
Ecological and Physiological Processes in Mixed Versus Monospecific Stands

3

David I. Forrester

Abstract

Tree growth depends on the resource availability, the proportion of resources acquired, and the efficiency with which those resources are used. Each of these variables can be influenced by species interactions. These interactions are dynamic and change spatially and temporally as resource availability and climatic conditions change. It is important to understand these processes when designing and managing mixed-species stands and also when modelling these processes. These interactions and their dynamics are the focus of this chapter. To begin with, the production ecology equation is described because it provides a useful framework to quantify the types of processes that influence the growth of forests and how these are influenced by species interactions. This equation describes growth as a function of resource availability, resource acquisition, and resource-use efficiency. Then, while referring to this equation, some of the main types of processes are described in terms of how they influence these variables and hence the productivity of mixtures. This is done for nutrients, then light, and then water. The influence of a given type of interaction on growth is not static. Instead, it changes with spatial and temporal variability in resource availability and climatic conditions and as a stand develops. Therefore, the next section describes a framework that explains these spatial and temporal dynamics and indicates when different types of interactions are important. Finally, stand density can influence the effect of these interactions. As stand density increases, interactions may become more favourable or less favourable, depending on how, and which, resources are influenced by the change in density. The final section therefore shows why stand density needs to be taken into account when examining how species interact.

D.I. Forrester (✉)

Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

e-mail: david.forrester@wsl.ch

Contents

3.1	The Production Ecology Equation	74
3.2	Types of Mixture Comparisons and Levels of Analyses	76
3.3	Nutrient Availability, Acquisition, and Use Efficiency	77
3.3.1	Nutrient Availability	77
3.3.2	Nutrient Uptake	80
3.3.3	Nutrient-Use Efficiency	81
3.4	Light Availability, Absorption, and Use Efficiency	82
3.4.1	Changes in Stand Structure and APAR	84
3.4.2	Changes in Tree Allometry and APAR	85
3.4.3	Changes in Tree Physiology	85
3.5	Water Availability, Use, and Use Efficiency	88
3.5.1	General Patterns and the Consideration of Spatial Scale	88
3.5.2	Processes That Influence Transpiration or WUE	92
3.5.3	The Influence of Stand Density and Water Stress	94
3.6	Spatial and Temporal Dynamics of Species Interactions	95
3.6.1	A Framework for Understanding the Dynamics of Species Interactions	95
3.6.2	Spatial Effects of Interactions That Influence Nutrient Availability	98
3.6.3	Spatial Effects of Interactions That Influence Water Availability	101
3.6.4	Spatial Effects of Interactions That Influence Light Absorption and Use	102
3.6.5	Temporal Dynamics of Species Interactions	102
3.6.6	Simultaneously Occurring Species Interactions	104
3.7	Stand Density	104
3.8	Synopsis	105
	Take-Home Messages	107
	References	108

3.1 The Production Ecology Equation

The relationship between growth, resource availability, resource acquisition, and the efficiency with which resources are used to fix carbon can be described using the production ecology equation (Monteith 1977):

$$\begin{aligned} \text{Gross primary production} &= \text{resource supply} \\ &\quad \times \text{fraction of resource acquired} \\ &\quad \times \text{resource use efficiency} \end{aligned} \quad (3.1)$$

When examining forest growth, the focus might be on above-ground biomass or wood production ($\text{Mg ha}^{-1} \text{ year}^{-1}$), which can be described using Eq. (3.1) as a function of the supply ($\text{Resource units ha}^{-1} \text{ year}^{-1}$), acquisition (a fraction), and use efficiency of light, water, or nutrients ($\text{Mg}_{\text{biomass}} \text{ Resource units}^{-1}$), minus allocation to respiration and nonwoody tissues (Binkley et al. 2004).

Interactions in mixtures are often described using terms such as facilitation, competition reduction, and competition (Chap. 2). However, it can be very difficult to separate the contribution of each of these on the growth dynamics of forests, and this is rarely attempted. The production ecology equation provides a framework that is useful for quantifying the processes driving these effects in order to understand how and why growth can change in mixtures (Richards et al. 2010). It has also been

Table 3.1 Many of the processes or species interactions that could influence the growth of mixtures compared with monocultures and an indication of whether they are facilitative or competitive reduction processes

Name of process or pattern	Facilitation (F) or competitive reduction (Cr)	Section
<i>Nutrient related</i>		
Symbiotic nitrogen fixation	F	3.3.1
Nutrient cycling	F	3.3.1
Chemical, spatial, or temporal stratification	Cr	3.3.2
Nutrient mineralisation	F	3.3.1
Canopy nitrogen retention	F	3.3.1
<i>Light related</i>		
Space occupation—canopy stratification	Cr	3.4.1
Space occupation—complementary crown shapes and architectures	Cr	3.4.1
Space occupation—intraspecific variability in crown architecture and size	Cr	3.4.2
Physiological differences	Cr	3.4.3
Phenology and interspecific effects on these	Cr	3.4.1
<i>Water related</i>		
Hydraulic redistribution	F	3.5.2
Shared mycorrhizal networks	F	3.5.2
Other spatial stratification	Cr	3.5.2
Canopy interception	Cr	3.5.2
Transpiration and WUE	Cr	3.5.1, 3.5.2
Litter layer as a sponge or barrier	F or Cr	3.5.2
Isohydric vs. anisohydric	Cr	3.5.2
Inter- and intraspecific differences in phenology	Cr	3.5.2
Modified within-stand environmental conditions	F	3.5.2
<i>Biotic</i>		
Insect herbivory and leaf pathogens	F	

The section column indicates where in the text their effect on the production ecology is described. See also Sect. 3.6 for the spatial and temporal implications of these interactions. Modified from Forrester and Bauhus (2016)

used in several reviews about the mechanisms driving growth responses to fertiliser application, irrigation, pruning, thinning, spacing, genotypes, species, stand age and geographic gradients (Binkley 2012; Forrester 2013) and even to examine the influence of species interactions on plant nutrition (Richards et al. 2010), transpiration (Forrester 2015), and light (Forrester and Albrecht 2014; Forrester et al. [in press](#)). Table 3.1 lists many of the processes and species interactions that have been found to influence mixtures. These are discussed in the text in relation to their influence on the production ecology of mixtures. The production ecology equation will provide the foundation for this chapter.

3.2 Types of Mixture Comparisons and Levels of Analyses

There are many ways experiments have been designed to make comparisons between mixtures and monocultures. Each type of comparison is useful for answering different questions, so it is important to describe the types of comparison that are often made and that will be referred to in this chapter.

Type 1 Comparing different species growing in a mixture in terms of their growth, morphology, physiology, and phenology (interspecific comparisons). This might be done to determine whether different species have traits that could complement each other and may not actually involve any measurements in monocultures at all.

Type 2 Comparisons of mixtures and monocultures in terms of total stand variables, such as growth, light absorption, transpiration, litterfall, etc. However, this total stand information does not show how each species contributes to the mixing effect. The individual species contributions are important because sometimes only one of the species contributes to the mixing effect. It is possible that an absence of any mixture effect at the total stand level is not due to an absence of a mixing (complementarity) effect, but rather results from opposing responses by different species. This Type 2 comparison does not provide information about individual species contributions to mixing effects.

Type 3 Compare the growth, morphology, physiology, or phenology of a given species in mixture with that of the same species in monoculture (intraspecific comparisons). This enables us to determine whether the species interactions actually changed the performance of a given species. This type of comparison, and the production ecology equation, has been used to examine mixture effects on nutrients (Richards et al. 2010), light absorption (Forrester and Albrecht 2014; Forrester et al. [in press](#)), and water pools or fluxes (Forrester 2015) and is frequently considered in this chapter.

A closely related issue is the level of analysis in terms of the scale of the variable being measured (Forrester and Pretzsch 2015). The main levels considered in this and the following chapters are the tree, neighbourhood, species, community, and landscape or estate. *Tree-level* analyses examine individual trees, such as when regression is used to examine how the relationship between tree diameter and tree biomass varies between treatments. *Neighbourhood-level* analyses are a form of tree-level analysis that take account of the characteristics of the trees' neighbourhood in terms of factors such as basal area and species composition (e.g. in terms of basal area, species composition; Vanclay 2006b; Boyden et al. 2005). The more typical tree-level analyses contrast with neighbourhood-level analyses because they either ignore the characteristics of the trees' neighbourhood or consider those characteristics only in terms of the stand-level treatment (where all trees within the plot have the same (mean plot) neighbourhood) (Forrester and Pretzsch 2015).

The next level up, *stand-level* analysis, considers totals and means of all trees within the plot, such as total above-ground biomass (B_T) or mean tree height. Stand-level analyses include *species-level* and *total stand-level* analyses. Species-level analyses divide the total stand by species to provide the totals and means for each species within the stand. For example, in a three-species mixture, $B_T = B_{\text{species1}} + B_{\text{species2}} + B_{\text{species3}}$. A species-level analysis could consider the B_{species1} , B_{species2} , and B_{species3} , whereas the total stand-level analysis could compare the B_T of different stands. The total stand-level analyses are commonly referred to as *community-level* analyses because they consider the totals or means of the whole community. The next level up includes the landscape level or the estate level. These are commonly used in forest planning and are referred to in Chaps. 10 and 11. While many other levels exist such as the leaf level and organ level (e.g. branches, roots) or coarser scales such as the region or continental levels, they are rarely considered in this book.

3.3 Nutrient Availability, Acquisition, and Use Efficiency

3.3.1 Nutrient Availability

Nutrient availability can increase when the size of the nutrient pool is increased, such as by symbiotic N fixation and atmospheric deposition or by increasing the proportion of the pool that is actually available to plants and the speed at which it is cycled (Forrester and Bauhus 2016). The available portion of the nutrient pool can be increased by increasing mineralisation rates, or when rates of nutrient cycling are accelerated by the production of more readily decomposable litter, by providing environments more favourable to litter decomposition and when nutrients that were inaccessible for one species are acquired and then cycled by another species. Roots require water to absorb and transport nutrients, so even when there are sufficient nutrient pool sizes, the availability can be low if the soils are dry or frozen. Therefore, processes that increase soil water availability (see Sect. 3.5) could also increase the available portion of nutrients. The proportion of nutrients available to a given species may also be increased when uptake by one species is lower than that of another, thereby leaving more nutrients for the latter, e.g. when there are interspecific differences in growth, in nutrient-use efficiency, or in the source of the given nutrient. Availability may also be increased by reducing nutrient losses that occur via leaching and erosion, or by combining species or altering stand structures to increase atmospheric deposition, but due to the more limited information on this aspect in mixtures, it will not be discussed (for Type 1 or 2 effects on soil fertility, see Augusto et al. 2002, 2015; Berger et al. 2009a, b). More detailed descriptions of processes that influence nutrition and nutrient cycling in forests are available in several reviews (Richards et al. 2010; Hinsinger et al. 2011; Binkley and Giardina 1998; Rothe and Binkley 2001; Knops et al. 2002; Gartner and Cardon 2004).

3.3.1.1 Nutrient Mineralisation

There can be large differences in the rates of mineralisation under different species (Binkley and Giardina 1998), and mixing species can result in increased mineralisation rates compared with monocultures of the species with slower rates of mineralisation. For example, N mineralisation rates and N uptake were 54% and 41% higher, respectively, in mixtures of *Picea sitchensis* and *Pinus sylvestris* than in *P. sitchensis* monocultures (Williams 1992). Mixtures of *Eucalyptus globulus* and *Acacia mearnsii* had N mineralisation rates that were about twice as high as those in *E. globulus* monocultures (Khanna 1997). N availability also increased with increasing proportions of *Albizia falcataria* in mixtures with *Eucalyptus saligna*, while P availability followed the opposite trend (Kaye et al. 2000). These effects clearly result from interspecific differences (Type 1 effects). It is also possible that mineralisation rates under a given species change when it is growing in a mixture compared with a monoculture (Type 3 effects). For example, Binkley and Valentine (1991) found that mineralisation rates under *Fraxinus pennsylvanica*, *Pinus strobus*, and *Picea abies* trees were modified by the identity of their neighbours. In contrast, antagonistic effects can reduce nutrient availability in mixtures compared with monocultures, and this occurred in mixtures of *Larix laricina* with either *Picea mariana* or *Pinus strobus*. In these mixtures, N mineralisation was lower than expected based on monocultures; however, above-ground biomass growth was greater than expected in *L. laricina*-*P. mariana* mixtures (Dijkstra et al. 2009). The mixing of lignin-rich litter from the conifers to the N-rich *L. laricina* litter was suggested to have suppressed the formation of lignolytic enzymes or formed complexes that were highly resistant to microbial degradation (Dijkstra et al. 2009).

3.3.1.2 Symbiotic N Fixation

Rates of symbiotic N fixation can be anything from 1 to 200 kg ha⁻¹ year⁻¹, and this can be 10% to >70% of the total N used by the N-fixing plant (Binkley and Giardina 1997; Khanna 1998; Fisher and Binkley 2000). This N can be transferred to non-N-fixing species after the plant and microbial tissues decompose (Van Kessel et al. 1994; Fisher and Binkley 2000). Smaller quantities may also be transferred via root exudation and common mycorrhizal connections (He et al. 2003). Soil N availability may also be increased for non-N-fixing species when the N-fixing species strongly rely on fixed N rather than soil N. Rates of N fixation and the proportion of N that is derived from the atmosphere (N_{dfa}) can increase with increasing soil P and decreasing with soil N and tend to vary with the same factors that influence growth. These effects have been the focus of several reviews (Crews and Peoples 2005; Peoples et al. 1995). However, the temporal dynamics of N fixation and the effects of competition from non-N-fixing species have received far less attention. These temporal dynamics clearly influence the balance between competition and facilitation and need to be understood in order to apply appropriate silvicultural treatments, such as thinning the N-fixing species.

It might be expected that as stands develop, rates of N fixation and N_{dfa} will increase to a peak and then decline as N availability increases, and internal N cycling within the trees provides some of the N demands of the trees. However,

while this has been observed in some stands, it has not in others, and there has not been enough research on N fixation dynamics in forests or plantations to confidently describe and generalise about these trends. In *Elaeagnus angustifolia*, rates of N fixation peaked at around age 2 or 3 years before declining at ages 4 and 5 years, but N_{dfa} continued to increase slowly (Khamzina et al. 2009). Rates of N fixation by *Acacia mearnsii* and *Acacia dealbata* in mixtures with *Eucalyptus* were about 40–90 kg ha⁻¹ year⁻¹ in at ages 5–10 years (May and Attiwill 2003; Forrester et al. 2007b) but were lower in older mixtures of *A. dealbata* or *A. melanoxylon* with *Eucalyptus* (Pfautsch et al. 2009a, b). In contrast, high rates of N fixation (75–85 kg ha⁻¹ year⁻¹) were still occurring at age 55 years in two *Alnus rubra*-*Pseudotsuga menziesii* mixtures (Binkley et al. 1992b). Rates of N fixation remained high between ages 1 and 3.5 years for *Leucaena leucocephala* and *Casuarina equisetifolia* (73–74 kg ha⁻¹ year⁻¹), and while N_{dfa} for *L. leucocephala* declined from 98% and 38%, there was no decline in that of *C. equisetifolia*, which fluctuated between 43% and 62% (Parrotta et al. 1996).

