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Are mixed-tree plantations including a nitrogen-fixing species more productive than monocultures?

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ABSTRACT

The inclusion of N_2-fixing tree species in tree plantations has the potential to increase biomass production compared to monocultures. Both successes and failures have been described in the literature; however, it is still difficult to distinguish a general pattern and to disentangle the factors influencing the mixture effect. The first objective of this study was to provide an overview of the published data on the effect of the introduction of N_2-fixing trees in tree plantations through a meta-analysis approach and to calculate a mean effect of mixed-tree plantations on biomass production compared to monocultures of the non N_2-fixing species in stands 2–20 years of age. The second objective was to evaluate the effects of *(1)* climate zone (temperate *vs.* tropical), *(2)* the species used (eucalypts *vs.* other non N_2-fixing species, and leguminous tree species *vs.* other N_2-fixing species), *(3)* the proportion of N_2-fixing species compared to the non-fixing species, and *(4)* plant developmental stage. A total of 148 case studies from 34 experimental plantations under tropical (68 case studies) and temperate (80 case studies) conditions were identified from the literature. The global mixture effect was significantly positive, mixed-tree plantations being 18% more productive than the non N_2-fixing monocultures, and this effect was significantly different from zero under temperate conditions (24% more productive) but not under tropical conditions (12% more productive). Indeed, the sites where the positive mixture effect was significantly different from zero were mostly located in a temperate climate, where soil nitrogen is generally considered less available than in tropical latitudes. Intermediate and high proportions of N_2-fixing species gave similar positive results (27% more productive), while low proportions had no significant impact. Neither plantation age nor type of N_2-fixing species (legume trees *vs.* other N_2-fixing species) had any significant effect. In conclusion, it appears that climate is the main factor influencing the success of the mixture; however, it also seems that the degree of mixture success is more marked on sites with low biomass production where the monoculture is the least productive.

1. Introduction

In 2012, nearly half of all industrial round wood harvested worldwide was removed from planted forests, the majority of which were large-scale tree plantations (Payn et al., 2015). Large-scale tree plantations, most of which are located in Asia and the Americas, can occupy anywhere from hundreds of hectares to hundreds of thousands of hectares and are generally under government or commercial management (Kanowski and Murray, 2008). Such plantations often comprise a single species or a few productive, and predominantly exotic, tree species that are intensively managed for varying commercial purposes, mainly for timber and pulpwood, but also for biofuels and carbon credits (Ingram et al., 2016; Malkamäki et al., 2017). Nearly three quarters of the world's industrial forest plantations are composed of *Pinus* (42%) and *Eucalyptus* species (26%) (Payn et al., 2015). However, concerns have arisen about the economic and environmental costs of fertilizers and pesticides, productivity losses from pests and diseases and reduced biodiversity in these monospecific production systems (FAO, 1992). Mixed-species plantations have the potential to address these concerns while simultaneously improving nutrient cycling (e.g. Koutika et al., 2017; Liu et al., 2015; Tchichelle et al., 2017), soil fertility (e.g. Montagnini, 2000), biomass production (e.g. Epron et al., 2013; Pretzsch et al., 2013) and carbon sequestration (e.g. Wang et al., 2009; Koutika et al., 2014) as well as providing other benefits through a diversification of products, improved risk management and protection from pests and diseases (Forrester, 2004; Kelty, 2006; Bauhus et al., 2017). Mixed-tree plantations containing N_2-fixing tree species are also thought to provide an additional benefit: a reduced need for nitrogen

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fertilization thanks to symbiotic N_2 fixation (Forrester et al., 2006a; Piotto, 2008; Bouillet et al., 2013).

However, the success of mixed-tree plantations (i.e. when the mixture is more productive than the monoculture) is highly variable (e.g. Bauhus et al., 2000 for a positive effect, Parrotta, 1999 for a negative effect and DeBell et al., 1987 for no effect). If the interspecific competition in the mixture is more intense than the intra-specific competition in the monoculture, the mixture is likely to be less productive. On the other hand, niche sharing and facilitation, especially when N_2-fixing species are introduced, are expected to promote biomass production in the mixture. However, it is very difficult to predict which kind of interaction will be preponderant and to guarantee the success of the mixture (Forrester et al., 2006a). According to the stress gradient theory (Bertness and Callaway, 1994), positive effects (complementarity) should prevail over negative effects (competition) in a mixture under stressful abiotic conditions. Positive interactions between species (i.e. facilitation and competition reduction) are generally more prevalent in sites with low nutrient availability (Forrester, 2014).

First of all, the design of the mixed-species plantation must be adapted to local conditions to maximize the chances of success. Many options have been illustrated in the literature (Forrester et al., 2006a; Piotto, 2008). Under tropical latitudes, the N_2-fixing species introduced with the economic target species (almost exclusively a eucalypt) most often belong to the *Acacia* genus, though species from the *Leucaena*, *Casuarina*, *Albizia* or *Enterolobium* genera are also occasionally used. Under temperate latitudes, N_2-fixing species mostly belong to the *Robinia* or *Alnus* genera, and more rarely to the *Caragana* genus, while the non-fixing species are more diverse: species from the *Populus*, *Salix*, *Pinus* and *Pseudotsuga* and other genera are used. N_2-fixing species are mainly legumes (*Fabaceae* Lindl. family) in which N_2 fixation is realized through their symbiosis with bacteria from the genus *Rhizobium*, except species from the *Alnus* and *Casuarina* genera, which form their symbiosis with bacteria from the genus *Frankia*. The mixing design can take the form of an additive series, where the density of the non-fixing species is kept constant, or a replacement series, where the N_2-fixing trees replace certain non-fixing trees to keep the total planting density constant. Tested proportions used to evaluate experimentally mixture effects range from 11 to 75% of N_2-fixing trees, but a fifty-fifty mixture remains the most widely used option (e.g. Bi and Turvey, 1994).

