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# High diversity mixed plantations in Brazil: *Eucalyptus* intercropped with native tree species

**Nino Tavares Amazonas**

Thesis presented to obtain the degree of Doctor in Science. Area: Forest Resources. Option in: Conservation of Natural Ecosystems

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# SUMMARY

RESUMO

**Plantações mistas de alta diversidade no Brasil: *Eucalyptus* intercalado com espécies arbóreas nativas**

O alto custo de se restaurar as florestas tropicais são um dos maiores obstáculos para se atingir a restauração em larga escala. Para superar essa barreira, nós desenvolvemos e implantamos plantações mistas que intercalam *Eucalyptus* e uma alta diversidade de espécies arbóreas nativas. O objetivo é criar condições favoráveis para a regeneração das espécies nativas e, ao mesmo tempo, obter retorno econômico da exploração de eucalipto como uma espécie pioneira comercial. O uso do eucalipto nesse sistema é temporário e ele deve ser substituído por espécies nativa adicionais após ser colhido. Nessa pesquisa, nós cobrimos os principais aspectos e abordagens relacionados aos efeitos da competição sobre o crescimento arbóreo utilizando dados dos nossos experimentos. O objetivo dessa pesquisa foi testar a viabilidade ecológica de plantios que consorciam temporariamente eucalipto e uma alta diversidade de espécies arbóreas nativas durante as fases iniciais da restauração ecológica como uma estratégia para compensar parte dos custos de implantação e manutenção. Essa alternativa é investigada com foco nas consequências das interações ecológicas sobre a sobrevivência e o crescimento das árvores em três experimentos implantados na Mata Atlântica do nordeste e sudeste do Brasil. Nós implantamos e comparamos talhões de espécies nativas intercaladas com eucalipto, plantios de restauração tradicionais e monocultivos de eucalipto. A tese é estruturada em três partes principais com foco em como os plantios mistos funcionam em comparação a plantios de restauração e monocultivos de eucalipto. Nós utilizamos inventários florestais para entender os efeitos da competição e estimamos parâmetros ecofisiológicos para investigar os mecanismos que afetam o crescimento arbóreo quando as árvores competem por água, luz e nutrientes. Na primeira parte do estudo, nó mostramos que os plantios mistos combinaram efetivamente alta produção de madeira com diversidade arbórea; que eucalipto cresceu mais em plantios mistos do que em monocultivos; que espécies nativas cresceram menos em consórcio com eucalipto; e que o efeito do consórcio foi maior para espécies de crescimento rápido e intermediário. Na segunda parte, mostramos que plantios mistos consumiram menos água do que monocultivos; que *Eucalyptus* reduziu a performance hidráulica de uma espécie nativa de rápido crescimento; e que o crescimento das árvores foi influenciado por mudanças na ecofisiologia do uso da água. Na última parte, nós mostramos que uma alta diversidade de espécies arbóreas fixadoras de nitrogênio facilitaram o crescimento de *Eucalyptus*; que *Eucalyptus* teve concentração de N ~30% mais alta na madeira, em plantios mistos; que o crescimento de árvores nativas não foi limitado pela competição por nutrientes com eucalipto; que eucalipto pode se beneficiar de maior disponibilidade de luz em plantios mistos; e que parcelas de espécies nativas interceptaram mais luz do que plantios mistos ou monocultivos de eucalipto. Essa pesquisa tem uma forte interface entre a ciência e a prática da restauração, e contribuiu para o desenvolvimento de novas maneiras de se restaurar as florestas tropicais por meio da aliança entre restauração e produção sob as perspectivas ecológica e econômica. Nossas descobertas indicam como avançar no futuro, a partir do estado da arte atual, em direção a sistemas de restauração florestal que minimizem a competição e maximizem o crescimento, como uma alternativa emergente e promissora para compensar os custos da restauração e superar a barreira econômica que ainda impede a restauração em larga escala. Essa pesquisa pode ser utilizada como uma base para se continuar adaptando a silvicultura a diferentes regiões e ecossistemas florestais. Olhando para o futuro mais distante, esses plantios mistos podem também representar um ponto inicial de um novo modelo de silvicultura que alia produção e conservação. A informação disponibilidade deve ser utilizada por cientistas, tomadores de decisão, planejadores e restauradores para avançar com a ciência e a prática da restauração e da silvicultura nos trópicos.

Palavras-chave: Plantações mistas de alta diversidade; Restauração de florestas tropicais; Crescimento arbóreo; Ecofisiologia florestal

# ABSTRACT

## High diversity mixed plantations in Brazil: *Eucalyptus* intercropped with native tree species

The high cost of restoring tropical forests is one of the greatest obstacle to achieving large-scale restoration. To overcome this barrier, we developed and implemented mixed plantations intercropping *Eucalyptus* with a high diversity of native tree species. The aim was to create favorable conditions for the regeneration of native species while simultaneously obtaining economic return from the exploitation of *Eucalyptus* as a commercial pioneer species. The use of *Eucalyptus* in this system is temporary and it shall be replaced by additional native species after it is harvested. In this research, we covered the main aspects and approaches of the effects of competition on tree growth using data from our restoration experiments. The objective of this research was to test the ecological viability of plantations that temporarily mix *Eucalyptus* spp. and a high diversity of native tree species during the initial phases of forest restoration as a strategy to offset implementation and maintenance costs. This alternative is investigated with a focus on the consequences of ecological interactions on tree survival and growth in three experiments implemented in the Atlantic Forest of Northeastern and Southeastern Brazil. We compared stands of native trees intercropped with *Eucalyptus*, traditional restoration plantations, and *Eucalyptus* monocultures. The thesis is structured in three main parts in which we focus in how the mixtures function compared to restoration plantations and *Eucalyptus* monocultures. We used forest inventories to understand the effects of competition and assessed ecophysiological parameters to provide insights about the mechanisms that affect tree growth when trees compete for water, light and nutrients. In the first part of the study, we showed that mixed plantations effectively combined high wood yield and tree diversity; that *Eucalyptus* grew larger in mixtures with native species than in monocultures; that native tree species grew less in mixtures with *Eucalyptus*; and that the mixing effect was stronger for fast- and intermediate-growing native species. In the second part, we found that mixtures consumed less water than monocultures; that *Eucalyptus* reduced the hydraulic performance of a fast-growing native species; and that tree growth was influenced by changes in the ecophysiology of water use. In the last part, we showed that a high diversity of nitrogen-fixing native trees facilitated *Eucalyptus* growth; that *Eucalyptus* had ~30% higher wood N concentration in mixtures; that native trees growth was not limited by nutrient competition with *Eucalyptus*; that *Eucalyptus* may benefit from increased light availability in mixed plantations; and that native species plots intercepted more sunlight than mixtures or *Eucalyptus* stands. This research has a strong interface between restoration science and practice, and contributed to the development of new ways to restore the tropical forests by allying restoration and production under the ecological and economic perspectives. Our findings indicate how to advance into the future, starting from the current state of art towards forest restoration systems that minimize competition and maximize growth, as an emergent promising alternative to finance tropical forest restoration and overcome the economic barrier that still holds large-scale restoration. This research may be used as a basis to continue adapting silviculture for different regions and forest ecosystems. Looking further into the future, these mixtures may also represent the starting point of a new silvicultural model that brings together production and conservation. The information available may be used by scientists, decision-makers, planners and restorationists to advance in the science and practice of restoration and silviculture in the tropics.

Keywords: High diversity mixed plantation; Tropical forest restoration; Tree growth; Forest ecophysiology

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# 1. INTRODUCTION

Nature has an intrinsic value of existence that is beyond the human perspective and has values for human societies that are both material and immaterial. Our modern societies are dependent on forests and other ecosystem types for the provision of goods and services and the way we manage natural resources have great impacts on biodiversity, the resilience and functioning of ecosystems and on the climate, at various scales. From an economic perspective, forests are important for many sectors such as the construction, food and pharmacological industries (FAO, 2016a). From a cultural perspective, forests provide cultural services (Daniel et al., 2012), recreation and are part of the identity of many communities. From a conservation perspective, forests harbor a great percentage of Earth's biodiversity (Beech et al., 2017a). To obtain what we need from forests, we manage natural, semi-natural and artificial forests using forestry systems that vary greatly in complexity, which results in considerable differences in forest structure and diversity.

Nowadays, forests are valued and desired, but achieving forest conservation and production goals is still a challenge (Rands et al., 2010). Many efforts are made to protect the remaining natural forests, to restore degraded forest lands and to exploit natural forests sustainably. Allied with this, is the development of commercial silviculture to provide forest products and alleviate the pressure on natural forests. Many different forestry systems were designed, tested and adopted, which are continuously being improved through the development of forestry techniques, mixed plantations, domestication of new tree species, artificial selection, hybridization, establishment of clonal plantations and even the recent use of genetically modified organisms.

The history of how humans influence forests is complex and as long as our own history (Chazdon, 2014). The management of the ecosystems on Earth have caused great variation in forest cover. As our capacity to convert natural systems into other types of land use increased, forest cover decreased to make space for human settlements, agriculture and other industrial activities. These complex patterns changed between the different regions and are explained by natural, climatic, demographic, economic, technological, cultural and other factors. Despite the still dynamic nature of land-use change, which is especially rapid in tropical regions, a recent increase in forest cover, known as forest transition (Mather, 1992), has been observed on the planet, and generally results from decreasing deforestation rates combined with the expansion of forest cover through natural regeneration, ecological restoration and the establishment of artificial commercial forests. This process is a global pattern with regional differences mainly driven by markets and legal factors. The restoration of forest landscapes is an important contribution to the forest transition and there is demand for the development of new forestry systems that attain multiple objectives. Today, most of the conversion from non-forest land use types into forests is surrounded by uncertainties and will only happen if silvicultural systems are flexible enough to be adapted according to changes in legal, financial and environmental conditions. These conversions occur mainly by the second growth of cleared natural forests, by the implementation of commercial silviculture stands and by forest restoration. Restoration may have high opportunity costs and enormous gains may be obtained if we develop and implement flexible systems that can be directed towards ecological restoration or forestry for wood production by adaptive management. This may be possible using mixed plantations.

Mixed species silviculture in the tropics is an emergent field that needs urgent development to meet the international demands for production and conservation. These new forestry systems need to be tested for their ecological and economic feasibility. Here, we test the effects of intercropping native species with *Eucalyptus* on tree survival and growth in three different experimental sites in Brazil.

Several national scale initiatives have made considerable efforts to promote large-scale restoration, with examples in the United States of America (Doyle e Drew, 2008), in Costa Rica (Arriagada et al., 2012; Sánchez-Azofeifa et al., 2007), in India, in the Republic of Korea, in South Africa, in Rwanda and also Colombia, Ecuador and Mexico (Aronson e Alexander, 2013; Murcia et al., 2016). During the Convention of the Parties, in 2010, an Strategic Plan for Biodiversity was defined for the period between 2011 and 2020. That document establishes in the aim 15 of the "*Aichi Biodiversity Targets*" that, by 2020, at least 15% of the world's degraded ecosystems must be restored (http://www.cbd.int/sp/targets/). In 2011, a ministerial conference in Bonn, Germany, established the aim of restoring 150 million hectares on the planet by 2020. In 2014, several organizations signed The New York Declaration on Forests and committed to make efforts towards the restoration of 150 million hectares of degraded lands by 2020 and another 200 million hectares by 2030 (United Nations, 2014). This perspective of expanding restoration initiatives though multi-sectorial coalitions has also been adopted at national scales, independently or derived from international agreements. In Brazil, the Pact for the Restoration of the Atlantic Forest (Pacto pela Restauração da Mata Atlântica, in Portuguese), aims at restoring 15 million hectares by 2050, in the 17 states where the ecosystem naturally exists (Rodrigues et al., 2009) and the National Plan for the Restoration of the Native Vegetation, the main public technical guideline tool for the implementation of the new federal law for the protection of the natural vegetation, has a goal of restoring 12 million hectares.

Despite the existence of initiatives at global, national and smaller scales, the leveraging of ecological restoration is still a great challenge. To achieve the goals of large-scale restoration, in Brazil, several obstacles need to be overcome. Amongst the barriers, are limitations in the technical, legal and economic spheres, governance problems, lack of trained human resources, lack of a specific market, not enough availability of seeds and seedlings in the quantity and diversity needed, and lack of information and environmental awareness. The main obstacle, however, is the cost-effectivity relationship that is still very discouraging, in a simplistic analysis, for rural landowners. Two possible approaches to change this scenario are the reduction of restoration costs and the generation of profit from the restoration activity, which can ideally be combined. Most of the restoration costs come from the implementation (fencing, soil preparation, seedlings and other inputs) and from the maintenance phase, especially weed control (Brancalion et al., 2012).

Currently, some initiatives focused on overcoming the financial obstacle for large-scale restoration are under development. There are proposals for the commercial exploitation of timber of high valued native species; but the time between plantation and harvesting is too long and there are many uncertainties regarding the silvicultural systems adopted and the quality of the wood produced in the future. Technological innovation, such as the mechanized plantation of native forest seeds, developed by “Grupo Mutirão Agroflorestal” and further improved by “Instituto Socioambiental-ISA”, in Mato Grosso, central Brazil, which achieved promising results and great cost reductions, although is restricted to degraded areas that can be mechanized and where seeds can be obtained for low prices (Durigan et al., 2013). Besides reducing costs, another possibility is profiting from restoration. It is necessary to transform restoration into an economically viable activity to make it more attractive to landowners and to displace low profit agricultural uses on marginal areas (Latawiec et al., 2015).

The demand for the development of a new profitable restoration system came up through exchanges with economists and executives from the forestry sector, which pointed to the need to anticipate the economic return of restoration projects. This anticipation of profits is essential for amortizing the elevated costs of forest implementation, which after 20 to 30 years of interest incidence and monetary correction would impair the project financially even if high value timber was harvested. The early harvest of lower value timber could eventually pay for most of the implementation costs within one rotation. Additionally, most restoration projects use around 50% of short lived trees which could be replaced by fast-growing commercial species in the beginning of the project, which could help to build the initial forest structure and also provide profit.

Aiming at overcoming the financial obstacle that hinders large-scale restoration in the Atlantic Forest, the Laboratório de Silvicultura Tropical (LASTROP) and the Laboratório de Ecologia e Restauração Florestal (LERF) from Escola Superior de Agricultura Luiz de Queiroz (ESALQ) of Universidade de São Paulo (USP), in partnership with the NGO Organização para a Conservação da Terra (OCT) and the companies Fibria Celulose S.A. and Suzano Papel e Celulose S.A. and collaborating with the Pacto pela Restauração da Mata Atlântica (PACTO), planed and implemented several forestry systems intended at improving the cost-effectivity relationship of tropical forest restoration of Legal Reserves within rural properties in the Brazilian Atlantic Forest. These experiments test directly the basis of the Brazilian National Law for the Protection of Native Vegetation (Brasil. Presidência da República, 2012), that allowed forest restoration through the intercropping of native and exotic tree species within the Legal Reserves of rural properties. The systems were implemented to test the concept of commercial pioneer species (exotic and native). These species are planted to play the role of pioneers and be harvested at the end of their production cycle. The profit must pay partially or totally, for the restoration costs and possibly generate profit, creating a favorable economic scenario for the future exploitation of high value native timber intercropped with the commercial pioneer trees. These pioneers shall contribute with the rapid formation of a forest, shading the soil and outcompeting invasive grasses, favoring secondary succession and the establishment of species characteristic of later successional stages. It has been demonstrated that grass control favors the survival and initial growth of native trees in restoration plantations (Campoe et al., 2010).

The species of the genus *Eucalyptus* may serve as good commercial pioneer species, since their cultivation is well known; *Eucalyptus* has a strong market, good prices and is easily traded; its short rotation offers the opportunity of early financial gains; the species are generally not invasive; they can play the role of pioneers and outcompete grasses; their implementation costs are low compared to a great variety of native species, especially for the low cost of seedlings (roughly three times cheaper on average). Additionally, *Eucalyptus* has multiple uses and may interest landowners to be used within their property regardless of the selling prospects.

In 2016, the area planted with *Eucalyptus* in Brazil reached 5.7 million hectares, representing 72% of all planted forests in the country. Other important genera are *Pinus* (1.6 million ha), *Hevea* (230 thousand ha), *Acacia* (160 thous. ha), *Schizolobium* (90 thous. ha), *Tectona* (87 thous. ha), *Araucaria* (11 thous. ha), *Populus* (4.2 thous. ha) and others (6.6 thous. ha) (Indústria Brasileira de Árvores, 2017). Most of the *Eucalyptus* planted in Brazil is within the Atlantic Forest region and the vast extension of the plantations highlights the strategic importance of developing systems adapted to the forestry sector, creating the necessary conditions for the expansion of the area under restoration. The forestry sector was responsible for 3.4% of the national gross primary product (Sociedade Brasileira de Silvicultura, 2008). Beyond its economic importance, recent research showed that commercial forest plantations favor natural regeneration and are even considered to facilitate forest restoration (Viani et al., 2010).

The challenge of conciliating production and nature conservation remains one of the biggest problems of our society (Godfray et al., 2010; Rands et al., 2010) and compromises the provision of the goods and services we obtain from natural ecosystems (Foley, 2005). The global demand for production land continues to grow (FAO, 2016a) and sustainable production allied with the conservation of forest biodiversity still needs to be achieved (Robertson e Swinton, 2005). Forest landscape restoration (Lamb, 2005) is a modern approach that contributes to the expansion of forest cover and integrates production and conservation at the landscape level. The increase in forest cover includes a variety of silvicultural systems (Wagner et al., 2013) with different specific objectives, from production to conservation, and the use of exotic and native species.

The objective of this research was to test the ecological viability of plantations that temporarily mix *Eucalyptus* spp. and a high diversity of native tree species during the initial phases of forest restoration as a strategy to offset restoration implementation and maintenance costs. This alternative is investigated with a focus on the consequences of ecological interactions on tree survival and growth in three experiments implemented in the Atlantic Forest of Northeastern and Southeastern Brazil. We implemented and compared stands of native trees intercropped with *Eucalyptus*, traditional restoration plantations, and *Eucalyptus* monocultures. We used forest inventories to understand the effects of competition and assessed ecophysiological parameters to provide insights about the mechanisms that affect tree growth when trees compete for water, light and nutrients. The thesis is structured in three main parts in which we focus in how the mixtures of *Eucalyptus* and a high diversity of native tree species function compared to restoration plantations and *Eucalyptus* monocultures.

In the first part of this research, we test this new silvicultural system to understand the consequences of the mixed plantation on tree survival and growth. We raised the following questions and hypotheses: (I) What are the consequences of intercropping *Eucalyptus* and native species? (II) Is size of neighboring trees the only factor influencing target tree diameter? (III) How do different native species respond to the intercropping with *Eucalyptus*? We tested the following hypotheses: (i) *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species is lower when intercropped with *Eucalyptus*; (ii) The diameter of target native trees is influenced by the size and by the identity of neighboring trees; (iii) The negative effect of competition from *Eucalyptus* on native species is directly related to their growth rate. We compared survival rate and growth, using inventory data and neighborhood analyses.

In the second part, we investigated how tree growth was influenced by water use and tree hydraulic performance. Our questions and hypotheses were: (I) What is the impact of high diversity mixed plantations of *Eucalyptus* intercropped with native trees on soil water? (II) How does the mixture affect the physiology of water use in native trees? We tested the hypothesis that (i) stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures, by measuring the temporal dynamics of soil water. Secondly, we tested if (ii) the mixing with *Eucalyptus* affects the hydraulic performance of fast- and slow-growing native species, by assessing the leaf water potential and the stomatal conductance of model species.

In the third part, we examine the influence of light and nutrient competition on the growth of trees in mixtures. This part of the research was oriented by the following questions and hypotheses: (I) Are N-fixing native species facilitating the growth of *Eucalyptus*? (II) Is the increased growth of *Eucalyptus* a result of higher nutrient acquisition in mixtures with native species? (III) Is the reduced growth of native species caused by competition from *Eucalyptus* for nutrients? (IV) Is competition for light important in these systems? First, we tested if (i) *Eucalyptus* trees were facilitated by N-fixing native tree species. Secondly, we hypothesized that (ii) *Eucalyptus* had higher nutrient concentrations in leaves and wood tissues in mixed plantations. Then, we tested if (iii) native species intercropped with *Eucalyptus* had lower nutrient concentration in leaves and wood than in native species plots. Lastly, we tested the hypothesis that (iv) the mixed forest had a denser canopy that intercepts more sunlight than the control treatments.

Finally, we finish with a summary of the main results of each part. As general considerations, we give practical recommendations of how to improve these new forestry models, based on the knowledge built. In the end, we raise important questions, pointing to perspectives for future research.

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# 2. HIGH DIVERSITY MIXED PLANTATIONS OF *EUCALYPTUS* AND NATIVE TREES: AN INTERFACE BETWEEN PRODUCTION AND RESTORATION FOR THE TROPICS

ABSTRACT

Despite the high diversity of trees in the tropics, very few species have been used in plantations. In a scenario of high international demand for nature conservation and for the provision of forest products, mixed species forestry in the tropics emerges as a promising option. In this study, we examine three large experiments that combine early *Eucalyptus* wood production with a high diversity of native tree species. We tested the following hypotheses: 1) *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species is lower when intercropped with *Eucalyptus*; 2) The diameter of target native trees is influenced by the size and by the identity of neighboring trees; 3) The negative effect of competition from *Eucalyptus* on native species is directly related to their growth rate. We compared mixtures of *Eucalyptus* and a high diversity of native tree species with *Eucalyptus* monocultures and with plots containing only native species. To test our hypotheses, we examined inventory data considering the stand- and the tree-levels. We calculated survival rate, diameter and height growth and basal area of whole stands and groups of species. We also used a neighborhood index analysis to separate the effect of total competition (i.e. stand density) and the influence of groups of species (intra- and inter-specific competition). The *Eucalyptus* trees in high diversity mixtures yielded nearly 75% of the basal area produced by *Eucalyptus* monocultures even though this species accounted for only 50% of seedlings in the mixtures. In the mixtures, individual *Eucalyptus* trees grew larger than in monocultures, and negatively affected the growth of native species proportionate to the native species' growth rate. With some exceptions, the mixed plantations had no overall effect on tree survival or height growth. The slower growth of native species is not of major concern in the short-term. We conclude that mixtures of *Eucalyptus* and a high diversity of native tree species are feasible and represent a potential alternative for establishing multipurpose plantations, especially in the context of forest and landscape restoration.

Keywords: Forest landscape restoration; High diversity mixed plantations; Mixing effect; Native species timber; Sustainable forestry; Tropical forest restoration

## 2.1. Introduction

Tropical forests host the vast majority of tree species on Earth (Beech et al., 2017b; Slik et al., 2015), but this potential remains underutilized as modern tropical silviculture is still dominated by monospecific plantations of a few genera, especially *Eucalyptus*, *Pinus*, *Acacia*, and *Tectona* (Kelty, 2006). Apart from being simplified from a biodiversity perspective, monocultures can also have a lower capacity to provide the ecosystem goods and services provided by diverse forests (Bauhus et al., 2017; Lindenmayer et al., 2012) in the context of forest landscape restoration. The combined outcomes of providing ecosystem services while delivering timber and non-timber products may be improved when production and conservation objectives are balanced and integrated. However, a complex set of factors currently hinder the adoption of alternative systems (Puettmann et al., 2015).

New forestry systems could be designed as stable mixes where species do not outcompete each other and may result in plantations that have ecological and economic resilience (Lamb, 2005). Mixed plantations usually comprise two to four species and are often only preferred when they produce a higher quantity or quality of wood (or biomass) than monocultures (Kelty, 2006), regardless of their benefits for biodiversity and ecosystem services. Together with the demand for timber products, there is growing international demand for forest and landscape restoration and for forests that can be used to achieve multiple objectives (Brancalion and Chazdon, 2017; Chazdon et al., 2017; FAO, 2016). In this scenario, mixed species forestry in the tropics emerges as a promising option to meet international demands for production and conservation at the stand and landscape scales while contributing to restoration objectives (Lamb, 2005) and serving as complementary forest habitat for wild species.

In this study, we explore a silvicultural option for the tropical region of Brazil that intercrops a fast-growing species of *Eucalyptus*, widely used by the industry and farmers in the tropics, with a high diversity of native tree species. In other tropical regions, mixtures of native tropical species, sometimes including *Eucalyptus*, have demonstrated that these systems can result in greater individual tree and stand productivity than monocultures and that the diversity of tree species is reflected in the diversity of growth responses and in the flexibility of potential silvicultural regimes (Erskine et al., 2006, 2005; Montagnini et al., 1995; Nguyen et al., 2014). For example, *Eucalyptus* can reduce establishment costs by providing early income from wood production, while planting native species can potentially enhance the conservation value of plantations and serve as an option for high value timber exploitation in the longer term.

An important challenge for the design of this new type of mixtures is to prevent the seedlings of the native species from becoming suppressed by *Eucalyptus*, which may result in reduced growth and/or high mortality, thus compromising the conservation value of mixtures in comparison with monocultures. The use of a fast-growing *Eucalyptus* species in this system aims to provide a rapid economic return due to its relatively short cycle, but is a challenge for its conservation viability. *Eucalyptus* species have been subject to extensive genetic improvement programs and are managed under intensive silvicultural regimes to achieve high biomass yield (Gonçalves et al., 2013), which is associated with a high demand for local resources. Commercial varieties of *Eucalyptus* might be, in comparison to native fast-growing trees, more efficient in acquiring and using the available water, light and nutrients. Native species have not gone through breeding programs and show a wide range of growth rates. This genetic diversity is desired for conservation purposes. It is necessary to understand how *Eucalyptus* and native species interact in these mixed plantations and further improve these systems to minimize competition while maximizing both wood production and restoration outcomes.

In this study we examined mixed plantations of *Eucalyptus* and a high diversity of native species using large experiments controlled for species diversity, stand density, age, disturbance regime and site characteristics such as soil type, topography and climate. We analyzed inventory data at the stand and tree levels from three different experimental sites in eastern Brazil containing (i) mixed plantations of *Eucalyptus* and a high diversity of native trees, (ii) *Eucalyptus* monocultures, and (iii) plantations composed exclusively of native trees. To investigate the silvicultural viability of these mixtures to produce high yields of *Eucalyptus* wood in mixed plantations with a high diversity of native tree species, our objective was to answer the following questions: What are the consequences of intercropping *Eucalyptus* and native species? Is the size of neighboring trees the only factor influencing target tree diameter? How do different native species respond to the intercropping with *Eucalyptus*? We tested the following hypotheses: 1) *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species is lower when intercropped with *Eucalyptus*; 2) The diameter of target native trees is influenced by the size and by the identity of neighboring trees; 3) The negative effect of competition from *Eucalyptus* on native species is directly related to their growth rate.

## 2.2. Material and Methods

### 2.2.1. The Mixed Forests and the control treatments

We implemented three experimental sites with three treatments, where mixture plots (hereafter MIX) contained rows of clonal *Eucalyptus* alternating with high diversity rows comprising of 23-30 native tree species (hereafter, diversity group); monospecific *Eucalyptus* stands (hereafter EUC) as the control for *Eucalyptus*; and plots planted with native species (hereafter NAT), as the control for native tree species, in which we used the same 23-30 native species (diversity group) that were intercropped with *Eucalyptus*, but *Eucalyptus* rows were replaced by rows containing a mix of 9-10 fast-growing shading native tree species (APPENDIX A). All seedlings in each experimental site were planted at the same time and were cultivated with the same silvicultural techniques commonly used in short-rotation *Eucalyptus* plantations in the region. This includes fertilization according to *Eucalyptus* nutritional demands for the local soil conditions, grass control with glyphosate spraying, ant control with insecticide baits and replanting after very low mortality within 1-2 months. All treatments of a given experimental site had the same spacing between the rows and between trees within rows.

### 2.2.2. Study sites and experimental design

We implemented three experimental sites within the Atlantic Forest region along the Brazilian East coast, located in Aracruz, ES, Mucuri, BA, and Igrapiúna, BA. The geographic distribution of the experimental sites represents a gradient of latitude, altitude, precipitation and temperature (Table 1; APPENDIX B). To control for the variability of ecological interactions, each native species was planted in the same position within all plots. The list of species used in each treatment is shown in APPENDIX C. Stand development is illustrated in Figure 1 and the visual difference between mixtures and native species plots is shown in Figure 2.

