

## Nutritional interactions in mixed species forests: a synthesis

Andreas Rothe and Dan Binkley

**Abstract:** For more than a century, scientists have considered whether mixtures of tree species may differ in nutrition and yield relative to monocultures. We review the empirical evidence on the nutritional interactions of tree species in mixtures, including information on foliar nutrition, soil nutrient supply, rates of nutrient input, and patterns of root distribution. Linear effects were most common, with mixtures intermediate in value between monocultures. In some cases, values for mixtures were lower than expected, indicating an antagonistic interaction. A few cases that included nitrogen-fixing species showed a synergistic interaction, with mixtures showing higher values than monocultures. Nutrient concentrations in foliage of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) were improved in mixtures with other conifers in three studies, in contrast to four studies with mixtures of various conifers and hardwoods that showed no effect of mixtures on foliage nutrient concentrations. Mixtures that combine species with and without the ability to fix atmospheric nitrogen have shown a full range of foliar responses from decreases to increases in phosphorus, to increases in nitrogen, to no effect of mixtures. Rates of litter decomposition usually showed no effect of species mixtures, but a few cases demonstrated both increases and decreases in decomposition relative to monocultures. Pools of soil nutrients generally did not differ between mixtures and monocultures. Root distributions in mixtures of Norway spruce (*Picea abies* (L.) Karst.) and beech (*Fagus sylvatica* L.) were altered in mixtures; compared with monocultures, spruce rooted more shallowly in mixtures with beech, and beech rooted more deeply in mixtures with spruce. General conclusions are limited by the small number of studies that directly addressed mixed-species effects in forests, and the wide variety of observed interactions. Further research would be particularly helpful in identifying situations where nonlinear interactions may develop, including the species and site conditions that promote nonlinear interactions. Neighborhood methods, which analyze the relationship between stand composition and nutritional properties on a small spatial scale, offer great potential for exploring nutritional effects in mixed-species stands.

**Résumé :** Depuis plus d'un siècle, les scientifiques ont cherché à déterminer si les peuplements mélangés se distinguent des peuplements purs par leur nutrition et leur rendement. Nous avons passé en revue les données empiriques sur les interactions nutritionnelles entre les espèces d'arbre en peuplements mélangés, incluant l'information sur la nutrition foliaire, la disponibilité des nutriments dans le sol, les taux d'apport de nutriments et les patrons de distribution des racines. Les effets linéaires sont les plus communs et les peuplements mélangés prennent des valeurs intermédiaires entre les peuplements purs. Dans certains cas, les valeurs qu'affichent les peuplements mélangés sont plus faibles que prévu, suggérant une interaction antagoniste. Quelques cas comportant des espèces fixatrices d'azote montrent une interaction synergique. Dans ce cas les peuplements mélangés affichent des valeurs plus élevées que les peuplements purs. La concentration de nutriments dans les feuilles de l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière.) est plus élevée en mélange avec d'autres conifères selon trois études contrairement à quatre autres portant sur des peuplements mélangés comprenant divers conifères avec des feuillus qui ne rapportent aucun effet des mélanges sur la concentration de nutriments dans les feuilles. Les peuplements mélangés qui combinent des espèces sans et avec la capacité de fixer l'azote atmosphérique montrent toute la gamme de réponses foliaires qui se traduisent par une diminution ou une augmentation du phosphore, une augmentation d'azote et aucun effet des mélanges. Le taux de décomposition de la litière n'est généralement pas affecté par un mélange d'espèces. Dans quelques cas cependant, des augmentations et des diminutions dans la décomposition de la litière ont été rapportées comparativement aux peuplements purs. Les pools de nutriments dans le sol des peuplements mélangés ne diffèrent généralement pas de ceux des monocultures. La distribution des racines dans les peuplements mélangés d'épicéa commun (*Picea abies* (L.) Karst.) et de hêtre commun (*Fagus*

Received January 24, 2001. Accepted June 24, 2001. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on October 12, 2001.

**A. Rothe.** Bayerisches Staatsministerium für Landwirtschaft und Forsten Referat Waldau und Nachhaltssicherung, Ludwigstraße 2, 80539 München, Germany.

**D. Binkley.**<sup>1</sup> Department of Forest Sciences, Graduate Degree Program in Ecology and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, U.S.A.

<sup>1</sup>Corresponding author (e-mail: [dan@cnr.colostate.edu](mailto:dan@cnr.colostate.edu)).

*sylvatica* L.) n'est pas la même dans les peuplements mélangés. Comparativement aux peuplements purs, l'épicéa a un système racinaire moins profond en mélange avec le hêtre et ce dernier s'enracine plus profondément en mélange avec l'épicéa. Il est difficile de tirer des conclusions à cause du petit nombre d'études qui examinent directement les effets dus au mélange d'espèces en forêt et de la grande variété d'interactions observées. D'autres travaux de recherche seraient particulièrement utiles pour identifier les situations où des interactions non linéaires pourraient se produire, incluant les espèces et les types de stations qui favorisent les interactions non linéaires. Les méthodes de voisinage, qui analysent les relations entre la composition du peuplement et les propriétés nutritionnelles sur une petite échelle spatiale offrent un potentiel élevé pour explorer les effets nutritionnels dans les peuplements mélangés.

[Traduit par la Rédaction]

## Introduction

Tree species differ substantially in their effects on soil development and nutrient supply (reviewed by Rhoades 1997; Binkley and Giardina 1998). The mechanisms behind these differences in the effects of species are poorly known, and the interactions among species in mixtures could be important. If two species are sufficiently distinct in resource use, they may utilize limited resources more efficiently (competitive production principle; Vandermeer 1989). Second, one species may improve the environment experienced by another species (facilitative production principle; Vandermeer 1989). The combined effects of differences in resource use and facilitation depend in large part on the intensity of competition among the species. Much work on mixed plant communities has been performed with herbaceous plants, mostly in agriculture (cf. Harper 1977; Francis 1986; Vandermeer 1989; Hobbie 1992; Horst 1995; Ong and Huxley 1996; Joliffe 1997; Hooper and Vitousek 1998). The results are complex and the production of mixtures is usually lower than or equal to the production in monocultures. The economic production may differ from ecological production in some cases, and several instances of synergistic production (mixture higher than expected from the monocultures) have been noted (particularly in cases including nitrogen-fixing species).

Intensive forest management typically focuses on the use of monoculture stands, even though most natural forests are mixtures of several to dozens of species. Some basic insights are available on the silviculture and productivity of mixtures of tree species (see Leibundgut 1984; Hart 1991; Kelty 1992a, Olsthoorn et al. 1999). Higher production of wood in mixed-species forests has often been ascribed in part to improved nutrition (cf. Assmann 1961; Kelty 1992b; Burkhardt and Tham 1992; Mård 1996; Frivold and Kolström 1999). Nutrition could be improved in mixtures if the mixtures experienced higher inputs of nutrients, if species exploited nutrients at different times of the season or depths in the soil, if the species were limited by different nutrients, or if the mixtures increased rates of nutrient recycling.

In this paper, we summarize the empirical evidence of nutritional interactions in mixed-species stands of trees and identify future research needs. The nutritional status of trees in mixtures might be assessed with a variety of features (Fig. 1). The effect of mixtures on some features, such as the foliar concentrations of nutrients, are comprised of separate effects on each species; one species in a mixture may show an increase in phosphorus (P) concentration compared with monoculture stands, whereas the other species may show a

decrease. The mixture effects on other features, such as the size of the pools of available soil nitrogen (N), would be an integrated, single effect. Some features, such as decomposition rates, have been analyzed both separately (for each species) and as an integrated response (overall decomposition of the litter layer).

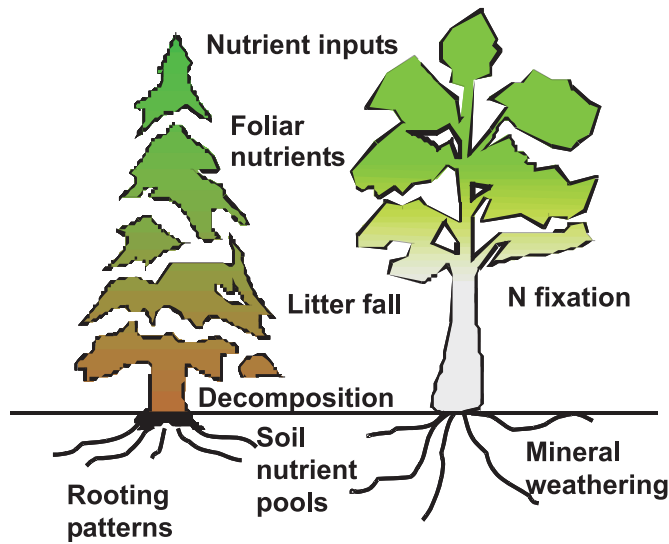
We considered two aspects of mixtures (Fig. 2). For single-species factors (such as foliar nutrient concentration), we focused on whether the values for each species in a mixture differed from the respective monocultures. For the integrated responses, such as soil available N, we focused on whether the value in the mixtures was intermediate between the monocultures or whether a nonlinear response (either antagonistic or synergistic) was evident.

## Nutrient inputs

### Atmospheric deposition

Atmospheric deposition is difficult to measure directly, but the nutrient content of throughfall may be used as a measure of deposition for ions that show minimal uptake by leaves or leaching from leaves. The quantity of nutrients in throughfall depends in part on leaf area and the duration of leaf area (Hultberg 1985; Lovett and Lindberg 1993; Ranger and Nys 1994; Matzner and Meiwes 1994; Rothe et al. 2001b), and spatial variation is large even in single-species stands (Pedersen 1992; Robson et al. 1994; Manderscheid and Matzner 1995). In mixed-species stands, the crowns of individual species create a complex spatial pattern of throughfall quantity and chemistry (Edmonds et al. 1991; Wilpert and Mies 1995). Heitz and Rehfuess (1999) found a close relationship between the crown density of individual overstory spruce trees and N deposition in Norway spruce (*Picea abies* (L.) Karst) stands underplanted with spruce, European beech (*Fagus sylvatica* L.), and European silver fir (*Abies alba* Mill.). The effect of a particular species on rates of deposition did not appear to vary between monocultures and mixtures. Wilpert and Mies (1995) found no differences in throughfall underneath individual spruce trees growing in monocultures or in mixed stands. This seems plausible as dry deposition is mainly a physical process and depends primarily on the surface properties of an individual tree (Lovett 1994), and Rothe (1997) found a linear increase of N in throughfall with increasing crown cover of spruce (Fig. 3). We note that the magnitude of the effect of species on deposition inputs may scale nonlinearly with the degree of atmospheric pollution; differences between evergreens and

**Fig. 1.** Diagram of key features examined in this review of tree nutrition in mixed-species forests.



deciduous species may be more pronounced in more polluted air (Rothe et al. 2001b).

**Nitrogen fixation**

Nitrogen fixation appears to relate linearly with the proportion of the N-fixing species in the mixture (Table 1). This tentative conclusion may not be robust. The rate of N accretion appeared linear with respect to the amount of nitrogen-fixing *Albizia facaltaria* (L.) Fosberg mixed with *Eucalyptus saligna* Sm. in the study by Kaye et al. (2000), but this linear trend was apparent only when the proportion of *Albizia* was expressed as number of trees (Fig. 4). The actual biomass of the *Albizia* trees did not relate linearly with the proportion of trees planted (DeBell et al. 1997; Kaye et al. 2000), and the trend of N accretion related nonlinearly to the proportion of biomass of *Albizia* in the stands.

