Combining the light-demanding *Araucaria angustifolia* with the shade-tolerant *Cabralea canjerana:* mixed plantations to produce tropical timber trees outside the Atlantic rainforest

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Abstract

Many trees of high timber value require canopy cover to become established and at present, they are only harvested from native rainforests. Other species require high radiation to establish and can be planted in monospecific stands. The main question was if the canopy generated by a light demanding rainforest species could protect mid-successional timber species from high radiation and extreme temperatures. We evaluated the establishment of *Cabralea canjerana* under the canopy of *Araucaria angustifolia* stands. We related growth with the number of neighbors to determine the better positions to plant *C. canjerana*. In one stand, we measured environmental and physiological traits and we determined that seedling did not suffer light or water stress. *C. canjerana* plants establishment was successful in stands of different basal areas and trees reached the highest growth with up to two *A. angustifolia* neighbors within a 5m radius. Therefore, the number of neighbors is a tool to choose the planting location to convert even-aged to uneven-aged mixed stands. In this way, valuable native timber species that requires canopy protection during the first years can be planted outside the rainforest. This is the first report of an uneven-aged mixed plantation of two Atlantic Forest timber species.

Keywords: Mixed stand; Competition index; Atlantic forests; Plant physiology; tropical timber species

Declarations

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Conflicts of interest

The authors declare that there is no conflict of interest regarding the publication of this manuscript.

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Authors’ contributions

Corina Graciano, Juan F. Goya, Martín A. Pinazo did the conceptualization and methodology. Flavia Yesica Olguin, Ana Paula Moretti, Martín Alcides Pinazo, Fermín Gortari, José Vera Bahima, Corina Graciano did field measurement, data acquisition, and data analysis. Flavia Y. Olguin and Corina Graciano performed data curation and formal analysis. Flavia Y. Olguin, Corina Graciano: wrote the original draft. All authors contributed to the writing and editing of the paper. Corina Graciano was responsible for funding acquisition, project administration, and resources.

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1 Introduction

The demand for timber products is growing internationally, as well as the need for forest restoration and silvicultural systems to achieve multiple objectives (i.e., food, water, CO_2 sequestration) (Brancalion and Chazdon 2017; Chazdon et al. 2017; Liu et al. 2018). New forest stands for timber should be designed as stable species mixtures where trees have low competition to obtain plantations with more ecological and economic resilience (Lamb et al. 2005). Mixed forest silviculture emerges as a promising option to meet demands for wood production and conservation, while contributing to restoration objectives as complementary forest habitat for wild species (Lamb et al. 2005; Amazonas et al. 2018; Naumov et al. 2018). In addition, mixed plantations with native species represent an opportunity to mitigate the loss of local biodiversity, connect rainforest remnants and contribute to the conservation of endangered species (Montagnini 2000).

Plantation forests make up 45% of the total planted forests in the world (FAO 2020), and most plantations for timber production are conducted as even-aged monospecific stands (Puettmann et al. 2015; Messier et al. 2022). If they are converted to even-aged mixed stands, all the species must tolerate full sun at planting, then only light-demanding species may be used. However, if they are converted to uneven-aged mixed plantations, valuable species that require canopy protection can be planted (i.e., species that do not tolerate frosts, high radiation, high temperatures, high evaporative atmospheric demand) (for example: Dordel et al. 2011; Yan et al. 2016; Zhang et al. 2018). These environmental requirements are related to the physiological characteristics of each species, such as shade tolerance, acclimation to low water availability, or temperature stress, among other aspects (Ashton 1992). Although large trees can limit light availability for shade-intolerant species, they can also increase growth of shade-tolerant species through reduction of abiotic stresses as was observed in temperate forests (Kothari et al. 2021). In this context, the reduction of environmental stresses mainly during the first two years after planting trees form the Atlantic forest in a restoration experiment, increased the probability of survival (Campoe et al. 2014). Then, the interactions generated between plants of different species in mixed-stands can positively or negatively affect their growth and mortality (Forrester 2014; Grossiord 2020). The type of interaction that prevails depends on the pool of species and their ecological requirements, plant ages, and the environment where plants develop (del Río et al. 2018). The partitioning in space and time in the use of resources leads to the reduction of competition through complementarity (Barry et al. 2019), and even increases stand productivity when monospecific stands are compared with mixed- stands (Erskine et al. 2006; Ishii et al. 2013). Then, uneven-aged mixed stands may be a good opportunity to produce valuable timber species that nowadays are extracted from the native rainforests, mainly to small-holders and communities that rely on forests and support their livelihood through multiple products (Vanclay et al. 2022). *Araucaria angustifolia* (Bertol.) Kuntze is the Gymnosperm species that gives identity to the Araucaria Humid Forest and it is listed as a critically endangered species (CR) in the IUCN Red List of Threatened Species (Thomas 2013). Its population was reduced mainly by the over-extraction of trees from the native forests for its high-quality wood, and by the expansion of agricultural and urban lands (Zandavalli and Dillenburg 2015; Souza 2020). Furthermore, natural regeneration of *A. angustifolia* in the understory of native forests is poor and mortality of the remaining population is high because adult trees need a wide area to growth and competition in the native rainforest is high (Moreira Beckert et al. 2014). The replacement of native forests by exotic monospecific plantations as *Pinus* and *Eucayiptus* sp decreases specific, structural, and functional diversity in the area (Zurita et al. 2006). However, there are 16,500 ha with commercial plantations of *A. angustifolia* managed for timber production in Misiones, Argentina. Nowadays *A. angustifolia* is the only native tree species of the Atlantic forest that is planted outside the rainforest for wood production. On the other hand, *Cabralea canjerana* (Vell.) Mart is a mid-succession timber broadleaved species, native from the same eco-region with a wide distribution in Central and South America (from 10°N to 35.5°S), that acclimates to different shade intensities within the rainforest (Moretti et al. 2019b; Olguin et al. 2020). *C. canjerana* trees are extracted for sawing from the native rainforest and there are no plantations with this high economic value species as plantations in deforested areas are not possible (Aimi et al. 2020). This background suggests that both species are suitable to be combined in uneven-aged-mixed stands as they have complementary eco-physiological demands: *A. angustifolia* is a light-demanding species

(Olguin et al. 2019) that is planted in deforested areas, whereas *C. canjerana* is a shade-tolerant species that needs protection from high radiation and extreme temperatures during its earlier establishment (Moretti et al. 2019b, 2019a). Therefore, *A. angustifolia* plantations could be used as nurse to establish *C. canjerana* seedlings as natural native tree species regeneration was reported in mature *A. angustifolia* plantations (Barbosa et al. 2009; Figueiredo Filho et al. 2017; Medina et al. 2020). The main question is whether the microenvironment generated by the umbrella-shaped open canopy of *A. angustifolia* buffers extreme soil and air temperatures and reduces incident radiation so it provides sufficient protection for the establishment of a mid-succession species.