**Table 1.** Characteristics of study sites. MIX= native trees intercropped with *Eucalyptus*; NAT= native trees intercropped with fast-growing shading native tree species; EUC= *Eucalyptus* monoculture.

| | 1 Aracruz-ES | 2 Mucuri-BA | 3 Igrapiúna-BA | References |
|---|---|---|---|---|
| Coordinates | 19°49′12″S, 40°16′22″W | 18°05′09″S, 39°33′03″W | 13°49′0″S, 39°9′0″W | |
| Altitude | 41 m | 78 m | 121 m | (Alvares et al., 2013) |
| Annual average rainfall | 1,412 mm | 1,531 mm | 2,191 mm | (Alvares et al., 2013) |
| Annual average air temperature | 23.4°C | 23.9°C | 25.0°C | (Alvares et al., 2013) |
| Climate Köppen | Aw; with a dry cold winter and a hot wet summer | Af; | Af; without a dry season | (Köppen, 1936) |
| Water deficit | Feb-Sep | Jan-Apr | Nov-Mar | (Sentelhas et al., 2013a, 2013b, 2013c) |
| Soil | Typical Yellow Argisol (Ultisol); sandy/medium/clayey texture | Argisol; clayey (40%) | Dystrophic Yellow-Red Oxisol; clayey | (EMBRAPA. Centro Nacional de Pesquisa de Solos, 2000; EMBRAPA, 2013) |
| Relief | Flat | Flat | Rounded hills with soft slopes; | (Ab'Sáber, 2003) |
| Experimental design | Randomized block design; 5 blocks | Randomized block design; 4 blocks | Randomized block design; 6 blocks | |
| Treatments | MIX; NAT; EUC | MIX; NAT; EUC | MIX; NAT | |
| Planting date | July 2011 | May 2012 | June 2011 | |
| Experimental area | 11.23 ha | 10.37 ha | 3.24 ha | |
| Total number of seedlings | 9,600 | 11,520 | 5,400 | |
| Plot area | 2,160 $m^2$ | 2,160 $m^2$ | 1,080 $m^2$ | |
| Number of seedlings in effective plot | 120 | 120 | 130 | |
| Plot design | 10 rows of 24 trees; two outer rows as border | 10 rows of 24 trees; two outer rows as border | 15 rows of 12 trees; one outer row as border | |
| Seedlings per hectare | 1,111 | 1,111 | 1,667 | |
| Spacing | 3x3 m | 3x3 m | 3x2 m | |
| Eucalypt planted | *E. grandis* x *E. urophylla* | hybrid of *E. urophylla* | 4 different clones | |
| Fast-growing shading native tree species | 10 species | 10 species | 9 species | |
| Native species of the diversity group | 30 species | 28 species | 23 species | |

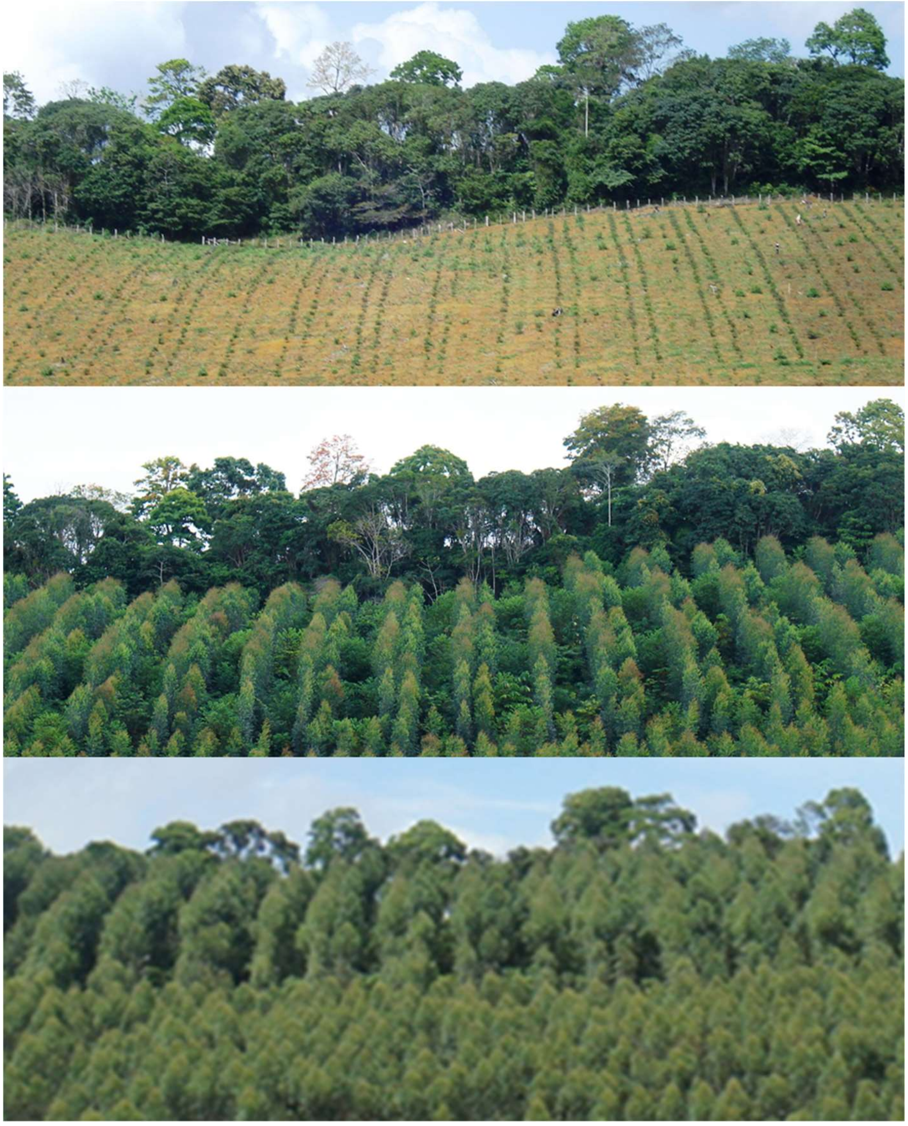

**Figure 1.** Stand development at the experimental site in Igrapiúna, BA, Brazil. One week after planting (upper image), 30- (middle) and 44-months after planting (bottom).

**Figure 2.** View of mixture (left) and native species (right) plots, in Aracruz, Espírito Santo State, Brazil. Picture taken 51 months after planting. Notice the difference in height between *Eucalyptus* and native trees and the two-layered canopy in mixture plots, with *Eucalyptus* above and native species crowns. bellow.

### 2.2.3. Data Collection

We measured the survival rate while considering planted trees of any size. The Diameter at Breast Height-DBH (cm) and total height (m) were measured for all planted trees ≥ 1.3 m tall. Dead trees were not measured. In the experimental sites of Aracruz and Mucuri, trees that branched below 1.3 m had up to five of the largest stems measured. In Igrapiúna, we measured up to three of the largest stems. Height data was not available for the experiment in Igrapiúna. We inventoried the experiment in Aracruz at 38, 51 and 58 months after planting; the one in Mucuri at 48 months; and the one in Igrapiúna at 31, 45, 53 and 60 months after planting.

### 2.2.4. Data analysis

We divided species into different functional groups within each site according to their taxonomic identity and growth rate. These included *Eucalyptus*, fast-growing shading native tree species, and all other native species grouped in terms of fast- (DBH>10 cm), intermediate- (DBH between 5 and 10 cm), and slow-growth rates (DBH< 5 cm). Native species growth-rate classification was based on the mean diameter of native species intercropped with fast-growing shading native tree species in the native species plots recorded in the last inventory of each site (APPENDIX D).

### 2.2.5. Growth and survival in mixtures compared with Eucalyptus or native species plots

To test the hypotheses that *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species was lower when intercropped with *Eucalyptus*, we compared their survival, diameter growth, height growth and basal area in all inventories and sites. We compared these variables between treatments at the stand level (community) using Welch's Two Sample t-test.

### 2.2.6. 2.4.2 The influence of neighbor size and identity on the diameter of target native trees

At the stand level, there were only three treatments, however at the neighborhood level, where a neighborhood could include the neighbors of a given target tree within different search radii, there is a much greater number of taxonomic diversity, functional diversity and stand density (due to differences in tree sizes). To test if the diameter of target native trees is influenced by the size (DBH) and by the identity (species functional group) of neighboring trees and the spatial scale (neighborhood search radii) to which these interactions occur, we examined the relationship between the diameter of target trees and a neighborhood index of target groups. We used inventory data to calculate neighborhood indices to quantify spatial (across site) and temporal tree interactions and growth dynamics. We performed tree-level analyzes to separate the effects of stand density from the effects of species composition on the growth of trees in the mixed species plots and used this to facilitate the interpretation of the stand-level analysis. This approach allows the partitioning of total competition effects into the effects of inter- and intra-functional group competition.

Trees were mapped at each site and we defined four neighborhood search radii to calculate the neighborhood index as the sum of neighbor diameters within a given radius. When there was no mortality, radius A included the four first order neighbors and corresponded to 3.1 m; radius B included eight neighbors and corresponded to 4.3 m in Aracruz and Mucuri and to 3.7 m in Igrapiúna; radius C included 20 neighbors and corresponded to 6.1 m in Aracruz and Mucuri and 4.1 m in Igrapiúna; radius D included 24 neighbors and corresponded to 8.5 m in Aracruz and Mucuri and 6.1 m in Igrapiúna. We avoided neighborhoods that exceeded the effective plot borders. We used the *nlme* (Pinheiro et al., 2016) package perform a linear mixed effects analysis of the relationship between the diameter of target trees and Neighborhood Index (NI) of the form shown in Equation 1. All statistical analyses were performed in R 3.2.1 (R Core Team, 2016).

$$y_{tijkl} = X_{tijkl}\,\beta + Z_{ijkl}\,b_{ijk\,l} + e_{tijkl} \quad (1)$$

With random effects:

$$b_i \overset{iid}{\sim} N(0,\sigma_i^2);\ b_{ij} \overset{iid}{\sim} N\left(0,\sigma_{ij}^2\right);\ b_{ijk} \overset{iid}{\sim} N\left(0,\sigma_{ijk}^2\right);\ b_{ijk\,l} \overset{iid}{\sim} N\left(0,\sigma_{ijk\,l}^2\right);\ \varepsilon_{tijk\,l} \overset{iid}{\sim} N(0,\sigma^2)$$

where $y_{tijk}$ is the dependent variable (DBH), $X_{tijkl}$ is the independent variables matrix (fixed effects matrix which included age, species functional groups (with an interaction term between NI and species group)), $Z_{ijkl}$ is the random effects matrix, $\beta$ and *b* are the parameters' vector of fixed and random effects, *t* is the index for time of measurement*, i* is the index for site, *j* is the index for block, *k* is the index for plot, *l* is the index for tree, $e_{tijkl}$ is the error component, $\rho$ is the autocorrelation coefficient and $\varepsilon_{tijkl}$ is the within group error vector. Visual evaluation using residual plots did not reveal any obvious deviation from normality or homoscedasticity. We used mixed models to be able to analyze data from repeated inventories of the same sites in different ages and to control for differences between sites, blocks and plots.

### 2.2.7. 2.4.3 Competitive effect of Eucalyptus in relation to native species growth rates

To test if the negative effect of competition from *Eucalyptus* on native species was related to their growth rate, we compared the diameters of trees in each diversity group in mixture and the control at the stand and tree-levels. At the stand level, this comparison was performed using a linear regression, by plotting the mean diameter of a species growing in mixture versus its mean diameter in control, for all different sites and ages measured. Then, we contrasted the fitted line against the null model (slope = 1). The lower the slope, the greater the competitive effect.

At the tree level, we performed a linear regression of tree diameter (DBH) as a function of total neighborhood index. The steeper the slope, the greater the effect of NI on DBH. We accounted for the effects of the different diversity groups based on the different growth rates (fast-, intermediate-, and slow-growth), the four different search radii, and the total neighborhood index as the sum of the diameters of all trees around a given target tree with a given search radius.

## 2.3. Results

### 2.3.1. Species' performance in mixtures of Eucalyptus and a high diversity of native trees

Total basal area was higher in stands of *Eucalyptus* monoculture, intermediate in mixtures and lowest in native species plots Figure 3.

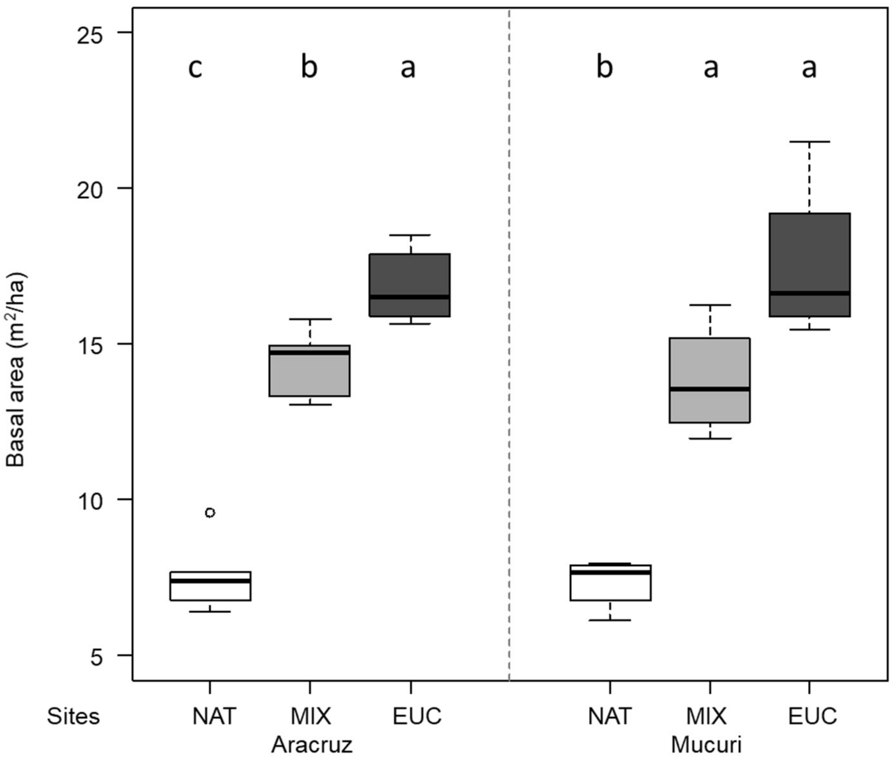


**Figure 3.** Total basal area in three different forestry systems planted in Eastern Brazil: Native species (NAT) (fast-growing shading native tree species + native species of the diversity group, 1:1), Mixture (MIX) (*Eucalyptus* + native species of the diversity group, 1:1); *Eucalyptus* monoculture (EUC). In Aracruz, ES, trees were aged 57 months and in Mucuri, BA, trees were aged 48 months.

Individual *Eucalyptus* trees had larger diameters in the mixed plantation than in monoculture ($p<0.01$), achieving an average increase of 21.4% in Aracruz and of 18.2% in Mucuri. In the mixture (555 *Eucalyptus* trees/ha), *Eucalyptus* alone produced approximately 75% of the basal area ($p<0.001$) produced in *Eucalyptus* monocultures (1,111 trees/ha). *Eucalyptus* survival and height were similar in monoculture and in mixtures with native trees (Figure 4; APPENDIX E).

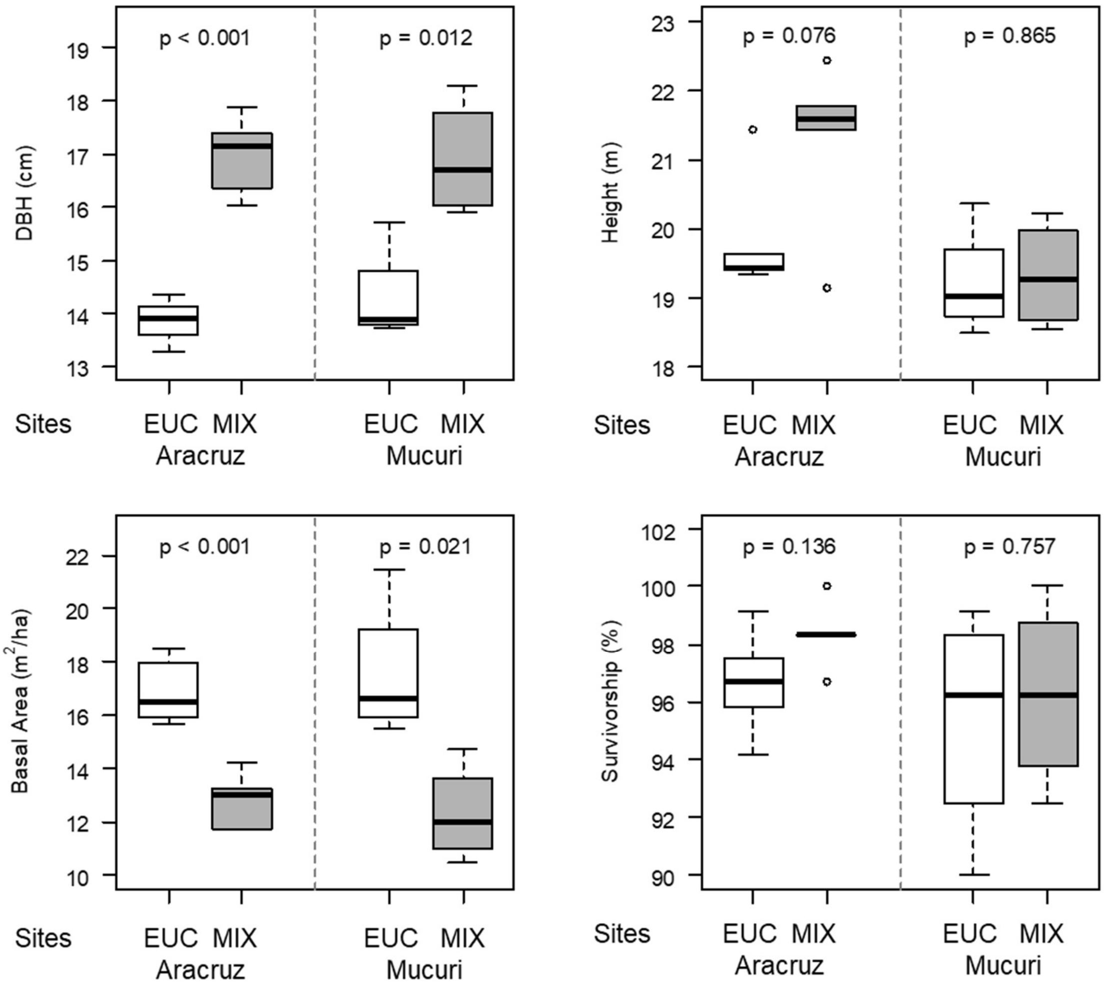


**Figure 4.** Comparison of DBH, height, basal area and survivorship for *Eucalyptus* planted in monoculture (EUC) or intercropped (MIX) with 28-30 native tree species (diversity group) in Brazil. At the Aracruz site, ES, trees were 57 months old and at the Mucuri site, BA, trees were 48 months old.

Native trees of the diversity group had smaller diameters when intercropped with *Eucalyptus* than intercropped with fast-growing shading native tree species (Figure 5) at all sites and ages (APPENDIX F; $p<0.01$). The reduction was equivalent to -17.9% at Aracruz, -19.0% at Mucuri and -23.0% at Igrapiúna. Fast- and intermediate-growing species had smaller diameters in mixtures, except for the intermediate-growing species at Mucuri, which had similar values. The diameter of slow-growing species did not differ among sites and ages (APPENDIX F). The basal area of native trees intercropped with *Eucalyptus* was 61.8% of that produced in native species plots in Aracruz ($p=0.019$), 45.7% in Mucuri ($p=0.003$) and 48.6% in Igrapiúna ($p=0.004$). Smaller basal areas occurred for species in all sites and ages for fast- and for intermediate-growing species, but not for the latter at Mucuri (APPENDIX G). We observed no difference in the basal area of slow-growing species at Aracruz or Igrapiúna at all ages, but this group presented a lower basal area in the mixture at Mucuri

(APPENDIX G). The survival of native trees of the diversity group did not differ between treatments, except at Mucuri, where mortality was higher in the mixture as a result of increased mortality of fast-growing native species (at 48 months; p=0.02). The survivorship of intermediate-growing native species was not affected by mixing with *Eucalyptus*. No difference in survival was observed for slow-growing native species at the beginning of experiments, but their survivorship became significantly lower in the mixtures at Aracruz as stands developed (at 51 and 57 months) (Figure 5; APPENDIX H). Tree height was similar for native species of the diversity group in both treatments in the last inventory (Figure 5), but changed through time as shown in APPENDIX I.

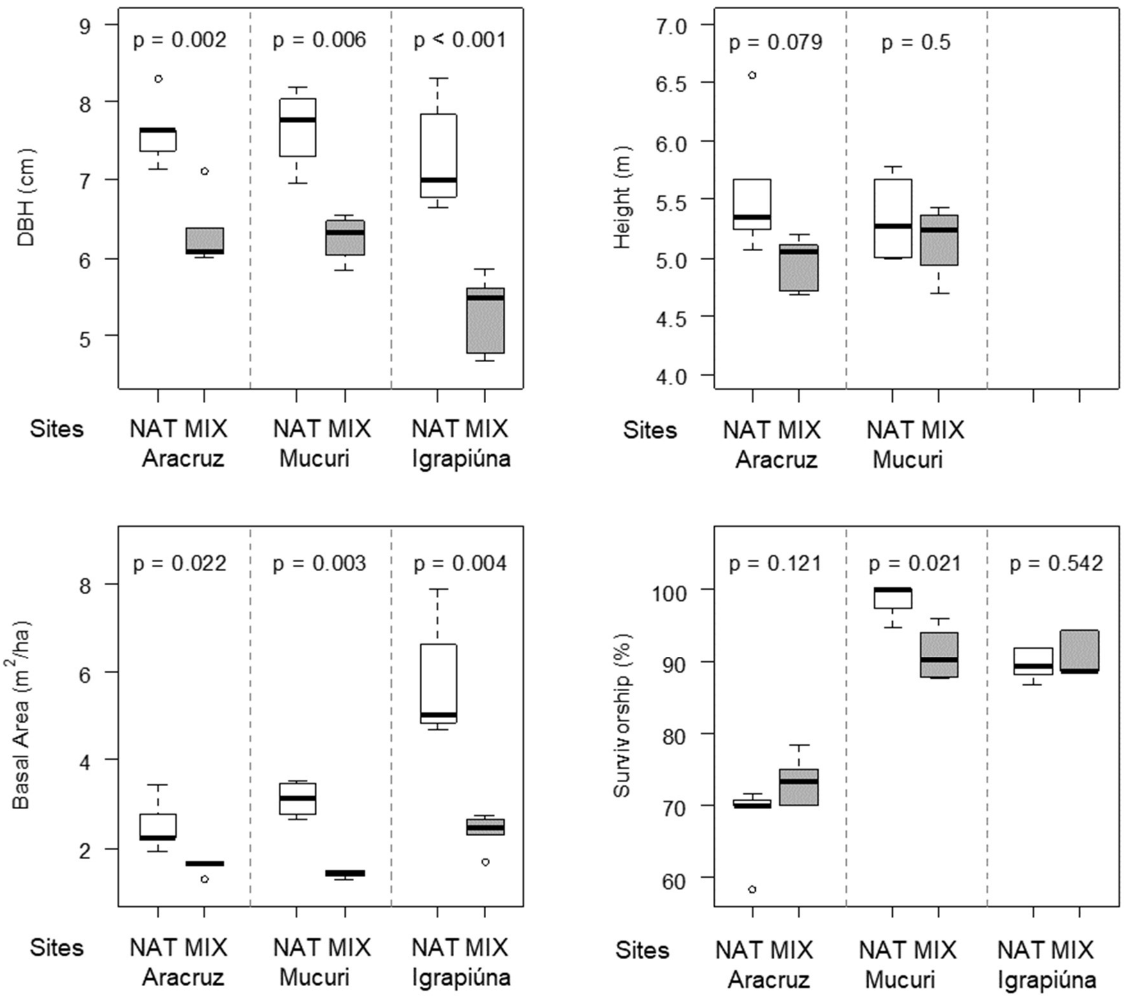


**Figure 5.** Comparison of DBH, height, basal area and survivorship for native trees of the diversity group intercropped with fast-growing shading native tree species (NAT) or with *Eucalyptus* (MIX) in Brazil. At Aracruz, ES, trees were 57 months old, at Mucuri, BA, trees were 48 months old and at Igrapiúna, trees were 60 months old. Tree height was not available at Mucuri, BA.

### 2.3.2. Target tree diameter is affected by size and identity of neighbors

*Eucalyptus'* diameter was negatively correlated with the size of the closest *Eucalyptus* neighbors, but was not influenced by native species neighbors, regardless of the search radii used (Table 2). Across sites, ages and treatments, the diameter of target native trees was negatively related to the size of neighbors (total neighborhood index) and this effect was modified by the identity of the neighbors (as indicated by the interaction between NI and species groups, data not shown).

**Table 2.** Effect of neighboring trees on the diameter of target trees. Bold letters indicating the number of potential neighbors included in the search radii followed by asterisks mean a significant effect; plain text letters indicate no significant effect for that search radius. For details on search radii and the number of neighboring trees within the given radius, refer to the Data analysis section.

| Group of target tree | Factor influencing target tree diameter | Number of potential neighbors |
|---|---|---|
| *Eucalyptus* | Neighborhood index of *Eucalyptus* | **4****** |
| | | **8*** |
| | | 20 |
| | | 24 |
| *Eucalyptus* | Neighborhood index of Diversity group | 4 |
| | | 8 |
| | | 20 |
| | | 24 |
| Diversity group | Total neighborhood index (including all species) | **4****** |
| | | **8****** |
| | | 20 |
| | | 24 |
| Diversity group | Neighborhood index of *Eucalyptus* or fast-growth shading native species | 4 |
| | | **8****** |
| | | 20 |
| | | 24 |
| Diversity group | Identity of neighbor (species group neighbors belong to: *Eucalyptus*; fast-growth shading native species; native species of fast-; intermediate-; or slow-growth) | **4****** |
| | | **8****** |
| | | **20****** |
| | | **24****** |

*p<0.05; **p<0.01; ***p<0.001

### 2.3.3. Tree growth rate and mixing effect intensity

At the plot level, competitive effect of *Eucalyptus* on diameter in mixtures was greater for native species of fast- than for species of intermediate- and slow-growth rates (**Erro! Fonte de referência não encontrada.**). At the neighborhood level, the interaction between fast-growing shading native tree species neighborhood index and the group of target tree species within radii including the nearest 8, 20 and 24 potential neighbors was important ($p<0.01$) for the diameter reduction in mixtures. Fast-growing native species' diameter and total neighborhood index had the strongest negative relationship; whereas tree species of intermediate- and slow-growth showed a weaker negative relationship with the neighborhood index of fast-growing shading species (*Eucalyptus* or native) (Figure 7), which is consistent with the differences shown in Figure 6.

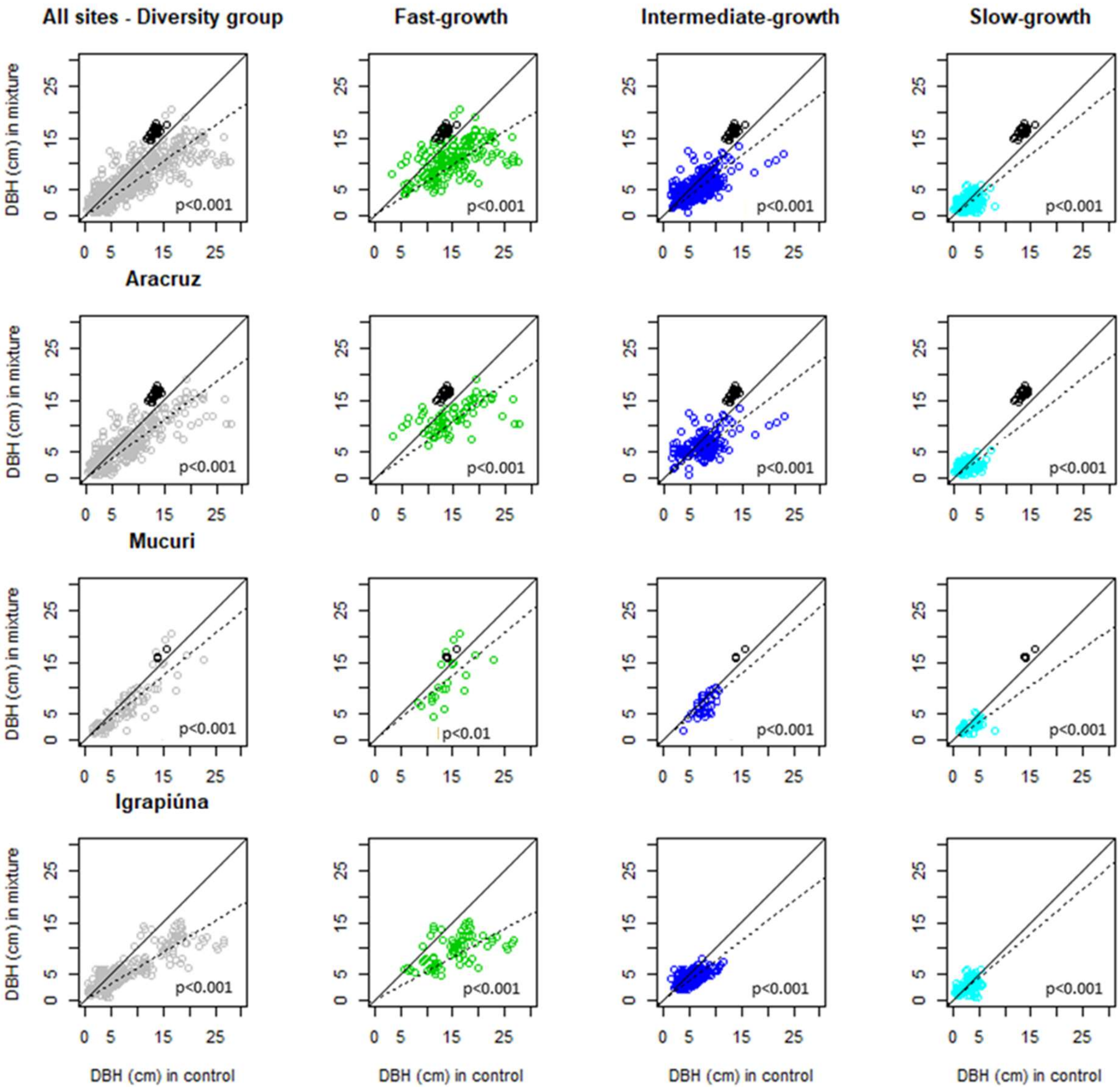


**Figure 6.** Mixing effect on tree diameter for *Eucalyptus* (black) and native species of the diversity groups (grey), classified at fast-, intermediate- and slow-growing species. The points are the mean for all trees of the given diversity group in a given plot at a given age. Note that points above the diagonal continuous line indicate that diameters were often larger in mixtures and points below the line indicate that species had smaller diameters in the mixture than in control treatments (*Eucalyptus* monoculture or native species plots). The dashed lines are fitted to the native species and not to *Eucalyptus* (black circles), which are shown only to indicate the corresponding *Eucalyptus* Diameter at Breast Height (DBH) in the same treatments. The p-values provided indicate that the diameter of native species in mixtures is significantly smaller than in native species plots. Data from all experimental sites are shown in the first row; from Aracruz in the second row; from Mucuri

in the third row; and from Igrapiúna in the fourth row, which does not have a *Eucalyptus* monoculture as a treatment. Data includes all inventories.

