Universidade de São Paulo
Escola Superior de Agricultura “Luiz de Queiroz”

Alelopatia ou restrição física? Influência da serapilheira na regeneração de espécies nativas em eucaliptais

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Trabalho de Conclusão de Curso apresentado para obtenção do título de Graduado em Ciências Biológicas.

Piracicaba
2023

Dados Internacionais de Catalogação na Publicação
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP

Melman, Guilherme Almeida

Alelopatia ou restrição física? Influência da serapilheira na regeneração de espécies nativas em eucaliptais / Guilherme Almeida Melman. - - Piracicaba, 2023.

18 p.

Trabalho de Conclusão de Curso - - USP / Escola Superior de Agricultura "Luiz de Queiroz".

1. Alelopatia 2. Serrapilheira 3. Eucalipto 4. Germinação.

Alelopatia ou restrição física? Influência da serapilheira na regeneração de espécies nativas em eucaliptais

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Resumo

A alelopatia vem sendo apontada como a principal causa da escassez de regeneração da vegetação nativa em plantações de eucalipto, afetando diretamente a germinação de sementes. No entanto, não há evidências suficientes para afirmar que o efeito alelopático do eucalipto seja o fator mais determinante. O presente projeto se propõe a avaliar a influência da camada de serapilheira na regeneração de espécies nativas arbóreas no sub-bosque de eucaliptais, buscando isolar o efeito de restrições físicas e químicas da serapilheira. Amostras de serapilheira de ambas as tipologias foram caracterizadas quanto à sua biomassa seca, teor de lignina, relação C/N, concentração de macronutrientes, teor de água e capacidade retenção hídrica (CRH). Em experimentos de campo, seis espécies nativas (três com fisiologia ortodoxa e três com fisiologia recalcitrante) foram submetidas a dois tratamentos (semeadura com e sem cobertura de serapilheira). Em experimentos de viveiro, as mesmas espécies de sementes foram submetidas a dois tratamentos: germinação sobre cobertura de serrapilheira de eucalipto e de florestas nativas; com cinco níveis de biomassa (150g, 120g, 90g, 60g, 30g), além do tratamento controle. A serrapilheira de eucalipto apresentou uma maior relação C/N e acúmulo de biomassa em comparação com a serrapilheira de nativas, enquanto uma menor concentração de macronutrientes, teor de lignina e CRH. Nos experimentos de viveiro, apenas a serrapilheira de eucalipto desempenhou um efeito restritivo significativo. Nos experimentos de campo, também só houve redução da taxa de germinação em função do acúmulo de biomassa nas áreas de eucalipto. Já comparando os tratamentos com e sem cobertura de serrapilheira, se observou um padrão inverso, em que a presença da serrapilheira de nativa inibiu mais intensamente a germinação, sugerindo a presença de compostos alelopáticos no solo dos plantios de eucalipto. Se concluiu que o impacto da camada de serrapilheira de eucalipto na germinação de espécies nativas se dá devido a uma restrição física, provocada pela sua maior resistência e elevado acúmulo no sub-bosque, e não a um mecanismo químico fisiológico. Contudo, não se descarta a possibilidade de haverem compostos alelopáticos no solo dos eucaliptais.

Allelopathy or physical restriction? Litter influence on the regeneration of native species in eucalypts plantations

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Abstract

Allelopathy has been identified as the main cause of limited native vegetation regeneration in eucalypt plantations, directly affecting seed germination. However, there is not enough evidence to claim that the allelopathic effect of eucalypt is the most determining factor. This project aims to assess the influence of the litter layer on the regeneration of native tree species in the understory of eucalypt stands, specifically isolating the effects of physical and chemical constraints imposed by the litter. Litter samples from both typologies were characterized for dry biomass, C/N ratio, macronutrient concentration, lignin content, water content and water holding capacity (WHC). In field experiments, six native species (three with orthodox physiology and three with recalcitrant physiology) were subjected to two treatments (seeding with and without litter cover). In nursery experiments, the same seed species were subjected to two treatments: germination on eucalypt and native forest litter cover, with five biomass levels (150g, 120g, 90g, 60g, 30g), in addition to the control treatment. Eucalypt litter showed a higher C/N ratio and biomass accumulation compared to native litter, while exhibiting lower macronutrient concentration, lignin content and WHC. The nursery results showed that only eucalypt litter had a significant restrictive effect on germination. In the field results, germination rates decreased only in relation to biomass accumulation in eucalypt areas. However, when comparing treatments with and without litter cover, an opposite pattern was observed, where the presence of native litter more intensely inhibited germination, suggesting the presence of allelopathic compounds in the soil of eucalypt plantations. It was concluded that the impact of eucalypt litter layer on the germination of native species is due to physical restriction caused by its higher resistance and accumulation in the understory, rather than a physiological chemical mechanism. However, the possibility of allelopathic compounds in eucalypt soil cannot be completely ruled out.

1. Introduction

Commercial tree plantations now cover vast areas worldwide and play an increasingly relevant role in supplying society with timber and non-timber forest products. Currently, plantation forests occupy an area of 131 million hectares globally, approximately 3% of the total forest area, but supply nearly 35% of the roundwood demand (FAO, 2020). Efforts have been made to make these plantations more sustainable, maximizing their contribution to biodiversity conservation and the provision of ecosystem services (Silva, Freer-Smith & Madsen, 2019; Löf et al., 2018). Forest plantations have also been used for restoring forest landscapes, economically enabling an increase in tree cover in degraded landscapes (Lamb, Erskine & Parrotta, 2005; Brancalion et al., 2020).