This study aimed to provide updated and complementary information compared to previously published reviews or meta-analyses, about eucalypt – acacia mixtures (Forrester et al., 2006a), and about forest mixed-species plantations in general (Piotto, 2008; Jactel et al., 2018; Zhang et al., 2012). All these studies suggested that mixed stands were globally more productive than pure ones. Zhang et al. (2012) calculated that mixed-species forests are globally 15% more productive than the average of their component monocultures, and Jactel et al. (2018) estimated that polycultures were 24% more productive than monocultures. However, these two meta-analyses reported that the positive effect of the mixtures was independent of the presence of N_2-fixing species in the mixture.

We carried out a quantitative study compiling the data available in the scientific literature about all kinds of mixed-tree plantations which included N_2-fixing species and undertook a meta-analysis – a set of statistical tools that makes it possible to combine the outcomes of independent studies to evaluate the overall effect of a particular factor and to test the influence of covariates on this effect (Gurevitch and Hedges, 1999). Our main objectives were to calculate a mean effect of mixed-tree plantations on biomass production compared to the monoculture of the non N_2-fixing species from the data reported in the literature. We then sought to evaluate the effects of plantation attributes in terms of *(1)* climate (temperate *vs.* tropical), *(2)* the species used (eucalypt *vs.* other non N_2-fixing species, and leguminous species *vs.* other N_2-fixing species), *(3)* the proportion of N_2-fixing species compared to the non-fixing species (high, low or equal proportions), and *(4)* the developmental stage for short rotation stands (juvenile or shortly after planting *vs.* nearing rotation age). Planting density was not tested since only two studies compared this factor. Only replacement series designs were considered in order to hold planting density constant. We chose to compare the mixed-tree plantations to the monocultures of the non N_2-fixing species and not to the monocultures of the N_2-fixing species because we considered that if the N_2-fixing monoculture was more productive than the mixture, the mixture would be useless in economic terms. We tested the following hypotheses: *(1)* globally, mixed-tree plantations including an N_2-fixing species should be more productive than the monoculture because of the additional nitrogen symbiotically fixed; *(2)* this better performance of the mixture should be more marked under temperate latitudes where soil nitrogen is generally considered to be less available than in tropical latitudes (Martinelli et al., 1999); *(3)* a balanced mixing proportion (50/50) would give the best results as this proportion would provide enough N_2-fixing trees to promote biomass production of the non-fixing species and not too many N_2-fixing trees lowering overall stand biomass production; *(4)* older developmental stages should give better results than juvenile stages since the interactions between species are likely to be limited in very young plantations; it has also been shown that synergistic effects between species are long lasting (Forrester et al., 2004; Zhang et al., 2012).

2. Materials and methods

2.1. Data collection

We examined existing literature up to December 2017 via an online scientific citation indexing service (Web of Science, Clarivate Analytics, U.S.A.) with various combinations of relevant terms such as: (mixed or mixture or mixing), (pure or monoculture), (tree plantation or forest) and (N-/N_2-/nitrogen-fixing or N/N_2/nitrogen fixation), and Latin names of the most frequently used tree N_2-fixing genera. We also surveyed the cited references in the relevant articles we retrieved. Studies were retained if they met the following conditions: *(1)* studies used a replacement series design in order to hold planting density constant; *(2)* a monoculture of the non N_2-fixing species was present under the same conditions as the mixture; *(3)* sufficient information on environmental conditions and experimental design was given; and *(4)* production data per unit area were presented in terms of aboveground dry matter, stem volume, stem volume index or basal area. Almost all studies that met these conditions deal with short rotation forests.

Mean production data were extracted from the articles for the mixed-tree plantation and the non N_2-fixing monoculture; when presented, standard deviations or standard errors were also extracted. In some cases, means and standard deviations were extrapolated from graphs with the computer tool Plot Digitizer 2.6.6 (http://plotdigitizer.sourceforge.net/). This program allows quickly digitizing values off a graph just by clicking on each data point and by comparing them to a scale. Forty articles reporting 148 case studies (differing in mixing proportions, planting densities, species or plantation age) on 34 experimental sites worldwide were found (Table 1 and Appendix A for soil characteristics). The sites were positioned on Google Maps using the GeoFree website (www.geofree.fr) (Appendix B).

2.2. Data analysis

For each case study, effect size (log-transformed response ratio, RR) was calculated as the log of the ratio between the mean aboveground biomass (or volume or basal area) in the mixture (*M*) and in the monoculture of the non N_2-fixing species (*NF*):

Table 1
Main characteristics of the 34 mixture sites identified from the literature: location (country, locality, geographic coordinates, altitude), climate (mean annual precipitation, MAP; mean annual temperature, MAT), N_2-fixing and non-fixing species, mixture proportion, age of stand at the last measurement, planting density and bibliographical references. NA stands for “not available” when data are not provided.