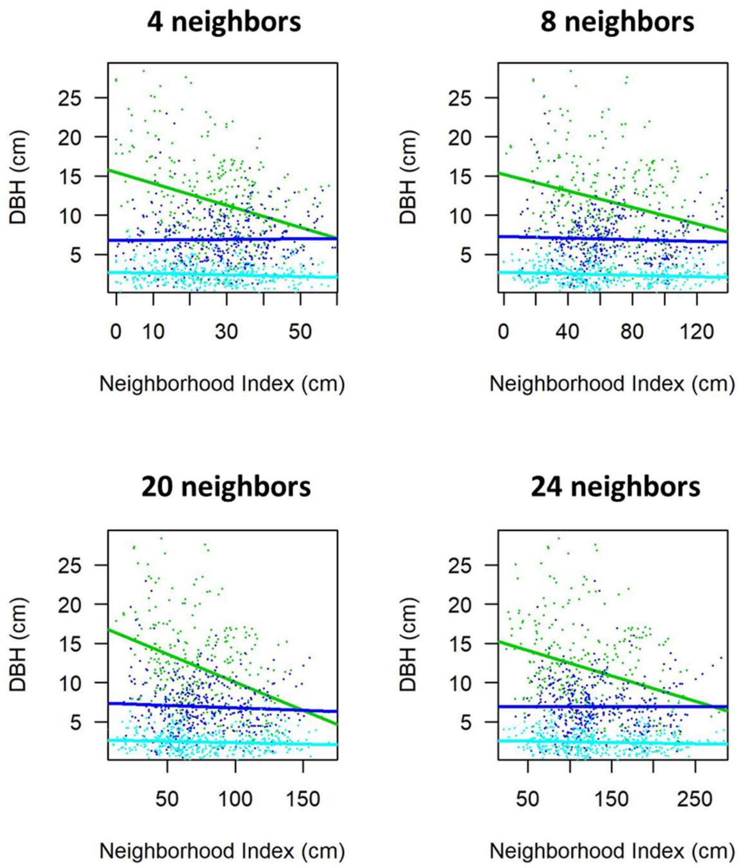


**Figure 7.** Relationship between tree diameter at breast height (DBH) and total neighborhood index for species of fast- (green), intermediate- (dark blue) and slow-growths (pale blue). Fast: $p<0.001$ (4, 8, 20 and 24 potential neighbors); $R^2$ = 0.08 (4 potential neighbors), 0.06 (8 potential neighbors), 0.15 (20 potential neighbors), and 0.09 (24 potential neighbors). Slow-growth: $p<0.05$ (4, 8 potential neighbors); $R^2$ = 0.0115 (4 potential neighbors), 0.0145 (8 potential neighbors).

### 2.3.4. Discussion

Commercial *Eucalyptus* species are well known in Brazil for their fast growth and high productivity in large-scale monocultures (Gonçalves et al., 2013). However, very little is known about the performance of *Eucalyptus* in mixed plantations with several native trees, as well the performance of native trees when intercropped with *Eucalyptus* (Erskine et al., 2006, 2005) or other tropical species (Montagnini et al., 1995; Nguyen et al., 2014; Parrotta, 1999) and this makes it difficult to design and manage these plantations. This study shows that it is feasible to establish a mixture of *Eucalyptus* and native species in high diversity plantations. Our first hypothesis was supported, since *Eucalyptus* grew faster in the mixtures while native species did not perform as well in mixtures. Our second hypothesis was also supported because both the size and the identity of neighbors were important factors influencing the diameter of target native trees. The results also supported the third hypothesis that *Eucalyptus* had a greater competitive effect on the fastest growing group of native species and a smaller competitive effect on the species with slower-growth rates. Even though competition slowed the diameter growth of native species, their survivorship and height were not affected, and they were not outcompeted in the mixture.

At the stand level, our results showed that, in mixtures, *Eucalyptus* produced as much as nearly 75% of the basal area produced by *Eucalyptus* monocultures, even though mixtures had only half the density of *Eucalyptus* seedlings (555 trees $ha^{-1}$) compared to monocultures (1,111 trees $ha^{-1}$). This resulted from the considerably greater diameters that individual *Eucalyptus* trees grew when intercropped with native species. Similar results were found for mixtures of *Eucalyptus* and *Acacia* (Forrester et al., 2004; Santos et al., 2016) and *Eucalyptus* and *Falcataria* (Binkley et al., 2003), in which individual *Eucalyptus* trees grew larger than in monocultures and produced disproportionately higher biomass per hectare than in monospecific stands. This outcome is advantageous when larger trees are worth more than smaller trees or when earlier harvesting can be anticipated because trees reach merchantable sizes earlier. In the mixture, *Eucalyptus* trees were much larger and taller than in *Eucalyptus* monoculture, and we found no evidence of competition from the smaller and shorter neighboring native species. The *Eucalyptus* species that are grown in plantations are often strong competitors and commonly benefit from growing in mixtures (Forrester et al., 2006). However, there are exceptions where *Eucalyptus* have been planted on sites where other species have been able to compete strongly enough to reduce the growth of the *Eucalyptus*, even if this was only for part of the rotation (Bouillet et al., 2013; David I. Forrester et al., 2007). Therefore, even for *Eucalyptus*, careful consideration of site and the mixed species is critical for success.

In this study, individual *Eucalyptus* trees may have benefited from more access to light especially at the lateral parts of their crowns above the rows of shorter native species canopies, as illustrated in Figure 2. These results clearly show that *Eucalyptus* benefited from the mixture plantations, which could be explained by competitive reduction and/or facilitation interactions (Kelty, 2006; Vandermeer, 1989), often collectively described using the term complementarity. The competitive advantage of *Eucalyptus* over native species that led to a reduction in competition, originates from many years of artificial selection and genetic improvement, which enables *Eucalyptus* to capture more resources than native trees (Gonçalves et al., 2013). The competitive reduction would also be related to a density effect because the native trees contribute a relatively low proportion of the stand basal area even though they represent about half the number of trees. That is, the basal area of the *Eucalyptus* monocultures was significantly greater than that of the mixtures. Facilitation could arise from higher soil nitrogen availability incorporated to the system by the abundant N-fixing native trees in our experiments (roughly 25% of the native trees). It is also possible that the rate of litter decomposition and nutrient cycling was higher in the mixtures (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Richards et al., 2010; Rothe and Binkley, 2001). Further research is then needed to decouple competitive reduction from facilitation in this silvicultural system so that these processes can be efficiently manipulated and utilized by managers. We highlight that other forms of facilitation such as mycorrhizae may be involved and we did not measure in this study.

Stand-level analyzes showed that the mixture with *Eucalyptus* negatively affected the size of native species (diameter, but not height). Thus, the mixtures were intermediate in productivity between the more productive *Eucalyptus* monocultures and the less productive native species stands. Similarly, the productivity of tropical plantations in the Philippines was related more to the productivity of the species within the plantation than to the tree species richness of the plantation (Nguyen et al., 2012). Tree-level analyzes showed that in these systems, the effect of neighbor size on target tree diameter depends both on the identities of target trees and neighbors. The growth of native species was influenced by fast-growing shading native tree species and by *Eucalyptus*, and the effect of treatment was important, meaning that using *Eucalyptus* instead of fast-growing shading native tree species resulted in greater competition. Similarly, previous research on mixtures of *Eucalyptus* and *Acacia* showed that competition slowed the diameter growth but not height of *Acacia* (Laclau et al., 2008). Amazonas et al., (in press) showed that native species may face stronger water limitation in these mixtures. This could cause shifts in carbon partitioning from above to belowground, ultimately resulting in less wood production (Nouvellon et al., 2012).

The different groups of native trees were affected differently by the competition with *Eucalyptus* according to their growth rate. The faster the native species grew, the more (in relative and absolute amounts) their growth was constrained by competition with *Eucalyptus*. This may simply be because the faster species require correspondingly more resources to maintain their growth, and therefore they are more likely to be affected by a faster growing and highly competitive tree species, like *Eucalyptus*. This effect may also be related to shade tolerance and could thus explain why the growth decrease of native species was related to growth rate with shade-tolerant late-successional species (which are slower growing) being less affected by the mixture.

At our experimental sites, *Eucalyptus* survived equally well in monospecific stands and in the mixtures. Native species had lower survival rates than *Eucalyptus* in general, but we found almost no difference between their survivorship in the mixtures and in the controls. Our results show that intercropping with *Eucalyptus* instead of fast-growing shading native tree species does not cause additional mortality to native species seedlings, except for fast-growing species at the Mucuri site. Tree mortality varied in different studies examining mixtures of two species. Survival rates did not change amongst treatments or sites for mixtures of *Eucalyptus* and *Acacia* in Brazil and the Congo (Bouillet et al., 2013). Similar survival rates were observed between monocultures and mixtures of *Eucalyptus* and *Albizia* in Hawaii (DeBell et al., 1997) while *Acacia* had higher survival rates in mixtures with *Eucalyptus* than in monocultures in Australia (Forrester et al., 2004).

This study shows that mixed species plantations can be established with *Eucalyptus* and a high diversity of native tropical Brazilian tree species. The economic and restoration success of these plantations will also depend on the silvicultural approach that follows. Many silvicultural options are likely to be appropriate for diverse mixtures such as these, depending on the objectives. A selective thinning regime that removes poorly formed and suppressed trees as well as trees that have reached merchantable sizes has been recommended for other tropical mixed species plantations (Erskine et al., 2005; Nguyen et al., 2014). In contrast, thinning the smallest trees will likely reduce the tree species richness by removing the slower growing species (Erskine et al., 2005). This thinning would release the retained trees from competition, provide some income and may also be used to encourage regeneration of the native species in the canopy gaps (Erskine et al., 2005; Nguyen et al., 2014). If necessary, the regeneration may be supplemented by enrichment planting. In addition, while the planting design worked on each site, other designs could be tested such as where the slower growing species are planted a year earlier to give them a head start (Kelty e Cameron, 1995; Nguyen et al., 2014).

Plantation design is essential for the further development of these systems and different spatial and temporal strategies could be used to optimize ecological interactions (Kelty and Cameron, 1995). One option to cope with possible incompatibilities between the *Eucalyptus* and fast-growing native species, regarding competition for water, nutrients and light, would be to establish high diversity mixtures without these sensitive native species, and then to add these native species when the *Eucalyptus* is removed from the system, assuming there is still enough light available for them to establish between the other species. Alternatively, of the *Eucalyptus* could be harvested as soon as it has reached a minimum merchantable size. Another option, is the implementation of mixtures in different spatial arrangements using an intermediate- or a coarse-, instead of a fine-grid design, to minimize competition between *Eucalyptus* and native trees (Bauhus et al., 2017; Kelty and Cameron, 1995). These designs could, however, increase competition between *Eucalyptus* trees and result in decreased *Eucalyptus* wood production.

From a production point of view, these mixtures proved to have the potential to combine wood production and land rehabilitation, since it is possible to produce eucalypt wood in the short-term in stands containing a high diversity of native tree species. The increased growth and the greater basal area produced by *Eucalyptus* in the mixtures, allied with high survival rates of native species, encourage further consideration and testing of this type of mixture in the tropics. The provision of ecosystem services, non-timber products and the future exploitation of native timber may increase the value of these systems, however the economic feasibility of these mixtures still needs to be studied while also considering incentives related to reducing silviculture's footprint (Robertson and Swinton, 2005).

These systems may be maintained as a mixture where *Eucalyptus* provides the financial income and native species are maintained for conservation purposes and potentially for to be exploited in the future to produce timber and non-timber products. Using another strategy, the system could start as a mixture of *Eucalyptus* and native species for a few rotations and then be converted at some point for the exclusive production of native species products after *Eucalyptus* is harvested. The intercropping with *Eucalyptus* slowed down the growth-rate of native trees, but we believe this may be reversed after *Eucalyptus* is harvested and this growth decrease may be compensated by the early income provided by *Eucalyptus*.

This is also important to note that the harvest of *Eucalyptus* wood will be associated with the export of some nutrients from the site (Gonçalves et al., 2008; Laclau et al., 2000), which could reduce the size of a site's nutrient pool, even though the availability of resources will likely be increased for native species after thinning the *Eucalyptus*.

These mixed forests also represent an opportunity to use the wood produced by *Eucalyptus* to finance the first years of tropical forest restoration, during which *Eucalyptus* provides early income for one or a few rotations and plays the role of pioneers, while native species grow more slowly in the understory. This is a real possibility for forest landscape restoration, for example, in Brazil, where the intercropping of exotic and native trees is allowed in some cases, making the use of these systems in millions of hectares (Brancalion et al., 2016; Brasil. Presidência da República, 2012). In regions where *Eucalyptus* does not have a well-established market, its role may be replaced by commercially valuable species of other genera, for example, *Pinus, Tectona, Acacia* or *Khaya*. Previous studies have tested the use of commercial fast-growing plantations of exotic species (*Pinus* and *Grevillea*) as nurse crops to facilitate the establishment of a few late-successional species (native or exotic) planted in their understory (Ashton et al., 1997; Dordel et al., 2010). These studies also suggested that beyond the ecological roles played by these nurse species, they could provide revenues from thinning while the other species grow more slowly. Continued research will provide insights related to the improvement of plantation design to balance ecological interactions and the interests of landowners, considering the ecological and socioeconomical aspects of the adoption of high diversity mixed plantations (Nguyen et al., 2014).

Increasing the diversity of forestry systems also adds complexity to the management, and operational practices, such as harvesting, which need to be adapted to maintain efficiency and simultaneously minimize damage to the trees that remain in the system. This is especially challenging when mixtures are designed as a fine grid and the space for harvesting is limited. Future research needs to address harvesting strategies in these systems to understand the implications of current design in time and costs, and suggest new designs, techniques and training for operators. Also, if we want to adapt these systems to be used in other regions and ecosystems, we need to understand the mechanisms of competition through which *Eucalyptus* affects the growth of native species. This could be obtained by research on the mechanisms of competition for water, light and nutrients in these mixtures and their importance for a given region and set of environmental conditions. Having this information available, will make it possible to adapt silviculture to minimize competition and maximize growth, with considerable biodiversity gains.

## 2.4. Conclusions

The mixed plantations we studied are beneficial for the growth of *Eucalyptus*, which produced almost 75% of the basal area of monocultures using only half the number of *Eucalyptus* seedlings. Even though competition for resources with *Eucalyptus* slowed the growth of native species, it was not strong enough to affect their survival or outcompete the native trees. The slower growth of native species is not of major concern in the short-term and may be reversed if the forests are managed for purposes other than the production of *Eucalyptus* in the future, but this reversal still needs to be assessed in the future. We conclude that mixtures of *Eucalyptus* and a high diversity of native tree species are technically feasible and represent an important alternative for establishing multipurpose plantations, especially in the context of forest and landscape restoration.

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# 3. COMBINING *EUCALYPTUS* WOOD PRODUCTION WITH THE RECOVERY OF NATIVE TREE DIVERSITY IN MIXED PLANTINGS: IMPLICATIONS FOR WATER USE AND AVAILABILITY

ABSTRACT

Mixed forest plantations now emerge as an alternative to traditional silviculture in the tropics and represent ecological gains associated with production, wood quality and nutrient cycling. Mixed plantations with higher diversity may also be advantageous concerning their use of soil water. To shed light onto water-related issues of mixing *Eucalyptus* and a high diversity of tropical native trees, we explored the following questions: What is the impact of high diversity mixed plantations of *Eucalyptus* intercropped with native trees on soil water? How does the mixture affect the physiology of water use by native trees? Firstly, we tested the hypothesis that stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures, by measuring the temporal dynamics of soil water. Secondly, we tested how mixing with *Eucalyptus* affects the hydraulic performance of fast- and slow-growing native species in these forestry systems. This is the first time a large experiment has been implemented to compare the effects of monospecific *Eucalyptus* plantations, native species mixtures and mixed plantations of *Eucalyptus* and native species on soil water dynamics under controlled conditions in terms of site, age, soil type, topography and climate. We found that high diversity mixed plantations of *Eucalyptus* and native trees use less soil water, than *Eucalyptus* monocultures. However, the soil in the mixtures was drier than in native species stands. The mixing with *Eucalyptus* affected the hydraulic performance of native species by decreasing the leaf water potential and stomatal conductance of the fast-growing species, suggesting that fast-growing species performance may be especially constrained by competition for water with *Eucalyptus*. These findings have important implications for forest management and ecological restoration in the tropics. They will help to further develop silvicultural options to adapt to climate change and improve plantation forestry by using mixed plantations for production purposes or rehabilitation of degraded lands.

Keywords: Atlantic forest restoration pact; Ecophysiology; High diversity mixed plantation; Leaf water potential; Soil volumetric water content; Stomatal conductance

## 3.1. Introduction

New silvicultural systems have been developed to meet the growing demand for forests of multiple uses (Lamb, 2005), including the emergent need to achieve environmental benefits allied to production (Stanturf et al., 2014). Mixed forest plantations now emerge as an alternative to traditional silviculture in the tropics, conferring ecological gains associated with production, wood quality, nutrient cycling and water use efficiency (Bouillet et al., 2013; Forrester, 2015; Forrester et al., 2006; Kelty, 2006; Piotto, 2008). These systems are more resilient and aggregate benefits associated with carbon-pool stability and other ecosystem services (Hulvey et al., 2013), but are often only preferred when their productivity is higher than that of monocultures. Higher productivity in mixtures is often achieved by combining a nitrogen fixing tree (ex: exotic *Acacia* species) with non-legume trees used for wood production, to take advantage of the higher nutrient inputs supplied (Bouillet et al., 2013). However, two-species mixed plantations designed for wood production make minimal contributions to biodiversity conservation. This may be increased with the offer of economic incentives associated with the additional values of these systems, such as payments for ecosystem services like biodiversity conservation, carbon storage, or water regulation, to compensate for lower yields (Brancalion et al., 2012).

Mixed plantations with higher diversity may also be advantageous concerning their higher resilience (Jactel e Brockerhoff, 2007) and lower vulnerability to extreme climate events such as droughts. Mixtures of *Eucalyptus* and *Acacia*, for example, can use water more efficiently than monocultures (Forrester et al., 2010). Reductions, but also increases, in water stress during droughts have also been found in mixed species forests (Forrester et al., 2016). These effects may become more pronounced as dry periods become more intense, longer and more frequent (Allison et al., 2009; IPCC, 2015), negatively affecting tree growth. Moreover, the drought-induced mortality of trees may rise rapidly with extreme or repeated severe-droughts (Meir et al., 2015).

The high productivity of *Eucalyptus* plantations, the most important commercial species in the tropics (Del Lungo et al., 2006), is associated with a high demand for water (Whitehead e Beadle, 2004). Water supply is a key resource determining the productivity of *Eucalyptus* plantations in some regions (Stape et al., 2010) and climate change may negatively affect the hydraulic performance of trees and plantations in regions where climate change increases temperatures, decreases precipitation and causes soil moisture drought (IPCC, 2015), ultimately compromising wood production and increasing the susceptibility of these forests to die-off (Allen et al., 2010). *Eucalyptus* can obtain water from deep soil layers (Christina et al., 2017) from the early stages of stand development, but may depend on precipitation and moisture of superficial soil layers at the end of the rotation when deep soil layers have dried out (Nouvellon et al., 2011). Other species have different ecological strategies and demand less water. Increasing species diversity in plantations could thus lead to complementary resource use by trees and a decrease in water demand at the stand level, reducing vulnerability to droughts caused by climate change and resulting in more sustainable wood production.

To examine how the water-use and physiological performance of native species are affected by mixing with *Eucalyptus* or a high diversity of tropical native trees, we explored the following questions: What is the impact of high diversity mixed plantations of *Eucalyptus* intercropped with native trees on soil water? How does the mixture affect the physiology of water use in native trees? We tested two hypotheses related to the water use strategies of trees in the tropics, with implications for forest management and restoration. Firstly, we tested the hypothesis that stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures, by measuring the temporal dynamics of soil water. We expected intermediate values of soil water content in mixtures compared to *Eucalyptus* monocultures (drier soils) and native species stands (wetter soils). Secondly, we tested if the mixing with *Eucalyptus* affects the hydraulic performance of fast- and slow-growing native species, by assessing the leaf water potential and the stomatal conductance of model species. We expected to find a decreased hydraulic performance of native trees. There is a widespread concern in society about the impact of *Eucalyptus* monoculture plantations on the conservation of water resources, and natural forests that grow more slowly are believed to have smaller impacts. Reliable information on water use by native and exotic trees derived from controlled experiments is, however, limited. This is the first time a large experiment has been implemented to compare the effects of monospecific *Eucalyptus* plantations, native species mixtures and mixed plantations of *Eucalyptus* and native species on soil water dynamics under controlled conditions in terms of site, age, soil type, topography and climate.

## 3.2. Material and methods

### 3.2.1. Study Site

The experimental site is located in Aracruz, ES, Brazil, (19°49’12”S, 40°16’22”W), within the Atlantic Forest region, managed by Fibria Celulose S.A. The site has a flat relief with a typical Yellow Argisol (Ultisol) presenting a sandy/medium/clayey texture. The region has a tropical climate with a dry winter (Aw) (Köppen, 1936) and a hot wet summer, with annual average temperature of 23.4 °C and annual average rainfall of 1,412 mm (Alvares et al., 2013). Historically, the region experiences a water deficit from February to September (Sentelhas et al., 2013a). Precipitation was markedly lower during the period we measured soil moisture compared to historical averages (APPENDIX J). The weather data from the meteorological station of the seedling nursery located approximately 12 km from the experimental site is shown in APPENDIX K.

### 3.2.2. Experimental Design and Sampling

The experiment had a randomized block design, with three treatments and five blocks (15 plots). Each plot consisted of 10 rows of 24 trees, including two outer rows as borders. Each effective plot measured 18 m x 60 m (1,080 $m^2$) and included six rows of 20 trees. The three treatments included a *Eucalyptus* monoculture (hereafter EUC); a mixed plantation of *Eucalyptus* intercropped with 30 native tree species, in alternated single rows (hereafter MIX); and native species plots consisting of 10 native pioneer species (instead of *Eucalyptus*) intercropped with the same 30 native tree species, in alternating single rows (hereafter NAT). In the mixture or native species treatments, half of the seedlings were *Eucalyptus* or 10 native pioneers, and the other half were seedlings from 30 native tree species common to both treatments. The site was planted in July 2011 using a 3 m x 3 m spacing at a density of 1,111 trees $ha^{-1}$. The *Eucalyptus* used was a clone of *E. grandis x E. urophylla*. All seedlings were planted at the same time using the same silvicultural techniques that are commonly used in *Eucalyptus* plantations in the region (fertilization according to the nutritional demands of *Eucalyptus* to local soil conditions, weed control using glyphosate spraying, and ant control using insecticide baits). All treatments had the same spacing in between rows and trees within rows. To control for the variability of neighborhood effects, each native species was planted in the same position within all plots. The list of species used in each treatment is shown in APPENDIX L. *Eucalyptus* and three native species with contrasting growth rates were chosen as model species for the ecophysiological traits, all presenting high survival rates and equal numbers of individuals (only one native tree missing). We chose two Fabaceae to reduce the effect of genetic distance on physiological behavior. *Paubrasilia echinata* Lam. is a slow-growing, late-successional species, while *Mimosa artemisiana* Heringer & Paula is a fast-growing species with traits common to early-successional tree species. We measured two individuals per plot (20 trees of each species). Because *Eucalyptus* trees were too tall and special equipment and training would be required, and because of time and equipment constraints, we could only measure stomatal conductance and leaf water potential of *Mimosa artemisiana* and *Paubrasilia echinata*. We measured the Diameter at Breast Height (DBH) (1.3 m) of all trees in the plots prior to ecophysiological measurements at age 47 months.

### 3.2.3. Soil volumetric water content

Soil volumetric water content was measured weekly for one year (from May 2015 through June 2016) in 30 positions, two in each plot (APPENDIX M), including the three treatments and covering all seasons. We installed tubes and used a portable device (Diviner 2000, Sentek) to measure soil volumetric water content (Sentek Pty Ltd., 2009) for every 10-cm soil layer down to 1.3 m.

### 3.2.4. Xylem water potential and stomatal regulation

We compared xylem water potential ($\Psi_{xylem}$) and stomatal conductance ($g_s$) of the model species intercropped with *Eucalyptus* with trees in native species plots. We estimated xylem water potential (MPa) using a pressure chamber (model 600, PMS Instrument Company), by measuring the water potential of leaves detached from small branches (<2 cm diameter) in the outer part at the middle third of the crown, facing south and shaded. Leaf water potential tends to vary considerably across complex canopies because of contrasting light conditions, so our leaf sampling was designed to estimate the xylem water potential of trees instead of leaf water potential. To estimate the predawn xylem water potential, a branch was enclosed with a black plastic bag in the evening before the measurement, to avoid nocturnal stomatal opening, and detached from the tree just before measurement. We used two leaves per individual for water potential measurements. We measured stomatal conductance ($g_s$; $mmol/m^2 \cdot s^{-1}$) using a portable Leaf Porometer (Decagon Devices, Inc.) for leaves from the outer part of the middle third of the crown, facing north and not shaded. We marked two leaves per individual attached to the branches and used the same leaves to make repeated measures of stomatal conductance. Leaf sampling was designed to estimate the $g_s$ of leaves under stressful conditions. We built daily curves for these variables using measurements made every two hours (from 6 am to 4pm and predawn at 4 am) in days without rain in June 2015 and January 2016, the historical dry and wet seasons, respectively.

### 3.2.5. Statistical Analysis

We tested if stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures by modeling soil volumetric water content as a function of treatment and depth as fixed factors, and time (year, month, day) and position (block, plot, tube) as nested random factors with an autocorrelation structure. We tested if the mixing affects the physiology of water use of trees by modeling leaf water potential and stomatal conductance using, first, treatment and species as fixed factors and date, block and time of measurement as nested random factors; and then separately per species entering treatment as a fixed factor and date, block and time of measurement as nested random factors. Linear Mixed Models were built using the *lme* function of the package *nlme* (Pinheiro et al., 2016). All analyses were performed in R 3.2.1 (R Core Team, 2016).

## 3.3. Results

### 3.3.1. Soil Volumetric Water Content

Treatment and depth were highly significant factors to explain soil water (p<0.0001). Soil volumetric water content increased with depth and was lowest in *Eucalyptus* monoculture, intermediate in mixtures and highest in native species stands. This pattern was stronger in drier months, consistent across the soil profile (0-130 cm) and during most of the year (Figure 8; Figure 9). The time change in volumetric soil water contents across different depths in each treatment are shown in APPENDIX N.

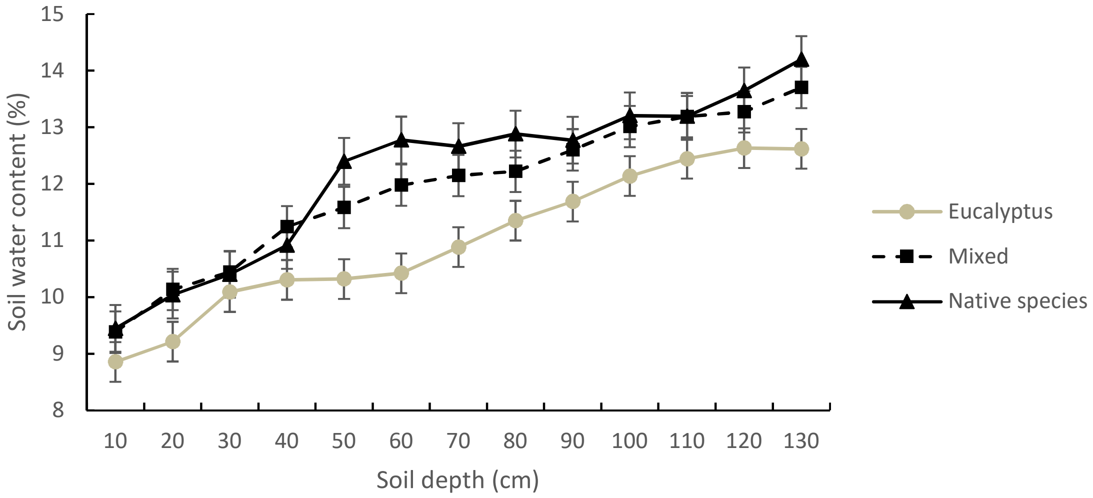


**Figure 8.** Average soil moisture differences among three types of forestry system implemented in Aracruz, ES, Brazil. Each point represents annual averages ± standard error for every 10-cm layer from 0-130 cm.