**Weathering**

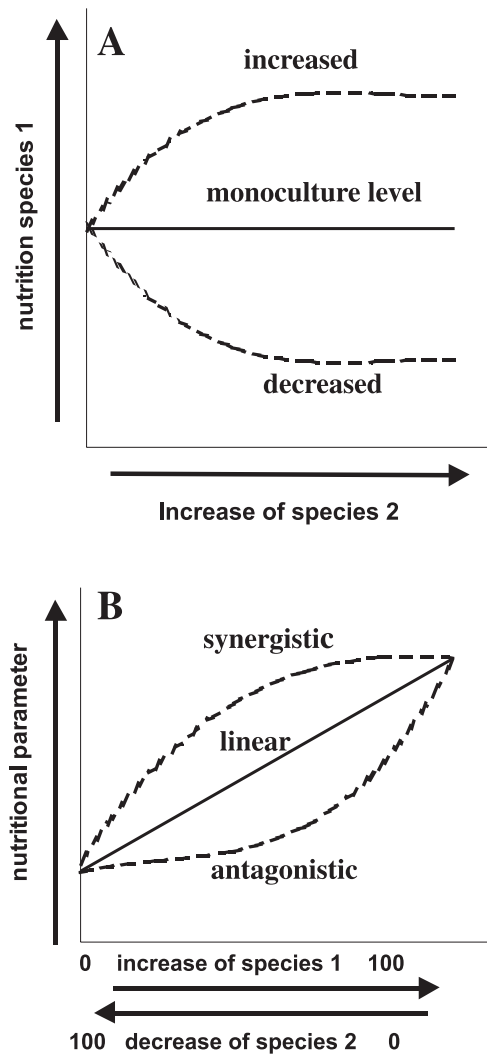
A variety of methods have been used to produce a few dozen estimates of rates of mineral weathering in forest soils (Fisher and Binkley 2000). Weathering estimates that contrasted the effects of species in monocultures are available from only two sites. Both studies from Sweden (Bergqvist and Folkesson 1995; Eriksson 1996) presented nutrient budgets that indicate species differ in rates of calcium (Ca) release from mineral weathering by 20 kg·ha<sup>-1</sup>·year<sup>-1</sup> or more. No studies have estimated rates of mineral weathering in mixed-species stands, but the large effects of individual species in these two studies leads us to expect the effects may be large.

**Site fertility**

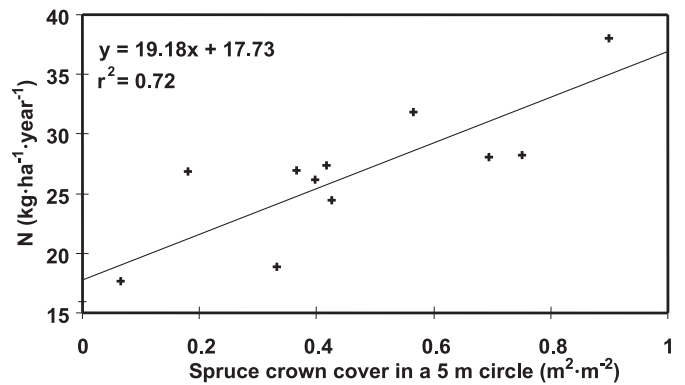
**Foliar nutrients**

The concentrations of nutrients in foliage are often used to gauge the nutritional status of trees, but surprisingly few studies have contrasted nutrient concentrations for species in mixtures (Table 2). These studies examined only a few forest types, often measuring only N and P concentrations and

**Fig. 2.** Hypothetical nutritional interactions in mixed forests: (A) criteria measured for individual species (e.g., foliar nutrients); (B) criteria for integrated responses in mixtures (e.g., pool of available soil N).



**Fig. 3.** Relationship between nitrogen throughfall deposition on 1-m<sup>2</sup> subplots and Norway spruce crown cover in a 5-m radial circle in a mixed spruce-beech forest. Each subplot had three throughfall collectors and was investigated for 2 years. (From Rothe 1997, reproduced with permission of Forstl. Forschungsber. München 163, © 1997 Bavarian State Institute of Forestry.)

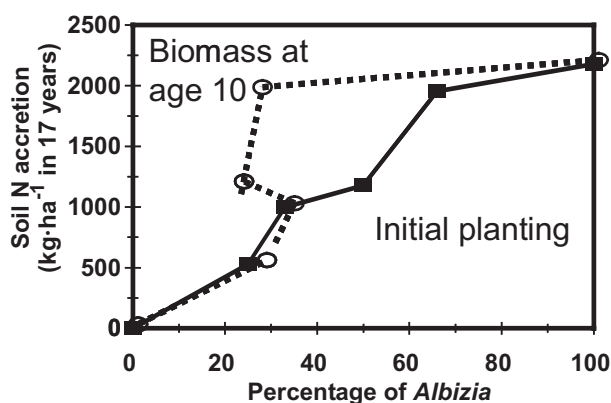


**Table 1.** Effect of species mixtures on rates of nitrogen fixation relative to monocultures.

Linear	Synergistic	Reference
<i>Casuarina equisetifolia</i> with <i>Eucalyptus robusta</i> ; <i>Leucaena leucocephala</i> with <i>Eucalyptus robusta</i>		Parrotta et al. 1996
<i>Albizia facaltaria</i> with <i>Eucalyptus saligna</i> , based on initial planting proportions	<i>Albizia facaltaria</i> with <i>Eucalyptus saligna</i> based on actual biomass proportions	Kaye et al. 2000
<i>Alnus rubra</i> with <i>Populus trichocarpa</i>		DeBell and Radwan 1979

**Note:** No studies reported antagonistic interactions.

**Fig. 4.** Soil N accretion increased linearly with the initial planting proportion of *Albizia facaltaria* in mixtures with *Eucalyptus saligna* (solid line), but a synergistic pattern developed with respect to the actual proportion of *Albizia* biomass in the stands (broken line) (based on data from DeBell et al. 1997; Kaye et al. 2000).



mostly only considered the more valuable species. No general trend is apparent; foliar nutrient concentration of trees in mixtures may be higher, identical, or lower compared with the pure stands. We might expect that the interactions of species would lead to the greatest effects of mixtures on poorer soils, but the available literature does not allow any classification by site variables.

Several studies included species comparisons in commercial plantations on oligotrophic peatland soils in Great Britain and Ireland (Morgan et al. 1992; Kerr et al. 1992; Brown 1992; Gardiner 1999). Commercially valuable Sitka spruce (*Picea sitchensis* (Bong.) Carrière) was interplanted with various species such as Japanese larch (*Larix kaempferi* (Lamb.) Carrière), hybrid larch (*Larix ×eurolepis* Henry), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Scots pine (*Pinus sylvestris* L.), black alder (*Alnus glutinosa* (L.) Gaertn.), and sessile oak (*Quercus petraea* L.). Mixtures of spruce with other conifers showed greater increases in spruce foliar N than mixtures with N-fixing alder, perhaps as a result of lower competitive stress with the other conifers (Yanai 1992), a conifer-induced reduction in competitive stress from *Calluna* species (Kerr et al. 1992), or enhanced mineralization of soil N as a result of improved soil aeration (McKay and Malcolm 1988).

For more than a century, foresters in central Europe have believed that conifers in mixtures with broad-leaved species would show better nutrition than in conifer monocultures (cf. Gayer 1886). Several studies have documented the effect of mixtures on the properties of the upper soil (Wiedemann 1942; Wittich 1961; Brown 1992; Frank 1994; Brandtberg et

al. 2000; Rothe et al. 2001a), and little evidence for improved tree nutrition has been found. Mixing European beech into conifer plantations did not influence foliar nutrient concentrations of Norway spruce on fertile luvisols (Neft and Stangl 1985; Burchardt 1998), or Scots pine on nutrient poor Podzols (Heinsdorf 1997). Mixing birch species (*Betula pendula* Roth and *Betula pubescens* Ehrh.) with Norway spruce on four N-deficient sites in southern Sweden had no effect on concentrations of N, Ca, magnesium (Mg), or manganese (Mn) in current-year spruce needles, but increased concentrations of P and potassium (K) (Brandtberg 2001).

Mixed stands that contain N-fixing species commonly show strong but inconsistent effects. In 8-year-old mixed-species stands of *Eucalyptus saligna* and N-fixing *Albizia falcataria* in Hawaii, N and P concentrations of *Eucalyptus* trees were about 20–30% higher in mixed plots with 66% *Albizia* (Binkley and Giardina 1997). In contrast, Khanna (1997) found no effect of stand type on N concentration of fully expanded leaves of *Eucalyptus globulus* Labill. or *Acacia mearnsii* De Wild. in mixed 2-year-old plantations, but N concentrations of senescent *Eucalyptus* leaves increased with the proportion of *Acacia* in mixture. Phosphorus concentrations of *Eucalyptus* decreased significantly in the mixed stands through the competition of *Acacia*.

Nutrient concentrations of leaves vary with leaf and stand age (Fisher and Binkley 2000), and the results of young plantations are not necessarily relevant for the subsequent phases of stand development (Khanna 1998). Mixtures of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with red alder (*Alnus rubra* (Bong.) Carrière) had higher concentrations of N in Douglas-fir needles but lower concentrations of P (Binkley 1992); this pattern does not appear to be consistent across sites.

### Bioassays

Bioassays are miniature field trials of soils in pots; extrapolation to field conditions may be problematic, but major effects of species in mixtures may be apparent. The number of bioassay studies investigating nutritional interactions in mixed-species stands is low; some have used tree seedlings, whereas others used agricultural species to assess soil fertility. Bioassays indicated that soils from mixed stands had higher nutrient supply than monoculture soils for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) with Gambel oak (*Quercus gambelii* Nutt.; Klemmedson 1991); Douglas-fir with red alder or Sitka alder (*Alnus sinuata* (Regel) Rydb.; Binkley 1982) and *Eucalyptus saligna* – *Albizia falcataria* mixtures (Binkley 1997). The fertility of soils from the mixed stand of ponderosa pine and Gambel oak appeared to depend on the species used in the bioassay (Klemmedson

**Table 2.** Foliar nutrient concentrations in mixed stands compared with the pure stands.

Higher	Similar	Lower	Reference
<b>Non-N-fixing mixtures</b>			
<i>Picea sitchensis</i> ,* <i>Larix kaempferi</i> – <i>L. ×eurolepis</i> (N)			Kerr et al. 1992; Morgan et al. 1992; Gardiner 1999
<i>Picea sitchensis</i> ,* <i>Pinus contorta</i> (N)			Kerr et al. 1992; Morgan et al. 1992; Gardiner 1999
<i>Picea sitchensis</i> ,* <i>Pinus sylvestris</i> (N)			Brown 1992
	<i>Picea sitchensis</i> ,* <i>Quercus petraea</i> (N, P)		Brown 1992
	<i>Picea abies</i> ,* <i>Fagus sylvatica</i> (N, P, K, Ca, Mg)		Neft and Stangl 1985; Burchardt 1998
<i>Picea abies</i> ,* <i>Betula pendula</i> , and <i>B. pubescens</i> (P, K)	<i>Picea abies</i> ,* <i>Betula pendula</i> , and <i>B. pubescens</i> (N, Ca, Mg, Mn)		Brandtberg 2001
	<i>Pinus sylvestris</i> ,* <i>Fagus sylvatica</i> (N, P, K, Ca, Mg)		Heinsdorf 1997
<b>N-fixing mixtures</b>			
	<i>Picea sitchensis</i> ,* <i>Alnus glutinosa</i> (tendency towards higher) (N, P)		Brown 1992
<i>Eucalyptus saligna</i> ,* <i>Albizia</i> <i>falcataria</i> (N, P)			Binkley and Giardina 1997
	<i>Eucalyptus globulus</i> * – <i>Acacia</i> <i>mearnsii</i> * (N)	<i>Eucalyptus</i> *– <i>Acacia</i> (P)	Khanna 1997
<i>Pseudotsuga menziesii</i> ,* <i>Alnus rubra</i> (N)	<i>Pseudotsuga menziesii</i> ,* <i>Alnus</i> <i>rubra</i> (P)		Binkley 1992

**Note:** Elements investigated are given in parentheses.

\*Species investigated in the study.

