



FERNANDA LEITE CUNHA

**CARBON SEQUESTRATION AND EMISSIONS IN
BRAZILIAN PLANTED FORESTS: INTEGRATING
ECOPHYSIOLOGICAL AND LIFE CYCLE MODELING**

**LAVRAS - MG
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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do programa de Pós-Graduação em Ciência Florestais, área de concentração em Silvicultura e melhoramento genético, para a obtenção do título de Doutor.

Orientador

Prof. Dr. Otávio Camargo Campoe

Coorientadora

Prof.^a Dr. Rachel Cook

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Fernanda Leite Cunha

**SEQUESTRO E EMISSÕES DE CARBONO EM FLORESTAS PLANTADAS
BRASILEIRAS: INTEGRANDO ECOFISIOLÓGICA E MODELAGEM DO CICLO DE
VIDA**

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Dr. Otávio Camargo Campoe UFLA

Dr. Márcio Montagnana Vicente Leme UFLA

Dr. José Leonardo Gonçalves Esalq

Dr. Rafael Rubilar UdeC

Dr. Clayton Alcarde Álvares UNESP

Orientador

Prof. Dr. Otávio Camargo Campoe

Coorientadora

Prof.^a Dra. Rachel Cook

LAVRAS – MG

2025

Ao meu avô, que fez da vida um verso simples, bonito e sincero (in memoriam)

Dedico

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RESUMO

As plantações florestais são estratégicas na mitigação climática pelo sequestro e armazenamento de carbono. Contudo, há lacunas sobre seus impactos sob eventos climáticos extremos e o destino do carbono na cadeia produtiva. Esta tese teve como objetivo quantificar o balanço de carbono em plantações de *Eucalyptus* e *Pinus* no Brasil e avaliar a contribuição climática de seus produtos derivados, com foco nos produtos de papel e celulose. Para isso, foram conduzidos três estudos integrados. O primeiro avaliou os fluxos e o particionamento de carbono em plantações comerciais distribuídas ao longo de um amplo gradiente climático nacional. O segundo investigou estratégias fisiológicas de tolerância à seca por meio do particionamento de carbono em clones de *Eucalyptus* com diferentes características genéticas. O terceiro consistiu na adaptação e parametrização de um modelo de Avaliação do Ciclo de Vida (LCA), o ForestWise, para estimar emissões e estoques de carbono associados a produtos de papel provenientes de plantações brasileiras de *Eucalyptus*. Os resultados indicaram que a produção primária bruta (GPP) variou mais de cinco vezes entre os sítios avaliados, sendo a temperatura máxima o principal fator limitante da produtividade. Plantios submetidos a estresse térmico apresentaram maior alocação de carbono para o sistema radicular, em detrimento da biomassa aérea, afetando o potencial de sequestro de carbono. Clones de *Eucalyptus* classificados como tolerantes à seca (DT) demonstraram menor sensibilidade às variações climáticas em comparação aos clones de crescimento rápido (FG). No terceiro estudo, o modelo ForestWise foi aplicado para simular o ciclo de vida de produtos de papel ao longo de um período de 18 anos. Os resultados indicaram que esses produtos armazenam aproximadamente 12,7 MtC no momento em que entram no mercado. A fase industrial foi responsável por mais de 90% das emissões totais do ciclo de vida, destacando a necessidade de melhorias na eficiência energética e nos processos de produção. O estudo mostra que plantações de *Eucalyptus* e *Pinus* no Brasil têm alto potencial de sequestro de carbono, sensível ao clima e ao material genético. A inclusão dos produtos de papel via LCA evidencia seu papel como extensão do sumidouro, especialmente com reciclagem, reforçando as florestas plantadas como soluções de mitigação climática.

Palavras-chave: modelagem de carbono florestal; plantio clonal; mitigação das mudanças climáticas; produtos de floresta plantada; papel e celulose.

ABSTRACT

Planted forests are strategic for climate mitigation through carbon sequestration and storage. However, knowledge gaps remain regarding their impacts under extreme climate events and the fate of carbon along the production chain. This thesis aimed to quantify the carbon balance in *Eucalyptus* and *Pinus* plantations in Brazil and assess the climate contribution of their derived products, focusing on pulp and paper. Three integrated studies were conducted. The first evaluated carbon fluxes and partitioning in commercial plantations across a broad national climatic gradient. The second investigated physiological drought-tolerance strategies through carbon allocation in *Eucalyptus* clones with different genetic traits. The third involved adapting and parameterizing a Life Cycle Assessment (LCA) model, ForestWise, to estimate carbon stocks and emissions associated with paper products from Brazilian *Eucalyptus* plantations. Results showed that gross primary production (GPP) varied more than fivefold among sites, with maximum temperature as the main limiting factor for productivity. Plantations under thermal stress allocated more carbon to root systems at the expense of aboveground biomass, affecting sequestration potential. Drought-tolerant (DT) *Eucalyptus* clones showed less sensitivity to climate variation compared to fast-growing (FG) clones. In the third study, the ForestWise model simulated the life cycle of paper products over 18 years, showing that these products store approximately 12.7 MtC upon entering the market. The industrial phase accounted for over 90% of total life cycle emissions, highlighting the need for improved energy efficiency and production processes. Overall, *Eucalyptus* and *Pinus* plantations in Brazil have high carbon sequestration potential, sensitive to climate and genetic material. Including paper products in climate accounting via LCA underscores their role as an extension of the carbon sink, especially with recycling, reinforcing planted forests as key nature-based climate solutions.

Keywords: forest carbon modeling; clonal plantations; climate change mitigation; harvested wood products; pulp and paper

INDICADORES DE IMPACTO

Esta tese apresenta contribuições significativas com potenciais impactos tecnológicos, econômicos e ambientais no contexto da produção florestal brasileira, especialmente nas cadeias de papel e celulose. Ao integrar dados ecofisiológicos com modelagem do ciclo de vida (LCA) de produtos florestais, os resultados possibilitam uma compreensão mais precisa do papel das plantações de *Eucalyptus* e *Pinus* na mitigação das mudanças climáticas, promovendo práticas mais sustentáveis e alinhadas às exigências de neutralidade de carbono. Do ponto de vista tecnológico e produtivo, os modelos e parâmetros desenvolvidos, como o ajuste do modelo ForestWise para a realidade brasileira, podem ser incorporados por empresas do setor florestal e de papel e celulose, subsidiando tomadas de decisão mais sustentáveis e baseadas em evidências. A inclusão de informações regionais detalhadas, oriundas de redes experimentais como o TECHS, permite que gestores avaliem a produtividade e o balanço de carbono considerando os impactos das variações climáticas e da escolha genética. Isso fortalece a inovação e eficiência no setor, caracterizando impacto direto nas áreas temáticas de Tecnologia e Produção (7) e Meio Ambiente (5) da Política Nacional de Extensão. Em relação aos impactos extensionistas, o trabalho contou com parceria direta com empresas do setor florestal e instituições nacionais e internacionais, como o Instituto de Pesquisa e Estudo Florestal (IPEF), a Indústria Brasileira de árvores (IBÁ), Forest Productivity Cooperative (FPC) e a Universidade North Carolina State University (NCSU - EUA). Esses parceiros representam os principais atores da cadeia de valor da silvicultura internacional, e o conhecimento gerado já está sendo discutido com o setor privado em oficinas técnicas e eventos científicos. Dessa forma, o público externo à UFLA foi envolvido diretamente na construção e validação dos resultados, com potencial de beneficiar centenas de profissionais do setor produtivo, gestores ambientais, pesquisadores e formuladores de políticas públicas. Além disso, a pesquisa está alinhada diretamente aos Objetivos de Desenvolvimento Sustentável (ODS) da ONU, especialmente: ODS 13 (Ação contra a mudança global do clima), e ODS 12 (Consumo e produção responsáveis).

IMPACT INDICATORS

This dissertation presents significant contributions with potential technological, economic, and environmental impacts within the context of Brazilian forest production, particularly in the pulp and paper value chains. By integrating ecophysiological data with Life Cycle Assessment (LCA) modeling of forest-based products, the results provide a more accurate understanding of the role of *Eucalyptus* and *Pinus* plantations in climate change mitigation, promoting more sustainable practices aligned with carbon neutrality goals. From a technological and productive standpoint, the models and parameters developed, such as the adaptation of the ForestWise model to the Brazilian context, can be incorporated by forestry and pulp and paper companies, supporting more sustainable and evidence-based decision-making. The inclusion of detailed regional information, sourced from experimental networks such as TECHS, enables managers to evaluate productivity and carbon balance while considering the impacts of climate variation and genetic selection. This strengthens innovation and efficiency in the sector, representing a direct impact within the thematic areas of Technology and Production (7) and Environment (5) of the Brazilian National Extension Policy. Regarding extension-related impacts, the work involved direct collaboration with national and international forestry companies and institutions, such as the Institute for Forestry Research and Studies (IPEF), the Brazilian Tree Industry (IBÁ), the Forest Productivity Cooperative (FPC), and North Carolina State University (NCSU – USA). These partners represent key stakeholders in the global forest value chain, and the knowledge generated is already being discussed with the private sector through technical workshops and scientific events. Thus, audiences beyond UFLA were directly engaged in the development and validation of the results, with the potential to benefit hundreds of professionals in the production sector, environmental managers, researchers, and policy makers. Furthermore, this research is directly aligned with the United Nations Sustainable Development Goals (SDGs), particularly SDG 13 (Climate Action) and SDG 12 (Responsible Consumption and Production).

LISTA DE SIGLAS

AIC / AICc	Akaike Information Criterion
ANAP	National Association of Paper Apparatus
ANPP	Aboveground Net Primary Production
BEF	Biomass Expansion Factor
BEPP	Brazilian <i>Eucalyptus</i> Productivity Program
C	Carbon
CAD	Available Water Capacity
CG	Clonal Group
CL	Carbon Stock in the Litter Layer
CO ₂	Carbon Dioxide
CR	Root Dry Mass Increment
CS	O Horizon Mass Change and Stump Decomposition
DT	Drought-Tolerant
DOCf	Degradable Organic Carbon Fraction
EPA	Environmental Protection Agency
EUCFLUX	Cooperative Program on Productivity and Carbon and Water Fluxes in <i>Eucalyptus</i>
FA	Aboveground Litterfall
FG	Fast-Growing
FNPP	Foliage Net Primary Production
FPC	Forest Productivity Cooperative
GAM	Generalized Additive Model
GHG	Greenhouse Gases
GLMM	Generalized Linear Mixed Model
GPP	Gross Primary Production
IBÁ	Brazilian Tree Industry
IPEF	Institute of Forestry Research and Studies
IPCC	Intergovernmental Panel on Climate Change
LAI	Leaf Area Index
LCA	Life Cycle Assessment
ForestWise	Forest Wood Inventory, Storage, and Emissions Model
MAI	Mean Annual Increment
MAPE	Mean Absolute Percentage Error
NCSU	North Carolina State University
NEP	Net Ecosystem Productivity
ODS / SDGs	Sustainable Development Goals

AIC / AICc	Akaike Information Criterion
PET	Polyethylene Terephthalate
PPPIB	Cooperative Program on Pinus Productivity in Brazil
PVC	Polyvinyl Chloride
R	Root-to-Shoot Ratio
R ²	Coefficient of Determination
Ra	Aboveground Tree Respiration
RH	Relative Humidity
Rf	Foliage Dark Respiration
Rw	Wood CO ₂ Efflux
RW20	Region Wide 20 Project
SLA	Specific Leaf Area
TBCF	Total Belowground Carbon Flux
TECHS	Tolerance of <i>Eucalyptus</i> Clones to Hydric, Thermal and Biotic Stresses
Tmean, Tmax, Tmin	Mean, Maximum and Minimum Air Temperature
UFLA	Federal University of Lavras
UNESP	São Paulo State University “Júlio de Mesquita Filho”
WD	Water Deficit
WNPP	Wood Net Primary Production

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FISRT PART

1 INTRODUCTION

In recent decades, scientific evidence on global warming has become increasingly compelling (ABBASS *et al.*, 2022). Between 2011 and 2020, the global average temperature was 1.1 °C above pre-industrial levels, and extreme weather events have become more frequent and intense (WARREN *et al.*, 2024). The scientific community warns that, without the urgent implementation of structural measures, the 1.5 °C target set by the Paris Agreement may be exceeded as early as 2036 (CHILTON *et al.*, 2025).

Rising temperatures, combined with reduced water availability in several tropical regions, threaten the growth and biomass accumulation of forest species (CAMPOE *et al.*, 2020). In commercial *Eucalyptus* plantations, for instance, there is evidence that productivity may be reduced by up to two-thirds in regions experiencing severe water deficits compared to more favorable sites (ELLI *et al.*, 2020; GONÇALVES, JOSÉ LM *et al.*, 2017). This scenario becomes even more concerning as forest expansion increasingly takes place in areas with higher climatic risk, marginal soils, and growing competition with the agricultural sector (ALVARES and MAFIA, 2023; GONÇALVES *et al.*, 2013).

To more accurately assess the real climate impact of actively managed planted forests, it is essential to account for the total carbon balance of the forest stand (CAMPOE *et al.*, 2020; MATTHEWS *et al.* 2023), including all management activities and post-harvest carbon flows (MATTHEWS *et al.*, 2023; PULS *et al.*, 2024). Carbon movement within forests is primarily driven by the assimilation of carbon dioxide through photosynthesis (Gross Primary Production – GPP), part of which is allocated to biomass production in different tree compartments (Net Primary Production – NPP), as well as to symbiotic organisms, mycorrhizae, and respiration (RODRIGUES; SILVA; NOUVELLON, 2021).

There are different methodologies for monitoring the carbon balance in forest ecosystems, each with its own specificities and limitations (LANDSBERG *et al.* 2001; LITTON; RAICH; RYAN, 2007; BINKLEY; RYAN, 2004). The most commonly used method is based on the concept of functional equilibrium between carbon inputs and outputs in forests, tracking growth through destructive sampling of individuals in the field and quantifying both above- and belowground carbon stocks (LITTON; RAICH; RYAN, 2007). In this approach, Gross Primary Production (GPP) is estimated as the sum of aboveground

Net Primary Production (ANPP: including leaf, branch, bark, and wood production), total belowground carbon flux (TBCF: encompassing carbon allocated to coarse and fine root production and respiration, root exudates, and substrates used by mycorrhizae), and aboveground autotrophic respiration (Ra), measured using respiration chambers (GIARDINA e RYAN, 2002; RYAN et al., 2004).