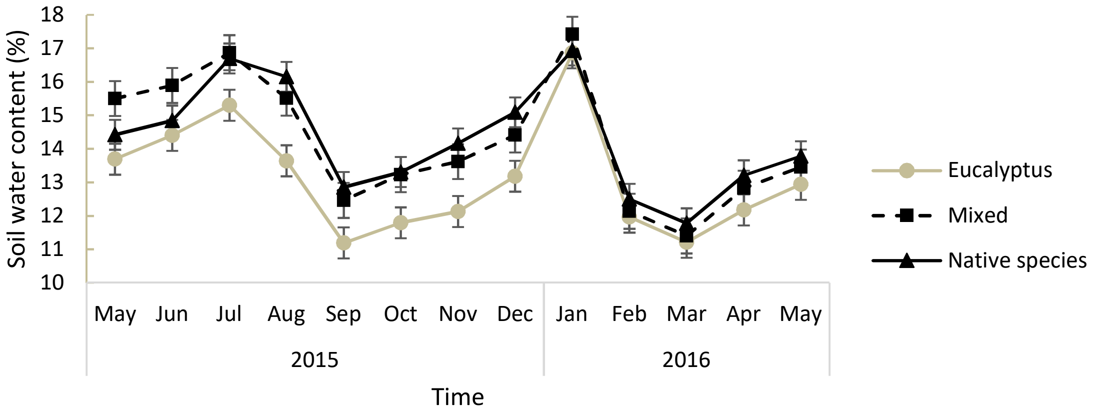


**Figure 9.** Annual variation of soil moisture among three types of forestry system implemented in Aracruz, ES, Brazil. Values are averages ± standard error for every month across the whole profile.

### 3.3.2. The mixing effect and the physiology of water use in model species

Native trees mixed with *Eucalyptus* grew less than their counterparts that were intercropped with native pioneers. This effect was statistically significant for the fast-growing, but not for the slower-growing species (Table 3). The survival rate of *Paubrasilia echinata* was 100% in both treatments. *Mimosa artemisiana* had a survival rate of 100% in the mixed plantation and 90% in native species stands.

**Table 3.** Mixing effect on the DBH of model species [a,b]. The control for native species are native species plots and the control for *Eucalyptus* are monocultures.

| | Treatments | | | |
|---|---|---|---|---|
| | Mixture | Controls | | |
| **Species** | DBH (cm) | | Mixing effect | p-value |
| *Eucalyptus* | 16.2 ± 0.1 | 12.9 ± 0.2 | +25.0% | <0.0001 |
| *Mimosa artemisiana* | 14.9 ± 1.6 | 21.0 ± 0.6 | -28.9% | 0.014 |
| *Paubrasilia echinata* | 2.2 ± 0.3 | 2.4 ± 0.2 | -7.8% | 0.673 |

[a] Results are presented as means ± standard error

[b] p-values from Welch's t test are shown.

We found contrasting xylem water potential values between species (p<0.0001) and treatments (p=0.0294). The fast-growing species *Mimosa artemisiana* showed less negative leaf water potential than *Paubrasilia echinata* in the two periods measured, June 2015 and January 2016. Daily variation also contrasted between these species, with greater differences in xylem water potential observed for *Paubrasilia echinata* during the day. The lowest potentials were observed around midday and both species showed lower values when intercropped with *Eucalyptus*. Values at 06:00 am were usually higher than predawn measures (Figure 10; Figure 11).

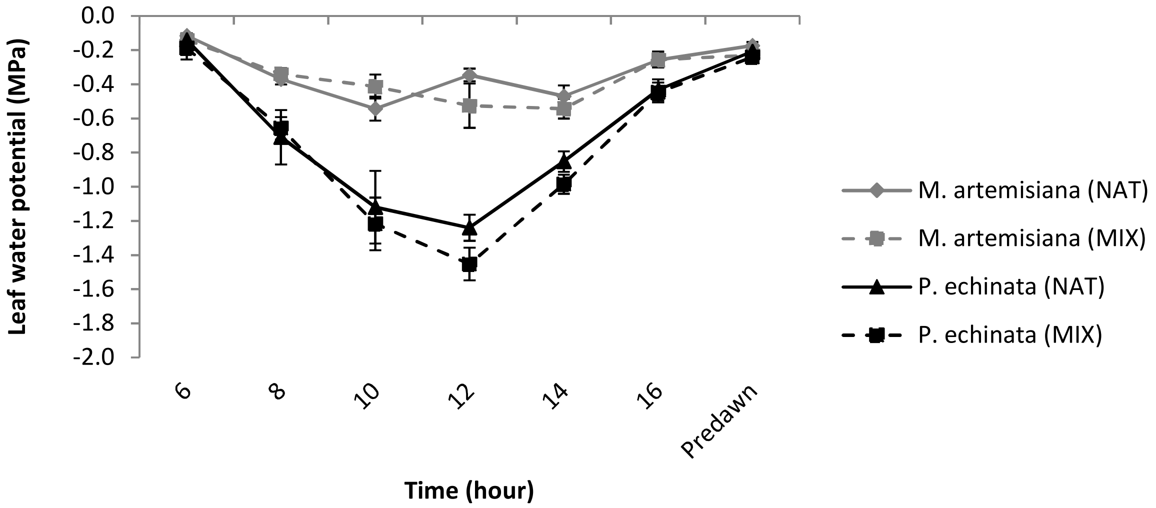


**Figure 10.** Xylem water potential daily variation curve of *Mimosa artemisiana* and *Paubrasilia echinata* planted intercropped with native pioneers or *Eucalyptus*. June 2015, historical dry season. MIX= native trees intercropped with *Eucalyptus*; NAT= native trees intercropped with native pioneers.

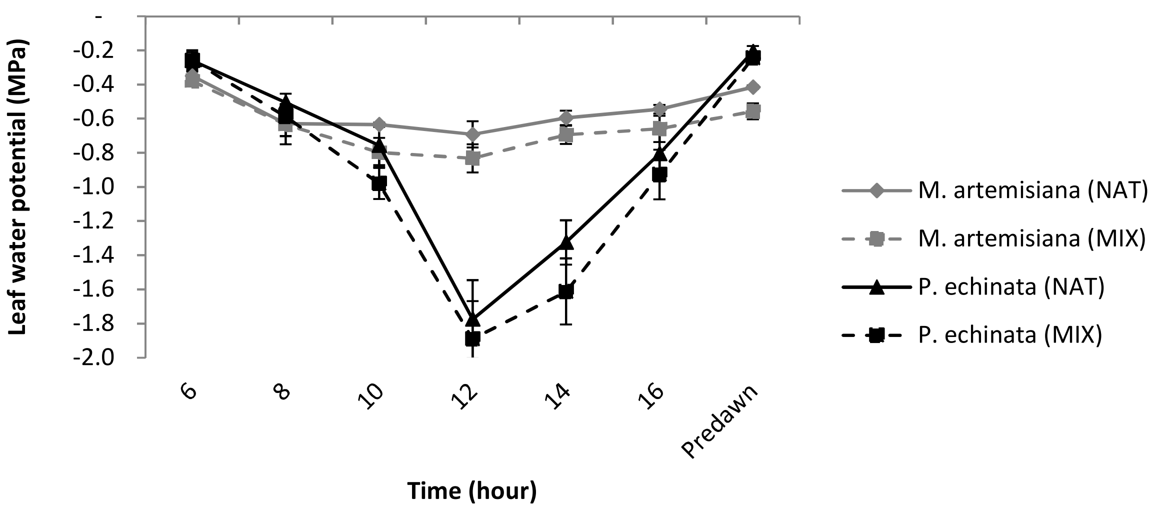


**Figure 11.** Xylem water potential daily variation curve of *Mimosa artemisiana* and *Paubrasilia echinata* planted intercropped with native pioneers or *Eucalyptus*. January 2016, historical wet season. MIX= native trees intercropped with *Eucalyptus*; NAT= native trees intercropped with native pioneers.

Stomatal conductance was different between species ($p<0.0001$) but not between treatments ($p=0.4608$). *Paubrasilia echinata*, the slow-growing species, had more similar values of stomatal conductance between the measurement periods and varied less during the day, while

*Mimosa artemisiana* showed the greatest differences both within days and across measurement periods (Figure 12; Figure 13). Considering treatments, *Paubrasilia echinata* showed similar stomatal regulation (Figure 12) with a tendency to higher conductance when intercropped with *Eucalyptus* (Figure 13). *Mimosa artemisiana* tended to lower conductance in mixtures (Figure 12; Figure 13).

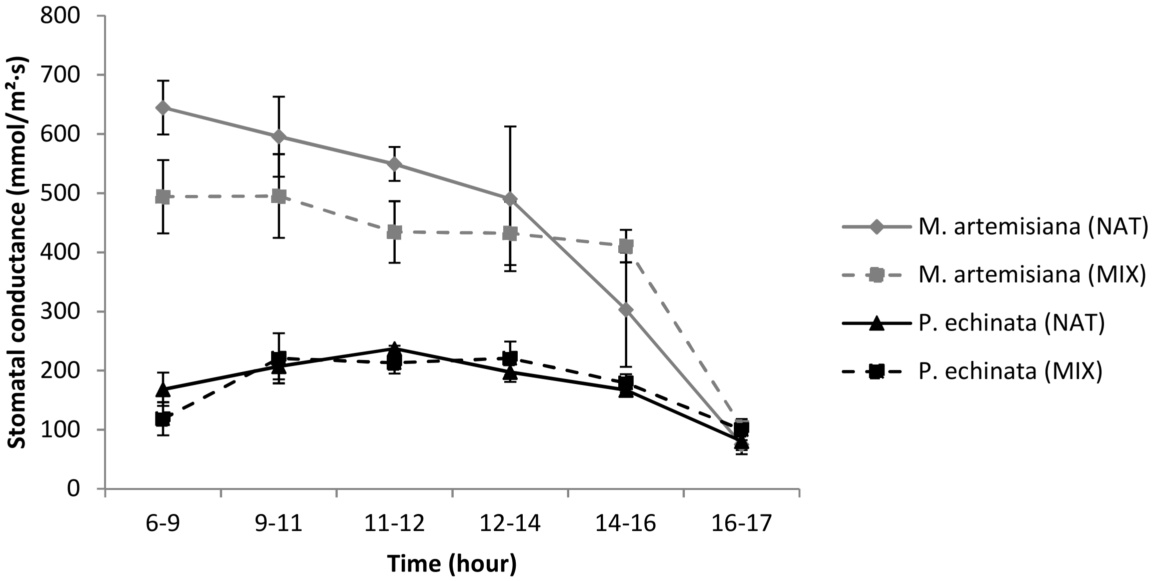


**Figure 12.** Daily variation curve of stomatal conductance of *Mimosa artemisiana* and *Paubrasilia echinata* planted intercropped with native pioneers or *Eucalyptus*. June 2015, historical dry season. MIX= native trees intercropped with *Eucalyptus*; NAT= native trees intercropped with native pioneers.

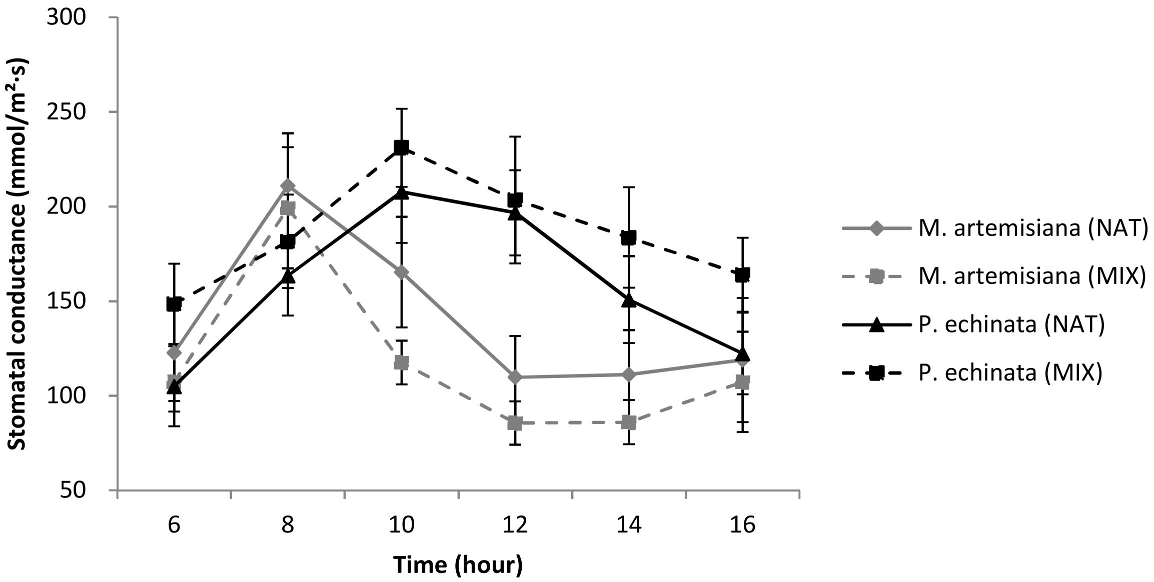


**Figure 13.** Daily variation curve of stomatal conductance of *Mimosa artemisiana* and *Paubrasilia echinata* planted intercropped with native pioneers or *Eucalyptus*. January 2016, historical wet season. MIX= native trees intercropped with *Eucalyptus*; NAT= native trees intercropped with native pioneers.

### 3.4. Discussion

In support of our first hypothesis, differences in soil water content showed that mixed plantations of *Eucalyptus* and a high diversity of native trees had less impact on soil water than *Eucalyptus* monocultures. However, the soil under the mixtures was still drier than that of native species stands. Similarly, the *Eucalyptus* monocultures were the most productive, the mixtures intermediate and the native species least productive (**Chapter 2**). This is consistent with the general finding that more productive stands use more water (Law et al. 2002) and that mixtures are less productive than monocultures they use less water, and when they are more productive they use more water (Forrester, 2015). That is, the transpiration of a stand appears more likely to depend on its productivity, species identity and the species functional traits than tree species diversity (Kunert et al., 2012; Lübbe et al., 2015).

It is important to note that *Eucalyptus* plantations can take up water from soil depths up to 10 m (Christina et al., 2017), however, we monitored soil water down to 1.3 m, and part of the interaction between *Eucalyptus* and the native species may have occurred deeper within the soil profile. Despite this limitation, we emphasize the importance of superficial soil water for fast-growing species of this genus especially from the age of around three years towards the end of the rotation, when *Eucalyptus* may depend on precipitation after most water in the deep soils layers has been depleted (Nouvellon et al., 2011). Even earlier in stand development, the proportion of water acquired from deep soil layers is generally low when water is available in shallower layers (Christina et al., 2017). Moreover, a global analysis of root distribution has showed that most of the roots in tropical forests are concentrated in the first 1-1.5 m of the soil, including as much as 78% in the first 50 cm (Jackson et al., 1996).

Xylem water potential and leaf stomatal conductance may change in response to mixing (Gebauer et al., 2012; Jonard et al., 2011) and species growing in mixtures have been found to experience increased or decreased water stress, depending on the species they are mixed with (Gebauer et al., 2012; Forrester et al., 2016). Low soil moisture may decrease xylem water potentials and force plants to close their stomata to avoid water loss, which in turn can lead to decreased photosynthetic rates and ultimately to decreased biomass production and growth. Taking advantage of higher water availability in the mixtures we studied, *Eucalyptus* could reach approximately 75% of the basal area produced by *Eucalyptus* monocultures, even though the mixtures contained only 50% of the number of *Eucalyptus* trees (**Chapter 2**). That is, the replacement of half of the *Eucalyptus* seedlings by native species increased diversity while significantly reducing water consumption disproportionately to the reduction in overall aboveground biomass production (9%; unpublished data). Despite the advantages related to increased biodiversity and lower water consumption, and even though there may be some degree of niche separation and competitive reduction in the mixtures (Vandermeer, 1989), the ecological interactions were also associated with a negative mixing effect for native species, with decreased growth caused by competition for water, and possibly other resources, with *Eucalyptus*.

The negative mixing effect was higher for the faster growing native species. These species may have a correspondingly high demand for water than the slower growing species, which makes the faster growing native species more constrained by competition for water from *Eucalyptus*. The growth reduction is in accordance with the observed changes in the water use physiology of our model native species, which presented lower leaf water potential in mixtures. In one extreme, the growth of *Paubrasilia echinata* (a slow growing species) was not significantly affected by *Eucalyptus* and presented equivalent performance in both treatments, consistent with a conservative water-balance strategy to avoid water losses, without compromising growth. At the other extreme, *Mimosa artemisiana* (a fast-growing species) experienced a large negative mixing effect, associated with more pronounced changes in the physiology of water use. Especially in the drier period, its pre-dawn leaf water potential was as low as -0.6 MPa, suggesting that leaves did not rehydrate overnight. The tendency of *Mimosa* to reduce $g_s$ in mixtures may have occurred in response to lower soil water potential. These patterns were probably caused by greater water uptake by *Eucalyptus* in mixtures than by native pioneers in native species plots, thereby significantly reducing the water potential in the rooting zone of *Mimosa artemisiana*.

*Eucalyptus* mixed with *Acacia* has been found to increase the vertical segregation and increase the density of *Acacia* fine roots in deep soil layers (Laclau et al., 2013). Even though a similar niche separation is possible in our experiment, we believe the physiological changes observed are related to some level of water limitation experienced by native species growing on soil containing lower water content which we attribute to the presence of *Eucalyptus*. Despite the marked differences in soil moisture and leaf water potential, the high variance in stomatal conductance led only to a non-significant tendency of lower values in the mixtures.

The adoption of forestry systems that consume less water have direct implications for watersheds important for water yield and may result in greater yields than those from catchments with high proportions of *Eucalyptus* monocultures. At the catchment scale, the combination of the proportion of the area occupied by plantations, the growth rate of species planted and their water use efficiency is a key-element influencing the impact of forests on water yield (Forrester et al., 2010; White et al., 2014). Therefore, fast-growing species like *Eucalyptus* which often have high water use efficiency, could use a smaller area and consume less water than slow-growing species of low water use efficiency to produce the same amount of biomass. Beyond the reduced impacts on water yield, the use of mixed forests, like the systems we tested here, may reduce the vulnerability of plantations to droughts since the water content of soils is higher, at least in these young stands. In the design of new forestry systems, it is important to consider the growth rate and the strategies of water use by different tree species, such as their ability to drop leaves and escape competition for water during the dry period, for example.

Considering the predictions of climate change in the near future, with the dry season expected to become drier and longer, this new silvicultural system can be considered as an alternative to *Eucalyptus* monocultures in regions important for water production. We tested this system in Brazil, which is an important global player in *Eucalyptus* silviculture, tree species biodiversity conservation (Beech et al., 2017a) and in tropical forest restoration (Aronson e Alexander, 2013; Calmon et al., 2011; Holl, 2017). The country has ambitious restoration objectives and these highly diverse mixed forest intercrops of *Eucalyptus* and native tree species may also be considered when rehabilitation of degraded lands is an option to restoration, representing positive gains for production and conservation.

### 3.5. Conclusion

The mixed plantation of *Eucalyptus* intercropped with native species had less water in the soil than *Eucalyptus* monocultures, but the mixing reduced the hydraulic performance of fast-growing native trees and constrained their growth. These findings have important implications for forest management and ecological restoration in the tropics. They may help to further develop silvicultural options to adapt to climate change and improve plantation forestry by using mixed plantations for production purposes and rehabilitation of degraded lands. Further research is necessary to test similar systems in other regions, while adapting the design and species composition in relation to the natural distributions of the native species. In addition, a complete hydrological study that includes measurements in deep soil layers, direct measurements of tree transpiration and catchment water yield would provide a more comprehensive understanding of how mixed forests influence water production.

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# 4. DRIVERS OF TREE GROWTH IN MIXED PLANTATIONS OF *EUCALYPTUS* AND A HIGH DIVERSITY OF NATIVE TREE SPECIES


## ABSTRACT

New forestry mixtures composed of *Eucalyptus* intercropped with a high diversity of native tree species are a promising option for allying wood production with biodiversity recovery in forest landscape restoration. These systems favor ecological interactions that minimize competition and maximize growth by means of different species compositions and designs in order to succeed. Our objective was to investigate facilitation by N-fixing species and competition for light and nutrients in mixed plantations of *Eucalyptus* with several native tree species. Our assessments were made on a 5-year old, 10-hectare experiment established in the Atlantic Forest of SE Brazil, consisting of monoculture plantations of *Eucalyptus*, mixed plantations made with 40 native tree species (10 pioneer species and 30 of the diversity group), and mixed plantations intercropping the same 30 native tree species in the diversity group with *Eucalyptus* (instead of pioneers). We performed a tree-level analysis using a neighborhood index to investigate a facilitation effect mediated by N-fixing native trees for the growth of *Eucalyptus* in mixtures. We also compared leaf and wood nutrient concentration to assess competition for nutrients as well as photosynthetically active radiation (PAR) to investigate competition for light between *Eucalyptus* and native species of the diversity group. At the tree-level, we found that native N-fixing trees enhanced the growth of *Eucalyptus*, as evidenced by a ~30% higher N concentration in the wood of *Eucalyptus* trees when intercropped with native trees. Despite the lack of a differential nutrient concentration in both leaves (except for Na) and wood (except for N) among species groups growing in different treatments, native species showed lower community-weighed means of all macronutrients when intercropped with *Eucalyptus*. At the community level, PAR interception was higher in plantations made exclusively with native tree species while plantations established with *Eucalyptus* in monoculture or in mixtures did not differ. Contrary to our expectations, native species of the diversity group faced stronger competition for light from native pioneer trees than from *Eucalyptus.* Facilitation and competition play an important role in these novel tree mixtures and should be further manipulated to increase silvicultural performance.


Keywords: Atlantic forest; Competition; Complementarity; Facilitation; Forest landscape restoration; High diversity mixed plantation

## 4.1. Introduction

The performance of trees in mixed plantations is driven by intra- and interspecific interactions, which can promote growth through complementarity effects or hinder it through competition (Vandermeer, 1989). The physiological mechanisms underlying these interactions are related to resource availability, acquisition, and use-efficiency. The interactions species develop are dynamic and may shift between positive, neutral, and negative relationships according to changes in resource availability as stands develop (Forrester et al., 2011). Thus, the advantages or disadvantages of being in a mixture are relative and may change for an individual tree throughout its lifecycle.

Water, nutrients, and light influences on plant development are interconnected, and their relative importance changes depending on the environment, stand development phase, and the species under consideration. In some cases, tree mixtures can increase water use efficiency (Forrester et al., 2010). However, mixed plantations can also be disadvantageous and increase water stress during droughts (Forrester et al., 2016). Mixed forests develop a more stratified canopy which can also be more efficient than monocultures in capturing and using light (Binkley et al., 1992; Menalled et al., 1998). It is important to notice that tree mixtures may not always favor all species and, depending on species composition, can result in greater competition for light. With respect to nutrients, the combination of nitrogen-fixers and non-fixers may help overcome N limitation on the growth of trees during the secondary succession of degraded natural areas (Amazonas et al., 2011; Siddique et al., 2008) as well as in N-limited forest plantations (Forrester et al., 2006). Regarding growth-rate, mixed plantations may represent a disadvantage to later-successional species at least in the first years of growth, because pioneer species more efficiently acquire and use nutrients (Gonçalves et al., 1992) and may win the competition for nutrients in the short-term.

When new tree mixtures are designed, species are usually selected based on functional traits that favor positive interactions and maximize the growth. Sometimes, other criteria are considered for the design of mixed plantation such as biodiversity conservation or the provision of ecosystem services. In Chapter 2 we presented a novel forestry system consisting of a mixture of *Eucalyptus* and a high diversity of native tree species representing an interface between production and restoration. It has been shown that individual *Eucalyptus* trees grew much more in diameter in these high diversity mixtures than in monocultures. *Eucalyptus* overtopped native trees, which, in turn, grew less in mixtures with *Eucalyptus* than in plantations where they were intercropped with native pioneers instead of *Eucalyptus*. In Chapter 3, we reported that the soils under these mixtures have more water than *Eucalyptus* monocultures, but less water than native species plots. The study related the increased growth of *Eucalyptus* and poorer performance of native trees to changes in the ecophysiology of water use. Thus, increased water availability in the soils under mixtures could partly explain the increased growth of *Eucalyptus* and the decreased growth of native tree species in these systems. Considering that competition for water and nutrients may be coupled (Jose et al., 2006), that nutrient limitation of photosynthesis is widespread in tropical trees (Santiago e Goldstein, 2016), and that native trees were overtopped by *Eucalyptus* in mixtures, the question that remains is how important are the ecological interactions influencing nutrient and light availability in determining tree growth in these high diversity mixed plantations.

To understand the underlying ecophysiological mechanisms influencing tree growth in mixed plantations of *Eucalyptus* intercropped with a high diversity of native tree species, we raised the following questions and hypotheses:

(I) Are N-fixing native species facilitating the growth of *Eucalyptus*? Considering the numerous examples of how non-fixing trees can benefit from the proximity of nitrogen-fixers (Binkley et al., 2003; Bouillet et al., 2013; Epron et al., 2013; Forrester et al., 2006; Paula et al., 2015), we hypothesized that (i) *Eucalyptus* trees were facilitated by N-fixing native tree species;

(II) Is the increased growth of *Eucalyptus* in mixtures a result of higher nutrient acquisition with native species? We hypothesized that (ii) *Eucalyptus* had higher nutrient concentrations in leaves and wood tissues in mixed plantations;

(III) Is the reduced growth of native species caused by competition from *Eucalyptus* for nutrients? We hypothesized that (iii) native species intercropped with *Eucalyptus* had lower nutrient concentration in leaves and wood than in native species plots;

(IV) Is competition for light important in these systems? Considering that *Eucalyptus* grew faster and overtopped native species, forming a stratified canopy different from *Eucalyptus* monocultures and from native species plots, we hypothesized that (iv) the mixed forest intercepts more sunlight than the control treatments.

The major difference between mixtures and native species plots in our study is the replacement of native pioneers by *Eucalyptus* in mixtures. Therefore, any additional growth of *Eucalyptus* in mixtures in comparison to monocultures may be the result of complementarity (Kelty, 2006; Vandermeer, 1989). Moreover, any reduction in the growth of native species of the diversity group in mixtures is attributable to additional competition posed by *Eucalyptus* rather than the competition already posed by native pioneers in plantations made exclusively with native species. The investigation of the relative contribution of light, water, and nutrients in the balance between competition and facilitation in such novel tree mixtures is an essential step for manipulating species composition, spatial distribution of species, and resource availability in these systems to increase silvicultural performance according to different project objectives.

## 4.2. Materials and Methods

### 4.2.1. Study Site

The experimental site is located in the Atlantic Forest of Aracruz, a municipality in the state of Espírito Santo in southeastern Brazil (19°49′12″S, 40°16′22″W). The site has a flat relief with a typical Yellow Argisol (Ultisol) presenting a sandy/medium/clayey texture. The climate in the region is Aw (Köppen, 1936) with an annual average air temperature of 23.4 °C, an annual average rainfall of

1,412 mm (Alvares et al., 2013), and a cold dry winter and hot wet summer. Historically, the region experiences a water deficit February through September (Sentelhas et al., 2013a).

### 4.2.2. Experimental Design

The experiment has a randomized block design, with three treatments and five blocks (15 plots). Each plot consisted of 10 rows of 24 trees, including two outer rows as borders. Each effective plot measured 18 m x 60 m (1,080 $m^2$) and included six rows of 20 trees. The three treatments included a *Eucalyptus* monoculture (EUC), a mixed plantation of *Eucalyptus* intercropped with 30 native tree species of the diversity group in alternated single rows (MIX), and a plantation made exclusively with native species in which 10 native pioneer species (instead of *Eucalyptus*) were intercropped with the same 30 native tree species from the diversity group intercropped with *Eucalyptus* in the MIX treatment (NAT). The site was planted in July 2011 using 3 m x 3 m spacing at a density of 1,111 trees $ha^{-1}$, in which each group of species (*Eucalyptus*, native pioneers, and native trees of the diversity group) was planted in alternated single rows. The *Eucalyptus* used was a clone of *E. grandis x E. urophylla*. To control for the variability of ecological interactions, each native species was planted in the same position within all plots. The list of all species used is shown in APPENDIX O, where the species with biological nitrogen fixation capacity are indicated. Note that the three n-fixing pioneers are not present in MIX plots, which contains six n-fixers out of 30 species in the diversity group. In MIX plots, *Eucalyptus* made up 50% of all individuals and represented an average of 89.7% of the total basal area. N-fixers of six species in the diversity group made up 10% of all individuals and accounted for 5.6% of basal area while non-N-fixers of 24 species in the diversity group represented 40% of all individuals and represented 4.7% of total basal area.

### 4.2.3. Nutrient concentrations

We collected leaves and stem disks of native pioneer species, native species of the diversity group, and *Eucalyptus*. The material for nutrient analysis was collected 57 months after plantation. We obtained fully expanded healthy leaves from branches distributed around the outer part of the crown in the second third of the vertical distribution. We weighed leaves in the field, scanned them using a Leaf Scan, and dried them for 48 hours at 60°. We collected stem disks of the same trees at 1.30 m in height, weighed them in the field, transported them refrigerated in ice boxes, determined their fresh volume in the laboratory, and then dried them at 60°C until they reached a stable weight. Dry samples were ground and used to determine the concentration of macro- and micronutrients following published methods for extraction and determination of concentrations (Malavolta et al., 1997). The concentration of metals was determined using inductively coupled plasma mass spectrometry (ICP-MS). The species used for nutrient analyzes are indicated in the list available in APPENDIX O.