Considering the need to promote the planting of native forest species that belong to the most biodiverse rainforests in the world, particularly in timber plantations that surround the remnants of native forests, in order to collaborate with their connectivity and considering that small-holders can supply the demands of multiple timber products, we propose mixed plantations with native species as a desirable silviculture to replace monospecific plantations. Although there are no records of *A. angustifolia* in uneven-aged mixed stands, the species was evaluated experimentally in agroforestry systems, in which low-density *A. angustifolia* trees were used as shelter to produce leaves of yerba mate (*Ilex paraguariensis*) (Ilany et al. 2010). Moreover, in Australia, *Araucaria cunninghamii* established successfully in even-aged mixed experimental plantation with a broad-leaved tree species (Vanclay et al. 2013). The aims were: 1) to evaluate the establishment and acclimation of *C. canjerana* seedlings in an *A. angustifolia* plantation, and 2) to assess the initial competition between species to establish a practical way to choose the planting position within the stand. In this sense, the hypothesis is that the canopies of *A. angustifolia* plantations generate coverage and environmental conditions that favor *C. canjerana* seedlings during their establishment, and that competition generates different microenvironments that result in differential seedling growth rates within the stand.

2. Materials and methods

2.1. Study area and experimental design

The experiments were performed in the Campo Anexo Manuel Belgrano (CAMB), Misiones, Argentina (26°03'11.8"S, 53°44'59.6"W), where 450 ha are planted with *A. angustifolia* of different ages. We first worked in a 14-year-old *A. angustifolia* stand that covers 2.3 ha, with a 4x2m initial spacing. Stand management followed standard practices in the area for timber production: it received two low-thinnings, with a final density of 340 trees ha^{-1} before *C. canjerana* seedlings were planted in October 2015 (spring). The *A. angustifolia* trees mean diameter at breast height (DBH) (1.3 m above soil surface) was 27±3cm (mean ± standard deviation), the mean height was 18±1m and the basal area (BA) was 20m^2 ha^{-1}. Six plots measuring 20m wide (five rows of *A. angustifolia*) and 50m long were selected from the stand. In three plots, *C. canjerana* seedlings were planted along the five plantation lines, 10 plants per line (50 *C. canjerana* plants per plot, n=150), randomly interspersed with *A. angustifolia.* The proportion of *C. canjerana* and *A. angustifolia* plants was 60:40 per plot. The final density considering both species was 840 trees ha^{-1}. Distance among plants was different because of previous *A. angustifolia* low-thinning and *C. canjerana* random plantation. Each seedling was identified with a number on a metal label. The seedlings were produced in the same location, from seeds collected in the native rainforest. *C. canjerana* seedlings were 4-months old at planting and their height was 11±3cm (Figure 1). The remaining three plots were maintained as a pure *A. angustifolia* plantation.

Later, in order to analyze initial competition in other intermediate stands, with similar age but different BA, we selected three *A. angustifolia* stands in the same location, in October 2018. We installed a 20x50m plot per stand and we randomly interplanted 50 4-month-old *C. canjerana* seedlings per plot, 10 seedlings per line, as in the previously explained experiment. Stands had 17, 21 and 23 years-old, they received standard practices in the area for timber production, including two thinnings, and had 18, 17 and 27 m^2 ha^{-1} of BA when *C. canjerana* seedlings were planted (Table S1).

2.2. Growth measurements

Araucaria angustifolia DBH was measured in all the plants within the six plots in 2015, 2017, 2019 and 2022. *C. canjerana* survival was registered by counting alive plants. Height and collar diameter were registered in all *C. canjerana* plants every six months during seven years.

2.3. Environmental and physiological measurements in *Cabralea canjerana* seedlings

To describe covering conditions where *C. canjerana* plants were growing, we measured, on 1-3 clear sunny typical days of each season, on six, 12, and 24 months after planting, the photosynthetic photon flux density (PPFD) at midday above the highest bud of each *C. canjerana* seedling, with a ceptometer (BAR-RAD 100, Cavadevices, Buenos Aires, Argentina). In addition, we measured soil temperature at 5cm depth and 10cm apart from the seedling collars, and air temperature and air relative humidity next to the bottom of 15 randomly selected *C. canjerana* seedlings per plot (n=45) with a TFA thermohygrometer (TFA 30.5000.02, Wertheim, Germany). In the same seedlings, we carried out morphological and physiological traits measurements. Specific leaf area (SLA) was measured in one leaflet of an upper complete expanded leaf per plant. The leaflet area was measured on a digital photograph taken from full- hydrated leaflets, with a 5cm-scale as reference and after that, it was dried at 65°C to constant weight. The photographs were analyzed with the software Image Tool v.1.28 CMEIAS Update (Liu et al. 2001). SLA was calculated as the leaflet area divided by its dry weight. We took a sample of a similar leaflet to measure chlorophyll concentration. Chlorophyll was extracted from an intact leaf disc of 19.6mm^2 area, submerged in 1ml of N, N- dimethylformamide for 48 hours at dark (Wellburn 1994). We registered the absorbance at 664 and 647nm in a spectrophotometer (UV-160A, Shimadzu, Kyoto, Japan) to calculate chlorophyll a concentration, chlorophyll b concentration, and chlorophyll a:b concentration ratio (Hallik et al. 2012). To estimate the photosynthetic rate, the electron transport rate (ETR; μmoles e$^-$ m^{-2} s^{-1}) was measured at midday (from 11am to 1pm) under natural light conditions, in the upper fully expanded leaf with a modular fluorometer (FMSII, Hansatech, Norfolk, United Kingdom). Simultaneously, stomatal conductance (gs) was measured with steady-state porometers Decagon SCI (Decagon Devices, Pullman, Washington, USA) as a predictor of the hydric status of the plants.

