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# The role of species mixtures in plantation forestry

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## Abstract

Nearly all forest plantations are established as monocultures, but research has shown that there are potential advantages to be gained by using carefully designed species mixtures in place of monocultures. This paper reviews recent studies that compare stand development and productivity of mixed and pure plantations. Higher stand-level productivity in mixtures has been found with two kinds of species interactions: (1) complementary resource use between species that arises from development of a stratified canopy (and possibly root stratification); (2) facilitative improvement in nutrition of a valuable timber species growing in mixture with a nitrogen-fixing species (but only if combined with complementary resource use as well). These mixtures can also improve economic return through greater individual-tree growth rates and provision of multiple commercial or subsistence products. More complex plantation mixtures of 5–70 species have been used for ecological restoration of degraded lands; these large numbers of species of different successional stages are combined to reduce the need for a series of sequential plantings. Future research needs to examine many more tree species across a wider range of sites. Innovative planting designs have been developed to reduce the land area needed for mixed-species plantation experiments, by focusing on individual-tree analysis rather than plot-level analysis.

*Keywords:* Species mixture; Plantation; Silviculture; Planting design; Species trial; Forest restoration

## 1. Introduction

Forest plantations are being established at an increasing rate throughout much of the world, and now account for 5% of global forest cover (FAO, 2001). These plantations provide perhaps as much as 35% of global roundwood (FAO, 2001), so their importance for production of merchantable wood is quite clear. Their status with regard to ecological conservation has been less positive, particularly where natural forest has been cleared for plantation establishment. However, this practice is declining, because a substantial amount of abandoned agricultural land and other disturbed areas is available for planting (Evans and Turnbull, 2004). There is also growing recognition of the conservation value of plantations in reducing logging pressure on natural forests, sequestering carbon, and restoring degraded lands. For these reasons, plantations are now commonly considered one part of the management ‘‘triad’’ consisting of ecological reserves, managed natural forests, and high-yield plantations, with the key question being how to allocate land among these three types on a landscape (Seymour and Hunter, 1999).

The papers in this special issue of *Forest Ecology and Management* focus on forest plantations of one type—those that consist of a mixture of tree species. The vast majority of the world's plantations are monocultures, with just a small number of tree genera in common use (FAO, 2001; Evans and Turnbull, 2004). *Eucalyptus*, *Pinus*, *Acacia*, and *Tectona* are the most widely planted worldwide, with *Picea*, *Pseudotsuga*, *Swietenia*, *Gmelina* and others being quite important in some regions. Thus, the papers in this issue deal with a very small segment of the world's plantations, so it is reasonable for proponents of mixed-species plantations to be asked, ‘‘Why mixtures?’’ As a prelude to presenting an answer, it is logical to first review the reasons for the dominant practice, and ask, ‘‘Why monocultures?’’

A principal advantage of monocultures over mixed-species forests is the ability to concentrate all site resources on the growth of a species with the most desirable characteristics, generally relating to growth rate and wood quality. In addition, the simplicity of stand management is of great importance. There are substantial economic benefits to be gained from using simple, standardized silviculture and harvest operations that produce uniform products (Evans and Turnbull, 2004). The same is true of the simplicity of nursery practice when working with one or a very few species. If genetic improvement programs are undertaken, the large investments of time and

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money cause an even greater reliance on the few species included in these programs.

Returning to the initial question regarding the reasons for studying mixed-species plantations, the objective of much of the research is to examine whether mixtures can provide greater yields or other benefits than monocultures at a level that may outweigh the advantages of management simplicity. Much of the interest among researchers is in mixtures of 2, 3, or 4 tree species. These are the types most likely to substitute for monocultures where wood production is the main objective, whether the forest land is in industrial or family/community ownership. The goal is to combine particular species to produce specific interactions that will increase stand-level productivity or individual-tree growth rates relative to monocultures, allow harvest products from different species on different rotations, reduce risk of market shifts or insect or disease impacts, or achieve some combination of these. There is also interest in using mixed-species plantations in ecological restoration of degraded land; these are composed of a moderate to very large number of planted species in order to directly reestablish part of the native diversity of tree vegetation, and to foster the establishment of additional native plant species in the plantation understory.

Experimental mixed-species plantations have been established by innovative forest managers for centuries; these were mostly in the form of adaptive management, generally without detailed measurements. Rigorous research began in the 1980s with the establishment of replicated plots of mixtures and monocultures on the same site, with extensive data collection. This paper briefly reviews the principal lines of research examining the various uses of mixtures, and presents some examples of these recent experiments and operational applications; the papers in this special issue then expand further on many of the topics. This paper is not intended to be a comprehensive review; specific aspects have been reviewed in greater depth elsewhere (Cannell et al., 1992; Kelty, 1992; Wormald, 1992; Rothe and Binkley, 2001; Forrester et al., 2005; Lamb et al., 2005). The paper is organized by the various objectives associated with the management of plantation mixtures, with some suggestions for future research at the conclusion.

## 2. Increasing stand-level productivity using complementary characteristics

High stand-level productivity is clearly an important characteristic for wood production, and it is also associated with carbon and other nutrient sequestration objectives. A key concept for designing highly productive mixed-species stands is the need to combine species that differ in characteristics such as shade tolerance, height growth rate, crown structure (particularly leaf area density), foliar phenology (particularly deciduous versus evergreen habit), and root depth and phenology (Kelty, 1992). If the species differ substantially in these characteristics, they may capture site resources more completely and/or use the resources more efficiently in producing biomass, resulting in greater total stand biomass production than would occur in monocultures of the component species. Such species are said to have complementary resource use (Haggar and Ewel, 1997) or good ecological combining ability (Harper, 1977). This interaction is often described in terms of competition intensity. Two species with similar growth characteristics have interspecific competition in mixture that is equal to that of intraspecific competition in monoculture. Species with complementary characteristics have interspecific competition that is much lower than intraspecific. For that reason, the phenomenon of higher production from this type of interaction is also called the competitive production principle (Vandermeer, 1989).