1991); the yield of barley (a nonmycorrhizal grass) was about three times higher on soils originating from the 1:1 mixture compared with soils from the pure stands, whereas pine seedlings showed no substantial effect of the mixed stand's soil relative to the monoculture soils.

### Soil assays

Soil assays have been used widely to diagnose the nutritional status of forest stands, but assay methods may or may not represent the nutrient supply to plants accurately (Fisher and Binkley 2000). In this section we consider the effects of mixtures on the pool sizes of nutrients, and the next section deals with fluxes or supply rates.

For all studies of mixtures that did not include an N-fixing species, the size of the soil N pools were within the range reported for the pure stands, giving no strong evidence of any increase or decrease in the mixtures (Table 3). We note that the distribution of nitrogen within the soil profiles may differ in mixtures. The mixed stands of ponderosa pine and Gambel oak had less N in the forest floor than in the pine monoculture (Klemmedson 1987), and similar patterns have been reported for mixtures of Norway spruce and European beech relative to spruce monocultures (Rothe 1997). Lower quantities of N in the forest floors of the mixtures were balanced by higher quantities of N in the upper mineral soils.

Mixtures that contained N-fixing species generally show larger soil pools of N than in monocultures of the non-N-fixing species. Nitrogen fixation rates in mixed Douglas-fir – red alder stands usually were within 50 to 100 kg·ha<sup>-1</sup>·year<sup>-1</sup>

compared with 100 to 200 kg·ha<sup>-1</sup>·year<sup>-1</sup> in pure red alder stands (Binkley 1992; Binkley et al. 1994). Bormann and Gordon (1984) concluded that rates of N fixation may not relate linearly to the proportion of red alder in mixed stands, but more investigation would be needed to determine if this is a general trend for red alder mixtures. An increase of soil nitrogen in mixed stands has also been documented for plantations of *Eucalyptus saligna* and *Albizia falcataria* in Hawaii. Nitrogen accretion increased linearly with the proportion of *Albizia* up to a maximum of 140 kg·ha<sup>-1</sup>·year<sup>-1</sup> in the pure *Albizia* stands (Kaye et al. 2000). No significant effects of species were obvious in pure and mixed plantations of *Eucalyptus robusta* Sm. and N-fixing *Casuarina equisetifolia* L. or N-fixing *Leucaena leucocephala* (Lam.) de Wit (Parrotta 1999). Since the least significant difference was more than half of the original soil N content, a possible effect may be hidden by the variability of the measurement.

Mixtures that contain N-fixing species have also shown all possible interactions for extractable pools of soil P. Extractable P in mixed stands was higher (Giardina et al. 1995), lower (Compton and Cole 1998; Binkley et al. 2000; Kaye et al. 2000) or similar (Brown 1992; Malcolm and Mason 1999) compared with the pure stands. The picture is still vague even for well-studied mixtures with Douglas-fir and red alder, and the relative contributions of potential mechanisms remain largely unexplored (Binkley 1992; Zou et al. 1995).

Even less information is available on the effects of mixtures on extractable pools of soil cations. Several studies re-

**Table 3.** Soil nitrogen pools in mixtures compared with the pure stands.

Higher than one monoculture	Not higher than either monoculture	Reference
<b>Non-N-fixing mixtures</b>		
	<i>Pinus ponderosa</i> , <i>Quercus gambelii</i>	Klemmedson 1987
	<i>Picea abies</i> , <i>Fagus sylvatica</i>	Rothe 1997; Weber et al. 1993; Heitz and Rehfuess 1999
	<i>Picea abies</i> , <i>Betula pendula</i> , and <i>B. pubescens</i>	Brandtberg et al. 2000
	<i>Picea sitchensis</i> , <i>Larix kaempferi</i> – <i>L. ×eurolepis</i>	Brown 1992; Morgan et al. 1992
	<i>Picea sitchensis</i> , <i>Pinus contorta</i>	Brown 1992; Morgan et al. 1992
	<i>Pinus sylvestris</i> , <i>Betula pendula</i>	Malcolm and Mason 1999
	<i>Chamaecyparis obtusa</i> , <i>Quercus mongolica</i> , <i>Carpinus japonica</i> , <i>Acer rufinerve</i>	Takahashi et al. 1999
<b>N-fixing mixtures</b>		
	<i>Pseudotsuga menziesii</i> , <i>Alnus rubra</i>	Binkley 1992; Binkley et al. 1994
	<i>Eucalyptus saligna</i> , <i>Albizia falcataria</i>	Kaye et al. 2000
	<i>Eucalyptus robusta</i> , <i>Casuarina equisetifolia</i> , <i>Leucaena leucocephala</i>	Parrotta 1999

ported no significant differences between mixed and pure stands (Klemmedson 1987; Binkley and Sollins 1990; Wittkopf 1995; Malcolm and Mason 1999; Heitz 1999), whereas others have reported higher concentrations in the topsoil beneath mixed stands (Heitz 1999; Takahashi 1999; Brandtberg et al. 2000).

### Decomposition

The rates of decomposition and nutrient release from litter depends in large part on the direct effects of litter quality and the indirect effects of litter quality on soil communities (Wittich 1961; McLaugherty et al. 1985; Scott and Binkley 1997; Ferrari 1999). The results of these studies are complex and inconsistent. Nonlinear effects (both synergistic and antagonistic) of litter mixtures occur in some cases, but even a qualitative classification according to different species combinations or according to site variables seems far away (Table 4). Some of the variety could result from differences in methods among studies, including field versus laboratory studies, time span of observation, and use of controlled or ambient environmental conditions.

The complex nature of mixed litter decomposition is revealed by the comprehensive work of Wardle et al. (1997), which included eight species of broad-leaved trees and some nontree species. They conducted a field experiment with 32 species and compared decomposition rates, N release, and microbial biomass of 70 litter mixtures containing two to eight species with the values expected from the pure litters. Decomposition of mixed litters showed nonadditive effects that were difficult to generalize. The N concentration in the litters could explain some of the observed patterns only for the early stages of decomposition.

The importance of litter quality for decomposition patterns in mixtures is confirmed by the work of Ferrari (1999). The lignin/N ratio of leaf litter and total litter fall correlated negatively with soil N mineralization and nitrification rates

at 50 subplots in an old-growth forest of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and hardwoods.

The effect of mixtures on litter decomposition could vary during the course of decomposition (Wardle et al. 1997; McTiernan et al. 1997). However, 5 years of decomposition of pure and mixed litters of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.) in British Columbia showed no effect of mixtures (Prescott et al. 2000). Rates of decomposition differed between species; aspen litter generally decayed faster than conifer litter in the initial stages of decomposition, but rates did not differ between species during later stages of decomposition (Fig. 5).

The effects for mass loss may not correspond with the effects on nutrient release. Saetre (1998a, 1998b) and McTiernan et al. (1997) reported that N mineralization in soils from mixtures was mostly lower than predicted from soils from pure stands, whereas CO<sub>2</sub> release was higher or identical.

Soil fauna and microbes play a key role in decomposition (Brussaard 1998; Lavelle 1994; Ellenberg et al. 1986), and faunal communities are strongly influenced by tree species (Kienzler et al. 1986; Weidemann and Schauer mann 1986; Boettcher and Kalisz 1991; Zou 1993). Mixture effects on decomposition appear to be driven at least in part by soil fauna and microbial community, but this area remains largely unexplored. The addition of earthworms to microcosms increased rates of C and N mineralization in soils mixed from spruce and birch stands, but earthworms survived only in mixed soils that contained at least 25% birch soil (Saetre 1998a). In field experiments with the same tree species, the densities of Coleoptera, Collembola, and Diptera larvae were significantly higher in the mixed species stands compared with the pure spruce stands, while populations of spiders and gamasid mites showed no effect. Nonlinear mixture effects have also been reported for nematodes (Blair et al. 1990), earthworms, enchytraeid worms (Brown 1992),

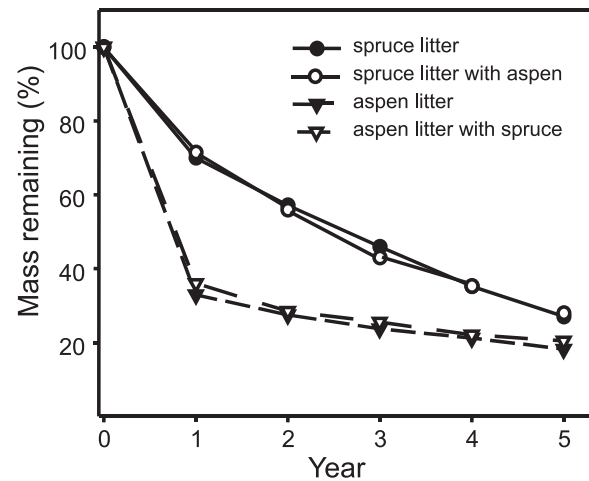
**Table 4.** The effects of species mixtures on rates of decomposition and nutrient release.