2.4. Calculation of competition indices

In order to analyze the relationship among the proximity of *A. angustifolia* trees and the growth rate of *C. canjerana* seedlings, we calculated three individual simple distance competition indices (Pommerening and Grabarnik 2019) to analyze the competition exerted on *C. canjerana* plants in mixed plots: total number of neighbors (NT), number of larger neighbors (NL), and total basal area (BAT). Position in the x-y grid was registered for all *A angustifolia* and *C. canjerana* plants in each plot. We calculated NT, NL and BAT for each *C.canjerana* plant. NT was calculated by counting all *C. canjerana* and *A. araucaria* trees present within the 5-m radius of the target tree (NT), which is the tree in the center of the 5-m radius circle. NL was evaluated by counting the number of *C. canjerana* and *A. araucaria* trees with a collar diameter larger than the target tree present within a 5-m radius of the target tree. The third competition index was calculated as the addition of the basal area of all the trees present in a 5-m radius around the target tree (BAT), considering *A. angustifolia* DBH and *C. canjerana* collar diameter. Given the high difference between the diameter of *A. angustifolia* and *C. canjerana*, BAT mainly describes the presence of *A. angustifolia*. For each index calculation, we calculate each index for each target tree and the other *C. canjerana* trees and *A. angustifolia* trees within a 5m radius are considered neighbors. A 5m radius was chosen for every index, to include neighbors in the same row and those of contiguous rows, as the initial *A. angustifolia* planting distance was 4x2m. Calculations were performed with a script written by ourselves in R software (R Core Team 2020).

In order to analyze if the inter-planting of *C. canjerana* seedlings had some negative effect in *A. angustifolia* growth seven years after the interplanting, we calculate the competition indices, NT, NL and BAT, in the same way as described for *C. canjerana*, but considering each *A. angustifolia* tree as a target tree and, as neighbors, other *A. angustifolia* trees and *C. canjerana* trees present in a 5m radius.

2.5. Statistical analysis

The correlation between the competition indices with the *C. canjerana* mean height and mean collar diameter and with DBH increments of *A. angustifolia* in mixed and pure plots, were analyzed with Pearson’s correlation. We reported the correlation coefficient (r) and 95% confidence interval for each significant correlation. We considered that correlations were significant if $p<0.05$. Then, we selected the NL index to further analysis as it yielded the best result in the Pearson´s correlation analysis. *C. canjerana* environmental and physiological traits were analyzed by GLM (General Linear Models) ($p<0.05$) considering time (6, 12, and 24 months) and ranges of the competition index NL (1–2, 3–4, and 5–8) and their interaction (time x NL) as main factors and plot as random effect. *C. canjerana* heights in the different basal area stands were analyzed by GLM ($p<0.05$) considering time and NL and their interaction as main factors. The *A. angustifolia*

DBH increment in the 2015–2017, 2017–2019 and 2019-2022 periods in mixed and pure plots was analyzed by GLM ($p<0.05$). Each plant was considered an experimental unit, with plot as random effect. To analyze DBH along time, GLM was used with treatment, time and NL as main factors, all the possible interactions were included (T x Y, T x NL, Y x NL and T x Y x NL), plot was considered a random effect and variance was modeled with time as VarIdent to consider repeated measurements. Normality and homoscedasticity were corroborated in every analysis. Analysis were performed with Infostat (Di Rienzo et al. 2020).

3. Results

3.1. NL is the better competition index to explain *Cabralea canjerana* growth

Cabralea canjerana survival was 80% six months after planting and 75% after seven years. Height increased 50-fold after the first seven years, with a range of the height from 0.6 to 12m in the last measurement (Figure 1). Collar diameter increased 6-fold in the same time lapse.

NL was the competition index with a better negative correlation with collar diameter and height increments. NT had a negative correlation with height increment, while BAT had a negative correlation with collar diameter (Figure 2).

3.2. Environmental conditions are similar among NL ranges and *C. canjerana* seedlings acclimate equally to every competition level

Environmental conditions were similar in *C. canjerana* seedlings with different ranges of competition index (NL) (Figure 3). Soil temperature at midday was 20-22°C on every date analyzed; usually 4°C lower than air temperature. Air relative humidity was 50–60% at midday on every date analyzed. The PPFD that reached to *C. canjerana* seedlings below the canopy of *A. angustifolia* at midday was 100–450 µmoles photons $m^{-2}s^{-1}$, representing 20–40% of the total incident light.

There were no differences in the physiological traits evaluated between seedlings in the different competition levels (NL: 1–2, 3–4, and 5–8). However, physiological traits changed over time (Table 1). Stomatal conductance (gs) and electron transport rate in photosystem 2 (ETR) increased over time, while chlorophyll a:b and SLA decreased 24 months after planting.

3.3 In other three *A. angustifolia* stands *C. canjerana* growth is conditioned by NL

The lower the competition (NL), the taller *C. canjerana* seedlings in the *A. angustifolia* stands with any basal area (BA) (Figure 4, Table S2 and Table S3). Height increased over time in *C. canjerana* seedlings with any level of competition index (NL). However, in the *A. angustifolia* stand with highest BA (27m^{2}ha^{-1}), *C. canjerana* seedlings grew to their minimum among plots.

