Title: **Growth Performance, Wind-throw, Insects - Meta-Analyses of Parameters Influencing Performance of Mixed Species Stands in Boreal and Northern Temperate Biomes**

Authors: Verena C. Griess[a*] (verena.griess@forst.wzw.tum.de),
Thomas Knoke[a] (knoke@forst.wzw.tum.de)

*Corresponding author. Tel.: +49 8161 71 4699; Fax: +49 8161 71 4545

Affiliation: [a]Institute of Forest Management, Center of Life and Food Sciences Weihenstephan, Technische Universität München

Address: Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

Abstract

Stand structure is a key attribute of forest ecosystems. Mixed tree plantations are widely felt to be the appropriate option for providing a broad range of goods, environmental services, and to reduce susceptibility to natural hazards. However, the debate continues whether mixed plantations can achieve greater financial return than monocultures can. In this study, mixed-species stands of conifers and hardwood species were analyzed in consideration of economically relevant factors. Growth performance and resistance to hazards and pests are widely noted in the literature and are of general economic interest. Thus meta-analyses of relevant studies were conducted to test the following hypotheses:

> *($H_{0,1}$) Mixing tree species has no significant influence on growth performance or resistance against hazards and pests;*

and if refuted

> *($H_{0,2}$) Mixing tree species causes mainly negative effects on growth performance and resistance against hazards and pests.*

A positive impact of mixing tree species was proven for resistance against windthrow and pests. The meta-analysis on growth performance just as well indicates a positive effect of mixing tree species.

Overall, these positive results underscore the need for a large number of additional studies to examine different silvicultural systems to develop optimal management prescriptions to benefit from positive interactions.

Keywords

Meta-analysis; mixed-species stand; ecological interdependence; ecosystem resistance; growth

Introduction

Until the end of the 18th century, Central European deciduous forests were degraded. Although foresters as well as scientists have been discussing whether or not pure or mixed-species stands would be the most advantageous planting scheme (Hartig, 1791; Cotta, 1828; Gayer, 1886), the rehabilitation of such forests led to monocultures in many cases. First, excellent growth performance allowed single-species stands to appear to be advantageous for all intents and purposes. Also, the lack of success of mixed-species management, that was often self-inflicted by silviculturists, was used as justification for the preference for single-species stands (Puettmann *et al.* 2009). Industry and government promoted fast growing monoculture plantations to satisfy a growing demand for industrial wood products (Cossalter & Pye-Smith, 2003). In many countries, this is still the case.

Mono-species stands require special care and management however, especially in terms of density control to keep individual tree vigor high (Kelty, 2006). Otherwise, mono-species stands appear to be more susceptible to natural hazards. Frequent windfalls and the European bark-beetle outbreak that has persisted now for over a decade, underline this susceptibility. These problems become more and more evident as climate conditions change. In the 20th century, the average temperature in central Europe increased by almost one degree Celsius (Badeck *et al.*, 2004). The years 1995-2006 were the warmest since temperature recording began, with the vegetation period increasing by eleven days (Biermayer, 2008; Walther *et al.*, 2002). Summer precipitation has declined, while increasing over the winter months. All these factors favor extreme weather incidents as well as insect calamities and other natural hazards (Bässler *et al.* 2010).

Foresters and governments have reacted to this situation, as evidenced by increasing calls for growing mixed-species stands. Still, only a weak understanding of the complex structure and dynamics of these mixed forests exists. The question whether or not multi-species forests can cope with the upcoming challenges gains importance (Puettmann *et al.*, 2009). Intuitively we would expect these mixtures to have advantages from the perspective of non-market values (recreation, biodiversity etc.). But we can also find advantages that lead to financial consequences (e.g. effects of mixing on yield, Knoke *et al.*, 2008). Possible ecological interrelation of species is particularly important when natural assets are estimated. Assuming species in a mixed stand are independent, only the combined risk is not proportional to changes in fractions of species. Yet the average economic performance changes proportionally. In this case, diversification has analogies to that of financial assets (Koellner & Schmitz, 2006). But if species interact because of ecological interdependence the direct analogy to financial assets dissolves. Mixed-species stands can thus not be treated as a summation of the corresponding monocultures, a fact that makes them highly interesting as objects for financial analysis.

Given the above, the following research question arises: In what ways will a stand be affected by species interaction, and how are they economically relevant? To ascertain this, we will have to take a closer look at the effects that have recently shown an impact on financial risk and return (Knoke & Seifert, 2008).

1) Growth performance, measured as MAI in volume over entire measurement period.

2) Stand resistance to hazards and pests (possibly increased due to higher single tree stability and reduced susceptibility to pests).

Quantifying these effects also allows for a ranking of the financial importance of different ecological information. This would link ecological and economic research in order to prioritize ecological investigations from a management perspective.

Another aspect that is often named when discussing species mixtures is a potential decline in timber quality in the border zones, where species directly interact (Röhrig *et al.*, 2006). These effects that would certainly influence economics significantly are however strongly determined by the specific type of mixture (Knoke & Seifert, 2008). As the aggregation of tree species in mixed stands seems more important for the impact of mixture than mixture itself, the aspect of changes in timber quality was not estimated within this study.

However, studies which quantify potential impacts are hard to find. Furthermore, most known studies relate to growth performance and disregard the fact, that mixture can lead to higher stability and risk apportionment (Pretzsch & Schütze, 2009). Hence it is still an open question whether or not integrating the ecological reality in models of mixed forests would change the results substantially. A first attempt to estimate the consequences of interdependent tree species, mixed at the stand level, was undertaken by Knoke & Seifert (2008). This paper emphasized the importance of stand resistance and timber quality in mixed stands according to financial parameters. A narrative review on the effects of admixing broadleaves to coniferous forests in terms of yield, ecological stability and economics also made obvious the necessity of improved bioeconomic modeling (Knoke *et al.*, 2008) considering the importance of species interaction (Knoke & Seifert, 2008). With improved bioeconomic modeling in forest science, the field of "silvicultural economics" (Knoke, 2010) may now emerge.

Materials and methods

Currently, there is still no universally accepted definition of "mixed-forest". Johansson (2003) found that in Europe several different definitions of mixed-species stands exist. In Norway and Finland for example, a stand is called mixed forest if 20% of its basal area is made up of another species, mostly broadleaves. The proportions vary in other countries. In Sweden it is 30%, in Italy only 10% and so on. Colloquially, a mixed-species stand is understood as a mixed stand of conifers and broadleaved species. For the purpose of this paper, a mixed stand is defined as a stand of trees with two or more species comprising the usable volume following a definition by Burkhart & Tham (1992). The share of the least abundant species must cover at least 10% of the total basal area. A comparable definition has first been proclaimed by Gayer (1886), and was also applied for the BWI², Germanys second Federal Forest Inventory, carried out in 2002. Burschel & Huss (2003) described several types of planting patterns for mixed-species stands that have been used most frequently in Europe. This classification of the areal composition also plays an important role as the intensity of the mixture is affected by the structure of a stand. A mixture of different species in large blocks, for instance, shows more or less the ecological characteristics of a pure stand. Ecological interdependence in such a mixture only occurs within the contact zones of the different species. This study focuses on more intimate mixtures such as groups or rows as common in international plantation forestry (Nichols *et al*., 2006).