Site	Site number	Latitude	Longitude	Altitude (m)	Climatic zone	MAP (mm)	MAT (°C)	Non-fixing species	N_2-fixing species	Proportion tested (% fixator: %non fixator)	Age of measurement (years)	Planting density (trees/ha)	References
Australia, Atherton-Tablelands	1	17°00′S	145°00′E	760	Tropical	1413	20.2	*Eucalyptus pellita*	*Acacia peregrina*	NA	10	1000	Bristow et al. (2006)
Australia, Canberra	2	35°15′S	149°10′E	650	Temperate	625	13.1	*Pinus radiata*	*Acacia decurrens; Acacia mearnsii*	34:66	4.5	1010	Forrester (2004)
Australia, Cann-River	3	37°35′S	149°10′E	110	Temperate	1009	14.2	*Eucalyptus globulus*	*Acacia mearnsii*	25:75 ; 50:50 ; 75:25	from 3 to 11	1010 ; 1515	Forrester (2004); Forrester et al. (2004); Khanna (1997); Forrester et al. (2005); Bauhus et al. (2004); Bauhus et al. (2000)
Australia, Eden	4	37°20′S	149°53′E	40	Temperate	751	15.4	*Eucalyptus nitens*	*Acacia mearnsii*	50:50	from 2 to 5	2500	Forrester (2004)
Australia, Nowra	5	34°50′S	150°15′E	109	Temperate	1048	16.3	*Eucalyptus saligna*	*Acacia mearnsii*	50:50	2	2500	Forrester (2004)
Brazil, Bofete	6	23°11′S	48°25′W	NA	Tropical	1420	21.4	*Eucalyptus grandis*	*Acacia mangium*	50:50	from 2 to 6	1666	Bouillet et al. (2013)
Brazil, Itatinga	7	23°02′S	48°38′W	860	Tropical	1380	19.0	*Eucalyptus grandis*	*Acacia mangium*	50:50	from 2 to 6	1111	Bouillet et al. (2013); Epron et al. (2013)
Brazil, Luiz Antônio	8	21°35′S	47°31′W	NA	Tropical	1420	23.3	*Eucalyptus urophylla × grandis*	*Acacia mangium*	50:50	from 2 to 6	1111	Bouillet et al. (2013)
Brazil, Minas do Leao	9	30°07′S	52°02′W	64	Temperate	1342	19.3	*Eucalyptus saligna*	*Acacia mearnsii*	50:50	4	1667	Vezzani et al. (2001)
Brazil, Rio de Janeiro	10	22°45′S	43°40′W	NA	Tropical	1370	24.0	*Eucalyptus urophylla × grandis*	*Acacia mangium*	50:50	from 2 to 5	1111	Santos et al. (2016)
Brazil, Santana do Paraíso	11	19°16′S	41°47′W	NA	Tropical	1240	24.4	*Eucalyptus urophylla × grandis*	*Acacia mangium*	50:50	from 2 to 6	1111	Bouillet et al. (2013)
Brazil, São Mateus	12	18°50′S	39°50′W	NA	Tropical	1350	25.0	*Eucalyptus urophylla*	*Leucaena leucocephala*	50:50	7	1342	Moraes de Jesus and Brouard (1989)
Canada, Mt. Benson	13	50°80′N	124°20′W	510	Temperate	1200	11.1	*Pseudotsuga menziesii*	*Alnus rubra*	NA	23	NA	Binkley (1983)
Canada, Laval	14	46°41′N	71°16′W	90	Temperate	1200	15.5	*Populus nigra × trichocarpa*	*Alnus glutinosa*	70:30; 30:70	2	90,000	Coté and Camire (1984)
Canada, Harris	15	51°67′N	107°66′W	541	Temperate	400	2.7	*Salix miyabeana*	*Caragana arborescens*	50:50; 34:66	4	14,818	Moukoumi et al. (2012)
Canada, Saskatoon 1	16	52°13′N	106°61′W	587	Temperate	347	3.3	*Salix miyabeana*	*Caragana arborescens*	50:50; 34:66	4	14,818	Moukoumi et al. (2012)
Canada, Saskatoon 2	17	52°09′N	106°46′W	510	Temperate	347	3.3	*Salix miyabeana*	*Caragana arborescens*	50:50; 34:66	4	14,818	Moukoumi et al. (2012)
China, Yuanmou	18	25°40′N	101°51′E	1110	Tropical	634	21.6	*Eucalyptus camaldulensis*	*Leucaena leucocephala*	50:50	10	816	Tang et al. (2013)
Congo, Kissoko	19	4°44′S	12°01′E	100	Tropical	1430	25.7	*Eucalyptus urophylla × grandis*	*Acacia mangium*	50:50	from 2 to 7	800	Epron et al. (2013); Koutika et al. (2014); Bouillet et al. (2013); Tchichelle et al. (2017)
England, Gisburn forest	20	54°10′N	2°22′W	275	Temperate	1400	10.0	*Picea abies, Pinus sylvestris, Quercus petraea*	*Alnus glutinosa*	50:50	from 6 to 20	4444	Mason and Connolly (2014)
France, Ardon	21	47°46′N	1°52′E	110	Temperate	637	10.6	*Populus trichocarpa × deltoides*	*Alnus glutinosa*	50:50	from 2 to 3	3333	Teissier du Cros et al. (1984)
France, Saint-Cyr-en-Val	22	47°48′N	1°58′E	NA	Temperate	620	11.0	*Populus nigra × deltoides*	*Robinia pseudoacacia*	50:50	from 1 to 4	1428	Gana (2016); Marron et al. (2018)
Iran, Foman	23	35°50′N	49°15′E	10	Temperate	1260	20.3	*Populus deltoides*	*Alnus glutinosa*	30:70; 50:50; 70:30	13	1250	Koupar et al. (2011)
Iran, Mazandaran	24	36°29′N	51°59′E	100	Temperate	803	16.2	*Populus deltoides*	*Alnus subcordata*	33:67; 50:50; 67:33	7 and 20	625	Ghorbani et al. (2018); Sayyad et al. (2006)

(continued on next page)

Table 1 (*continued*)

Site	Site number	Latitude	Longitude	Altitude (m)	Climatic zone	MAP (mm)	MAT (°C)	Non-fixing species	N_2-fixing species	Proportion tested (% fixator: %non fixator)	Age of measurement (years)	Planting density (trees/ha)	References
Puerto Rico, Tao Baja	25	18°27′N	66°10′W	NA	Tropical	1600	26.6	*Eucalyptus × robusta*	*Casuarina equisetifolia; Leucaena leucocephala*	50:50	4	1000	Parrotta (1999); Parrotta et al. (1996)
Spain, Alcalá de Henares	26	40°28′N	3°22′W	595	Temperate	447	14.0	*Populus alba*	*Robinia pseudoacacia*	25:75; 50:50; 75:25	3	10,000	Oliveira et al. (2018)
Thailand, Ratchaburi	27	13°32′N	99°48′E	NA	Tropical	980	29.3	*Eucalyptus camaldulensis*	*Acacia auriculiformis*	25:75; 50:50; 75:25	from 2 to 4	1250; 2500	Wichiennopparat et al. (1998); Snowdon et al. (2003)
USA, Onomea 1	28	19°30′N	155°15′W	420	Tropical	5080	21.0	*Eucalyptus saligna / Eucalyptus grandis*	*Acacia melanoxylon; Albizia falcataria*	50:50	5	2500	DeBell et al. (1985)
USA, Onomea 2	29	19°30′N	155°15′W	480	Tropical	4600	21.0	*Eucalyptus saligna / Eucalyptus grandis*	*Acacia melanoxylon; Albizia falcataria*	11:89; 25:75; 33:67; 50:50; 75:25	from 3 to 20	2500	Binkley et al. (1992); Binkley et al. (2003); DeBell et al. (1989); DeBell et al. (1997)
USA, Waimanalo	30	21°20′N	158°20′W	20	Tropical	1023	24.6	*Eucalyptus grandis*	*Albizia falcataria; Enterolobium cyclocarpum; Leucaena leucocephala × L. diversifolia*	50:50	from 1 to 4	6667	Austin et al. (1997)
USA, Cascade Head	31	45°05′N	124°00′W	330	Temperate	2500	10.0	*Pseudotsuga menziesii*	*Alnus rubra*	50:50	15	1111	Moore et al. (2011); Radosevich et al. (2006); D'Amato and Puettmann (2004)
USA, HJ Andrews	32	44°14′N	122°10′W	800	Temperate	2300	8.5	*Pseudotsuga menziesii*	*Alnus rubra*	50:50	15	1111	Moore et al. (2011); Radosevich et al. (2006); D'Amato and Puettmann (2004)
USA, Camas	33	45°35′N	122°24′W	NA	Temperate	1200	12.2	*Populus trichocarpa*	*Alnus rubra*	50:50	2	13,889	DeBell and Radwan (1979)
USA, Skykomish	34	47°50′N	121°50′W	35	Temperate	2000	11.1	*Pseudotsuga menziesii*	*Alnus rubra*	NA	23	NA	Binkley (1983)