In tropical regions, species of the *Eucalyptus* and *Corymbia* genus are the most cultivated, covering approximately 20 million hectares globally (IUFRO, 2018) and 7 million hectares in Brazil (IBA, 2020). Eucalypt plantations are typically intensively managed in short cycles (~7 years) for pulp and charcoal production, which limits the opportunities for natural regeneration of native species in the understory and increases the demand for water and nutrients (Bremer & Farley, 2010). Various hypotheses have been proposed to explain the lack of natural regeneration in eucalypt plantations, such as the release of allelopathic compounds from leaves and roots, soil acidification, and limited water availability (Cannell, 1999; Zhang & Fu, 2009; Rhoades & Binkley, 1996). However, few field studies have tested these effects, particularly in humid tropical regions (Amazonas et al., 2018).

The allelopathic potential of eucalypt species has been widely discussed in the literature (May & Ash, 1990; Chu et al., 2014) and generally accepted as a fact by environmentalists. However, there is insufficient evidence to support allelopathy as the main cause of understory regeneration scarcity in commercial eucalypt stands. Several studies have observed high plant diversity in unmanaged eucalypt plantations, contradicting the central idea that eucalypts inhibit germination and establishment of native seedlings (Brockerhoff et al., 2013; Wu et al., 2015). Furthermore, most allelopathy studies are conducted through laboratory tests, extracting compounds and performing bioassays, without considering several field variables that could mitigate the activity of allelopathic compounds. Some field studies have obtained results similar to bioassays, confirming the allelopathic effect of eucalypts on other species (Zhang & Fu, 2009; Chu et al., 2014). However, few studies of this nature have been conducted in the context of humid tropical forests, where high temperatures, precipitation, and soil microbial activity contribute to the rapid degradation of potential allelopathic compounds.

The limited understory regeneration in some eucalypts stands can also be explained by factors unrelated to the species characteristics, such as intensive land use before plantation establishment, isolation of seed sources, and short harvesting cycles that prevent the recruitment of regenerating individuals (Bremer & Farley, 2010). In a controlled experiment conducted in three regions of the Atlantic Forest, no difference in natural regeneration diversity was observed between mixed plantations of eucalypt and native species and plantations consisting exclusively of native species (Brancalion et al., 2020). Natural regeneration was found to be more dependent on landscape context than the presence of eucalypts, as it was more abundant in planting areas with higher native vegetation coverage in the landscape.

The litter layer also plays a crucial role in the microsite conditions for forest regeneration, but for reasons unrelated to the release of allelopathic compounds. The composition and thickness of the litter layer influence the humidity, temperature, nutrient availability, and light conditions of the regeneration micro-site, which are crucial for seed germination and seedling establishment (Santos & Válio, 2002; Vazquez-yanes et al., 1990). Eucalypt plantations usually exhibit a thicker litter layer compared to native forests, despite having lower annual litter production (Barlow et al., 2007; Lisanework & Michelsen, 1994). This is due to the lower decomposition rates of eucalypts litter, which consists of hydrophobic leaves with a high C/N ratio, making it unfavorable for decomposers (Garcia et al., 2012; Kainulainen & Holopainen, 2002; Hua Guo et al., 2019; Santos et al., 2019). These characteristics result in lower nutrient release from eucalypt litter, leading to its accumulation on the forest floor, forming a thick layer of organic debris. This layer of eucalypt-derived organic material may make seeds more susceptible to desiccation and act as a physical barrier to seedling establishment, restricting seedlings' shoot emergence and root penetration into the soil (Santos & Válio, 2002; Chambers & MacMahon, 1994).

Different morphological, physiological, and phenological adaptations allow seeds to establish in diverse environments (Roberts, 1973). Each species has a distinct ecological strategy to integrate and persist in ecosystems, responding differently to regeneration conditions (Chambers & MacMahon, 1994). For instance, small wind-dispersed seeds may be greatly hindered by the accumulation of litter, as they may fail to come into contact with the soil, and the low reserve availability could prevent the primary root from growing enough to overcome the thick litter layer (Leishman et al., 2000). Litter impacts of regeneration could be particularly relevant for recalcitrant seeds, which do not tolerate desiccation and may be more adversely affected when deposited on top of a thicker and, supposedly, drier layer of litter. In this case, orthodox seeds, which are desiccation-tolerant, may have a competitive advantage over recalcitrant seeds in this regeneration environment.

Characterizing the ecological attributes of litter in eucalypt plantations is essential to understand the modulation of understory recolonization by native tree species. This knowledge can serve as a basis for the development of more sustainable silvicultural practices that increase the regeneration of native species in the understory and, consequently, the contributions of commercial timber plantations for biodiversity conservation and some ecosystem services, such as pollination and pest control. Here, we aimed at understanding the potential physical barriers imposed by eucalypt litter to native species regeneration. To do so, we first characterized the litter of eucalypt and mixed-native species plantations (chemical composition and biomass), then performed greenhouse experiments manipulating litter composition (eucalypt and native species) and thickness, and finally performed field experiments in eucalypt monocultures and mixed-native species plantations.