The relationship between juvenile height growth rate and degree of shade tolerance plays an important role in mixed plantations (Menalled et al., 1998). In general, intolerant species grow rapidly in height, allocate more growth to stem and branches, and have crowns with low leaf area density (Haggar and Ewel, 1995; Canham et al., 1994; Sheil et al., 2006). These species can form an upper canopy stratum that transmits a substantial portion of light to shade tolerant species that form a lower stratum with greater leaf area density. Canopy stratification of this kind is an important aspect of complementary resource use. Root stratification may also occur, but there is much less information about below ground processes.

In species combinations where complementarity of crown or root structure is an important interaction, a fine-grained spatial pattern (i.e., with the species intermixed on a tree-by-tree basis) is necessary to maximize interspecific interactions (Fig. 1A). A coarse-grained spatial pattern (i.e., with species segregated into blocks or multiple rows) will reduce the frequency of such interactions.

An example of mixed-species stand development can be found in a study in which *Cordia alliodora*, *Cedrela odorata*, and *Hyeronima alchorneoides* were planted in mixture on a highly productive site in Costa Rica together with two understory monocot species (Menalled et al., 1998). A stratified canopy formed within 4 years, with *C. alliodora* in an upper canopy above the more shade tolerant *H. alchorneoides*; *C. odorata* had poor survivorship in the mixture. *C. alliodora* has a more open canopy than *H. alchorneoides* (less than half the leaf area index) and is partially deciduous in the dry season, whereas, *H. alchorneoides* is evergreen. *H. alchorneoides* also has higher fine root density at greater depths than *C. alliodora* (Haggar and Ewel, 1995).

Several studies have tested the question of whether biomass productivity in mixed plantations with complementary characteristics exceeds that in monocultures of the component species. Early studies involved plantations established in the late 19th century in Germany and Switzerland (Assmann, 1970). Mixtures of *Larix decidua* with *Fagus sylvatica* and of *Picea abies* with *Abies alba* formed stratified canopies, with the mixtures producing greater stem biomass than either monoculture of the component species. Two plantation studies of *Pinus sylvestris* and *P. abies* in the Czech Republic (Poleno, 1981) and in the Perm region of Russia (Prokopev, 1976) also produced stratified stands with the mixtures having greater yields than monocultures of either species. Mixed-species

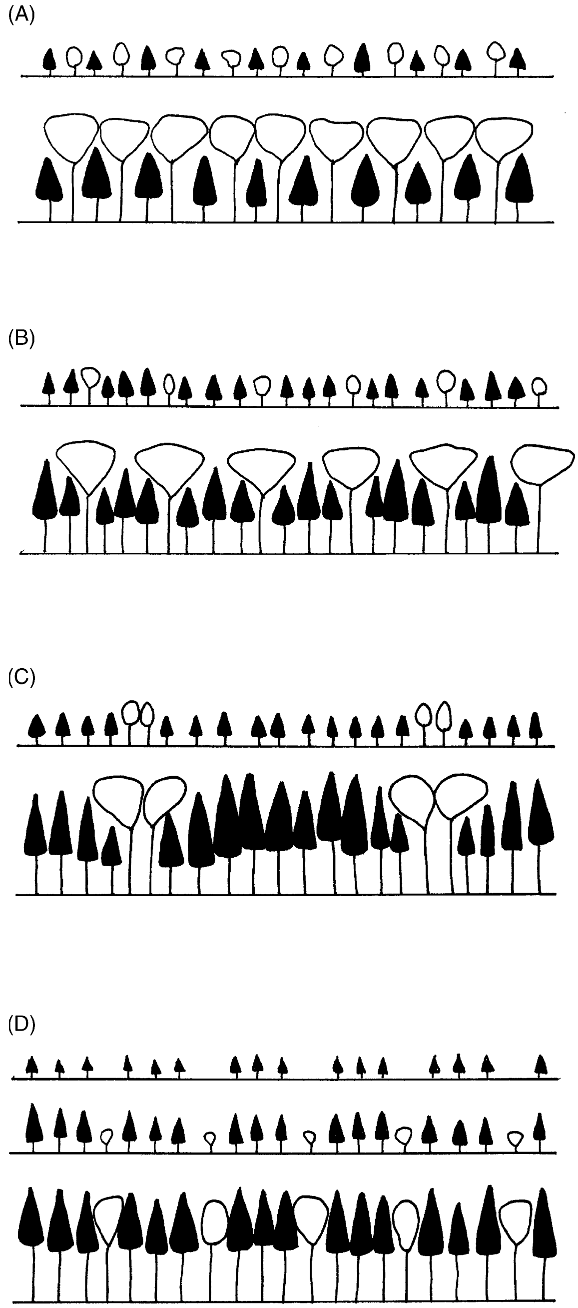

Fig. 1. Schematic diagrams of four mixed-species plantation designs, each with two species. Each diagram shows the plantation at the sapling stage and mature stage: (A) fine-grained mixture with stratified canopy with equal proportions of species, for complementary resource use (facilitative interaction may also be present); (B) fine-grained mixture similar to (A) but with unequal proportions of species, to promote individual-tree growth of upper canopy species and reduce suppression of lower canopy; (C) coarse-grained mixture for facilitative interaction, to limit the overtopping of timber species by fast-growing N-fixing species; (D) fine-grained mixture with delayed planting of fast-growing N-fixing species, for same objective as in (C). See text for specific examples of each design.

stands of *Pinus densiflora* and *Chamaecyparis obtusa* in Japan developed stratified canopies by age 30, with *P. densiflora* in the upper canopy (Kawahara and Yamamoto, 1982, 1986). Total stand volume was greater in mixed stands, with the maximum values occurring with 35% *P. densiflora* and 65% *C. obtusa.*

There has been a great deal of interest in the management of mixtures of *Betula* spp. and *P. abies* in boreal forests of Scandinavia (e.g., Bergqvist, 1999; Fahlvik et al., 2005). *P. abies* is commonly seeded or planted at 2000–3000 trees/ha after clearcut harvests, and *Betula pendula* and *Betula pubescens* regenerate naturally from seedlings or sprouts. *Betula* quickly outgrows the *P. abies* seedlings in height, and the standard practice had been to completely remove the *Betula*. In one of a number of experiments, the tall *Betula* canopy was thinned to leave 300–600 trees/ha (Bergqvist, 1999). *P. abies* growth was reduced somewhat by the upper canopy, but the *Betula* growth more than compensated for that reduction. Thinning, rather than eliminating, the *Betula* overstory is now a part of operational management. A similar situation in both stand dynamics and management considerations occurs in central British Columbia, with natural regeneration of *Betula papyrifera* growing above planted *Pseudotsuga menziesii* or other conifer species (Simard and Hannam, 2000).