Species	Investigated parameter	Results	Reference
<b>Mass (carbon) loss</b>			
<i>Pinus taeda</i> , <i>Cornus florida</i>	Mass loss of mixed litter compared with pine litter	No mixture effect	Thomas 1968
<i>Picea glauca</i> , <i>Populus tremuloides</i>	Mass loss of mixed litter with two species compared with the pure litters	No mixture effect	Prescott et al. 2000
<i>Picea rubens</i> , <i>Pinus strobus</i> , <i>Acer rubrum</i>	Mass loss of mixed litter compared with spruce litter	No mixture effect	Rustad 1994
<i>Betula pendula</i> , <i>Empetrum hermaphroditum</i> (dwarf shrub), <i>Pleurozium schreberi</i> (feather moss)	Mass loss of mixed litter compared with beech litter	No mixture effect	Nilsson et al. 1999
<i>Callophylum brasiliense</i> , <i>Jacaranda copaia</i> , <i>Vochysiam guatemalensis</i> , <i>Strypnodendron microstachyum</i>	Mass loss of mixed litter of all four species compared with the pure litters	No general mixture effect, but varying patterns over time	Byard et al. 1996
<i>Pseudotsuga menziesii</i> , <i>Alnus rubra</i> , <i>Gaultheria shallon</i>	Mass loss of mixed litter with two species compared with Douglas-fir litter	Mixtures with red alder decomposed faster, mixtures with salal slower compared with pure Douglas-fir	Fyles and Fyles 1993
<i>Quercus serrata</i> , <i>Pinus densiflora</i> , <i>Sasa veitchii</i>	Mass loss of mixed litter compared with pure litters	Two mixtures with <i>Sasa veitchii</i> decomposed significantly faster	Kaneko and Salamanca 1999
<i>Picea abies</i> , <i>Betula pendula</i>	CO <sub>2</sub> release of soil mixtures ranging from pure spruce to pure birch	Linear increase with increasing proportions of birch	Saetre 1998a, 1998b
<i>Quercus petraea</i> , <i>Alnus glutinosa</i> , <i>Pinus sylvestris</i> , <i>Picea abies</i> , <i>Picea sitchensis</i> , <i>Fraxinus excelsior</i> , <i>Betula pendula</i>	CO <sub>2</sub> release of all 21 two-litter combinations in comparison to the CO <sub>2</sub> release expected from the monocultures	Eight significantly higher; one significantly lower, 12 mixtures no significant effect	McTiernan et al. 1997
Thirty-two plant species including eight broad-leaved tree species	Mass loss of mixed litter with two to eight species in comparison with the mass loss expected from the monocultures	All patterns and directions, effects changed over time, after 300 days mass loss of 3 of 10 mixtures with trees significantly higher	Wardle et al. 1997
<b>Nutrient release</b>			
<i>Picea rubens</i> , <i>Pinus strobus</i> , <i>Acer rubrum</i>	Nutrient release from mixed litters	No mixture effect	Rustad 1994
<i>Tsuga canadensis</i> , <i>Acer saccharum</i> , <i>Tilia americana</i>	Correlation between N mineralization–nitrification and litter variables	Significant positive correlation with the amount of broad-leaved litter	Ferrari 1999
<i>Fagus grandifolia</i> , <i>Tsuga canadensis</i> , <i>Acer saccharum</i> , <i>Acer rubrum</i> , <i>Fraxinus americana</i> , <i>Quercus rubra</i>	Correlation between soil N mineralization and litter input	Nonlinear (antagonistic) mixture effect	Finzi and Canham 1998
<i>Picea sitchensis</i> , <i>Pinus sylvestris</i> , <i>Quercus petraea</i>	N and P release from forest floor in mixtures compared with the spruce monoculture	Mineralization rates in spruce + pine mixture higher than spruce and spruce + oak mixture	Chapman et al. 1988; Brown 1992
<i>Acer rubrum</i> , <i>Quercus prinus</i> , <i>Cornus florida</i>	N release of litter mixtures compared with the monocultures	Initial N release greater in mixtures	Blair et al. 1990
<i>Picea sitchensis</i> , <i>Pinus sylvestris</i> , <i>Larix kaempferi</i>	Influence of litter composition on soil N mineralization	Mineralization rates in mixture higher compared to pure spruce	Williams and Alexander 1991

Table 4 (concluded).

Species	Investigated parameter	Results	Reference
<i>Chamaecyparis obtusa</i> , <i>Quercus mongolica</i> , <i>Carpinus japonica</i> , <i>Acer rufinerve</i>	Soil N mineralization of mixtures from 0 to 100% broad-leaved trees	Mineralization rates in mixture lower than expected	Takahashi et al. 1999
<i>Picea abies</i> , <i>Betula pendula</i>	Soil N mineralization of soil mixtures ranging from pure spruce to pure birch	Mineralization rates in mixture lower than expected	Saetre 1998a, 1998b
<i>Quercus petraea</i> , <i>Alnus glutinosa</i> , <i>Pinus sylvestris</i> , <i>Picea abies</i> , <i>Picea sitchensis</i> , <i>Fraxinus excelsior</i> , <i>Betula pendula</i>	NH <sub>4</sub> release of all 21 two-litter combinations in comparison with the values expected from the monocultures	One significantly higher, four significantly lower, 16 mixtures no significant effect	McTiernan et al. 1997

Fig. 5. Decomposition of spruce and aspen litter, in single-species litter bags, and in mixed-species litter bags, in a boreal forest near Dawson, B.C. Mixing litter from the two species had no effect on decomposition rates (after Prescott et al. 2000).



microbial activity (Morgan et al. 1992; Wardle et al. 1997), and oribatid mites and faunal abundance (Kaneko and Salamanca 1999), whereas no mixture effects were apparent for oribatid mites (Migge et al. 1998).

### Litter fall

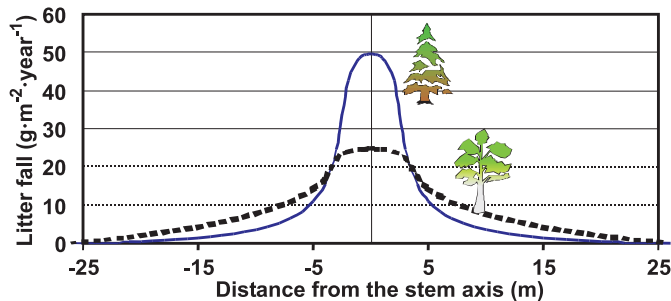
Litter production varies widely among forest ecosystems (Bray and Gorham 1964; Binkley et al. 1997), and some of this variation results from the differences among tree species in the quality and quantity of litter fall (Ebermayer 1876; Binkley and Giardina 1998). The effects of mixtures of species may derive from effects on litter quantity and quality of litter (as described above), or from patterns in the spatial distribution of litter fall.

The most striking effects on nutrient quantity may be found in mixtures with N-fixing species. Mixed stands of Douglas-fir and red alder cycle three to eight times more N in litter fall than Douglas-fir stands, and litter fall contents of P, Ca, Mg, and K are also significantly greater compared with the conifer monocultures (Binkley 1992). Similar magnitudes are reported from *Eucalyptus-Albizia* mixtures in Hawaii, where N and P cycling in litter fall was about three times higher in the mixed plots compared with the *Eucalyptus* monoculture (Binkley 1997).

Litter fall measurements in stands of European beech and Norway spruce (Bücking 1987; Rothe 1997) revealed significantly higher contents of the base cations (K, Ca, and Mg) for beech, while for N and P the differences among species were small. In mixed spruce-beech stands, the cycling of nutrients in litter fall increased linearly with increasing proportions of beech when calculated on a stand level.

Litter from broad-leaved species may be blown farther by wind than needle litter (Fig. 6), leading to a characteristic distribution of litter with higher amounts underneath conifers and smaller amounts beneath broad-leaved trees. This effect was noted long ago by foresters (e.g., Gayer 1886; Hoffmann 1923). In forests containing European beech and Norway spruce, between 20 and 70% of the beech litter is

**Fig. 6.** Horizontal distribution of litter fall for spruce and beech. To transfer this one-dimensional figure to a spatial scale, it has to be considered that the area of the radial rings increases with the square root of the distance. (From Rothe 1997, reproduced with permission of Forstl. Forschungsber. München 163, © 1997 Bavarian State Institute of Forestry.)



transported to areas beneath spruce canopies, whereas 5–20% of spruce litter is moved to beneath canopies of beech (Mettin 1986; Rothe 1997). The net gain of litter in the parts of the stand covered by spruce resulted in an additional input of 15–40 kg N·ha<sup>-1</sup>·year<sup>-1</sup>, 1–3 kg P·ha<sup>-1</sup>·year<sup>-1</sup>, 2–5 kg Mg·ha<sup>-1</sup>·year<sup>-1</sup>, and 5–12 kg K·ha<sup>-1</sup>·year<sup>-1</sup> for a 1:1 mixture. Ferrari and Sugita (1996) examined spatial patterns in litter fall within a mixed forest of eastern hemlock and different broad-leaved species (*Fagus grandifolia* Ehrh., *Acer saccharum* Marsh, and *Betula papyrifera* Marsh). The differences were small but statistically significant. About 90% of the litter of an average hardwood tree fell within about 1000 m<sup>2</sup> (18 m radius), whereas 90% of the litter of an average hemlock tree was found within 800 m<sup>2</sup> (16 m radius). Horizontal distribution patterns of nutrients in litter fall are also obvious from a mixture experiment in Connecticut, U.S.A., using a checkerboard design with 11 × 11 m plots (Binkley and Valentine 1991). Plots with Norway spruce or white pine (*Pinus strobus* L.) had 50–100% more litter fall Ca and Mg when the adjacent plots were green ash (*Fraxinus pennsylvanica* Marsh.) than when the adjacent plots were coniferous.

These studies all focused on the aboveground inputs of litter, but the inputs of organic matter and nutrients in dead roots and mycorrhizae may be of equal (or greater?) importance as a mechanism of interaction in mixed-species forests. Unfortunately, the state of knowledge on belowground interactions is limited to rooting patterns and zones of nutrient uptake; we hope future studies will be able to include the mass balance of belowground inputs to decomposition processes.

### Rooting patterns and nutrient uptake

The patterns of root development differ among species, including the spatial distribution of roots in the soil and rates of root turnover (Köstler et al. 1968; Vogt et al. 1996, 1997). Differences in rooting patterns could lead to differences in soil exploitation among species. This idea is supported in some agricultural situations (Vandermeer 1989), but root studies are scarce in mixed-species forests.

Fine-root distribution of Sitka spruce in mixture with Scots pine may be more shallow (Brown 1992) or deeper

**Table 5.** Vertical distribution (percent of total mass) of fine roots <2 mm of beech and spruce (>1 m from boles) according to stand type on a Typic Hapludalf at the Höglwald research area, southern Germany (modified from Wittkopf 1995).

Soil layer	Stand type			
	Spruce pure stand	Spruce mixed stand	Beech pure stand	Beech mixed stand
Forest floor	14 <sub>a</sub>	21 <sub>a</sub>	2 <sub>b</sub>	0 <sub>c</sub>
0–10 cm	60 <sub>a</sub>	66 <sub>a</sub>	40 <sub>b</sub>	18 <sub>c</sub>
10–30 cm	22 <sub>b</sub>	13 <sub>b</sub>	45 <sub>a</sub>	63 <sub>a</sub>
30–50 cm	4 <sub>b</sub>	0 <sub>c</sub>	13 <sub>a</sub>	19 <sub>a</sub>

**Note:** Different letters indicate significantly different values among stand types at the 95% level.

(McKay and Malcolm 1988) compared with the pure spruce stands. The different patterns might derive from differences in soil moisture on the peatland soils. McKay and Malcolm (1988) speculated that increased water use by pine on the wet peatland soils in Scotland improved soil aeration in mixed stands, allowing spruce roots to exploit deeper soils.

Root interactions have also been documented for mixed stands with Norway spruce and European beech (Mackenthun 1990; Fölster et al. 1991; Wittkopf 1995; G. Glatzel, personal communication) and for mixtures of ash (*Fraxinus excelsior* L.) and European beech on nutrient rich loamy soils (Rysavy and Roloff 1994). On all soil types investigated, spruce or ash tended to root more shallowly in mixture than in the pure stands, while beech tended to root deeper in the mixed stand compared with the pure beech stand (Table 5). The effect was most pronounced for fine roots in the interstem area, while differences among stand types concerning the coarse roots in the proximity of the trunks and concerning the maximum depth of rooting were small (Kern et al. 1961; Fölster et al. 1991).