2. Material and methods

2.1 Site description

Field experiments were conducted at the Experimental Stations of Forest Sciences of Itatinga (23°10' S, 48°40' W) and Anhembi (22°40' S, 48°10' W), of the University of São Paulo. Itatinga station is situated at an altitude of 850m and is characterized by a Cwa climate (Köppen classification). The annual average temperature and precipitation are 20°C and 1,350 mm, respectively, and the predominant soils are classified as Latosols and Podzols. The Anhembi station is located at an altitude of 400m and also has a Cwa regional climate, with annual average temperature of 23°C and precipitation of 1,100 mm, and the predominant soils are Latosols and Quartzarenic Neosols. The controlled germination experiments and the litter physiochemical analysis were conducted at the forest nursery of the Department of Forest Sciences, University of São Paulo, located in Piracicaba-SP, Brazil (Fig 1).

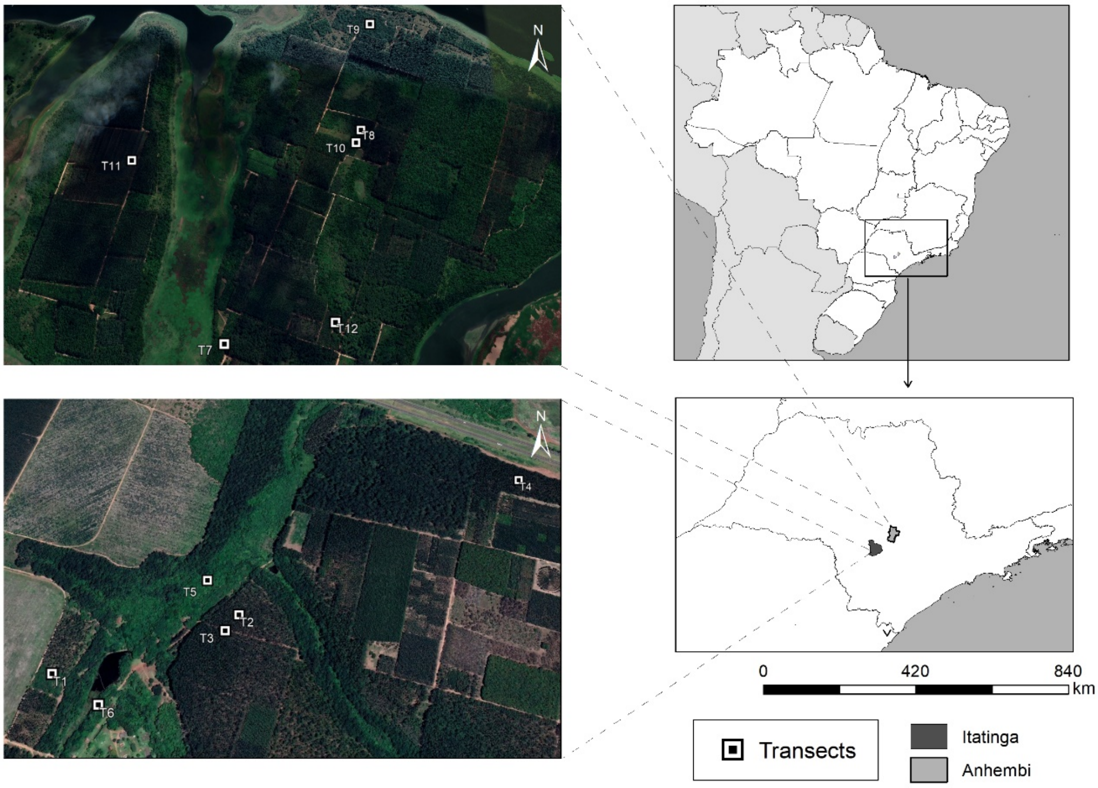

Fig. 1. Location of the twelve transects in the two study sites, at Itatinga and Anhembi provinces, São Paulo State, Brazil.

2.2 Physiochemical characterization of litter

We established six transects of 30 meters each within each study site, distant at least 5 m from the edge, being three in eucalypt plantations and three in restoration plantations (Table 1). Within each transect, we collected a litter sample in four 1000cm² plots, spaced 10 m from each other intervals. Plantations with dense grass coverage in the understory or with a high number of regenerating individuals were avoided due to potential alterations in litter composition. The collected samples were evaluated for dry biomass, litter thickness, lignin content, macronutrient concentration, C/N ratio, water content, and water retention capacity. Dry biomass and thickness were evaluated for each plot (n=48), while the other analyses were performed on a composite sample from the entire transect (n=12). Biomass accumulation was obtained by measuring the dry weight of the sample (oven-dried in at 45°C for 3 days and weighed using a precision balance with a sensitivity of 0.001g). Macronutrient concentration was determined through nitroperchloric digestion (Malavolta, E.; Vitti, G.C.; Oliveira, S.A, 1989) and sulfuric digestion (Kjeldahl method), while total lignin content was determined using the Goldschmidt (1971) and Gomide and Demuner (1986) method. The wet weight of litter samples was measured using a precision balance with a sensitivity of 0.01g immediately after field collection. Subsequently, the litter samples were oven-dried at 105°C for 24 hours and weighed again, thus obtaining the water mass and water content of the litter. The water holding capacity (WHC) of the litter was experimentally determined using the Blow method (1955), according to Equation 1. The samples of dried litter of each typology (eucalypt plantations and forest restoration) were rehydrated by immersing them in water for 90 minutes. They were then placed on sieves for 30 minutes to allow the surface water to drain, and their wet mass (Mu) was measured using a precision balance with an accuracy of 0.01g.