To quantify growth performance and resistance of mixed-species stands, three meta-analyses were performed, following a comparable approach on tropical plantations by Piotto (2008). This approach allows a straightforward analysis of species composition and growth respective to relative total yields. Furthermore analyzing mixed stands resistance against hazards and pests implies an enlargement of Piotto´s (2008) appraisal which was limited to tree growth.

In contrast to Piotto (2008), who focused on tropical and temperate ecosystems, the review at hand is placing emphasis on commercial species of the boreal and temperate biomes. Not only do boreal and temperate forests of Europe and North America cover the largest area compared to other forest types worldwide (Bailey, 2009), but also, growing mixed forests in the boreal and temperate zone will become increasingly viable under changing climate conditions (Eggers *et al.*, 2008; Garcia-Gonzalo *et al.*, 2007). The following hypotheses are to be tested:

(1) Interdependence of tree species has no significant influence on growth performance or resistance against hazards and pests; and if refuted

(2) Interdependence of tree species causes mainly negative effects on growth performance and resistance against hazards and pests.

Meta-analysis

For each meta-analysis an extensive literature search through the database ISI Web of Knowledge and the scientific search engines Google scholar and Scirus was conducted, using various combinations of specific sets of keywords for each factor, mainly: mixed, species; forest, growth, species interactions, windthrow, pests, resistance, temperate, boreal, intercropping, hazard as well as combinations of the above. Literature providing information on both mixed- and mono-species stands conjointly delivered the basis for each meta-analysis. To perform the analysis for each of the factors (growth performance, resistance against hazards and pests) the results of each experiment respectively had to be distilled in the form of a measure of the magnitude for the effect in that experiment. This magnitude is called the "effect size" and has to be distilled out of the results of each experiment in the form of a measure of the magnitude of the effect in each specific experiment (XiangDong *et al.*, 2007). In the present study the effect size summarizes the magnitude of the response of growth performance to species interaction for the first analysis, and the magnitude of the response of resistance against hazards and pests due to species interaction for the second analysis. There are various indices to display the effect size. For the study at hand "Hedges' d index", or standardized mean difference is used. It is calculated as:

$$d = \left[\frac{M_E - M_C}{SD} \right] J$$

Where M_E is the mean of the experimental group, M_C is the mean of the control group, SD is the pooled standard deviation, and J is a correction factor (Borenstein *et al.*, 2009). J is needed to avert the production of too large estimates that occur especially with small samples. It is adapted from Gurevitch & Hedges (2001) and calculated as:

$$J = 1 - \left[\frac{3}{4(N_E + N_C - 2) - 1} \right]$$

The pooled standard deviation SD can be calculated from the standard deviations of the two groups "experimental group" and "control group". It is just as well adapted from Gurevitch & Hedges (2001) and calculated as:

$$SD = \sqrt{\frac{(N_E - 1)(SD_E)^2 + (N_C - 1)(SD_C)^2}{N_E + N_C - 2}}$$

Where N_E is the sample size of the treatment, N_C the sample size of the control.

The experimental effect is indicated by the effect size d. If d is not significantly different from zero no experimental effect is indicated (Cohen, 1988). Values above 0 indicate that the experiment had a positive effect on the variable; values below 0 indicate a negative effect. According to Cohen (1988), effect sizes of 0.2, 0.5 and 0.8 indicate small, medium and large effect sizes. However, it has to be mentioned that in new areas of research inquiry, effect sizes are likely to be small. This is because the phenomena under study are typically not under good experimental or measurement control or both (Cohen, 1988).

The variance around d is calculated with standard methods, and used to determine weighted average effects across studies and the confidence intervals around those effects (Rustad *et al.*, 2001). Following the calculation of d, the variance in the effect v has to be estimated. It is a measure for the dispersion of the indicator *d* for each study and is calculated using the equation below:

$$v = \left[\frac{N_E + N_C}{N_E N_C} \right] + \left[\frac{d^2}{2(N_E + N_C)} \right]$$

Using the variance v the weighting factor w can be calculated. It allows for provision of the sample size of each study.

$$w = \frac{1}{v}$$

In a last step, the studies were combined to get the cumulated effect size d+, and its variance.

$$d^{+} = \frac{\sum wd}{\sum w} \quad \text{and} \quad s^{2}(d^{+}) = \frac{1}{\sum w}$$

Using the calculations of the cumulated effect size *d+* and its variance *s^2(d+)*, it is tested whether the estimated effect size is significantly different from zero using a confidence interval of 95%. If the region between the upper and lower bounds did not include zero, the null hypothesis of no effect is rejected.

Results

The results obtained by carrying out meta-analysis on growth performance, resistance against windthrow and resistance against pests in mixed-species stands are furthermore displayed in Fig. 1 shown below in form of a box-whisker plot.

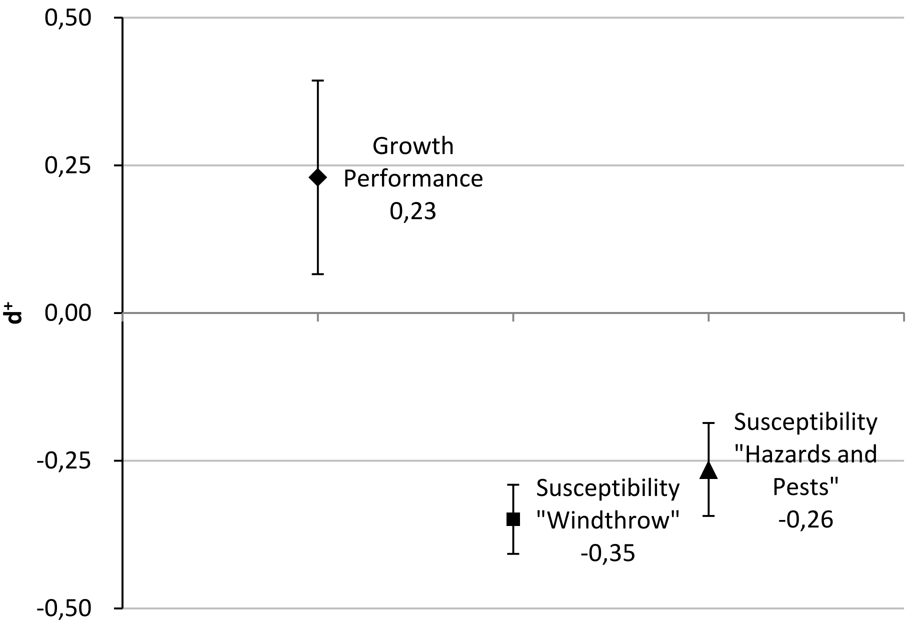

Fig. 1: Cumulated effect size d^+ and 95% CI for mixed-species stands in comparison with mono-species stands referring to growth performance, resistance against windthrow and resistance against pests.