The proportions of the species in mixtures can have important effects on stand development. When two species are combined in a fine-grained mixture in a 1:1 proportion, the upper canopy species may suppress the lower canopy species to the extent that the stand will shift toward the production levels of a monoculture of the upper canopy. It may be necessary with many species combinations to reduce the proportion of the taller species to achieve highest production, as shown in the examples from Japan and Scandinavia above (Fig. 1B).

## 3. Increasing stand-level productivity using facilitation

Much more research has been focused on mixed-species plantations designed to produce facilitative interactions than those designed solely for complementarity of resource use (e.g., Forrester et al., 2006a). The facilitative production principle (Vandermeer, 1989) involves one species directly benefiting the growth of another. The greatest use of facilitation in forest plantations has been through the combination of an N-fixing tree species (those with root symbionts that fix atmospheric $N_2$) and a non-N-fixing, valuable timber tree species that shows substantial growth responses to increased N availability. The species are grown in mixture to allow N to be transferred from the N-fixing species to the companion species. The transfer mechanism is: the N-fixing species produces leaf and root tissues with high N content; decomposition of dead leaves and roots increases the N soil pool (compared to that in a stand without the N-fixing species); the N in soils is then available to both species for root uptake. The more rapid nutrient cycling of the N-rich litter may increase available pools of other nutrients as well, but in some cases available P has been found to decrease, due apparently to the high demand for P by some N-fixing species (Rothe and Binkley, 2001). With some species combinations, there may also be a more direct transfer of N and other nutrients between trees species through an ectomycorrhizal connection if the tree species share the same ectomycorrhizal species (Simard et al., 1997).

Generally the principal goal is to improve the nutrition and thereby increase the growth of the non-N-fixing species, but the production of the N-fixing species is important as well, as a key part of achieving greater stand-level productivity than monocultures of either component species. Studies indicate that the species in these plantations must have complementary characteristics in addition to the facilitative nutritional interaction, in order to achieve this higher production level. One example of that situation is the 20-year study on the island of Hawaii of *Eucalyptus saligna* and the N-fixing *Falcataria moluccana* grown in monocultures and varying proportions of the two species in mixture, with density held constant for all stands (DeBell et al., 1997; Binkley et al., 2003). *E. saligna* grew taller than *F. moluccana* in mixed stands, forming a stratified canopy. Soil N pools were greater with higher *F. moluccana* proportion in mixed stands, and the N concentration in *E. saligna* foliage was higher in mixed stands than in monoculture. *E. saligna* total biomass was similar in all stands (i.e., was not related to the proportion of *E. saligna*), but *F. moluccana* biomass increased with greater initial proportion of *F. moluccana*, resulting in the highest stand biomass occurring with the proportion of 1:3 of *E. saligna* and *F. moluccana*. Measurements indicated that this mixture had greater total canopy light interception than the *E. saligna* monoculture and had greater light use efficiency than the *F. moluccana* monoculture (Binkley et al., 1992).

Similarly, *Eucalyptus globulus* and *Acacia mearnsii* were studied in mixtures and monocultures in Victoria, Australia (Forrester et al., 2004). *A. mearnsii* had greater height growth in the first 5 years, but then fell behind; a stratified canopy developed with *E. globulus* overtopping *A. mearnsii* by age 9 years. N concentrations of foliage and fine roots of *E. globulus* were higher in mixtures than in the *E. globulus* monoculture, and total stand biomass was greater in the mixed stands than in either monoculture. This study was the most complete of any in analyzing the mechanisms of facilitative and complementary interactions, yet it was still not clear how the increased N concentration in *E. globulus* foliage resulted in increased productivity; it did not appear to increase total canopy density, thereby increasing total light capture in the mixture (the *A. mearnsii* monoculture had the highest light capture), nor to increase the crown efficiency of *E. globulus* in mixture compared to monoculture (Forrester et al., 2005).

Contrasting results were found in a study in Puerto Rico, in which *Eucalyptus robusta* was grown in mixed plantations at 1:1 proportions with either of the N-fixing species *Casuarina equisetifolia* or *Leucaena leucocephala* (Parrotta, 1999). In this case, neither mixture formed a stratified canopy—the mean heights of species did not differ greatly from one another. The N-fixing species were both strong competitors of *E. robusta* which had only 15% and 35% of total stand basal area in the mixtures with *C. equisetifolia* and *L. leucocephala*, respectively, at age 8 years. The biomass production rates with stand types were highly variable, and there were no significant differences in total biomass production between mixtures and monocultures (Parrotta, 1999). When species combinations are found to show these development patterns and relative production levels, it may be possible to plant them in a coarse-grained mixture that allows facilitation to occur through wind dispersal of leaf litter but reduces the competitive effects of the N-fixing species on the companion species. Studies of the distance that leaf litter of various species is dispersed into adjacent blocks of a different tree species (reviewed in Rothe and Binkley, 2001) can be used to design the spacing of rows or blocks of N-fixing species within the matrix of the valuable timber species.

The problem of highly competitive N-fixing species has also occurred in studies of the valuable conifer timber species *P. menziesii* with the N-fixing species *Alnus rubra* in the northwestern United States. An early study of this mixture was established in 1929 on an N-deficient site in the state of Washington, comparing a mixed stand with a pure *P. menziesii* stand (Binkley, 2003). The rapid growth of *A. rubra* had already been recognized at that time, so *A. rubra* seedlings were planted 4 years after *P. menziesii* had been planted. Total stem biomass growth of the mixed stand was consistently higher than that of the pure *P. menziesii* stand over 73 years. *A. rubra* increased N content of the combined soil and vegetation to more than double that of the *P. menziesii* stand. *P. menziesii* increasingly dominated most *A. rubra* in height, and nearly all *A. rubra* died between ages 55 and 73 years (Binkley, 2003).