Equation 1:

$$WRC\ (\%) = \frac{Wm - Dm}{Dm} \times 100$$

Where WHC (%): Water Holding Capacity; Wm: wet mass; Dm: dry mass.

Tabel 1. Description of the study area plantations.

transect	typology	specie	planting year
1	restoration	mixed native	2007
2	eucalypt	*E. saligna*	2004
3	eucalypt	*E. grandis*	2004
4	eucalypt	*E. grandis*	1997
5	restoration	mixed native	2000
6	restoration	mixed native	2000
7	restoration	mixed native	2000
8	restoration	mixed native	2005
9	restoration	mixed native	2006
10	eucalypt	*E. grandis, E. maculata*	2015
11	eucalypt	*E. grandis x E. camaldulensis*	2011
12	eucalypt	*E. urophylla*	2019

2.3 Greenhouse experiments

We sowed seeds of six native tree species - three with orthodox (*Handroanthus impetiginosus, Ceiba speciosa, and Anadenanthera peregrina*) and three with recalcitrant seeds *(Eugenia uniflora, Myrciaria floribunda, and Genipa americana*) – in 5.5L pots (20 cm diameter and height) filled with substrate and covered with eucalypt and native species litter, with five levels of litter biomass (30g, 60g, 90g, 120g, and 150g) and a control treatment, with no litter. We sowed 20 seeds of each recalcitrant-seeded species or 20 seeds of each orthodox-seeded species per pot (60 seeds per pot), totaling 110 pots. The pots were placed under a shade net greenhouse in order to simulate the shading conditions of the understory and monitored weekly according to seedling emergence for four months (Nov/2022 to April/2023). During this period, the pots were maintained at natural rainfall conditions, without irrigation, which may have not limited water supply as this period is the rainy season (932 mm of precipitation accumulated during the experiment) (INMET). The litter used in the experiment was collected from a native species restoration area and a *E. Urograndis* plantation, both located on the ESALQ campus in Piracicaba-SP, Brazil. There was no treatment of the collected litter. The pots were prepared with it immediately after harvest, without any drying process.

2.4 Field experiments

The tests were conducted under two litter conditions: seed sowing on the local litter and seed sowing on bare soil after removing the litter. A circular frame was installed to delimit the plots, restricting the lateral movement of litter and seeds, and facilitating periodic cleaning of fallen leaves in the *without litter treatment*. Six arboreous native species were selected, three with orthodox physiology (*Tabebuia avellanedae, Ceiba speciosa, and Anadenanthera peregrina*) and three with recalcitrant physiology *(Eugenia uniflora, Myrciaria floribunda, and Genipa americana*). In each plot, 20 seeds of each species were sown, totaling 120 seeds per plot and 960 seeds per transect. In total, 11,520 seeds were sown. The germination tests implementation occurred between October 26th and 28th of 2022, on the beginning of the rainy season. After the implementation, the germination tests were monthly monitored for a three-month period, until its stabilization. During field trips, the transects were revisited, and the progress of germination was recorded. The germinated seedlings were then removed to avoid the risk of double counting.

2.5 Data analyses

Physical and chemical characterization of leaf litter:

To compare the means of biomass accumulation, thickness, macronutrients, lignin content, C:N ratio, water content and water retention capacity among the different typologies, the T-Student test was used in the R software. To analyze the correlation between biomass accumulation and layer thickness, a Pearson correlation coefficient was calculated in the R software.

Controlled germination experiments:

To assess whether there was a significant impact of the treatments (biomass level and leaf litter composition) on germination rate, a factorial analysis of variance was applied in the R software. This allowed not only evaluating the isolated effect of each predictor variable but also their interaction. The applied model included both orthodox and recalcitrant seeds without distinguishing between them. To evaluate the effect of the treatments on orthodox and recalcitrant seeds independently, another factorial ANOVA was performed, relating the germination rate to the levels of biomass and seed physiology.

Field germination experiments:

To assess whether biomass accumulation influenced the germination rate in different forest typologies, a simple linear regression was performed. In this regression, only data from the litter treatment were considered. To verify if there were differences between the sowing treatments with and without biomass cover in different typologies, a factorial ANOVA with two criteria was applied: treatment (with and without leaf litter cover) and forest typology (eucalypt or native restoration). The results were further analyzed with estimated means (Post Hoc test) with Bonferroni correction for better detail.

3. Results

3.1 Physiochemical characterization of litter

The accumulation of litter was higher in the eucalypt plantations compared to the similarly aged forest restoration plantations (maximum 5-year difference) (Fig. 2). The samples collected in the eucalypt plantations had an average of 162.8 g more litter than those found in the restoration plantations ($t_{31} = 7.23$ and $P < 0.001$). The water retention capacity was significantly higher in the litter collected from the restoration plantations ($t_{34} = -5.85$ and $P < 0.001$) (Fig. 2), while the water content did not show a significant difference between the two groups.