Understanding carbon partitioning is essential for accurately estimating forest productivity. Over the past decades, numerous studies have been conducted on *Eucalyptus* and *Pinus* species (CAMPOE *et al.*, 2020; DELIBERARI, 2015; DRAKE *et al.*, 2019; ELLI *et al.*, 2020; LITTON; RAICH; RYAN, 2007; STAPE, JOSE LUIZ *et al.*, 2010). The main findings indicate that, under elevated temperature conditions, forest plantation productivity tends to increase; however, under resource-limited stress conditions, such as water and nutrient scarcity, trees allocate a greater proportion of carbon belowground as a growth strategy (CAMPOE *et al.*, 2020; LITTON; RAICH; RYAN, 2007). Temperature is a key climatic variable that influences tree physiology, including photosynthesis, respiration, and growth, and thus affects carbon allocation patterns (WAY e OREN, 2010). According to (QUEIROZ et al., 2023), the optimal growth temperature for hybrid *Eucalyptus* plantations is approximately 20 °C, with reduced growth observed at both higher and lower temperatures.

The effects of drought on forest plantations are a growing concern, particularly in the context of climate change, which is increasing the frequency and severity of such events (JUMP *et al.*, 2017). Studies on *Eucalyptus* clones across different climatic conditions have shown that under water stress, carbon uptake is reduced and allocation shifts toward belowground compartments (Campoe et al., 2020). Although increased root investment during drought is generally expected, carbon allocation responses can be more complex and context-dependent (DRAKE *et al.*, 2019). Furthermore, the combined effects of drought and rising temperatures may exacerbate physiological stress, intensifying water loss and increasing the risk of tree mortality (ALLEN *et al.*, 2010).

Silvicultural practices such as planting density and fertilization significantly influence carbon flux and partitioning patterns throughout the production cycle. Planting density regulates competition for resources such as water, light, and nutrients, directly affecting CO₂ uptake and the allocation of photoassimilates (Gonçalves et al., 2013; Ryan et al., 2010; Stape et al., 2010). Studies have shown that denser spacing can lead to higher GPP during the early years of rotation, although it does not necessarily result in consistent changes in above- and

belowground carbon partitioning (CAMPOE *et al.*, 2020; RODRIGUES; SILVA; NOUVELLON, 2021). Fertilization, in turn, tends to reduce carbon allocation to roots under conditions of greater nutrient availability (DELIBERARI, 2015; STAPE, JOSE LUIZ; BINKLEY; RYAN, 2008). In more productive environments, the combination of irrigation and fertilization can more than double GPP, as observed in *Pinus taeda* plantations in the southeastern United States (MAIER *et al.*, 2004), highlighting the central role of management in modulating productivity and carbon balance in forest plantations.

In addition, drought-tolerant genetic materials such as the clones *Eucalyptus grandis* × *E. camaldulensis* (C3) and *E. urophylla* × *E. brassiana* (P7) exhibit greater belowground carbon allocation at the expense of carbon allocation to wood production, when compared to other high-yielding clones such as *E. urophylla* (CAMPOE *et al.*, 2020). The resilience of forest plantations in environments exposed to water and heat stress is strongly associated with both adaptive (genetic) and acclimatory (climatic gradient) strategies adopted by different genetic materials (SERRAJ; SINCLAIR; PURCELL, 2012). Drought-tolerant clones tend to invest more energy in developing survival strategies under water stress than in biomass production. These clones typically prioritize survival mechanisms, such as increased allocation of carbon to fine and deep roots (BASÍLIO *et al.*, 2024; CAMPOE *et al.*, 2020), higher stomatal density (PECH, 2024) more efficient stomatal control (SANTOS *et al.*, 2024), and leaf angles that minimize direct solar exposure during the most critical hours of the day (DE MATTOS *et al.*, 2020). These traits enable access to deeper water reserves and confer greater resistance to severe water deficits (HUBBARD *et al.*, 2020). On the other hand, fast-growing clones prioritize carbon allocation to aboveground biomass, which maximizes productivity under favorable conditions but makes them more vulnerable to climatic variability (BINKLEY *et al.*, 2020; CAMPOE *et al.*, 2020). This vulnerability is further influenced by site conditions, particularly the position relative to the water table. In landscapes where groundwater is deep and less accessible, fast-growing clones face chronic water deficits, reduced productivity, and increased mortality during dry years (STAPE and ALVARES, 2024). These effects highlight the importance of considering water availability in clone-site matching strategies.

This contrast highlights an important trade-off between productivity and stress tolerance, with direct implications for the productivity and sustainability of forest plantations (BINKLEY *et al.*, 2020). The balance between growth and resilience influences the potential

for Net Ecosystem Production (NEP), especially in regions where water limitation is expected to worsen due to climate change (CAMPOE *et al.*, 2020; STAPE, JOSE LUIZ; BINKLEY; RYAN, 2008). High-yielding clones tend to accumulate more biomass over time and, consequently, exhibit greater NEP compared to drought-tolerant clones (CAMPOE *et al.*, 2020).

NEP is defined as the net change in carbon stored within an ecosystem over a given time period and is calculated as the difference between Gross Primary Production (GPP) and ecosystem respiration. When NEP is negative, the ecosystem emits carbon to the atmosphere; when positive, it functions as a carbon sink, absorbing atmospheric carbon through photosynthesis. *Eucalyptus* plantations in Brazil exhibit rapid growth and quickly become carbon sinks, with high carbon uptake rates (BINKLEY *et al.*, 2020). Guillemot *et al.* (2019), through an eddy covariance study, using a flux tower, in *Eucalyptus* plantations in the state of São Paulo, observed that within three years the plantations had established themselves as strong carbon sinks, absorbing an average of 19.2 Mg C ha⁻¹ yr⁻¹.

In addition to on-site monitoring of carbon fluxes in forest plantations, it is essential to consider the emissions associated with other stages of the production cycle, particularly those related to harvesting, processing, and the end-of-life of wood products (PULS *et al.*, 2024). Life Cycle Assessment (LCA) emerges in this context as a robust methodology for quantifying environmental impacts throughout the entire life cycle of forest products, from raw material extraction to product end-of-life (CHANG; LEE; CHEN, 2014; ISO, 2006). Regulated by ISO standards 14040 and 14044 (ABNT, 2009), LCA enables the integration of carbon emissions and stocks both within and beyond the ecosystem (in situ and ex situ), providing a comprehensive view of the carbon balance in the forestry sector (FINKBEINER *et al.*, 2006; SAHOO *et al.*, 2019).

The inclusion of Harvested Wood Products (HWPs) in carbon balance estimates has advanced significantly in recent decades, reflecting their growing recognition as a relevant component of climate mitigation strategies. The Intergovernmental Panel on Climate Change (IPCC) first acknowledged the carbon storage potential of HWPs in its 1996 guidelines, later revised in the 2006 Guidelines and the 2013 Supplementary Methods (IPCC, 2006; 2013). Beginning with the 17th Conference of the Parties (COP17), carbon stocks in HWPs were officially accepted as part of national contributions toward emission reduction commitments under the United Nations Framework Convention on Climate Change (UNFCCC) (PULS *et*

al., 2024). In parallel, the United States Environmental Protection Agency (EPA) adopted the methodology developed by Skog (2008) to estimate HWP carbon stocks in its national greenhouse gas inventories, which is now incorporated into the EPA's regular assessment processes (EPA, 2023; LOEFFLER *et al.*, 2014).

HWPs provide additional mitigation benefits by extending the retention time of carbon originally sequestered by forests, reducing emissions along the value chain, and enabling the substitution of fossil fuel-intensive materials such as cement and steel (LESKINEN *et al.*, 2018; MATTHEWS *et al.*, 2023). However, despite this progress, many models still overlook the interactions between forest carbon flows and the industrial end-uses of wood, which can limit the accuracy of mitigation projections. Recent studies, such as (PULS *et al.* 2024), highlight the importance of integrating both in situ and ex situ carbon stocks across specific value chains. The authors found that in the U.S. South, pulp and paper products derived from *Pinus* plantations can account for up to 63% of harvested wood product carbon stocks in the year the products enter the market, with the main carbon pool concentrated in product end-of-life, particularly in landfills.

In this context, paper and pulp products produced in Brazil exhibit a high potential for carbon storage throughout their life cycle. According to the Brazilian Tree Industry (IBÁ, 2024), Brazil has approximately 10 million hectares of planted forests, with 2.8 million hectares allocated to pulp and paper production. These plantations, primarily composed of *Eucalyptus* (76%) and *Pinus* (19%) species, have the highest forest productivity in the world, averaging $33 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$, which contributes to an estimated carbon stock of 1.82 GtCO₂eq. Life Cycle Inventory (LCI) analysis of pulp products demonstrates that the carbon fixed in plantations can be retained for extended periods in short- and medium-lived products, contributing significantly to the sector's climate balance (PULS *et al.* 2024). Thus, in addition to capturing carbon during forest growth, the pulp and paper sector plays a strategic role in prolonging carbon retention time, enhancing the climate benefits associated with planted forests in Brazil.

Given this scenario, integrating ecophysiological approaches with Life Cycle Assessment (LCA) becomes essential to fully understand the carbon cycle, from the sequestration mechanisms in plantations to the end-of-life of wood-derived products. Understanding tree growth strategies, biomass allocation, and responses along climatic gradients allows for improved forest management and greater efficiency in carbon

sequestration at the base of the production chain (Campoe et al., 2020). Brazil, with its broad latitudinal range and diverse edaphoclimatic conditions, offers a great opportunity for this type of integrated investigation.

This study aimed to quantify the total carbon balance in *Eucalyptus* and *Pinus* plantations in Brazil by integrating data from various ecophysiological studies conducted across distinct climatic gradients. Additionally, we sought to extend this analysis beyond the forest ecosystem by incorporating the Life Cycle Assessment approach applied to pulp and paper products, in order to identify the main carbon stock and emission compartments throughout the entire value chain, from plantation establishment to product end-of-life.

Specific objectives

Paper 1:

- (1) Characterize the amplitudes of carbon fluxes and partitioning between genera to be used as parameters for ecophysiological models;
- (2) Characterize the amplitudes of carbon fluxes and partitioning between different management practices in Brazil;
- (3) Characterize the amplitudes of carbon fluxes and partitioning between different temperature gradients, and different water deficits;
- (4) Evaluate the carbon sequestration potential of *Eucalyptus* and *Pinus* plantations in Brazil through Net Ecosystem Productivity (NEP) and investigate how climatic conditions, management, and age influence the values of this variable.

Paper 2:

- (1) Which carbon allocation strategy is adopted by drought-tolerant and fast-growing clones?
- (2) What is the interaction between clonal groups when submit to different temperature gradients and water deficit;
- (3) How does increased temperature and water deficit influence gross primary production (GPP) and carbon partitioning?

Paper 3

- (1) Adjust and parameterize the HWP life cycle model (Puls et al., 2024), which uses elements of the Life Cycle Assessment, developed for the Southern United States, for paper and pulp products, produced from *Eucalyptus* forests in Brazil;
- (2) Provide a comprehensive analysis of C fluxes from paper and pulp sector in Brazil, assessing their contribution to atmospheric C removal and emissions.

Hypotheses

Paper 1:

- (1) The range of carbon fluxes of *Eucalyptus* is higher than *Pinus*;
- (2) Management practices that favor nutrient availability increase carbon partitioning to wood net primary production (WNPP) at the expense of root system growth (TBCF);
- (3) C fluxes decrease when the stands are under water and thermal stress, favoring partitioning belowground;
- (4) NEP is directly related to the growth potential of plantations; in other words, the greater the water and thermal stress, the lower the carbon sequestration potential.
- (5) NEP tends to decrease with age.

Paper 2

- (1) The drought-tolerant clonal group allocates more carbon to root growth than to wood production, compared to fast-growing clones;
- (2) expect that FG are more sensitive to climate variation, while the DT clone presents less variation in C partition;
- (3) Increased temperature and water deficit decrease GPP and increase C partitioning to root growth at the expense of wood production.

Paper 3

- (1) Brazilian forestry sector plays a strategic yet underestimated role in global climate mitigation, significantly contributing to sustainability goals and the development of nature-based solutions.

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SECOND PART - PAPERS

The papers were written in accordance with the guidelines of the journals to which they were submitted.

Paper 1: Carbon fluxes and partitioning in *Eucalyptus* and *Pinus* plantations across a climatic gradient in Brazil

Submitted to agricultural and forest meteorology

Fernanda Leite Cunha^{1*}, Otávio Camargo Campoe¹, Cléber Rodrigo de Souza¹, Isaira Leite & Lopes¹, Yann Nouvellon², Timothy Albaugh³, David R. Carter³, Rafael Rubilar^{4,5}, Isabel Deliberari⁶, Rachel Cook⁷, Joannès Guillemot², Guerric Le Maire², Jean-Paul Laclau², Jose Luiz Stape⁶, Clayton Alcarde Alvares^{8,9}

^{1*} Department of Forestry Sciences, Federal University of Lavras (UFLA), Lavras 37200, Brazil

² Eco&Sols, University of Montpellier, CIRAD, INRA, IRD, Montpellier, SupAgro, Montpellier, France

³ Virginia Tech Department of Forest Resources and Environmental Conservation, 228 Cheatham Hall, Blacksburg, VA 24061.

⁴ Cooperativa de Productividad Forestal. Departamento de Silvicultura, Facultad de Ciencias Forestales, Universidad de Concepción. Victoria 631, Casilla 160-C, Concepción, Chile

⁵ Centro Nacional de Excelencia para la Industria de la Madera (CENAMAD) - ANID BASAL FB210015, Pontificia Universidad Católica de Chile, Santiago, Chile.