The cumulated effect size for the analysis of growth performance in mixed stands compared to pure stands is d+=0.23. Confidence limits are 0.07 and 0.39. Studies used in the analysis on growth performance in mixed stands cover a wide diversity of species, with a total of 12 tree species (Table 4). Of the seven studies included in the analysis, three showed positive effects and four showed negative effects of mixing tree species on growth performance, as indicated in the column titled d^+ of

Table 1.

All studies were analyzed together in order to test hypothesis 1 and 2. As displayed in Fig. 1, interdependence in mixed-species stands did show positive effect on growth performance in comparison to single-species stands.

Table 1: Results of the single analysis on growth performance

Growth performance	∑ w	∑ wd	d^+	$s^2(d^+)$
Amoroso & Turnblom (2006)	8,89	-0,99	-0,11	
Brown (1992)	32,90	13,28	0,40	
Chen *et al*. (2003)	5,40	-1,41	-0,26	
Erickson *et al.* (2009)	8,12	-4,67	-0,58	
Gobakken & Naesset (2002)	0,95	0,63	0,66	
Johansson (2003)	0,92	-0,75	-0,81	
Kennel (1965)	17,65	-0,57	-0,03	
Pretzsch & Schütze (2009)	74,21	28,72	0,39	
Summe	***149,04***	***34,24***	***0,23***	***0,0067***

Studies used for the analysis on windthrow in mixed cover the principal tree species planted in Central Europe (

Source	Species	Age (years)	Location	Experimental design
Amoroso & Turnblom (2006)	Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)	12	Olympic Peninsula, Washington, USA	Two species mixture
Brown (1992)	Norway spruce (*Picea abies* (L.) Karst.) Sessile oak (*Quercus petraea*) Common alder (*Alnus glutinosa*) Scots pine (*Pinus sylvestris* L.)	4-26	North-West, Great Britain	6 two species mixtures
Chen *et al.* (2003)	Western red cedar (*Thuja plicata* Donn. ex D. Don) Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) Western larch (*Larix occidentalis* Nutt.) Black spruce (*Picea mariana* (Mill.) BSP)	55 55-62 69-83 68-80 87	British Columbia and Alberta, Canada	3 two species mixtures a: Hemlock – Red Ceda b: Pine – Larch c: Pine – Spruce
Erickson *et al*. (2009)	Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) Western white pine (*Pinus monticola* Dougl. Ex. D. Don)	10-20 10-20	Southern Washington State, USA	Two species mixtures
Gobakken & Naesset (2002)	Norway spruce (*Picea abies* (L.) Karst.) Birch (*Betula pendula* Roth *B. pubescens* Ehrh.)	7-23	Eastern and southern counties, Norway	Two species mixture
Johansson (2003)	Norway spruce (*Picea abies* (L.) Karst.) Birch (*Betula pendula* Roth *B. pubescens* Ehrh.)	35-37	Sweden	Two species mixture
Kennel (1965)	Norway spruce (*Picea abies* (L.) Karst.) Beech (*Fagus sylvatica*)	76-83	Südharz and Bayrischer Wald, Germany	Two species mixture
Légaré *et al.* (2004)	Black spruce (*Picea mariana*) Trembling aspen (*Populus tremuloides* Michx.)	23-75	Abitibi–Témiscamingue, NW Quebec, Canada	Two species mixture
Pretzsch & Schütze (2009)	Norway spruce (*Picea abies* (L.) Karst.) Beech (*Fagus sylvatica*)	37-155	South Bavaria, Germany	Two species mixture

*** the first number represents the proportion of the first species for each study. In most cases studies contain analyses of several stands with varying speci**

Table 5). All studies were analyzed together in order to test hypothesis 1 and 2. The results obtained from analyzing the single studies are displayed in Table 2.

Table 2: Results of the single analysis on resistance against windthrow

Resistance against windthrow	$\sum w$	$\sum wd$	d^+	$s^2(d^+)$
Heupel & Block (1991)	282,60	-161,57	-0,57	
König (1995)	49,88	-7,04	-0,14	
Rau (1995)	99,18	-24,54	-0,25	
Schmid-Haas & Bachofen (1991)	141,32	-96,27	-0,68	
Wangler (1974)	495,42	-99,76	-0,20	
Winterhoff (1995)	99,51	-18,55	-0,19	
Zindel (1991)	148,52	-40,07	-0,27	
Total	***1167,90***	***-407,74***	***-0,35***	***0,0009***

As displayed in Fig. 1, an effect on resistance of mixed-species stands against windthrow in comparison to single-species stands does exist. The cumulated effect size is d+=-0.35 with confidence limits of -0.29 and -0.40. The given analogies in the studies used are mirrored in the confidence limits that have been computed. The CI for resistance against windthrow shows the smallest dissemination of the three analyses carried out. Confidence limits do not include 0; therefore for windthrow the 0-hypothesis of no effect can be refuted. As single-species stands were used as control and mixed stands as experimental group within the analysis of windthrow, results below zero indicate lesser damage. The shown effect clearly indicates a positive effect of mixing tree species on resistance against windthrow. The 0-hypothesis of mainly negative effects of mixing tree species on resistance against windthrow can therefore be refuted.

Regarding the effects of mixing tree species on resistance against pests, of the five studies included in the analysis, three showed negative effects on resistance, as indicated in

Table 6. The detailed results obtained by analyzing all single studies are displayed in Table 3.

Table 3: Results of the single analysis on resistance against pests

Resistance against pests	$\sum w$	$\sum wd$	d^+	$s^2(d^+)$
MacLean (1980)	129,29	-67,91	-0,53	
Moore *et al*.(1991)	149,51	18,07	0,12	
Vehviläinen et al. (2006)	150	-0,61	-0,004	
Bergeron *et al.* (1995)	147,91	33,67	0,23	
Su *et al.* (1996)	148,54	-38,98	-0,26	
Total	***644,73***	***-170,75***	***-0,26***	***0,0016***

The five studies were analyzed together in order to test hypothesis 1 and 2. As displayed in Fig. 1, an effect on resistance of mixed-species stands against pests in comparison to single-species stands does exist. The cumulated effect size is d+=-0.26 with confidence limits of -0.19 and -0.34 (Fig. 1). Confidence limits do not include 0 therefore the 0-hypothesis of no effect can be refuted. The shown results also clearly indicate a positive effect of mixing tree species on resistance against pests. The 0-hypothesis of mainly negative effects can therefore also be refuted.