Competition from non-N-fixing species appears to have little influence on rates of N fixation. Rates of N fixation per tree and linear relationships between N accretion and the proportion of N-fixing species in mixtures have been found in several mixtures (ordered as N-fixing species with non-N-fixing species) including *Falcataria moluccana* with *E. saligna*, *A. mearnsii* with *E. globulus*, and *Alnus rubra* with *Populus trichocarpa* (DeBell and Radwan 1979; Kaye et al. 2000; Forrester et al. 2007b). In most of these mixtures, the growth of each species increased compared with monocultures. However, when competition from the non-N-fixing species is intense enough to significantly reduce the growth of the N-fixing species, it may also reduce rates of N fixation. This occurred in mixtures of *E. grandis* (1111 trees ha⁻¹) and a N-fixing tree, *A. mangium* (556 trees ha⁻¹), where growth of *A. mangium* was reduced and N fixation at age 30 months was 7–31 kg ha⁻¹ compared with 66 kg ha⁻¹ in *A. mangium* monocultures (1111 trees ha⁻¹) (Bouillet et al. 2008).

3.3.1.3 Accelerating Rates of Nutrient Cycling

As plant material decomposes, the nutrients it contains return to a mineral form in the soil, which plants can use. Nutrient inputs into forests are often low, and growth is often limited by nutrient availability, so the rate at which litter decomposition and nutrient cycling occurs is important. Litter decomposition depends on the microclimate and quality (e.g. nutrient concentrations, lignin contents) of the litter and surrounding soil, which influence decomposer composition and activity, and these factors differ between mixtures and monocultures (Rothe and Binkley 2001; Gartner and Cardon 2004; Hättenschwiler et al. 2005). The differences between mixtures and monocultures can be a combination of interspecific differences (Type 1 effects) as well as intraspecific differences, such as when the quality of litter from a given species varies between mixtures and monocultures (Type 3 effects) (Hättenschwiler et al. 2005; Richards et al. 2010). Several reviews of litter decomposition found that, in about half of the studies, litter decomposition was faster in mixtures than expected based on monocultures (mean of 17% faster), but in about

30% of studies, there was no effect, and in about 20% of studies, there was an antagonistic effect (Hättenschwiler et al. 2005; Gartner and Cardon 2004). These reviews contained tree mixtures but also grass mixtures. A review that focussed on tree mixtures found that the most common result was no effect but that synergistic and antagonistic effects all occurred (Rothe and Binkley 2001).

3.3.2 Nutrient Uptake

The N and P uptake of mixed-species stands was reviewed by Richards et al. (2010). In >50% of studies, the N or P uptake, by a given species, increased by at least 10% in mixtures compared with monocultures, and this was not dependent on whether the mixtures contained N-fixing species. It is important to note that nutrient uptake was quantified as the nutrient content of above-ground biomass ($\text{kg nutrient ha}^{-1}$), so this indicates the net effect of changes in availability as well as the proportion of nutrient taken up. Some of the processes described in Sect. 3.3.1 that influence nutrient availability will also increase the proportion of nutrients that are taken up. In addition to these processes, the proportion of nutrients taken up by plants might increase when there are differences (Type 1 or 3) in nutrient preferences and symbiotic associations, temporal differences in nutrient uptake, contrasting spatial distributions of fine roots or more fine roots, and hence a greater potential nutrient uptake.

Spatial fine-root distributions vary between species (Type 1 differences), which may result in the use of a higher proportion of soil nutrients when the species are mixed. The spatial distribution of fine roots in mixtures can also be influenced by the species interactions, such that the fine-root distributions for a given species in mixture are significantly different to its monocultures (Type 3) (Rothe and Binkley 2001). Rothe and Binkley (2001) suggested that differences in fine-root distributions could be exploited if deeper rooting species are used to ‘pump’ nutrients from the subsoil to upper layers where shallow-rooted species can make use of them.

Several studies have found that fine-root biomass or fine-root production is higher in mixtures than at least one of the monocultures (sometimes with transgressive below-ground overyielding) and that fine-root biomass or production of a given species is greater than expected based on monocultures (Fredericksen and Zedaker 1995; Wang et al. 2002; Brassard et al. 2011; Schmid and Kazda 2002; Laclau et al. 2013). The mixing effect appears to be greater when the species are mixed more homogeneously within the forest enabling a greater proportion of the soil space to be filled due to interspecific differences in fine-root positioning and proliferation (Brassard et al. 2013), compared with mixed-species forests with a less uniform distribution of species where there is a higher probability that individual trees will be growing in neighbourhoods dominated by other individuals of the same species. In some cases, the fine-root biomass of one species increases at the expense of another species, whose fine-root biomass production is suppressed (Laclau et al. 2013; Bolte and Villanueva 2006).

These studies rarely link the changes in fine-root distributions, biomass, or growth with actual nutrient (or water) uptake, which would indicate whether the below-ground complementarity effects were associated with increased nutrient uptake. This is important because greater growth or nutrient uptake in mixtures might result from, but does not require, any differentiation in fine-root distributions between species or that mixtures have greater fine-root biomass or fine-root growth. Several studies have found no spatial differences in fine-root distributions and/or no differences in fine-root biomass in mixtures and monocultures, even though above-ground biomass (shown in Fig. 4.16) was much greater in mixtures (Bauhus et al. 2000). One explanation is that nutrient uptake was not a major process influencing this complementarity effect; complementarity may have been driven more by increased nutrient availability (which may even reduce fine-root biomass) or light or water resources. Another explanation is that nutrient uptake does not directly relate to fine-root distributions, biomass, or growth. Nutrient uptake also depends on the fine-root architecture, mycorrhizal associations, and the root physiology and phenology (Richards et al. 2010).

Chemical stratification is another process whereby competition for nutrients may be reduced and the proportion of the total nutrient pool taken up is increased in mixtures compared with monocultures (McKane et al. 2002; Richards et al. 2010). Chemical stratification occurs when different species take up different forms, or sources, of a given nutrient (e.g. organic or inorganic forms) due to contrasting mycorrhizal associations and the ability to influence nutrient acquisition by secreting enzymes and organic acids (Ewel 1986; Turner 2008; Richards et al. 2010; Hinsinger et al. 2011). Interspecific differences in N preferences (Type 1), such as symbiotically fixed N, nitrate, ammonium, and amino acids, have been found in mixtures (McKane et al. 2002; Pfautsch et al. 2009b; Kranabetter and MacKenzie 2010), and there may also be differences in P preferences (Turner 2008; Hinsinger et al. 2011).

3.3.3 Nutrient-Use Efficiency

When comparing the N- or P-use efficiency of trees growing in mixtures with that of the same species growing in monocultures, Richards et al. (2010) found that decreases, increases, and no changes in N- and P-use efficiency all occurred and that declines were more common than increases. In some studies, N- and P-use efficiency declined even when growth increased in mixtures. It is important to note that Richards et al. quantified nutrient-use efficiency as above-ground biomass growth per unit of nutrient in litterfall (following Vitousek 1982) or in foliage mass (following Harrington et al. 1995). These nutrient contents are rough approximations of actual nutrient uptake and require an assumption that litterfall mass or foliage mass is a fixed proportion of growth, which is often not the case. Nitrogen-use efficiency calculated from actual measurements of nutrient uptake is not common in mixtures. One example is mixtures that contained *Pseudotsuga menziesii* with a N-fixing species, *Alnus rubra* (Binkley et al. 1992b). The growth of

P. menziesii was significantly faster in mixtures but only on low N sites, and this was related to increases in nutrient uptake (N, Mg, and K); N-use efficiency in mixtures was only 25%, and 16% of those in *P. menziesii* stands on low- and high-N sites, respectively (Binkley et al. 1992b). However, N-use efficiency can also increase as nutrient uptake increases. For example, in *Eucalyptus* monocultures, growth and N-use efficiency increased with increasing nitrogen use and increasing precipitation (Stape et al. 2004). These studies indicate that there may not be a general trend for changes in nutrient-use efficiency in mixtures, unlike those for water- and light-use efficiency (see below).

3.4 Light Availability, Absorption, and Use Efficiency

The absorption of photosynthetically active radiation (APAR) by trees and stands is the basis for their growth. Increases in tree growth rates are often accompanied by increases in APAR, light-use efficiency (LUE), or both, according to a literature review by Binkley (2012) that included a wide range of treatments, such as productivity gradients, fertiliser application, irrigation, mixed-species systems, stand structures, and stand age. When growth increased, APAR also increased by a median of 40% and a mean of 85%. In about 90% of studies, when growth rates increased, LUE also increased by a median of 50% and a mean of 70%. In about half of the studies, there were increases in APAR and LUE, while in the other half, either one or the other increased, not both.

So what does this mean for mixtures? It suggests that for a given species, when its growth increases in mixture, due to some sort of complementarity effect, this may be associated with increased APAR and/or LUE (Type 3 difference). In addition, Type 1 differences will probably exist because the species in mixture are likely to vary in terms of their APAR and LUE due to interspecific differences in physiology, morphology, and phenology. For example, if a fast-growing species with high LUE overtops a slower-growing and more shade-tolerant species that is capable of high LAI and APAR, then mixtures could have a greater LUE than monocultures of the more shade-tolerant species and could have a greater APAR than monocultures of the less shade-tolerant species in the upper canopy.

Only a few studies have measured and compared APAR and LUE in mixtures with monocultures (Fig. 3.1), and Type 1 and Type 3 differences have both been observed (Forrester and Bauhus 2016). For example, mixtures of *Eucalyptus saligna* with *Falcataria moluccana* in Hawaii and *Eucalyptus globulus* with *Acacia mearnsii* in Australia had greater APAR and LUE than monocultures (Binkley et al. 1992a; Forrester et al. 2012b). The *Eucalyptus* species had higher LUE than the other species (Type 1 difference), but their growth was limited by N. *F. moluccana* and *A. mearnsii* are both N-fixing species. In mixtures, the higher LUE of the eucalypts (Type 1 difference) was combined with the higher N availability under the N fixers, which increases the growth of the eucalypts (Type 3). Since the LUE of the mixtures was greater than each monoculture, rather than a weighted average, the LUE of at least one of the species must have increased in each mixture compared

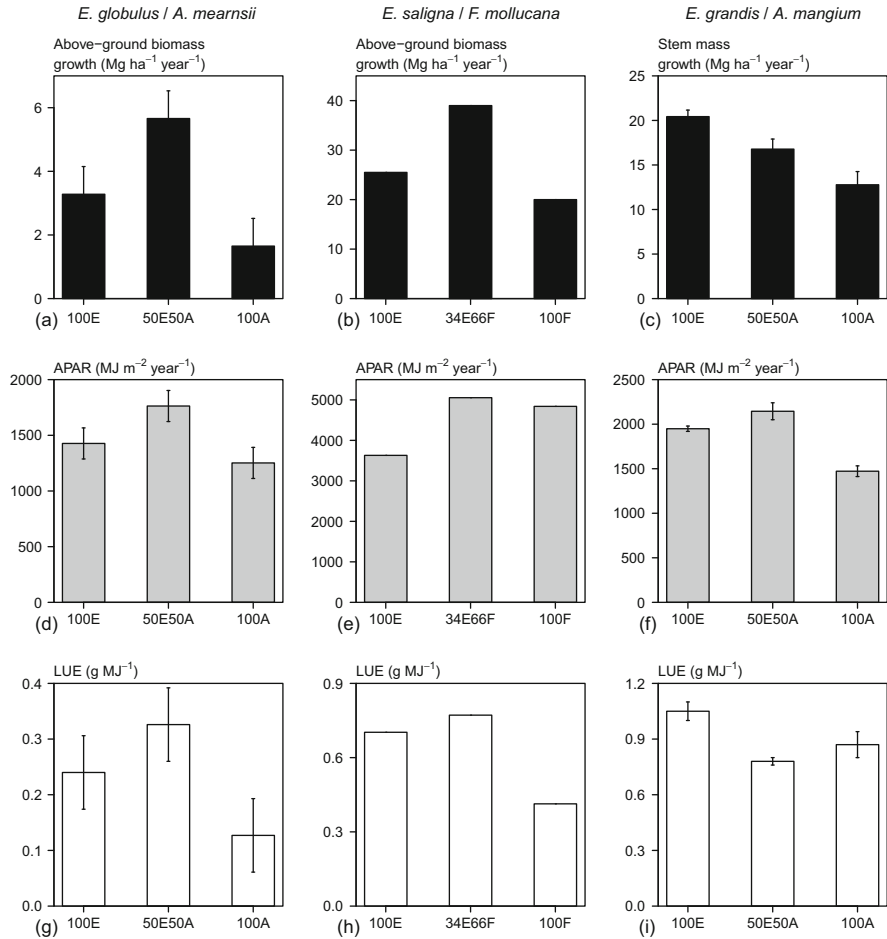


Fig. 3.1 Biomass growth, absorption of photosynthetically active radiation (APAR), and light-use efficiency (LUE) in monocultures and mixtures of (a, d, g) *Eucalyptus globulus* with *Acacia mearnsii* between ages 14 and 15 years (Forrester et al. 2012b), (b, e, h) *Eucalyptus saligna* with *Falcattaria moluccana* between ages 5 and 6 years (Binkley et al. 1992a), and (c, f, i) *Eucalyptus grandis* and *Acacia mangium* during a 6-year rotation (le Maire et al. 2013). Error bars are standard errors of difference for *E. globulus*/*A. mearnsii*, or standard deviations for *E. grandis*/*A. mangium*. The numbers on the x-axes are the percentage of all planted trees belonging to a given species (e.g. 100E is 100% *Eucalyptus*; 34E66F is 34% *Eucalyptus* and 66% *Falcattaria*)

with its monoculture (Type 3). The increases in APAR resulted, at least in part, from greater leaf areas associated with increases in growth due to a higher availability of, or reduced competition for, other resources. Several processes that could increase resource availability are described in Sect. 3.3 (nutrients) and Sect. 3.5 (water).