### 4.2.4. Light measurements

We used intercepted photosynthetically active radiation (IPAR) as proxy for light competition to compare mixtures and controls (native species plots or *Eucalyptus* monocultures). IPAR was calculated as 1 – transmitted PAR / incident PAR (iPAR). We performed measurements in June 2015 (47 months after plantation) and in January 2016 (54 months after plantation), which corresponded with the middle of the dry and the wet seasons according to historical records. We measured light in a fine grid of 30 points, equally spaced within each plot, between four trees so that every tree was next to one measurement point (APPENDIX P). We used a Ceptometer AccuPAR LP-80 (Decagon Devices, Inc.) pointing northward to measure PAR one meter above the soil between 09:00 and 15:00 on days with predominantly clear sky. We also measured PAR in open areas outside the forest before and after measuring the 30 points within each plot.

### 4.2.5. Data analyses

First, we used inventory data (**Chapter 2**) to perform tree-level analysis and obtain the neighborhood index (NI) (Forrester et al., 2011) of N-fixing native species to test if the increased growth of *Eucalyptus* in the mixture could be explained by facilitation. To do so, we performed tree-level analyzes to separate the effects of stand density from the effects of species composition on the growth of trees in the mixed species plots. Further details are described in **Chapter 2**. Then, we used *lme* (Pinheiro et al., 2016) to perform a linear mixed effects analysis of the relationship between the diameter of target *Eucalyptus* trees and the NI of nitrogen-fixing neighbors. As fixed effects, we entered age, block, plot and site into the model. As a random effect, we had a by-tree random slope for the effect of NI. We used mixed models to be able to analyze data from repeated inventories of the same sites in different ages to control for differences between sites, blocks and plots, and for idiosyncrasy. Prior to modeling, we checked for the assumptions of linearity, absence of collinearity, homoscedasticity, normality of residuals, the absence of influential data points, and independence. Visual evaluation using residual plots did not reveal any obvious deviation from normality or homoscedasticity.

We used Student's t-test to compare nutrient concentration in the leaves and wood of each group of species between treatments. We calculated Community-Weighted Means (CWM) of macronutrients in the wood as a proxy for the amount of nutrients absorbed by each group in order to investigate the accumulated result of competition for nutrients. The wood nutrient concentration of each group of species within each treatment was weighed by the basal area of that group in the community (wood concentration*basal area of group/total basal area). All statistical analyses were performed in R 3.2.1 (R Core Team, 2016).

## 4.3. Results

### 4.3.1. Facilitation and Nutrient competition

The diameter of *Eucalyptus* was positively correlated with the neighborhood index of N-fixing neighbors (radius 4.3 m; p=0.01). *Eucalyptus* diameter was not related to the size of native species of the diversity group (for any radii). Except for higher foliar Na for native trees in mixtures, we found no differences in the average foliar nutrient concentration of *Eucalyptus* and native trees growing in mixtures and controls (Table 4). Similarly, we found almost no differences in wood nutrient concentration between mixtures and controls. The only significant differences were that both *Eucalyptus* and native species of the diversity group had significantly higher N concentration in wood when cultivated in mixtures (Table 4). *Eucalyptus* foliar Ca/K ratios were 1.1 in mixtures and 1.3 in monocultures and foliar Ca/Mg ratios were 2.3 in mixtures vs 2.4 in monocultures. Detailed results of foliar and wood nutrient concentration per species in each treatment are available in APPENDIX Q and APPENDIX R. Native trees in the diversity group had higher community-weighed means (CWM) of wood nutrients in native species plots for all macronutrients. In general, *Eucalyptus* wood showed similar CWM in monoculture and mixtures (Figure 14). Detailed values are available in APPENDIX S.

**Table 4.** Mean nutrient concentration in leaves and wood of trees planted in mixed plantations of 30 native tree species of the diversity group intercropped with 10 native pioneers (NAT), mixed plantations intercropping 30 native tree species of the diversity group and *Eucalyptus* (MIX), and monocultural plantations of *Eucalyptus* (EUC) in the Atlantic Forest of Southeastern Brazil. Species grouping is indicated under "Group" using EU for *Eucalyptus*, DG for diversity group and NP for native pioneers. Significant results (p<0.05; Student's t test) of comparisons between of the same group of species in different treatments were indicated with bold font.

| Group | Diversity | | *Eucalyptus* | | Pioneers |
|---|---|---|---|---|---|
| Treatment | NAT | MIX | EUC | MIX | NAT |
| Leaf | | | | | |
| N (g/kg) | 24.2±4.5 | 24.7±6.1 | 17.97±1.86 | 19.18±1.92 | 24.14±4.33 |
| P (g/kg) | 1.1±0.2 | 1.1±0.3 | 1.1±0.1 | 1.1±0.1 | 1.1±0.2 |
| K (g/kg) | 8.7±2.9 | 8.2±2.5 | 6.4±0.2 | 6.5±0.3 | 7.4±2.6 |
| Mg (g/kg) | 2.5±0.7 | 2.4±0.73 | 3.5±0.7 | 3.1±0.3 | 2.6±0.8 |
| Ca (g/kg) | 11.6±4.6 | 11.8±4.84 | 8.2±0.3 | 7.3±0.6 | 11.9±4.4 |

| Group | Diversity | | *Eucalyptus* | | Pioneers |
|---|---|---|---|---|---|
| Treatment | NAT | MIX | EUC | MIX | NAT |
| S (g/kg) | 2.5±0.6 | 2.5±0.67 | 1.7±0.0 | 1.7±0.1 | 2.9±1.3 |
| Na (mg/kg) | **479±535** | **793±672** | 1516±492 | 1301±183 | 515.8±279 |
| Mn (mg/kg) | 65.7±54.7 | 90.8±103.9 | 142.8±31.7 | 123.1±7.3 | 85.8±43 |
| Fe (mg/kg) | 117.1±50.2 | 132.5±47.8 | 100.0±0.8 | 81.3±8.7 | 118.6±33.9 |
| Cu (mg/kg) | 1.6±0.9 | 1.6±0.8 | 1.0±0.5 | 0.9±0.3 | 2.1±0.9 |
| B (mg/kg) | 56.9±27.2 | 52.5±27.6 | 53.6±1.9 | 49.5±4.9 | 38.9±12.7 |
| Mo (mg/kg) | 0.2±0.2 | 0.1±0.1 | 0.2±0.2 | 0.2±0.2 | 0.2±0.2 |
| Wood | | | | | |
| N (g/kg) | **3.2±1** | **3.7±0.9** | **2.1±0.1** | **2.8±0.35** | 3.02±0.89 |
| P (g/kg) | 0.3±0.1 | 0.3±0.2 | 0.1±0.0 | 0.1±0.01 | 0.37±0.16 |
| K (g/kg) | 2.1±0.8 | 2.1±0.6 | 1.1±0.2 | 1.0±0.14 | 3.18±1.53 |
| Mg (g/kg) | 0.4±0.3 | 0.4±0.3 | 0.1±0.0 | 0.1±0.02 | 0.43±0.13 |
| Ca (g/kg) | 2.3±1.0 | 2.4±0.9 | 0.7±0.0 | 1.0±0.18 | 2.58±2.36 |
| S (g/kg) | 0.4±0.4 | 0.4±0.4 | 0.0±0.0 | 0±0 | 0.26±0.21 |
| Na (mg/kg) | 96.3±104 | 95.9±106 | 239.1±73.5 | 244.5±96.8 | 149.6±178 |
| Mn (mg/kg) | 3.8±2.7 | 5.2±3.9 | 3.2±1.3 | 2.8±0.49 | 10.6±18.7 |
| Fe (mg/kg) | 20.2±14.8 | 15.2±7.3 | 9.7±1.9 | 12.9±4.93 | 19.68±9.5 |
| Cu (mg/kg) | 0.8±0.4 | 0.8±0.4 | 0.3±0.3 | 0.2±0.17 | 1.03±0.64 |
| B (mg/kg) | 4.2±0.7 | 4.3±0.9 | 3.9±0.3 | 4.0±0.36 | 4.07±0.67 |
| Mo (mg/kg) | 0.1±0.2 | 0.1±0.3 | 0 | 0±0 | 0.2±0.3 |

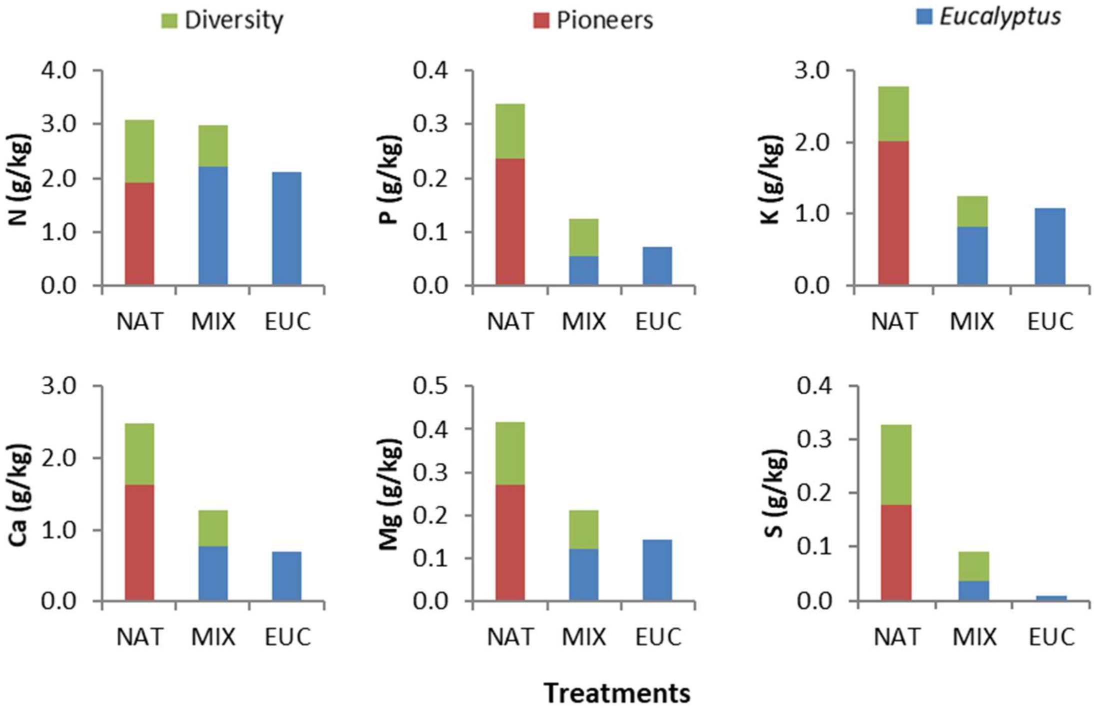


**Figure 14.** Community-weighed means of wood nutrients of trees planted in mixed plantations made exclusively with 40 native tree species (NAT), mixed plantations intercropping 30 native tree species and *Eucalyptus* (MIX) and monoculture plantations of *Eucalyptus* (EUC) in the Atlantic forest of southeastern Brazil. The diversity group comprises 30 native species intercropped with *Eucalyptus* in MIX or with 10 native pioneer species in NAT.

### 4.3.2. Light

Intercepted PAR did not differ among treatments in the first (47 months) measurement period (Shapiro-Wilk, p= 0.6505; ANOVA, p=0.3676) but was higher in NAT compared with EUC and MIX which did not differ among themselves in the second (54 months) measurement (Shapiro-Wilk, p=0.1071; ANOVA, p=0.01086; Tukey, α=0.05) (Figure 15).

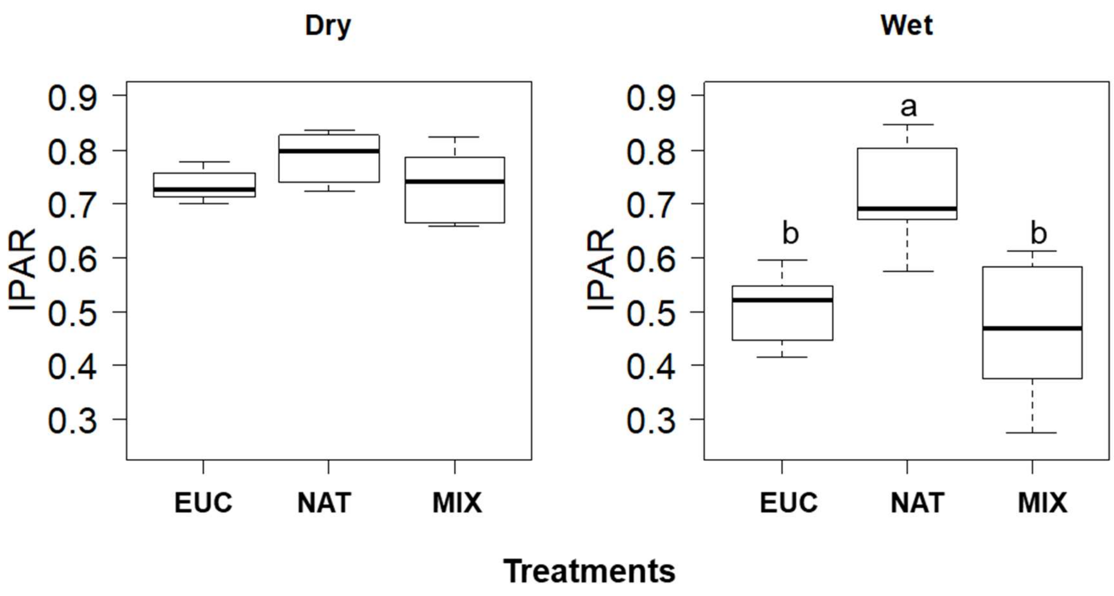


**Figure 15.** Intercepted Photosynthetically Active Radiation (IPAR) by stands planted in mixed plantations made exclusively with 40 native tree species (NAT), mixed plantations intercropping 30 native tree species and *Eucalyptus* (MIX) and monoculture plantations of *Eucalyptus* (EUC) in the Atlantic forest of southeastern Brazil. Measurements were made in June 2015, historical dry season, and in January 2016, historical wet season, 47 and 54 months after plantation, respectively.

## 4.4. Discussion

We found evidence to support the hypothesis that native N-fixing trees facilitated the growth of *Eucalyptus* in highly diverse mixed plantations. However, we found no strong evidence of increased nutrient availability in mixtures except for slightly higher N concentrations in *Eucalyptus* leaves - partially supporting our second hypothesis. Larger individual *Eucalyptus* trees were significantly associated with greater neighborhood indices of N-fixing species. This indicates that the higher the number of N-fixing neighbors, and the larger they are, the larger *Eucalyptus* will grow in mixtures. These N-fixing neighbors may increase the amount of N available in the system (Siddique et al., 2008) that can be acquired by *Eucalyptus* after decay or below-ground transfer (Paula et al., 2015) and result in higher foliar N concentration and photosynthetic rates. Species grown in mixtures generally have greater above-ground nutrient content (Richards et al., 2010). Higher foliar N concentration is a common trait when *Eucalyptus* grows in mixed plantations containing nitrogen-fixers (David I Forrester et al., 2007) and increased nitrogen concentration may result in higher photosynthesis and resource-use efficiency (Richards et al., 2010). Beyond the evidence for facilitation, the neighborhood analysis also showed that non-N-fixing native neighbors were not strong competitors of *Eucalyptus*. These relationships suggest a density effect favoring the extra growth of individual *Eucalyptus* trees in mixtures which is potentially mediated by competition reduction with other *Eucalyptus* trees and weaker competition from native species. Despite the similar values in foliar nutrient concentrations, the ratios among different elements also point to better nutritional status of *Eucalyptus* in mixtures. High productivity of *E. grandis* was related to foliar Ca/K ratios between 0.55 and 0.85 (Silveira et al., 2005). We found that Ca/K ratios are out of the optimum range for *Eucalyptus* in our experimental site, but values were more adequate in mixtures (1.1) than in monocultures (1.3). Lower foliar Ca/Mg ratios were also related to higher productivity (Silveira et al., 2005) and we found better values in mixtures (2.3 vs 2.4 in monocultures). Altogether, these differences in nutrients may have caused *Eucalyptus* to allocate more carbon to aboveground biomass (Litton et al., 2007).

Nutrient concentrations in foliar and wood tissues of native species of the diversity group were similar between mixtures and native species plots. This does not support the hypothesis that nutrient competition from *Eucalyptus* affects the growth of native trees. The only exceptions were higher foliar Na concentrations and higher N wood concentrations of native species in mixtures. Increased Na concentrations in leaves can affect growth (Anthraper e DuBois, 2003) and may arise from higher salinity in the soils, which were also shown to be drier under mixtures (**Chapter 3**). Drought and salinity alter nutrient availability, transport and partitioning (Hu e Schmidhalter, 2005). In contrast with almost no differences in foliar and wood nutrient concentration, the lower community-weighed means of all macronutrients showed that, as native species intercropped with *Eucalyptus* grew, they acquired and stored a smaller proportion of the nutrients (at the community level) in their wood. The assessment of nutrient limitation is species-specific and depends on previous knowledge about the relationship between plant growth and the concentration of a given nutrient in plant tissues (Bouma, 1983). This knowledge simply does not exist for most of the tropical tree species which makes nutrient limitation hard to identify, especially when growth is constrained by nutrient limitation below the levels causing deficiency that would result in common symptoms. This limits comparison of the results obtained with any published standards or previous research. Despite this limitation, nutrient competition does not seem to be the major factor explaining the reduced growth of native species in our mixed forests and when nutrient availability is high, plants may compete mainly for light (Aerts, 1999).

Several studies found that higher tree diversity in plantations increased leaf area index and light interception or absorbance. This was always associated with more stratified canopies (Binkley et al., 1992; Forrester et al., 2012; le Maire et al., 2013; Menalled et al., 1998; Nouvellon et al., 2012). We observed that mixtures and monocultures were similar and intercepted less photosynthetically active radiation, suggesting that competition for light did not limit native species growth in mixtures with *Eucalyptus*. On the other hand, *Eucalyptus* seem to benefit from higher availability of sunlight in mixtures compared to monocultures because it grew much taller than native trees and formed a clear upper canopy layer in mixtures (**Chapter 2**) which provided it with access to direct sun light at the lateral parts of the crown (field observation), and this advantage may contribute to the better performance of *Eucalyptus* in mixtures. Due to their architecture defined by apical dominance, *Eucalyptus* trees occupied fewer of the available lateral canopy gaps and canopy structure was much more homogeneous than the canopy of native species plots. In contrast, the ten different native pioneers that substituted *Eucalyptus* in native species plots formed a shorter canopy but was structurally much more diverse even though it had some degree of overlap with the crowns of native species in the diversity group. Native pioneers were more plastic and could colonize gaps more efficiently, both horizontally and even vertically, with greater heterogeneity (field observation). Thus, native species in the diversity group occupying the lower part of the canopy stratum had more light available when intercropped with *Eucalyptus* in mixtures than when intercropped with native pioneers in native species plots. At a minimum, this is true for the period of the day between 10 am and 3 pm, when we made our measurements (following the guidelines for equipment use). During this period, sunlight passed through the linear canopy openings between *Eucalyptus* rows and reached the canopy of native species in the diversity group and the ground. We do not rule out the possibility, however, that *Eucalyptus* filtered a greater proportion of solar radiation earlier in the morning, when solar radiation crossed longer distances through the upper canopy layer before reaching native trees. In that case, native species could face light competition in hours of intense photosynthetic activity (**Chapter 3**). We also need to point out that competition for light may have been more important in earlier phases of stand development when *Eucalyptus* leaf area index peaked, possibly around the second or third year after plantation (Almeida et al., 2007; Laclau et al., 2009).

We believe the higher light irradiance in mixtures stimulated native trees to allocate more to roots, since they transpired more and needed to capture more water (Poorter, 1999). This could partly explain their reduced stem diameter growth (**Chapter 2**). Using the same logic, the higher competition for light in native species plots may promote native trees in the diversity group to allocate more to the production of leaf biomass. This matches the decreased soil water availability and related lower hydraulic performance of native species observed in these mixtures (**Chapter 3**) compared to native species plots. On the other hand, mixtures had more water in their soil than *Eucalyptus* monocultures (**Chapter 3**). This, in addition to increased light availability, nutrient acquisition, more appropriate element ratios, and more allocation to aboveground biomass may explain the increased growth of *Eucalyptus*.

Commercial mixed plantations are usually composed of two to four species of trees (Kelty, 2006). The growth patterns of different species may be affected by different factors. Despite the accumulated knowledge, understanding these factors is still a challenge, especially when new combinations of species are tested and a high diversity of species is employed. Here, this challenge is increased for several reasons. First, the objective of combining production and restoration in the same stands is *per se* ambitious and poorly explored by research. Second, we intercropped an unprecedently high diversity of native tree species with a fast-growing commercial variety of *Eucalyptus*. Third, there is an alarming lack of information about the physiology and the silvicultural aspects of native tree species in the tropics. In addition to this complexity, combining species gives rise to emergent properties originating from these interactions. Together, this makes it hard to design and understand the functioning of highly diverse mixtures. Moving forward, we suggest that future plantations should first combine fast-growing commercial species and a high proportion of nitrogen-fixers with intermediate growth rate that can facilitate the growth of non-fixers and sustain their own growth-rates without significant reductions in diameter. This would be especially advantageous if these nitrogen-fixers have ecological strategies to cope with water limitations such as leaf deciduousness in the dry season to scape competition for water. Latter successional species of slow-growth, native non-fixers in general, and fast-growing native species could be added after the commercial species (e.g. *Eucalyptus*) is harvested. Future research on the physiology and silvicultural characteristics of native tree species are important to understanding current mixtures in more detail and to serve as input information for the modeling and design of new mixed plantations.

## 4.5. Conclusions

Facilitation and competition play an important role in the functioning of highly diverse mixed plantations of native species and *Eucalyptus*. We believe the explanation for the increased growth of individual *Eucalyptus* trees in mixtures reported in **Chapter 2** is mainly the increased availability of water and light and facilitation from several nitrogen-fixing native trees species which stimulated growth and carbon allocation aboveground. The decreased growth of native species intercropped with *Eucalyptus* on the other hand, may result from higher light availability combined with less water in the soil, increasing competition for water, decreasing their hydraulic performance, and resulting in lower biomass production and more allocation to the roots rather than stem growth

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# 5. FINAL CONSIDERATIONS

To continue increasing global forest cover and meet conservation and production goals, we need to manage forests at the landscape level using different complementary approaches and the development of new forestry systems that aim at multiple objectives. Reforestation may have high opportunity costs and the financial benefits take longer to achieve than those of many other non-forest land use types. Most of the planned conversion from non-forest land use types into forests is surrounded by uncertainties and will only happen if silvicultural systems are flexible enough to be managed according to changes in legal, financial and environmental conditions. Positive gains may be obtained if we develop and implement forest systems that can be directed through adaptive management towards ecological restoration or commercial forestry.

Initially, the experiments described in this thesis were designed for anticipating the economic returns from sites undergoing forest restoration to overcome the financial barrier that hinders its large-scale adoption. Bringing exotic *Eucalyptus* into restoration as a temporary ally was strategic and a paradigm shift *per se*, since commercial *Eucalyptus* plantations have been assumed to cause environmental degradation. As this research developed, we started seeing this alternative restoration model as a new forestry system. At one end, we had traditional restoration plots, with high species diversity, but high implementation costs and no direct economic return, at least in the short and intermediate terms. At the other end, we had commercial monocultures of clonal *Eucalyptus*, which have the lowest implementation costs, fastest economic returns, but negligible contribution for biodiversity conservation compared to native tropical forests. In the middle, these high diversity mixtures effectively combined biodiversity conservation and wood production at the stand scale, with intermediate implementation costs, and produced wood, providing economic return from restoration sites in the short run. Essentially, these mixed plantations of *Eucalyptus* and a high diversity of native tree species are flexible forestry systems that can direct adaptive management towards restoration, if the *Eucalyptus* component is exploited and replaced by other native species, but it can also be kept as a production forest that combines wood production and biodiversity conservation.

The objective of this research was to test the ecological viability of plantations that temporarily mix *Eucalyptus* spp. and a high diversity of native tree species during the initial phases of forest restoration as a strategy to finance part of its costs. We showed that these new mixtures are a viable option for that objective. In the first part of the study, we showed that mixed plantations effectively combined high wood yield and tree diversity; that *Eucalyptus* grew larger in mixtures with native species than in monocultures; that native tree species grew less in mixtures with *Eucalyptus*;

and that the mixing effect was stronger for fast- and intermediate-growing native species. In the second part, we found that the mixture of *Eucalyptus* and native species consumed less water than *Eucalyptus* monocultures; that *Eucalyptus* reduced the hydraulic performance of fast-growing native trees; and that tree growth was influenced by changes in the ecophysiology of water use. In the last part, we showed that a high diversity of nitrogen-fixing native trees facilitated *Eucalyptus* growth; that *Eucalyptus* had ~30% higher wood N concentration when intercropped with native trees; that the growth of native trees was not limited by nutrient competition with *Eucalyptus*; that *Eucalyptus* may benefit from increased light availability in mixed plantations; and that native species plots intercepted more sunlight than mixtures or *Eucalyptus* monocultures. There comes an even bigger paradigm shift. This is supported by the high production of *Eucalyptus* in these systems, reaching as much as nearly 75% of the basal area produced by *Eucalyptus* monocultures, but using only half the number of trees, while the other half of seedlings consist of a high diversity of native species. The way these mixed forests function also represents advantages. First, they use less water than *Eucalyptus* monocultures. Second, native species with the capacity for biological nitrogen fixation facilitate the growth of *Eucalyptus*. Third, there seems to be more photosynthetically active radiation for all components compared to the other systems, with possible advantages for *Eucalyptus* from increased light exposure of the lateral parts of individual tree crowns. All together, these facts raised the possibility that these mixtures could be used as an alternative for traditional commercial plantations. This would be especially advantageous in areas sensitive for water production or areas which will likely be subjected to drier conditions due to climate change. Also, despite some decreased growth of native trees, the disproportionate increase in biomass in the system originating from the *Eucalyptus* component, compared to native pioneers, represent an opportunity for higher carbon sequestration in the short term. Of course, these mixtures do not represent a final solution for financing tropical forest restoration nor for the challenges of combining the production of forest products with biodiversity conservation. It does represent an important step towards a paradigm shift or a contemporary solution for these problems.

From the scientific results and the practical field experience obtained during this research, we suggest improvements for the implementation of new sites. To facilitate harvesting, mixtures should be planted in double or triple rows of *Eucalyptus*, since single rows can be mechanically harvested, but may require extra training and time from machine operators. However, if the system is managed for restoration and all *Eucalyptus* is harvested at once, it is likely that fast-growing native species will need to be planted to fill the space left by *Eucalyptus* if the potential for natural regeneration is low and the seed bank of grasses is still active. Thinking of promoting positive ecological interactions, native trees could also be planted in triple rows, using a large proportion of nitrogen fixing species in the outer rows, next to *Eucalyptus*, to diminish the effects of competition on native trees and increase facilitation, while placing most of the other native species in the central row. The fastest-growing native trees could be avoided at time zero, to be included in the system to replace *Eucalyptus* when it is harvested. We also highlight the need for *Eucalyptus* stump sprout control after its last rotation in the system if the native species are not large enough to outcompete it.

For the first time, the basis for intercropping native and exotic trees in a 1:1 proportion for tropical forest restoration was tested. Our research showed that it is possible to temporarily intercrop *Eucalyptus* and trees native from the Atlantic Forest during the first stages of forest restoration. These findings support one part of the basis of the new Law for the Protection of the Native Vegetation of Brazil (Brasil. Presidência da República, 2012) which replaced the former Forest Code. However, we highlight that the extrapolation of how these mixtures functioned during the first five years to the outcome of a permanent intercrop of these species in these proportions is limited.

This research has a strong interface between restoration science and practice, which more than testing hypotheses, contributed to the development of new ways to restore the tropical forests, allying restoration and production from ecological and economic perspectives. Our findings indicate how to advance into the future, starting from the current state of the art towards forest restoration systems that minimize competition and maximize growth, as an emergent promising alternative to finance tropical forest restoration and overcome the economic barrier that still holds large-scale restoration. This research may be used as a basis to continue adapting silviculture for different regions and forest ecosystems. Looking further into the future, these mixtures may also represent the starting point of a new silvicultural model that brings together production and conservation.