Table 4: Studies and species used for the meta-analysis on growth performance

Source	Species	Age (years)	Location	Experimental design	Intensity of mixture (Basal area in %, unless indicated differently)*	Effect
Amoroso & Turnblom (2006)	Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)	12	Olympic Peninsula, Washington, USA	Two species mixture	50 / 50	(-)
Brown (1992)	Norway spruce (*Picea abies* (L.) Karst.) Sessile oak (*Quercus petraea*) Common alder (*Alnus glutinosa*) Scots pine (*Pinus sylvestris* L.)	4-26	North-West, Great Britain	6 two species mixtures	50 / 50	(+)
Chen *et al.* (2003)	Western red cedar (*Thuja plicata* Donn. ex D. Don) Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) Western larch (*Larix occidentalis* Nutt.) Black spruce (*Picea mariana* (Mill.) BSP)	55 55-62 69-83 68-80 87	British Columbia and Alberta, Canada	3 two species mixtures a: Hemlock – Red Cedar b: Pine – Larch c: Pine – Spruce	a + b: stands with >20% difference in basal area between species considered mixed. c: stands with 15-40% Spruce considered mixed.	(-)
Erickson *et al*. (2009)	Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) Western white pine (*Pinus monticola* Dougl. Ex. D. Don)	10-20 10-20	Southern Washington State, USA	Two species mixtures	50 / 50	(-)
Gobakken & Naesset (2002)	Norway spruce (*Picea abies* (L.) Karst.) Birch (*Betula pendula* Roth *B. pubescens* Ehrh.)	7-23	Eastern and southern counties, Norway	Two species mixture	Number of trees: ≥80% species 1; ≥10% species 2	(+)
Johansson (2003)	Norway spruce (*Picea abies* (L.) Karst.) Birch (*Betula pendula* Roth *B. pubescens* Ehrh.)	35-37	Sweden	Two species mixture	70 / 30	(-)
Kennel (1965)	Norway spruce (*Picea abies* (L.) Karst.) Beech (*Fagus sylvatica*)	76-83	Südharz and Bayrischer Wald, Germany	Two species mixture	32-50 / 50-68	(-)
Légaré *et al.* (2004)	Black spruce (*Picea mariana*) Trembling aspen (*Populus tremuloides* Michx.)	23-75	Abitibi–Témiscamingue, NW Quebec, Canada	Two species mixture	74 / 26	(-)
Pretzsch & Schütze (2009)	Norway spruce (*Picea abies* (L.) Karst.) Beech (*Fagus sylvatica*)	37-155	South Bavaria, Germany	Two species mixture	15-89 / 16-36	(+)

*** the first number represents the proportion of the first species for each study. In most cases studies contain analyses of several stands with varying species proportions.**

255 **Table 5: Studies and species used for the meta-analysis on resistance against windthrow (according to Lüpke & Spellmann (1997))**

Source	Species	Age (years)	Location	Aspects of the appraisal	Intensity of mixture (Basal area in %, unless indicated differently)*	Effect
Heupel & Block (1991)	Norway spruce (*Picea abies* (L.) Karst.) Beech *(Fagus sylvatica)*	>60	Hunsrück/ Rhineland-Palatinate/ Germany	Damaged area in % of the total area	≤85 / ≥15	(+)
König (1995)	Norway spruce (*Picea abies* (L.) Karst.) Beech *(Fagus sylvatica)*	74 145	Eichstätt/ Bavaria/ Germany	Damaged area in % of the total area	n.a. (at least 10 percent Beech)	(+)
Rau (1995)	Norway spruce (*Picea abies* (L.) Karst.) Beech *(Fagus sylvatica)*	106-149	Virngrund/ Baden-Württemberg/ German	Damaged area in % of the total area	50-90 / 10-50	(+)
Schmid-Haas & Bachofen (1991)	Norway spruce (*Picea abies* (L.) Karst.) Fir *(Abies alba)* Beech *(Fagus sylvatica)*		Switzerland	Damaged area in % of the total area	Three groups with a proportion of coniferous species of 0-10, 11-50 and 51-90 percent.	(+)
Wangler (1974)	Norway spruce (*Picea abies* (L.) Karst.) Beech *(Fagus sylvatica)* Fir *(Abies alba)* Pine *(Pinus sylvestris)*	>60	Baden-Württemberg/ Germany	Damaged area in % of the total area	n.a. (at least 10 percent Beech)	(+)
Winterhoff *et al.* (1995)	Norway spruce (*Picea abies* (L.) Karst.) Beech *(Fagus sylvatica)*	n.a.	Hesse/ Germany	Damaged volume in % of the total volume	≤90 / ≥10	(+)
Zindel (1991)	Norway spruce (*Picea abies* (L.) Karst.) Beech *(Fagus sylvatica)*	80-109	Hesse/ Germany	Damaged area in % of the total area	10-90 / 10-90	(+)

*** the first number represents the proportion of the first species for each study. In most cases studies contain analyses of several stands with varying species proportions.**

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257 **Table 6: Studies and species contained analysed for the resistance against pests**

Source	Species	Type of pest	Location	Aspects of the appraisal	Intensity of mixture (Number of trees in %, unless indicated differently)*	Effect
Bergeron *et al*. (1995)	Balsam fir (*Abies balsamea* (L.) Mill.)	Spruce budworm (*Choristoneura fumiferana* (Clem.))	Northwestern Quebec, Canada	Stem mortality in %	Mixed decidous: 51-75% hardwoods and mixed coniferous with 51-75% conifers.	(+)
MacLean (1980)	Red Spruce (*Picea rubens* Sarg.) White spruce (*P. glauca* (Moench) Voss) Black Spruce (*P. mariana* (Mill.) B.S.P.) Balsam fir (*Abies balsamea* (L.) Mill.)	Spruce budworm (*Choristoneura fumiferana* (Clem.))	Quebec and New Brunswick, Canada	Stem mortality in %	Mixed stand with ≥20% hardwood	(-)
Moore *et al.* (1991)	Oak (*Quercus petraea* (Mattuschka) Liebl.) Alder (*Alnus glutinosa* (L.) Gaertn.) Norway spruce (*Picea abies* (L.) Karst.) Scots Pine (*Pinus sylvestris* L.)	*Phyllobius argentatus, Tuberculoides neglectus, Eurhadina pulchella, E. concinna, Phyllonorycter spp.*	Gisburn Forest, Lancashire, Great Britain	Leaf area damaged in % of total leaf area	50 / 50	(+)
Su *et al*. (1996)	Balsam fir (*Abies balsamea* (L.) Mill.) Various hardwood species	Spruce budworm (*Choristoneura fumiferana* (Clem.))	New Brunswick, Canada	Relationship between Balsam fir defoliation and hardwood content [%]	Hardwood proportion 25%, 50% and 75%	(-)
Vehviläinen et al. (2006)	Norway spruce (*Picea abies* (L.) Karst.) Scots pine (*Pinus sylvestris* L.) Silver birch (*Betula pendula* Roth)	*Insect defoliators, leaf rollers, gall mites, aphids*	Ähtäri and Jokioinen, Finnland; Östad, Sweden	Percentage of leaves with defoliators present	50 / 50 and 25 / 75	(-)

*** the first number represents the proportion of the first species for each study. In most cases studies contain analyses of several stands with varying species proportions.**

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Discussion

"Certain tree species will have higher yield if grown in mixed stands rather than pure stands!" This promising assumption led to an extensive search for the "mixed-species effect", which can be defined as the effect of interrelations between tree species in a stand (Jonsson, 1962).