$RR = log(M/NF)$

Log response ratios and their corresponding variances were calculated in R with the "escal" function in the Metafor package (Viechtbauer, 2010). A positive *RR* value indicated that production was higher in the mixture than in the monoculture. For studies that reported only mean values, standard deviations were imputed from the weighted average of the standard deviations from the other studies (Robertson et al., 2004). Many studies included in our meta-analysis provided more than one effect size (e.g. comparisons of different species, mixture proportions, planting densities or ages). Effect sizes originating from the same given site cannot be considered statistically independent (Nakagawa and Santos, 2012). To account for this non-independence, we included "site" as a random factor in the model, calculated with the "rma" function in the Metafor package. We first ran the model on the whole dataset, then restricted the dataset to eucalypt for the non-fixing genera (104 case studies), or to *Fabaceae* for the nitrogen-fixing family (117 case studies). Log response ratios were back-transformed to provide a direct estimate of the magnitude of tree mixture effect as a percentage of the decrease or increase in biomass production compared to the non-fixing monoculture.

We tested the significance of several explanatory variables (moderators) to account for variations in *RR*. We first split the dataset into temperate versus tropical climates. We considered a site as tropical when its latitude is below 25° and as temperate when its latitude is above 30°. This separation can be considered as arbitrary, but it separated the species without ambiguity, since almost all were found exclusively in one of the two climatic zones. The only exception was *E. saligna* that was found in both climate zones, consistent with its distribution area, but which was associated with a different N_2 fixing species. We could have distinguished several climatic subzones within each main zone (e.g. Mediterranean in temperate) but the number of sites within each zone would have been too low. We also tested the effects of mixing proportion by retaining only those studies with at least three mixing proportions, i.e. low (33% or less of N_2-fixing trees), equal (50%) and high (66% or more). This represented 69 case studies (23 per mixing proportion). We also compared young (measurements taken a maximum of two years after planting) and older (measurements taken at up to the end of a rotation) stands. Only short rotation stands (composed of eucalypts and poplars) were included in the analysis because only one study compared ages for species grown for saw timber production. Sixty case studies allowed this comparison (30 case studies per development stage).

To verify the lack of publication bias, Rosenberg's fail-safe number (Rosenberg, 2005) was calculated corresponding to the number of case studies with a null effect size to be added to the meta-analysis to reduce the mean effect to zero. The number was 11597, a much greater value than Rosenthal's conservative critical value (750, Rosenthal, 1979), indicating that our results are robust to publication and that our meta-analysis does not represent a bias where researchers were not more inclined to investigate species mixtures with synergistic effects between the species rather than to investigate mixtures where antagonistic effects prevailed.

3. Results

3.1. Dataset characteristics

The studies included in our analysis contain a wide range of species (Table 1). At tropical latitudes, the non-fixing species belong exclusively to the *Eucalyptus* genus (5 species and 2 interspecific hybrids), while at temperate latitudes, a wider diversity of genera is represented: *Populus* (3 species and 3 interspecific hybrids), *Eucalyptus* (3 species), *Pinus* (2 species), *Quercus*, *Salix*, *Pseudotsuga* and *Picea* (1 species each). The N_2-fixing species under tropical conditions mainly belong to the *Acacia* genus (4 species), and, less frequently, to the *Leucaena*, *Albizia*, *Casuarina* and *Enterolobium* genera. Under temperate conditions, N_2-fixing species were from the *Alnus* (3 species), *Acacia* (2 species), *Robinia* or *Caragana* (1 species each) genera. All the N_2-fixing species belong to the *Fabaceae* family and establish symbiosis with the proteobacteria *Rhizobium*, except for *Casuarina* and *Alnus* which belong to other families and establish symbiosis with the actinobacteria *Frankia*. Overall, the non N_2-fixing species were eucalypts in 70% of the case studies, while the N_2-fixing species were legumes in 79% of the case studies.

The 148 case studies are fairly well distributed between temperate and tropical conditions: 80 *vs.* 68 case studies, respectively. The 34 experimental plantations are located on all continents, with quite a high concentration in Brazil, in eastern Australia and in Pacific Northwest (Appendix B). It is noteworthy that some large regions (e.g. China and Africa) are underrepresented in the international literature.

Plantation ages range between two and 23 years, with the majority of the case studies dealing with two-to-four-year-old plantations. Planting densities ranged between 625 and 90,000 trees per ha, but most plantations had densities between 1000 and 2500 trees per ha. Fixing / non-fixing species mixing proportions were fifty-fifty in most cases, but proportions of one third to two thirds or one quarter to three quarters (and conversely) also occurred in several studies.