No clear pattern of vertical stratification of roots was found in mixtures of Scots pine and European beech on nutrient poor sandy soils in eastern Germany (Ehwald et al. 1961). Root mass and root distribution in the mixed stands appeared to be a linear addition of the patterns in monocultures.

Mixtures of Norway spruce and birch species in Sweden showed similar masses of fine (<1 mm) roots in the humus layer, whereas the mineral soil in the spruce monocultures has greater fine root mass than in the mixed stands (Brandtberg et al. 2000). The rooting pattern was reflected in a higher annual rate of Ca incorporation into aboveground tissues in the monoculture (Brandtberg 2001). Although birch has been promoted as a “soil improver” as a result of deeper rooting and uptake of base cations below the rooting zone of spruce, Brandtberg (2001) found that uptake of <sup>32</sup>P and <sup>45</sup>Ca was proportionally the same between the humus and mineral soil for birch and spruce. The combination of similar (or greater) fine-root development with depth, and similar uptake of radioisotopes, provided no support for ideas of a differentiation in the distribution of roots and nutrient uptake between these species.

The timing of root growth and the stage of plant development may also be important for root interactions in mixtures,

as shown by Hooper and Vitousek (1998) for mixed communities of herbaceous plants. Fine root density in the deeper soil layers of mixed stands of Douglas-fir and European beech on sandy, podzolic soils in the Netherlands was significantly higher compared with the monocultures. The 40-year-old mixed stands had a higher fine root density of Douglas-fir than beech, while the 60-year-old stands had a lower fine root density of Douglas-fir than of beech (Hendriks and Bianchi 1995). These authors speculated that this might be part of a temporal rooting strategy with faster growing Douglas-fir expanding the root system first, but much more work (including replication of stands) would be needed to test this idea. Differences in the timing of root growth were reported for mixed stands of pedunculate oak (*Quercus robur* L.) and European beech on nutrient-poor sandy soils in northern Germany (Büttner and Leuschner 1994). Fine root biomass peaked in August for beech and in September for oak.

We conclude that knowledge is still very limited on the interactions among root systems of tree species, and the available literature does not allow a differentiation according to site properties. The overall implications of root interactions for nutrient uptake could be large, but root distribution patterns may not necessarily coincide with nutrient uptake patterns (Vogt et al. 1995; George and Marschner 1996). The strongest effects for tree nutrition can be expected in situations where a deeper rooting species exploits nutrient-rich layers in the subsoil and facilitates nutrient uptake by the shallow-rooted species (a "nutrient pump" effect). Similar patterns should occur on Aquic soils, where a species less susceptible to anoxic conditions (e.g., alder, oak) may utilize moist soil horizons and facilitate a species susceptible to anoxic conditions (e.g., spruce). Nutritional effects resulting from differences in the timing of root growth and activity are most likely in mixtures of conifers and hardwoods, since conifers usually start transpiration and nutrient uptake before leaf flush of broadleaf species (Rothe 1997). All of these ideas need further experimentation before strong confidence would be warranted.

## Conclusions and approaches for future research

Empirical studies on nutrition of mixed-species stands support few generalizations about the influence of tree species in mixtures, or about the interaction between environmental factors and nutritional effects. Systematic studies of particular mixtures across gradients in soil types are almost nonexistent; only the decomposition studies of Wardle et al. (1997) and McTiernan et al. (1997) investigated mixture effects of multiple-species combinations under controlled environmental conditions. The interpretation of the literature is hampered by differing methodology, experimental conditions, and even confusing use of terminology.

Most investigations have focused on patterns of interaction among species, rather than directly addressing the nutritional status of the trees. Different patterns of soil nutrient pools, nutrient availability, root distribution, or litter quality may not indicate differences in the nutritional status of trees (e.g., enhanced N availability is unlikely to influence N foliar concentrations on sites where N is not limiting) and it is

debatable whether we should draw conclusions about "nutritional interactions" in such cases.

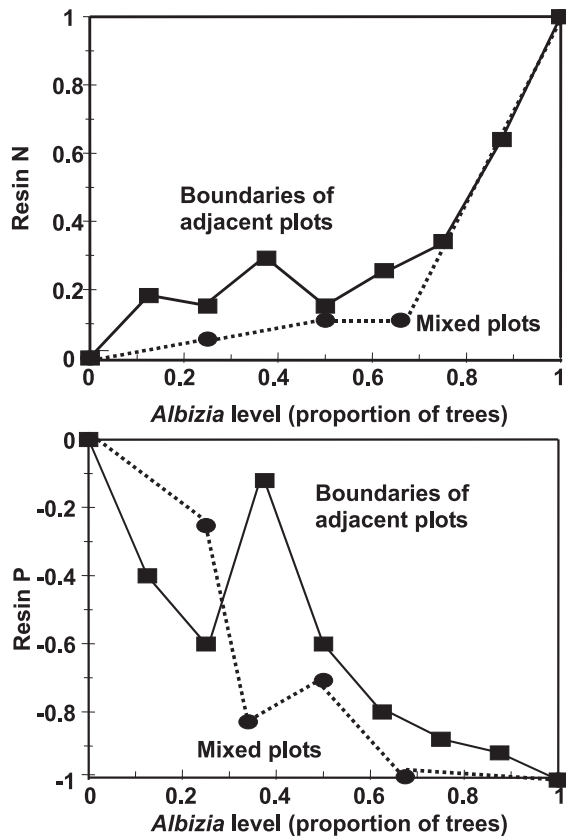
At the end of this review, we would like to offer several hypotheses that would take the wide variety of empirical observations and condense them into coherent, useful simplifications. The empirical data have not supported general simplifications. The strongest expectation might be that mixtures that include N-fixing species will show improved nitrogen nutrition in the non-N-fixing trees, but even these cases are inconsistent. Mixtures that include N-fixing species generally show increased N availability relative to the non-N-fixing monocultures, but foliar N concentrations do not always reflect high soil N supply. The effects on P are variable, and several case studies found antagonistic effects of the N fixer on the P nutrition of the non-N-fixing species in mixtures. A second expectation is that, in the absence of N-fixing species, nonlinear nutritional interactions seem to be less common than classic expectations. Interaction effects for foliar and soil nutrients will only occur for special site conditions and species combinations (e.g., mixtures of Sitka spruce with other conifers on peatland soils; see above). Where nonlinear patterns occurred, the interactions were mostly synergistic.

We think that this broad range of empirical results is realistic and that unifying hypotheses or concepts may not capture the real breadth of interactions among species. Given this conclusion, we recommend two tracks for future research. A statistical approach (also called a phenomenological approach; sensu Vandermeer 1989) is needed to increase the degrees of freedom in the analysis of tree nutrition in mixtures. How many sites with spruce mixed with beech will show higher N concentrations in spruce than in monocultures? At present, the number of available studies is too small to provide a frequency distribution for the effects categorized in Tables 1–4. A modest network of coordinated experiments including the same mixture type under similar site conditions as well as different species combinations under comparable site conditions could provide insights on the frequencies with which mixtures fall into the columns of Tables 1–4.

The second approach is a mechanistic one. If we knew that about half of the mixed stands of spruce and beech would show improved N nutrition for spruce than in monocultures, then research could focus on identifying which components of Fig. 1 differed among sites that showed different responses in spruce nutrition. The variation in nutrition responses among sites might be linked to differences in the observed effect of mixtures on atmospheric inputs, or rates of litter decomposition, further reducing the uncertainty in predicting the general effect of spruce and beech mixtures.

Both the statistical approach and the mechanistic approach can utilize experimental designs at the scales of plots and of single-tree neighborhoods. Plot studies have dominated in the past, and have compared mixed stands with monocultures on a plot level. Site factors have often confounded the effects of species, because the mixtures developed under site conditions (or stand histories) that also influenced tree nutrition. This confounding is avoided in common-garden designs (Binkley 1995), but these powerful approaches may be difficult to apply in many situations. A

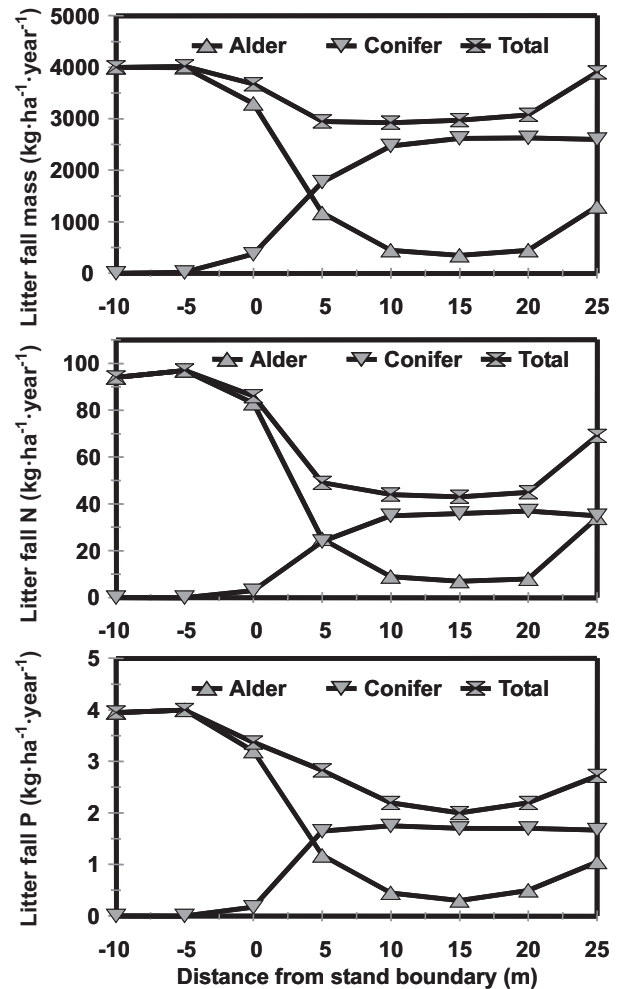
**Fig. 7.** The effect of species mixture on the accumulation of ammonium + nitrate and phosphorus on resin bags was similar when evaluated with transects across boundaries of adjacent stands, and when evaluated in mixed-species plots. For comparability between sites, values are scaled to pure *Eucalyptus* equals 0, pure *Albizia* equals 1 or -1. *Albizia* level for the boundary plots was calculated as the proportion of species in two rows of trees to each side of the sampling point. Boundary data are from D. Binkley and M. Bashkin (unpublished data), and mixed-species plot data are from Kaye et al. (2000).



simple experiment with three species, all possible species combinations, two forms of mixtures, and five replications would require 55 plots to characterize the mixture effects for a single site!