Bachmann (2005) outlined how growth of a mixed-species stand could outperform the growth of a single-species stand: Mixed-species stands can fully utilize radiation caused by varying need of light. By accessing different rooting depths and horizons, available nutrients can be fully used. In addition, different species neighbors – for example N fixing trees – can have positive effects on neighboring trees. Erskine *et al*. (2006) as well as Piotto (2008) support these ideas and verify that significant productivity gains could be made if multi-species plantations were more broadly pursued. Species rich plantations are able to more efficiently access and utilize limiting resources if they contain species with a diverse array of ecological attributes (Kelty, 1992). In reverse it must be stated that using species with similar ecological niches in the mixture won't produce a greater yield (Chen *et al*., 2003). In such a case, even a declining yield can occur because of antagonistic effects.

Keeping in mind that improved growth performance is economically desirable, the evaluation of growth performance in mixed-species stands has become a research field of great importance. Larson (1992) described tree growth as gene-environmental interactions. The large genetic variability of mixed-species stands therefore must result in greater variation in growth rates among individual trees in a stand. In addition, because the "environment" of each tree is greatly modified by the neighboring individuals there is greater environmental variation within mixed-species stands. Compared to mono-species stands, in mixed-species stands the possibilities for divergence from general growth development are very wide.

Summarizing the above conclusions, we expected mixed-species stands composed of species with different ecological niches to have a higher net primary production, translating into larger relative wood yields (Brown, 1992) compared to mono-species stands (Binkley *et al*., 2003; Forrester *et al*., 2006). But to definitely answer the question whether or not mixing tree species will lead to higher yields we had to quantify growth performance in both mixed- and single-species stands and compare productivity (Pretzsch, 2005). Information on comparative yields of pure stands and mixed-species stands was needed. Chen *et al.* (2003) stated that ideally, studies on the productivity of mixed-species stands have to be conducted by growing even-aged single- and mixed-species stands under equal conditions. Therefore, to gain the desired information, the results of research that has been carried out on existing stands with corresponding qualities were taken into account (e.g., Brown 1992; Burkhart & Tham 1992; Schläpfer & Schmid 1999; MacPherson *et al.* 2001; Pretzsch & Schütze, 2009) within this study. The total number of studies providing all information necessary is very small. Only few studies were accomplished aiming at a direct comparison of mixed- and mono-species stands. Hence it has to be pointed out that the used method is based on observations within studies rather than studies itself. Therefore the results gained are based on data taken on 26 sites in the case of growth performance, 27 sites in the case of wind throw and 21 sites regarding resistance against pests, which is a good data base. All details are provided in the appendix.

The results on growth performance are less clear than the results on resistance. The confidence limits of the standardized difference comprise a large range compared to those in the cases of resistance. Therefore, growth performance has thus to be integrated into bioeconomic models with great care.

For the analysis on resistance against hazards and pests research is likewise scarce. These two factors are crucial for economic evaluation of a forest stand, as forest stands are exposed to numerous risks during their long lifetime. Risks are either abiotic - meaning physical hazards like storms, fire, snow break, mechanical damage, acidification of the soil etc. - or biotic - meaning damage caused by herbivores, fungal pathogens or others. These hazards can even be related to each other in some way, as the ecological resilience of the ecosystem forest that is highly compatible with complexity science, shows (Puettmann *et al.*, 2009). Every single risk a stand is exposed to influences economic outcomes.

The paper at hand focused on the two most important disturbances for forests in the boreal and temperate zones: windthrow and pest damage (Brassel *et al*., 1999; Burschel & Huss, 2003; Schelhaas *et al*., 2003; Ministerkonferenz zum Schutz der Wälder in Europa, 2007, Albrecht *et al.* 2010).

Windthrow has always been an important risk factor in forest management, especially in the temperate and boreal zone. No later than in 1886 Karl Gayer pointed out, that the occurrence of windthrow is directly related to the prolongation of mono-species stands. Bosshard (1967), who evaluated storm damage in Switzerland, confirmed Gayers (1886) statement by proving that no other attributes have higher influence on susceptibility to storm damage than the proportion of spruce in a stand. The importance of windthrow at least in Central Europe is affirmed by a series of severe storm events during the last decades, interspersed with numerous smaller events (Schelhaas *et al*., 2003). Within the literature found, one of the most significant predisposing factors was, once more, the mixture. An admixture of 10% or more broadleaved tree species or wind-firm conifers, such as Douglas fir, significantly reduced the vulnerability of spruce stands by a factor of more than three (Schütz, *et al.*, 2006). Generally and regardless of the structure of the stand, the vulnerability to wind damage increases with tree height (indirectly with the age of a stand) (Watt, 1992). For tree heights of over 29m the probability of storm damage increases more than 50% (Lüpke & Spellmann, 1997). Therefore the vulnerability of conifers to wind damage increases more rapidly than that of broadleaves (Quine & Miller, 1991), as coniferous trees gain height quicker. Schmid-Haas & Bachofen (1991) compared windthrow occurrences over several stand types. They found a twice greater resistance of mixed stands (10-50% broadleaved) vs. pure stands (100% conifers). Schütz *et al.* (2006) assessed the form and magnitude of storm damage and stand disclosure patterns in pure stands of spruce (*Picea abies* L.) and beech (*Fagus sylvatica* L.) after a major storm in 1999. One of the most significant predisposing factors was, once more, the mixture.

Furthermore, species themselves are a major predictor in many empirical storm damage studies (Albrecht *et al.*, 2010). This means that a decrease of the amount of damage that is reported in all studies in mixed stands might occur because the stands are at least partly composed of more stable tree species than the pure stands (Lüpke & Spellmann, 1999). This is certainly the case for many studies comparing highly risk-prone pure stands of Norway spruce to mixed stands including spruce and deciduous trees such as beech, but only König *et al.* (1995) were able to isolate influencing parameters other than mixture.

That mixed-species stands show a higher resistance against windthrow is clear. Yet, all information on resistance against windthrow had to be transformed into a mode of direct comparability, as possible by taking out a meta-analysis on according studies, where the number of available studies delivering the needed data once again turned out to be the limiting factor. However, confidence limits comprise the smallest range in the case of resistance against windthrow.

Regarding pest damages under climate change scenarios, bark beetle damage is predicted to increase up to more than 200% in terms of timber volume losses (Seidl *et al*., 2008) in Central Europe. This prediction underlines the importance of resistance against pests. Jactel *et al.* (2005) quantitatively confirmed that mixed stands suffer less pest damage or have smaller pest populations than single-species stands in a meta-analysis. In their approach, only five studies from boreal forests were used and none of these studies were experimental, which was criticized by Koricheva *et al*. (2006). The paper at hand therefore expanded the approach by Jactel *et al*. (2005). Another meta-analysis was carried out by Jactel & Brockerhoff (2007) to gain information on the resistance of mixed-species stands against insects. This analysis was based on a variety of over 100 studies worldwide that compared herbivory by defoliators and other insects in single-species and mixed forests. A significant reduction of herbivory was proven for oligophagous insects such as bark beetles in diverse forests.