⁶ Department of Forestry Sciences, “Luiz de Queiroz” College of Agriculture, São Paulo State University, Piracicaba, SP, 13418-900, Brazil

⁷ Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

⁸ Department of Forestry Sciences, São Paulo State University “Júlio Mesquita Filho” (UNESP), Botucatu 18600, Brazil

⁹ Suzano SA, Limeira 13473, Brazil

* Correspondence: fernandaleitecunha@gmail.com, Tel.: +55-31-9-99450-1613, ORCID: 0000-0001-7707-0910

Highlights

- 1) Maximum temperature is strongly correlated with Carbon (C) dynamics in Brazil
- 2) Under climatic stress conditions, plants allocate more C to TBCF at the expense of WNPP.
- 3) Spacing had a greater influence on C balance than planting fertilization
- 4) Brazilian forests have a high potential for C storage, with NEP $\sim 1787 \text{ g C m}^{-2}$

Abstract

Brazilian *Eucalyptus* and *Pinus* forests are the most productive forests worldwide. The growth rates of these intensively managed plantations depend strongly on environmental conditions and matching genotypes to local environments. Changing climates underscore the value of understanding the intricacies of how these plantations can fix high amounts of carbon (C) and grow so much wood. We measured the full C budgets of *Eucalyptus* and *Pinus* forests across climate gradients in Brazil, focusing on the rates of C uptake, the allocation of C to belowground roots and mycorrhizae, and stem growth. Carbon balance was estimated using a destructive biomass sampling approach to quantify total above- and belowground carbon stocks. We found that gross primary production (GPP) varied more than fivefold across the climate conditions in Brazil. The annual mean of maximum temperature was the main climatic driver of productivity, where extreme temperatures reduced fluxes to stem production while increasing fluxes to root production. Net ecosystem production varied with management and age across the sites. The ecophysiological investigation presented in this work is fundamental for understanding C partitioning behavior under extreme temperature conditions. In this way, our results provide tools for forest managers to support their decision-making processes as well as starting points for strategies to be implemented in projects aimed at mitigating the effects of climate change.

Keywords: Gross primary production, Carbon sequestration, Carbon allocation, Belowground allocation, Wood productivity, Thermal stress

1 Introduction

Climate changes caused by anthropic action have imposed a series of novel environmental conditions and challenges. Recent research based on simulations with different large-scale climate models suggests significant changes in air temperature ranges and an increase in the seasonality of rainfall distribution in the future (Almazroui et al., 2021). Nature-based solutions (NBSs), including forest plantations for timber production or restoration purposes, have the potential to mitigate the effects of climate change by reducing the atmospheric concentration of CO₂ (Brancalion et al., 2019). Reforestation with native species is a natural solution to sequester CO₂ and contribute to mitigating the negative effects of climate change (Andres et al., 2023). Similarly, forest plantations, which typically utilize non-native species, also have potential in carbon credit compensation projects (Brazilian tree industry - IBÁ, 2023; Sanquetta et al., 2011). In order to better measure the real climate

impact of planted forests, it is necessary to understand the total C balance of the forest stand, including all management activities, as well as the life cycle of C in forest products and by-products (Matthews et al., 2023; Van Der Gaast et al., 2018). These conditions justify the development of carbon balance and modeling studies for planted forests under different climate scenarios (Campoe et al., 2020; Van Der Gaast et al., 2018).

According to Brazilian Tree Industry - IBÁ, (2023) there are 9.93 million hectares of *Eucalyptus* and *Pinus* plantations in Brazil, which store an average of 1.82 Gt CO₂ equivalent annually. Despite the recognized potential of these plantations as a climate mitigation tool, there is a gap in understanding how much carbon can be captured in monoculture plantations. The lack of concrete data on the carbon stock potential of plantation forestry has led to uninformed and, consequently, controversial interpretations about planted forests and their contribution to carbon sequestration.

Net Ecosystem Production-NEP is a good measure of the total amount of carbon retained by the system over a given measurement period (Catovsky et al., 2002). NEP is defined as the net amount of carbon retained within plant biomass and is calculated as the total carbon fixed by vegetation (Gross Primary Productivity, GPP) minus plant respiration and soil respiration. Soil respiration includes a combination of autotrophic respiration from roots and associated mycorrhizae, as well as heterotrophic respiration from microorganisms that utilize root exudates and organic material Bond-Lamberty et al., (2004), Maier et al., (2004) and Verlinden et al., (2013). NEP theoretically tends to reach its maximum value near canopy closure, when the ratio of leaf biomass to wood biomass is higher (Gower et al., 1994). The time it takes for a planted forest to transition from being a carbon source to a carbon sink depends on climatic conditions, forest age, genetic growth potential, management practices, and environmental conditions (Law et al., 2001). Guillemot et al. (2019) observed that *Eucalyptus* plantations in Brazil achieve a positive NEP after 19 months, indicating that all carbon emitted through the decomposition of organic matter in the initial months is offset. By the third year, these plantations are firmly established as significant carbon sinks, absorbing an average of 19.2 Mg C ha⁻¹ yr⁻¹.

The capacity of a forest to store carbon is directly influenced by the growth potential of the genetic material, environmental and climatic conditions (Campoe et al., 2020), and as well as to very specific site conditions like physiographic positions that offer water table access to trees growth (Stape and Alvares, 2025). According to Martins et al. (2022) if

temperatures increase by 1.5°C to 2.0°C, *Eucalyptus* cultivation may be significantly reduced or restricted to a few regions in Brazil, specifically the southernmost and southeastern areas. This would have important consequences for the *Eucalyptus* production chain and its role as a carbon sink.

One way to understand the growth patterns of trees is through studies of carbon balance, which include carbon flux (the rate at which carbon moves between specific tree components) and carbon partitioning (the allocation of carbon to a given component as a fraction of gross primary production (GPP) (Ryan et al., 2010). Studies in this context provide significant and necessary gains into carbon partitioning among different tree components, including aboveground net primary productivity (ANPP) and belowground flux, such as total belowground carbon flux (TBCF) (Litton et al., 2007). Thus, over the last few decades, several studies have investigated C balances in *Eucalyptus* and *Pinus* plantations (Campoe et al., 2020; Deliberari, 2015; Drake et al., 2019; Elli et al., 2020; Litton et al., 2007; Ryan et al., 2010; Stape et al., 2008). These studies obtained important results, e.g., under conditions of mild temperatures without water restriction, there is an increase in the productivity of forest plantations; however, with limited water and nutrients, the trees increase carbon partitioning to TBCF, as a growth strategy (Campoe et al., 2020; Litton et al., 2007).

Despite significant advances in the literature, gaps remain regarding the responses of *Eucalyptus* and *Pinus* to varying environmental conditions, underscoring the need for studies that explore genotype x environment interactions and resource availability across different climatic gradients. Studies on the integration of carbon balance data are scarce, e.g., Litton et al. (2007) reported low sampling in tropical locations. In contrast, Campoe et al. (2020) achieved considerable gains in understanding the C balance in *Eucalyptus* plantations in Brazil, however, they just sampled plantations at mid-rotation (aged 22-33 months) and did not sample sites in southernmost Brazil or frost-tolerant clones. Understanding and modeling the response of the main genetic materials planted in Brazil to potential variations in temperature and water deficit in the current climate change scenario is essential for predicting changes in forest productivity and determining the true potential contributions of productive plantations in carbon sequestration (Bukoski et al., 2022; Campoe et al., 2020). Moreover, understanding carbon partitioning strategies in productive forests under different climatic scenarios is crucial for developing management strategies and creating effective sustainable programs and policies to achieve productivity and carbon sequestration goals (Rubilar et al.,

2024). In addition, knowledge of carbon partitioning is essential for accurately estimating forest production through process-based modeling, which involves simulating physiological processes that influence growth and understanding how these processes are influenced by the environment (Elli et al., 2020).

The scope of this study encompasses integrating the results of different C balance studies of the *Eucalyptus* and *Pinus* genera in Brazil to evaluate the C flux and partitioning patterns for the major genotypes planted in Brazil under different silvicultural treatments and climatic stress conditions. Our specific objectives were to (1) Characterize the amplitudes of carbon fluxes and partitioning between genera to be used as parameters for ecophysiological models (2) different management practices in Brazil, (3) different temperature gradients, and different water deficits; and (4) To evaluate the carbon sequestration potential of *Eucalyptus* and *Pinus* plantations in Brazil through Net Ecosystem Productivity (NEP) and investigate how climatic conditions, management, and age influence the values of this variable. We hypothesize that (1) the range of carbon fluxes of *Eucalyptus* is higher than *Pinus*; (2) management practices that favor nutrient availability increase carbon partitioning to wood net primary production (WNPP) at the expense of root system growth (TBCF); (3) C fluxes decrease when the stands are under water and thermal stress, favoring partitioning belowground; and (4) we hypothesize that NEP is directly related to the growth potential of plantations; in other words, the greater the water and thermal stress, the lower the carbon sequestration potential. (5) Additionally, NEP tends to decrease with age.

2 Materials and methods

2.1 Dataset

We compiled a dataset with 377 observations that included carbon balance from five independent experiments conducted at 12 different locations from northeast to south Brazil, covering contrasting climate conditions in the country (Fig. 1). During the experiments, the mean annual temperatures of the sites ranged from 17 to 27.3 °C and the average annual rainfall from 713 to 1572 mm. Each experiment had one or several specific silvicultural treatments, such as planting density, uniformity, fertilization, and water availability (details can be found in the references listed in Table 1).

Table 1: Location, climatic characteristics, age, and management of the different stands included in this study

Genus	Local Code	City and State	Lat., Long.	Köppen classification	Tmean (°C)	Rainfall (mm yr ⁻¹)	Age (months)	Fertility	Water Availability	Spacing	Uniformity	N	Project	Reference
E	S1	Urbano Santos, Maranhão	-3.4, -43.1	As	27.3	1461	22–36	TF	R, TE	3x3	U	14	TECHS	(Campoe et al., 2020).
E	S2	Teixeira de Freitas, Bahia	-17.5, -39.7	Af	25.3	1040	36–48	TF, SF	R, I	3x3	U, H	48	BEPP	(Ryan et al., 2010)
E	S3	Eunápolis, Bahia	-16.4, -39.6	Aw	23.2	1100	23–60	TF, SF	R, I	3x3	U, H	80	BEPP	(Ryan et al., 2010)
E	S4	Bocaiúva-Minas Gerais	-17.3, -43.8	As	23.3	713	22–33	TF	R, TE	3x3	U	14	TECHS	(Campoe et al., 2020).
E	S5	Aracruz, Espírito Santo	-19.4, -39.4	Am	23.4	1140	23–57	TF, SF	R, I	3x3	U, H	22	BEPP	(Ryan et al., 2010)
E	S6	Mogi Guaçu, São Paulo	-22.4, -47	Cwa	21.6	1320	22–60	TF, SF	R, I	3x3	U, H	80	BEPP	(Ryan et al., 2010)
E	S7	Mogi Guaçu, São Paulo	-22.4, -47	Cwa	22.1	1097	20–31	TF	R, TE	3x3	U	16	TECHS	(Campoe et al., 2020).

E	S8	Itatinga, São Paulo	-23, - 48.7	Cwa	19.2	1391	69–81	TF	R	3x2	U	12	EucFlux	Campoe et al. (2013)
E	S9	Telêmaco Borba, Paraná	-24.2, -50.5	Cwb	19.6	1492	20–31	TF	R, TE	3x3	U	16	TECHS	(Campoe et al., 2020).
E	S10	Otacílio Costa, Santa Catarina	-27.5, -50.1	Cfb	17	1520	63–75	TF	R, TE	3x3	U	8	TECHS	Not published
P	S11	Itatinga, São Paulo	-23.1, -48.6	Cwa	19.4	1319	77–101	TF, NF	R, I	3x2	U	32	PPPIB	(Deliberari, 2015)
P	S12	Rio Negrinho, Paraná	-26.3, -49.8	Cfb	18.3	1572	89–115	TF	R	2.4x6.8/ 2.4x2.2	U	33	RW20	(Hincapie, 2020)

Note: Lat., long.: latitude (south) and longitude (west) of the site; Aw: tropical savanna climate with dry winters; As: tropical savanna climate with dry summers; Af: tropical rainforest climate; Am: tropical monsoon and trade-wind littoral climate; Cfb: temperate oceanic climate or subtropical highland climate; Cwa: monsoon-influenced humid subtropical climate; Cwb: subtropical highland climate or temperate oceanic climate with dry winters. Tmean: mean annual temperature; TF: traditional fertilization - the traditional fertilization regime that represents the current operational best practices for *Eucalyptus* and *Pinus* and varies by site based on the current operations of each company.; SF: super fertilization - a non-limiting fertilization regime was applied quarterly throughout the study; I: irrigated - water from a well or nearby stream was applied weekly if needed to maintain soil water near field capacity; R: rainfall, subjected to rainwater; TE: throughfall exclusion - rainfall was reduced by about 30% with under-canopy troughs, details can be found in (Campoe et al., 2020); U: uniform planting - trees in each plot were planted on the same day; H: heterogeneous planting - trees in each plot were planted in three stages, each spaced 40 days apart; N: number of samples; TECHS: cooperative project Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses; BEPP: Cooperative Program on Potential *Eucalyptus* Productivity in Brazil; Eucflux: Cooperative Program on Productivity and Carbon and Water Fluxes in *Eucalyptus*; PPPIB: Cooperative Program on *Pinus* Research in Brazil.

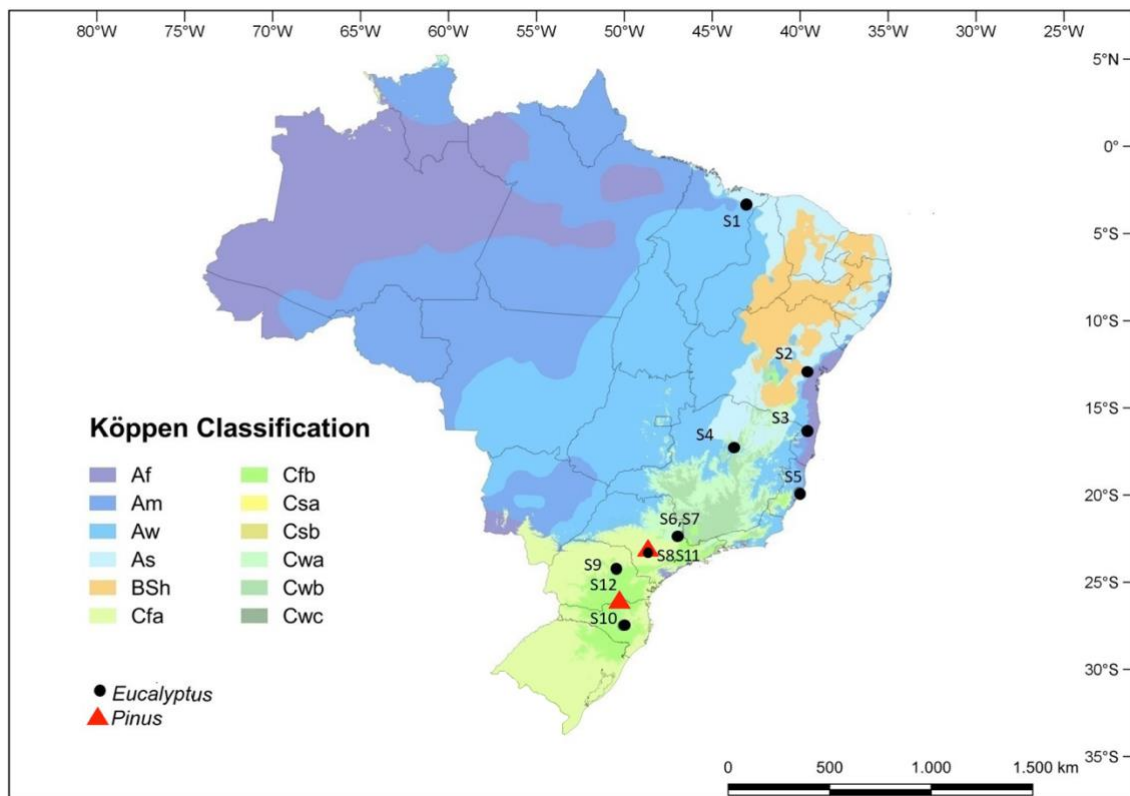


Fig. 1: Spatial distribution of the study sites in Brazil and its climate gradient.