The litter collected in the forest restoration areas showed a higher concentration of macronutrients and a lower C:N ratio compared to the litter found in the eucalypt plantations (Fig. 3). The litter from native forests exhibited higher average concentrations of Nitrogen (N), Phosphorus (P), Magnesium (Mg), and Calcium (Ca), along with a lower C:N ratio. Only Potassium (K) and Sulfur (S) did not show significant differences between the two groups ($P > 0.05$) (Fig. y). The lignin content, on the other hand, was higher in the litter from native forests, averaging 15.8% more than in the eucalypt litter samples ($t_{34} = -13.4$ and $P < 0.001$) (Fig. 2). The eucalypt plantations also showed greater thickness measurements ($t_{23} = 5.16$, $P < 0.001$). A positive relationship was found between biomass accumulation and layer thickness, with a significant Pearson correlation coefficient ($r = 0.52$ and $p < 0.001$) (Fig. 4). Furthermore, eucalypt litter layers have greater thickness values for the same biomass compared to native litter layers.

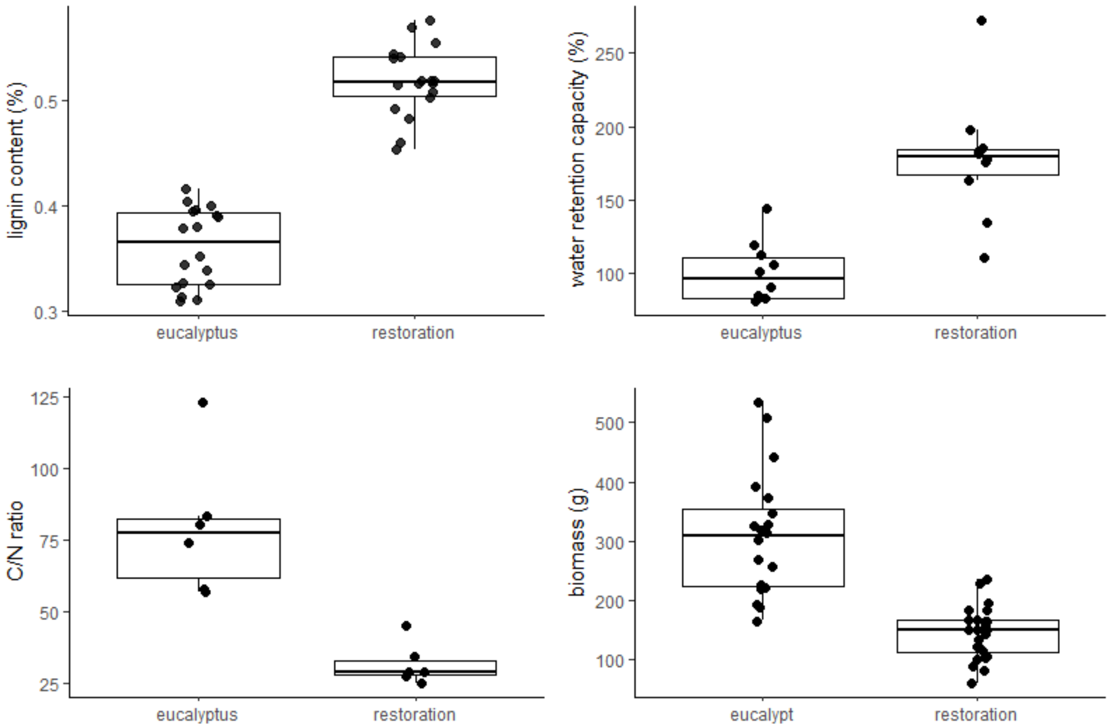

Fig. 2. Lignin content (%), water retention capacity (WRC) (%), C/N ratio and biomass accumulation (g) in different forest typologies (eucalypt plantations and forest restoration). There was a significant difference (P-value < 0.05) for all presented litter attributes.

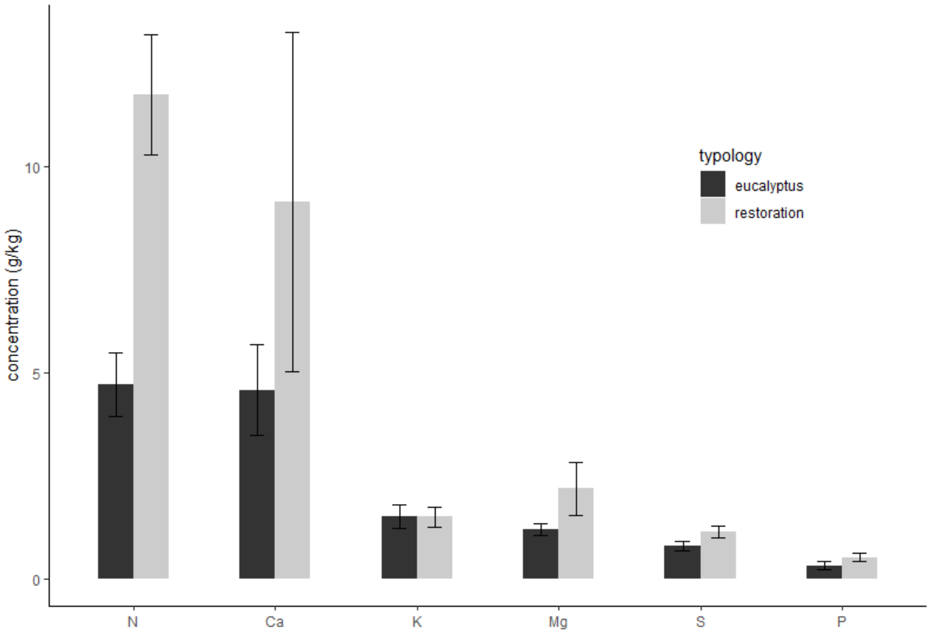

Fig. 3. Litter macronutrient concentration (g/kg) among the two typologies.