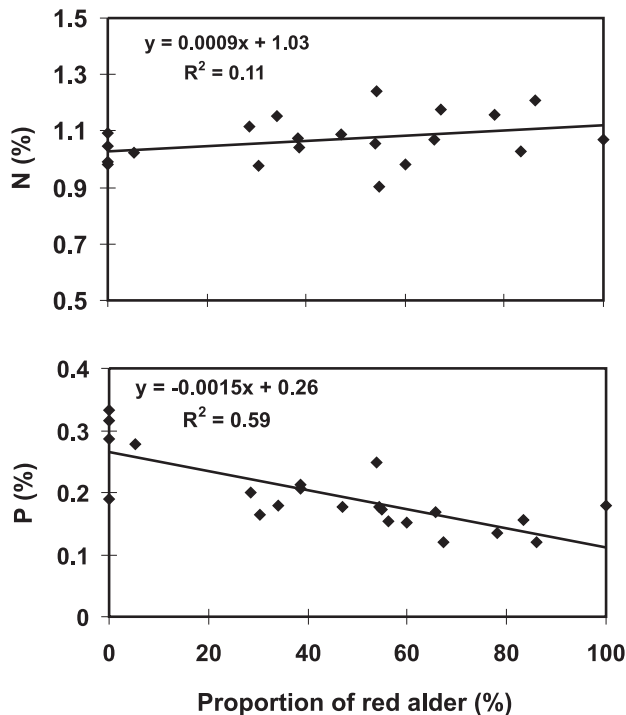
In the absence of replicated-plot experiments, research could take advantage of the spatial scale at which trees interact. Individual trees influence soil properties primarily within the radius of the canopy (Zinke 1962; Turner and Franz 1985; Boettcher and Kalisz 1990; Rhoades and Binkley 1992; Vogt et al. 1995; Rothe 1997; Ewers et al. 1996; review by Rhoades 1997), while litter fall and microclimate may influence nutritional interactions up to one tree height (Rothe 1997; Ferrari and Sugita 1996; Shure and Phillips 1987). This provides an opportunity for a neighborhood approach to investigate the correlation between nutritional properties and the type and location of species on a small spatial scale. Such approaches, similar to the competition assessment used in single tree based growth models (Pretzsch 1992; Biging and Dobertin 1995), might offer a great potential to provide reliable insights into the pattern expected for mixed-species stands.

**Fig. 8.** Litter fall mass and nutrient content along transects perpendicular to the boundaries between three stands of nitrogen-fixing red alder and conifers. Negative distances from the boundary are in the pure alder stands, and positive distances are in the pure conifer stands (from data in Lavery 2000).



Binkley (1995) suggested that the effects of mixtures of species might be determined by examining the boundary between monocultures of different species. Forest management activities have created many boundaries between stands of different species, and the exact location of these boundaries often relates to a treatment prescription rather than any boundary in soil conditions. This approach has been used to investigate relative differences in resin-available N and P among mixed stands of *Eucalyptus* and *Albizia* in Hawaii (Binkley et al. 2000; D. Binkley and M. Bashkin, unpublished data). The data for the mixed stands come from four replicated plots of six proportions of *Albizia*, and the boundary data come from a similar site 1 km away, where three pairs of adjacent pure plots of each species had been planted at the same time. Both experimental designs showed the same overall effect of species (Fig. 7). Resin N declined dramatically with even minor components of *Eucalyptus*, whereas the effect of species on resin P appeared more linear. Lavery (2000) examined the trends in litter fall biomass and nutrient content across the boundary between stands of red alder and conifers (mostly Douglas-fir) at three sites in

**Fig. 9.** Example of the neighborhood design, with nitrogen and phosphorous concentrations of 2-year-old Douglas-fir needles related to the proportion of red alder (basal area) in a 5-m circle. For nitrogen no mixture effect was apparent ( $p = 0.17$ ) while there seems to be a competitive effect for phosphorus ( $p = 0.000$ ). Data are from the H.J. Andrews forest in Oregon, U.S.A. (Rothe et al., paper submitted).<sup>2</sup>



British Columbia. Conifers had little effect on litter fall mass or nutrient content beyond the boundary of the stands; no conifer litter fell more than 5 m into the red alder stand (Fig. 8). In contrast, the broad-leaved litter fall of alder fell at least 25 m into the conifer stand, comprising about a quarter of the N and P content of litter fall.

Alternatively, a single-tree, within-stand design may be used to relate soil or tree properties to the number, size, and species of neighboring plants and the distances between them (Klemmedson 1987; Kelty and Cameron 1995). Planting design usually does not consider small-scale soil properties, and therefore, confounding soil effects are unlikely in the case of artificial regeneration. Rothe (1997) analyzed the small-scale influence of individual trees on throughfall deposition, seepage water, rooting patterns, litter fall, and different soil properties in a mixed European beech – Norway spruce forest in southern Germany. All properties were strongly related with the trees within a 5-m circle around the sampling point, but only for litter fall the influence of trees outside the 5-m circle was significant. The single-tree neighborhood design might also be useful for identifying nutritional interactions in mixed-species stands (Fig. 9), but it has barely been used up to now.

The importance of mixed-species management is likely to increase in the future, as social demands shift the focus of

forestry away from widespread, extensive monocultures. The current state of knowledge shows that tree nutrition in mixtures commonly matches nutrition in monocultures, but that nonlinear interactions do occur. The complete story of interaction in mixed-species stands is still more complex and depends on the interaction of all growth resources and site variables. We expect that the greatest interaction between species will develop when one species increases the rate of supply of a limiting resource (such as N in soils beneath N-fixing species) and another species has a greater rate of growth per unit of resource used (such as high production per kilogram of N used by *Eucalyptus* species; Binkley 1992). The ability to understand and predict the impacts of mixed-species silviculture will require a substantial (and hopefully coordinated) set of statistical and mechanistic studies that examine the frequency and magnitude of the changes in ecosystem pools and fluxes. These studies could not test all reasonable combinations of tree species across the range of forest soils, but key combinations (including species with nutrient-rich litter fall, and species with high nutrient-use efficiencies) could be chosen to map the likely occurrence and magnitudes of the interacting effects of species on tree nutrition.

## Acknowledgements

We thank Heidi Steltzer, Jason Kaye, and several anonymous reviewers for helping to improve this manuscript. This work was supported in part by the German Research Council (DFG), and by McIntire-Stennis appropriations to Colorado State University.

## References

- Assmann, E. 1961. Waldtragskunde. BLV Verlag, München, Germany.
- Bergkvist, B., and Folkesson, L. 1995. The influence of tree species on acid deposition, proton budgets and element fluxes in south Swedish forest ecosystems. *Ecol. Bull.* **44**: 90–99.
- Biging, G.S., and Dobertin, M. 1995. Evaluation of competition indices in individual tree growth models. *For. Sci.* **41**: 360–377.
- Binkley, D. 1982. Alder effects on forest soil nutrient availability. MacMillan Bloedel, Ltd., Nanaimo, B.C. Project Rep. 552-8.
- Binkley, D. 1992. Mixtures of nitrogen<sub>2</sub>-fixing and non nitrogen<sub>2</sub>-fixing tree species. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. *Br. Ecol. Soc. Spec. Publ.* **11**. pp. 99–124.
- Binkley, D. 1995. The influence of tree species on forest soils: processes and patterns. *In* Proceedings of the Trees and Soils Workshop, Canterbury, N.Z. *Edited by* D.J. Mead and I.S. Cornforth. Lincoln University Press, Canterbury, N.Z. *Agron. Soc. N.Z. Spec. Publ.* **10**. pp. 1–34.
- Binkley, D. 1997. Bioassays of the influence of *Eucalyptus saligna* and *Albizia falcataria* on soil nutrient supply and limitation. *For. Ecol. Manage.* **91**: 229–234.
- Binkley, D., and Giardina, C. 1997. Nitrogen fixation in tropical forst plantations. *In* Management of soil, nutrients and water in tropical plantation forests. *Edited by* S.E.K. Nambiar and A.G.

<sup>2</sup>A. Rothe, J. Ewald, and D.E. Hibbs. Do admixed broadleaves improve foliar nutrient status of conifer tree crops? Submitted to *For. Ecol. Manage.*