3.2. Grand mean effect size

The grand mean effect size calculated on the whole dataset (0.17 ± 0.06) was significantly positive ($P < 0.01$, Fig. 1), mixed-tree plantations being 18% more productive than the non N_2-fixing species monocultures (after back-transformation of the log response ratio). However, the magnitude of the effect varied significantly according to climate, the species concerned, mixing proportion and the development stage of the plantation. Biomass production was 24% higher in mixed-tree plantations than in monocultures under temperate latitudes ($P < 0.05$), while it was only 12% higher under tropical latitudes (not significantly different from zero); however, effect size did not

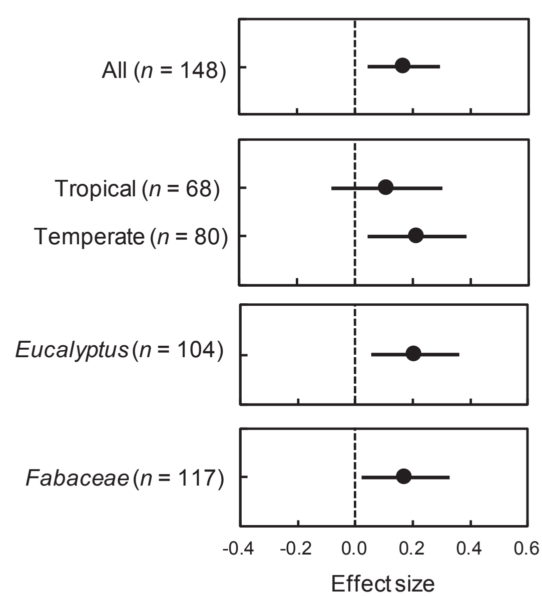

Fig. 1. Effect size (and confidence intervals) for all the case studies (top), tropical and temperate conditions (second down), eucalypt plantations only (third down), and only plantations with leguminous (*Fabaceae*) as N_2-fixing tree species (bottom).

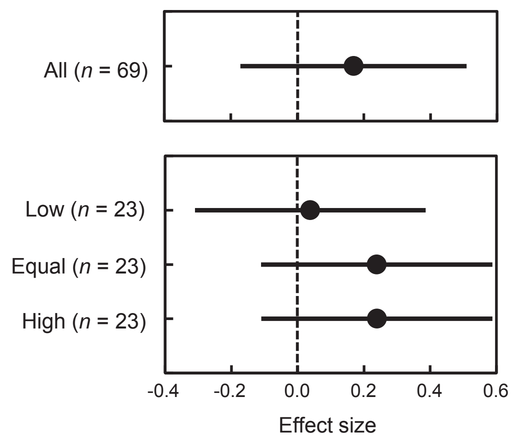

Fig. 2. Effect size (and confidence intervals) for all studies where low, high and equal mixing proportions were compared (top), and separating effect sizes for the three proportions (bottom).

significantly differ between tropical and temperate conditions ($P = 0.42$). Mixed eucalypt plantations were 24% more productive than their monocultures ($P < 0.05$). The number of case studies with species other than eucalypts was too small to make statistical comparisons possible; the mixture effect on production averaged only 11%. In terms of N_2-fixing species, mixed-tree plantations composed of leguminous species (*Fabaceae*) were 19% more productive than monocultures ($P < 0.05$); similar results were found when all N_2-fixing species were combined. Here also, the number of case studies with N_2-fixing species other than *Fabaceae* was too small to make statistical comparisons possible.

When only those studies containing three mixing proportions (high, low and equal) were retained in the analysis, the mixture effect on growth was 18%; however due to the limited number of case studies in this category, the effect was non-significantly different from zero (Fig. 2). However, both high and equal proportions resulted in biomass production 27% higher than the monoculture, a significantly higher effect size than the mean effect size of the low proportion (4%, $P < 0.01$).

Finally, when only studies comparing young and older short rotation plantations were retained in the analysis, young mixtures were 24% more productive than the monoculture while mixtures nearing rotation age were 17% more productive. Yet again, due to the small number of case studies, neither effect was significantly different from zero ($P = 0.07$) or significantly different from each other ($P = 0.51$) (Fig. 3).

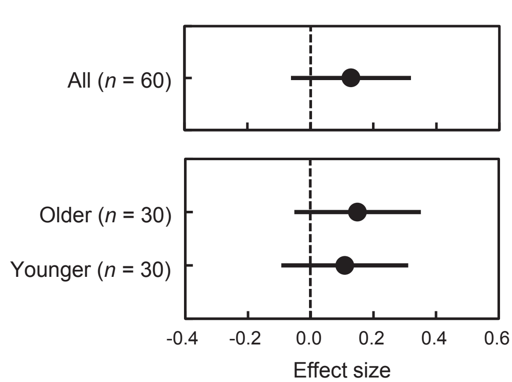

Fig. 3. Effect size (and confidence intervals) for all studies where juvenile and mature developmental plantation stages were compared (top), and separating effect sizes for the two stages (bottom).

3.3. Effect size per site

Fig. 4 represents the mean effect size for each of the 34 sites inventoried from the literature. The sites showed a wide range of effect sizes, ranging from highly positive to highly negative (Fig. 4). Most plantations showing negative or null effects were beyond the 95% confidence interval of the global effect size calculated on the whole dataset. Both the most successful and the worst-performing mixed plantations were located in temperate zones. Under temperate conditions, positive effects were highly significant in the USA, Australia and Canada, with one exception in Harris, Canada, where the mixture effect was significantly negative. Under tropical conditions, effects were weakly positive or negative, with the exception of the six plantations located in Congo, Thailand, Puerto Rico and Hawaii (three sites) where the effect was strongly positive.

Biomass production of the non N_2-fixing species monoculture, expressed in Mg ha^{-1} $year^{-1}$ and calculated as the biomass at the oldest age of the plantation divided by this age, was negatively correlated to effect size ($r = -0.61$, $n = 25$, Fig. 5); when only eucalypt plantations were included, the correlation coefficient rose to 0.84 ($n = 15$). The correlation was not tested for significance because of the inter-dependence of the two variables.