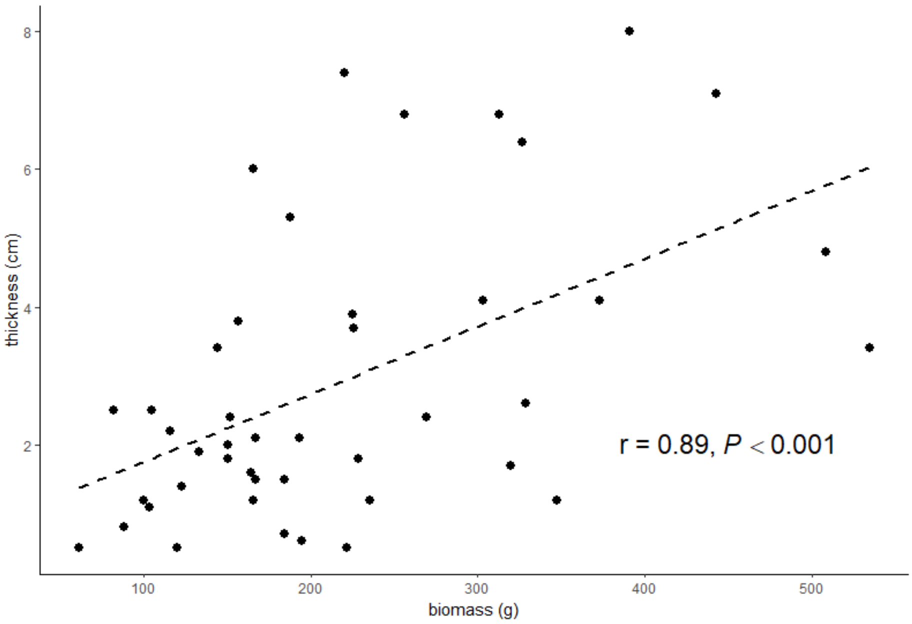

Fig. 4. Correlation between biomass accumulation (g) and litter layer thickness (cm).

3.2 Controlled germination experiment:

Only the eucalypt litter biomass cover exhibited a significant restrictive power on germination ($P<0.001$) (Fig. 5), and the decreases in germination due to biomass was similar between orthodox and recalcitrant seeds (Fig. 6).

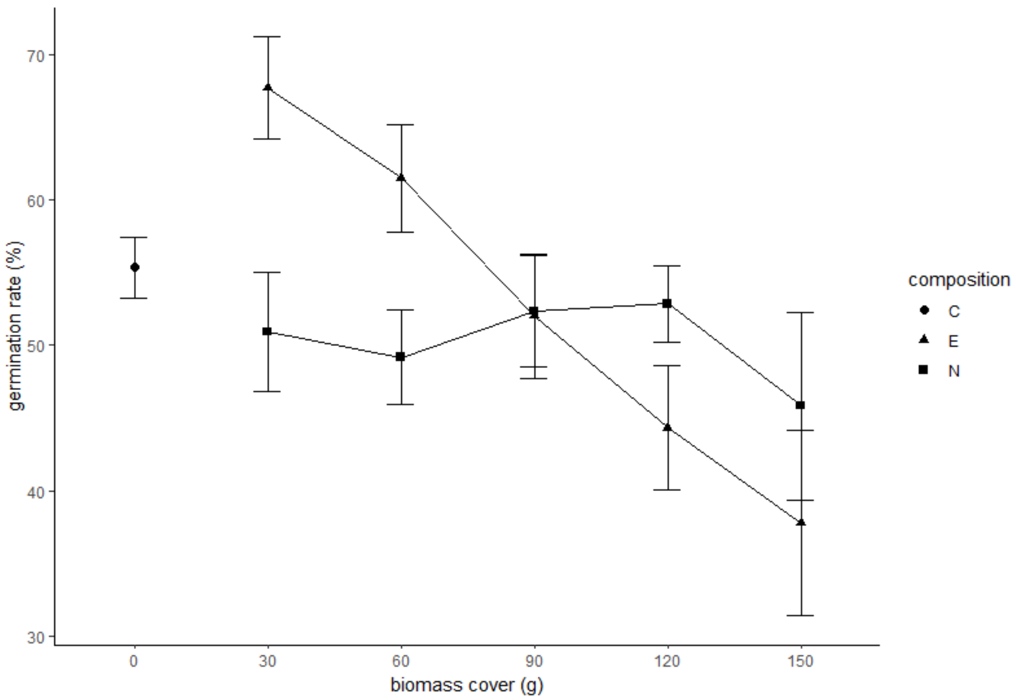

Fig. 5. Germination rate (%) as a function of biomass levels (0g; 30g; 60 g; 90g; 120g; 150g) and litter composition (C - Control; E – Eucalypt litter; N – Native litter).