Accomplishing the meta-analysis, an overall positive impact of mixing tree species was proven for resistance against windthrow and pests. The conducted meta-analysis on growth performance did indicate a clear positive effect - only if the latest study (Pretzsch & Schütze, 2009) was included. The result of the meta-analysis on growth performance indeed shows a positive trend leaving out the study by Pretzsch & Schütze (2009), but confidence limits then include 0. This result may lead to the impression that the data basis in general is too weak to provide sound information. But the method allows us to include studies weighted regarding the number of stands or area compared within them. The study in question by Pretzsch & Schütze (2009) delivers by far the largest dataset of all studies found (see Detailed data used for the meta-analysis on growth performance in appendix). Still the positive effect on growth performance by mixing tree species has to be interpreted quite carefully.

Furthermore it has to be kept in mind that benefits obtained by an increase in growth performance have to be put into perspective by a possible increase in costs for stand establishment or the conversion of an existing stand. At least in Germany increased costs for establishment of mixed species stands are buffered by governmental grants for corresponding silvicultural practices. The yield increase necessary to offset additional costs associated with mixed-species plantings has been estimated by Nichols *et al.* (2006) who postulate ranges between 0.2% and 11% necessary for various silvicultural systems employing mixed species stands.

The absence of a larger number of adequate studies in literature (Rothe & Binkley, 2001) as well as the extreme diversity of possible influences and interactions of the various species used in each mixture (Légaré *et al.* 2004) demonstrate the importance of further research to be carried out. Furthermore the inclusion of such a wide variety of individual studies based on forest stands growing under very specific terms and conditions limits the potential application of the delivered results. Still the study at hand aims at prompting a further study in the field now opened up for additional research, especially as close-to-nature forestry is becoming a topic of major concern an so are mixed-species stands.

Meta-analysis – useful method or shenanigan?

Meta-analysis as a method itself has been criticized. Critics may argue that narrative reviews provide better solutions (Borenstein *et al*., 2009). Bailar (1997) gives general conspectus of numerous critiques. First, results of meta-analysis are said to be of little validity as all studies found, irrespective of their methodological quality, can be used (Liberati, 1991). To avoid an impairment of the meta-analysis for the paper at hand, only studies of authoritative results were used. Reliability and appropriateness is warranted by choosing only studies that were published in reviewed journals or magazines and excluding grey literature. Furthermore, meta-analysis is criticized because of a possible appearance of a study bias (Spector, 1991). This occurs quite often if only studies that support a desired or supposed hypothesis, or studies offering significant results are taken into account, which leads to a bias of the result of the meta-analysis itself (Egger, 1998). Possible publication biases are in fact a problem for meta-analysis. However, the idea that equivalent problems do not occur in narrative reviews is wrong (Borenstein *et al*., 2009). In the study at hand it is unlikely that this bias was present. If all studies would have favored mixed-species stands we could expect a clear advantage in all three tested characteristics for mixed-species stands. However, for the growth performance, as explained above, we could only find a relatively uncertain effect, although this aspect was investigated extensively. Given this fact we may conclude that the clear advantages found for the resistance of mixed-species stands are actually present and substantial.

A third point of critique is the commonly used expression of comparing apples and oranges with regard to the combination of different kinds of studies in meta-analysis. It has to be remembered, that the meta-analysis carried out addresses a broader question than any of the individual studies used in the analysis. Therefore the meta-analysis may be thought of as asking a question about fruit, for which both apples and oranges contribute valuable information (Borenstein *et al*. 2009).

Bearing in mind all the above points, we conclude that meta-analysis is generally not to be understood as an exact statistical science, but rather as a valuable and objective descriptive technique that furnishes a clear qualitative conclusion on the objective of this paper (Thompson and Pocock, 1991). As a matter of course, one number cannot summarize the whole research field of economically relevant effects from forest stand level mixtures. Especially, because heterogeneity plays an important role regarding mixed-species stands. Direct observation of species-mixtures and the occurring interdependences, concurrently gaining information on behavior of the involved species in single-species stands which are comparable in consideration of environmental variables is a task that was rarely successful. There are very few studies dealing with both mixed- and single-species stands on a comparable site, especially for regions outside the tropics. Data usually comes from studies that were not established specifically to address the relevant issues. Also, differences in the detailed composition of mixtures, site conditions and silvicultural treatments leave open many questions (Pretzsch, 2005). Nevertheless, the results of the present study indicate that interspecific effects do exist. These effects have to be taken into account when it comes to evaluating economic results of growing mixed-species stands.

Conclusions

The paper at hand addresses research questions on mixed forests that are largely neglected in consequence of a severe lack of appropriate data. All three meta-analysis are confined to deliver a first overview and existing tendencies in the literature. With more information about mixed-species compared to mono-species stands, the basic meta-analysis can be extended into meta-regressions that furthermore reveal relationships between one or more covariates and a dependent variable (Borenstein *et al.,* 2009) such as the influence of age, structure or others.

As the intensive literature research carried out for the study at hand has shown, many detailed publications have not been translated into widely known languages such as English. To extend the given database, not only for this study, but also for many other fields of interest, researchers should contribute to the available literature by translating and officially publishing such existing information.

The prominent effects of resistance of mixed-species stands in comparison with no effect in growth performance point to the necessity of a suitable modeling approach. Modeling growth and yield for mixed-species stands in a first step is essential for evaluating biological potential as well as for the making of sound management decisions (Burkhart & Tham, 1992). Forest modeling has been focused more on mono-species stands (Porté & Bartelink, 2002). Notwithstanding the need for modeling mixed-species stands, only a small number of potentially suitable models has been developed. A first approach was made by Turnbull in 1964, followed by the development of “gap-models” to specifically simulate mixed forest growth by Hahn and Leary (1979) and numerous others through the years, as depicted in an extensive survey by Vanclay & Skovsgaard (1997). All model approaches had one thing in common: They do not consider interdependences. But as this paper shows, interdependences do exist and have to be taken into account. Linking information on productivity with other variables is indispensable. Pretzsch *et al.* (2008) consider solutions for prospective model research. Inter alia they suggest combining empirical and mechanistic model approaches with management risks by means of sudden events such as storm or insect attacks. The paper at hand underlines this requirement. However, it clarifies a pronounced priority. First and foremost, the resistance of mixed stands has to be incorporated in economically oriented modeling. This conclusion is well in line with the results of Knoke & Seifert (2008), who found the resistance of mixed forest stands being of outstanding economical importance, while volume growth showed only minor effects on economical indicators. An improved bioeconomic modeling, combined with economic optimization under uncertainty (especially concentrating on risk avoidance) will be the next step towards proper financial analysis in forestry focusing on mixed-species stands, which serve economical and ecological objectives.