The carbon balance dataset covers a total of 12 different genetic materials of *Eucalyptus* (10) and *Pinus* (2) (Table 2). The age of the *Eucalyptus* and *Pinus* stands ranged from 13 to 75 months and from 77 to 105 months, respectively.

Table 2: Species or genotypes of *Eucalyptus* and *Pinus* used in this study.

Code	Species/ Genotype	Origin*	Climate of the origin region of the clone	Site	N
PT1	<i>P. taeda</i>	Clonal	Subtropical	S12	3
PT2	<i>P. taeda</i>	Clonal	Subtropical	S12	9
PT3	<i>P. taeda</i>	Clonal	Subtropical	S12	9
PT4	<i>P. taeda</i>	Clonal	Subtropical	S12	3
PTO	<i>P. taeda</i>	Seed	Subtropical	S12	9
PC	<i>P. taeda</i>	Seed	Subtropical	S11	16
PT5	<i>P. caribaea</i> var. <i>hondurensis</i>	Seed	Tropical	S11	16
E1	<i>Eucalyptus grandis</i>	Seed	Tropical	S8	12
E2	<i>E. grandis</i> x <i>urophylla</i>	Clonal	Tropical	S5	22
E3	<i>E. grandis</i> x <i>sp</i>	Clonal	Tropical	S6	80
E4	<i>E. urophylla</i>	Clonal	Tropical	S3	80
E5	<i>E. grandis</i>	Clonal	Tropical	S2	48
K2	<i>E. saligna</i>	Clonal	Tropical	S1, S4, S7, S9	10
A1	<i>E. urophylla</i>	Clonal	Tropical	S1, S4, S7, S9, S10	17
P7	<i>E. urophylla</i> x <i>E. brassiana</i>	Clonal	Tropical	S1, S4, S7, S9	14
C3	<i>E. grandis</i> x <i>E. camaldulensis</i>	Clonal	Tropical	S1, S4, S7, S9	8
B2	<i>E. grandis</i> x <i>E. urophylla</i>	Clonal	Tropical	S1, S4, S7, S9	14
I9	<i>E. dunnii</i>	Clonal	Subtropical	S10	2
E12	<i>E. benthamii</i>	Clonal	Subtropical	S10	1
J1	<i>E. benthamii</i>	Clonal	Subtropical	S10	2

* seedlings obtained through seed or through vegetative propagation (clonal).

2.2. Estimation of the Carbon Balance

The carbon balance in each experiment was quantified using techniques described in Giardina and Ryan (2002) and Ryan et al. (2004), and all details of the data collected can be found in the Table 1 references. Each flux and carbon partitioning value were measured at least every 2 years and expressed as $\text{g C m}^{-2} \text{ yr}^{-1}$ (Table 3); the detailed methods are presented in Table 3. The partitioning was calculated as the ratio between a specific carbon flux (WNPP, ANPP, TCBF, and Rag) and GPP.

Table 3: Carbon balance variables and the methodology used for calculation.

Variable	Definition	Methodology
TBCF	Total belowground carbon flux	Estimated based on measurements of soil CO ₂ efflux (FS). Variation in soil C and losses of C through leaching or erosion (FE) were considered negligible (Giardina & Ryan, 2002; Ryan et al., 2004). Aboveground litterfall (foliage, branches, bark, flowers, cones and fruits) (FA). O horizon mass change and decomposition of stumps from the previous rotation (CS). Root dry mass increment (CR). Variation in C stock in the litter layer at the soil surface (CL). The TBCF (g C m ⁻² yr ⁻¹) was calculated as follows: TBCF = FS + FE – FA + CS + CR + CL.
WNPP	Wood net primary production	Estimated as the annual production of wood biomass, which was calculated from tree diameter measurements using site and species-specific allometric equations; trees were sampled in two different years to estimate diameter changes. Clone and site-specific dry mass equations were applied to the annual measurements, and then dry mass was converted into carbon (Campoe et al. 2020).
FNPP	Foliage net primary production	Estimated from leaf area index which was converted into dry mass using specific leaf area, plus foliage litterfall.
ANPP	Aboveground net primary production	Estimated as the sum of WNPP and FNPP.
Ra	Aboveground tree respiration	Estimated as the combination of foliage dark respiration (Rf) and wood CO ₂ efflux (Rw), based on Ryan et al. (2009).
GPP	Gross primary production	Estimated as the sum of ANPP, TBCF, and Ra.
NEP	Net ecosystem productivity	The NEP was calculated as follows: NEP = GPP - Ra – FS (Maier et al., 2004).

2.3 Data Analysis

We initially conducting an exploratory analysis using scatter plots and stacked bar charts to examine the behavior of carbon flux and partitioning data across groups of genus, site, Köppen classification, and forest management.

For analyzed the effects of the genera (*Eucalyptus* vs. *Pinus*), age, minimum and maximum temperatures (tmin and tmax), soil water deficit (WD), and silvicultural treatments on the NEP, carbon flux and partitioning variables we used generalized linear mixed models (GLMMs) for fluxes and generalized additive models (GAMs) for partitioning. GLMMs were applied to capture linear relationships between the dependent variables and minimum and maximum temperatures, for fluxes. GAMs were

employed to model nonlinear (second-degree) relationships with temperature variables, providing flexibility in capturing curvilinear responses of carbon fluxes to temperature, thus allowing for more precise modeling where nonlinearity is expected. Campoe et al. (2020) already reported the effect of mean temperature on the carbon balance in Brazil, in that way we chose to use only the minimum and maximum temperatures to determine the effect of extreme climatic conditions on the carbon balance in forest plantations. Climatic information was obtained from the Xavier et al. (2022) database. To calculate the minimum and maximum temperature variables, we averaged the daily minimum (Tmin) and maximum (Tmax) temperatures over each month. The water deficit (WD) was calculated based on the sequential scaled water balance proposed by Camargo (1962) using the specific water-retention capacity of the local soil. Silvicultural treatments were analyzed by incorporating spacing (S) and fertilization (F) to improve the quality of the models. We omitted the treatments with throughfall exclusion, irrigation, and heterogeneous planting for the best performance of the models, resulting in a total of 216 observations.

We first built a global model by assuming a Gaussian family for fluxes and a binomial family for partitioning data for each response variable. While we initially tested interactions between categorical variables and genus (i.e., genera $\times$ Köppen, genera $\times$ water availability, and genera $\times$ spacing), these interactions were not significant and did not yield meaningful biological insights within the context of our study. Therefore, we proceeded with the simpler model: $y = \text{genus} + S + F + \text{Köppen} + T_{\text{max}} + T_{\text{min}} + \text{WD} + x|\text{sitio}$. We included "site" as the random variable to control dependence between measurements performed in the same experiment and at the same collection site. We adopted $x = 1$, for Ra and all carbon partitioning variables, and for the other variables, we adopted $x = \text{precipitation}$. From this global model, we obtained all submodels with combinations of uncorrelated variables ($r < |0.6|$) using the dredge function of the MuMIN package (Bartón, 2020). The selection of the best models was made using the AICc (second-order Akaike information criterion), as described by (Santos et al., 2024). When the proposed models indicated a significant effect for categorical variables, Tukey's HSD test ($P < 0.05$) was applied to compare means among treatments. For continuous variables showing significant effects, we generated predictor-response plots, which were used to assess model fit quality for GLM and GAM models through simple linear regression plotting. All analysis were performed in R software version 4.3.1 (R Core Team, 2023).

For carbon partitioning for WNPP and TBCF, we also evaluated the probability of a given observation occurring over specific ranges of possible values. For this, we extracted 1000 random samples from the dataset (with replacement), and for each sample we quantified the percentage of values of each variable present in five different classes, defined based on the average (Avg), standard deviation (Sd), minimum (Min), and maximum (Max) values: of the dataset. The classes were structured as follows:

- 1) Min to $\text{Avg} - 2 * \text{Sd}$;
- 2) $\text{Avg} - 2 * \text{Sd}$ to $\text{Avg} - 0.5 * \text{Sd}$;
- 3) $\text{Avg} - 0.5 * \text{Sd}$ to $\text{Avg} + 0.5 * \text{Sd}$;
- 4) $\text{Avg} + 0.5 * \text{Sd}$ to $\text{Avg} + 2 * \text{Sd}$;
- 5) $\text{Avg} + 2 * \text{Sd}$ to Max.

We calculated the probability of carbon partitioning values occurring in each of the five maximum temperature classes, based on the 1000 sampled. To help interpret the influence of maximum temperature on carbon partitioning, we created a density plot showing the distribution of temperatures during the study period. This visualization highlights how likely each carbon flux value is to occur within each temperature class, making it easier to understand the relationship between temperature and carbon allocation.

3 Results

3.1 Carbon Partitioning patterns

3.1.1 Responses of genetic materials

The different genera showed distinct patterns in terms of fluxes and carbon partitioning under the studied climate conditions (Fig. 2). On average, gross primary production (GPP) for *Pinus* was approximately $5200 \text{ g C m}^{-2} \text{ yr}^{-1}$ while *Eucalyptus* showed a mean of $4315 \text{ g C m}^{-2} \text{ yr}^{-1}$. Higher ranges of GPP fluxes were found for *Pinus* ($\sim 1365\text{--}11443 \text{ g C m}^{-2} \text{ yr}^{-1}$) compared to *Eucalyptus* ($\sim 1791\text{--}12159 \text{ g C m}^{-2} \text{ yr}^{-1}$). *Eucalyptus* presented wood production ($\sim 1582 \text{ g C m}^{-2} \text{ yr}^{-1}$) nearly 22% higher than that of *Pinus* ($\sim 1238 \text{ g C m}^{-2} \text{ yr}^{-1}$). *Pinus* tended to increase TBCF:GPP at the expense of WNPP:GPP, whereas *Eucalyptus* showed the opposite trend. For net ecosystem production, *Eucalyptus* presented a range of 12 to $7482 \text{ g C m}^{-2} \text{ yr}^{-1}$, with an average of approximately $2106 \text{ g C m}^{-2} \text{ yr}^{-1}$. In contrast, *Pinus* exhibited a range of 254 to $4370 \text{ g C m}^{-2} \text{ yr}^{-1}$, with an average of around $1462 \text{ g C m}^{-2} \text{ yr}^{-1}$. In general, we found that the GPP varied more than fivefold across the climate conditions in Brazil.

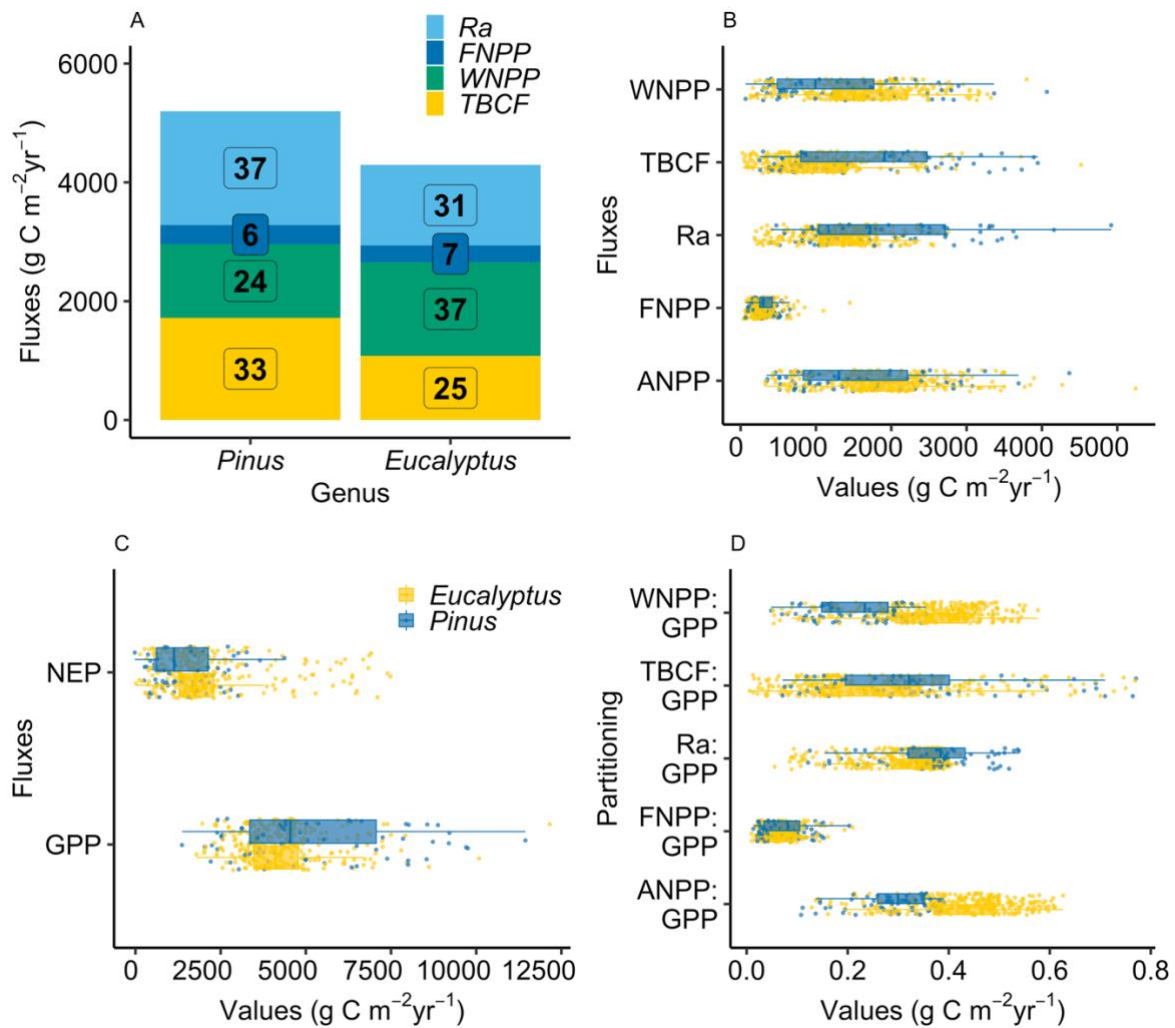


Fig. 2: (A) Carbon fluxes of the different genera; partitioning (%) is numerically presented in the boxes, (B) range of the carbon fluxes for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), total belowground carbon flux-TBCF, (C) net ecosystem production (NEP), gross primary production and (GPP) and (D) partitioning values (%).