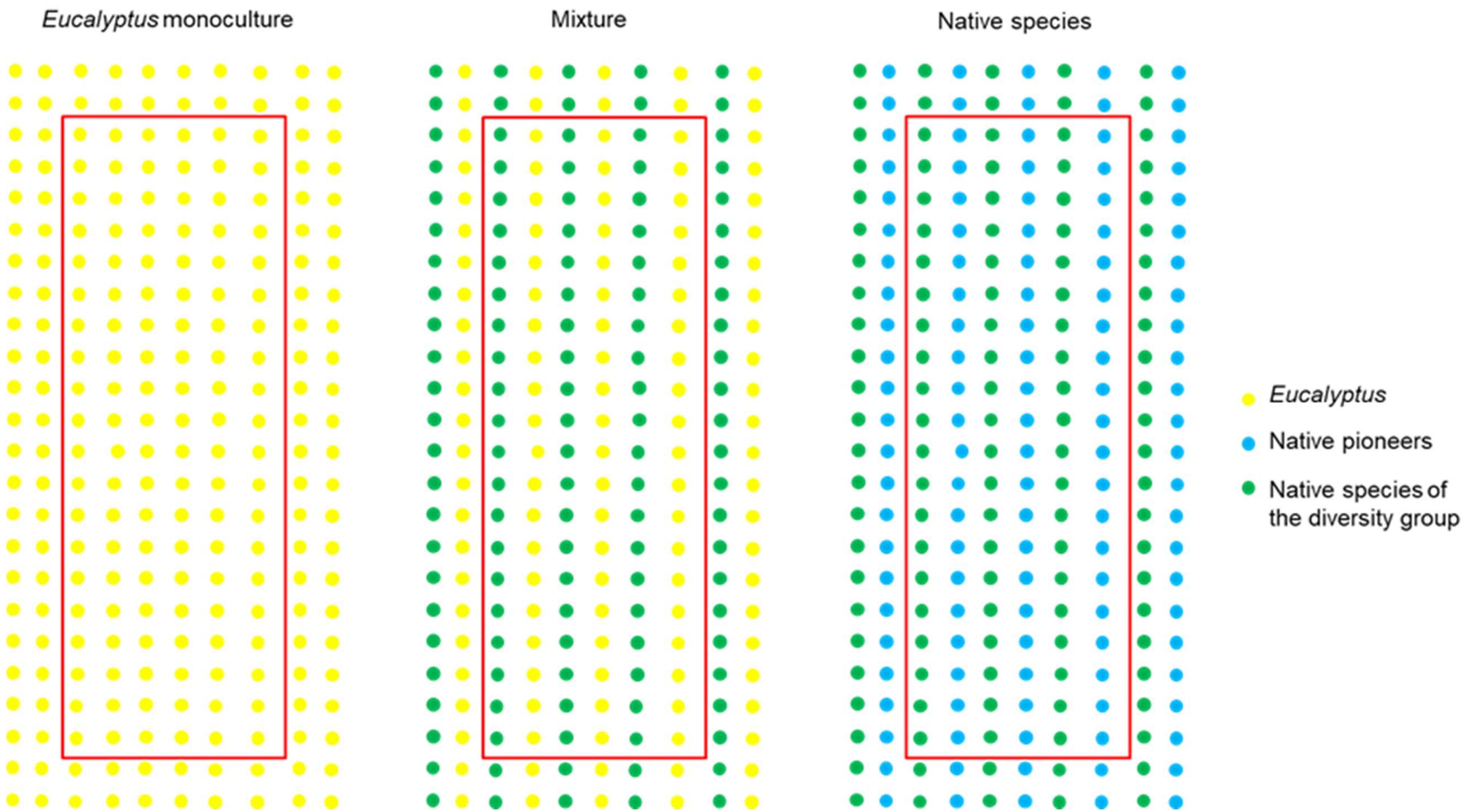
This study represents a big step forward but also raises several questions that remain to be answered. How will the system react to the harvesting of *Eucalyptus* at the end of the rotation? How do plantation mixtures of *Eucalyptus* and a high diversity of native species function regarding species survival and growth if we manage for additional rotations of *Eucalyptus*? What is the hydraulic performance of the other native species? Does the mixing result in niche partitioning belowground? Does the mixture change how deep species acquire water from? How could climate change or different plantations designs affect the functioning of these forestry systems? Which other species could be mixed with a high diversity of native trees with the objective of providing early economic return from restoration? These and many other questions inspire future studies. Future research could use growth models to investigate how similar mixtures would behave under different climatic scenarios and plantation designs. Using this approach, it is possible to understand how this restoration system responds to climate change and infer how silviculture can be adapted accordingly. Also, we need to build up knowledge about the physiology and silviculture of native tree species to make it possible to do the modeling and for the well-informed creation of new mixtures. The information available may be used by scientists, decision makers, planners and restorationists to advance the science and practice of restoration and silviculture in the tropics.

## References

Brasil. Presidência da República, 2012. Lei Nº 12.651, de 25 de Maio de 2012.

# APPENDICES

**APPENDIX A.** Representation of the plot designs for the three different treatments used in the experimental sites.



**APPENDIX B.** Monthly rainfall and temperature historical averages of the study sites.

| State | Municipality | Region | Climate | Altitude | Month | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | Annual mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Rainfall (mm) | | | | | | | | | | | | |
| BA | Igrapiúna | Northeast | Af | 121 | | 141 | 157 | 199 | 186 | 180 | 206 | 202 | 132 | 140 | 129 | 191 | 160 | 168.5 |
| BA | Mucuri | Northeast | Af | 78 | | 142 | 93 | 128 | 113 | 93 | 80 | 98 | 70 | 91 | 160 | 174 | 172 | 117.8 |
| ES | Aracruz | Southeast | Aw | 41 | | 157 | 90 | 118 | 91 | 65 | 47 | 65 | 59 | 80 | 140 | 193 | 199 | 108.7 |
| | | | | | | Temperature (°C) | | | | | | | | | | | | |
| BA | Igrapiúna | Northeast | Af | 121 | | 26.3 | 26.6 | 26.5 | 25.7 | 24.4 | 23.1 | 22.5 | 23.1 | 24.3 | 25.5 | 25.7 | 26.0 | 25.0 |
| BA | Mucuri | Northeast | Af | 78 | | 25.8 | 26.2 | 26.0 | 24.9 | 23.2 | 21.7 | 20.9 | 21.4 | 22.6 | 23.9 | 24.5 | 25.1 | 23.9 |
| ES | Aracruz | Southeast | Aw | 41 | | 25.6 | 26.1 | 25.8 | 24.6 | 22.6 | 21.2 | 20.2 | 20.7 | 21.8 | 23.2 | 23.9 | 24.8 | 23.4 |

**APPENDIX C.** List of species planted in each experimental site. For each species, we list scientific names including authors, family, common names in Portuguese and the functional grouping. The groupings are: *Eucalyptus*; pioneer for native species planted in the native species plots in the same positions where *Eucalyptus* was planted in the mixture; and fast, interm and slow for fast-, intermediate- and slow-growing native species, respectively. Species planted in a given experimental site are indicated with the corresponding group name.

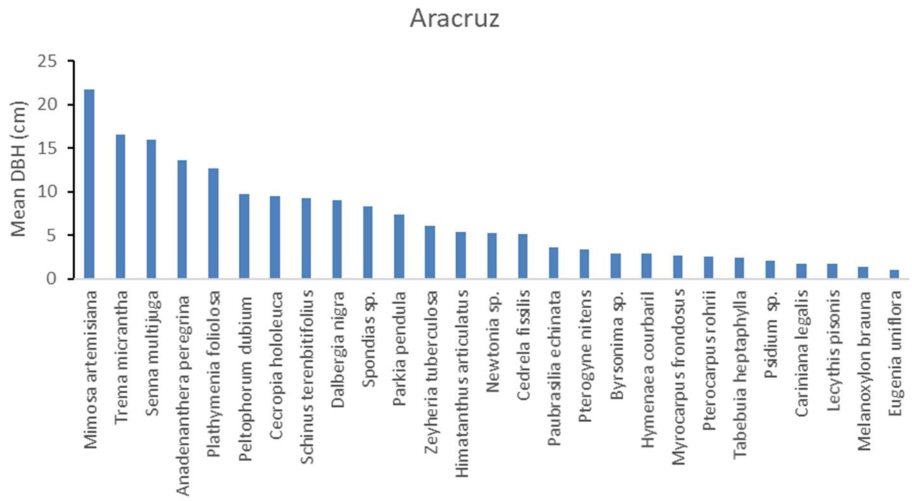
| Species | Author | Family | Common name | Grouping in Sites | | |
|---|---|---|---|---|---|---|
| | | | | Aracruz | Mucuri | Igrapiúna |
| *Acnistus arborescens* | (L.) Schltdl. | Solanaceae | Fruto-de-sabiá | slow | interm | |
| *Aegiphila sellowiana* | Cham. | Lamiaceae | Mululo | pioneer | pioneer | pioneer |
| *Anadenanthera peregrina* | (L.) Speg. | Fabaceae | Angico-curtidor | fast | interm | interm |
| *Annona neosericea* | H.Rainer | Annonaceae | Pinha-da-mata | | | interm |
| *Apuleia leiocarpa* | (Lambin *et al.*) J.F.Macbr. | Fabaceae | Garapa | | slow | |
| *Bowdichia virgilioides* | Kunth | Fabaceae | Macanaíba | | interm | |
| *Byrsonima sericea* | DC. | Malpighiaceae | Murici | | interm | interm |
| *Byrsonima* sp. | Rich. ex Kunth | Malpighiaceae | Murici | slow | | |
| *Calophyllum brasiliense* | Cambess. | Calophyllaceae | Guanandi | | slow | |
| *Cariniana estrellensis* | (Raddi) Kuntze | Lecythidaceae | Jequitibá-branco | slow | | slow |
| *Cariniana legalis* | (Mart.) Kuntze | Lecythidaceae | Jequitibá-rosa | slow | | interm |
| *Cecropia hololeuca* | Miq. | Urticaceae | Embaúba-branca | interm | fast | fast |
| *Cedrela fissilis* | Vell. | Meliaceae | Cedro | interm | | |
| *Centrolobium microchaete* | (Mart. ex Benth.) H.C.Lima | Fabaceae | Putumuju | | interm | interm |
| *Citharexylum myrianthum* | Cham. | Verbenaceae | Pau-viola | pioneer | pioneer | pioneer |
| **Cordia myxa* | L. | Boraginaceae | Baba-de-boi | | | fast |

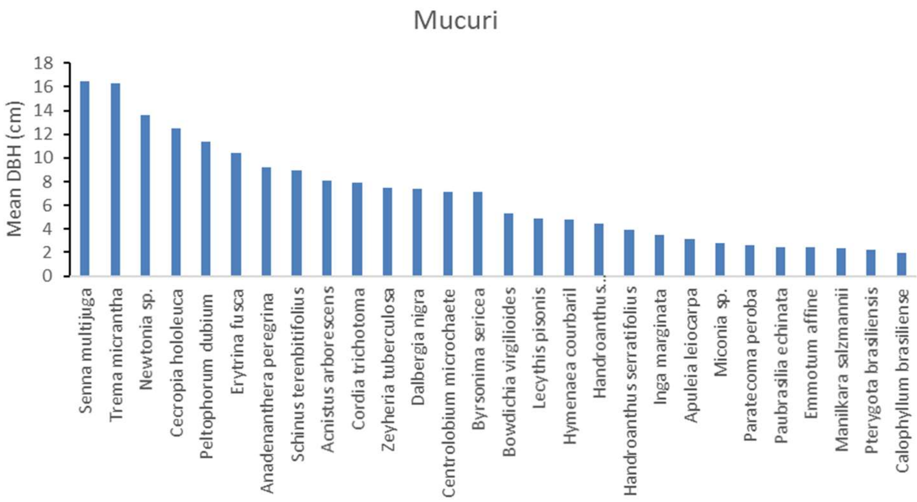
| Species | Author | Family | Common name | Grouping in Sites | | |
|---|---|---|---|---|---|---|
| | | | | Aracruz | Mucuri | Igrapiúna |
| *Cordia superba* | Cham. | Boraginaceae | Baba-de-boi | | | fast |
| *Cordia trichotoma* | (Vell.) Arráb. ex Steud. | Boraginaceae | Louro-curtidor | | interm | |
| *Cupania* sp. | L. | Sapindaceae | Camboatã | pioneer | | |
| *Dalbergia nigra* | (Vell.) Allemão ex Benth. | Fabaceae | Jacarandá-da-Bahia | interm | interm | interm |
| *Emmotum affine* | Miers | Icacinaceae | Aderno | | slow | |
| *Enterolobium contortisiliquum* | (Vell.) Morong | Fabaceae | Tamboril | pioneer | pioneer | fast |
| *Erythrina fusca* | Lour. | Fabaceae | Eritrina | | fast | |
| *Eucalyptus spp.* | | Myrtaceae | Eucalipto | *Eucalyptus* | *Eucalyptus* | *Eucalyptus* |
| *Eugenia uniflora* | L. | Myrtaceae | Pitanga | slow | | |
| *Guazuma ulmifolia* | Lam. | Malvaceae | Mutambo | | pioneer | |
| *Handroanthus impetiginosus* | (Mart. ex DC.) Mattos | Bignoniaceae | Ipê-roxo | | slow | interm |
| *Handroanthus serratifolius* | (Vahl) S.Grose | Bignoniaceae | Ipê-ovo | | slow | |
| *Himatanthus articulatus* | (Vahl) Woodson | Apocynaceae | Agoniada | interm | | slow |
| *Hymenaea courbaril* | L. | Fabaceae | Jatobá | slow | slow | slow |
| *Inga edulis* | Mart. | Fabaceae | Inga-de-metro | pioneer | pioneer | pioneer |
| *Inga laurina* | (Sw.) Willd. | Fabaceae | Inga | pioneer | | pioneer |
| *Inga marginata* | Willd. | Fabaceae | Inga marginata | | slow | |
| *Joannesia princeps* | Vell. | Euphorbiaceae | Boleira | pioneer | pioneer | pioneer |

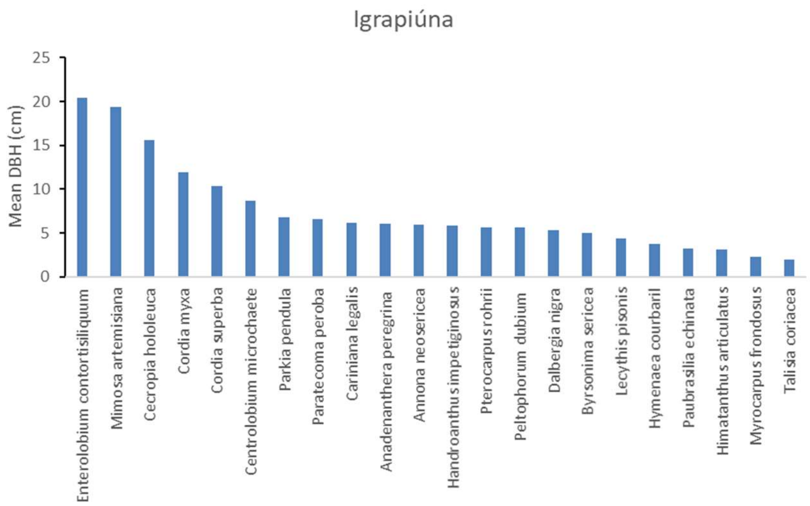
| Species | Author | Family | Common name | Grouping in Sites | | |
|---|---|---|---|---|---|---|
| | | | | Aracruz | Mucuri | Igrapiúna |
| *Lecythis pisonis* | Cambess. | Lecythidaceae | Sapucaia | slow | slow | slow |
| *Luehea* sp. | | Malvaceae | Açoita-cavalo | | pioneer | |
| *Manilkara salzmannii* | (A.DC.) H.J.Lam | Sapotaceae | Maçaranduba | | slow | |
| *Melanoxylon brauna* | Schott | Fabaceae | Brauna | slow | | |
| *Miconia* sp. | | Melastomataceae | Quaresminha | | slow | |
| *Mimosa artemisiana* | Heringer & Paula | Fabaceae | Angico-cangalha | fast | | fast |
| *Myrocarpus frondosus* | Allemão | Fabaceae | Balsamo | slow | | slow |
| *Newtonia* sp. | | Fabaceae | Angico-vermelho | interm | fast | |
| *Paratecoma peroba* | (Record) Kuhlm. | Bignoniaceae | Peroba-amarela | slow | slow | interm |
| *Parkia pendula* | (Willd.) Benth. ex Walp. | Fabaceae | Juerana-vermelha | interm | | interm |
| *Paubrasilia echinata* | (Lam.) E. Gagnon, H.C. Lima & G.P. Lewis | Fabaceae | Pau-Brasil | slow | slow | slow |
| *Peltophorum dubium* | (Spreng.) Taub. | Fabaceae | Angico-canjiquinha | interm | fast | interm |
| *Plathymenia foliolosa* | Benth. | Fabaceae | Vinhático | fast | | |
| *Psidium* sp. | | Myrtaceae | Araçá | slow | | |
| *Pterocarpus rohrii* | Vahl | Fabaceae | Pau-sangue | slow | | interm |
| *Pterogyne nitens* | Tul. | Fabaceae | Madeira-nova | slow | | |
| *Pterygota brasiliensis* | Allemão | Malvaceae | Farinha-seca | | slow | |
| *Schinus terenbitifolius* | Raddi | Anacardiaceae | Aroeira | interm | interm | |

| Species | Author | Family | Common name | Grouping in Sites | | |
|---|---|---|---|---|---|---|
| | | | | Aracruz | Mucuri | Igrapiúna |
| *Senna macranthera* | (DC. ex Collad.) H.S.Irwin & Barneby | Fabaceae | Fedegoso | pioneer | pioneer | pioneer |
| *Senna multijuga* | (Rich.) H.S.Irwin & Barneby | Fabaceae | Pau-cigarra | fast | fast | |
| *Sparattosperma leucanthum* | (Vell.) K.Schum. | Bignoniaceae | Cinco-folhas | pioneer | pioneer | pioneer |
| *Spondias* sp. | | Anacardiaceae | Cajá-mirim | interm | | |
| *Spondias venulosa* | (Engl.) Engl. | Anacardiaceae | Cajá-do-mato | | pioneer | pioneer |
| *Tabebuia heptaphylla* | (Vell.) Toledo | Bignoniaceae | Ipê-roxo | slow | | |
| *Talisia coriacea* | Radlk. | Sapindaceae | Pitomba | | | slow |
| *Tapirira guianensis* | Aubl. | Anacardiaceae | Peito-de-pombo | pioneer | | pioneer |
| *Trema micrantha* | (L.) Blume | Cannabaceae | Corindiba | fast | fast | |
| *Zeyheria tuberculosa* | (Vell.) Bureau ex Verl. | Bignoniaceae | Ipê-felpudo | interm | interm | |

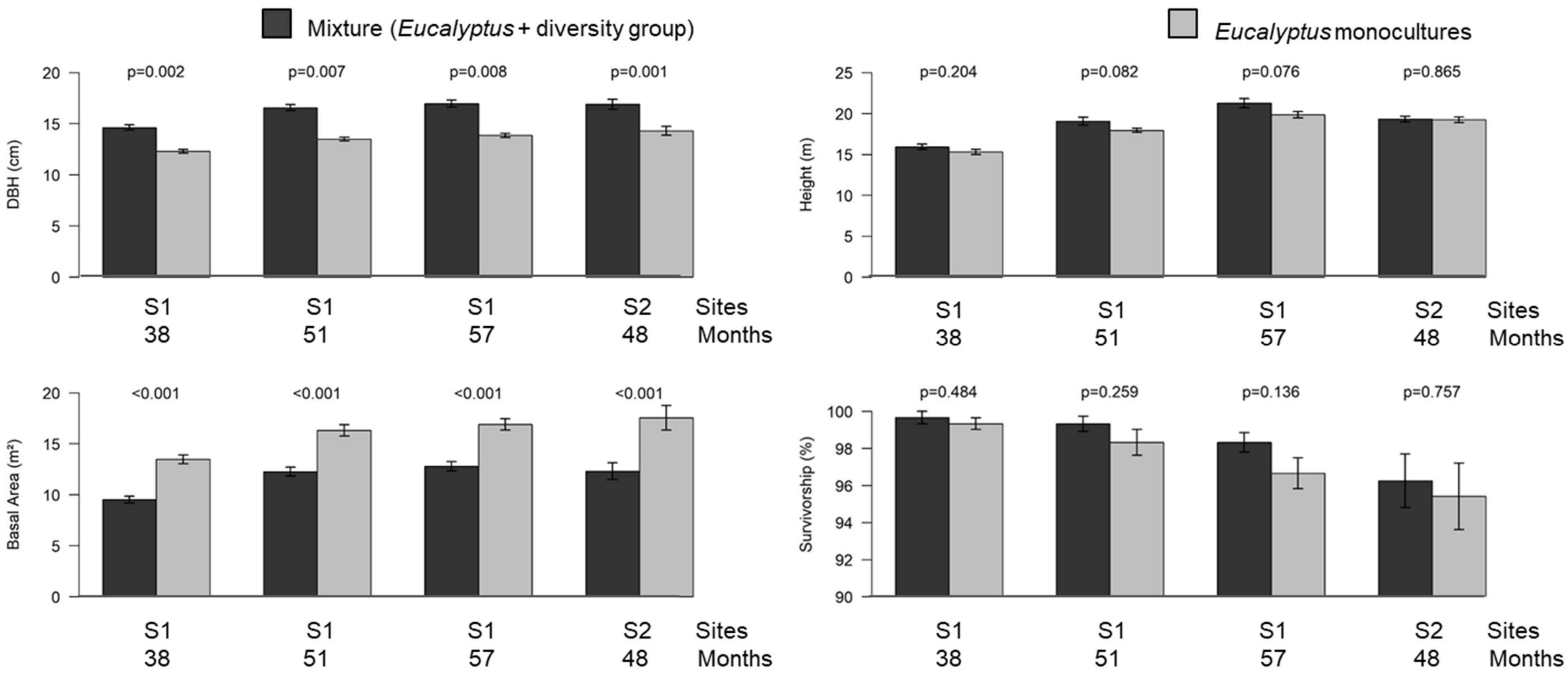
**APPENDIX D.** Average diameter of native species intercropped with native pioneers. The Diameter at Breast Height represented here was measured at 57 months in Aracruz-ES, 48 months in Mucuri-BA and at 60 months in Igrapiúna-BA.



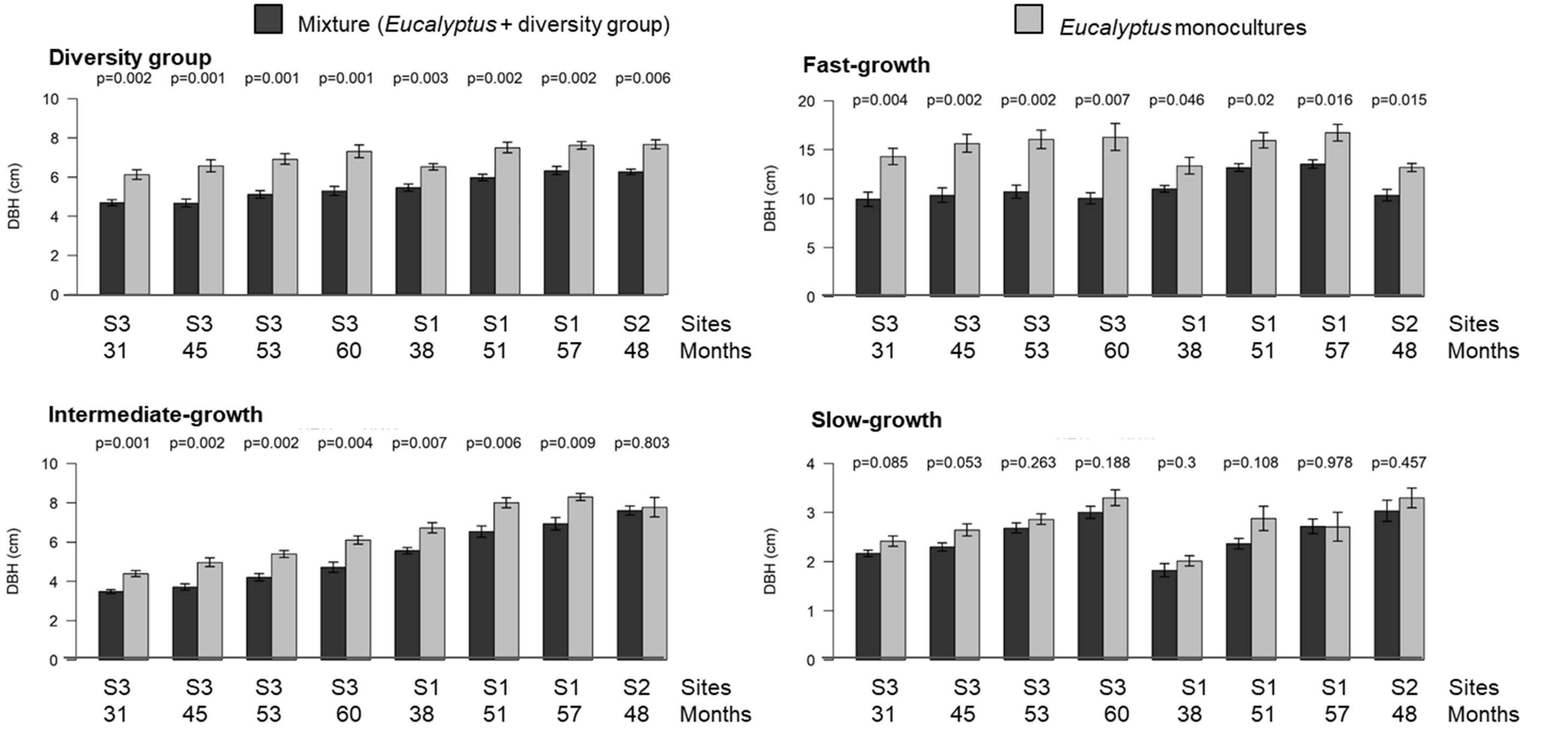



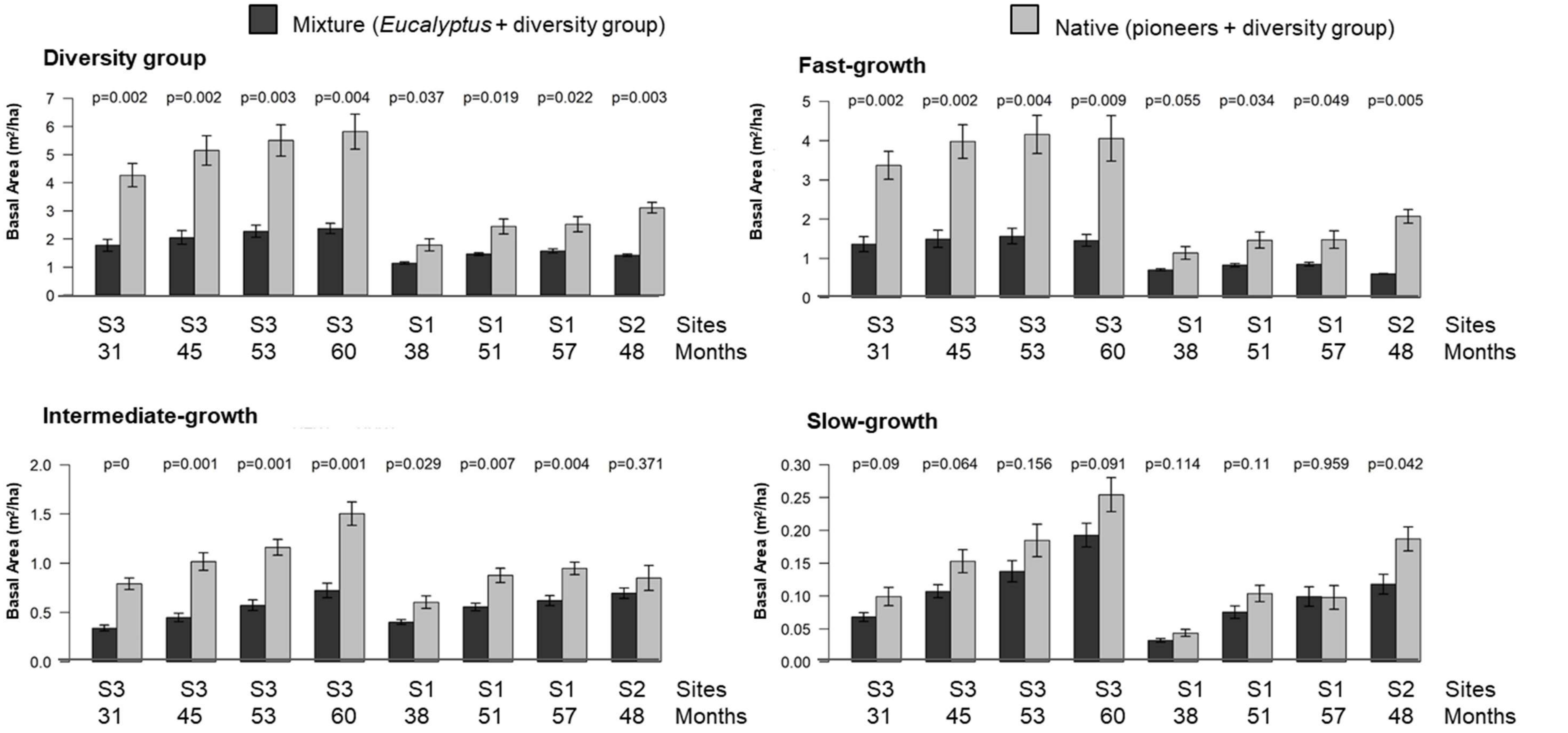
**APPENDIX E.** Diameter, height, basal area and survivorship of *Eucalyptus* in different experimental sites, treatments and ages. Sites are Aracruz (S1), Mucuri (S2), and Igrapiúna (S3). Age is shown in months below site label. Bars represent treatment averages across blocks with Standard Error. T test p-values are shown above bars.