3.4.1 Changes in Stand Structure and APAR

Contrasting stand structures between mixtures and monocultures can result in higher APAR for some of the species in mixtures, often the taller species (Forrester and Bauhus 2016). The total planting densities (trees per ha) of all mixtures and monocultures were kept constant in each experiment in Fig. 3.1, and the eucalypts overtopped the N-fixing species. Therefore, before the eucalypt canopy closes above the N-fixing species, there should be more space between the eucalypt crowns in mixtures than in monocultures. This could result in less shading of eucalypt crowns, at least from the sides, and higher APAR per eucalypt tree in mixtures compared with monocultures. In the mixtures of Fig. 3.1a, b, the trees of both species were larger in mixtures than in monocultures, except for *F. moluccana*, which was a similar size in both treatments. In extreme cases, such as Fig. 3.1c, the growth and APAR per tree of one species can increase because it outcompetes and reduces the growth of the other species. This was the case in 1:1 mixtures of *E. grandis* and *A. mangium*. In these mixtures, stand APAR was higher than that of monocultures of either species (Fig. 3.1f) (le Maire et al. 2013), similar to the *E. saligna*–*F. moluccana* and *E. globulus*–*A. mearnsii* mixtures described in Fig. 3.1. However, the LUE of both *E. grandis* and *A. mangium* were lower in mixtures than monocultures, and as a result, the growth of mixtures was intermediate between faster-growing *E. grandis* monocultures and slower-growing *A. mangium* monocultures (Fig. 3.1c, f, i). That is, mean tree *E. grandis* growth and APAR increased compared with trees in monocultures, but this was at the expense of lower mean tree *A. mangium* growth and APAR in the mixtures.

In addition to changes in the vertical structure of the canopy, there can be temporal changes in structure when mixtures contain species that have leaves when others do not, in which case the APAR of the given species can increase while the other species are leafless. This interspecific difference in phenology (Type 1) may not be very useful in forests where the deciduous trees lose their leaves outside most of the main growing season of the other species, such as during cold temperate or boreal winters when the other species are not growing much anyway (Forrester et al. in press). However, this may be particularly useful in forest types where trees grow all year, such as in the tropics and subtropics (Sapjanskas et al. 2014).

Individual tree APAR (for a given crown leaf area) could also be increased when the different species have crowns with complementary shapes that fit together more efficiently in the mixtures than in the monocultures (Bauhus et al. 2004). For example, in mixtures of *A. alba* and *P. abies*, the APAR of *A. alba* crowns with a given leaf area, and at a given stand density, was greater when its neighbourhood was mostly composed of *P. abies* than when it was composed of other *A. alba* trees, even though the mean height of *A. alba* trees was usually lower than that of *P. abies* trees (Forrester and Albrecht 2014). More efficient ‘packing’ (see also Chap. 4) of crowns is one explanation for this increase in APAR. Another is changes in crown architecture (Type 3) for a given species when growing in mixture compared with monocultures (Forrester et al. in press).

3.4.2 Changes in Tree Allometry and APAR

The crown architecture of a given species often varies in response to competition and changes in resource availability (Ryan et al. 2004; Forrester et al. 2012a), such that trees in mixture might have wider or longer crowns compared with monocultures even when they have the same stem diameters (Bauhus et al. 2004; Getzin and Wiegand 2007; Bayer et al. 2013; Forrester et al. 2016). One possible reason for this change in allometry is to increase APAR and to shade competitors. In mixtures of *P. abies* and *A. alba*, a 10% increase in crown size, in terms of either width, length, or leaf area, resulted in predicted increases in APAR of up to about 15% (Forrester and Albrecht 2014). Interestingly, increasing leaf area by 10% resulted in the smallest increase (only about 2.5%) in APAR. Increasing leaf area without also increasing crown volume will result in a higher leaf area density and self-shading, and this appears to be a relatively inefficient way for trees to increase APAR. Leaf area density tends to change much less than crown lengths and widths in response to many different treatments, including thinning, fertiliser application, and pruning (Forrester et al. 2012a; Ligot et al. 2014; Guisasola et al. 2015). Inter- and intraspecific changes in crown architecture were also found to influence tree and stand APAR in *P. sylvestris* and *F. sylvatica* mixtures (Forrester et al. *in press*) and to increase total stand APAR in a planted biodiversity experiment (Sapjanskas et al. 2014).

3.4.3 Changes in Tree Physiology

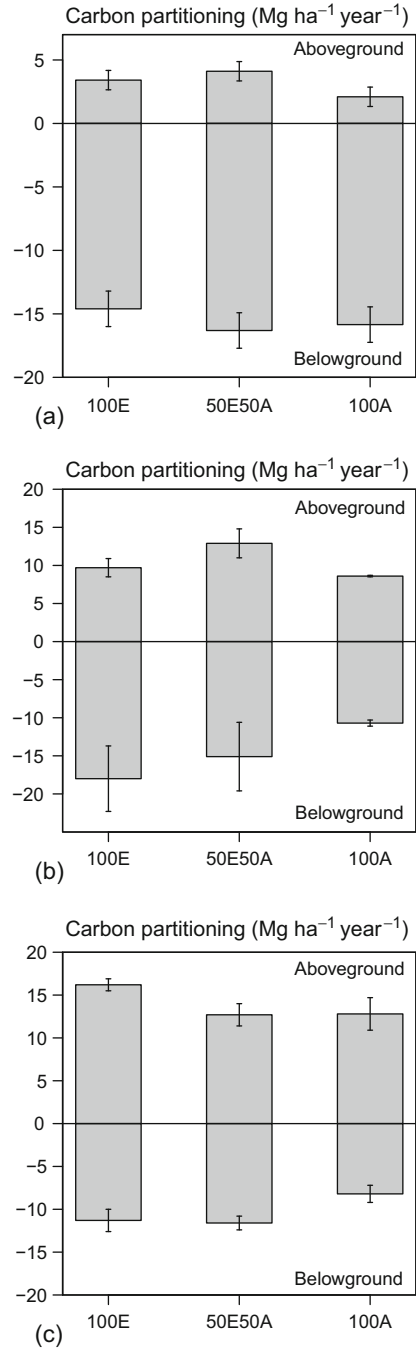
So what are the processes that lead to increases in LUE? LUE could increase if photosynthesis increases and/or if there is a higher allocation of biomass above ground, to capture more light per unit of net primary production. Photosynthetic rates were higher for *E. globulus* in mixture (same experiment shown in Fig. 3.1a, d, g) with the N-fixing *A. mearnsii* (Forrester et al. 2012b), and many studies have found that photosynthesis can increase following fertiliser application (Forrester 2013). However, photosynthesis certainly does not always increase following fertiliser application, and many studies have found that increases in above-ground growth resulted from increases in carbon partitioning to above-ground growth (Box 3.1) (Forrester 2013). Two studies where carbon partitioning was measured in mixed-species stands found that when mixtures of *Eucalyptus* and N-fixing *Acacia* species were more productive than monocultures, they also allocated a higher proportion of carbon above ground than monocultures (Box Fig. 3.1-1 in Box 3.1).

Box 3.1 Carbon Partitioning and Implications for Mixtures

Carbon (C) partitioning is important to consider when comparing mixtures with monocultures because even when there are no differences in net primary production, the above-ground biomass or wood mass may still differ, simply due to differences in C partitioning (Box Fig. 3.1-1). Two important

(continued)

Box Fig. 3.1-1 Carbon partitioning to above-ground net primary production (including above-ground biomass + litterfall – mortality) and the total below-ground flux (including respiration), in (a) *Eucalyptus globulus* and *Acacia mearnsii* stands between ages 10.5 and 11.5 years, at Cann River, Australia (Forrester et al. 2006a); (b) *Eucalyptus grandis* and *Acacia mangium* between ages 4 and 6 years at Itatinga, Brazil; and (c) *E. urophylla* × *grandis* clone and *A. mangium* between ages 6 to 7 years at Kissoko, Congo (Epron et al. 2013). Error bars are standard errors of difference for *E. globulus*/*A. mearnsii*, or standard deviations for *E. grandis*/*A. mangium*. The numbers on the x-axes are the percentage of all planted trees belonging to a given species (100E is 100% *Eucalyptus*, 50E50A is 50% *Eucalyptus* and 50% *Acacia*, and 100A is 100% *Acacia*)



Box 3.1 (continued)

factors that influence C partitioning are (1) ontogeny and (2) resource availability. Both of these are likely to differ between mixtures and monocultures. In terms of ontogeny, as stands age and trees get larger, there is often a decline in the partitioning of C below ground and to leaves and an increase in partitioning to stems (Litton et al. 2007; Poorter et al. 2012). When growth is increased in mixtures, there may therefore be changes in C partitioning due to changes in tree size, and the rate and magnitude of this change may vary between species.

Regarding the second factor, as resource availability increases, plants tend to partition less C to the plant tissues that forage for that resource. So as nutrient or water availability increase, partitioning to roots decreases, and plants allocate more resources above ground, to capture more light and fix more C (Litton et al. 2007; Poorter et al. 2012; Reich et al. 2014).

The photosynthetic capacity of the canopy might also be improved if mixtures have a closer-to-optimal distribution of nutrients in relation to light availability (Wacker et al. 2009). This ‘optimality theory’ (Field 1983; Hirose and Werger 1987; Anten et al. 1995; Sands 1995) predicts that canopy photosynthesis will be maximised when leaf mass and leaf N concentrations are high at the top of the canopy and decrease continuously towards the lower canopy in relation to the vertical gradient in light availability. The higher leaf N concentration at the top means that leaves can make use of the higher light availability and have high rates of photosynthesis, while the lower leaf N at the bottom of the canopy prevents N from being wasted where there is not enough light to maintain high rates of photosynthesis. Studies with grasses, shrubs, and trees have shown that monocultures generally do not develop such an ‘optimal’ distribution of leaf N for reasons including the following:

- Vertical distributions in leaf-specific hydraulic conductance that are not optimal. Optimal N distribution is of no use if there is not enough water for photosynthesis (Peltoniemi et al. 2012).
- The availability of light within the entire canopy can be very variable. Even though there can be a general decline in light from the top to the bottom of the canopy, it is likely that some high leaves will be more shaded than some lower leaves, but leaves on branches of the upper canopy may still have higher leaf N concentrations than those on branches in the lower canopy, thereby preventing an optimal relationship between light availability and foliar nutrition (Osada et al. 2014). That is, Osada et al. (2014) found that for a given range in light availability, there was a smaller range in leaf N concentrations for leaves within a single branch than there was for leaves in different branches throughout the canopy.

- Leaf N may be more dependent on the light availability that existed when the leaf was produced than current conditions. The light availability for a given leaf may therefore change more rapidly than the leaves can re-acclimate (Niinemets 2012).
- The optimality theory assumes that there is no competition between individual plants and that they distribute the N within their crowns in a way that is optimal for the whole stand rather than the individual. However, there is typically strong competition between individuals, and stand leaf area is often higher than optimal, perhaps in an attempt to outcompete neighbours (Anten 2005). This strategy maximises the carbon gain of individuals but not the entire canopy.
- There is an upper bound constraint on specific-leaf area (leaf area per unit leaf mass) that leaves cannot go above, which is determined by a minimal physical strength that prevents structural damage from wind, herbivory, etc., and this constrains the morphology and nutrition of the lower canopy leaves. This can prevent an optimal distribution of leaf N concentrations such that N concentrations decline less rapidly than light availability from the top to the bottom of the canopy (Dewar et al. 2012).

In contrast, interspecific differences in leaf nutrition and leaf morphology, as well as differences in biomass allocation in terms the trade-off between height growth and leaf area, may enable mixtures to achieve a closer-to-‘optimal’ distribution than monocultures (Anten 2005; Wacker et al. 2009). The interspecific differences may be exaggerated further by intraspecific variability in mixtures resulting from interspecific interactions. This has not been tested in tree mixtures, but in grass mixtures, there was a shift in leaf biomass to greater heights and a greater APAR than in monocultures, although only a few of the mixtures examined had an optimal vertical distribution of leaf N (Wacker et al. 2009).

3.5 Water Availability, Use, and Use Efficiency

3.5.1 General Patterns and the Consideration of Spatial Scale

A major argument that is often used in favour of mixtures is their greater productivity; however, the faster trees grow, the more water they are likely to use (Law et al. 2002), which may in turn make them more susceptible to drought periods, as well as reducing water supplies for downstream users. Despite this, few studies have compared the transpiration (E_T), water-use efficiency (WUE, tree, or stand growth per unit E_T), and their seasonality in mixtures and monocultures (Forrester 2015). In contrast, there is far more information about the production ecology of monocultures with regard to tree or stand E_T and WUE, and these studies indicate that generally when tree or stand growth increases, there is also an increase in E_T and/or WUE (Binkley 2012; Binkley et al. 2004), and there are usually no reductions in E_T or WUE when growth increases. This pattern has been found for a wide range of treatments including genetics, tree age, irrigation/drought, fertiliser

application, pruning, thinning, species comparisons, and geographic gradients (Binkley 2012; Forrester 2013). Specifically, when (monospecific) stands were more productive than control treatments, in 90% of cases, they also used more water (median of 25%) and used it more efficiently (median of 70%). There were also increases in E_T and WUE in about half of the studies, while in the other half, there were increases in one or the other, and not both.

Based on these patterns, it could be expected that if the growth of a given species is greater in mixture, there were probably also increases in E_T and/or WUE. Furthermore, the interspecific interactions in mixtures, which improve growth, could be used and manipulated to improve tree or stand WUE. The few studies that have compared rates of water use in mixtures with monocultures have shown that, when mixtures were more productive, they also used more water and they were also more water-use efficient (Fig. 3.2) (see review by Forrester 2015). For example, by age 15 years, the above-ground biomass of mixed-species stands of *Eucalyptus globulus* and *Acacia mearnsii* was 85% and 58% greater than *E. globulus* or *A. mearnsii* monocultures, respectively. Between ages 14 and 15 years, the mixtures used 17% and 93% more water than the monocultures, respectively, but the mixtures were also more water-use efficient than the monocultures because the water-use efficiency of *E. globulus* trees was 80% greater in the mixtures (Fig. 3.2). The processes that increased the growth of these particular *Eucalyptus-Acacia* mixtures are described in detail as a case study in Sect. 4.2.2.

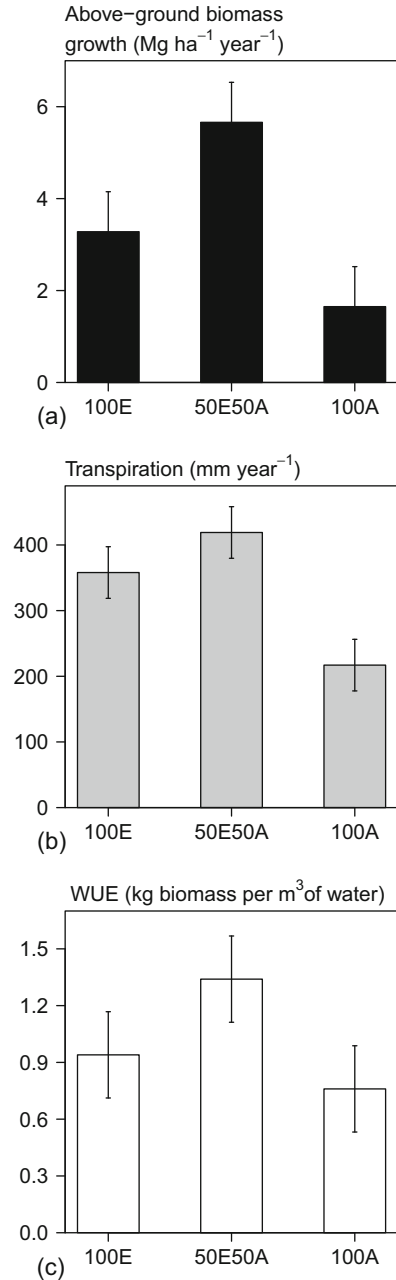
In contrast, when there are no complementarity effects on growth in mixtures, there are also generally no complementarity effects on E_T or WUE (Forrester 2015). In such stands, the growth, E_T , or WUE of the mixtures is a function of the properties of the monocultures of each individual species and the proportion of stand basal area, sapwood area, or stand crown projection area that each species contributed to the mixture (Moore et al. 2011; Gebauer et al. 2012).