4. Discussion

4.1. Are mixed plantations more productive than monocultures?

In line with our first hypothesis, a significant positive mixture effect on biomass production was revealed: tree plantations with introduced N_2-fixing species were, on average, 18% more productive than the corresponding monoculture of the non-fixing species. Previous meta-analyses focusing on forest mixtures in general have reported a positive effects of mixture over monoculture, but this effect was independent of the presence of N_2-fixing species in the mixture (Jactel et al., 2018; Zhang et al., 2012). We therefore cannot confirm that the positive effect of the mixture we found was always related to N_2 fixation. Other differences in plant functional traits promoting a more efficient resource exploitation and utilization (complementarity effects) may also account for the positive effect of the mixture in our study (e.g. reduced competition for water, improved light interception or light use efficiency, Forrester, 2014).

The positive mixture effect on biomass production was significantly different from zero for temperate plantations (21%), but not for tropical ones. The lack of correlation between site effect size and either the mean annual temperature or the annual rainfall (data not shown) suggests that the difference between temperate and tropical plantations may be more related to edaphic characteristics than to climate characteristics, thus supporting our second hypothesis based on soil nitrogen being generally less available under temperate than tropical conditions (Martinelli et al., 1999). On average, it has indeed been shown that more N circulates annually through lowland tropical forests, and does so at higher concentrations, than through temperate forests (Vogt et al., 1986). Comparable data on rates of nitrogen mineralization and leaching losses also generally show greater rates of nitrogen cycling in many lowland tropical forests (Neill et al., 1995). However, exceptions exist under certain tropical conditions; quite high positive effect sizes were observed, notably in Congo, Thailand, Puerto Rico and Hawaii (Epron et al., 2013; Wichiennopparat et al., 1998; Parrotta, 1999; DeBell et al., 1985, respectively). In Congo, the plantation was located on an arenosol, a soil type with very low nutrient content (Mareschal

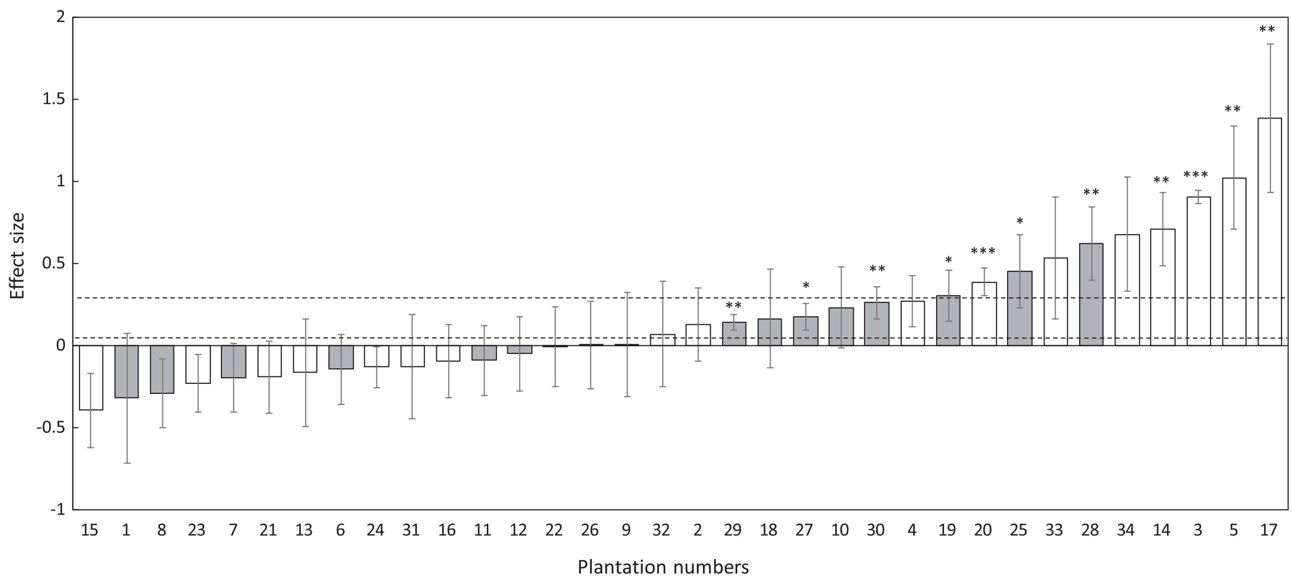

Fig. 4. Effect sizes (and their standard errors) of the 34 experimental mixture sites inventoried from the literature. Negative effect sizes indicate that the mixed-tree plantation was less productive than the non-fixing species monoculture. The dotted line represents the 95% confidence interval of the global effect size. Significant effects (different from zero) are indicated as * for $P \leq 0.05$, ** for $P \leq 0.01$ and *** for $P \leq 0.001$. Grey rectangles correspond to tropical plantations. Numbers correspond to plantation numbers in Table 1.

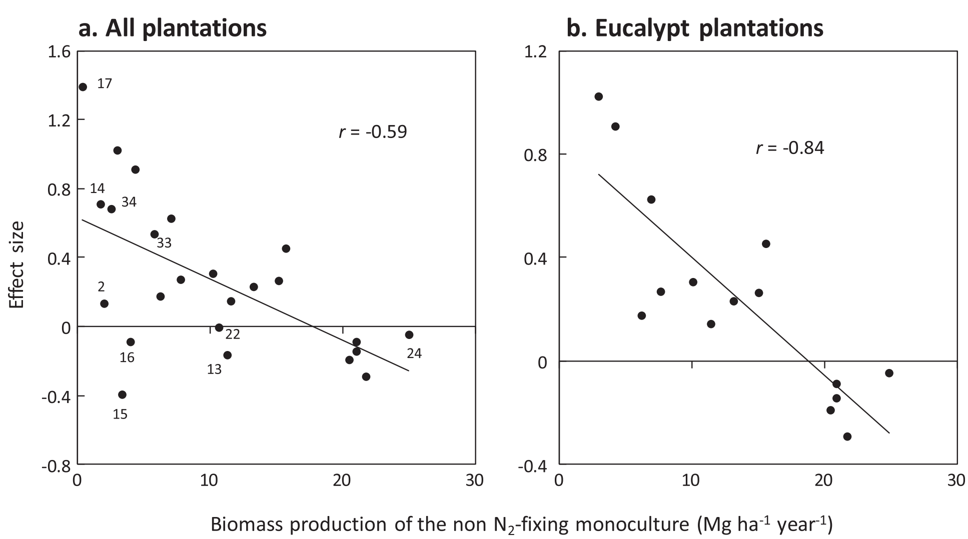

Fig. 5. Relations between site effect size and biomass production for the non N_2-fixing monocultures when expressed in Mg ha^{-1} in the articles, for all plantations (panel a, $n = 25$) and for eucalypt plantations only (panel b, $n = 15$). Numbers on the left panel refer to the numbers of the non-eucalypt plantations in Table 1.