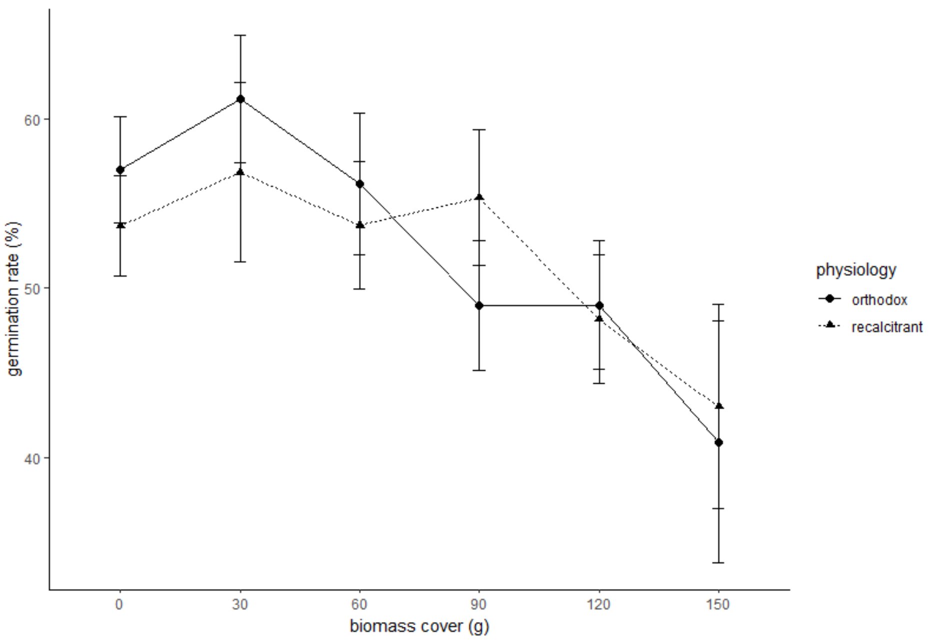

Fig. 6. Germination rate (%) as a function of biomass levels (0g; 30g; 60 g; 90g; 120g; 150g) and seed physiology (orthodox and recalcitrant).

3.3 Field germination experiment:

The field results are consistent with those found in the controlled experiments. As the biomass accumulation increases, the germination rate decreases, but only in the eucalypt litter ($P<0.05$)

(Fig. x). For every 100g of eucalypt litter, there was a 3% decrease in the germination rate. The germination rate of recalcitrant seeds was very low in the field experiments, leading to the decision to exclude them from the analysis. Therefore, the results only refer to orthodox species. When considering the treatments with and without litter cover, a decrease in germination was only observed in the forest restoration areas (P = 0.02), but not in the eucalypt areas (Fig. x). There was a 63,6% relative decrease in average germination between the treatments in the experiments conducted in the restoration areas.

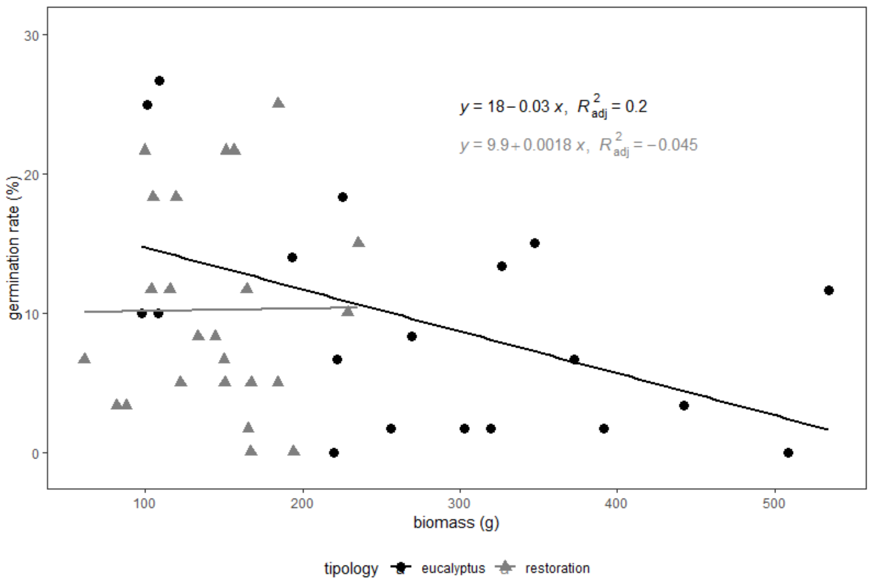

Fig. 7. Germination rate (%) as a function of biomass accumulation gradient (g) and forest typology (eucalypt plantation and forest restoration).