All of the patterns described so far in this section are at the species stand level or total stand level. However, stand-level patterns are determined by individual trees and the interactions between them. Stand-level responses are simply the net effect of a much wider range of individual tree-level responses. This is because there is considerable spatial and temporal variability in soil and canopy conditions within mixed-species forests (Schume et al. 2004; Boyden et al. 2012; Canham et al. 1999; He et al. 2014), and this, together with inter-tree variability in genetics, pest damage, etc., is reflected in tree-level relationships. Therefore, the tree-level patterns include fundamental information about the processes underlying the species stand-level and total stand-level responses.

Tree-level patterns of growth, E_T , or WUE were therefore examined in the same stands shown in Fig. 3.2. Even within the same mixtures, growth, E_T , or WUE only increased for some of the trees (compared with trees in monocultures) and not for others (Fig. 3.3). The response of the individual trees depended on their size and the species composition or basal area of their neighbourhoods (Fig. 3.3), and the stand-level patterns simply reflected the mean tree-level response (Forrester 2015).

In contrast to these species-specific patterns (at the tree or stand levels), it is far more difficult to make total stand-level generalisations about how the net effect of

Fig. 3.2 Above-ground biomass growth (a), transpiration (b), and water-use efficiency (c; WUE) in monocultures and mixtures of *Eucalyptus globulus* with *Acacia mearnsii* between ages 14 and 15 years (Forrester et al. 2010b). Error bars are standard errors of difference. (100E = 100% *Eucalyptus*, 50E50A = 50% *Eucalyptus* and 50% *Acacia*, and 100A = 100% *Acacia*)



all species in the mixture will influence stand water availability, E_T , and WUE. This is because regardless of the complementarity effects (significant Type 3 differences), there may be significant interspecific differences in E_T and WUE, and this Type 1 difference will also contribute to total stand-level differences

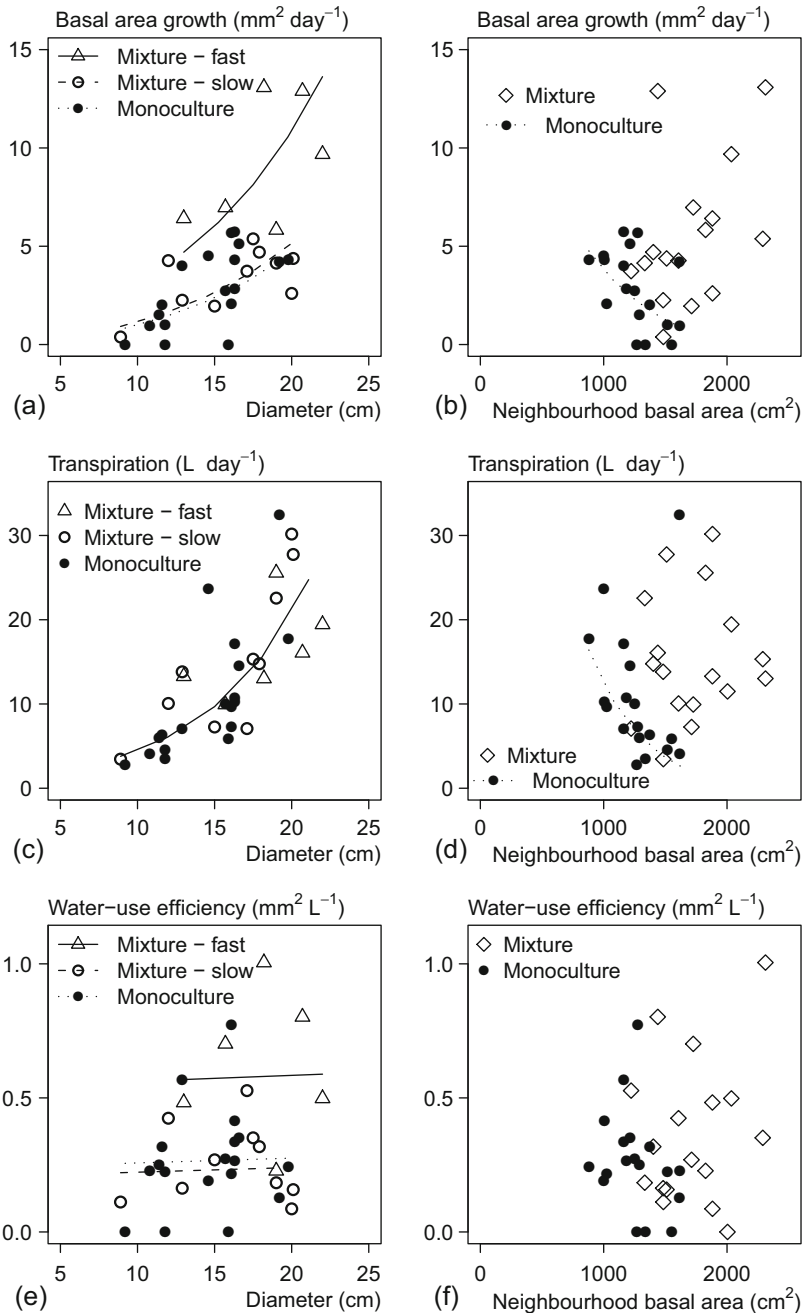


Fig. 3.3 The relationship between diameter and basal area growth (a), transpiration (E_T ; c) and water-use efficiency (e), or between neighbourhood basal area and basal area growth (b), transpiration (E_T ; d), and water-use efficiency (WUE; f) of *E. globulus* trees growing in monocultures or in 1:1 mixtures with *A. mearnsii* trees. For (d) the monoculture line is fitted without the outlier with a transpiration of 32 L day⁻¹. Modified from Forrester (2015)

between mixtures and monocultures. If a management aim is to increase growth and WUE of mixtures, the best suggestion appears to be to combine very water-use-efficient species with species that will increase the growth of that water-use-efficient species, which could be via any process appropriate for the site and species. Another useful management tool is the observation that for a given species, if there is no increase in its growth in the mixtures, then there is unlikely to be any increase in its E_T or WUE (Forrester 2015). Therefore, growth measurements, which are much easier and cheaper than E_T measurements, could provide a good initial indication about whether mixtures are likely to be using more water (Forrester 2015).

3.5.2 Processes That Influence Transpiration or WUE

There are many processes that could influence the water availability or water stress of trees in mixtures compared with monocultures (Forrester and Bauhus 2016). However, few have actually been quantified and compared between mixtures and monocultures. Therefore, even if they occur in mixtures, it is unclear whether they often have a significant effect on growth, water availability, E_T , or WUE. Some of these processes are described below.

- *Interception losses*: Part of the precipitation received by a forest never actually reaches the soil because it is caught by the canopy and evaporates back into the atmosphere. The proportion of precipitation that is ‘intercepted’ by the canopy depends on variables such as canopy leaf area (larger leaf areas have higher interception), the roughness of the bark and funnel-like architecture (rough-barked and porous-barked trees have less stem flow and more interception loss), and the size of the rainfall events; following small rainfall events, a higher proportion of precipitation will probably be intercepted by, and evaporated from, the canopy (Gash et al. 1995; Augusto et al. 2002, 2015; Levia and Frost 2003; Schume et al. 2004). The funnel-like crown architectures might also help to distribute the water around the base of a given tree where it is harder to reach by neighbours (Gerrits et al. 2010). These traits clearly vary a lot between species and may also be influenced by the species interactions, such as when growth and leaf areas are increased in mixtures. For example, even with similar leaf areas, *P. abies* monoculture canopies intercepted more rain than *F. sylvatica* monocultures or mixtures of these species (Schume et al. 2004). Therefore, the mixtures might have more available water than *P. abies* monocultures.
- *Increased storage*: Water availability could be increased if the mixtures develop a thicker O horizon that is capable of storing more water than the O horizons in one, or all, of the monocultures (Ilek et al. 2015). In contrast, water availability could be lower if infiltration of precipitation into the O horizon is reduced resulting in higher evaporation and runoff (Schume et al. 2004).

- *Contrasting water requirements*: If one species transpires (or intercepts) less water per unit area than another, then water availability will increase for the other species, while the less water demanding species may have to deal with more intense interspecific competition for water compared with the intraspecific competition in its monocultures. High water-using species could be those with high growth rates or low water-use efficiency.
- *Contrasting sources*: If one species obtains water from deeper depths than another, it could have less competition in the mixture than in its monoculture. Several studies have shown interspecific differences in water sources by species growing in mixtures. For example, *Q. petraea* was found to use deeper soil water than *F. sylvatica* (Zapater et al. 2011). Similarly, *E. globulus* dried the soil out more at deeper layers than *A. mearnsii* and may therefore have experienced less competition in the mixtures (Forrester et al. 2010b). Contrasting fine-root distributions (Sect. 3.3.2) could also differ between species or change as a result of species interactions, thereby influencing competition for water.
- *Differences in phenology* might leave one species free of competition or with reduced competition for water during parts of its growing season (e.g. Vandermeer 1989; Moore et al. 2011; Rouspard et al. 1999; Schwendenmann et al. 2015). For example, many forests are composed of deciduous and evergreen species, and an extreme case is the deciduous N fixer *Faidherbia albida* that has a ‘reverse phenology’ where it loses its leaves during the wet season (Rouspard et al. 1999). Most studies that have compared the transpiration of mixtures and monocultures were done over complete growing seasons (Forrester et al. 2010b; Kunert et al. 2012; Moore et al. 2011; Gebauer et al. 2012) rather than for short periods (several days or weeks) to account for the seasonality in the ranking of E_T and WUE between mixtures and monocultures that results from interspecific differences in phenology (e.g. time of peak E_T) and the effects of intra-annual climatic conditions on E_T or WUE.
- *Hydraulic redistribution*: This is a process where roots take up water from moist soil and release it into drier soil (Prieto et al. 2012; Neumann and Cardon 2012). Reported mean magnitudes of hydraulic redistribution vary between about 0.04 to 1.3 mm of water per day, and these have come from a wide range of forest types and from the tropics to temperate and Mediterranean climates (Neumann and Cardon 2012). The significance of this process will clearly depend on its magnitude and timing, and the potential benefits can include increasing dry-season transpiration and photosynthesis, lifting water so shallow-rooted plants can use it, increasing plant nutrient uptake (which requires soil moisture), extending the life span of roots, and moving water into deeper layers where it does not evaporate (Neumann and Cardon 2012).
- *Anisohydric or isohydric*: Different species tend to show one of two types of stomatal behaviour in response to the soil drying out. Isohydric species close their stomata during earlier stages of drought. This conserves water and reduces the risk of embolisms in their water transport systems. However, closing their stomata also prevents them from fixing carbon, and if the drought goes for a long time, they may use up all their carbon reserves and die. This conservative

strategy may result in higher water availability for more anisohydric species during the early stages of drought. Anisohydric species open their stomata for longer into drought periods. They invest more carbon into their transport systems to reduce their vulnerability to embolisms. But if the drought is severe enough, then eventually tension within the water transport system builds up, the water columns break, and the trees suffer an embolism. If this occurs at a faster rate than the trees can repair themselves, some branches will begin to die, and eventually the tree may die. If they do not die, then after the drought they will need to rebuild their canopies, and the isohydric species may then have less competition.

- *Changes in canopy microclimate*: Transpiration from one species (in the overstorey) could reduce the vapour pressure deficit within the canopy and hence facilitate an understorey plant (Saccone et al. 2009). This potential process has received very little attention with respect to tree–tree interactions in forests (as opposed to tree-seedling or shrub-seedling interactions).
- *Processes that improve light or nutrient availability and use*: Growth, E_T , or WUE can increase in response to processes that improve light and nutrient availability or uptake. When these processes increase growth, they are also likely to increase E_T . They can also increase WUE by shifting C partitioning from below ground to above ground or by increasing the availability or uptake of nutrients or light enabling the plants to increase photosynthesis and make more efficient use of their water.

The processes listed here will often occur simultaneously and in opposite directions. Therefore, information about one process may not give a good indication of the total or average effects of all water-related interactions. For example, in monocultures and mixtures of *F. sylvatica* and *P. abies*, the *F. sylvatica* (a deciduous deeper rooter) used more water per crown projection area, but this was compensated for by higher interception rates of *P. abies* (an evergreen shallower rooter) (Schume et al. 2004).

3.5.3 The Influence of Stand Density and Water Stress

Mixed-species forests are often recommended for their potential to provide higher levels of ecosystem services than monocultures, including a reduced susceptibility to droughts (Grossiord et al. 2014). At first glance, this might appear to contradict the case studies described above where E_T was higher in mixtures than monocultures and could therefore result in reduced water availability and increased drought stress in mixtures. However, while this may sometimes be true, it will certainly not always be the case and may be related to stand density. This is because E_T is only one of the processes listed above that could influence the water availability and drought stress of mixtures. The other water-related processes could be beneficial during periods of water stress.

There is likely to be a trade-off between increasing productivity (and hence E_T), but not increasing it so much that there is a large enough reduction in water availability that outweighs the complementarity effect on water stress during a drought period (Forrester 2015). This trade-off may require minimal differences in stand density between the mixtures and monocultures. If a mixture is growing faster than a monoculture, it probably has a higher stand density in terms of basal area, sapwood area, leaf area, and biomass and is therefore likely to transpire more water. If stand density and productivity are significantly greater in mixtures, then mixtures may use more water than monocultures, but if stand density is similar, the water-related processes listed above could reduce the water stress of trees in mixtures. Controlling stand density is a common and important silvicultural treatment used in forests to manage water availability (Hawthorne et al. 2013), and density can be similar in mixtures and monocultures when it is managed by thinning or when each species has similar growth rates. An example of the interaction between stand density and growth, E_T , and WUE is shown in Fig. 3.3 (see also Sect. 3.7), where *E. globulus* growth and E_T are negatively correlated with neighbourhood density (basal area) in the monocultures but not in the mixtures.

3.6 Spatial and Temporal Dynamics of Species Interactions

Interactions between a given pair of species are dynamic and change as resource availability or climatic conditions change (see reviews by Forrester 2014; Forrester and Bauhus 2016). Net complementarity interactions between a given pair of species can transform into net competitive interactions and vice versa (Forrester et al. 2011; Bouillet et al. 2013; Binkley 2003; Pretzsch et al. 2010; Boyden et al. 2005). It is important to understand how these interactions might change when managing mixed-species stands and designing mixed-species plantations. Furthermore, mixed-species forests are an important component of climate adaptation and risk-reduction strategies (Reif et al. 2010), and to ensure that mixtures are used appropriately, it is critical to understand how climatic variability influences species interactions. These spatial and temporal dynamics were reviewed by Forrester (2014), and this forms the basis for the following sections.