3.4. A. angustifolia growth is not affected by the interplanting of *C. canjerana* seedling during the first seven years after conversion from a pure to mixed plots

A. angustifolia increment in DBH was similar in mixed plots and in pure plots. In the 2015–2017 period DBH increment was 1.33±0.03cm y^{-1} in mixed plots and 1.23±0.03cm y^{-1} in pure plots (GLM F=4.10, p=0.113). Increment in DBH in 2017–2019 period was 1.44±0.05cm y^{-1} and 1.33±0.05cm y^{-1} (GLM F=2.74, p=0.173), and in 2019–2022 period it was 0.59±0.02cm y^{-1} and 0.57±0.02cm y^{-1} (GLM F=0.39, p=0.568) for mixed and pure plots, respectively. There was a positive correlation between DBH and the yearly increment in DBH of *A. angustifolia* in mixed and pure plots (Figure S1). The number of neighbors with larger DBH (NL) was the index that better correlated with the increment in DBH (Figure S2). DBH of *A. angustifolia* trees was higher with lower competition (NL 0) than with higher competition (NL 1 and 2–3) in pure and mixed plots, and differences among competition index increased along time (GLM F=3.91, p=0.0204) (Figure 5, Table S4 and Table S5).

4. Discussion

4.1. Growth and acclimation of *C. canjerana* seedlings under *A. angustifolia* canopy

To promote new ways to produce wood without further affecting rainforests, it is essential to evaluate the production of native forest species in already deforested areas. This is the first experiment centered on the study of physiological acclimation of a native Atlantic Forest species in the conversion from monospecific to mixed stands. *C. canjerana* seedlings were successfully established under the canopy of a 14-year-old *A. angustifolia* plantation, with an incident PFDD ranging from 4 to 58% with respect to that of open areas. Previous studies indicated that *C. canjerana* seedlings have high phenotypic plasticity, which gives them the ability to acclimate to different coverage conditions, even at more extreme low light intensities (below 10 µmol photons m^2s^{-1}) registered in the native forest (Moretti et al. 2019b; Olguin et al. 2020). The monolayer flat umbrella-shaped crown of *A. angustifolia* produced a sparse canopy cover and high light intensity; sunflecks reached the understory and allowed high growth rates of *C. canjerana* seedlings. The microenvironmental conditions generated by the canopy of *A. angustifolia* were similar among *C. canjerana* seedlings, with different levels of competition (Figure 3), i.e., regardless of the number of larger neighbors (NL), which are those that mostly modify the environmental conditions. Thereby, the *C. canjerana* morpho-physiological response was similar at different NL. The plasticity of *C. canjerana* allowed it to acclimate to the different microenvironments and maintain high growth rates through physiological modifications during the first years. Two years after planting, *C. canjerana* decreased the SLA and the chlorophyll a:b ratio. The higher concentration of chlorophyll b is related to bigger light-harvesting antennas, which makes the plants capable of using low radiation (Valladares et al. 2015; dos Santos and Ferreira 2020). Then, seedlings increased the capacity to intercept more light and thus the electron transport rate (ETR), with the subsequent higher carbon gain per unit of surface area (Kalaji et al. 2014). In none of the microenvironments generated by the canopy of *A. angustifolia*, where *C. canjerana* was planted, we found any physiological indicator of water stress, excess or lack of light, such as partial or total stomatal closure, reduction in the photosynthetic rate, or changes in leaf morphology as was found in open areas (Moretti et al. 2019b). Then, the canopy of *A. angustifolia* prevented *C. canjerana* stress during its establishment.

The increment in height in *C. canjerana* seedlings was affected by the number of total neighbors (NT) and, specifically, by the number of larger neighbors (NL) (Figure 2). It is known that shade tolerant species have higher survival and growth rate as light availability is higher (Lin et al. 2001). BAT had a positive correlation with collar diameter increment, but there was no correlation with height increment; therefore, higher BAT diminished stem thickness. As higher BAT implied more *A. angustifolia* trees near the *C. canjerana* seedlings, the growth in height and collar diameter of *C. canjerana* seedlings was affected mainly by the competition of the largest neighbors. Consistently, NL was the competition index that best explained the relationship between the increase in height and collar diameter and competition. In other words, *C. canjerana* seedlings growth was lower when the number of *A. angustifolia* neighbors within a 5m radius was higher.

This result was also observed in other *A. angustifolia* stands with different basal area (Figure 4). However, in the *A. angustifolia* stand with higher basal area (BA=27m^{2}ha^{-1}), *C. canjerana* growth in height was low as any microenvironment was good enough for *C. canjerana* seedlings. A higher basal area produces more shaded microenvironments, where the growth of *C. canjerana* seedlings can be light-limited, as was observed in different positions within the rainforest gaps (Moretti et al. 2019a; Olguin et al. 2020). In *C. canjerana* seedlings interspecific competition would prevail over intraspecific competition as the large trees are mainly represented by *A. angustifolia* trees. Despite these competitive relationships, *C. canjerana* seedlings survival and growth rates were very high (Figure 4), higher than the growth registered in plantations in gaps in the native rainforest (Moretti et al. 2019a; Olguin et al. 2020). The initial growth registered seems to be better than the results reported in a previous experiment that obtained plants with 22cm DBH and 12m height, 22 years after planting (Paniagua et al. 2006). Thus, it can be stated that although further measuring until harvest is required to be able to assess its yield, the initial *C. canjerana* establishment under the canopy of *A. angustifolia* was successful, and conversion from an even-aged monospecific *A. angustifolia* stand to a mixed uneven-aged stand is possible. Similar results were registered when the shade-tolerant *Acacia mearnsii* was planted below the light-demanding *Eucalyptus globulus* (Bauhus et al. 2004). In mixed uneven-aged plantations, the differences in planting moment produced microenvironmental heterogeneity, which is advantageous in the establishment of both species. The species planted first has the advantage of establishing and growing without interspecific competition. The species planted later, in this case *C. canjerana*, benefits from being protected by a canopy during the first years, as the canopy buffers high and low temperatures, wind speed, and reduces soil drying compared to deforested open areas. Then, there is a trade-off between facilitation and competition that allows species to coexist. In this sense, the facilitation seven years after planting *C. canjerana* below the canopy of *A. angustifolia* would have a higher incidence than the incipient competition for resources for both species when mixed. However, in more advanced stages, sustained competition could affect growth rates (Ledo et al. 2014).