3.1.2 Site and Climate Effects

GPP and wood production showed trends associated with location and Köppen classification (Fig. 3). For *Pinus*, (Fig.3 - A), we observed a trend of increased carbon fluxes with the increase in GPP under conditions of lower temperature (S12) compared with higher temperatures (S11). However, despite the increase in carbon partitioning to wood production (22 to 25%), there was also an unexpected increase in carbon partitioning to TBCF of around 87% (21 to 39%). This trend may be linked to the greater partitioning to the root system of the genetic material (*Pinus taeda*) planted at

this Cfb site (S12) compared with that of *Pinus caribaea* var. *hondurensis* planted at the Cwa site (S11). For *Eucalyptus*, (Fig 3 - B), subtropical (Cwa and Cwb) and temperate (Cfb) sites had GPPs and WNPPs higher than tropical climates (Af, Am, and As). We noticed that in environments with extreme low temperatures, frost occurrence, and higher temperatures with high water deficit, there was a trend of greater partitioning of C for TBCF at the expense of WNPP.

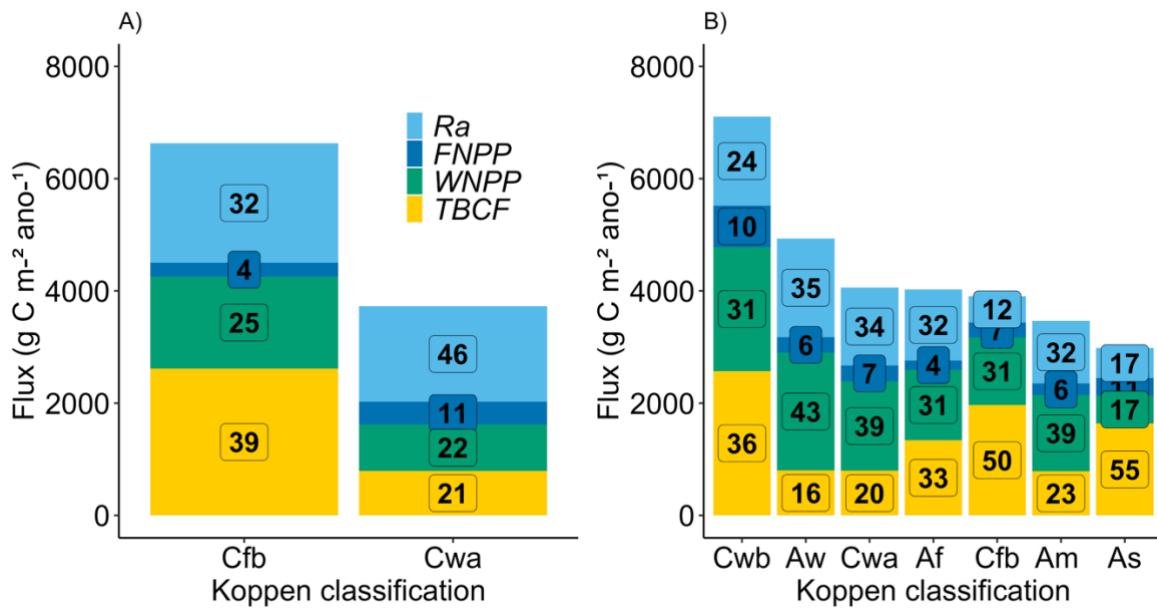


Fig.3: Carbon fluxes for all Köppen climate classifications (averaged across sites) for *Pinus* (A) and *Eucalyptus* (B) plantations. Partitioning (%) is numerically presented in the boxes of each bar. TBCF: total belowground carbon flux, WNPP : wood net primary production, FNPP: foliage net primary production, Ra: aboveground tree respiration Note: As: Savanna climate with dry summers (S4); Am: Monsoon climate with a drier period (S5); Aw: Savanna climate with dry winters (S1, S3); Cwa: Humid subtropical climate (S6, S7, S8, S11); Af: Equatorial climate, (S2); Cwb: Subtropical high-altitude climate (S9); Cfb: Temperate oceanic climate (S10, S12).

3.1.3 Silvicultural Effects

For *Pinus* (Fig.4 – A and supplementary Fig. 3, 4, 5 and 6), the rainfall treatment in the S12 project (higher genetically improved materials) presented a GPP value ($\sim 6628 \text{ g C m}^{-2} \text{ yr}^{-1}$). This value appeared to be higher than those observed in the PPPIB project, which included genetic materials from seeds with a low degree of improvement. The irrigated plantations in the PPPIB project (lower genetically improved materials-seed plantations) had approximately 10% and 13% higher GPP and WNPP, respectively, compared to rainfall treatments. In the fertility analysis, the plantations

that received fertilization had higher GPP ($\sim 5751 \text{ g C m}^{-2} \text{ yr}^{-1}$) and WNPP ($\sim 1394 \text{ g C m}^{-2} \text{ yr}^{-1}$) than the non-fertilized plantations. The smallest spacing presented the highest GPP ($\sim 7587 \text{ g C m}^{-2} \text{ yr}^{-1}$) and the highest partitioning to WNPP ($\sim 2099 \text{ g C m}^{-2} \text{ yr}^{-1}$). Plantations from improved seeds ($3 \times 2 \text{ m}$), seemed to have lower carbon fluxes compared to others.

For *Eucalyptus* (Fig.4 – B and supplementary Fig. 3, 4, 5 and 6), the irrigated treatment resulted in higher GPP ($\sim 4500 \text{ g C m}^{-2} \text{ yr}^{-1}$) than the other treatments, with an increase in wood production of around 41%. We also observed that the throughfall exclusion treatment (clonal plantation) resulted in higher GPP and carbon partitioning to TBCF (45%) than the treatment that received ambient rainfall (mix of seedlings originating from seeds and clones – 27%). The fertilized treatments had similar GPP values, but the super fertilizer treatment resulted in the highest carbon partitioning to WNPP (41%). Uniform planting resulted in higher GPP than heterogeneous planting, but the heterogeneous plantations had higher carbon partitioning to WNPP (38%). Regarding planting density, the greater the spacing, the higher the GPP ($\sim 4325 \text{ g C m}^{-2} \text{ yr}^{-1}$) and WNPP ($\sim 1600 \text{ g C m}^{-2} \text{ yr}^{-1}$) values.

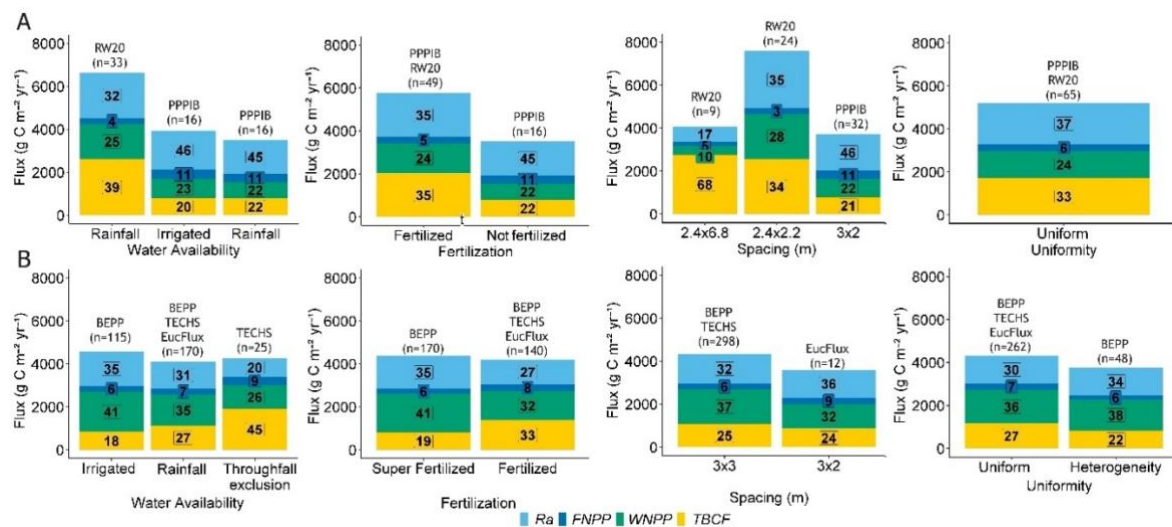


Fig. 4: Carbon fluxes in response to water availability, fertilization, spacing, and uniformity, averaged across sites and clones. Partitioning (%) is numerically presented in the box of each bar for *Pinus* (A) and *Eucalyptus* (B). TBCF: total belowground carbon flux, WNPP: wood net primary production, FNPP: foliage net primary production, Ra: aboveground tree respiration. Note: RW20: S12; PPPIB: S11; TECHS: S1, S4, S7, S9, and S10; BEPP: S2, S5, S6, and S3; EucFlux: S8.

3.2 Climate and Silviculture modeling of plantation carbon balance

We found a significant effect between the categorical groups based on the GLMM and GAM results (Fig. 5). The Tukey test ($P < 0.05$) results are presented in Supplementary Fig.1 and 2. With respect to genus, higher WNPP and ANPP values were recorded for *Eucalyptus* (~ 1451 and $1736 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively), and higher Ra higher values were recorded for *Pinus* ($\sim 1948 \text{ g C m}^{-2} \text{ yr}^{-1}$). Regarding spacing, all variables had significant response except FNPP, FNPP: GPP, and GPP. The highest flux values were found for the $2.4 \times 2.2 \text{ m}$ spacing, and the $3 \times 3 \text{ m}$ spacing resulted in the highest partitioning to wood production at the expense of root system production. Regarding fertility, only ANPP:GPP presented a significant effect, with the best results in response to super fertilization (45%). Regarding the Köppen classification, only partitioning presented a significant response. We found that subtropical sites (CWa and CWb) had relatively higher wood production (35% and 29%, respectively) and low partitioning to root growth (20% and 27%, respectively).



Fig. 5: Sizes of the effects (estimates shown inside the rectangles) of the explanatory variables (categorical and continuous) on the carbon fluxes and partitioning in *Eucalyptus* and *Pinus* plantations in Brazil based on GLMM and GAM analyses. Cells colored green, blue, yellow and white correspond to significant categorical positive effects and continuous positive, negative and not significant effects, respectively, on fluxes and carbon partitioning. Note: T-min: minimum temperature, T-max: maximum temperature, WD: water deficit. FNPP: foliage net primary production, WNPP: wood net primary production, ANPP: aboveground net primary production, TBCF: total belowground carbon flux, Ra: aboveground tree respiration, GPP: gross primary production, NEP: net ecosystem production. Ra and GPP had an inverse relationship between age and the fluxes for NEP, as

observed in GLMM and GAM results (Fig. 5). As tree age increased, the NEP fluxes decreased (Fig. 6). The model indicated a negative effect for GPP and Ra, but we did not observe a significant effect with age (Fig. 6), which may be related to the limited sampling of data from the *Pinus* plantations. The maximum temperature (Fig. 7 and 8) had a positive effects for C flux and partitioning to TBCF, while for WNPP, ANPP, GPP, NEP, WNPP:GPP, ANPP:GPP and Ra:GPP, we observed negative effects (Fig. 7 and 8). For C partitioning, we observed non-linear behavior, i.e., extreme maximum temperatures (Fig. 8 - A) caused a reduction in wood productivity and increase in root system growth.

Minimum temperature had a positive linear effect on FNPP:GPP and a negative non-linear effect on ANPP:GPP and Ra:GPP (Fig. 5), for which the extreme minimum temperatures caused a reduction in carbon partitioning. Notably, for the non-linear models, at both the lower and higher extremes of minimum temperature, we observed a reduction in C partitioning (Fig. 8 - B). The water deficit had a negative effect only on TBCF:GPP (Fig. 9 - A). The effects of water deficit and maximum temperature on TBCF:GPP showed that under water and thermal (low and high temperatures) stresses, carbon partitioning tended to increase for TBCF:GPP (Fig. 9 - B).

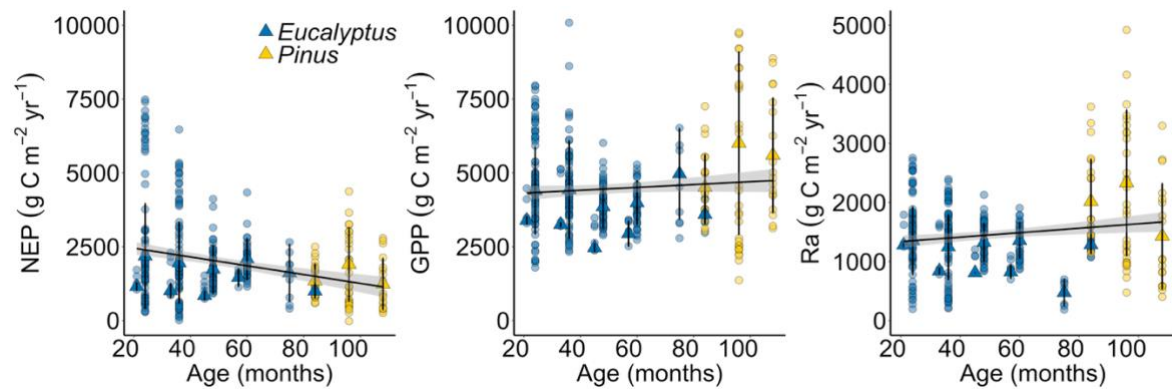


Fig. 6: Changes in net primary production (NEP), gross primary production (GPP), and aboveground tree respiration (Ra) with age in *Eucalyptus* (yellow) and *Pinus* (blue) plantations, relationships identified as significant in the GLMM and GAM model. Shaded regions on regression lines represent the standard error. The circles represent the observed data, and the triangles represent the average for each age.