3.6.1 A Framework for Understanding the Dynamics of Species Interactions

The spatial and temporal dynamics of species interactions can be summarised in Fig. 3.4. This framework is based on the assumption that complementarity effects are related to (1) the types of species interactions (e.g. N fixation) and (2) how resource availability changes along the spatial or temporal gradient (Forrester 2014). Complementarity increases as the availability of resource 'X' declines (or climatic condition 'X' becomes harsher) if the species interactions improve

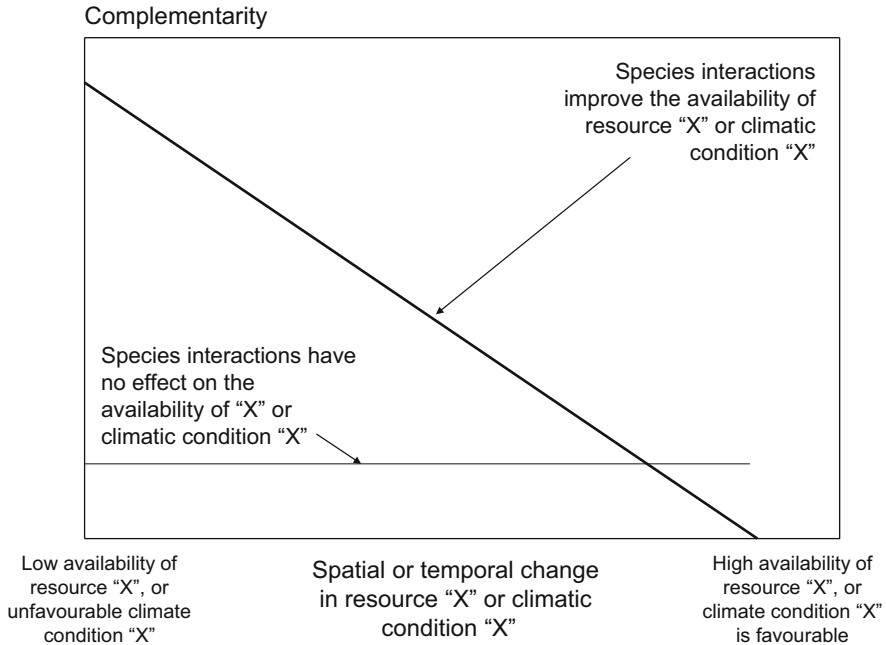


Fig. 3.4 A framework to describe the relative complementarity response of a species growing in a mixture in relation to gradients in growing conditions and the types of species interaction that occur between the species in that mixture. The thick diagonal line shows a pattern where complementarity increases as the availability of resource "X" declines or climatic condition "X" becomes harsher. This occurs when the species interactions improve the availability, uptake or use efficiency of resource "X" or interactions improve climatic condition "X". For example, complementarity could increase as competition for light becomes more intense (and light availability per tree declines) when interactions increase light interception or light-use efficiency. This type of interaction would be less useful if nutrients or water limit growth, but its usefulness should increase as soil resource availability increases (or climatic conditions become more favourable). The thin horizontal line shows what could result when the species interactions do not lead to any change in complementarity along the gradient because complementarity does not result from interactions that influence "X". This figure ignores the possible interactions between multiple X factors on the x-axis (see Sect. 3.6.6). Modified from Forrester (2014) and Forrester and Bauhus (2016)

the availability, uptake, or use efficiency of resource 'X' (or interactions improve climatic condition 'X') (Forrester and Bauhus 2016).

The spatial and temporal shifts in the way species interact can occur on small to large scales. There is spatial variability in light and soil resource availability in forests at the scale of a few square metres (Boyden et al. 2012) and climatic conditions within a stand vary due to canopy gaps, shading, or wind protection from neighbours (Rao et al. 1998). At larger spatial scales, abiotic factors vary along slopes and with aspect and of course from one stand or region to another. Temporally, climatic conditions vary from 1 year to another and may even change in the long term. Species interactions can also change as stands develop because the

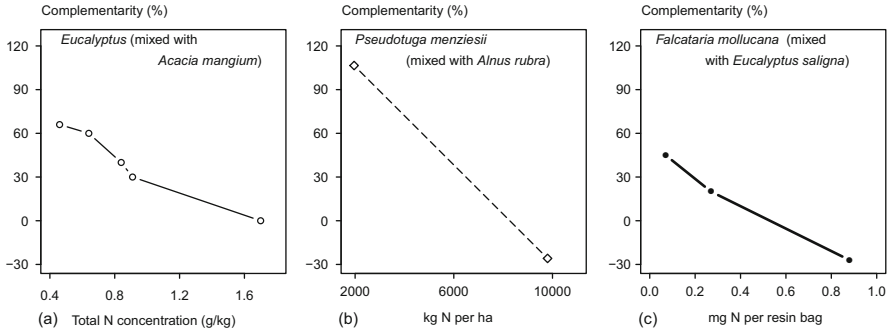


Fig. 3.5 Relationships between complementarity (%), calculated using Eqs. (3.2) and (3.3), and soil N availability, which were quantified differently in each study. The stands contained (a) *E. grandis* or *E. urophylla* \times *grandis* clones with *A. mangium* (Bouillet et al. 2013), (b) *P. menziesii* with *A. rubra* (Binkley 2003), and (c) *F. mollucana* with *E. saligna* (Boyden et al. 2005)

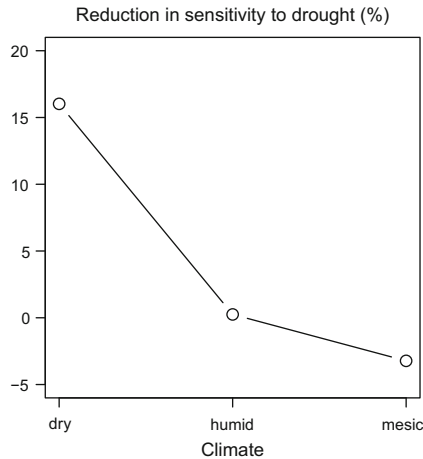
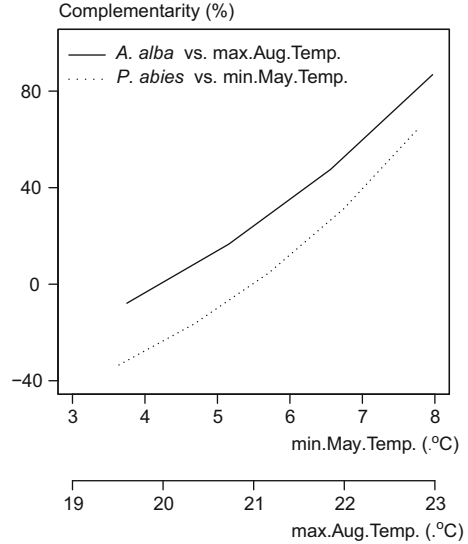


Fig. 3.6 The relative reduction in drought sensitivity (%) of *A. alba* (in mixtures with *P. abies*) in relation to climate (Lebourgeois et al. 2013). The reduction in sensitivity is the mean sensitivity of trees in mixtures compared with monocultures. Figure modified from Forrester (2014)

demand and availability of light, water, and nutrients will often change as growth rates and stand biomass changes.

Using studies from the literature, Figs. 3.5, 3.6, and 3.7 summarise the relationships between complementarity and gradients in resource availability or climatic conditions. The complementarity effects that are shown in these figures were calculated using tree or stand species-level information. Using tree-level information, complementarity was calculated for mean tree sizes and medium density stands based on the relative productivity (Eq. 3.2) (Forrester and Pretzsch 2015).

Fig. 3.7 Relationships between complementarity (%), calculated using Eq. (3.2), and the mean maximum temperature in August or the mean minimum temperature in May, both of which varied between six sites at which there were *A. alba* and *P. abies* forests (Forrester et al. 2013)



$$\text{Relative Productivity (\%)} = \frac{\text{growth in mixture} - \text{growth in monoculture}}{\text{growth in monoculture}} \times 100 \quad (3.2)$$

Using stand-level information, complementarity was calculated using Eq. (3.3)

$$\text{Relative Productivity (\%)} = \left(\frac{\text{growth or yield in mixture}}{\text{growth or yield in monoculture} \times \text{species proportion}} - 1 \right) \times 100 \quad (3.3)$$

where the species proportion is the stand density of the given species in mixture divided by the total stand density, and density can be expressed as the initial planting density (trees ha⁻¹) or stand biomass.

3.6.2 Spatial Effects of Interactions That Influence Nutrient Availability

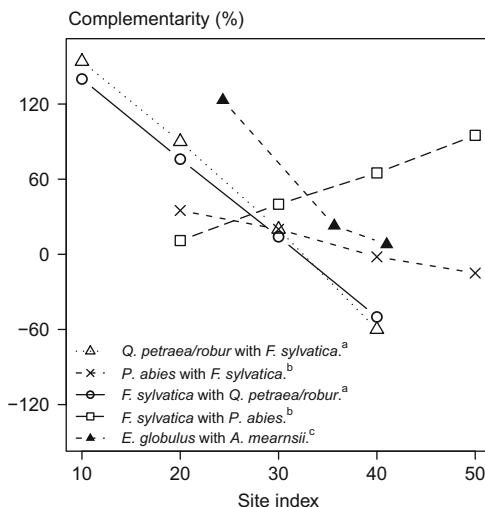
Species interactions that improve nutrient availability, uptake, and use efficiency often result in greater facilitative effects on sites where those nutrients are limited (Forrester 2014, Fig. 3.5). The most well-known example is probably the increasing facilitative effect of N-fixing species on the growth of non-N-fixing species as soil N becomes more limiting (Binkley 2003; Forrester et al. 2006b, c; Bouillet et al.

2013). For example, the N-fixing *Alnus rubra* significantly increased the growth of *Pseudotsuga menziesii* on a low-N site, but not on a high-N site (Binkley 2003). The complementarity effect by age 70 years was as high as 100% (Fig. 3.5b) and was related to greater nutrient uptake rather than changes in availability or efficiency. The rates of N, Mg, and K uptake were greater in mixtures than in *P. menziesii* stands at both sites, but the relative increases were much greater at the low-N site (Binkley et al. 1992b). Rates of N fixation by *A. rubra* were high at both sites, and the N-use efficiency of mixtures was <30% of *P. menziesii* stands on both sites (Binkley et al. 1992b).

The studies in Fig. 3.5 imply that facilitative (complementarity) effects that result from increases in the availability of a given resource (e.g. N) can be outweighed by competition when other resources are strongly limiting growth. There are many examples where mixture productivity was not improved by N-fixing species because N was not limiting enough or the N-fixing species were outcompeted by the non-N-fixing species (Forrester et al. 2007a; Bouillet et al. 2013; Epron et al. 2013). Managers could make use of these dynamics to increase facilitative effects. That is, the availability of resources that are not greatly influenced by species interactions, but that are limiting growth, could be increased, thereby increasing the likelihood that the resources influenced by the species (e.g. N) are the major limiting resources. For example, as phosphorus availability increases, the facilitative effects of N-fixing species on eucalypts also increase (Boyden et al. 2005; Forrester et al. 2006c), so the application of phosphorus fertiliser might increase the facilitative effect of the N-fixing species in these stands.

N fixation is an example of how N availability can be increased by increasing the size of the N pool. Nutrient availability can also be increased by increasing the proportion of the total soil nutrient pool that is actually available to plants. Section 3.3 discussed some of the mechanisms, including accelerating rates of nutrient cycling, contrasting mycorrhizal associations, and contrasting fine-root distributions. When any of these do actually improve nutrient availability, the facilitative effect on growth should be more useful on sites where the given nutrient is limiting growth. No studies could be found that measured complementarity in growth and nutrient cycling along gradients in nutrient availability. However, traits or interactions that reduced competition for, or improved, the availability of nutrients, including faster nutrient cycling, were suggested to have contributed to the increasing complementarity effects of *F. sylvatica* on the growth of *P. abies* (Pretzsch et al. 2010), *Quercus petraea*, or *Q. robur* (Pretzsch et al. 2013a) as site quality increased (Box Fig. 3.2-1 in Box 3.2). This was also suggested for *Picea mariana* and *Populus tremuloides* mixtures (Cavard et al. 2011).

Box Fig. 3.2-1 Relationship between complementarity ($C\%$) and site indices. $C\%$ was calculated using Eq. (3.3). The site index is the mean or maximum height at age 100 years (a, b) or the stand volume (of monocultures) at age 15 years ($\text{m}^3 \text{ha}^{-1}/\beta$).^a Pretzsch et al. (2013a),^b Pretzsch et al. (2010),^c Forrester et al. (2011). Figure modified from Forrester (2014)



Box 3.2 Examining the Spatial Dynamics of Species Interactions Using Site Indices

Site quality or site indices are often used to quantify differences in growing conditions. Site quality or site indices are the net effect of many different factors, including climatic variables such as temperature, vapour pressure deficit, precipitation and climatic extremes, and soil properties relating to the availability of water and many different nutrients. Site quality and site indices are used a lot in forestry because they ‘summarise’ the net effects of all these factors. However, this strength becomes a weakness and is problematic when examining the spatial dynamics of species interactions, which are related directly to actual gradients in specific resources (Figs. 3.5, 3.6, and 3.7), and not the productivity (site index) of the site per se (Box Fig. 3.2-1). For example, some of the largest facilitative effects of N-fixing trees on the growth of eucalypts have been found in relatively productive plantations (Binkley et al. 2003; DeBell et al. 1987), and a review of these effects found that there was no significant relationship between the mean annual biomass or volume growth of eucalypt monocultures (a measure of site quality) and the mixing effect in 1:1 mixtures (Forrester et al. 2006b). That is, very productive sites had plenty of water, phosphorus, and favourable climatic conditions but were N limited, whereas sites that were not so N limited had low productivities because other resources, such as water availability, limited growth.

Similarly, complementarity effects were found to increase with increasing site quality for *F. sylvatica* mixed with *P. abies* (Pretzsch et al. 2010) and for

(continued)

Box 3.2 (continued)

A. alba mixed with *P. abies* (Forrester et al. 2013). However, in different studies, but for the same species combinations, complementarity effects for *F. sylvatica* that occurred during low-growth years were absent during more favourable growth periods (del Río et al. 2014), or complementarity effects for *A. alba* that were found on dry sites were not significant on mesic or humid sites (Lebourgeois et al. 2013). Thus, in some studies, complementarity effects increased as growing conditions improved, and in other studies, complementarity for the same species in the same mixture combinations decreased as growing conditions improved. As explained in Sect. 3.6.6, this is probably the result of measurements of complementarity during average conditions in one study (when interactions influencing light were important) but during slow-growth periods in another study (when interactions influencing water were important). This shows the risk of relying on site quality or site indices when studying how plant interactions change (perhaps with the exception of light-related interactions).