It is important to highlight that the microenvironmental conditions were not significantly affected by the number of larger neighbors near each seedling (Figure 3), so all the seedlings were similarly acclimated to those microenvironments (Table 1). In this sense, the selection of the planting site in the stand should not seek the protective effect of the proximity of many neighbors, neither systematically nor randomly. It is important to highlight that during the first 24 months, *C. canjerana* growth was indifferent to the number of *A. angustifolia* neighbors within a 5m radius. This time lapse coincides with that reported for tropical species as the most critical to ensure establishment (Campoe et al. 2014). After two years of planting, the growth rate markedly increased in *C. canjerana* seedlings with only one or two larger neighbors, probably due to the difference between seedling shade tolerance and sapling light demand to maintain bigger non-photosynthetic tissues (Sendall et al. 2015). Therefore, within the *A. angustifolia* stand, the plantation of *C. canjerana* should be carried out in positions that imply the seedling will have zero, one or two neighbors within a 5m radius, and positions with a higher number of neighbors should be avoided. The information reported in this work is relevant to small landholders, who need practical recommendations to convert monospecific plantations in mixed-plantations, with the consequence increase in economic income and natural resilience (Nguyen et al. 2018).

***4.2. A. angustifolia* growth in mixed and pure plots**

At the beginning of the experiment, when *C. canjerana* seedlings were planted, the *A. angustifolia* trees with the highest DBH were those without neighbors within a 5m radius, both in mixed and pure plots (Figure 5). Furthermore, in pure plots where only *A. angustifolia* was present, the negative correlation between the DBH increment and NL confirms that *A. angustifolia* is affected by intraspecific competition of larger trees. These results are consistent with the demand of this species of large disturbs to regenerate in the native forest (Souza et al. 2008), as it is a sun-demanding species with a wide monolayer crown. Also, in an unthinned commercial monospecific plantation, with an initial density of 2,500 trees ha^{-1}, 62% mortality was registered 21 years after planting (Salto and Lupi 2019), reinforcing the idea that intraspecific competition is high.

Therefore, seven years after the conversion from pure to mixed stands, the complementarity of niches and the difference in age between *A. angustifolia* and *C. canjerana* implied to maintain the growth of the conifer in spite of the presence of the young broadleaved trees. This is an important point considering that in mixed plots, the density of trees was higher than in pure plots, as the second species was added without removing the preexisting plants and no mortality of *A. angustifolia* occurred. In other experiments, the growth of different species in mixed plantations was higher than in their corresponding monospecific plantations (Perot et al. 2010; Forrester and Smith 2012; You et al. 2018). The fact that in our experiment, the second species was planted when the first species was 14 years old is important to ensure the optimal microenvironment for both species, which have very different requirements. Likewise, the establishment of five native tree species under 12 to 15-year-old *Pinus elliottii* plantations did not negatively affect the growth or the volume produced 23 years after the conversion to mixed stands (Simpson and Osborne, 2006). However, experiences carried out even with a difference of three months in the planting of a shade-intolerant and a shade-tolerant species, have shown stratification and higher productivity in mixed plots rather than in their corresponding pure plots (Bauhus et al., 2004). The predominant interaction among species in the stand can change, as was observed 4 years after mixed stand conversion, when competition of *Robinia pseudoacacia* over *Populus* hybrids was higher than the initial facilitation (Rebola-Lichtenberg et al. 2021). In our results, during the first 7 years after interplanting *C. canjerana* under *A. angustifolia,* a neutral effect of the mixture followed by similar growths of the sun-demanding species was observed, but this result needs to be confirmed over a longer period. In fact, to ensure the maximum growth rate in *A. angustifolia*, it is important to ensure that no other bigger tree is present in 5-m radius. The presence of smaller neighbor trees has no negative effect on *A. angustifolia* growth. Although measurements must continue, it is important to note that this is the first report of an uneven-aged mixed plantation with two native timber species of the Atlantic Forest, one of them critically endangered. This experience is extremely relevant as efforts are done in reforest tropical regions with native species, and few eco-physiological information of mixed-plantations is available in South-America (Nguyen et al. 2014, 2018). We reported an experimental methodology to determine competition and to choose the better position to plant the seedlings, when converting the stands to mixed-plantations. This methodology can be easily replicated with other native species below the *A. angustifolia* canopy, or other monospecific plantations.

5. Conclusions

The canopy of an *A. angustifolia* plantation with BA around 17-20 m^{-2}ha^{-1} reaches adequate levels of light and promotes the initial establishment of *C. canjerana*, protecting the seedlings in the first stages from high and low temperatures, and no stress was observed in any microenvironment within the stand.

The addition of *C. canjerana* seedlings, a shade tolerant species, in a 14 to 21-year-old monospecific stands of *A. angustifolia*, a light-demanding species, allowed the establishment of mixed stands without affecting the growth of the older species by interspecific competition. Moreover, the effect of intraspecific competition can be reduced or even canceled if conifers do not coincide within a 5m radius. We found an easy way to choose the site to plant broadleaved seedlings within the stand: in positions where up to two trees are present within 5-m radius the seedling growth will be maximum. Moreover, each *A. angustifolia* tree needs a 5-m radius without any larger neighbor to reach its maximum DBH increment, but smaller neighbors do not decrease its growth.

It is possible to convert monospecific *A. angustifolia* plantations to mixed uneven-aged plantations with *C. canjerana* as an option to produce high valuable rainforest timber species, and to meet international and local demands for wood production and ecosystem conservation, as mixed plantations would increase biodiversity and reduce economic and ecological risks. This is the first report of an uneven-aged mixed plantation of two native Atlantic Forest timber species.

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Table 1 Physiological and morphological traits 6, 12, and 24 months after planting *Cabralea canjerana* seedlings in a 14-year-old *Araucaria angustifolia* plantation. GLM was performed considering the period of time (6, 12, and 24 months), the ranges of the competition index NL (1–2, 3–4, and 5–7) and the interaction (time x NL). For each factor and interaction, the p-value is shown. Different letters indicate significant differences ($p<0.05$) between means.