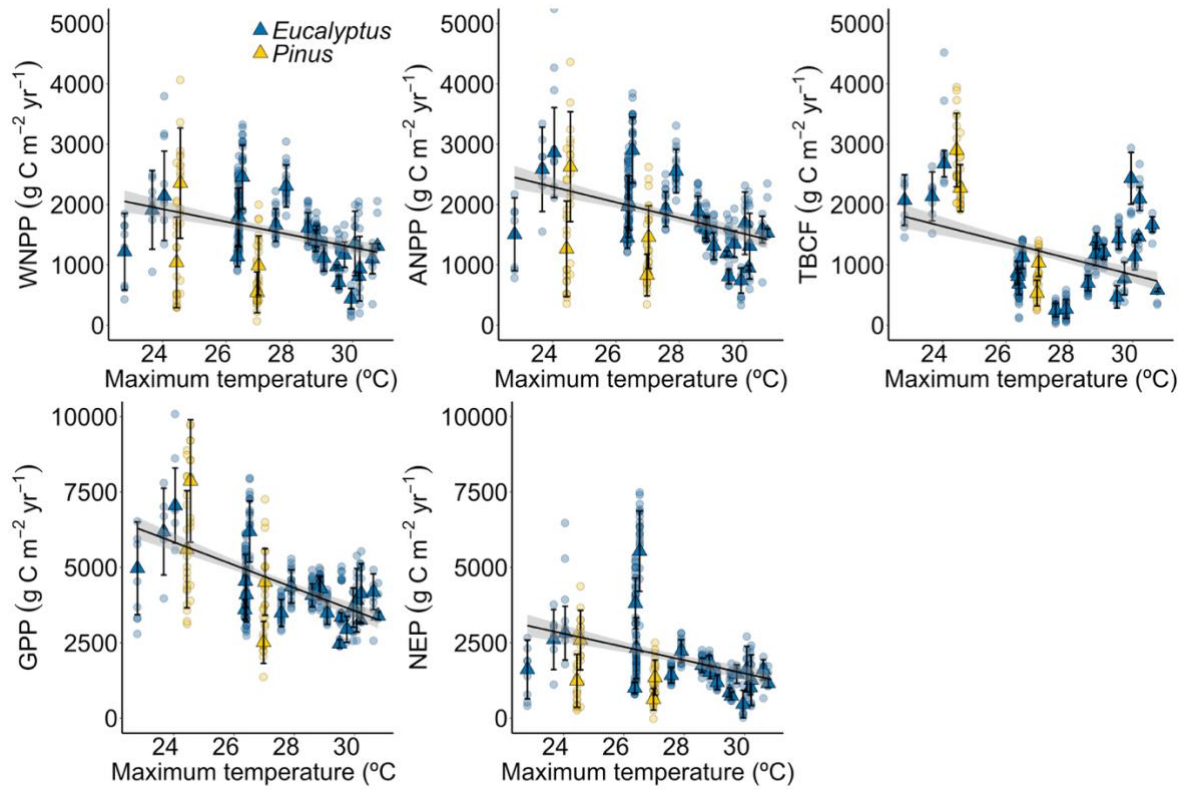


Fig. 7: The negative effect of maximum temperature on wood net primary production (WNPP), aboveground primary production (ANPP), total belowground carbon flux (TBCF), gross primary production (GPP), and net ecosystem primary production (NEP) in *Eucalyptus* (blue) and *Pinus* (yellow) plantations, relationships identified as significant in the GLMM and GAM model. Shaded regions on regression lines represent the standard error. The circles represent the observed data, and the triangles represent the average for each temperature.

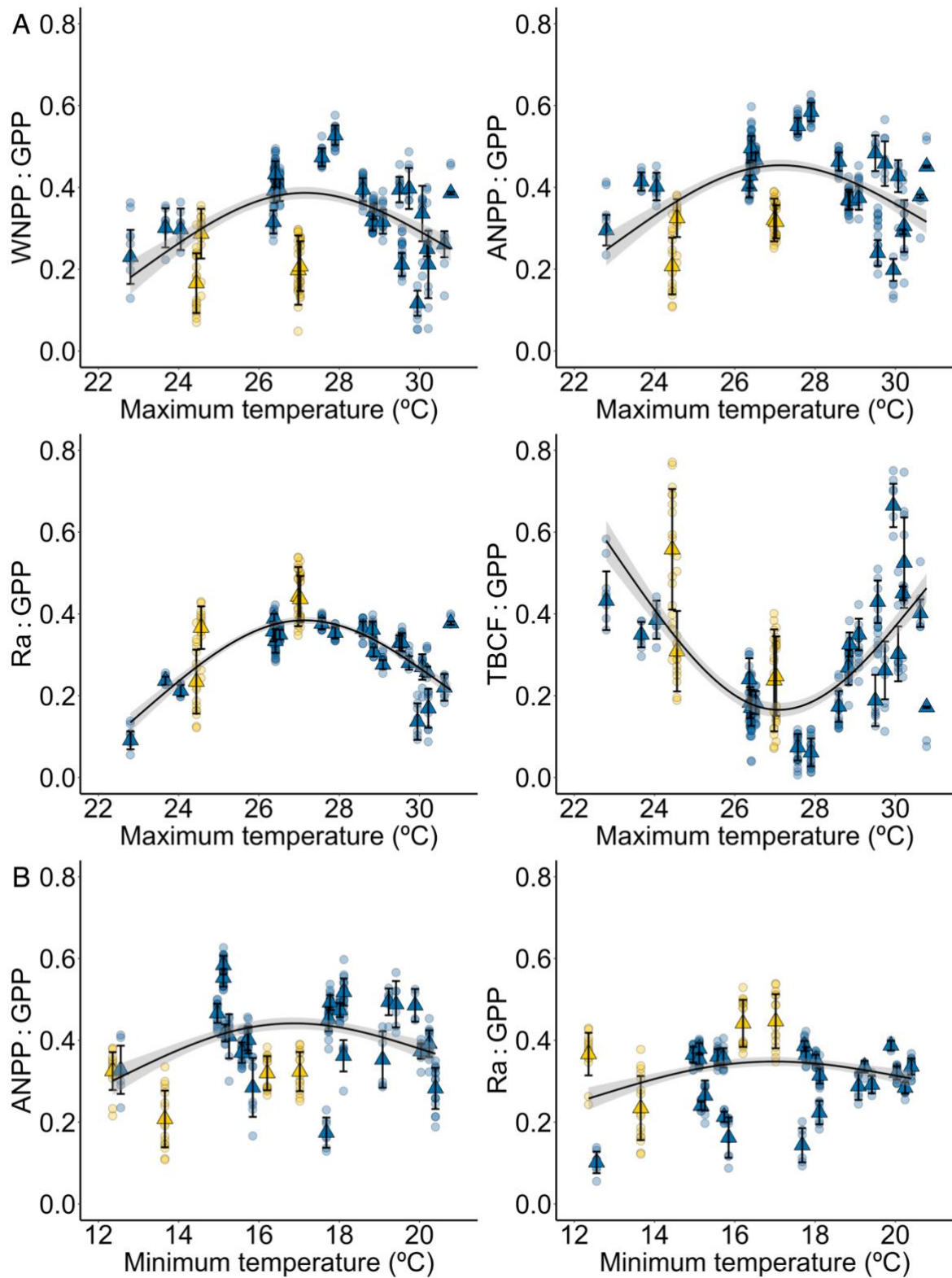


Fig. 8 : The effect of the maximum temperature on carbon partitioning to wood net primary production (WNPP), foliage net primary production (FNPP), aboveground net primary production (ANPP), aboveground tree respiration (Ra), and total belowground

carbon flux (TBCF) (A) and the effect of the minimum temperature on carbon partitioning to ANPP, and Ra (B) in *Eucalyptus* (blue) and *Pinus* (yellow) plantations, relationships identified as significant in the GLMM and GAM model. Shaded regions on regression lines represent the standard error. The circles represent the observed data, and the triangles represent the average for each temperature.

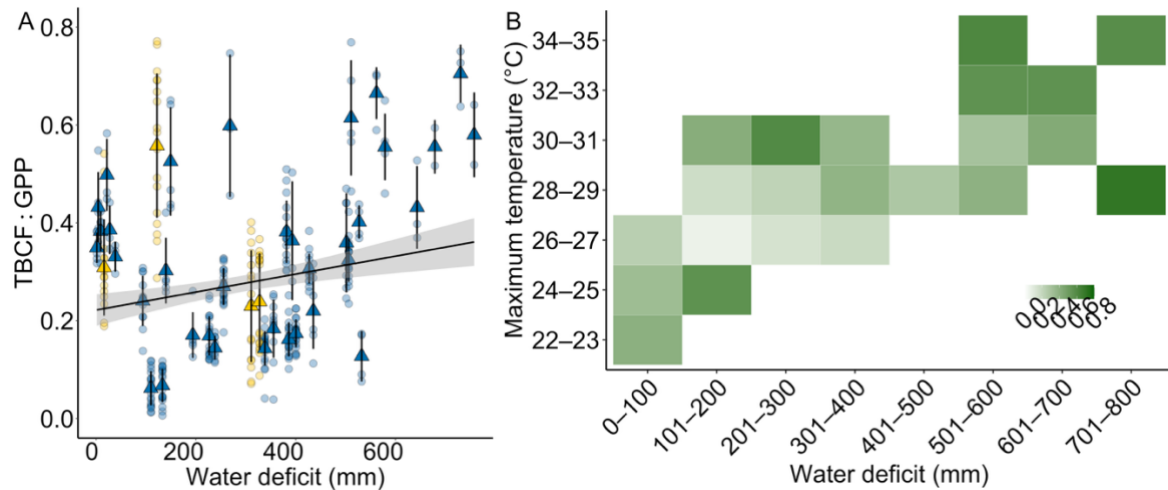


Fig. 9: (A) The positive effect of water deficit (WD) on carbon partitioning to total belowground carbon flux (TBCF:GPP) in *Eucalyptus* (blue) and *Pinus* (yellow) plantations. Relationships identified as significant in the GLMM and GAM model. Shaded regions on regression lines represent the standard error. The circles represent the observed data, and the triangles represent the average for each water deficit. (B) Relationship between the maximum temperature and water deficit and the effect on TBCF:GPP.

3.3 Carbon partitioning probability

For genus *Pinus* the maximum temperature had a significant effect only on TBCF:GPP, with a decrease in maximum temperature resulting in higher carbon allocation to belowground, showing a 22% probability of values exceeding 0.41 (Fig. 10 - A). For *Eucalyptus* (Fig. 10 - B), the variables exhibited antagonistic effects, with non-linear behavior. The extreme temperatures caused a reduction in wood production at the expense of root system growth. The most productive plantations with low TBCF:GPP are located in areas with maximum temperatures between 24 and 30°C, with a 78% probability of TBCF:GPP being below 0.33 and a 73% probability of WNPP:GPP exceeding 0.30, within this temperature range.

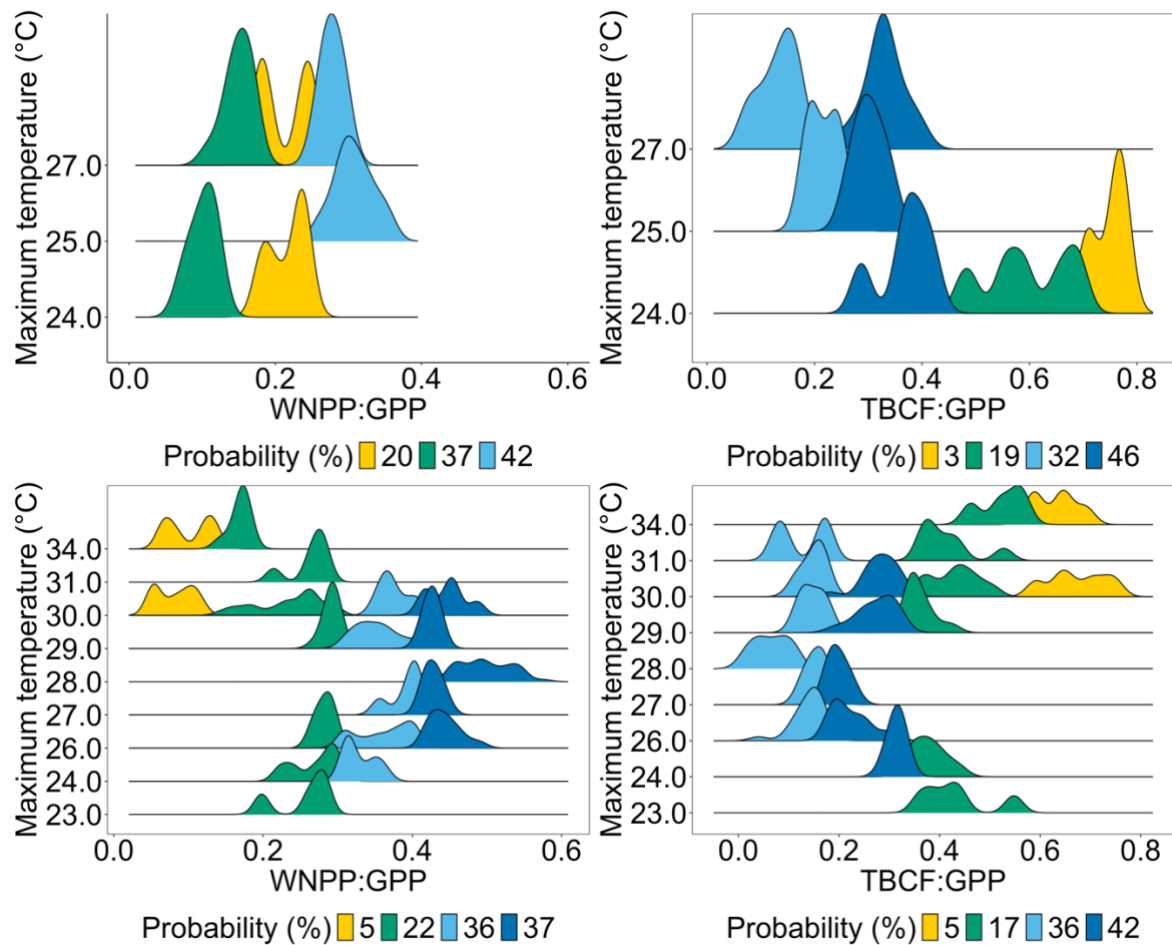


Fig. 10: Probability of occurrence for carbon partitioning to wood net primary production (WNPP:GPP) and total belowground carbon flux (TBCF:GPP) for each data occurrence class, derived from the standard deviation, in *Pinus* (A) and *Eucalyptus* (B) plantations in different maximum temperature environments in Brazil. The partitioning classes for WNPP (Wood Net Primary Production) were defined as: 1) 0.05-0.14, 2) 0.14-0.30, 3) 0.30-0.41 and 4) 0.41-0.57, and for TBCF (Total Belowground Carbon Flux): 1) 0.0-0.17; 2) 0.17-0.33; 3) 0.33-0.57; 4) 0.57-0.77. These classes are represented by the colors yellow, green, light blue, and dark blue, respectively. The probability of carbon allocation to WNPP and TBCF is indicated by the numbers in the legend of the density curves.