3.6.3 Spatial Effects of Interactions That Influence Water Availability

As water availability declines, any interactions or mechanisms that influence water availability and uptake should have a greater complementarity effect (Fig. 3.4). For example, the sensitivity of *Abies alba* to summer droughts declined in mixtures with *Picea abies* or *Fagus sylvatica* compared with monospecific neighbourhoods, but this complementarity effect was only found at dry sites and not at mesic or humid sites (Fig. 3.6). The mechanisms responsible for this effect were not measured, but it was suggested that competition for water was reduced for *Abies alba* because the other species have shallower roots systems, and the canopies of *F. sylvatica* may intercept less rain, allowing more to reach the soil. Increasing complementarity effects of *Quercus petraea* or *Q. robur* on *F. sylvatica* with declining site quality were suggested to result from mechanisms that improved water availability, including hydraulic redistribution (see Sect. 3.5.2) (Pretzsch et al. 2013a). However, water availability or use was not measured in that study, and another study using the same species found that although *Q. petraea* redistributed water from deeper to more shallow regions of the soil, there was no evidence that *F. sylvatica* actually acquired that water (Zapater et al. 2011). The contribution of processes that could improve water relations and complementarity does not appear to have been quantified along gradients in water availability in forests. All examples of complementarity effects in this paragraph were observed at drier ends of spatial gradients; however complementarity involving improved water relations may also occur at sites that are not considered to be dry but that experience seasonal water deficits or periodic droughts (see Sect. 3.6.5).

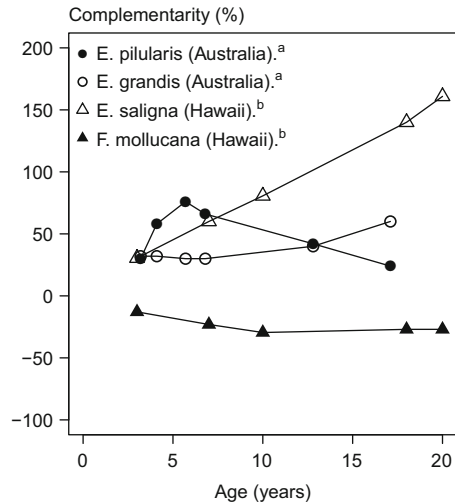
3.6.4 Spatial Effects of Interactions That Influence Light Absorption and Use

Mixtures that contain a fast-growing and light-use efficient species that overtops a slower-growing but more shade-tolerant species could have a greater LUE than monocultures of the shade-tolerant species and greater APAR than monocultures of the less shade-tolerant upper canopy species. Complementarity effects resulting from interactions that improve APAR or LUE should increase as light availability declines (Fig. 3.4). As climatic conditions improve or the availability of water and nutrients increase, stand leaf area and APAR should also increase. As this happens, light availability will decline, and trees tend to respond by allocating a higher proportion of their growth above ground, which improves light absorption (Box 3.1) (Litton et al. 2007; Poorter et al. 2012). Several studies have found increases in complementarity with improvements in growing conditions, such as better climatic conditions and site quality (Box Fig. 3.2-1 in Box 3.2 and Fig. 3.7). Increasing relative and absolute complementarity effects were found with improved growing conditions in *Picea abies* and *Abies alba* stands in south-western Germany (Forrester et al. 2013). The complementarity appeared to result from greater APAR and LUE due to contrasting crown physiologies, crown architectures, and canopy structure (Forrester and Albrecht 2014). Similarly, the complementarity effect for *Picea abies* growing with *Abies alba* in Switzerland also increased with increasing site quality (Huber et al. 2014). Complementarity effects for *F. sylvatica* mixed with *P. abies* increased with increasing site quality in Central European forests (Pretzsch et al. 2010). *F. sylvatica* trees of a given diameter had larger crown projection areas in mixtures than in monocultures, and this effect increased with site quality (Dieler and Pretzsch 2013). These greater crown sizes may have improved light interception by trees in mixtures. In Canadian forests, relative growth reductions of *Picea glauca* × *engelmannii* growth (compared with hypothetical free-growing trees) due to competition from *Pinus contorta* were lower at higher-quality sites (Coates et al. 2013), which may indicate that species interactions resulted in improved APAR or LUE of *Picea glauca* × *engelmannii*.

3.6.5 Temporal Dynamics of Species Interactions

As stands develop, there are often changes in complementarity effects or the relative dominance of each species (Fig. 3.8) (Binkley 2003; Filipescu and Comeau 2007; Cavard et al. 2011; Forrester et al. 2011; Bouillet et al. 2013; Forrester 2014). These temporal changes can result from abiotic factors, such as climatic conditions and stand disturbances, or stands developing and influencing the availability of light and soil resources. The temporal dynamics in Fig. 3.8 illustrate the value of long-term measurements and the likelihood that measurements at a single point in time may not reflect actual long-term complementarity effects (see also Figs. 4.17 and 4.18). As an example, several studies have shown that complementarity can change with temporal changes in water availability. As even-aged stands develop, leaf

Fig. 3.8 Temporal dynamics of complementarity in 1:1 mixtures of *E. pilularis* with *E. grandis* or *E. saligna* with *F. moluccana*. ^aForrester and Smith (2012), ^bBinkley et al. (2003). Figure modified from Forrester (2014)



areas, growth rates, and transpiration initially increase before peaking and then declining (Dunn and Connor 1993; Vertessy et al. 1996; Ryan et al. 1997; Forrester et al. 2010a). As transpiration increases, soil water availability may decline, leaving the stands more water limited and susceptible to dry or hot conditions. When mixtures are more productive than monocultures, they can also use more water (Forrester et al. 2010b; Kunert et al. 2012), and this may increase their susceptibility to water-limiting conditions. Several studies have reported early complementarity effects in mixtures that were lost later due to excessive competition for water (Snowdon et al. 2003; Forrester et al. 2007a; Bouillet et al. 2013). In these mixtures, the main complementarity effects resulted from higher N availability due to N-fixing species. In contrast, when interactions or contrasting species traits reduce competition for water, the mixtures may be less sensitive to hot and dry periods. For example, complementarity effects in mixtures of *Q. petraea*, *P. abies*, and *F. sylvatica* were observed during low-growth years but not during high-growth years (del Río et al. 2014). The *F. sylvatica* trees were also more resistant and resilient to droughts when growing in mixtures (Pretzsch et al. 2013b), and it was speculated that the complementarity effects resulted from improved water relations.

The magnitude of complementarity effects could also vary with the intensity of light competition (Sect. 3.6.4). As stands develop and leaf areas increase, so does competition for light, and trees can allocate a higher proportion of growth above ground, which improves light interception (Litton et al. 2007). As competition for light increases, it becomes more important for shade-intolerant species to overtop more shade-tolerant species (Kelty 1992). When shade-intolerant species, such as eucalypts, are unable to overtop the admixed species, complementarity effects are more likely to be smaller or absent (Forrester et al. 2006b, 2011).

3.6.6 Simultaneously Occurring Species Interactions

In any one mixture, there are almost certainly several different processes that influence the net complementarity effects. For example, it has been well documented that complementarity effects of mixtures containing N-fixing species do not only result from improved N availability, but there can also be accelerated rates of P cycling, reductions in competition for light and greater APAR or LUE, and greater transpiration or WUE (Binkley et al. 1992a; Forrester et al. 2005; Richards et al. 2010; Hinsinger et al. 2011). Furthermore, as discussed above, the contribution that each process makes to the net complementarity effects changes with spatial and temporal variability in resource availability and climatic conditions (Forrester 2014). This also implies that for a given species combination, there are likely to be several complementarity—resource availability relationships depending on the resource gradients that are being examined and when they are being examined (see Box 3.2). Many studies focus, understandably, on a single resource gradient and may therefore underestimate the total complementarity effects. Similarly, productivity-biodiversity relationships will be the net result of many interactions between each specific species combination and their spatial and temporal dynamics (Forrester and Bauhus 2016). The asymptotic productivity-biodiversity relationships that are often found (Forrester and Bauhus 2016) might suggest that some species are redundant in more diverse stands. However, grassland mixture studies have shown that when more functions (growth, nutrient cycling, etc.) and more growing conditions are considered (ages, resources, climatic conditions), the number of species required to reach an asymptote is higher because there is a greater chance that each will be useful under specific conditions (Hector and Bagchi 2007; Isbell et al. 2011). The absence of productivity-biodiversity relationships in some forests (Vilà et al. 2013) may result because the species in those forests do not interact in ways that improve the availability or use of the limiting resources during the measurement period (Forrester and Bauhus 2016). For example, when water limits growth, having a wide range of nutrient uptake strategies may be of little benefit.

3.7 Stand Density

The interactions between species can also be influenced by stand density, which is important for two reasons. The first is that stand density can be positively correlated with species diversity (e.g. Vilà et al. 2013; Chisholm et al. 2013), and so greater productivity in mixtures may sometimes, at least partly, result from higher densities or higher structural diversity, rather than from direct effects of species diversity or interactions per se (Forrester and Bauhus 2016). Therefore, if stand density is not taken into account, complementarity effects may be over- or underestimated. These density effects are well known, and various approaches for dealing with them have been developed (Chap. 4). At the stand level, replacement and additive series designs have been used for planted experiments (Kelty and Cameron 1995) (see

Chap. 2), while in forests, plots that are close to their maximum density are used (see Chap. 4). At the tree level, competition indices are sometimes used to separate the effects of inter- and intraspecific interactions and stand density (Boyden et al. 2005; Vanclay 2006a; Forrester et al. 2013; Forrester 2015).

The second reason why density is important is that all of the complementarity effects described in this chapter could potentially be influenced by stand density (e.g. light-related effects in Forrester and Albrecht 2014, or water-related effects in Forrester 2015; Fig. 3.3). At low densities (and following thinning), species interactions will be weak whether they are complementary or competitive because the trees need to be close enough to interact in the first place. At the other extreme, when stand density is very high, competition will probably be high enough to outweigh any complementarity effects. This has been shown in *Eucalyptus* and *Acacia* mixtures, for which there are many examples of strong complementarity effects (Forrester et al. 2006b). However, at very high densities, when up to 20,000 *Acacia* weeds invade monospecific *Eucalyptus* plantations, there are net competitive effects on *Eucalyptus* growth, even though soil nitrogen increases with *Acacia* density (Hunt et al. 1999). Between these extremes of very low and very high densities, the relationship between density and complementarity effects depend on the resources that are limiting and that are influenced by changes in density, as well as the types of species interactions (following Fig. 3.4). Depending on the study, increasing stand density has increased or reduced complementarity effects in mixed-species forests or plantations (Fig. 3.9) (Garber and Maguire 2004). For example, complementarity effects increased with stand density on sites where mixtures of *P. abies* and *A. alba* were more productive than monocultures but increased competition on sites where mixtures were less productive (Fig. 3.9, Forrester et al. 2013). Complementarity effects were higher at lower densities for each species in *P. sylvestris* and *Q. pyrenaica* mixtures (Fig. 3.9, del Río and Sterba 2009). Complementarity effects increased with increasing density for *F. sylvatica*, which is a relatively strong competitor, but declined for associated *P. sylvestris* (Condés et al. 2013). Complementarity effects increased or decreased with stand density for *Falcataria moluccana* and *Eucalyptus saligna*, depending on how soil N and P availability changed (Boyden et al. 2005).

These effects of density on complementarity indicate that thinning is likely to significantly influence complementarity effects and may therefore be a useful management tool in mixtures. However, it also has important implications for studies that use plots in forests where previous thinning intensities are unknown, in which case it may be difficult to separate complementarity effects from density effects that are an artefact of previous management.

3.8 Synopsis

This chapter describes how species interactions can influence some of the main physiological and ecological processes that occur in mixed-species forests and plantations. Firstly, the production ecology equation is introduced as a framework

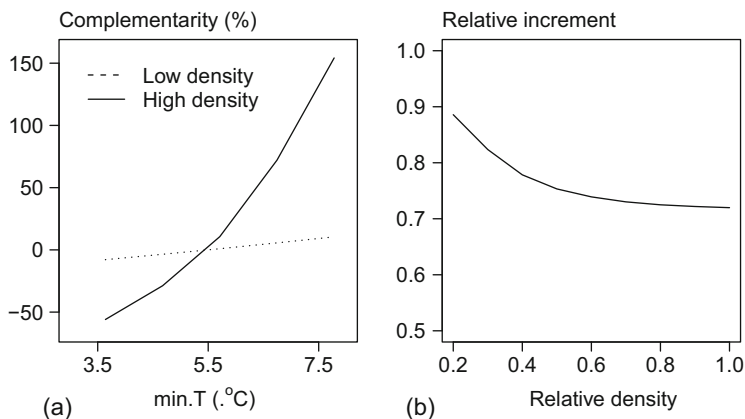


Fig. 3.9 Increasing stand density (a) increased complementarity effects for *P. abies* in mixtures with *A. alba* along a 6-site gradient in mean minimum temperature in May (min.T) (Forrester et al. 2013). Increasing stand density (b) decreased complementarity effects (in terms of relative increment) for *Pinus sylvestris* in mixture with *Quercus pyrenaica* (modified from del Río and Sterba 2009). Relative increment is the increment ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) of *P. sylvestris* in mixture divided by its increment in monoculture, and relative density is the basal area per ha of *P. sylvestris* in monoculture divided by the maximum observed basal area per ha of *P. sylvestris* stands

for quantifying the types of processes that influence tree growth and how these are influenced by species interactions. This equation describes growth as a function of resource availability, resource acquisition, and resource-use efficiency. Nutrient availability can increase when the size of the nutrient pool is increased, such as by symbiotic N fixation or by increasing the proportion of the pool that is actually available to plants and the speed at which it is cycled. Nutrient-use efficiency can increase, decrease, or remain unchanged when productivity increases in mixtures. This contrasts with light- and water-use efficiency (tree growth per unit of light absorption or transpiration), which increase or remain unchanged, but generally do not decline, as productivity increases. With regard to light, if a fast-growing species with high light-use efficiency overtops a slower-growing and more shade-tolerant species that is capable of high leaf areas and high light absorption, then mixtures could have a greater light-use efficiency than monocultures of the more shade-tolerant species and could absorb more light than monocultures of the less shade-tolerant species of the upper canopy. The few studies that have compared the water availability, transpiration, and water-use efficiency of a given species growing in a mixture compared with a monoculture have indicated that when growth increases (at the tree or stand levels), there are also likely to have been increases in transpiration or water-use efficiency, and several different processes can contribute to this response.