	Months after planting			p-value		
	6	12	24	time	NL	time*NL
gs (mmoles m^2 s^{-1})	114.6$^{(c)}$	169.4$^{(b)}$	254.0$^{(a)}$	<0.001	0.46	0.11
ETR (µmoles m^2 s^{-1})	38.9$^{(b)}$	64.1$^{(a)}$	80.3$^{(a)}$	<0.001	0.74	0.50
SLA (cm^2 g^{-1})	244.5$^{(a)}$	270.6$^{(a)}$	201.6$^{(b)}$	<0.001	0.15	0.88
Chlorophyll a:b	1.95$^{(a)}$	1.96$^{(a)}$	1.60$^{(b)}$	<0.001	0.25	0.15

Figure captions

Fig. 1. *Araucaria angustifolia* stand at the moment of *Cabralea canjerana* interplanting (a); *Cabralea canjerana* 4-month old seedling at planting (b), *C. canjerana* seedling examples at the first year (c), two (d), three (e), four (f) and seven (g) years after planting. (Photo credits: Flavia Yesica Olguin, Corina Graciano)

Fig. 2. Annual increment in height (cm year^{-1}) and collar diameter (mm year^{-1}) in *Cabralea canjerana* seedlings with different competition indices seven years after planting. NT is the total number of neighbors within a 5m radius, NL is the number of neighbors with larger diameter within a 5m radius and BAT is the total basal area (m^2) within a 5m radius. Pearson determination coefficient (r) and the p-value of the correlation are reported inside each panel. Bars indicate standard errors. Points with no error bars had no replications. Dotted lines indicate 95% confidence interval.

Fig. 3. Environmental conditions at midday in the dates where physiological traits were measured 6, 12, and 24 months after planting *Cabralea canjerana* seedlings below the canopy of *A. angustifolia* (Autumn, Spring, and Autumn respectively): air temperature next to the plant, soil temperature in the upper 5cm next to plant collar, air relative humidity and quotient between the photosynthetic photon flux density (PPFD) (μmol photons m^{-2} s^{-1}) above each plant and the maximum PPFD measured at midday on sunny days. Seedlings were classified in three ranges according to the competition index NL: 1–2, 3–4, or 5–8 neighbors with a larger diameter within a 5m radius. Data are means, and bars are standard errors. There was no significant difference between NL ranges for any variable on any date.

Fig. 4. Total height in *Cabralea canjerana* seedlings along the time after planting in a 20 m^{2}ha^{-1} (340 trees ha^{-1}, 14 years old) 17m^{2}ha^{-1} (250 trees ha^{-1}, 21 years old), 18m^{2}ha^{-1} (220 trees ha^{-1}, 17 years old) and 27 m^{2}ha^{-1} (340 trees ha^{-1}, 23 years old) *Araucaria angustifolia* plantations. Seedlings were classified in three ranges according to the competition index NL (1–2, 3–4, 5–8) neighbors with a larger diameter within a 5m radius). Inside each panel, GLM p-values for time,

NL, and its interaction are reported. Different letters indicate significant differences ($p<0.05$) between means, at the end of the experiment. Differences between means at every date are showed in Table S3. Bars indicate standard errors.

Fig. 5. *Araucaria angustifolia* DBH for the year 2015, 2017 2019 and 2022 according to range of competition in pure plots and mixed plots (treatments). Plants were divided into three ranges according to the competition index NL (number of neighbors with a larger diameter in a 5-m radius). Inside each panel, GLM p-values for treatment (T), year (Y), competition index (NL), and their interactions are reported. Different letters indicate significant differences ($p<0.05$) between means, at the end of the experiment. Complete comparisons of means are reported in Table S5. Bars indicate standard errors.

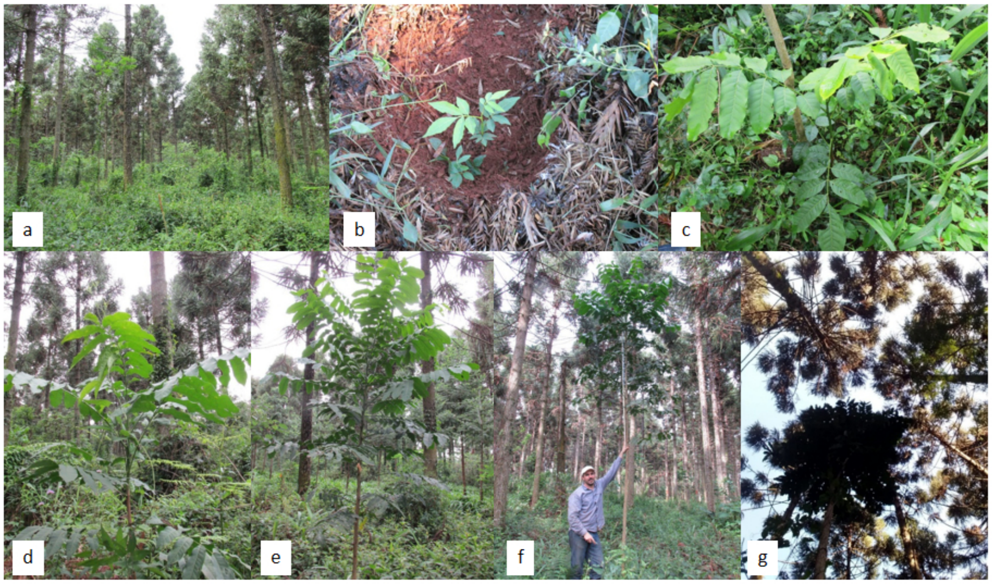

Fig. 1. Araucaria angustifolia stand at the moment of Cabralea canjerana interplanting (a); Cabralea canjerana 4-month old seedling at planting (b), C. canjerana seedling examples at the first year (c), two (d), three (e), four (f) and seven (g) years after planting. (Photo credits: Flavia Yesica Olguin, Corina Graciano)

614x364mm (38 x 38 DPI)