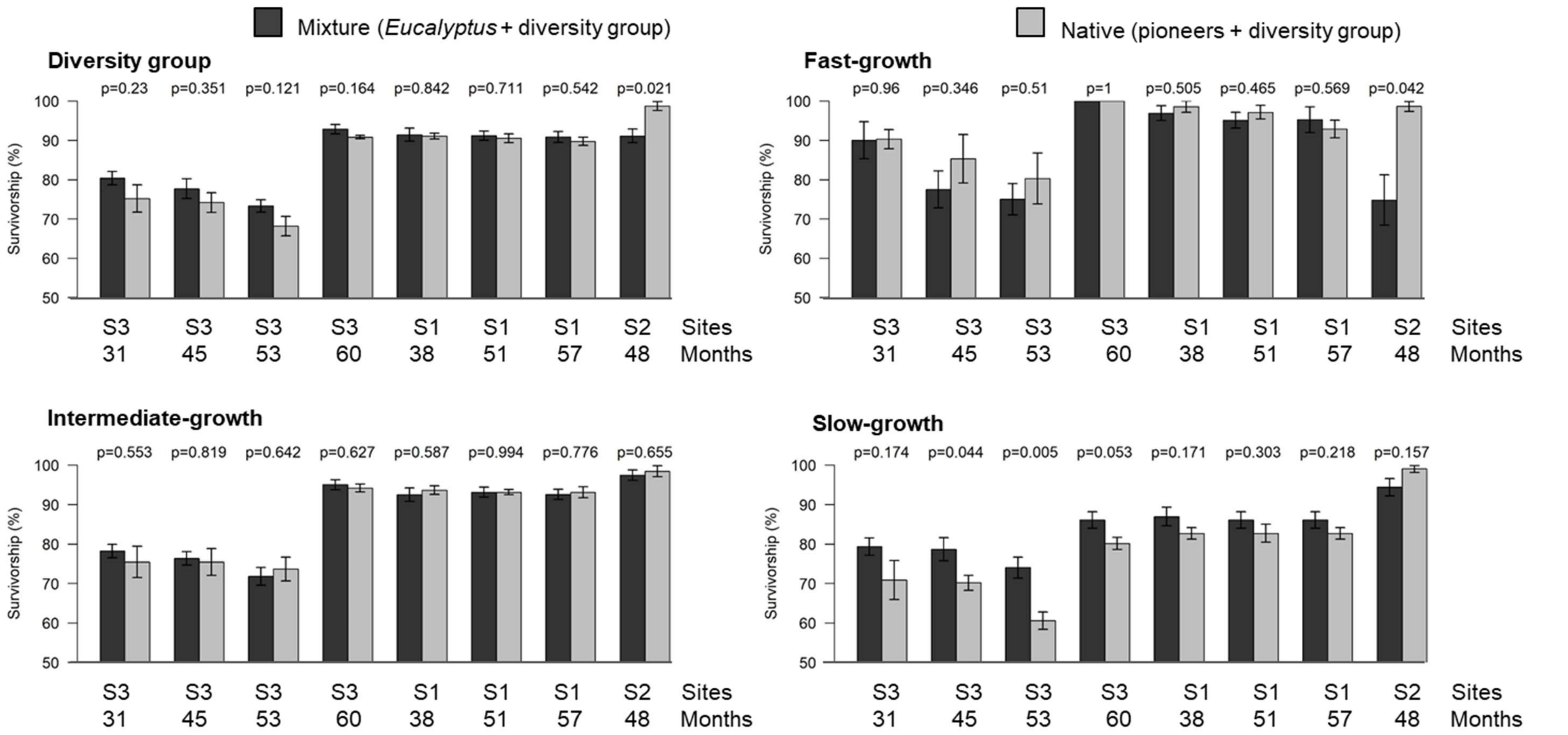
**APPENDIX F.** Diameter in different experimental sites, treatments and ages. All native species common to both treatments (Diversity group) are divided into Fast-, Intermediate- and Slow-growth. Sites are Aracruz (S1), Mucuri (S2), and Igrapiúna (S3). Age is shown in months below site label. Bars represent treatment averages across blocks with Standard Error. T test p-values are shown above bars.



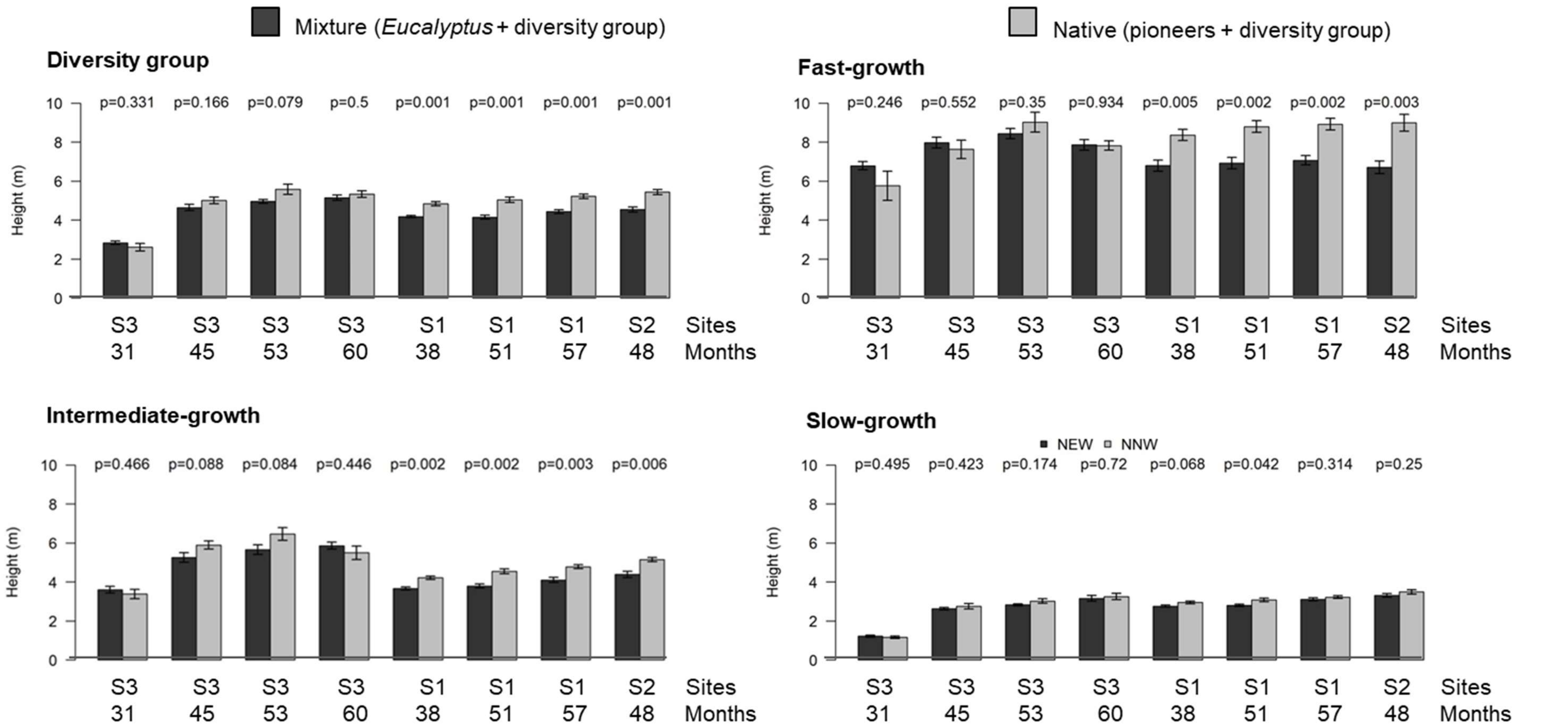
**APPENDIX G.** Basal area in different experimental sites, treatments and ages. All native species common to both treatments (Diversity group) are divided into Fast-, Intermediate- and Slow-growth. Sites are Aracruz (S1), Mucuri (S2), and Igrapiúna (S3). Age is shown in months below site label. Bars represent treatment averages across blocks with Standard Error. T test p-values are shown above bars.



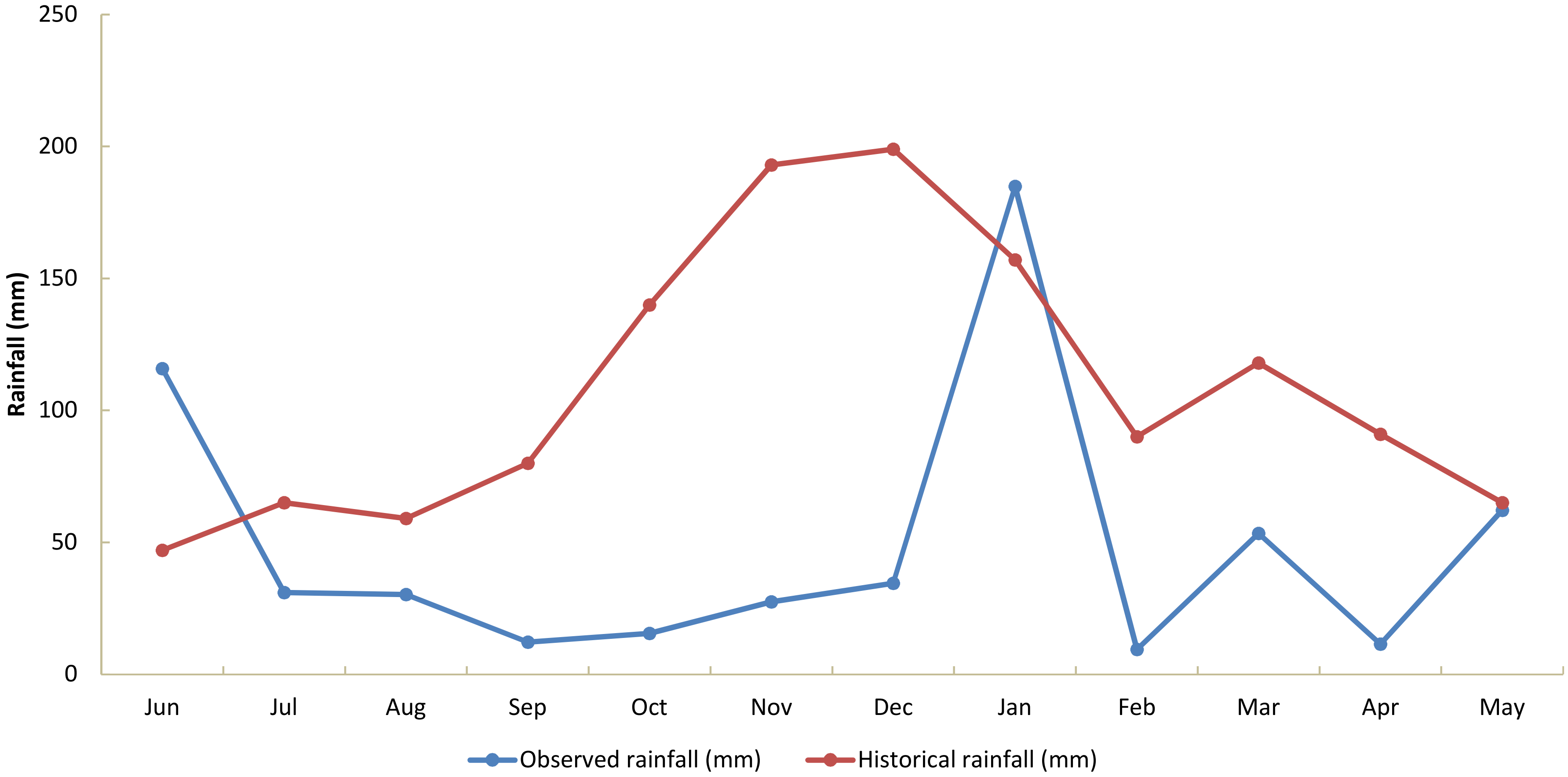
**APPENDIX H.** Survivorship of seedlings in different experimental sites, treatments and ages. All native species common to both treatments (Diversity group) are divided into Fast-, Intermediate- and Slow-growth. Sites are Aracruz (S1), Mucuri (S2), and Igrapiúna (S3). Age is shown in months below site label. Bars represent treatment averages across blocks with Standard Error. T test p-values are shown above bars.



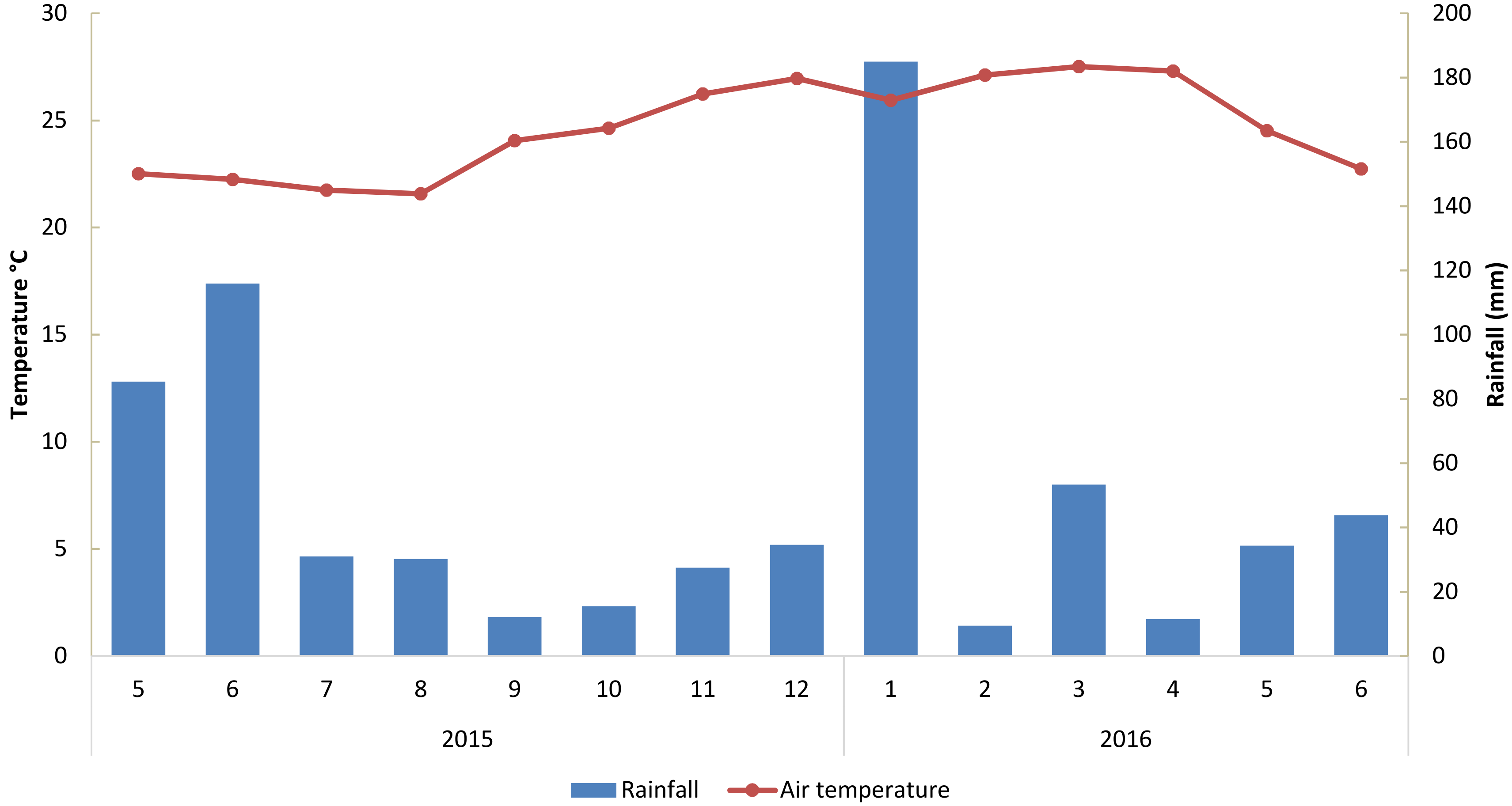
**APPENDIX I.** Tree height in different experimental sites, treatments and ages. All native species common to both treatments (Diversity group) are divided into Fast-, Intermediate- and Slow-growth. Sites are Aracruz (S1), Mucuri (S2), and Igrapiúna (S3). Age is shown in months below site label. Bars represent treatment averages across blocks with Standard Error. T test p-values are shown above bars.



**APPENDIX J.** Historical average versus observed monthly rainfall in Aracruz, ES, Brazil.



**APPENDIX K.** Monthly rainfall and air temperature in Aracruz, ES, Brazil. Data obtained from the seedling nursery meteorological station near the experimental site.



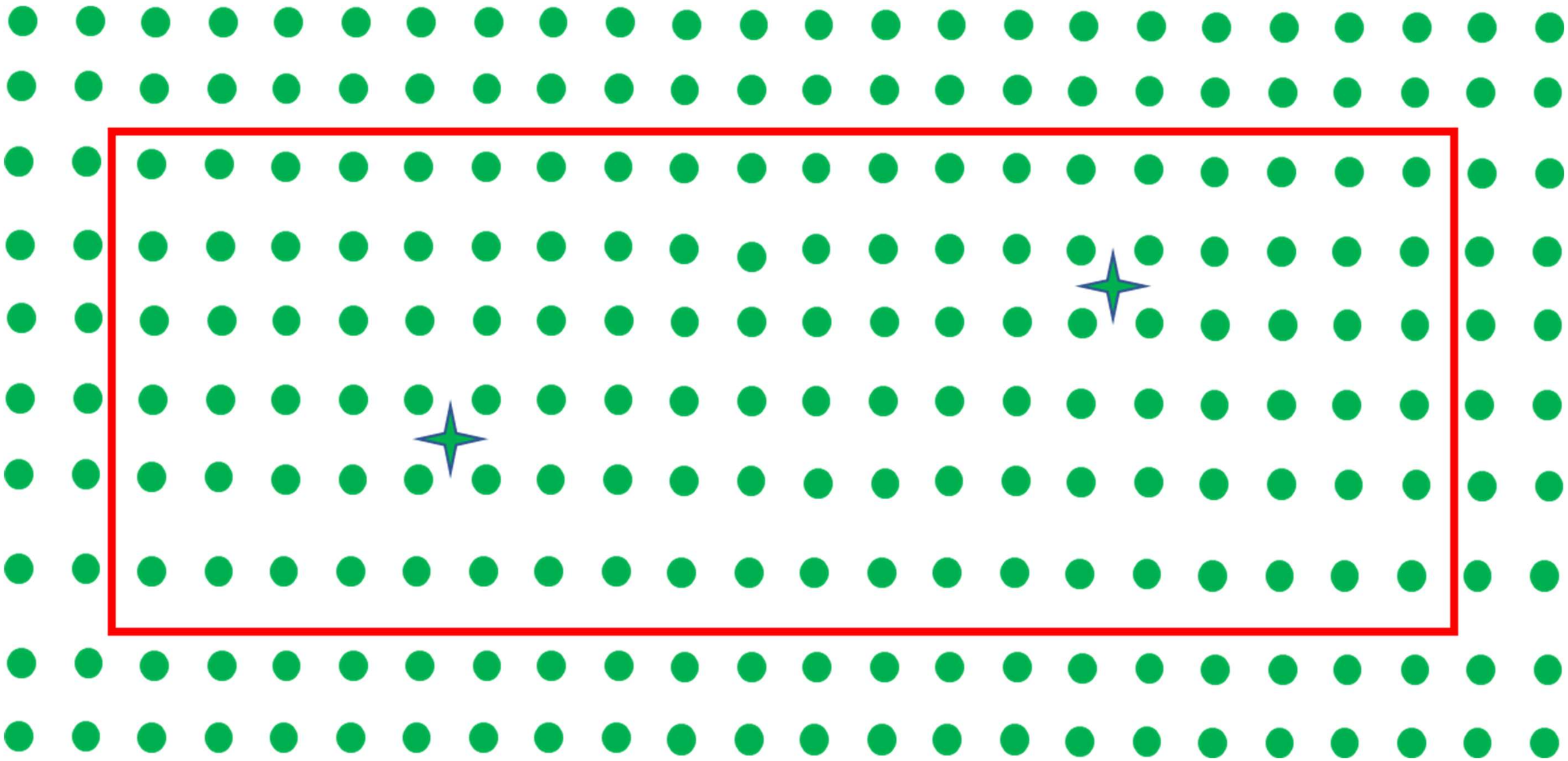
**APPENDIX L.** List of species used in each treatment in the experiment. EUC= *Eucalyptus* monoculture; MIX= Mixed plantation of *Eucalyptus* intercropped with native species; NAT= Native species intercropped with native pioneers. Common names are shown in Portuguese.

| Scientific name | Author | Family | Common name | Treatments |
|---|---|---|---|---|
| *Acnistus arborescens* | (L.) Schltdl. | Solanaceae | Fruto-de-sabia | NAT, MIX |
| *Aegiphila sellowiana* | Cham. | Lamiaceae | Mululo | NAT |
| *Anadenanthera peregrina* | (L.) Speg. | Fabaceae | Angico-curtidor | NAT, MIX |
| *Byrsonima spp.* | Rich. ex Kunth | Malpighiaceae | Murici | NAT, MIX |
| *Cariniana estrelensis* | (Raddi) Kuntze | Lecythidaceae | Jequitiba-branco | NAT, MIX |
| *Cariniana legalis* | (Mart.) Kuntze | Lecythidaceae | Jequitiba-rosa | NAT, MIX |
| *Cecropia hololeuca* | Miq. | Urticaceae | Embauba-branca | NAT, MIX |
| *Cedrela fissilis* | Vell. | Meliaceae | Cedro | NAT, MIX |
| *Citharexylum myrianthum* | Cham. | Verbenaceae | Pau-viola | NAT |
| *Cupania* sp. | L. | Sapindaceae | Camboata | NAT |
| *Dalbergia nigra* | (Vell.) Allemão ex Benth. | Fabaceae | Jacaranda-da-Bahia | NAT, MIX |
| *Enterolobium contortisiliquum* | (Vell.) Morong | Fabaceae | Tamboril | NAT |
| *Eucalyptus spp.* | | Myrtaceae | Eucalipto | EUC, MIX |
| *Eugenia uniflora* | L. | Myrtaceae | Pitanga | NAT, MIX |
| *Himatanthus articulates* | (Vahl) Woodson | Apocynaceae | Agoniada | NAT, MIX |

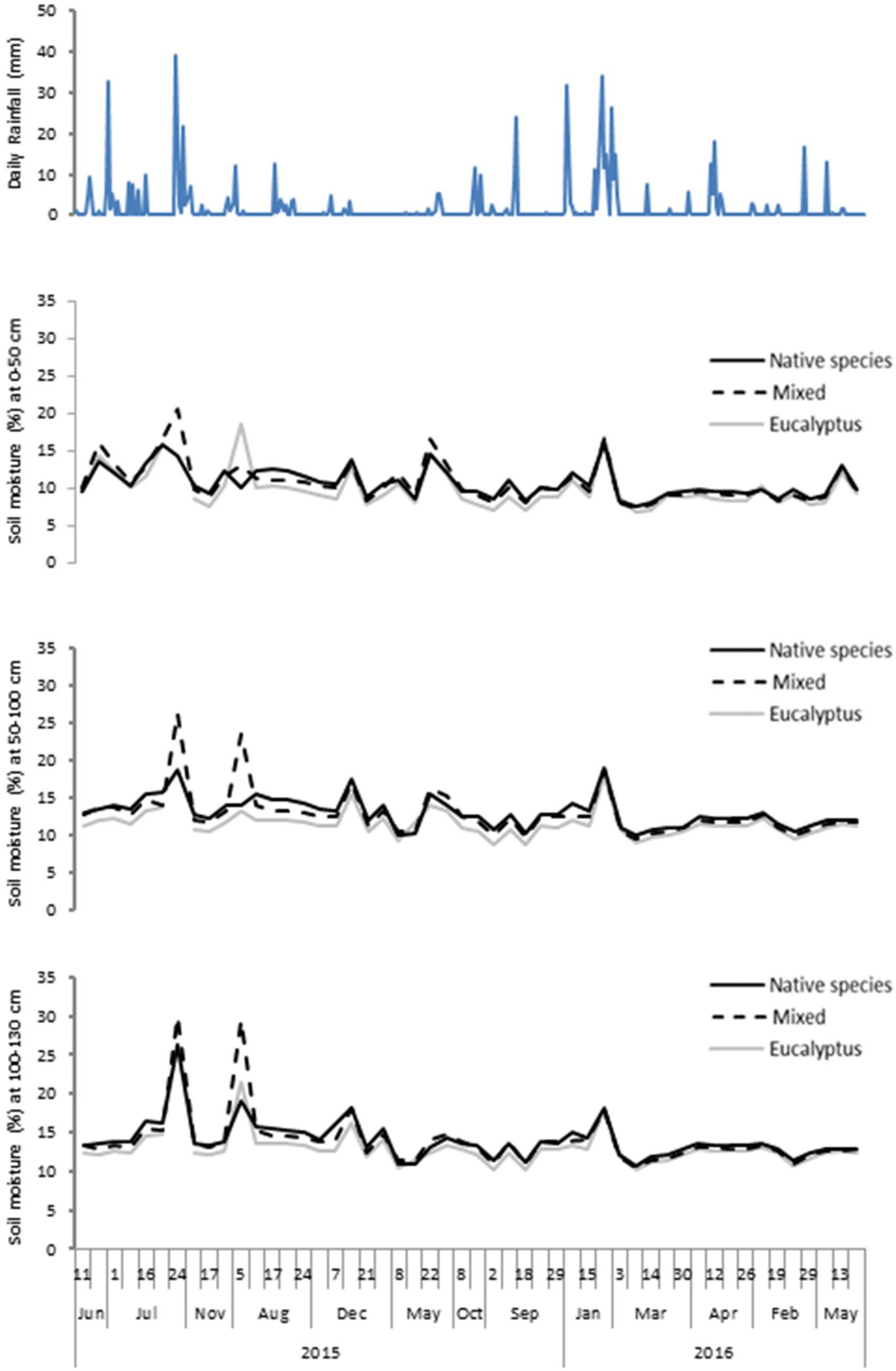
| Scientific name | Author | Family | Common name | Treatments |
|---|---|---|---|---|
| *Hymenaea courbaril* | L. | Fabaceae | Jatoba | NAT, MIX |
| *Inga edulis* | Mart. | Fabaceae | Inga-de-metro | NAT |
| *Inga laurina* | (Sw.) Willd. | Fabaceae | Inga | NAT |
| *Joannesia princeps* | Vell. | Euphorbiaceae | Boleira | NAT |
| *Lecythis Pisonis* | Cambess. | Lecythidaceae | Sapucaia | NAT, MIX |
| *Melanoxylon brauna* | Schott | Fabaceae | Brauna | NAT, MIX |
| *Mimosa artemisiana* | Heringer & Paula | Fabaceae | Angico-cangalha | NAT, MIX |
| *Myrocarpus frondosus* | Allemão | Fabaceae | Balsamo | NAT, MIX |
| *Newtonia spp.* | | Fabaceae | Angico-vermelho | NAT, MIX |
| *Paratecoma peroba* | (Record) Kuhlm. | Bignoniaceae | Peroba-amarela | NAT, MIX |
| *Parkia pendula* | (Willd.) Benth. ex Walp. | Fabaceae | Juerana-vermelha | NAT, MIX |
| *Paubrasilia echinata* | (Lam.) E. Gagnon, H.C. Lima & G.P. Lewis | Fabaceae | Pau-Brasil | NAT, MIX |
| *Peltophorum dubium* | (Spreng.) Taub. | Fabaceae | Angico-canjiquinha | NAT, MIX |
| *Plathymenia foliolosa* | Benth. | Fabaceae | Vinhatico | NAT, MIX |
| *Psidium* sp. | | Myrtaceae | Araca | NAT, MIX |

| Scientific name | Author | Family | Common name | Treatments |
| --- | --- | --- | --- | --- |
| *Pterocarpus rohrii* | Vahl | Fabaceae | Pau-sangue | NAT, MIX |
| *Pterogyne nitens* | Tul. | Fabaceae | Madeira-nova | NAT, MIX |
| *Schinus terenbitifolius* | Raddi | Anacardiaceae | Aroeira | NAT, MIX |
| *Senna macranthera* | (DC. ex Collad.) H.S.Irwin & Barneby | Fabaceae | Fedegoso | NAT |
| *Senna multijuga* | (Rich.) H.S.Irwin & Barneby | Fabaceae | Pau-cigarra | NAT, MIX |
| *Sparattosperma leucanthum* | (Vell.) K.Schum. | Bignoniaceae | Cinco-folhas | NAT |
| *Spondias spp.* | | Anacardiaceae | Caja-mirim | NAT, MIX |
| *Tabebuia heptaphylla* | (Vell.) Toledo | Bignoniaceae | Ipe-roxo | NAT, MIX |
| *Tapirira guianensis* | Aubl. | Anacardiaceae | Peito-de-pombo | NAT |
| *Trema micrantha* | (L.) Blume | Cannabaceae | Corindiba | NAT, MIX |
| *Zeyheria tuberculosa* | (Vell.) Bureau ex Verl. | Bignoniaceae | Ipe-felpudo | NAT, MIX |

**APPENDIX M.** Location of tubes (cross) for the measurement of soil volumetric water content within effective plots (red line).



**APPENDIX N.** Time course of soil water contents at different depths in each treatment. Data are presented from depth 0-130 cm.