The influence of a given type of interaction on growth is not static; it changes with spatial and temporal variability in resource availability and climatic conditions and as a stand develops. A recently developed framework is used to explain these spatial and temporal dynamics and to indicate when different types of interactions

are important. This shows that complementarity effects depend on the types of species interactions and how resource availability changes along the spatial or temporal gradients. When interactions improve N availability (e.g. via symbiotic N fixation), then relative complementarity effects are highest when N availability is low, and they decline as N availability increases because there is then less need for any additional N. Similarly, interactions that improve water availability are likely to lead to greater relative complementarity effects when water availability is low, and these effects are likely to decline as water availability increases. In contrast, some studies have found that complementarity effects increase with increasing site qualities. These patterns appear to occur because as growing conditions improve, competition for light increases, and complementarity effects will result from interactions that improve light absorption or light-use efficiency. It is also important to consider that multiple types of interactions are likely to occur simultaneously in mixtures, such as interactions that influence nutrients, others that influence water, and others that influence light. Therefore, different resource availability-complementarity patterns can occur for a given pair of species, depending on the resource being examined. Finally, stand density can influence these interactions. As stand density increases, interactions may become more favourable or less favourable, depending on how, and which, resources are influenced by the change in density.

Take-Home Messages

1. The production ecology equation provides a useful framework to quantify the processes driving species interactions. This equation describes growth as a function of resource availability multiplied by the proportion of resource acquired by the trees, multiplied by the resource-use efficiency.
2. Nutrient availability can increase when the size of the nutrient pools increase (e.g. via N fixation, atmospheric deposition) and when a higher proportion of the nutrient pool is available to the trees (e.g. faster mineralisation or nutrient cycling). The proportion of nutrients used (nutrient uptake) can be increased when there are also spatial, chemical, or temporal differences in nutrient uptake. Nutrient-use efficiency can increase, decrease, or not change as growth increases.
3. Combining a shade-tolerant species that is capable of high light interception, with a very light-use efficient species, could result in mixtures that absorb more light than monocultures of the less shade-tolerant species and that are more light-use efficient than the more shade-tolerant species. In addition, when interactions increase growth, they are also likely to increase leaf area and light absorption, as well as light-use efficiency.
4. The few studies that have examined the transpiration and WUE of mixtures have found that when mixtures are more productive than monocultures, they

often also use more water and have a higher WUE. There are several processes that could increase the water availability in mixtures, but their influence on the complementarity effects that are sometimes observed in mixtures has rarely been quantified.

5. Species interactions are dynamic and vary spatially and temporally with resource availability and climatic conditions. The direction depends on the types of species interactions and how the resources change along the gradients. For example, interactions that increase water availability, transpiration, or WUE will become more useful as water availability declines along spatial gradients, or during periods of water stress, or as stands develop and competition for water changes.
6. For a given species combination, there are probably several different types of interactions occurring simultaneously (e.g. N fixation, reduced competition for light or water). Therefore, there can be different complementarity-resource availability relationships for a given species combination depending on the resource gradients that are being examined. For this reason, site quality or site indices can be problematic because they do not differentiate between the different resources that limit growth. Complementarity-site index relationships are the net effect of different types of interactions, and opposing relationships have been found for the same combinations of species in different studies that use site indices.
7. Stand density can modify the way species interact because it changes the balance between competitive and complementarity interactions. Furthermore, whether or not complementarity increases or decreases with increasing stand density depends on the types of species interactions that occur in the given mixture.

References

- Anten NPR (2005) Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. *Ann Bot* 95:495–506
- Anten NPR, Shieving F, Werger MJA (1995) Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C₃ and C₄ mono- and dicotyledonous species. *Oecologia* 101:504–513
- Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. *Ann For Sci* 59:233–253
- Augusto L, Schrijver AD, Vesterdal L, Smolander A, Prescott C, Ranger J (2015) Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biol Rev* 90:444–466
- Bauhus J, Khanna PK, 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 AP, Nicotra AB (2004) Above-ground interactions and productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*. *Can J For Res* 34:686–694

- Bayer D, Seifert S, Pretzsch H (2013) Structural crown properties of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in mixed versus pure stands revealed by terrestrial laser scanning. *Trees Struct Funct* 27:1035–1047
- Berger TW, Inselebacher E, Mutsch F, Pfeffer M (2009a) Nutrient cycling and soil leaching in eighteen pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*). *For Ecol Manag* 258:2578–2592
- Berger TW, Untersteiner H, Topf M, Neubauer C (2009b) Nutrient fluxes in pure and mixed stands of spruce (*Picea abies*) and beech (*Fagus sylvatica*). *Plant Soil* 322:317–342
- Binkley D (2003) Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. *Can J For Res* 33:2274–2279
- Binkley D (2012) Understanding the role resource use efficiency in determining the growth of trees and forests. In: Schlichter T, Montes L (eds) *Forests in development: A vital balance*. Springer, The Hague, pp 13–26
- Binkley D, Giardina C (1997) Nitrogen fixation in tropical forest plantations. In: Nambiar EKS, Brown AG (eds) *Management of soil, nutrients and water in tropical plantation forests*. Australian Centre for International Agricultural Research, Canberra, pp 297–337
- Binkley D, Giardina C (1998) Why do tree species affect soils? The Warp and Woof of tree-soil interactions. *Biogeochemistry* 42:89–106
- Binkley D, Valentine D (1991) Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. *For Ecol Manag* 40(1–2):13–25
- Binkley D, Dunkin KA, DeBell D, Ryan MG (1992a) Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. *For Sci* 38(2):393–408
- Binkley D, Sollins P, Bell R, Sachs D, Myrold D (1992b) Biogeochemistry of adjacent conifer and alder-conifer stands. *Ecology* 73:2022–2033
- Binkley D, Senock R, Bird S, Cole TG (2003) Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and N-fixing *Falcataria moluccana*. *For Ecol Manag* 182:93–102
- Binkley D, Stape JL, Ryan MG (2004) Thinking about efficiency of resource use in forests. *For Ecol Manag* 193:5–16
- Bolte A, Villanueva I (2006) Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) *Eur J For Res* 125:15–26
- Bouillet JP, Laclau JP, Goncalves JLM, Moreira MZ, Trivelin PCO, Jourdan C, Silva EV, Piccolo MC, Tsai SM, Galiana A (2008) Mixed-species plantations of *Acacia mangium* and *Eucalyptus grandis* in Brazil 2: nitrogen accumulation in the stands and biological N₂ fixation. *For Ecol Manag* 255:3918–3930
- Bouillet J-P, Laclau J-P, Gonçalves JLM, Voigtlaender M, Gava JL, Leite FP, Hakamada R, Mareschal L, Mabiala A, Tardy F, Levillain J, Deleporte P, Epron D, Nouvellon Y (2013) *Eucalyptus* and *Acacia* tree growth over entire rotation in single- and mixed-species plantations across five sites in Brazil and Congo. *For Ecol Manag* 301:89–101
- Boyden S, Binkley D, Senock R (2005) Competition and facilitation between *Eucalyptus* and nitrogen-fixing *Falcataria* in relation to soil fertility. *Ecology* 86(4):992–1001
- Boyden S, Montgomery R, Reich PB, Palik B (2012) Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure. *Ecol Appl* 22(5):1578–1588
- Brassard BW, Chen HYH, Bergeron Y, Paré D (2011) Differences in fine root productivity between mixed- and single-species stands. *Funct Ecol* 25:238–246
- Brassard BW, Chen HYH, Cavard X, Laganière J, Reich PB, Bergeron Y, Paré D, Yuan Z (2013) Tree species diversity increases fine root productivity through increased soil volume filling. *J Ecol* 101:210–219
- Canham C, Coates KD, Bartemucci P, Quaglia S (1999) Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Can J For Res* 29:1775–1783

- Cavard X, Bergeron Y, Chen HYH, Paré D, Laganière J, Brassard B (2011) Competition and facilitation between tree species change with stand development. *Oikos* 120:1683–1695
- Chisholm RA, Muller-Landau HC, Rahman KA, Bebbler DP, Bin Y, Bohlman SA, Bourg NA, Brinks J, Bunyavejchewin S, Butt N, Cao H, Cao M, Cardenas D, Chang L-W, Chiang J-M, Chuyong G, Condit R, Dattaraja HS, Davies S, Duque A, Fletcher C, Gunatilleke N, Gunatilleke S, Hao Z, Harrison RD, Howe R, Hsieh C-F, Hubbell SP, Itoh A, Kenfack D, Kiratiprayoon S, Larson AJ, Lian J, Lin D, Liu H, Lutz JA, Ma K, Malhi Y, McMahon S, McShea W, Meegaskumbura M, Razman SM, Morecroft MD, Nyctch CJ, Oliveira A, Parker GG, Pulla S, Punchi-Manage R, Romero-Saltos H, Sang W, Schurman J, Su S-H, Sukumar R, Sun I-F, Suresh HS, Tan S, Thomas D, Thomas S, Thompson J, Valencia R, Wolf A, Yap S, Ye W, Yuan Z, Zimmerman JK (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. *J Ecol* 101:1214–1224
- Coates KD, Lilles EB, Astrup R (2013) Competitive interactions across a soil fertility gradient in a multispecies forest. *J Ecol* 101(3):806–818
- Condés S, Rio MD, Sterba H (2013) Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. *For Ecol Manag* 292:86–95
- Crews TE, Peoples MB (2005) Can the synchrony of nitrogen supply and crop demand be improved in legume and fertilizer-based agroecosystems? A review. *Nutr Cycl Agroecosyst* 72:101–120
- DeBell DS, Radwan MA (1979) Growth and nitrogen relations of coppiced black cottonwood and red alder in pure and mixed plantations. *Bot Gaz* 140(Suppl.):S97–S101
- DeBell DS, Whitesell CD, Crabb TB (1987) Benefits of *Eucalyptus-Albizia* mixtures vary by site on Hawaii Island. USDA For. Serv. Res. Paper PSW-187
- del Río M, Sterba H (2009) Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. *Ann For Sci* 66:502
- del Río M, Schütze G, Pretzsch H (2014) Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biol* 16:166–176
- Dewar RC, Tarvainen L, Parker K, Wallin G, McMurtrie RE (2012) Why does leaf nitrogen decline within tree canopies less rapidly than light? An explanation from optimization subject to a lower bound on leaf mass per area. *Tree Physiol* 32:520–534
- Dieler J, Pretzsch H (2013) Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. *For Ecol Manag* 295:97–108
- Dijkstra FA, West JB, Hobbie SE, Reich PB (2009) Antagonistic effects of species on C respiration and net N mineralization in soils from mixed coniferous plantations. *For Ecol Manag* 257:1112–1118
- Dunn GM, Connor DJ (1993) An analysis of sap flow in Mountain Ash (*Eucalyptus regnans*) forests of different age. *Tree Physiol* 13:321–336
- Epron D, Nouvellon Y, Mareschal L, Moreira R, Koutika L-S, Geneste B, Delgado-Rojas JS, Laclau J-P, Sola G, Gonçalves JLM, Bouillet J-P (2013) Partitioning of net primary production in *Eucalyptus* and *Acacia* stands and in mixed-species plantations: two case-studies in contrasting tropical environments. *For Ecol Manag* 301:102–111
- Ewel JJ (1986) Designing agricultural ecosystems for the humid tropics. *Annu Rev Ecol Syst* 17:245–271
- Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56:341–347
- Filipescu CN, Comeau PG (2007) Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. *For Ecol Manag* 247:175–184
- Fisher RF, Binkley D (2000) Ecology and management of forest soils, 3rd edn. Wiley, New York, Chichester
- Forrester DI (2013) Growth responses to thinning, pruning and fertiliser application in *Eucalyptus* plantations: a review of their production ecology and interactions. *For Ecol Manag* 310:336–347

- Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For *Ecol Manag* 312:282–292
- Forrester DI (2015) Transpiration and water-use efficiency in mixed-species forests versus monocultures: effects of tree size, stand density and season. *Tree Physiol* 35:289–304
- Forrester DI, Albrecht AT (2014) Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. For *Ecol Manag* 328:94–102
- Forrester DI, Bauhus J (2016) A review of processes behind diversity – productivity relationships in forests. *Curr Forest Rep* 2:45–61
- Forrester DI, Pretzsch H (2015) Tamm Review: on the strength of evidence when comparing ecosystem functions of mixtures with monocultures. For *Ecol Manag* 356:41–53
- Forrester DI, Smith RGB (2012) Faster growth of *Eucalyptus grandis* and *Eucalyptus pilularis* in mixed-species stands than monocultures. For *Ecol Manag* 286:81–86
- Forrester DI, Bauhus J, Cowie AL (2005) Nutrient cycling in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *Can J For Res* 35(12):2942–2950. doi:[10.1139/x05-214](https://doi.org/10.1139/x05-214)
- Forrester DI, Bauhus J, Cowie AL (2006a) Carbon allocation in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. For *Ecol Manag* 233:275–284. doi:[10.1016/j.foreco.2006.05.018](https://doi.org/10.1016/j.foreco.2006.05.018)
- Forrester DI, Bauhus J, Cowie AL, Vanclay JK (2006b) Mixed-species plantations of *Eucalyptus* with nitrogen fixing trees: a review. For *Ecol Manag* 233:211–230. doi:[10.1016/j.foreco.2006.05.012](https://doi.org/10.1016/j.foreco.2006.05.012)
- Forrester DI, Cowie AL, Bauhus J, Wood J, Forrester RI (2006c) 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(1–2):267–277. doi:[10.1007/s11104-005-3228-x](https://doi.org/10.1007/s11104-005-3228-x)
- Forrester DI, Bauhus J, Cowie AL, Mitchell PA, Brockwell J (2007a) Productivity of three young mixed-species plantations containing N₂-fixing *Acacia* and non-N₂-fixing *Eucalyptus* and *Pinus* trees in Southeastern Australia. *For Sci* 53(3):426–434
- Forrester DI, Schortemeyer M, Stock WD, Bauhus J, Khanna PK, Cowie AL (2007b) Assessing nitrogen fixation in mixed- and single-species plantations of *Eucalyptus globulus* and *Acacia mearnsii*. *Tree Physiol* 27:1319–1328. doi:[10.1093/treephys/27.9.1319](https://doi.org/10.1093/treephys/27.9.1319)
- Forrester DI, Collopy JJ, Morris JD (2010a) Transpiration along an age series of *Eucalyptus globulus* plantations in southeastern Australia. For *Ecol Manag* 259:1754–1760. doi:[10.1016/j.foreco.2009.04.023](https://doi.org/10.1016/j.foreco.2009.04.023)
- Forrester DI, Theiveyanathan S, Collopy JJ, Marcar NE (2010b) Enhanced water use efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. For *Ecol Manag* 259:1761–1770. doi:[10.1016/j.foreco.2009.07.036](https://doi.org/10.1016/j.foreco.2009.07.036)
- Forrester DI, Vanclay JK, Forrester RI (2011) The balance between facilitation and competition in mixtures of *Eucalyptus* and *Acacia* changes as stands develop. *Oecologia* 166(1):265–272
- Forrester DI, Collopy JJ, Beadle CL, Baker TG (2012a) Interactive effects of simultaneously applied thinning, pruning and fertiliser application treatments on growth, biomass production and crown architecture in a young *Eucalyptus nitens* plantation. For *Ecol Manag* 267:104–116. doi:[10.1016/j.foreco.2011.11.039](https://doi.org/10.1016/j.foreco.2011.11.039)
- Forrester DI, Lancaster K, Collopy JJ, Warren CR, Tausz M (2012b) Photosynthetic capacity of *Eucalyptus globulus* is higher when grown in mixture with *Acacia mearnsii*. *Trees Struct Funct* 26:1203–1213
- Forrester DI, Kohnle U, Albrecht AT, Bauhus J (2013) Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. For *Ecol Manag* 304:233–242
- Forrester DI, Benneter A, Bouriaud O, Bauhus J (2016) Diversity and competition influence tree allometry – developing allometric functions for mixed-species forests. *J Ecol*. doi:[10.1111/1365-2745.12704](https://doi.org/10.1111/1365-2745.12704)
- Forrester DI, Ammer C, Annighöfer PJ, Barbeito I, Bielak K, Bravo-Oviedo A, Coll L, del Río M, Drössler L, Heym M, Hurt V, Löff M, den Ouden J, Pach M, Pereira MG, Plaga B, Ponette Q,