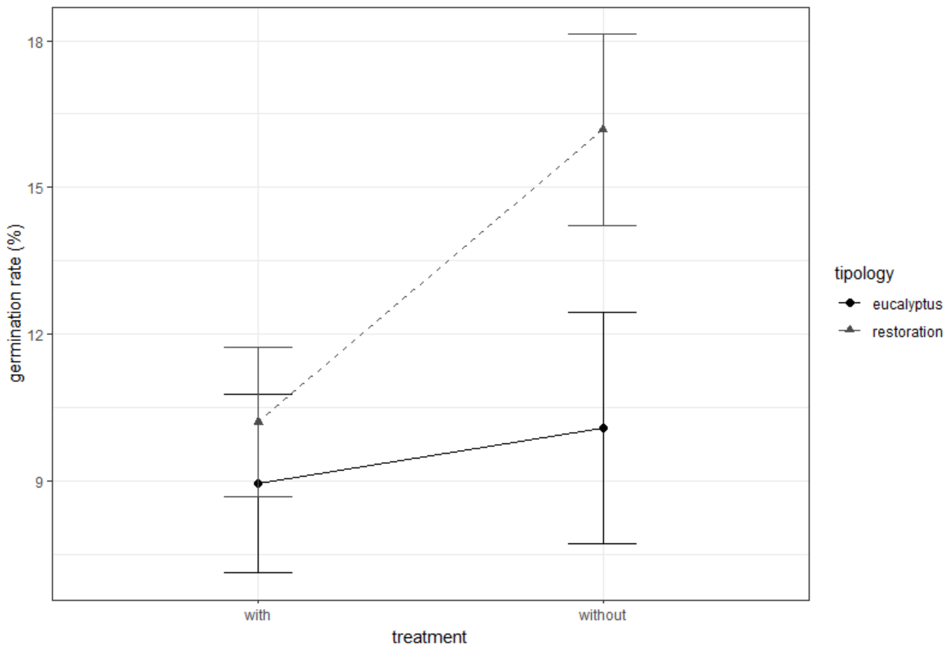

Fig. 8. Germination rate (%) as a function of treatment (seeding with and without litter cover) and forest typology (eucalypt plantation and native species forest restoration).

4. Discussion

Physiochemical litter characterization

The greater litter biomass found in eucalypt plantations indicates that the production rate is higher than decomposition, leading to its accumulation in the understory. This is due to the physicochemical attributes of eucalypt litter, which directly affect the abundance and activity of decomposer agents (Melillo et al., 1982; Taylor et al., 1989). The lower concentration of macronutrients and higher C:N ratio would hinder the action of decomposers (Yang et al., 2022), thus explaining its greater accumulation in the understory. The lignin content was lower in the litter samples collected from eucalypt plantations (Fig. 2), ruling out the hypothesis that this compound is the main responsible for the lower decomposition rate. The higher thickness-biomass ratio and lower water retention capacity found in eucalypt litter could also impair seed water availability, hindering root access to the soil and seedling emergence (Santos & Válio, 2002; Chambers & MacMahon, 1994). This is mainly due to the higher proportion of branches and, consequently, the greater accumulation of air in the eucalypt layer (Santos et al., 2020), as well as the hydrophobic compounds that coat its leaves, especially the wax covering the cuticle (Hua Guo et al., 2019).

Germination experiments

In controlled experiments, only the eucalypt litter biomass exhibited a restrictive power in germination rate, suggesting an allelopathic effect rather than physical (Fig. 5). However, during the experiment, a decrease in the volume of native litter was observed, attenuating the physical effect of this treatment. In contrast, in pots with eucalypt cover, there was no reduction in volume (likely due to a higher proportion of branches and the chemical composition of the leaves), supporting the hypothesis of physical restriction. The decrease in germination due to biomass was similar for both orthodox and recalcitrant species, contrary to the expected pattern (which predicted a greater decrease in germination rate for recalcitrant seeds) (Fig. 6).

The field results are consistent with those found in the controlled experiments. The germination rate significantly decreased in relation to biomass coverage, but only in the eucalypt areas (Fig. 7). However, the accumulation of litter in restored forest areas is much lower than in eucalypt plantations, supporting the hypothesis of physical restriction. Perhaps, if there were a restoration area with a large accumulation of litter, a restriction of germination would also be observed. When considering the treatments with and without litter cover, a decrease in germination was only observed in the forest restoration areas, but not in the eucalypt areas (Fig. 7.). This result indicates that the lower germination rate found in the eucalypt areas was not due to physical restriction, but rather to other causes, possibly allelopathic compounds present in the soil (not in the litter). There are other unassessed edaphoclimatic factors that may have also influenced the results, and it is not possible to attribute this effect solely to allelopathy.

Another relevant observation is that the differences between species within the physiological groups (orthodox and recalcitrant) were not considered. Although species is an influential variable, including it would add an additional level of complexity to the analyses. Seeds with higher reserve quantities, for example, would have a greater success in breaking through the physical barrier provided by the litter layer and would exhibit more vigorous seedlings (Leishman et al., 2000). However, the decision was made to use more species in order to increase the chances of germination in field experiments. In this project, only the effect of the litter layer on the germination rate was evaluated. However, it would also be very relevant, in future studies, to measure the impact of the treatments on seedling establishment.

5. Conclusion

The main objective of the project was to understand how the eucalypt litter layer interferes on the germination environment and whether its restrictive effect is due to a physical barrier caused by its accumulation in the understory or to allelopathic compounds. According to the results in controlled conditions, it can be concluded that there is a negative influence of litter biomass on seed germination, but this effect varies depending on the composition of the litter. At the same biomass levels, eucalypt litter was significantly more detrimental when compared to native litter. Due to its constitutive characteristics, eucalypt litter forms a thicker and more rigid cover at equivalent biomass cover, potentially creating a greater physical barrier to seed germination.

It is not believed that this restrictive power of eucalypt litter is superior due to allelopathic compounds because, in field conditions, the opposite was observed, with native litter producing a more intense negative effect than eucalypt litter. However, the possibility of allelopathic compounds being present in the soil cannot be ruled out, considering that in germination experiments without litter cover, the germination rate was significantly lower in the eucalypt areas. It is also possible that this lower germination on eucalypt soil is due to other unassessed edaphoclimatic factors in the project, such as soil permeability, nutritional quality, acidity, canopy openness, among others. To test this possibility, future studies can be conducted comparing germination on soils collected from different forest typologies.

With that said, it is possible to conclude that the impact of the eucalypt litter layer is due to a physical restriction caused by its greater resistance and high accumulation in the understory, rather than a physiological chemical mechanism. However, the possibility of allelopathic compounds being present in the soil (and not in the litter) cannot be ruled out, and further experiments are necessary to gather more evidence.

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