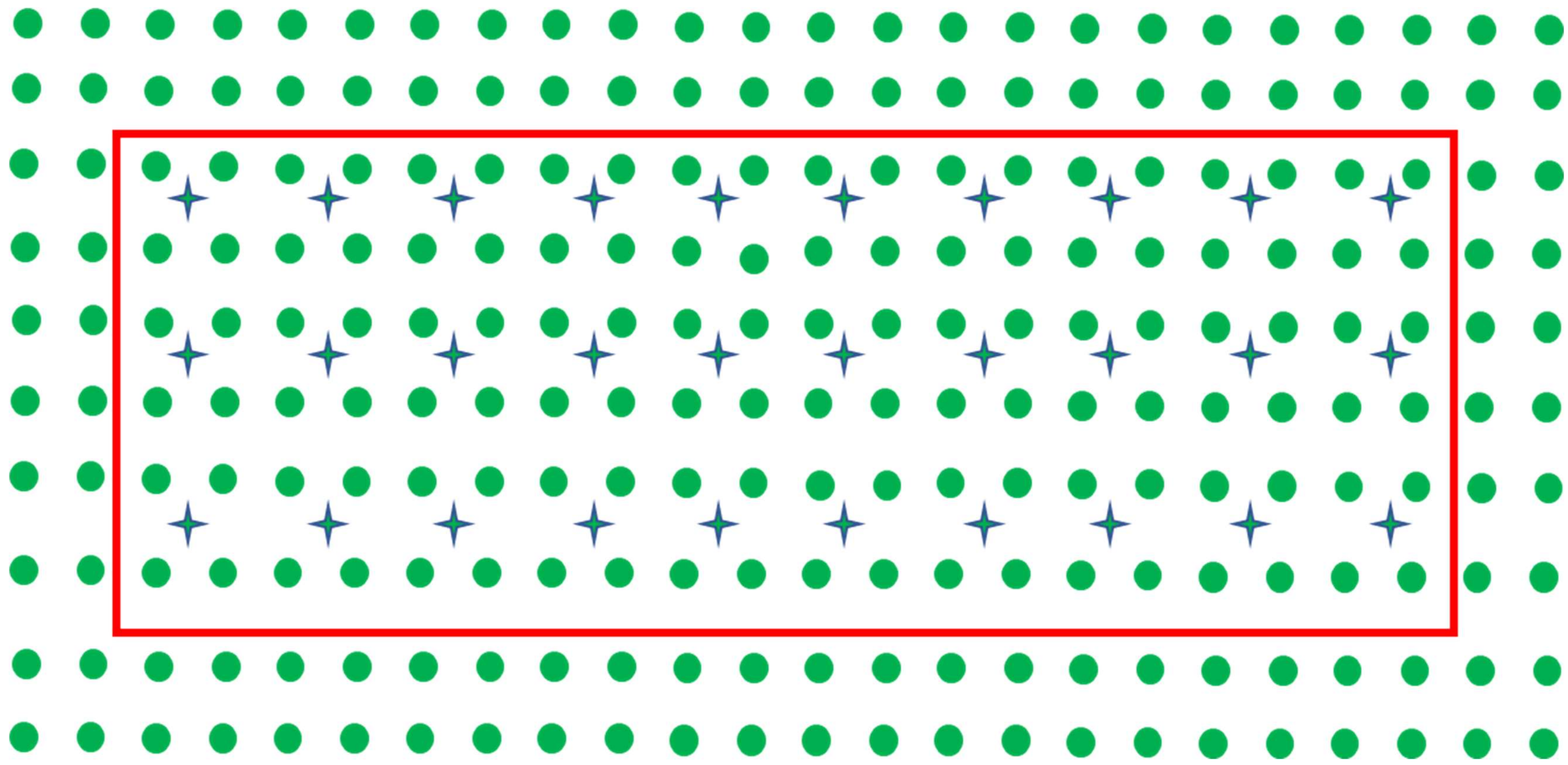
**APPENDIX O.** List of species planted in each experimental site. For each species, we list scientific names including authors, family, common names in Portuguese and the functional grouping. The groupings are: *Eucalyptus*; native pioneers; and native species of the diversity group, divided into fast-, intermediate- and slow-growing (Growth). Species used for nutrient analysis are indicated with an "x" (Nutrient). Biological nitrogen fixation capacity is indicated under "N-fixer" as fixers (yes), non-fixers (no). No information was found for some leguminous species (NA). References are provided for leguminous species under the column "Reference".

| Species | Author | Family | Common name | Growth | Nutrient | N-fixer | Reference |
|---|---|---|---|---|---|---|---|
| *Acnistus arborescens* | (L.) Schltdl. | Solanaceae | Fruto-de-sabiá | slow | | No | |
| *Aegiphila sellowiana* | Cham. | Lamiaceae | Mululo | pioneer | | No | |
| *Anadenanthera peregrina* | (L.) Speg. | Fabaceae | Angico-curtidor | fast | X | Yes | (Gross et al., 2002) |
| *Byrsonima* sp. | Rich. ex Kunth | Malpighiaceae | Murici | slow | | No | |
| *Cariniana estrellensis* | (Raddi) Kuntze | Lecythidaceae | Jequitibá-branco | slow | | No | |
| *Cariniana legalis* | (Mart.) Kuntze | Lecythidaceae | Jequitibá-rosa | slow | | No | |
| *Cecropia hololeuca* | Miq. | Urticaceae | Embaúba-branca | interm | | No | |
| *Cedrela fissilis* | Vell. | Meliaceae | Cedro | interm | | No | |
| *Citharexylum myrianthum* | Cham. | Verbenaceae | Pau-viola | pioneer | | No | |
| *Cupania* sp. | L. | Sapindaceae | Camboatã | pioneer | | No | |
| *Dalbergia nigra* | (Vell.) Allemão ex Benth. | Fabaceae | Jacarandá-da-Bahia | Interm | X | Yes | (Canosa et al., 2012) |
| *Enterolobium contortisiliquum* | (Vell.) Morong | Fabaceae | Tamboril | pioneer | | Yes | (Canosa et al., 2012) |
| *Eucalyptus spp.* | | Myrtaceae | Eucalipto | *Eucalyptus* | X | No | |
| *Eugenia uniflora* | L. | Myrtaceae | Pitanga | slow | | No | |
| *Himatanthus articulatus* | (Vahl) Woodson | Apocynaceae | Agoniada | interm | | No | |

| Species | Author | Family | Common name | Growth | Nutrient | N-fixer | Reference |
|---|---|---|---|---|---|---|---|
| *Hymenaea courbaril* | L. | Fabaceae | Jatobá | slow | X | No | (de Souza Moreira et al., 1992) |
| *Inga edulis* | Mart. | Fabaceae | Ingá-de-metro | pioneer | X | Yes | (Canosa et al., 2012) |
| *Inga laurina* | (Sw.) Willd. | Fabaceae | Ingá | pioneer | X | Yes | (Canosa et al., 2012) |
| *Joannesia princeps* | Vell. | Euphorbiaceae | Boleira | pioneer | X | No | |
| *Lecythis pisonis* | Cambess. | Lecythidaceae | Sapucaia | slow | | No | |
| *Melanoxylon brauna* | Schott | Fabaceae | Braúna | slow | | Yes | (Sprent e Parsons, 2000) |
| *Mimosa artemisiana* | Heringer & Paula | Fabaceae | Angico-cangalha | fast | X | Yes | (Canosa et al., 2012) |
| *Myrocarpus frondosus* | Allemão | Fabaceae | Bálsamo | slow | X | Yes | (Canosa et al., 2012) |
| *Newtonia* sp. | | Fabaceae | Angico-vermelho | interm | | Yes | (Sprent e Parsons, 2000) |
| *Paratecoma peroba* | (Record) Kuhlm. | Bignoniaceae | Peroba-amarela | slow | | No | |
| *Parkia pendula* | (Willd.) Benth. ex Walp. | Fabaceae | Juerana-vermelha | Interm | | No | (de Souza Moreira et al., 1992) |
| *Paubrasilia echinata* | (Lam.) E. Gagnon, H.C. Lima & G.P. Lewis | Fabaceae | Pau-Brasil | slow | X | NA | |
| *Peltophorum dubium* | (Spreng.) Taub. | Fabaceae | Angico-canjiquinha | interm | X | NA | |
| *Plathymenia foliolosa* | Benth. | Fabaceae | Vinhático | fast | X | Yes | (Souza, 2010) |

| Species | Author | Family | Common name | Growth | Nutrient | N-fixer | Reference |
|---|---|---|---|---|---|---|---|
| *Psidium* sp. | | Myrtaceae | Araçá | slow | | No | |
| *Pterocarpus rohrii* | Vahl | Fabaceae | Pau-sangue | slow | | NA | |
| *Pterogyne nitens* | Tul. | Fabaceae | Madeira-nova | slow | X | No | (de FARIA et al., 1984) |
| *Schinus terenbitifolius* | Raddi | Anacardiaceae | Aroeira | interm | X | No | |
| *Senna macranthera* | (DC. ex Collad.) H.S.Irwin & Barneby | Fabaceae | Fedegoso | Pioneer | X | No | (Barberi et al., 1998) |
| *Senna multijuga* | (Rich.) H.S.Irwin & Barneby | Fabaceae | Pau-cigarra | Fast | X | No | (de Faria et al., 1987) |
| *Sparattosperma leucanthum* | (Vell.) K.Schum. | Bignoniaceae | Cinco-folhas | pioneer | X | No | |
| *Spondias* sp. | | Anacardiaceae | Cajá-mirim | interm | | No | |
| *Tabebuia heptaphylla* | (Vell.) Toledo | Bignoniaceae | Ipê-roxo | slow | X | No | |
| *Tapirira guianensis* | Aubl. | Anacardiaceae | Peito-de-pombo | pioneer | X | No | |
| *Trema micrantha* | (L.) Blume | Cannabaceae | Corindiba | fast | | No | |
| *Zeyheria tuberculosa* | (Vell.) Bureau ex Verl. | Bignoniaceae | Ipê-felpudo | interm | | No | |

**APPENDIX P.** Location of measurement points (cross) for the assessment of Photosynthetically Active Radiation within effective plots (red line).



**APPENDIX Q.** Mean nutrient concentration in leaves of trees planted in mixed plantations of 30 native tree species of the diversity group intercropped with 10 native pioneers (NAT), mixed plantations intercropping 30 native tree species of the diversity group and *Eucalyptus* (MIX), and monocultural plantations of *Eucalyptus* (EUC) in the Atlantic Forest of Southeastern Brazil. Species grouping is indicated under "Group" using EU for *Eucalyptus*, DG for diversity group and NP for native pioneers.

| Species | Group | Treat. | DBH | N (g/kg) | P (g/kg) | K (g/kg) | Ca (g/kg) | Mg (g/kg) | S (g/kg) | Na (mg/kg) | Mn (mg/kg) | Fe (mg/kg) | B (mg/kg) | Cu (mg/kg) | Mo (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eucalyptus spp.* | EU | EUC | 13.83 | 17.97 | 1.07 | 6.39 | 8.19 | 3.47 | 1.74 | 1516.22 | 142.82 | 100.02 | 53.63 | 0.97 | 0.17 |
| | EU | MIX | 17.57 | 19.18 | 1.12 | 6.52 | 7.30 | 3.14 | 1.74 | 1301.05 | 123.10 | 81.32 | 49.48 | 0.87 | 0.20 |
| *Mimosa artemisiana* | DG | MIX | 15.96 | 39.62 | 1.72 | 7.98 | 9.68 | 2.93 | 3.54 | 1020.63 | 107.09 | 118.88 | 30.22 | 1.80 | 0.11 |
| | DG | NAT | 23.98 | 34.67 | 1.50 | 6.73 | 8.71 | 2.60 | 3.08 | 232.53 | 79.91 | 92.51 | 38.36 | 1.14 | 0.06 |
| *Peltophorum dubium* | DG | MIX | 9.32 | 24.62 | 1.06 | 8.25 | 8.01 | 2.15 | 3.54 | 163.35 | 77.85 | 125.51 | 35.34 | 1.70 | 0.21 |
| | DG | NAT | 10.86 | 23.29 | 1.00 | 6.81 | 8.98 | 1.89 | 3.37 | 101.84 | 59.91 | 79.43 | 38.89 | 1.84 | 0.00 |
| *Anadenanthera peregrina* | DG | MIX | 6.51 | 27.00 | 0.97 | 6.40 | 15.03 | 3.37 | 2.94 | 1344.60 | 339.50 | 241.55 | 52.22 | 1.10 | 0.20 |
| | DG | NAT | 4.40 | 26.06 | 0.96 | 7.71 | 9.87 | 2.31 | 2.72 | 658.24 | 206.06 | 140.14 | 47.85 | 0.67 | 0.25 |
| *Schinus terenbitifolius* | DG | MIX | 5.90 | 18.50 | 1.23 | 11.99 | 15.71 | 3.34 | 2.28 | 2493.38 | 55.52 | 144.27 | 22.92 | 2.03 | 0.13 |
| | DG | NAT | 10.04 | 18.29 | 1.30 | 13.31 | 15.61 | 3.51 | 2.85 | 2015.12 | 51.70 | 108.61 | 31.76 | 3.22 | 0.34 |
| *Myrocarpus frondosus* | DG | MIX | 2.27 | 25.36 | 1.51 | 11.40 | 15.43 | 2.53 | 2.42 | 554.78 | 27.53 | 84.63 | 69.76 | 1.32 | 0.14 |
| | DG | NAT | 2.76 | 24.34 | 1.38 | 10.80 | 16.11 | 2.84 | 2.11 | 411.38 | 25.85 | 81.74 | 76.65 | 0.99 | 0.11 |
| *Tabebuia heptaphylla* | DG | MIX | 3.44 | 22.17 | 0.92 | 7.77 | 17.10 | 2.65 | 1.78 | 642.13 | 40.15 | 141.22 | 78.81 | 2.41 | 0.06 |
| | DG | NAT | 4.06 | 23.87 | 1.17 | 10.76 | 18.01 | 3.59 | 1.92 | 498.78 | 52.65 | 244.23 | 103.70 | 2.14 | 0.09 |
| *Dalbergia nigra* | DG | MIX | 8.09 | 25.78 | 0.77 | 4.04 | 7.53 | 3.08 | 1.93 | 576.43 | 130.00 | 147.24 | 105.72 | 0.96 | 0.00 |
| | DG | NAT | 11.08 | 24.57 | 0.86 | 4.24 | 5.34 | 2.83 | 2.07 | 203.21 | 64.51 | 103.75 | 85.52 | 0.49 | 0.16 |
| *Hymenaea courbaril* | DG | MIX | 3.46 | 19.16 | 1.10 | 8.26 | 9.13 | 2.23 | 2.52 | 431.14 | 181.82 | 93.28 | 27.14 | 2.57 | 0.11 |
| | DG | NAT | 3.34 | 20.98 | 1.23 | 10.00 | 8.94 | 3.14 | 2.07 | 296.78 | 108.73 | 118.93 | 33.46 | 2.56 | 0.24 |
| *Pterogyne nitens* | DG | MIX | 4.32 | 25.01 | 1.16 | 8.99 | 15.19 | 1.88 | 1.53 | 116.70 | 22.39 | 135.14 | 71.09 | 1.30 | 0.08 |

| Species | Group | Treat. | DBH | N (g/kg) | P (g/kg) | K (g/kg) | Ca (g/kg) | Mg (g/kg) | S (g/kg) | Na (mg/kg) | Mn (mg/kg) | Fe (mg/kg) | B (mg/kg) | Cu (mg/kg) | Mo (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DG | NAT | 2.54 | 27.91 | 1.31 | 10.52 | 14.47 | 1.58 | 1.79 | 129.94 | 26.95 | 130.32 | 82.51 | 2.06 | 0.31 |
| *Paubrasilia echinata* | DG | MIX | 2.75 | 19.90 | 1.10 | 10.65 | 8.66 | 1.19 | 2.84 | 826.83 | 16.41 | 80.18 | 17.64 | 1.17 | 0.23 |
| | DG | NAT | 3.55 | 19.74 | 1.10 | 10.86 | 13.02 | 1.60 | 3.20 | 681.95 | 28.26 | 89.78 | 21.99 | 1.93 | 0.11 |
| *Senna multijuga* | DG | MIX | 15.85 | 19.39 | 0.85 | 7.45 | 17.10 | 2.13 | 2.55 | 948.98 | 35.37 | 133.96 | 55.67 | 0.96 | 0.00 |
| | DG | NAT | 17.84 | 22.42 | 0.91 | 8.28 | 15.51 | 2.24 | 2.56 | 383.39 | 33.59 | 115.39 | 51.15 | 0.92 | 0.08 |
| *Plathymenia foliolosa* | DG | MIX | 11.21 | 29.49 | 1.13 | 5.80 | 2.64 | 1.51 | 2.37 | 393.74 | 56.26 | 144.18 | 64.02 | 1.46 | 0.00 |
| | DG | NAT | 11.46 | 24.66 | 0.77 | 4.96 | 4.75 | 2.07 | 2.08 | 130.40 | 51.13 | 100.51 | 71.04 | 1.15 | 0.24 |
| *Tapirira guianensis* | NP | NAT | 10.38 | 18.55 | 0.88 | 5.69 | 13.91 | 3.23 | 2.77 | 422.62 | 37.41 | 90.76 | 34.02 | 0.91 | 0.24 |
| *Joannesia princeps* | NP | NAT | 17.43 | 24.48 | 1.20 | 7.11 | 8.60 | 3.26 | 1.56 | 996.14 | 52.98 | 104.27 | 41.05 | 2.11 | 0.15 |
| *Sparattosperma leucanthum* | NP | NAT | 6.90 | 19.60 | 1.01 | 12.31 | 10.05 | 3.21 | 2.48 | 517.56 | 159.88 | 98.31 | 50.04 | 3.04 | 0.46 |
| *Senna macranthera* | NP | NAT | 18.15 | 25.29 | 1.07 | 8.00 | 19.48 | 1.66 | 5.30 | 548.46 | 85.22 | 164.88 | 55.97 | 1.89 | 0.15 |
| *Inga* spp. | NP | NAT | 15.24 | 28.47 | 1.35 | 5.74 | 9.71 | 2.16 | 2.66 | 305.05 | 89.57 | 126.77 | 26.31 | 2.37 | 0.02 |

**APPENDIX R.** Mean nutrient concentration in the wood of trees planted in mixed plantations of 30 native tree species of the diversity group intercropped with 10 native pioneers (NAT), mixed plantations intercropping 30 native tree species of the diversity group and *Eucalyptus* (MIX), and monocultural plantations of *Eucalyptus* (EUC) in the Atlantic Forest of Southeastern Brazil. Species grouping is indicated under “Group” using EU for *Eucalyptus*, DG for diversity group and NP for native pioneers.

| species | Group | Treat. | DBH | N (g/kg) | P (g/kg) | K (g/kg) | Ca (g/kg) | Mg (g/kg) | S (g/kg) | Na (mg/kg) | Mn (mg/kg) | Fe (mg/kg) | B (mg/kg) | Cu (mg/kg) | Mo (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eucalyptus spp.* | EU | EUC | 13.83 | 2.12 | 0.07 | 1.08 | 0.70 | 0.14 | 0.01 | 239.13 | 3.17 | 9.71 | 3.91 | 0.30 | 0.00 |
| | EU | MIX | 17.57 | 2.78 | 0.07 | 1.03 | 0.96 | 0.15 | 0.00 | 244.51 | 2.78 | 12.88 | 4.02 | 0.17 | 0.01 |
| *Mimosa artemisiana* | DG | MIX | 15.96 | 3.59 | 0.29 | 2.74 | 2.08 | 0.55 | 0.85 | 24.77 | 7.49 | 15.29 | 3.70 | 0.66 | 0.05 |
| | DG | NAT | 23.98 | 2.99 | 0.16 | 2.24 | 2.22 | 0.43 | 0.86 | 31.89 | 3.22 | 12.70 | 3.89 | 0.45 | 0.00 |
| *Peltophorum dubium* | DG | MIX | 9.32 | 5.62 | 0.25 | 2.90 | 2.84 | 1.01 | 1.49 | 45.92 | 4.68 | 14.54 | 3.62 | 0.74 | 0.03 |
| | DG | NAT | 10.86 | 4.53 | 0.24 | 2.15 | 3.06 | 1.16 | 1.61 | 259.52 | 4.46 | 21.96 | 4.08 | 1.24 | 0.01 |
| *Anadenanthera peregrina* | DG | MIX | 6.51 | 2.82 | 0.31 | 1.64 | 1.94 | 0.15 | 0.40 | 50.83 | 11.06 | 13.23 | 3.98 | 0.66 | 0.70 |
| | DG | NAT | 4.40 | 2.47 | 0.26 | 1.60 | 1.25 | 0.15 | 0.31 | 95.76 | 9.00 | 9.83 | 4.17 | 0.72 | 0.29 |
| *Schinus terenbitifolius* | DG | MIX | 5.90 | 2.47 | 0.26 | 2.85 | 2.12 | 0.63 | 0.59 | 143.16 | 3.10 | 19.81 | 4.74 | 0.70 | 0.04 |
| | DG | NAT | 10.04 | 2.05 | 0.23 | 3.34 | 2.02 | 0.64 | 0.56 | 82.02 | 1.89 | 19.23 | 4.24 | 0.59 | 0.00 |
| *Myrocarpus frondosus* | DG | MIX | 2.27 | 3.15 | 0.23 | 2.06 | 2.58 | 0.27 | 0.19 | 82.83 | 2.39 | 11.05 | 5.19 | 1.06 | 0.00 |
| | DG | NAT | 2.76 | 3.17 | 0.25 | 2.26 | 2.64 | 0.26 | 0.24 | 33.26 | 1.93 | 12.72 | 5.31 | 0.86 | 0.05 |
| *Tabebuia heptaphylla* | DG | MIX | 3.44 | 3.76 | 0.39 | 1.61 | 1.55 | 0.42 | 0.47 | 34.94 | 2.95 | 15.00 | 3.97 | 1.67 | 0.22 |
| | DG | NAT | 4.06 | 3.48 | 0.35 | 2.65 | 2.04 | 0.40 | 0.49 | 78.39 | 2.58 | 14.85 | 4.14 | 0.95 | 0.37 |
| *Dalbergia nigra* | DG | MIX | 8.09 | 4.15 | 0.41 | 2.23 | 1.73 | 0.81 | 0.62 | 289.58 | 8.09 | 12.93 | 6.43 | 0.55 | 0.13 |
| | DG | NAT | 11.08 | 3.52 | 0.26 | 2.34 | 1.07 | 0.58 | 0.61 | 29.77 | 4.46 | 25.92 | 5.62 | 0.53 | 0.02 |
| *Hymenaea courbaril* | DG | MIX | 3.46 | 3.94 | 0.73 | 2.61 | 2.10 | 0.46 | 0.31 | 123.91 | 10.00 | 15.99 | 3.92 | 0.97 | 0.02 |
| | DG | NAT | 3.34 | 2.87 | 0.17 | 1.16 | 1.29 | 0.25 | 0.03 | 50.09 | 6.39 | 23.02 | 3.22 | 0.83 | 0.00 |
| *Pterogyne nitens* | DG | MIX | 4.32 | 4.32 | 0.43 | 1.75 | 3.16 | 0.27 | 0.03 | 21.51 | 1.09 | 13.95 | 4.05 | 0.97 | 0.03 |

| species | Group | Treat. | DBH | N (g/kg) | P (g/kg) | K (g/kg) | Ca (g/kg) | Mg (g/kg) | S (g/kg) | Na (mg/kg) | Mn (mg/kg) | Fe (mg/kg) | B (mg/kg) | Cu (mg/kg) | Mo (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DG | NAT | 2.54 | 4.15 | 0.59 | 1.65 | 3.48 | 0.29 | 0.08 | 58.26 | 0.78 | 15.53 | 4.05 | 1.10 | 0.06 |
| *Paubrasilia echinata* | DG | MIX | 2.75 | 3.36 | 0.21 | 1.35 | 4.21 | 0.11 | 0.14 | 162.85 | 1.90 | 16.50 | 3.96 | 0.89 | 0.11 |
| | DG | NAT | 3.55 | 2.54 | 0.23 | 1.32 | 3.87 | 0.14 | 0.20 | 212.70 | 2.89 | 45.34 | 4.02 | 1.13 | 0.14 |
| *Senna multijuga* | DG | MIX | 15.85 | 3.66 | 0.34 | 2.04 | 2.94 | 0.40 | 0.06 | 109.07 | 2.06 | 9.37 | 4.11 | 0.65 | 0.00 |
| | DG | NAT | 17.84 | 3.10 | 0.29 | 2.21 | 2.26 | 0.25 | 0.06 | 68.66 | 1.70 | 10.00 | 3.48 | 0.55 | 0.00 |
| *Plathymenia foliolosa* | DG | MIX | 11.21 | 3.85 | 0.25 | 1.99 | 2.19 | 0.27 | 0.22 | 61.22 | 7.88 | 24.80 | 3.94 | 0.72 | 0.00 |
| | DG | NAT | 11.46 | 3.73 | 0.32 | 1.82 | 2.86 | 0.29 | 0.33 | 155.30 | 5.81 | 31.76 | 4.57 | 0.53 | 0.00 |
| *Joannesia princeps* | NP | NAT | 17.43 | 3.34 | 0.52 | 5.38 | 7.02 | 0.51 | 0.40 | 450.06 | 38.07 | 24.76 | 4.37 | 1.12 | 0.51 |
| *Sparattosperma leucanthum* | NP | NAT | 6.90 | 2.99 | 0.38 | 4.59 | 1.41 | 0.53 | 0.47 | 152.57 | 7.70 | 14.44 | 3.70 | 1.32 | 0.07 |
| *Senna macranthera* | NP | NAT | 18.15 | 2.50 | 0.30 | 1.54 | 1.27 | 0.39 | 0.15 | 50.57 | 3.29 | 14.94 | 4.49 | 1.37 | 0.00 |
| *Inga* spp. | NP | NAT | 15.24 | 3.47 | 0.39 | 2.83 | 2.05 | 0.35 | 0.23 | 54.21 | 5.74 | 23.52 | 3.78 | 0.89 | 0.26 |
| *Tapirira guianensis* | NP | NAT | 10.38 | 2.38 | 0.27 | 1.90 | 1.66 | 0.44 | 0.08 | 135.84 | 3.29 | 16.91 | 4.31 | 0.57 | 0.00 |

**APPENDIX S.** Species means and Community-Weighed Means of macronutrients in wood of trees planted in mixed plantations of 30 native tree species of the diversity group intercropped with 10 native pioneers (NAT), mixed plantations intercropping 30 native tree species of the diversity group and *Eucalyptus* (MIX), and monocultural plantations of *Eucalyptus* (EUC) in the Atlantic Forest of Southeastern Brazil.

| Treatment | **NAT** | | | | | | **MIX** | | | | | | **EUC** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group | *Diversity group* | | | | | | *Diversity group* | | | | | | - | | | | | |
| Means | Species Mean | | | CWM | | | Species Mean | | | CWM | | | | | | | | |
| Nutrient | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | | | | | | |
| N | 3.22 | 3.09 | 3.36 | 1.17 | 1.14 | 1.20 | 3.73 | 3.54 | 3.93 | 0.75 | 0.70 | 0.84 | | | | | | |
| P | 0.28 | 0.27 | 0.30 | 0.10 | 0.09 | 0.11 | 0.34 | 0.31 | 0.36 | 0.07 | 0.06 | 0.08 | | | | | | |
| K | 2.06 | 1.88 | 2.32 | 0.75 | 0.63 | 0.86 | 2.15 | 1.94 | 2.28 | 0.43 | 0.38 | 0.49 | | | | | | |
| Mg | 0.40 | 0.37 | 0.43 | 0.15 | 0.14 | 0.15 | 0.45 | 0.41 | 0.50 | 0.09 | 0.08 | 0.11 | | | | | | |
| Ca | 2.34 | 2.01 | 2.67 | 0.85 | 0.78 | 0.99 | 2.45 | 2.24 | 2.62 | 0.49 | 0.43 | 0.56 | | | | | | |
| S | 0.31 | 0.16 | 0.51 | 0.15 | 0.10 | 0.19 | 0.28 | 0.00 | 0.43 | 0.05 | 0.00 | 0.08 | | | | | | |
| Group | *Pioneers* | | | | | | *Eucalyptus* | | | | | | *Eucalyptus* | | | | | |
| Means | Species Mean | | | CWM | | | Species Mean | | | CWM | | | Species Mean | | | CWM | | |
| Nutrient | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| N | 3.02 | 2.85 | 3.16 | 1.92 | 1.79 | 2.02 | 2.78 | 2.38 | 3.01 | 2.22 | 1.87 | 2.42 | 2.12 | 2.03 | 2.24 | 2.12 | 2.03 | 2.24 |
| P | 0.37 | 0.34 | 0.42 | 0.24 | 0.22 | 0.26 | 0.07 | 0.05 | 0.08 | 0.06 | 0.04 | 0.06 | 0.07 | 0.06 | 0.09 | 0.07 | 0.06 | 0.09 |
| K | 3.18 | 2.93 | 3.35 | 2.02 | 1.80 | 2.22 | 1.03 | 0.88 | 1.15 | 0.82 | 0.69 | 0.92 | 1.08 | 0.89 | 1.19 | 1.08 | 0.89 | 1.19 |
| Mg | 0.43 | 0.38 | 0.46 | 0.27 | 0.25 | 0.29 | 0.15 | 0.14 | 0.17 | 0.12 | 0.11 | 0.13 | 0.14 | 0.13 | 0.15 | 0.14 | 0.13 | 0.15 |
| Ca | 2.58 | 1.78 | 3.25 | 1.63 | 1.18 | 2.05 | 0.96 | 0.86 | 1.17 | 0.77 | 0.68 | 0.94 | 0.70 | 0.66 | 0.74 | 0.70 | 0.66 | 0.74 |
| S | 0.40 | 0.35 | 0.45 | 0.18 | 0.15 | 0.23 | 0.16 | 0.00 | 0.49 | 0.04 | 0.00 | 0.11 | 0.01 | 0.00 | 0.02 | 0.01 | 0.00 | 0.02 |