- Brown. Australian Centre for International Agricultural Research, Canberra. ACIAR Monogr. Ser. 43. pp. 297–337.
- Binkley, D., and Giardina, C. 1998. Why do tree species affect soils? The warp and woof of tree–soil interactions. *Biogeochemistry*, **42**: 89–106.
- Binkley, D., and Sollins, P. 1990. Factors determining differences in soil pH in adjacent conifer and alder conifer stands. *Soil Sci. Soc. Am. J.* **54**: 1427–1433.
- Binkley, D., and Valentine, D. 1991. Fifty-year biogeochemical effects on green ash, white pine and Norway spruce in a replicated experiment. *For. Ecol. Manage.* **40**: 13–25.
- Binkley, D., Cromack, K., Jr., and Baker, D.D. 1994. Nitrogen fixation rates by red alder: biology, rates, and controls. *In* The biology and management of red alder. *Edited by* D. Hibbs, D. DeBell, and R. Tarrant. Oregon State University Press, Corvallis, Ore. pp. 57–72.
- Binkley, D., O'Connell, A.M., and Sankaran, K.V. 1997. Stand development and productivity. *In* Management of soil, nutrients and water in tropical plantation forests. *Edited by* E.K.S. Nambiar and A.G. Brown. Australian Centre for International Agricultural Research, Canberra. ACIAR Monogr. Ser. 43. pp. 419–442.
- Binkley, D., Giardina, C., and Bahskin, M. 2000. Soil phosphorus supply under the influence of *Eucalyptus saligna* and nitrogen-fixing *Albizia facaltaria*. *For. Ecol. Manage.* **128**: 241–247.
- Blair, J.M., Parmelee, R.W., and Beare, M.H. 1990. Decay rates, nitrogen fluxes and decomposer communities of single- and mixed-species foliar litter. *Ecology*, **71**: 1976–1985.
- Boettcher, S.E., and Kalisz, J.P. 1990. Single tree influence on soil properties in the mountains of eastern Kentucky. *Ecology*, **71**: 1365–1372.
- Boettcher, S.E., and Kalisz, J.P. 1991. Single-tree influence on earthworms in forest soils in eastern Kentucky. *Soil Sci. Soc. Am. J.* **55**: 862–856.
- Bormann, B.T., and Gordon, J.C. 1984. Stand density effects in young red alder plantations: productivity, photosynthate partitioning, and nitrogen fixation. *Ecology*, **65**: 394–402.
- Brandtberg, P.-O. 2001. Mixing birch in Norway spruce stands: impacts on forest floor chemistry with implications for the buffering of acidity and the nutrition of spruce. Ph.D. thesis, Swedish University of Agricultural Sciences, Uppsala.
- Brandtberg, P.-O., Lundkvist, H., and Bengtsson, J. 2000. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. *For. Ecol. Manage.* **130**: 253–364.
- Bray, R.J., and Gorham, E. 1964. Litter production in forests of the world. *Adv. Ecol. Res.* **2**. pp. 101–157.
- Brown, A.H.F. 1992. Functioning of mixed-species stands at Gisburn, NW-England. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. Br. Ecol. Soc. Spec. Publ. 11. pp. 125–150.
- Brussaard, L. 1998. Soil fauna, guilds, functional groups and ecosystem processes. *Appl. Soil Ecol.* **9**: 123–135.
- Bücking, W. 1987. Streuanlieferung und Rückführung einiger Makroelemente mit der Streu in Fichten- und Buchenwaldökosystemen des Schönbuchs. *Mitt. Ver. Forstl. Standortsk. Pflanzenzüchtg.* **33**: 62–99.
- Büttner, V., and Leuschner, C. 1994. Spatial and temporal patterns of fine root abundance in a mixed oak–beech forest. *For. Ecol. Manage.* **70**: 11–21.
- Burchardt, U. 1998. Einflüsse von Buchengruppen auf angrenzende Fichtenreinbestände. Diplomarbeit, Fachhochschule Weihenstephan, Freising, Germany.
- Burkhardt, H.E., and Tham, A. 1992. Predictions from growth and yield models of the performance of mixed species stands. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. Br. Ecol. Soc. Spec. Publ. 11. pp. 21–34.
- Byard, R., Kristin, K.C., and Montagnini, F. 1996. Leaf litter decomposition and mulch performance from mixed and monospecific plantations of native tree species in Costa Rica. *Agric. Ecosyst. Environ.* **58**: 145–155.
- Chapman, K., Wittaker, J.B., and Heal, O.W. 1988. Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agric. Ecosyst. Environ.* **24**: 33–40.
- Compton, J., and Cole, D.W. 1998. Phosphorus cycling and soil P fractions in Douglas-fir and red alder stands. *For. Ecol. Manage.* **110**: 101–112.
- DeBell, D.S., and Radwan, M.A. 1979. Growth and nitrogen relations of coppiced black cottonwood and red alder in pure and mixed plantings. *Bot. Gaz. (Suppl.)* **140**: 97–101.
- DeBell, D.S., Cole, T.G., and Whitesell, C.D. 1997. Growth, development, and yield of pure and mixed stands of *Eucalyptus* and *Albizia*. *For. Sci.* **43**: 286–298.
- Ebermayer, E. 1876. Die gesamte Lehre der Waldstreu mit Rücksicht auf die chemische Statik des Waldbaues. Springer, Berlin.
- Edmonds, R.L., Thomas, T.B., and Rhodes, J.J. 1991. Canopy and soil modification in a temperate rain forest. *Soil Sci. Soc. Am. J.* **55**: 1685–1693.
- Ehwald, E., Grunert, F., Schulz, W., and Vetterlein, E. 1961. Zur Ökologie von Kiefern-Buchen-Mischbeständen. *Arch. Forstwesens*, **10**(4–6): 397–416.
- Ellenberg, H., Mayer, R., and Schaueremann, J. 1986. Ökosystemforschung – Ergebnisse des Sollingprojektes. Eugen Ulmer Verlag, Stuttgart, Germany.
- Eriksson, H.M. 1996. Effects of tree species and nutrient application on distribution and budgets of base cations in Swedish forest ecosystems. Ph.D. thesis, Swedish University of Agricultural Sciences, Uppsala.
- Ewers, B., Binkley, D., and Bashkin, M. 1996. Influence of adjacent stand on spatial patterns of soil carbon and nitrogen in *Eucalyptus* and *Albizia* plantations. *Can. J. For. Res.* **26**: 1501–1503.
- Ferrari, J.B. 1999. Fine-scale patterns of leaf litterfall and nitrogen cycling in an old-growth forest. *Can. J. For. Res.* **29**: 291–302.
- Ferrari, J.B., and Sugita, S. 1996. Aspatially explicit model of leaf litterfall in hemlock–hardwood forests. *Can. J. For. Res.* **26**: 1905–1913.
- Finzi, A.C., and Canham, C.D. 1998. Non-additive effects of litter mixtures on net N mineralization in a southern New England Forest. *For. Ecol. Manage.* **105**: 129–136.
- Fisher, R.F., and Binkley, D. 2000. Ecology and management of forest soils. Wiley, New York.
- Fölster, H., Degenhard, M., Flor, T., and Lux, M. 1991. Untersuchungen zur Tiefendurchwurzelung und Durchwurzelungsintensität auf Braunerde-Pseudogleyen im Vorderen Hunsrück in Abhängigkeit von Baumart und Bestandsstrukturparametern. *Mitt. Forstl. Versuchsanst. Rheinland-Pfalz* **19**.
- Francis, C.A. (Editor). 1986. Multiple cropping systems. Macmillan Publishing Co., New York.
- Frank, J. 1994. Use of broadleaved trees with conifers as a countermeasure to acidification—effects on soil properties. *In* Proceedings of the Seminar on Counteractions Against Acidification in Forest Ecosystems, 3–4 Mar. 1994, Mastermyr, Norway. Norsk Institutt for Skogforskning, As, Norway. pp. 28–31.

- Frivold, L.H., and Kolström, T. 1999. Yield and treatment of mixed stands of boreal tree species in Fennoscandia. *In* Management of mixed-species forest: silviculture and economics. *Edited by* A.F.M. Olsthoorn, H.H. Bartelink, J.J. Gardiner, H. Pretzsch, H.J. Hekhuis, and A. Franc. Institute for Forestry and Nature Research, Wageningen, the Netherlands. *IBN Sci. Contrib.* 15. pp. 98–117.
- Fyles, J.W., and Fyles, I.H. 1993. Interaction of Douglas-fir with red alder and salal foliage litter during decomposition. *Can. J. For. Res.* 23: 358–361.
- Gardiner, J.J. 1999. Mixed-species forest plantations on oligotrophic sites in the Republic of Ireland. *In* Management of mixed-species forest: silviculture and economics. *Edited by* A.F.M. Olsthoorn, H.H. Bartelink, J.J. Gardiner, H. Pretzsch, H.J. Hekhuis, and A. Franc. Institute for Forestry and Nature Research, Wageningen, the Netherlands. *IBN Sci. Contrib.* 15. pp. 58–64.
- Gayer, K. 1886. *Der gemischte Wald, seine Begründung und Pflege insbesondere durch Horst- und Gruppenwirtschaft.* Paul Parey Verlag, Berlin.
- George, E., and Marschner, H. 1996. Nutrient and water uptake by roots of forest trees. *J. Plant Nutr. Soil Sci.* 159: 11–21.
- Giardina, C.P., Huffmann, S., Binkley, D., and Cadwell, B.A. 1995. Alders increase soil phosphorus availability in a Douglas-fir plantation. *Can. J. For. Res.* 25: 1652–1657.
- Harper, J.L. 1977. *Population biology of plants.* Academic Press, London.
- Hart, C. 1991. *Practical forestry for the agent and the surveyor.* Alan Sutton Publishing Ltd., Gloucestershire, U.K.
- Heinsdorf, M. 1997. Soil and nutritional studies in pine and pine-beech mixed stands on different sites in Brandenburg. *Beitr. Forstwirtsch. Landschaftsökol.* 31: 119–124.
- Heitz, R. 1999. *Umbau von Fichtenreinbeständen in naturnahe Mischwälder—Auswirkungen auf bodenchemischen Zustand und Bioelementhaushalt.* Dissertation, Forstwissenschaftliche Fakultät, Universität München, München, Germany.
- Heitz, R., and Rehfuess, K.-E. 1999. Reconversion of Norway spruce (*Picea abies* (L.) Karst.) stands into mixed forests: effects on soil properties and nutrient fluxes. *In* Management of mixed-species forest: silviculture and economics. *Edited by* A.F.M. Olsthoorn, H.H. Bartelink, J.J. Gardiner, H. Pretzsch, H.J. Hekhuis, and A. Franc. Institute for Forestry and Nature Research, Wageningen, the Netherlands. *IBN Sci. Contrib.* 15. pp. 37–45.
- Hendriks, C.M.A., and Bianchi, F.J. 1995. Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. *Neth. J. Agric. Sci.* 43: 321–331.
- Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* 7: 336–339.
- Hoffmann, F. 1923. Mischungen von Buchen mit Nadelholz, insbes. mit der Fichte und Tanne. *Allg. Forst Jagdztg.* 99: 273–281.
- Hooper, D.U., and Vitousek, P.M. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* 68: 121–149.
- Horst, W.J. 1995. Efficiency of soil-nutrient use in intercropping systems. *Institute Nationale de la Recherche Agronomique, Guadeloupe, West Indies.* pp. 197–211.
- Hultberg, H. 1985. Budgets of base cations, chloride, nitrogen, and sulphur in the acid Lake Gardsjön catchment, SW Sweden. *Ecol. Bull.* 37: 133–158.
- Joliffe, P.A. 1997. Are mixed populations of plant species more productive than pure stands. *Oikos*, 80: 595–602.
- Kaneko, N., and Salamanca, E.F. 1999. Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecol. Res.* 14: 131–138.
- Kaye, J.P., Resh, S.C., Kaye, M.W., and Chimner, R.A. 2000. Nutrient and carbon dynamics in a replacement series of *Eucalyptus* and *Albizia* trees. *Ecology*, 81: 3267–3273.
- Kelty, M.J. (Editor). 1992a. *The ecology of mixed species forests.* Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Kelty, M.J. (Editor). 1992b. Comparative productivity of monocultures and mixed species stands. *In* The ecology of mixed species forests. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 125–141.
- Kelty, M.J., and Cameron, I.R. 1995. Plot design for the analysis of species interactions in mixed stands. *Commonw. For. Rev.* 74: 322–332.
- Kern, K.G., Moll, W., and Braun, H.J. 1961. *Wurzeluntersuchungen in Rein- und Mischbeständen des Hochschwarzwaldes.* *Allg. Forst Jagdztg.* 132: 241–259.
- Kerr, G., Nixon, C.J., and Matthews, R.W. 1992. Silviculture and yield of mixed-species stands: the UK experience. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. *Br. Ecol. Soc. Spec. Publ.* 11. pp. 35–52.
- Khanna, P.K. 1997. Comparison of growth and nutrition of young monocultures and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.* 94: 105–113.
- Khanna, P.K. 1998. Nutrient cycling under mixed-species tree systems in Southeast Asia. *Agrofor. Syst.* 38: 99–120.
- Kienzler, M., Alban, D.H., and Perala, D.A. 1986. Soil invertebrate and microbial populations under three species on the same soil type. *USDA For. Serv. Res. Note* NC-337.
- Klemmedson, J.O. 1987. Influence of oak in pine forests of central Arizona on selected nutrients of forest floor and soil. *Soil Sci. Soc. Am. J.* 51: 1623–1628.
- Klemmedson, J.O. 1991. Oak influence on nutrient availability in pine forests of central Arizona. *Soil Sci. Soc. Am. J.* 55: 248–253.
- Köstler, J.N., Brückner, H., and Biebelriether, H. 1968. *Die Wurzeln der Waldbäume.* Verlag Paul Parey, Hamburg, Berlin.
- Lavelle, P. 1994. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *In* Transactions of the 15th World Congress on Soil Science. *Edited by* J.D. Etchevers, A. Aguilar, R. Nunez, G. Alcantar, and P. Sanchez. International Society of Soil Science and Mexican Society of Soil Science, Mexico City. Vol. 1. pp. 189–220.
- Lavery, J.M. 2000. *The influence of red alder in adjacent conifer stands: nutrient cycling and light transmission.* M.Sc. thesis, University of British Columbia, Vancouver, B.C.
- Leibundgut, H. 1984. *Die Waldpflege.* Verlag Paul Haupt, Bern, Stuttgart.
- Li, Z., Yang, Y., and Wu, Z. 1993. Root system of mixed stand of Chinese fir and homana. *Chin. J. Ecol.* 12: 20–24.
- Lovett, G.M. 1994. Atmospheric deposition of nutrients and pollutants in North America: an ecological perspective. *Ecol. Appl.* 4: 629–650.
- Lovett, G.M., and Lindberg, S.E. 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. *Can. J. For. Res.* 23: 1603–1616.
- Mackenthun, G. 1990. *Vergleichende Ökologische Untersuchung eines Fichten-Buchen-Mischbestandes und verschiedener Reinbestände in Westerhof, Harzvorland.* Diplomarbeit, Universität Göttingen, Göttingen, Germany.
- Malcolm, D.C., and Mason, W.L. 1999. Experimental mixtures of Scots pine and birch: 30 year effects on production, vegetation and soils. *In* Management of mixed-species forest: silviculture and economics. *Edited by* A.F.M. Olsthoorn, H.H. Bartelink, J.J. Gardiner, H. Pretzsch, H.J. Hekhuis, and A. Franc. Institute for Forestry and Nature Research, Wageningen, the Netherlands. *IBN Sci. Contrib.* 15. pp. 143–158.
- Manderscheid, B., and Matzner, E. 1995. Spatial and temporal variation of soil solution chemistry and ion fluxes through the soil in a mature Norway spruce stand. *Biochemistry*, 30: 99–114.