Thus, three designs have been used to incorporate N-fixing species successfully into mixtures: a fine-grained mixture with a stratified canopy in which the lower canopy species is the N-fixer, and the overstory is at equal or reduced proportions relative to the N-fixer (Fig. 1A and B); a coarse-grained mixture with a highly competitive N-fixing species grown in blocks or multiple rows (Fig. 1C); a fine-grained mixture in which the planting of a highly competitive N-fixing species is delayed until several years after the other species has been planted (Fig. 1D).

Although most experimental plantings have been conducted on just a single site, there is evidence from some studies that facilitative interactions do not produce greater biomass in mixtures on sites with high N availability. These studies included manipulations of nutrient levels for small groups of trees growing in pots (Forrester et al., 2006b) and field studies on multiple sites (Binkley, 2003; Boyden et al., 2005).

There is also considerable interest in using facilitative interactions to improve tree nutrition with combinations of species that do not include an N-fixing species. A common practice in European forestry is to mix a broadleaf tree species with a valuable conifer species with one objective being to increase the rate of nutrient cycling (Matthews, 1989). Some conifers, particularly *Picea* spp. produce litter with high lignin/N ratios that make them resistant to rapid decomposition. The addition of the more readily decomposable broadleaf litter is expected to increase the microbial activity on that material, and the desired effect is for these higher decomposition rates to occur with the conifer litter as well, thus creating a synergistic effect.

Despite the application of this idea to silvicultural practice with *P. abies*-*Betula* spp. and *P. abies*-*F. sylvatica* mixtures in some regions, Rothe and Binkley (2001) noted that there are few studies that directly track the effect of such mixtures through the process of litterfall, decomposition, root uptake, and change in foliar nutrient concentrations of the conifer species. Their review found that soil nitrogen pools were increased relative to monocultures when the mixtures included an N-fixing species, but generally were not with non-N-fixing species, including *F. sylvatica* and *Betula* spp. In most studies, foliar nutrient levels were not affected by mixtures, although P and K (but not N or other nutrients) were higher in *P. abies* in mixture with *Betula* spp. Thus, the use of non-N-fixing species in mixtures for increasing rates of nutrient cycling does not have consistent support from empirical studies. There is some evidence for accelerated rates of nutrient cycling, but there are also cases where rates have not changed or even declined, and the processes leading to these opposing effects are unclear (Binkley et al., 1992; Rothe and Binkley, 2001; Gartner and Cardon, 2004).

## 4. Improving individual-tree growth rate and stem quality

The size and allometry of trees in monoculture stands are strongly affected by stand density, through its influence on the intensity of intraspecific competition. Plantations are generally established at densities that are high enough to cause shading of lower branches and thus improve stem quality in the early stage of stand development. Silviculturists then have the option of maintaining high density for maximum stand-level production or reducing density substantially to promote individual tree growth. In many situations, individual tree size is of primary importance for producing merchantable timber, to the extent that investments are made in pre-commercial thinning.

Mixed-species plantations with stratified canopies can provide an advantage in this regard. Initial planting densities can be as high as in monocultures, but then the effective density (in terms of crown competition) will begin to decline as canopy stratification develops. Crown and stem size may increase relative to trees in monoculture of the same initial density. The species of the upper canopy would be more likely to develop larger stems; the crowns of lower canopy species may expand laterally, but their overall growth rate would be affected by their shade tolerance as well as the density of upper canopy. The effect on growth increases of upper canopy species would be exaggerated by reducing the initial planting density of that species.

Larger individual tree sizes of one or both species in mixed stands compared to monocultures were found in several experimental stands described previously, including both *E. saligna* and *F. moluccana* (DeBell et al., 1997), both *E. globulus* and *A. mearnsii* (Forrester et al., 2004), and *P. menziesii* (Binkley, 2003). A study that included measures of crowns sizes found that both upper canopy *C. alliodora* and lower canopy *H. alchorneoides* had larger crowns and stem diameters in mixture than in monoculture (Menalled et al., 1998).

Stratified mixtures can also promote stem quality of the upper canopy species. For example, the valuable timber species *Quercus petraea* is commonly grown in mixture with *F. sylvatica* in France and Germany (Matthews, 1989) so that the crowns of the lower canopy *F. sylvatica* will shade any epicormic branches that develop on the *Q. petraea* stems. A more demanding management problem of this type concerns *Acacia melanoxylon*, an important timber species in eastern Australia; this species has poor apical control, so it often develops branchy, low quality stems when grown in plantations. In natural mixed-species regrowth in the region, the dense shade of the native tree species *Pomaderris apetala* has been found to produce sufficient shade such that the *A. melanoxylon* in these stands develop with single straight stems and few branches (Unwin et al., 2006). This finding can be applied to plantation design by incorporating *P. apetala* or another lower canopy species at high density, which would transmit no more than 15% of solar radiation to the boles of the upper canopy *A. melanoxylon* crop trees.

However, mixtures can create stem quality problems if the difference in juvenile height growth rate between the species is too great. When *P. menziesii* and *A. rubra* were planted at the same time to create mixed plantations, *A. rubra* grew into an upper canopy very rapidly; they developed long, wide crowns at the sapling stage, producing branchy lower stems (Grotta et al., 2004). With a 5-year delay in the planting of *A. rubra*, heights of the two species were more similar and there was better natural pruning of *A. rubra*, but higher light levels reached the *P. menziesii* lower stems through the more open crowns of *A. rubra*, possibly reducing long-term *P. menziesii* stem quality.

## 5. Growing multiple products on varying rotations

One advantage of mixed-species plantations is that market risk may be reduced by growing a variety of products. This involves the usual tradeoffs inherent in predicting markets—with the option of putting all resources into the single product that has highest value at present, or diversifying production; of course, the diversification option will not always give the highest return. There may also be a more predictable advantage for mixtures in the timing of production of commercial or subsistence products. Generally, the largest financial problem that forest landowners face when establishing plantations is the length of time from the large initial investment of site preparation, planting, and control of competing vegetation to the economic return in forest products at the end of the rotation. The management of many monocultures includes early thinnings undertaken as soon as a usable product can be harvested, but some species that are valuable as solid wood products at large diameters have little or no value when small. Growing multiple species in a plantation can give more options for providing periodic income throughout the rotation.