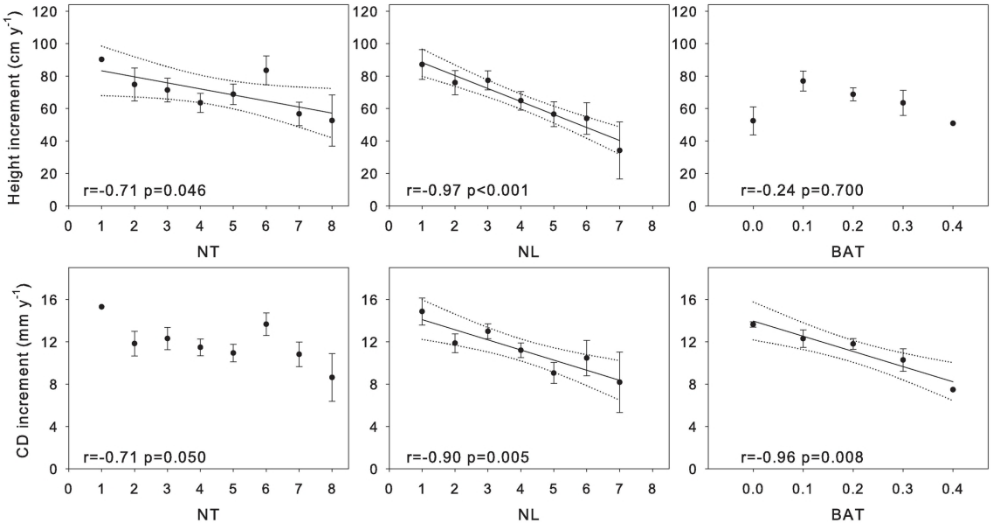

Fig. 2. Annual increment in height (cm year-1) and collar diameter (mm year-1) in Cabralea canjerana seedlings with different competition indices seven years after planting. NT is the total number of neighbors within a 5m radius, NL is the number of neighbors with larger diameter within a 5m radius and BAT is the total basal area (m2) within a 5m radius. Pearson determination coefficient (r) and the p-value of the correlation are reported inside each panel. Bars indicate standard errors. Points with no error bars had no replications. Dotted lines indicate 95% confidence interval.

181x99mm (300 x 300 DPI)

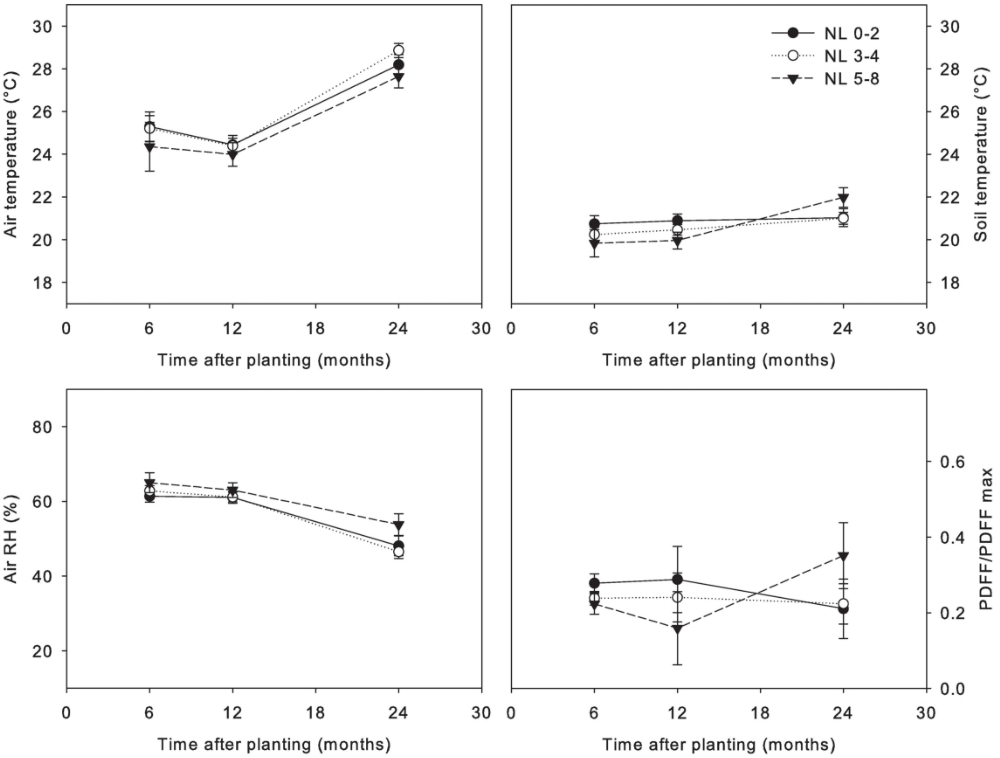

Fig. 3. Environmental conditions at midday in the dates where physiological traits were measured 6, 12, and 24 months after planting Cabralea canjerana seedlings below the canopy of A. angustifolia (Autumn, Spring, and Autumn respectively): air temperature next to the plant, soil temperature in the upper 5cm next to plant collar, air relative humidity and quotient between the photosynthetic photon flux density (PPFD) (µmol photons m-2 s-1) above each plant and the maximum PPFD measured at midday on sunny days. Seedlings were classified in three ranges according to the competition index NL: 1–2, 3–4, or 5–8 neighbors with a larger diameter within a 5m radius. Data are means, and bars are standard errors. There was no significant difference between NL ranges for any variable on any date.