- Matzner, E., and Meiwes, K.J. 1994. Long-term development of element fluxes with bulk precipitation and throughfall in two German forests. *J. Environ. Qual.* **23**: 162–166.
- Mård, H. 1996. The influence of a birch shelter (*Betula* spp.) on the growth of young stands of *Picea abies*. *Scand. J. For. Res.* **11**: 343–350.
- McClagherty, C.A., Pastor, J., Aber, J.D., and Melillo, J.M. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, **66**: 266–275.
- McKay, H.M., and Malcolm, D.C. 1988. A comparison of the fine root component of a pure and mixed coniferous stand. *Can. J. For. Res.* **18**: 1416–1426.
- McTiernan, K.B.P., Ineson, P., and Hasted, P.A. 1997. Decomposition of tree litters in mixture. *Oikos*, **78**: 527–538.
- Mettin, C. 1986. Inwieweit ist Laubstreu eine ökologische und ökonomische Hilfe in Nadelholzbeständen? *Allg. Forstz.* **37**: 918–922.
- Migge, S., Maraun, M., Scheu, S., and Schaefer, M. 1998. The oribatid mite community (Acarina) of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. *Appl. Soil Biol.* **9**: 115–121.
- Morgan, J.L., Campbell, J.M., and Malcolm, D.C. 1992. Nitrogen relations of mixed-species stands on oligotrophic soils. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford, U.K. *Br. Ecol. Soc. Spec. Publ.* **11**. pp. 65–86.
- Neft, R., and Stangl, J. 1985. Charakterisierung des Ernährungszustandes der Fichte auf frischen, tiefgründigen Lehmen im Forstamt Schongau. Diplomarbeit, Forstwissenschaftliche Fakultät, Universität München, München, Germany.
- Nilsson, M., Wardle, D., and Dahlberg, A. 1999. Effects of plant litter species composition and diversity on the Boreal forest plant–soil system. *Oikos*, **86**: 16–26.
- Olsthoorn, A.F.M., Bartelink, H.H., Gardiner, J.J., Pretzsch, H., Hekhuis, H.J., and Franc, A. (Editors). 1999. Management of mixed-species forest: silviculture and economics. Institute for Forestry and Nature Research, Wageningen, the Netherlands. *IBN Sci. Contrib.* **15**.
- Ong, C.K., and Huxley, P. (Editors). 1996. Tree–crop interactions: a physiological approach. CAB International, Wallingford, U.K.
- Parrotta, J.A. 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *For. Ecol. Manage.* **124**: 45–77.
- Parrotta, J.A., Baker, D.D., and Fried, M. 1996. Changes in dinitrogen fixation in maturing stands of *Casuarina equisetifolia* and *Leucaena leucocephala*. *Can. J. For. Res.* **26**: 1684–1691.
- Pedersen, B. 1992. Throughfall chemistry of Sitka spruce stands as influenced by tree spacing. *Scand. J. For. Res.* **7**: 433–444.
- Prescott, C.E., Zabek, L.M., Staley, C.L., and Kabzems, R. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type and litter mixtures. *Can. J. For. Res.* **30**: 1742–1750.
- Pretzsch, H. 1992. Konzeption und Konstruktion von Wuchsmodellen für Rein- und Mischbestände. *Forstl. Forschungsber. München* **115**.
- Ranger, J., and Nys, C. 1994. The effect of spruce (*Picea abies* Karst) on soil development: an analytical and experimental approach. *Eur. J. Soil Sci.* **45**: 193–204.
- Rhoades, C. 1997. Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. *Agrofor. Syst.* **35**: 71–94.
- Rhoades, C., and Binkley, D. 1992. Spatial extent of impact of red alder on soil chemistry in adjacent conifer stands. *Can. J. For. Res.* **22**: 1434–1437.
- Robson, A.J., Neal, C., Ryland, G.P., and Harrow, M. 1994. Spatial variations in throughfall chemistry at the small plot scale. *J. Hydrol. (Amsterdam)*, **158**: 107–122.
- Rothe, A. 1997. Influence of tree species composition on rooting patterns, hydrology, elemental turnover, and growth in a mixed spruce–beech stand in Southern Germany (Höglwald). [In German with English summary.] *Forstl. Forschungsber. München* **163**.
- Rothe, A., and Kreutzer, K. 1998. Wechselwirkungen von Fichte und Buche im Mischbestand. *Allg. Forstz.* **15**: 784–787.
- Rothe, A., Kreutzer, K., and Küchenhoff, H. 2001a. Influence of tree species composition on soil and soil solution properties in two mixed spruce–beech stands with contrasting history in southern Germany. *Plant Soil*. In press.
- Rothe, A., Huber, C., Kreutzer, K., and Weis, W. 2001b. Deposition and soil leaching in stands of Norway spruce and European beech: results from the Höglwald in comparison with other European case studies. *Plant Soil*. In press.
- Rustad, L. 1994. Element dynamics along a decay continuum in a red spruce ecosystem in Maine, (U.S.A.). *Ecology*, **75**: 867–879.
- Rysavy, T., and Roloff, A. 1994. Ursachen der Vereschung in Mischbeständen und Vorschläge zu ihrer Vermeidung. *Forst Holz*, **49**: 392–395.
- Saetre, P. 1998a. Decomposition, microbial community structure, and earthworm effects along a birch–spruce soil gradient. *Ecology*, **79**: 834–846.
- Saetre, P. 1998b. Soil organisms, ground vegetation and ecosystem processes in mixed stands of Norway spruce and birch. *Acta Univ. Agric. Suec. Silvestria* **54**.
- Scott, N.A., and Binkley, D. 1997. Foliage litter quality and annual net mineralization: comparison across North American forest sites. *Oecologia*, **111**: 151–159.
- Shure, D.J., and Philipps, D.L. 1987. Litter fall patterns within different-sized disturbance patches in a southern Appalachian Mountain forest. *Am. Midl. Nat.* **118**: 348–357.
- Takahashi, T., Toda, H., and Haibara, K. 1999. Changes in soil chemical and physical characteristics in Japanese cypress (*Chamaecyparis obtusa* Endl.) stands by mixture of deciduous broad-leaved trees in the northern Kanto region of Japan. *J. For. Res.* **4**: 223–228.
- Thomas, W.A. 1968. Decomposition of loblolly pine needles with and without additions of dogwood leaves. *Ecology*, **49**: 568–571.
- Turner, D.P., and Franz, E.H. 1985. The influence of western hemlock and western red cedar on microbial numbers, nitrogen mineralization, and nitrification. *Plant Soil*, **88**: 259–267.
- Vandermeer, J. 1989. The ecology of intercropping. Cambridge University Press, Cambridge, U.K.
- Vogt, K.A., Vogt, D.J., Asbjorsen, H., and Dahlgren, R.A. 1995. Roots, nutrients and their relationship to spatial patterns. *Plant Soil*, **168–169**: 113–123.
- Vogt, K.A., Vogt, D.J., Palkiotto, P.A., Boon, P., O'Hara, J., and Asbjorsen, H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil*, **187**: 159–199.
- Vogt, D.A., Asbjorsen, H., Ercelawn, A., Montagnini, F., and Valdes, M. 1997. Roots and mycorrhizas in plantation ecosystems. *In* Management of soil, nutrients and water in tropical plantation forests. *Edited by* S.E.K. Nambiar and A.G. Brown. Australian Centre for International Agricultural Research, Canberra. *ACIAR Monogr. Ser.* **43**. pp. 247–296.
- Wardle, D.A., Bonner, K.I., and Nicholson, K.S. 1997. Biodiversity and plant litter: experimental evidence which does not support

- the view that enhanced species richness improves ecosystem function. *Oikos*, **79**: 247–258.
- Weber, G., Rehfuss, K.E., and Kreutzer, K. 1993. Über den Einfluss naturnaher Waldwirtschaft auf den chemischen Bodenzustand. *Allg. Forstz.* 2. pp. 68–71.
- Wiedemann, E. 1942. Der ungleichaltrige Fichten-Buchen-Mischbestand. *Mitt. Forstwirtsch. Forstwiss.* **13**: 1–81.
- Weidemann, G., and Schauer, J. 1986. Die Tierwelt, ihre Nahrungsbeziehungen und ihre Rolle. *In Ökosystemforschung Ergebnisse des Sollingprojektes. Edited by S.E.K. Nambiar and A.G. Brown.* Eugen Ulmer Verlag, Stuttgart, Germany. pp 179–266.
- Williams, B.L., and Alexander, C.E. 1991. Interactions of mixing litters from beneath Sitka spruce and Scots pine and the effects on microbial activity and N-mineralization. *Soil Biol. Biochem.* **23**: 71–75.
- Wilpert, K.V., and Mies, E. 1995. The influence of stand structure and tree species on mineral cycling. *In Nutrient uptake and cycling in forest ecosystems.* European Commission, Brussels. Off. Publ. 8.
- Wittich, W. 1961. Der Einfluss der Baumart auf den Bodenzustand. *Allg. Forstz.* 16. pp. 41–45.
- Wittkopf, W. 1995. Wurzelintensität im Fichten-Buchen-Mischbestand im Vergleich zum Reinbestand. Diplomarbeit, Forstwissenschaftliche Fakultät, Universität München, München, Germany.
- Yanai, R.D. 1992. Competitive interactions between Norway spruce and Scots pine at Gisburn Forest, North England. *Forestry*, **65**: 435–451.
- Young, A. 1997. *Agroforestry for soil management.* CAB International, Wallingford, U.K.
- Zinke, P.J. 1962. The pattern of individual forest trees on soil properties. *Ecology*, **43**: 130–133.
- Zou, X. 1993. Species effects on earthworm density in tropical tree plantations in Hawaii. *Biol. Fertil. Soils*, **15**: 35–38.
- Zou, X., Binkley, D., and Caldwell, B.A. 1995. Effects of dinitrogen-fixing trees on phosphorus biogeochemical cycling in contrasting forests. *Soil Sci. Soc. Am. J.* **59**: 1452–1458.