Perhaps the best example of this involves mixtures of *P. abies* (or other conifers) and *Betula* spp. in Scandinavian countries. As was described previously, *P. abies* is generally planted at 2000–3000 trees/ha, and then *Betula* regenerates naturally. The density of *Betula* is reduced to 300–1200 trees/ha at the sapling stage, and a stratified canopy quickly develops with the *Betula* growing much taller than the conifers. The *Betula* upper canopy can then be harvested at age 20–30 years (all in one cut or in two or more partial cuts), and *P. abies* is grown to a rotation age of 80 years or more (Tham, 1994; Bergqvist, 1999).

In most plantations, size differences among species are not as extreme, but the same principle can hold, whether under in industrial or family/community ownership. In the case of legume tree species growing in a lower canopy beneath *Eucalyptus*, the legumes can be removed for timber or pulp products (having already increased ecosystem N content), leaving the higher value *Eucalyptus* to grow to large diameters. An example of management appropriate to small land holdings involves a mixture of the timber species *Terminalia amazonia* and the N-fixing species *Inga edulis* established on abandoned pasture land in Costa Rica (Nichols et al., 2001). *I. edulis* increased *T. amazonia* height growth rates, leading to rapid canopy closure and reducing the need for weeding. By the third year, *I. edulis* produced usable biomass for fuelwood, and began producing edible fruit pods. However, a net benefit cannot simply be assumed with these kinds of plantations. In this example, the planting of the *I. edulis* trees for earlier canopy closure and some low-value products could not be justified economically.

## 6. Reducing risk of pest damage

One desired benefit of using species mixtures is a reduction of insect or disease damage. This is the most difficult aspect of mixtures to study, because damage generally occurs episodically and is affected by vegetation composition and structure at the landscape level. For the most part, studies that are designed to address questions of competition, nutrition, and productivity on small plots cannot provide information on insect and disease damage. Much of the research that does focus on pest effects compares monocultures to complex natural forests (e.g., Jactel et al., 2002). Many potential managers of mixed-species plantations would be interested in whether only 2, 3, or 4 species in mixture reduce risk compared to monocultures, and there is very little information about these low-diversity mixtures.

The potential risk of monocultures is that the invasion of a pest would affect all or most of the trees because of the uniform genetic composition. Recent reviews on the vulnerability of plantations (Powers, 1999; Gadgil and Bain, 1999) noted that most plantations (which are nearly all monocultures) have low incidences of insect and disease problems, but stressed the importance of two factors: (1) monocultures must be managed well, especially in terms of control of stand density; periodic thinning must keep individual tree vigor high to reduce the impacts of most pest species; (2) many monocultures are not native to the region where they have been planted, and their natural pest species have not been introduced with the trees. In spite of these factors, considerable risk is still involved, because many plantations experience periods of poor management, and pest species (along with most other types of organisms) are increasingly being moved around the globe. Two mechanisms by which mixtures may reduce risk of pest damage are: (1) mixtures may dilute the host concentration for a pest organism and thereby impair the ability of the pest to find the host; (2) mixtures may provide more diverse habitats that tend to support higher populations of natural enemies of the pest species (Watt, 1992).

In spite of the limitations of productivity studies for providing information on pest risks, there are some lessons that can be learned from them. In a Costa Rica study described above (Menalled et al., 1998), *C. odorata* was repeatedly attacked by the native shoot borer *Hypsipyla grandella* in monoculture and in mixture with *C. alliodora* and *H. alchorneoides*. Stems of *C. odorata* in monoculture died back repeatedly from the damage, but gradually recovered as the stems grew above the maximum height that *Hypsipyla* will fly; however, most *C. odorata* in mixture could not recover because they were suppressed by the adjacent unaffected tree species. Thus, the impact of a species-specific pest may be greater in a mixture because of interspecific competition.

In another study in Costa Rica (Stanley and Montagnini, 1999; Montagnini, 2000), three sets of experimental plantations were established, with each set consisting of one N-fixing species and three non-N-fixing species in mixture and monocultures. In two of these sets, nearly all of the trees of the N-fixing species were killed or damaged by pests (a root herbivore in one case, and a fungal disease in the other), reducing or eliminating the sought-after nutrient facilitation effect (Montagnini et al., 1995). The third set of plantations was not seriously affected by pests. This experience suggests the importance of having at least two tree species for each functional role in a mixed plantation, especially when shifting to operational management.

## 7. Restoring degraded lands

Mixed-species plantations potentially have a very different role to play compared to objectives described above—as a part of the restoration of degraded lands. Tree planting has long been used as part of the reclamation of mining spoils; for example, a legal requirement that *Alnus* spp. be planted on abandoned coal mines was established in Germany in 1766 (Lögters and Dworschak, 2004). Early research focused on the selection of species for their ability to withstand difficult site conditions (e.g., low pH and organic matter, and high levels of certain elements). Species trials were often planted as mixtures, and this kind of planting became operational in many cases. Much of the goal was simply to vegetate the site in order to reduce erosion.

A good deal of recent research on the restoration of abandoned agricultural lands has been devoted to evaluations of commercial timber plantations (generally monocultures of non-native species) as initiators of forest succession (Parrotta et al., 1997). These plantations act as nurse trees to shade out grasses and other post-agricultural vegetation, and provide a forest habitat structure that attracts animal dispersers of many native plant species. Thus, they represent a low-cost method of restoring (at least partially) the native forest vegetation using the successional model of relay floristics, with a sequential establishment of species. It has been proposed that the restoration of highly structured and diverse forest plant communities *must* involve sequential introductions of species of different characteristics or stages of succession, as opposed to simultaneous introductions in a mixed planting (Dobson et al., 1997). This section describes some examples of experiments and operational programs that test this proposal by using mixed plantations of up to 70 tree species for restoration. The goal is generally to plant many of the native overstory species and to create conditions conducive to the natural regeneration of understory species.