et al., 2011); in Thailand, the podsolic soil carrying the mixed-tree plantation had previously been covered in degraded open woodland of no economic value; in Puerto Rico, the soil was sandy and had been subjected to frequent, and often intense, disturbance for at least a century. For these three sites, the success of the mixed-tree plantations (compared to the monoculture of the non N_2-fixing species) can be attributed to the harsh soil conditions and nutrient limitations. It should be noted that, in Puerto Rico, the higher overall biomass production in the mixture was mostly due to growth in the N_2-fixing species, not in the eucalypt target species, thus limiting the economic interest of the mixture. Interestingly, two tropical mixed-tree plantations in Hawaii were significantly successful even though there were no indication of soil N limitations at these sites (DeBell et al., 1985, 1987); this indicates that harshness of soil conditions and N limitation are not the only factors involved in the success or failure of a mixed-tree plantation.

Concerning mixture proportion (third hypothesis), low proportions of N_2-fixing species in the mixture had no significant impact on biomass production, while high and equal proportions had a more pronounced, and equal, effect (+27%). While for commercial production, the planting density of the species of greater economic value is typically between 70 and 80%, the fifty – fifty mixture proportion may be the most cost-effective option when the target species is not the N_2-fixing species, as higher proportions give similar results and lower proportions do not significantly improve production. This assumes that planting stock of both the N_2-fixing and the target species cost the same. If this is not the case, it might also influence the proportions used in the mixture.

Finally, the mixture effect was slightly, but not significantly, higher in older than younger plantations. With long-term monitoring (i.e. 11 years), Forrester et al. (2004) showed that differences between mixed and pure stands of eucalypt and acacia increased with time, indicating that the synergistic effects of the acacias were long-lasting, and that these effects started rapidly as biomass production peaked early in acacias. Zhang et al. (2012) showed that effect size increased weakly between 1 and 20 years, mostly in tropical plantations. They observed a stronger increase with age between 65 and 75 years, reflecting canopy transition in boreal and temperate forests. The limited age range present in our study did not allow us to consider similar age effects.

It should be noted that our analysis assumes that the biomass from the N_2-fixing species is as desirable for the market as that of the target species, but this may not always be true. Moreover, even if wood production is higher in mixed stands, the economic value of the wood may be lower if the amount of wood produced from the species of higher economic value is lower. However, reliable economic analyses of mixed stands, especially those including their ecological stability, are still scarce (Nichols et al., 2006; Knoke et al., 2008).

4.2. Interaction mechanisms underlying mixture effects

Facilitative and competitive processes have been shown to depend on resource availability, with higher competition in fertile environments and greater facilitation under harsh conditions (Paquette and Messier, 2011). The balance between negative and positive interactions in mixtures shifts in relation with soil fertility (Boyden et al., 2005; Forrester et al., 2006b; Bouillet et al., 2013). We confirmed this pattern; a general negative correlation occurred between biomass production in the monoculture and mixture effect size, meaning that the sites where the mixture was the most successful were those where conditions were the least favourable for growth, in agreement with the stress gradient theory postulated by Bertness and Callaway (1994). This overall effect has also been reported in individual studies comparing contrasting sites in the USA, Australia, Canada and Brazil (Binkley, 1983; Forrester, 2004; Moukoumi et al., 2012; Bouillet et al., 2013, respectively). In Moukoumi et al. (2012), the differences in the success of the mixed-tree plantations at different sites in Canada were probably once again due to soil N limitation; these differences were probably exacerbated by the high planting density (around 15,000 trees per ha) which likely provoked a rapid shading of the N_2-fixing species by the dominant non-fixing species at the most productive site, leading to canopy decline and dieback in the N_2-fixing species. The more positive response to mixing in eucalypt plantations than in plantations with other non-fixing species may be due to lower competition for light; indeed, most eucalypt species have an intrinsically low leaf area index and pendulous leaf position (King, 1997; Nouvellon et al., 2010). More light can therefore reach the lower part of the canopy when the eucalypts grow taller than the N_2-fixing species. Mixed-eucalypt plantations may still fail, however, when competition for another environmental resource is the driving force, as when water availability is low, for example (Nouvellon et al., 2012; le Maire et al., 2013).

4.3. A balance between mixture success and high biomass production

When observing the relationship between site productivity and mixture effect size, it is noteworthy that the outliers are all sites where, despite low productivity, the mixture effect size was negative or only moderately positive. In other words, we found no studies where a highly productive site was associated with a successful mixture. This indicates that harsh conditions are required to promote the success of a mixture, but are not sufficient to ensure it. Outliers in the relationships included sites with non-fixing species other than eucalypts (poplar, pine, willow, Douglas fir); when only eucalypt sites were retained, the correlation coefficient was improved ($r = 0.84$). For sites without eucalypts, no general pattern is obvious because only a few case studies occur for each of the four genera. However, when site conditions are harsh enough to promote mixture success, failure is likely to be due to other factors such as the varying ecological requirements of the two species (Marron et al., 2018). Based on their review of eucalypt / acacia mixtures, Forrester et al. (2005, 2006a), identified three major factors contributing to the success of mixed-tree plantations: compatibility between height growth rates of the two species, choice of an adequate N_2-fixing species, and appropriate site selection. Based on our results, it appears that site condition is the main factor influencing mixture success, and that biomass production of the non N_2-fixing monoculture is a good proxy for site conditions. On the other hand, the choice of the N_2-fixing species does not seem to be of great importance. We found no difference between mixture effect on growth with legumes (associated with *Rhizobium*) and with other N_2-fixing species (associated with *Frankia*), with the caveat that 87% of the N_2-fixing species were legumes in the case studies we inventoried, indicating that other N_2-fixing species are underrepresented in the literature.