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Figures

Tables

Detailed data used for the meta-analysis on growth performance

Table A 1: Detailed data used for the meta-analysis on growth performance, derived from Amoroso and Turnblom (2006)

Amoroso (2006)	*Vol. [m^3/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Douglas fir	39	36.53	0.80	-0.26	0.67	1.49	-0.39
Western Hemlock	26	36.53	0.80	0.02	0.67	1.50	0.03
Mixture	27						
Douglas fir	78	36.53	0.80	-0.39	0.68	1.47	-0.58
Western Hemlock	82	36.53	0.80	-0.48	0.69	1.46	-0.70
Mixture	60						
Douglas fir	104	36.53	0.80	0.11	0.67	1.50	0.16
Western Hemlock	94	36.53	0.80	0.33	0.68	1.48	0.49
Mixture	109						

Table A 2: Detailed data used for the meta-analysis on growth performance, derived from Brown (1992)

Brown (1992)	*Vol. [m^3/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Scots Pine	158	57.41	0.92	0.47	0.34	2.92	1.36
Norway Spruce	98	57.41	0.92	1.43	0.42	2.39	3.42
Mixture	187						
Scots Pine	158	57.41	0.92	-0.50	0.34	2.91	-1.45
Common Alder	24	57.41	0.92	1.66	0.45	2.23	3.70
Mixture	127						
Scots Pine	158	57.41	0.92	-0.29	0.34	2.97	-0.86
Sessile Oak	26	57.41	0.92	1.83	0.47	2.11	3.87
Mixture	140						
Common Alder	24	58.18	0.92	1.08	0.38	2.62	2.83
Norway Spruce	98	57.41	0.92	-0.10	0.33	3.00	-0.29
Mixture	92						
Common Alder	24	57.41	0.92	0.05	0.33	3.00	0.14
Sessile Oak	26	57.41	0.92	0.02	0.33	3.00	0.05
Mixture	27						
Norway Spruce	98	57.41	0.92	-0.48	0.34	2.92	-1.41
Sessile Oak	26	57.41	0.92	0.68	0.35	2.84	1.92
Mixture	68						

Table A 3: Detailed data used for the meta-analysis on growth performance, derived from Chen *et al*. (2003)

Chen (2003)	*Vol. [m^3/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Western Hemlock	1,036	5.65	0.80	-34.96	102.52	0.01	-0.34
Western Red Cedar	758	4.72	0.80	5.26	2.97	0.34	1.77
Mixture	789						
Lodgepole Pine	328	10.25	0.80	-3.51	1.70	0.59	-2.07
Western Larch	348	117.10	0.80	-0.44	0.68	1.46	-0.65
Mixture	283						
Lodgepole Pine	298	156.53	0.80	-0.08	0.67	1.50	-0.11
Black Spruce	n.a.	-	-	-	-	-	-
Mixture	283	156.53	0.00	0.00	0.67	1.50	0.00

Table A 4: Detailed data used for the meta-analysis on growth performance, derived from Erickson *et al.* (2009)

Erickson *et al.* (2003)	*Vol. [m³/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Douglas fir	10	3,34	0,80	0,32	0,68	1,48	0,48
Western white pine	16	3,34	0,80	-1,20	0,79	1,27	-1,52
Mixture	11						
Douglas fir	40	1,83	0,80	-1,55	0,87	1,15	-1,79
Western white pine	37	1,83	0,80	-0,44	0,68	1,46	-0,65
Mixture	36						
Douglas fir	84	8,48	0,80	-1,24	0,80	1,26	-1,56
Western white pine	68	8,48	0,80	0,25	0,67	1,49	0,37
Mixture	71						

Table A 5: Detailed data used for the meta-analysis on growth performance, derived from Gobakken and Naesset (2002)

Gobakken (2002)	*Vol. [m³/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Norway Spruce	31	1.73	0.57	0.66	1.05	0.95	0.63
Birch	n.a.	-	-	-	-	-	-
Mixture	33						

Table A 6: Detailed data used for the meta-analysis on growth performance, derived from Johansson (2003)

Johansson (2003)	*MAI [m³/ha/a]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Norway Spruce	7.9	0.49	0.57	-0.81	1.08	0.92	-0.75
Birch	n.a.	-	-	-	-	-	-
Mixture	7,2						

Table A 7: Detailed data used for the meta-analysis on growth performance, derived from Kennel (1965)

Kennel (1965)	*Vol. [m³/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Norway Spruce	899	422.85	0.92	-0.58	0.35	2.88	-1.67
Beech	509	422.85	0.92	0.27	0.34	2.97	0.81
Mixture	634						
Norway Spruce	436	422.85	0.92	-0.12	0.33	2.99	-0.35
Beech	311	422.85	0.92	0.15	0.33	2.99	0.46
Mixture	382						
Norway Spruce	553	422.85	0.92	-0.23	0.34	2.98	-0.70
Beech	347	422.85	0.92	0.22	0.34	2.98	0.64
Mixture	446						

Table A 8: Detailed data used for the meta-analysis on growth performance, derived from Pretzsch and Schütze (2009)

Pretzsch (2009)	*Vol. [m^3/ha]*	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech	137	160.15	0.95	0.24	0.22	4.47	1.06
Norway Spruce	73	132.11	0.95	0.75	0.24	4.20	3.15
Mixture	177						
Beech	255	160.15	0.95	0.90	0.24	4.09	3.67
Norway Spruce	424	132.11	0.95	-0.13	0.22	4.49	-0.58
Mixture	406						
Beech	209	160.15	0.95	1.41	0.28	3.60	5.08
Norway Spruce	409	132.11	0.95	0.27	0.22	4.46	1.19
Mixture	446						
Beech	337	153.51	0.95	0.99	0.25	4.01	3.96
Norway Spruce	358	132.11	0.95	0.99	0.25	4.00	3.98
Mixture	496						
Beech	517	160.15	0.95	-1.11	0.26	3.90	-4.33
Norway Spruce	330	132.11	0.95	0.00	0.22	4.50	0.00
Mixture	330						
Beech	321	160.15	0.95	0.20	0.22	4.48	0.91
Norway Spruce	253	132.11	0.95	0.74	0.24	4.22	3.10
Mixture	355						
Beech	363	160.15	0.95	1.30	0.27	3.71	4.84
Norway Spruce	422	132.11	0.95	1.15	0.26	3.86	4.45
Mixture	582						
Beech	683	160.15	0.95	-1.63	0.30	3.38	-5.51
Norway Spruce	392	132.11	0.95	0.12	0.22	4.49	0.55
Mixture	409						
Beech	693	160.15	0.95	-0.26	0.22	4.46	-1.17
Norway Spruce	493	132.11	0.95	1.12	0.26	3.89	4.37
Mixture	649						

Detailed data used for the meta-analysis on resistance against windthrow

Table A 9: Detailed data used for the meta-analysis on resistance against windthrow, derived from Heupel and Block (1991)

Heupel and Block (1991)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech with spruce	4	37.63	1.00	-0.40	0.02	49.03	-19.47
Pure spruce	19						
Beech with spruce	1	37.63	1.00	-0.29	0.02	49.48	-14.41
Pure spruce	12						
Beech with spruce	2	37.63	1.00	-0.45	0.02	48.77	-21.95
Pure spruce	19						
Beech with spruce	3	37.63	1.00	-1.03	0.02	44.12	-45.55
Pure spruce	42						
Beech with spruce	10	37.63	1.00	-0.13	0.02	49.89	-6.60
Pure spruce	15						
Beech with spruce	8	37.63	1.00	-1.30	0.02	41.31	-53.59
Pure spruce	57						