4 Discussion

4.1 Genetic materials and silvicultural effects

The study of genus $\times$ environment interactions is essential for understanding the growth behavior of forest plantations and informing management strategies to increase productivity. We discovered that *Eucalyptus* and *Pinus* have different

ecophysiological growth patterns. Besides the highest carbon partitioning to WNPP in *Eucalyptus* (37%), we also expected that this genus would present the highest average GPP due its rapid growth driven mainly by its efficiency in the use of light, water, and nutrients and carbohydrate assimilation (Hubbard et al., 2020; Viera et al., 2016; Campoe et al., 2012b). However, according to the GLMM, only the fluxes for WNPP, ANPP, and Ra were different between the genera, this leads us to partially accept our first hypothesis that all fluxes for *Eucalyptus* would be higher than those for *Pinus*.

Pinus GPP values reported in other studies were lower than those observed in our dataset, with maximum values of $2587 \text{ g C m}^{-2} \text{ yr}^{-1}$, at 12 years old, in the United States (Maier et al., 2004) and $3438 \text{ g C m}^{-2} \text{ yr}^{-1}$, at age 20 in Australia (Ryan et al., 2004). Furthermore, GPP and carbon fluxes tend to decrease with stand age (Larcher, 2000). Although we observed a reduction in carbon fluxes with stand age (Fig. 5), we expected that the *Pinus* plantations (aged 77–105 months) would present a lower flux than the *Eucalyptus* plantations (aged 22–75 months). However, due to the relatively slower growth of *Pinus* trees, we believe that the peak fluxes for *Pinus* occur at older stand ages. Uri et al. (2019) found that in a 6-year-old *Pinus sylvestris* plantation in Estonia, the NEP was still negative, meaning that trees had respiration fluxes that were higher than the GPP. Despite these studies being conducted in subtropical environments, where *Pinus* has lower growth, they indicate the slow increase in GPP with age, which tends to increase until the maximum average annual growth rate is reached.

The higher GPP of *Pinus* than *Eucalyptus*, may be consistent with the characteristics of the tree canopy of these two genera in the field at the time of the carbon balance measurement. The interception and absorption of radiation influence the productivity of the forest and are strongly correlated with the leaf area index (LAI). *Pinus* plantations had an average LAI of $6.67 \text{ m}^2 \text{ m}^{-2}$ (Hincapie, 2020; Deliberari, 2015), while *Eucalyptus* plantations had an average LAI of $3.51 \text{ m}^2 \text{ m}^{-2}$ (Campoe et al., 2012, 2020, Stape et al., 2008). The LAI is also related to climatic conditions. As temperature increases and the water deficit decreases, LAI tends to be greater. These indications, added to the fact that *Pinus* plantations are located in cold and humid places, may have resulted in greater respiration and GPP for the genus.

In recent decades, different studies have been carried out with *Eucalyptus* and *Pinus* that demonstrate a strong response of GPP and wood production to increased resource (Rubilar et al., 2024; Deliberari, 2015; Binkley et al., 2004, 2013; Stape et al.,

2008; Maier et al., 2004), similar to our observations for the uniformity and spacing (*Eucalyptus*) and fertility (*Eucalyptus* and *Pinus*) treatments. For the other silvicultural treatments, the increase in resource availability through water availability (*Eucalyptus* and *Pinus*) and spacing (*Pinus*) did not increase carbon fluxes, which is linked to the low productivity of the genotypes that originated from seed, *Eucalyptus* E1 and *Pinus* PT and PTC (Table 2) (Deliberari, 2015; Campoe et al., 2012). The lower productivity found for forest seed plantations may be linked to the lower uniformity as well as the capture and use-efficiency of resources by the trees (Binkley et al., 2002). We observed that management, especially the spacing of the stands (Fig. 4), directly affected forest productivity and the forest carbon stock. Planting density is a management strategy that can be used, particularly in areas with high water deficits (Hakamada et al., 2020; Ryan et al., 2010). Increasing the spacing between trees can increase individual biomass production and reduce planting water use (Aguilar, 2018; Hakamada et al., 2020; Rodrigues et al., 2021).

In general, management practices resulted in increased resources, increased carbon partitioning to WNPP, and decreased TBCF, which led us to accept our second hypothesis. Management practices can maximize the expression of the quality of the genetic material and the productive potential of the site by increasing the availability of resources essential to growth, mainly water, light, and nutrients (Binkley et al., 2004). Unfortunately, we do not have replicates for the genetic materials at all of the sites and for all of the management scenarios studied, which may have resulted in some genetic material or site condition being highlighted as having high carbon fluxes.

4.2 Climate effects

We observed a strong influence of maximum temperature on carbon fluxes and carbon partitioning (Fig. 5, 8), which led us to accept our third hypothesis. An increase in maximum temperature decreased the carbon fluxes and lead the trees allocated more carbon belowground at temperature extremes than to aboveground, with a maximum carbon partition range for wood production between 26 and 30°C maximum temperature. Corroborating the findings of Queiroz et al. (2020), studying the optimal temperature range for the growth of different *Eucalyptus* genetic materials in Brazil, found an optimal growth rate of around 20 °C, with a reduction in growth towards temperature extremes. Temperature extremes directly affect photosynthesis and the

physiological processes of plants, which reduces their growth (Aspinwall et al., 2016; Drake et al., 2016; Way & Oren, 2010).

Temperature also increases the vapor pressure deficit and consequently evaporation, reducing the availability of water in the soil (Grossiord et al., 2020). Which justifies the increase in TBCF:GPP observed with an increase in the water deficit (Fig. 9). Campoe et al. (2020) did not find a strong correlation with C partitioning and water deficit. Therefore, the productivity of forest plantations is subject to temperature variations, where temperature extremes affect carbon partitioning priorities. Temperature sensitivity generates concern about the expansion of forest to increasingly drier areas with high temperatures, in addition to predictions of increased temperatures and severe droughts for the tropic regions for the coming years, mainly due to El Niño (IPCC, 2014; Kay et al., 2022). Increases in maximum or minimum temperatures, reductions in precipitation, and extended drought periods have affected the sustained productivity of intensively managed plantations (Booth, 2013; Mitchell et al., 2016; Sun et al., 2018).

However, landscape-level factors such as physiography and groundwater accessibility, which are often overlooked in regional-scale approaches, may also significantly influence GPP and carbon partitioning (Alvares and Stape, 2025). Areas with greater access to ground water could buffer the negative effects of water deficit, sustaining higher productivity and modifying allocation patterns. Therefore, the expansion of plantations into drier and warmer regions should carefully consider local physiographic conditions to ensure long-term sustainability and carbon sequestration potential.

High temperatures have a negative influence on carbon sequestration in forests NEP as carbon sequestration is directly associated with biomass gains. We observed that the hottest (Am) and driest (As) locations presented the lowest NEP ($\sim 1261 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average), which leads us to accept our fourth hypothesis. In this climate context, it is important to adopt intelligent management strategies for new plantations to improve their potential to store carbon and be used in climate mitigation projects.

4.3 Carbon storage

In Brazil, assessments of carbon balance in *Eucalyptus* and *Pinus* forests is scarce, and most studies started with the principle of modeling and do not address the

flux of carbon belowground. Therefore, this work provides great insight into the potential of planted forests to act as carbon sinks and the identification of the main factors that influence NEP, for which *Eucalyptus* plantations had a range of ~ 12 to $\sim 7482 \text{ g C m}^{-2} \text{ yr}^{-1}$, while *Pinus* had range of ~ 271 to $\sim 4370 \text{ g C m}^{-2} \text{ yr}^{-1}$. We observed variation in NEP with plantation age; at a more advanced age, a forest's capacity to sequester carbon is reduced, which leads us to accept our fourth hypothesis. The time it takes for a forest to go from being a source of carbon to becoming a sink depends on the physiological conditions of the forest, which are associated with its age and the management of the area (Law et al., 2001). *Eucalyptus* plantations have fast growth, so they quickly become sinks, with high carbon absorption rates. *Pinus* plantations have a lower growth rate, and, therefore, take longer to become carbon sinks and have a lower NEP (Uri et al., 2019; Schulze et al., 2000; Cohen et al., 1996). Uri et al. (2019) reported that *Pinus sylvestris* plantations became a carbon sink at between 7 to 10 years of age in a temperate climate.

The results presented here emphasize the effectiveness of silvicultural management, especially the spacing of the stand (Fig. 4), for increasing the carbon stock, highlighting its effective contribution to reducing carbon emissions into the atmosphere. Robust scientific studies have shown the importance of considering fast-growing forest plantations to reach high C sequestration rates (Rubilar et al., 2024). Long-term studies have demonstrated that *Eucalyptus* and *Pinus* plantations are sustainable; Brazilian forests storing an average of 1.79 billion t CO₂eq in Brazil from 9.93 million hectares of planted forests Brazilian tree industry - IBÁ, (2023).

This work explored, for the first time, the carbon balance of different ages, genotypes and climate conditions. Based on the results, we conclude that Brazilian *Eucalyptus* and *Pinus* forests can store large amounts of carbon throughout the plantation cycle. The potential for carbon storage depends on the quality of the genetic material used and its adaptability to environmental conditions, the forest management that will be adopted during plantation growth, and local climate conditions. However, it is still necessary to account for the total carbon of all forestry activities from planting to harvesting. In addition, wood products have a potential role in mitigating greenhouse gas emissions, either by acting as carbon sinks and collectors or by replacing materials that require the consumption of fossil fuels and/or that emit high amounts of greenhouse gases at the end of their life (Behera et al., 2020; Burschel et al., 1993). Therefore, it is necessary to fully understand the fate of timber production and the life cycle stages

(production, use, cascade use, and end-of-life) of hierarchical timber value chains, as the final fate of timber affects the sector's global carbon balance (Forster et al., 2021; Leskinen et al., 2018; Matthews et al., 2023). In this way, we suggest that future work should aim to understand the main forest products and by-products produced in Brazil and map their uses and life cycles to be accounted for in carbon projects for climate mitigation.

5. Conclusion

The *Eucalyptus* and *Pinus* plantations showed different behaviors of carbon fluxes and partitioning across different climatic gradients in Brazil. Although *Pinus* had the highest flux values, *Eucalyptus* exhibited higher carbon partitioning to wood production at the expense of root system growth at the ages studied. For a better understanding of the fluxes for *Pinus* plantations, data which cover longer time series and tropical locations are needed. Despite the observed carbon fluxes and partitioning, forest management, especially spacing, proved to be an important tool for optimizing forest productivity and increasing the carbon stock of plantations at the expense of root system growth. For the management effect to be maximized, it needs to be planned according to climatic conditions, aiming for sustainable management of planted areas.

Maximum temperature had a non-linear relationship with C fluxes. Maximum partitioning for wood production was between 26 and 30°C maximum temperatures. Maximum temperature also reduced the NEP and C storage potential of plantations. Brazilian forests have a greater capacity of C storage (mean NEP $\sim 1787 \text{ g C m}^{-2} \text{ ha}^{-1} \text{ yr}^{-1}$, across sites, ages and management). So tropical forestry is a sustainable industry, but for better understanding of their eligibility in C mitigation projects it is necessary to know the life cycle of the C in different uses and also the total C balance resulting from all activities.

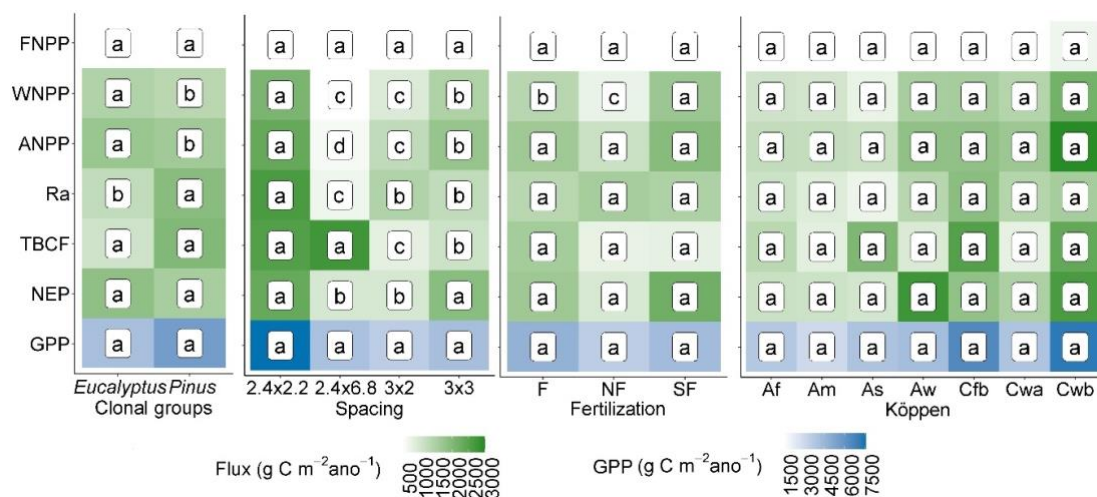
The results found here can be used as parameters in ecophysiological models, support the calibration of life cycle assessment models, and serve as tools for guiding forest management decisions. Additionally, carbon balance studies can help improve the understanding of clone-specific ecophysiological strategies, such as water use efficiency and drought tolerance, which can inform clonal deployment decisions, allowing forest managers to match genotypes to site conditions and enhance plantation resilience.