5. Conclusions

We found that mixed-tree plantations with N_2-fixing tree species were 18% significantly more productive than the corresponding monocultures of the non-fixing species. This mixture effect was significantly more evident under temperate than under tropical conditions (with a few exceptions). Intermediate mixing proportion gave the best results, with an equal effect for a high proportion of N_2-fixing species. In line with the stress gradient theory, mixed plantations were more productive than monoculture under conditions unfavourable for growth; so, the success of the mixture seemed to be conditioned to a low biomass production. However, almost all studies included in this meta-analysis dealt with short rotation forests. Any extrapolation to forests managed on longer rotations should therefore be done with care.

Our analysis also highlighted some research gaps in the scientific literature: (i) To isolate the underlying drivers, replicating experimental trials with the same combination of N_2-fixing and target species along soil fertility and/or soil water availability gradients would be appropriate; (ii) Tree species associated with *Frankia* actinobacteria are underrepresented in the literature and more experimental trials are needed to test the potential of these species for improving growth in forest plantations. Native nitrogen fixing species may be more easily accepted in ecological contexts where exotic legume trees are either unadapted or undesirable because of their invasiveness; (iii) Our study focused on experiments using the replacement series design but the additive-series design would be more suitable when the non-fixing species is much more productive than the N_2-fixing species (the density of the most productive species would not be reduced and no production would be lost), or when only the production of the non-fixing species is of interest for commercial purposes; (iv) Finally, mixing N_2-fixing tree species with non-fixing tree species potentially increases biomass production, especially in temperate climates. However, regional socio-economic studies are still needed to convince managers – especially those responsible for short rotation plantations for bioenergy – that mixtures can mitigate some of the negative environmental impacts of monocultures without having a negative impact on an owner's income.

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Appendix A. Soil characteristics of the 34 experimental mixed-tree plantations in terms of pH, carbon (C) and nitrogen (N) contents, ratio C/N, sand and clay contents and type. NA: Not available

Location	Site number	pH	C (g kg^{-1})	C/N	N (g kg^{-1})	Sand (%)	Clay (%)	Soil type
Australia, Atherton-Tablelands	1	NA	NA	NA	NA	NA	NA	Humic gley
Australia, Canberra	2	NA	NA	NA	NA	NA	NA	Yellow Kandosol
Australia, Cann-River	3	5.1	2.6	2.4	1.1	NA	NA	Yellow Podzolic
Australia, Eden	4	NA	NA	NA	NA	NA	NA	Brown friable earth
Australia, Nowra	5	NA	NA	NA	NA	NA	NA	Brown loam
Brazil, Bofete	6	4.5	12.0	14.3	0.8	NA	11.8	Ferralsols
Brazil, Itatinga	7	5.5	17.6	19.6	0.9	84.0	13.0	Ferralsols
Brazil, Luiz Antonio	8	4.8	8.5	13.3	0.6	NA	10.1	Ferralic arenosols
Brazil, Minas do Leao	9	4.4	NA	NA	NA	NA	NA	NA
Brazil, Rio de Janeiro	10	4.9	3.6	9.6	0.4	86.5	6.3	Haplic planosol
Brazil, Santana do Paraiso	11	5.5	19.0	11.2	1.7	NA	50.7	Ferralsols
Brazil, São Mateus	12	NA	NA	NA	NA	NA	NA	NA
Canada, Mt. Benson	13	4.2	NA	NA	3.1	NA	NA	Gravelly clay loam Typic Haplorthod
Canada, Laval	14	4.1	27.5	11.0	2.5	NA	NA	Acid loam/orthic dystric brunisol
Canada, Harris	15	5.9	11.8	9.5	NA	85.4	8.6	Loamy sand
Canada, Saskatoon 1	16	7.9	31.4	8.9	NA	13.0	67.4	Clay
Canada, Saskatoon 2	17	8.2	17.3	10.5	NA	52.3	32.9	Sandy clay loam
China, Yuanmou	18	6.2	4.6	NA	0.2	NA	NA	Ferralic arenosols
Congo, Kissoko	19	4.6	6.9	17.3	0.4	91.0	3.0	Ferralic arenosols
England, Gisburn forest	20	NA	NA	NA	NA	NA	NA	Water gleys
France, Ardon	21	NA	NA	NA	4.1	NA	NA	NA
France, Saint-Cyr-en-Val	22	5.6	10.0	12.5	0.8	68.0	9.0	Gleyic luvisol
Iran, Foman	23	4.7	17.1	6.2	2.8	NA	NA	Silty loam
Iran, Mazandaran	24	7.9	21.8	8.2	2.7	NA	NA	Silty loam
Puerto Rico, Tao Baja	25	8.2	NA	NA	NA	NA	NA	Calcareous sand
Spain, Alcala de Henares	26	8.1	NA	NA	NA	NA	NA	Silty loam
Thailand, Ratchaburi	27	NA	NA	NA	NA	NA	NA	Brown Podzolic
USA, Onomea 1	28	4.9	NA	NA	6.0	NA	NA	Thixotropic isomesic typic Hydrandept
USA, Onomea 2	29	5.9	NA	NA	5.0	NA	NA	Thixotropic isomesic typic Hydrudands
USA, Waimanalo	30	NA	NA	NA	NA	NA	NA	Isohyperthermic Vertic Haplustol
USA, Cascade Head	31	NA	NA	NA	NA	NA	NA	Gravelly clay loam
USA, HJ Andrews	32	NA	NA	NA	NA	NA	NA	Gravelly clay loam
USA, Camas	33	NA	NA	NA	0.9	NA	NA	NA
USA, Skykomish	34	4.5	NA	NA	0.9	NA	NA	Silty clay loam Dystric Xerochrept

Appendix B. GPS positioning of the 34 experimental mixed-tree plantations inventoried from the literature on a Google map planisphere (from www.geofree.fr)

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