The first example deals with a bauxite-mined site in the state of Pará in Brazil (Parrotta and Knowles, 1999), where a number of reforestation planting treatments were tested after the topsoil had been replaced on areas that had previously been disturbed by mining. A mixed commercial timber plantation (consisting of five *Eucalyptus* spp., *Acacia mangium*, and the native *Sclerolobium paniculatum*) had greatest canopy height and stand basal area of all treatments, but grass invasion beneath the sparse canopy reduced the establishment of native species in the understory. A native-species plantation (with more than 70 woody species from the region) had lower grass cover, and greater abundance, mean height, and species richness of woody plant regeneration in the understory. The natural regeneration treatment (no planting) had higher basal area and canopy cover than the native-species plantation, but it was composed of many short-lived pioneer tree species, so there was concern that much of the overstory would senesce before woody plants could dominate the understory, potentially leading to the expansion of grass cover. The native-species plantation was selected as the operational treatment at this mine (Parrotta and Knowles, 1999). However, it was recognized that several families of woody plant species were missing from the understories—mainly those that had poor survival when planted in the open or had few animal dispersers because of their large seeds. These species would likely have to be planted in the understory after the canopy was well established.

The second example is from the Rhineland region of Germany where brown coal (lignite) opencast mines are currently in operation, as they have been for 150 years throughout Germany, leaving extensive disturbed areas. In the brown coal mines west of Cologne, an operational forest restoration program began in the early 20th century, functioning concurrently with active mining. Since then, the concept of ecological restoration has undergone changes based on scientific, social, and legal developments, and the specific practices have been modified through continual research and adaptive management. In current practice (Dworschak, 2003; Lögters and Dworschak, 2004), after the coal layer has been removed from a section of the mine, the area is capped with native loess soils (mixed with sand and gravel), which had been removed from above the coal layer in another section of the mine. On this new soil, mixed plantations are established using *F. sylvatica*, *Acer* spp., and *Fraxinus* spp. on the moister sites, and *Quercus robur*, *Carpinus betulus*, and *Tilia* spp. on the drier sites. *Populus* spp. are planted at wide spacing as nurse trees on both kinds of sites to rise above the other species and provide partial shade (Ulf-Rainer Dworschak, personal communication). In addition, a ground cover of *Lupinus* spp. is established to increase soil nitrogen levels, and patches of topsoil and litter from intact stands are distributed on the forest floor of the new stand to reestablish soil fauna populations (Dworschak, 1997). These stands are being established primarily for ecological restoration objectives, but they will be managed for timber production as well. For example, the *Populus* nurse trees are cut at age 15–20 years to release the other species, and are sold for pulp when markets are available; the other species have not yet attained merchantable size.

Ashton et al. (2001) described a similar procedure for restoring abandoned agricultural land in Sri Lanka. Widely spaced, short-lived pioneer nurse trees and a leguminous ground cover were planted first, to provide shade, retain soil moisture, and increase soil nitrogen. Just 1 year later, a mixture of longer-lived pioneer tree species and more shade tolerant tree species were planted. Subcanopy species (those that never attain canopy height) were not included at this stage, but will be planted after the more shade tolerant species from the initial planting reach the height of the pioneer canopy.

These examples add insight to the generalization that forest restoration must follow a sequential establishment (relay floristics) model of succession. It appears that many species, from pioneer to climax in their characteristics, can be planted at one time, with their development following the initial floristics successional pattern. Differences in height growth rate and shade tolerance among the species lead to a stratified canopy that provides pioneer nurse trees to shelter the more shade tolerant mesic species, even though they are all the same age. However, there are likely to be subcanopy species that do not survive well as seedlings in the open, and require the high shade conditions that exist beneath a tall canopy; these would need to be planted later. Thus, it may be that only two sequential planting stages are necessary, even for highly diverse forest types.

## 8. Expanding the information base for designing mixtures

The results of recent studies (those reviewed here, and others) have substantially increased our knowledge base on the development and production of mixed-species plantations. However, there still has been little work on a number of aspects of the topic: the prevalence and mechanisms of beneficial below ground interactions; the effects of site factors and spacing on species interactions; and the prevalence of beneficial interactions across a broad range of tree species. Experiments on the mechanisms of interactions among species are so expensive that most are carried out on very small plots, nearly all are on one site type and at one spacing level, and only a small number of tree species have been included. Most studies have used replacement series designs, which focus on variations of species proportions at a constant overall spacing (Table 1) (Sackville Hamilton, 1994; Kelty and Cameron, 1995). Some also include additive series to incorporate variation in spacing, and some include both synchronous and delayed planting, where one species has a very rapid juvenile growth rate. However, it is unlikely that funding will be available to expand

Table 1
Examples of mixed-species plantation experiments

| Species | Location | Experimental design | Reference |
|---|---|---|---|
| *Betula papyrifera–Taxus brevifolia*,<br>*Betula papyrifera–Pseudotsuga menziesii* | Canada (British Columbia) | Two 2-species mixtures (replacement and additive series) | Simard (1996) |
| *Cedrela odorata–Cordia alliodora–Hyeronima alchorneoides* | Costa Rica | One 3-species mixture (replacement series) | Menalled et al. (1998) |
| *Genipa americana–Vochysia ferruginea–Pithecellobium elegans–Hieronyma alchorneoides*[a] | Costa Rica | Three 4-species mixtures (replacement series) | Stanley and Montagnini (1999),<br>Montagnini (2000) |
| *Eucalyptus saligna–Falcataria moluccana* | United States (Hawaii) | One 2-species mixture (replacement series) | DeBell et al. (1997),<br>Binkley et al. (2003) |
| *Eucalyptus globulus–Acacia mearnsii* | Australia (Victoria) | One 2-species mixture (replacement series at two spacings) | Forrester et al. (2005) |
| *Eucalyptus robusta–Casuarina equisetifolia*,<br>*Eucalyptus robusta–Leucaena leucocephala*,<br>*Casuarina equisetifolia–Leucaena leucocephala* | Puerto Rico | Three 2-species mixtures (replacement series) | Parrotta (1999) |
| *Pseudotsuga menziesii–Alnus rubra* | United States (Oregon) | One 2-species mixture (replacement and additive series; delayed and synchronous planting; early removal of one species) | Grotta et al. (2004) |

[a] Species for only one of three plantations given; see references for others.

many replicated replacement/additive experiments to include all these important factors. A variety of research approaches is needed, including species trials, continued studies of interaction mechanisms, and operational trials.