- Skrzyszewski J, Sterba H, Svoboda M, Zlatanov T, Pretzsch H (in press) Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. *J Ecol*
- Fredericksen TS, Zedaker SM (1995) Fine root biomass, distribution, and production in young pine-hardwood stands. *New For* 10:99–110
- Garber SM, Maguire DA (2004) Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. *For Sci* 50:92–105
- Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos* 104:230–246
- Gash JHC, Lloyd CR, Lachaud G (1995) Estimating sparse forest rainfall interception with an analytical model. *J Hydrol* 170:79–86
- Gebauer T, Horna V, Leuschner C (2012) Canopy transpiration of pure and mixed forest stands with variable abundance of European beech. *J Hydrol* 442–443:2–14
- Gerrits AMJ, Pfister L, Savenije HHG (2010) Spatial and temporal variability of canopy and forest floor interception in a beech forest. *Hydrol Process* 24:3011–3025
- Getzin S, Wiegand K (2007) Asymmetric tree growth at the stand level: random crown patterns and the response to slope. *For Ecol Manag* 242:165–174
- Grossiord C, Granier A, Ratcliffe S, Bouriaud O, Bruelheide H, Češko E, Forrester DI, Dawud SM, Finér L, Pollastrini M, Scherer-Lorenzen M, Valladares F, Bonal D, Gessler A (2014) Tree diversity does not always improve resistance of forest ecosystems to drought. *Proc Natl Acad Sci U S A* 111(41):14812–14815
- Guisasola R, Tang X, Bauhus J, Forrester DI (2015) Intra- and inter-specific differences in crown architecture in Chinese subtropical mixed-species forests. *For Ecol Manag* 353:164–172
- Harrington RA, Fownes JH, Meinzer FC, Scowcroft PG (1995) Forest growth along a rainfall gradient in Hawaii: *Acacia koa* stand structure, productivity, foliar nutrients, and water- and nutrient-use efficiencies. *Oecologia* 102:277–284
- Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu Rev Ecol Evol Syst* 36:191–218
- Hawthorne SND, Lane PNJ, Bren LJ, Sims NC (2013) The long term effects of thinning treatments on vegetation structure and water yield. *For Ecol Manag* 310:983–993
- He X-H, Critchley C, Bledsoe C (2003) Nitrogen transfer within and between plants through common mycorrhizal networks (CMNs). *Crit Rev Plant Sci* 22(6):531–567
- He Z-B, Yang J-J, Du J, Zhao W-Z, Liu H, Chang X-X (2014) Spatial variability of canopy interception in a spruce forest of the semiarid mountain regions of China. *Agric For Meteorol* 188:58–63
- Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nat Lett* 448:188–191
- Hinsinger P, Betencourt E, Bernard L, Brauman A, Plassard C, Shen J, Tang X, Zhang F (2011) P for two, sharing a scarce resource: soil phosphorus acquisition in the rhizosphere of intercropped species. *Plant Physiol* 156:1078–1086
- Hirose T, Werger MJA (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72(4):520–526
- Huber MO, Sterba H, Bernhard L (2014) Site conditions and definition of compositional proportion modify mixture effects in *Picea abies* – *Abies alba* stands. *Can J For Res* 44:1281–1291
- Hunt MA, Unwin GL, Beadle CL (1999) Effects of naturally regenerated *Acacia dealbata* on the productivity of a *Eucalyptus nitens* plantation in Tasmania, Australia. *For Ecol Manag* 117:75–85
- Ilek A, Kucza J, Szostek M (2015) The effect of stand species composition on water storage capacity of the organic layers of forest soils. *Eur J For Res* 134:187–197
- Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–203
- Kaye JP, Resh SC, Kaye MW, Chimmer RA (2000) Nutrient and carbon dynamics in a replacement series of *Eucalyptus* and *Albizia* trees. *Ecology* 81(12):3267–3273

- Kelty MJ (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty MJ, Larson BC, Oliver CD (eds) The ecology and silviculture of mixed-species forests. Kluwer Academic Publishers, Dordrecht, pp 125–141
- Kelty MJ, Cameron IR (1995) Plot designs for the analysis of species interactions in mixed stands. *Commonwealth For Rev* 74(4):322–332
- Khamzina A, Lamers JPA, Vlek PLG (2009) Nitrogen fixation by *Elaeagnus angustifolia* in the reclamation of degraded croplands of Central Asia. *Tree Physiol* 29(6):799–808
- Khanna PK (1997) Comparison of growth and nutrition of young monocultures and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii*. *For Ecol Manag* 94:105–113
- Khanna PK (1998) Nutrient cycling under mixed-species tree systems in southeast Asia. *Agrofor Syst* 38:99–120
- Knops JMH, Bradley KL, Wedin DA (2002) Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecol Lett* 5:454–466
- Kranabetter JM, MacKenzie WH (2010) Contrasts among mycorrhizal plant guilds in foliar nitrogen concentration and $\delta^{15}\text{N}$ along productivity gradients of a boreal forest. *Ecosystems* 13:108–117
- Kunert N, Schwendenmann L, Potvin C, Hölscher D (2012) Tree diversity enhances tree transpiration in a Panamanian forest plantation. *J Appl Ecol* 49:135–144
- Laclau J-P, Nouvellon Y, Reine C, Gonçalves JLM, Krushe AV, Jourdan C, le Maire G, Bouillet J-P (2013) Mixing *Eucalyptus* and *Acacia* trees leads to fine root over-yielding and vertical segregation between species. *Oecologia* 172:903–913
- Law BE, Falge E, Guc L, Baldocchi DD, Bakwind P, Berbigier P, Davis K, Dolman AJ, Falk M, Fuentes JD, Goldstein A, Granier A, Grelle A, Hollinger D, Janssens IA, Jarvis P, Jensen NO, Katul G, Mahli Y, Matteucci G, Meyers T, Monsont R, Munger W, Oechel W, Olson R, Pilegaard K, Paw KT, Thorgeirsson H, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric For Meteorol* 113:97–120
- le Maire G, Nouvellon Y, Christina M, Ponzoni FJ, Gonçalves JLM, Bouillet J-P, Laclau J-P (2013) Tree and stand light use efficiencies over a full rotation of single- and mixed-species *Eucalyptus grandis* and *Acacia mangium* plantations. *For Ecol Manag* 288:31–42
- Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For Ecol Manag* 303:61–71
- Levia DF, Frost EE (2003) A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *J Hydrol* 274(1–4):1–29
- Ligot G, Balandier P, Courbaud B, Claessens H (2014) Forest radiative transfer models: which approach for which application? *Can J For Res* 44(5):385–397
- Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Glob Chang Biol* 13:2089–2109
- May BM, 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 Manag* 181:339–355
- McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA, Murray G (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415:68–71
- Monteith JL (1977) Climate and the efficiency of crop production in Britain. *Philos Trans R Soc Lond B* 281:277–294
- Moore GW, Bond BJ, Jones JA (2011) A comparison of annual transpiration and productivity in monoculture and mixed-species Douglas-fir and red alder stands. *For Ecol Manag* 262:2263–2270
- Neumann RB, Cardon ZG (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytol* 194:337–352

- Niinemets Ü (2012) Optimization of foliage photosynthetic capacity in tree canopies: towards identifying missing constraints. *Tree Physiol* 32:505–509
- Osada N, Yasumura Y, Ishida A (2014) Leaf nitrogen distribution in relation to crown architecture in the tall canopy species, *Fagus crenata*. *Oecologia* 175:1093–1106
- Parrotta JA, Baker DD, Fried M (1996) Changes in dinitrogen fixation in maturing stands of *Casuarina equisetifolia* and *Leucaena leucocephala*. *Can J For Res* 26(9):1684–1691
- Peltoniemi MS, Duursma RA, Medlyn BE (2012) Co-optimal distribution of leaf nitrogen and hydraulic conductance in plant canopies. *Tree Physiol* 32:510–519
- Peoples MB, Herridge DF, Ladha JK (1995) Biological nitrogen fixation: an efficient source of nitrogen for sustainable agricultural production? *Plant Soil* 174(1–2):3–28
- Pfautsch S, Gessler A, Adams MA, Rennenberg H (2009a) Using amino-nitrogen pools and fluxes to identify contributions of understory *Acacia* spp. to overstory *Eucalyptus regnans* and stand nitrogen uptake in temperate Australia. *New Phytol* 183:1097–1113
- Pfautsch S, Rennenberg H, Bell TL, Adams MA (2009b) Nitrogen uptake by *Eucalyptus regnans* and *Acacia* spp. – preferences, resource overlap and energetic costs. *Tree Physiol* 29:389–399
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50
- Pretzsch H, Block J, Dieler J, Dong PH, Kohnle U, Nagel J, Spellmann H, Zingg A (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann For Sci* 76:712–723
- Pretzsch H, Bielak K, Block J, Bruchwald A, Dieler J, Ehrhart H-P, Kohnle U, Nagel J, Spellmann H, Zasada M, Zingg A (2013a) Productivity of mixed versus pure stands of oak (*Quercus petraea* (MATT.) LIEBL. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur J For Res* 132:263–280
- Pretzsch H, Schütze G, Uhl E (2013b) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol* 15:483–495
- Prieto I, Armas C, Pugnaire FI (2012) Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytol* 193:830–841
- Rao MR, Nair PKR, Ong CK (1998) Biophysical interactions in tropical agroforestry systems. *Agrofor Syst* 38:3–50
- Reich PB, Luo Y, Bradford JB, Poorter H, Perry CH, Oleksyn J (2014) Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proc Natl Acad Sci U S A* 111:13721–13726
- Reif A, Brucker U, Kratzer R, Schmiedinger A, Bauhus J (2010) Waldbewirtschaftung in Zeiten des Klimawandels – Synergien und Konfliktpotenziale zwischen Forstwirtschaft und Naturschutz. *Naturschutz und Landschaftsplanung* 42(9):261–266
- Richards AE, Forrester DI, Bauhus J, Scherer-Lorenzen M (2010) The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiol* 30:1192–1208. doi:10.1093/treephys/tpq035
- Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. *Can J For Res* 31(11):1855–1870
- Roupsard O, Ferhi A, Granier A, Pallo F, Depommier D, Mallet B, Joly HI, Dreyer E (1999) Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese west Africa. *Funct Ecol* 13:460–472
- Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. *Adv Ecol Res* 27:213–262
- Ryan MG, Binkley D, Fownes JH, Giardina CP, Senock RS (2004) An experimental test of the causes of forest growth decline with stand age. *Ecol Monogr* 74:393–414
- Saccone P, Delzon S, Pagès J-P, Brun J-J, Michalet R (2009) The role of biotic interactions in altering tree seedling responses to an extreme climatic event. *J Veg Sci* 20:403–414

- Sands PJ (1995) Modelling canopy production. I Optimal distribution of photosynthetic resources. *Aust J Plant Physiol* 22:593–601
- Sapjanskas J, Paquette A, Potvin C, Kunert N, Loreau M (2014) Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* 95:2479–2492
- Schmid I, Kazda M (2002) Root distribution of Norway spruce in monospecific and mixed stands on different soils. *For Ecol Manag* 159(1-2):37–47
- Schume H, Jost G, Hager H (2004) Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *J Hydrol* 289:258–274
- Schwendenmann L, Pendall E, Sanchez-Bragado R, Kunert N, Hölscher D (2015) Tree water uptake in a tropical plantation varying in tree diversity: interspecific differences, seasonal shifts and complementarity. *Ecohydrology* 8:1–12
- Snowdon P, Wichienopparat W, Khanna PK (2003) Growth, above-ground biomass and nutrient content of eucalypts and acacias grown in mixture in a tropical environment – evaluation for one full rotation. In: International Conference on Eucalypt Productivity, Hobart, Australia, 10–15 November 2003. pp 57–58
- Stape JL, Binkley D, Ryan MG (2004) *Eucalyptus* production and the supply, use and efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. *For Ecol Manag* 193:17–31
- Turner BL (2008) Resource partitioning for soil phosphorus: a hypothesis. *J Ecol* 96:698–702
- Van Kessel C, Farrell RE, Roskoski JP, Keane KM (1994) Recycling of the naturally-occurring ¹⁵N in an established stand of *Leucaena leucocephala*. *Soil Biol Biochem* 26:757–762
- Vanclay JK (2006a) Experiment designs to evaluate inter- and intra-specific interactions in mixed plantings of forest trees. *For Ecol Manag* 233:366–374
- Vanclay JK (2006b) Spatially-explicit competition indices and the analysis of mixed-species plantings with the Simile modelling environment. *For Ecol Manag* 233:295–302
- Vandermeer J (1989) The ecology of intercropping. Cambridge University Press, New York
- Vertessy RA, Hatton TJ, Benyon RG, Dawes WR (1996) Long-term growth and water balance predictions for a mountain ash (*Eucalyptus regnans*) forest catchment subject to clear-felling and regeneration. *Tree Physiol* 16(1-2):221–232
- Vilà M, Carrillo-Gavilán A, Vayreda J, Bugmann H, Fridman J, Grodzki W, Haase J, Kunstler G, Schelhaas M, Trasobares A (2013) Disentangling biodiversity and climatic determinants of wood production. *PLoS One* 8(2):e53530
- Vitousek PM (1982) Nutrient cycling and nutrient efficiency. *Am Nat* 119:553–572
- Wacker L, Baudois O, Eichenberger-Glinz S, Schmid B (2009) Effects of plant species richness on stand structure and productivity. *J Plant Ecol* 2(2):95–106
- Wang XL, Klinka K, Chen HYH, de Montigny L (2002) Root structure of western hemlock and western redcedar in single- and mixed-species stands. *Can J For Res* 32:997–1004
- Williams BL (1992) Nitrogen dynamics in humus and soil beneath Sitka spruce (*Picea sitchensis* (Bong.) Carr.) planted in pure stands and in mixture with Scots pine (*Pinus sylvestris* L.) *Plant Soil* 144:77–84
- Zapater M, Hossann C, Bréda N, Bréchet C, Bonal D, Granier A (2011) Evidence of hydraulic lift in a young beech and oak mixed forest using ¹⁸O soil water labelling. *Trees* 25:885–894