Table A 10: Detailed data used for the meta-analysis on resistance against windthrow, derived from König *et al.* (1995)

König *et al*. (1995)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech with spruce	1.6	11.29	1.00	-0.14	0.02	49.88	-7.04
Pure spruce	3.2						

Table A 11: Detailed data used for the meta-analysis on resistance against windthrow, derived from Rau (1995)

Rau (1995)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech with spruce	11	28.14	1.00	-0.18	0.02	49.80	-8.82
Pure spruce	16						
Beech with spruce	7	28.15	1.00	-0.32	0.02	49.37	-15.73
Pure spruce	16						

Table A 12: Table A 10: Detailed data used for the meta-analysis on resistance against windthrow, derived from Schmid-Haas & Bachofen (1991)

Schmid-Haas & Bachofen (1991)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Admixture of 10-49% conifers	15	60,79	1,00	-0,92	0,02	45,24	-41,51
Pure spruce	71						
Admixture of 50-89% conifers	11	111,83	1,00	-0,61	0,02	47,81	-28,96
Pure spruce	71						
Admixture of 90-100% conifers	3	111,83	1,00	-0,53	0,02	48,28	-25,80
Pure spruce	71						

Table A 13: Detailed data used for the meta-analysis on resistance against windthrow, derived from Wangler (1974)

Wangler (1974)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech-Spruce-Fir	14	45.47	1.00	-0.33	0.02	49.33	-16.21
Pure spruce	29						
Beech with spruce	3	45.47	1.00	-0.26	0.02	49.57	-13.03
Pure spruce	15						
Spruce with Pine	0	45.47	1.00	-0.64	0.02	47.60	-30.24
Pure spruce	29						
Spruce with Pine	1	45.47	1.00	-0.31	0.02	49.42	-15.16
Pure spruce	15						
Beech-Spruce-Fir	7	45.47	1.00	-0.07	0.02	49.97	-3.28
Pure spruce	10						
Beech-Spruce-Fir	4	45.47	1.00	-0.11	0.02	49.93	-5.47
Pure spruce	9						
Beech-Spruce-Fir	7	45.47	1.00	-0.02	0.02	50.00	-1.10
Pure spruce	8						
Spruce with Pine	2	45.47	1.00	-0.18	0.02	49.81	-8.73
Pure spruce	10						
Spruce with Pine	1	45.47	1.00	-0.18	0.02	49.81	-8.73
Pure spruce	9						
Spruce with Pine	10	45.47	1.00	0.04	0.02	49.99	2.19
Pure spruce	8						

Table A 14: Detailed data used for the meta-analysis on resistance against windthrow, derived from Winterhoff (1995)

Winterhoff *et al.* (1995)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech with spruce	9.5	38.70	1.00	-0.12	0.02	49.92	-5.78
Pure spruce	14						
Beech with spruce	4	38.70	1.00	-0.26	0.02	49.59	-12.77
Pure spruce	14						

Table A 15: Detailed data used for the meta-analysis on resistance against windthrow, derived from Zindel (1991)

Zindel (1991)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Beech with spruce	36	111.83	1.00	-0.16	0.02	49.84	-7.99
Pure spruce	54						
Beech with spruce	21	111.83	1.00	-0.29	0.02	49.47	-14.54
Pure spruce	54						
Beech with spruce	14	111.83	1.00	-0.36	0.02	49.22	-17.54
Pure spruce	54						

Detailed data used for the meta-analysis on resistance against pests

Table A 16: Detailed data used for the meta-analysis on resistance against pests, derived from Bergeron (1995)

Bergeron (1995)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Mixed decidous	45.3	1.00	1.00	30.16	2.29	0.44	13.15
Decidous	15.1						
Mixed coniferous	51	1.00	1.00	-12.68	0.42	2.37	-30.04
Coniferous	63.7						
Mixed decidous	58	1.00	1.00	25.17	1.60	0.62	15.70
Decidous	32.8						
Mixed coniferous	66.5	1.00	1.00	-9.29	0.24	4.24	-39.41
Coniferous	75.8						
Mixed decidous	48.6	1.00	1.00	-20.77	1.10	0.91	-18.91
Decidous	69.4						
Mixed coniferous	72.1	1.00	1.00	-10.39	0.29	3.45	-35.85
Coniferous	82.5						

Table A 17: Detailed data used for the meta-analysis on resistance against pests, derived from MacLean (1980)

MacLean (1980)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Mixed stand	25.5	1.00	1.00	-33.71	2.86	0.35	-11.78
Pure stand	59.25						
Mixed stand	47.5	1.00	1.00	-11.73	0.36	2.75	-32.22
Pure stand	59.25						
Mixed stand	61.25	1.00	1.00	17.48	0.78	1.28	22.30
Pure stand	43.75						
Mixed stand	61.25	1.00	1.00	23.22	1.37	0.73	16.97
Pure stand	38						

Table A 18: Detailed data used for the meta-analysis on resistance against pests, derived from Moore (1991)

Moore (1991)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Oak - Alder	22.33	1.00	1.00	5.22	0.09	11.34	59.22
Pure Oak	17.1						
Oak - Alder	22.33	1.00	1.00	0.08	0.02	49.96	3.99
Pure Oak	22.25						
Oak - Alder	30.77	1.00	1.00	13.65	0.49	2.06	28.09
Pure Oak	17.1						
Oak - Alder	30.77	1.00	1.00	8.51	0.20	4.97	42.33
Pure Oak	22.25						

Table A 19: Detailed data used for the meta-analysis on resistance against pests, derived from Su (1996)

Su (1996)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
Balsam fir + 25% Hardwood	63	280.75	1.00	-0.08	0.02	49.96	-3.90
Balsam fir	85						
Balsam fir + 50% Hardwood	41	280.75	1.00	-0.16	0.02	49.85	-7.78
Balsam fir	85						
Balsam fir + 75% Hardwood	18	280.75	1.00	-0.24	0.02	49.65	-11.80
Balsam fir	85						

Table A 20: Detailed data used for the meta-analysis on resistance against pests, derived from Vehviläinen (2006)

Vehviläinen (2006)	Damage [%]	*SD*	*J*	*d*	*v*	*w*	*wd*
50-50 Birch-Pine	0.85	1.00	1.00	-0.15	0.02	49.86	-7.47
Pure Birch	1						
25-75 Birch Pine	0.67	1.00	1.00	-0.33	0.02	49.33	-16.26
Pure Birch	1						
50-50 Birch-Pine	11.2	1.00	1.00	-0.20	0.02	49.75	-9.94
Pure Birch	11.4						
25-75 Birch Pine	7	1.00	1.00	-4.39	0.07	14.65	-64.36
Pure Birch	11.4						