### 8.1. Species trials

The most direct way to include more species is to expand upon the standard species trial, in which small monoculture blocks of trees are planted. This can be supplemented with a spatially randomized mixture of all the species in the monoculture blocks (e.g., Piotto et al., 2004; Erskine et al., 2005). These provide initial information on competitive interactions among species. It may be more informative to establish blocks of all possible two-species mixtures, but that would increase the land area and number of trees substantially (but see innovative designs below for alternatives). Trees located on edges of adjacent monoculture blocks can be useful in examining interactions (Rothe and Binkley, 2001), so small monoculture blocks in species trials could be arranged to create edges among all species involved in the trial.

### 8.2. Studies of species interactions

A combination of replacement and additive series plots is an important method to analyze interaction effects on stand development and productivity, but sufficient replication at the plot level quickly adds up to large land areas and high costs. A more efficient method is individual-tree analysis, which focuses on the effect of neighborhood tree variables (species, size, distance) on the growth of a subject tree. This kind of analysis can be done with any replacement or additive series experiment (e.g., D'Amato and Puettmann, 2004; Boyden et al., 2005; Vanclay, 2006a), but plots can be designed to take advantage of particular neighborhood structures (Kelty and Cameron, 1995). There are also innovative plot designs that are designed to be so efficient in land area that they can be used as species trials, and yet still allow quantitative analysis of species interactions at the individual tree-level. These have been described for two species (Nester, 1994, described in Kelty and Cameron, 1995), three species (Goelz, 2001) and four species (Vanclay, 2006b).

### 8.3. Operational trials

If the ideas developed in research are to be put into practice, it is necessary to have a better connection of using research results to design operational scale trials with industry and with family/community owners of small forest tracts. This holds the greatest likelihood of testing more species combinations across a greater variety of sites—the statistical approach described by Rothe and Binkley (2001) to increase the sample size for analysis of mixture results. Much research on monoculture plantations is conducted in operational plantings, which gives a great advantage in providing low cost replicates of research treatments. In addition, the adoption of mixed-species plantation silviculture will require forest managers to solve operation problems that are not encountered when planting small experimental plots, and any progress in this area will represent a major step in moving mixed-species plantations toward standard use in forest management.

## References

Ashton, M.S., Gunatilleke, C.V.S., Singhakumara, B.M.P., Gunatilleke, I.A.U.N., 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. For. Ecol. Manage. 154, 409–430.

Assmann, E., 1970. The Principles of Forest Yield Study. Pergamon Press, Oxford, 506 pp.

Bergqvist, G., 1999. Wood volume yield and stand structure in Norway spruce understorey depending on birch shelterwood density. For. Ecol. Manage. 122, 221–229.

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., Dunkin, K.A., DeBell, D., Ryan, M.G., 1992. Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. For. Sci. 38, 393–408.

Binkley, D., Senock, R., Bird, S., Cole, T.G., 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and N-fixing *Falcataria moluccana*. For. Ecol. Manage. 182, 93–102.

Boyden, S., Binkley, D., Senock, R., 2005. Competition and facilitation between *Eucalyptus* and nitrogen-fixing *Falcataria* in relation to soil fertility. Ecology 86, 992–1001.

Cannell, M.G.R., Malcolm, D.C., Robertson, P.A., 1992. The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific, Oxford, 312 pp.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. 24, 337–349.

D'Amato, A.W., Puettmann, K.J., 2004. The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/*Pseudotsuga menziesii* stands. J. Ecol. 92, 450–463.

DeBell, D.S., Cole, T.G., Whitesell, C.D., 1997. Growth, development, and yield in pure and mixed stands of *Eucalyptus* and *Albizia*. For. Sci. 43, 286–298.

Dobson, A.P., Bradshaw, A.D., Baker, A.J.M., 1997. Hopes for the future: restoration ecology and conservation biology. Science 277, 515–522.

Dworschak, U., 1997. Earthworm populations in a reclaimed lignite open-case mine of the Rhineland. Euro. J. Soil Biol. 33, 75–81.

Dworschak, U., 2003. The role of succession in reclamation—opportunities and constraints: experience gained in the Rhenish lignite mining area. Surf. Min. Braunkohle Other Miner. 55 (1), 51–60.

Erskine, P.D., Lamb, D., Borschmann, G., 2005. Growth performance and management of a mixed rainforest tree plantation. New For. 29, 117–134.

Evans, J., Turnbull, J.W., 2004. Plantation Forestry in the Tropics, 3rd ed. Oxford University Press, Oxford, 467 pp.

Fahlvik, N., Agestam, E., Nilsson, U., Nyström, K., 2005. Simulating the influence of initial stand structure on the development of young mixtures of Norway spruce and birch. For. Ecol. Manage. 213, 297–311.

FAO, 2001. Global Forest Resources Assessment 2000. Main Report. FAO Forestry Paper 140, Food and Agriculture Organization of the United Nations, Rome, 479 pp.

Forrester, D.I., Bauhus, J., Khanna, P.K., 2004. Growth dynamics in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. For. Ecol. Manage. 193, 81–95.

Forrester, D.I., Bauhus, J., Cowie, A.L., 2005. On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. For. Ecol. Manage. 209, 147–155.

Forrester, D.I., Bauhus, J., Cowie, A.L., Vanclay, J.K., 2006a. Mixed-species plantations of eucalyptus with nitrogen fixing trees: a review. For. Ecol. Manage. 233, 211–230.

Forrester, D.I., Cowie, A.L., Bauhus, J., Wood, J., Forrester, R.I., 2006b. Effects of changing the supply of nitrogen and phosphorus on growth and interactions between *Eucalyptus globulus* and *Acacia mearnsii* in a pot trial. Plant Soil 280, 267–277.

Gadgil, P.D., Bain, J., 1999. Vulnerability of planted forests to biotic and abiotic disturbances. New For. 17, 227–238.

Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.

Goelz, J.C.G., 2001. Systematic experimental designs for mixed-species plantings. Native Plants J. 2, 90–96.

Grotta, A.T., Gartner, B.L., Radosevich, S.R., 2004. Influence of species proportion and timing of establishment on stem quality in mixed red Alder-Douglas-fir plantations. Can. J. For. Res. 34, 863–873.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, New York, 892 pp.