181x144mm (300 x 300 DPI)

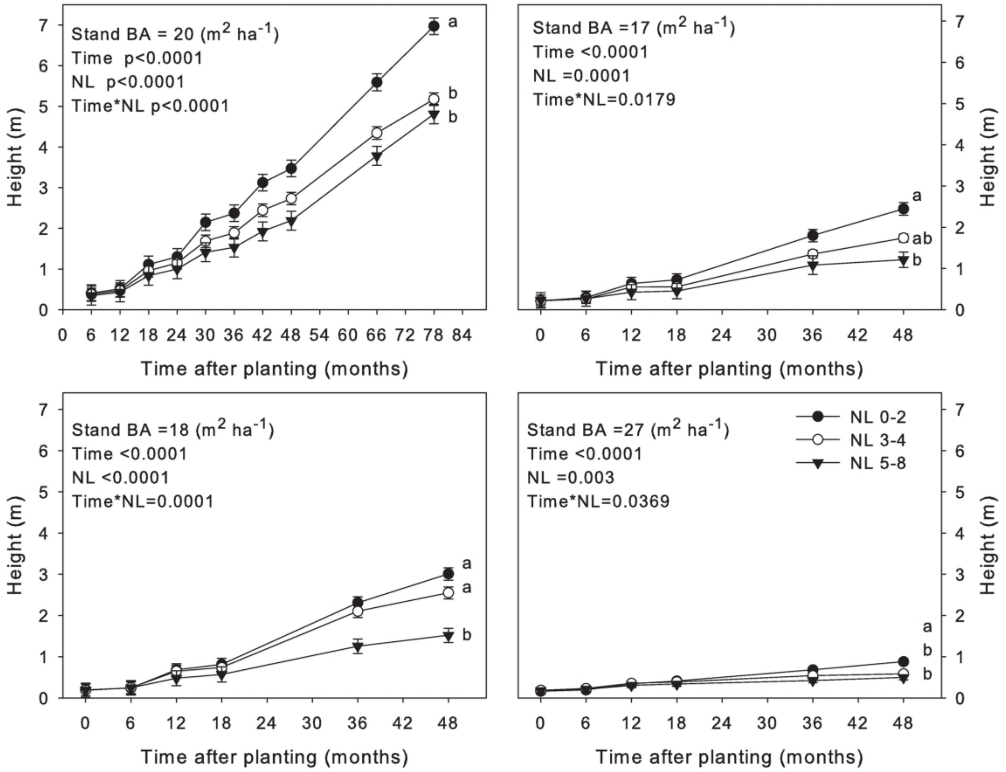

Fig. 4. Total height in Cabralea canjerana seedlings along the time after planting in a 20 m2ha-1 (340 trees ha-1, 14 years old) 17m2ha-1 (250 trees ha-1, 21 years old), 18m2ha-1 (220 trees ha-1, 17 years old) and 27 m2ha-1 (340 trees ha-1, 23 years old) Araucaria angustifolia plantations. Seedlings were classified in three ranges according to the competition index NL (1–2, 3–4, 5–8) neighbors with a larger diameter within a 5m radius). Inside each panel, GLM p-values for time, NL, and its interaction are reported. Different letters indicate significant differences (p<0.05) between means, at the end of the experiment. Differences between means at every date are showed in Table S3. Bars indicate standard errors.

181x147mm (300 x 300 DPI)

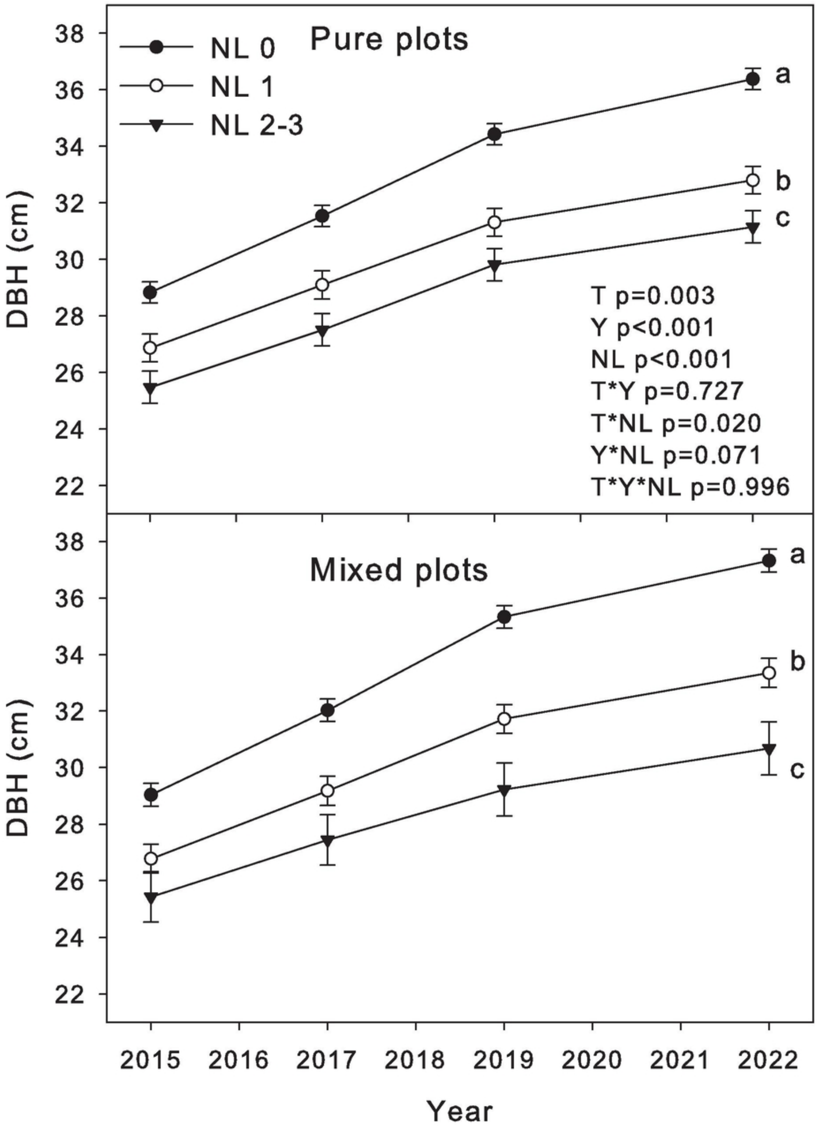

Fig. 5. Araucaria angustifolia DBH for the year 2015, 2017 2019 and 2022 according to range of competition in pure plots and mixed plots (treatments). Plants were divided into three ranges according to the competition index NL (number of neighbors with a larger diameter in a 5-m radius). Inside each panel, GLM p-values for treatment (T), year (Y), competition index (NL), and their interactions are reported. Different letters indicate significant differences ($p<0.05$) between means, at the end of the experiment. Complete comparisons of means are reported in Table S5. Bars indicate standard errors.

82x114mm (300 x 300 DPI)