Haggar, J.P., Ewel, J.J., 1995. Establishment, resource acquisition, and early productivity as determined by biomass allocation patterns of three tropical tree species. For. Sci. 41, 689–708.

Haggar, J.P., Ewel, J.J., 1997. Primary productivity and resource partitioning in model tropical ecosystems. Ecology 78, 1211–1221.

Jactel, H., Goulard, M., Menassieu, P., Goujon, G., 2002. Habitat diversity in forest plantations reduces infestations of the pine stem borer *Dioryctria sylvestrella*. J. Appl. Ecol. 39, 618–628.

Kawahara, T., Yamamoto, K., 1982. Studies on mixed stands of akamatsu (*Pinus densiflora*) and hinoki (*Chamaecyparis obtusa*). I. Productivity and decomposition rate of organic matter. J. Jap. For. Soc. 64, 331–339 (in Japanese with English summary).

Kawahara, T., Yamamoto, K., 1986. Studies on mixed stands of akamatsu (*Pinus densiflora*) and hinoki (*Chamaecyparis obtusa*). III. Stem volume of mixed stands. J. Jap. For. Soc. 68, 327–3332 (in Japanese with English summary).

Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), The Ecology and Silviculture of Mixed-Species Forests. Kluwer Academic Publishers, Dordrecht, Boston, pp. 125–141.

Kelty, M.J., Cameron, I.R., 1995. Plot designs for the analysis of species interactions in mixed stands. Common. For. Rev. 74, 322–332.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632.

Lögters, C., Dworschak, U., 2004. Recultivation of opencast mines—Perspectives for the people living in the Rhineland. World Min. Surf. Underground 56 (2), 126–135.

Matthews, J.D., 1989. Silvicultural Systems. Clarendon Press, Oxford, 284 pp.

Menalled, F.D., Kelty, M.J., Ewel, J.J., 1998. Canopy development in tropical tree plantations: a comparison of species mixtures and monocultures. For. Ecol. Manage. 104, 249–263.

Montagnini, F., 2000. Accumulation in above ground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland. For. Ecol. Manage. 134, 257–270.

Montagnini, F., Gonzalez, E., Rheingans, R., Porras, C., 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. Common. For. Rev. 74, 306–314.

Nester, M.R., 1994. A Compendium of Designs and Plant Arrangements for the Study and Control of Plant Interactions. Unpublished Report, Queensland Forest Research Institute, Gympie, Australia, 51 pp.

Nichols, J.D., Rosemeyer, M.E., Carpenter, F.L., Kettler, J., 2001. Intercropping legume trees with native timber trees rapidly restores cover to eroded tropical pasture without fertilization. For. Ecol. Manage. 152, 195–209.

Parrotta, J.A., 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. For. Ecol. Manage. 124, 45–77.

Parrotta, J.A., Knowles, O.H., 1999. Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restor. Ecol. 7, 103–116.

Parrotta, J.A., Turnbull, J.W., Jones, N., 1997. Catalyzing native forest regeneration on degraded tropical lands. For. Ecol. Manage. 99, 1–7.

Piotto, D., Viquez, E., Montagnini, F., Kanninen, M., 2004. Pure and mixed forest plantations with native species of the dry tropics of Costa Rica: a comparison of growth and productivity. For. Ecol. Manage. 190, 359–372.

Poleno, Z., 1981. Development of mixed forest stands. Prace VULHM 59, 179–202 (in Czech with English summary).

Powers, R.F., 1999. On the sustainable production of planted forests. New For. 17, 263–306.

Prokop'ev, M.N., 1976. Mixed plantings of pine and spruce. Lesnoe Khozyaistvo 5, 37–41 (in Russian with English summary).

Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. Can. J. For. Res. 31, 1855–1870.

Sackville Hamilton, N.R., 1994. Replacement and additive designs for plant competition studies. J. Appl. Ecol. 31, 599–603.

Seymour, R.S., Hunter, M.L., 1999. Principles of ecological forestry. In: Hunter, M.L. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, pp. 22–61.

Sheil, D., Salim, A., Chave, J., Vanclay, J., Hawthorne, W.D., 2006. Illumination-size relationships of 109 coexisting tropical forest tree species. J. Ecol. 94, 494–507.

Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., Molina, R., 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388, 579–582.

Simard, S.W., Hannam, K.D., 2000. Effects of thinning overstory paper birch on survival and growth of interior spruce in British Columbia: implications for reforestation policy and biodiversity. For. Ecol. Manage. 129, 237–251.

Simard, S.W., 1996. In: Comeau, P.G., Thomas, K.D. (Eds.), Proceedings of the Workshop on Design of a Birch/Conifer Mixture Study in the Southern Interior of British Columbia. Designing Mixedwood Experiments. British Columbia Working Paper 20, 8-11. BC Ministry of Forests, Victoria, BC.

Stanley, W.G., Montagnini, F., 1999. Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica. For. Ecol. Manage. 113, 91–103.

Tham, A., 1994. Crop Plans and Yield Predictions for Norway Spruce (*Picea abies* (L.) Karst) and Birch (*Betula pendula Roth* and *Betula pubescens* Ehrh.) Mixtures. Studia Forestalia Suecica (195) Swedish University of Agricultural Sciences, Uppsala, 21 pp.

Unwin, G.L., Jennings, S.M., Hunt, M.A., 2006. Light environment and tree development of young *Acacia melanoxylon* in mixed-species regrowth forest, Tasmania, Australia. For. Ecol. Manage. 233, 240–249.

Vanclay, J.K., 2006a. Spatially explicit competition indices and the analysis of mixed-species plantings with the Simile modelling environment. For. Ecol. Manage. 233, 295–302.

Vanclay, J.K., 2006b. Experiment designs to evaluate inter- and intra-specific interactions in mixed plantings of forest trees. For. Ecol. Manage. 233, 366–374.

Vandermeer, J., 1989. The Ecology of Intercropping. Cambridge University Press, Cambridge, 237 pp.

Watt, A.D., 1992. Insect pest population dynamics: effects of tree species diversity. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 267–275.

Wormald, T.J., 1992. Mixed and Pure Forest Plantations in the Tropics and Subtropics. FAO Forestry Paper 103, Food and Agriculture Organization of the United Nations, Rome, 152 pp.