6 Acknowledgments

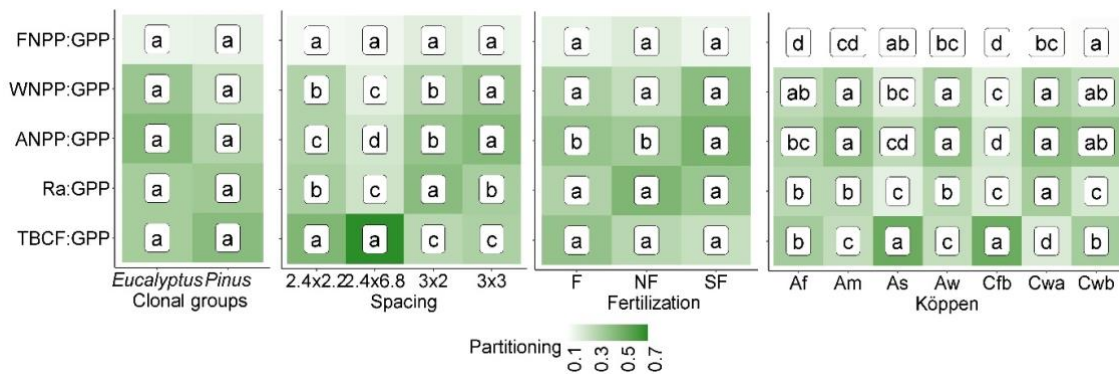
The data used in this work were provided by the projects BEPP, TECHS, EUCFLUX, PPPIB, and RW20, funded by the Forestry Science and Research Institute (IPEF, <https://www.ipef.br/>) and Forest Productivity Cooperative (FPC, www.forestproductivity.org). We thank Dan Binkley for his contributions to draft versions and all the companies that funded the projects. The following universities and institutes also supported this study: Federal University of Lavras, University of São Paulo, São Paulo State University, Colorado State University, North Carolina State University, Virginia Tech, Universidad de Concepción, and the USDA Forest Service.

7 Supplementary material

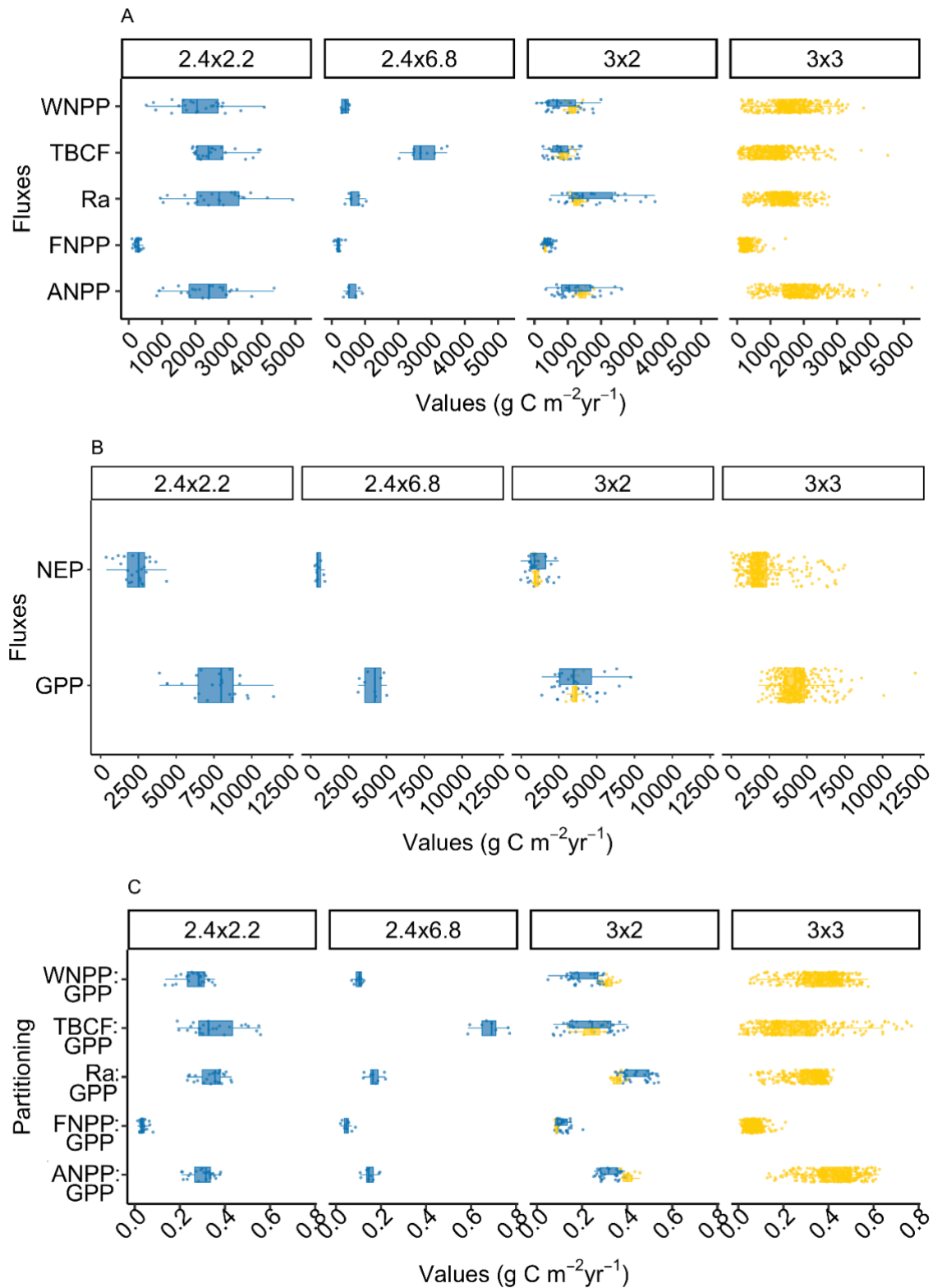
Supplementary Fig. 1: Influence of categorical variables, planting spacing, fertilization and Köppen classification on carbon partitioning in forest plantations in Brazil based on the Tukey test ($P < 0.05$) made from GLMM models, for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), total belowground carbon flux (TBCF), net ecosystem production (NEP), and gross primary production (GPP). F: fertilized; NF: not fertilized; SF: super fertilized; Aw: tropical savanna climate with a dry winter; As: tropical savanna climate with a dry summer; Af: tropical rainforest climate; Am: tropical monsoon and trade-wind littoral climate; Cfb: temperate oceanic climate or subtropical highland climate; Cwa: monsoon-influenced humid subtropical climate; Cwb: subtropical highland climate or temperate oceanic climate with dry winters.



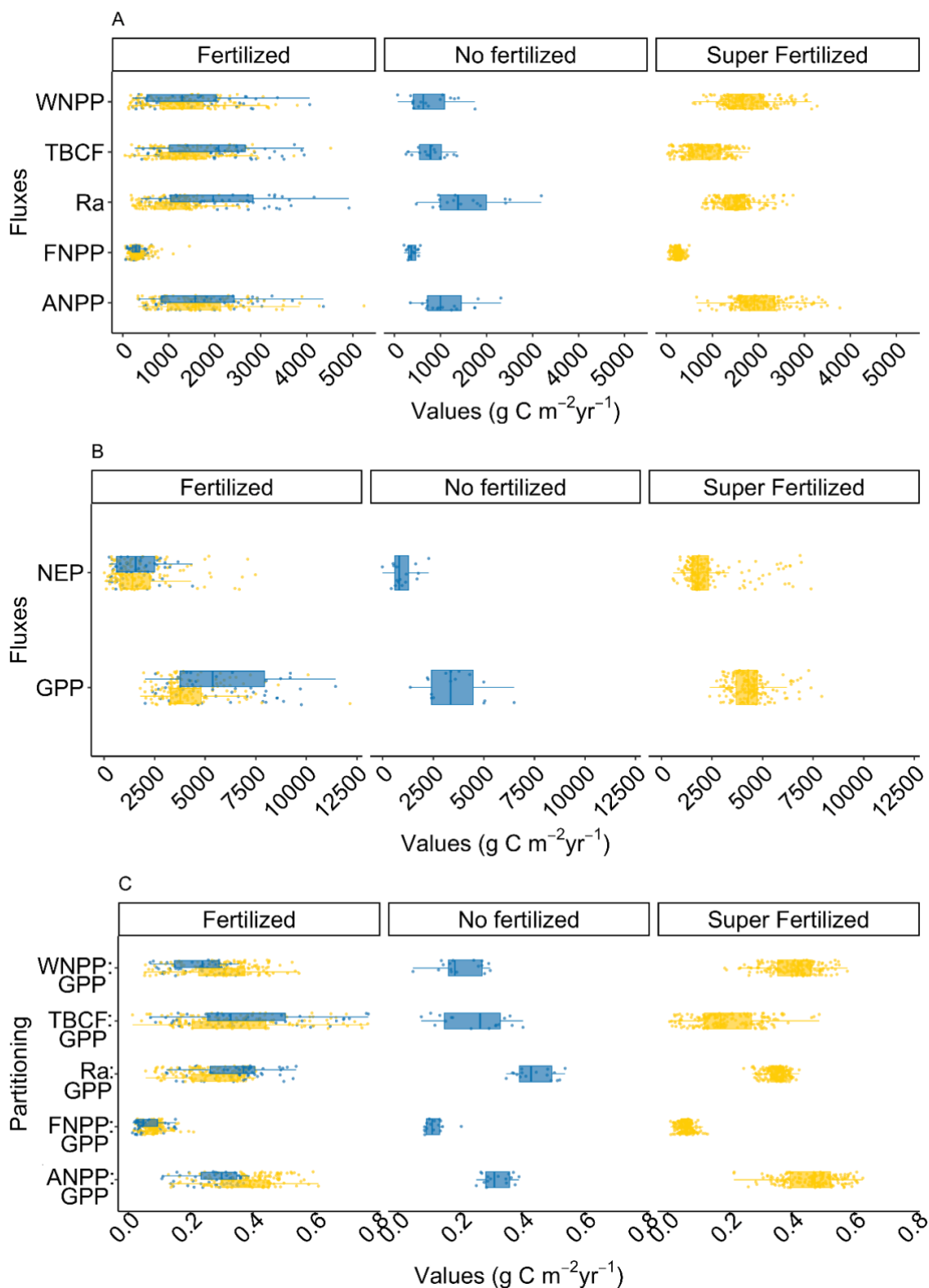
Supplementary Fig. 2: Influence of categorical variables, planting spacing, fertilization and Köppen classification on carbon partitioning in forest plantations in Brazil based on the Tukey test ($P < 0.05$) made from GAM models, for carbon partitioning for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), and total belowground carbon flux (TBCF). F: fertilized; NF: not fertilized; SF: super fertilized; Aw: tropical savanna climate with a dry winter; As: tropical savanna climate with a dry summer; Af: tropical rainforest climate; Am: tropical monsoon and trade-wind littoral climate; Cfb: temperate oceanic climate or subtropical highland climate; Cwa: monsoon-influenced humid subtropical climate; Cwb: subtropical highland climate or temperate oceanic climate with dry winters.



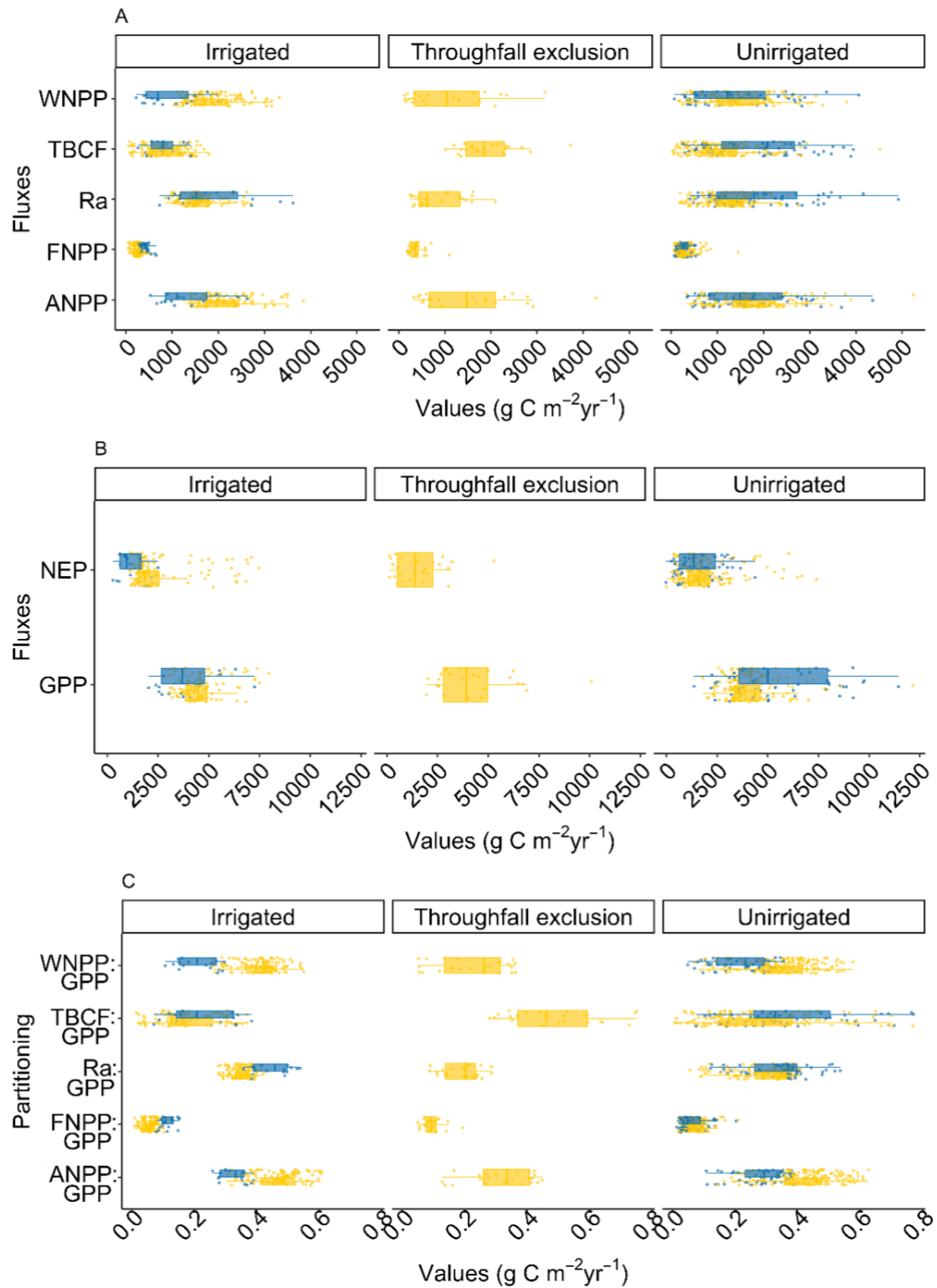
Supplementary Fig 3: (A) Range of the carbon fluxes of the different planting spacing for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), total belowground carbon flux (TBCF), and (C) net ecosystem production (NEP), gross primary production and (GPP), and (C) partitioning values (%).



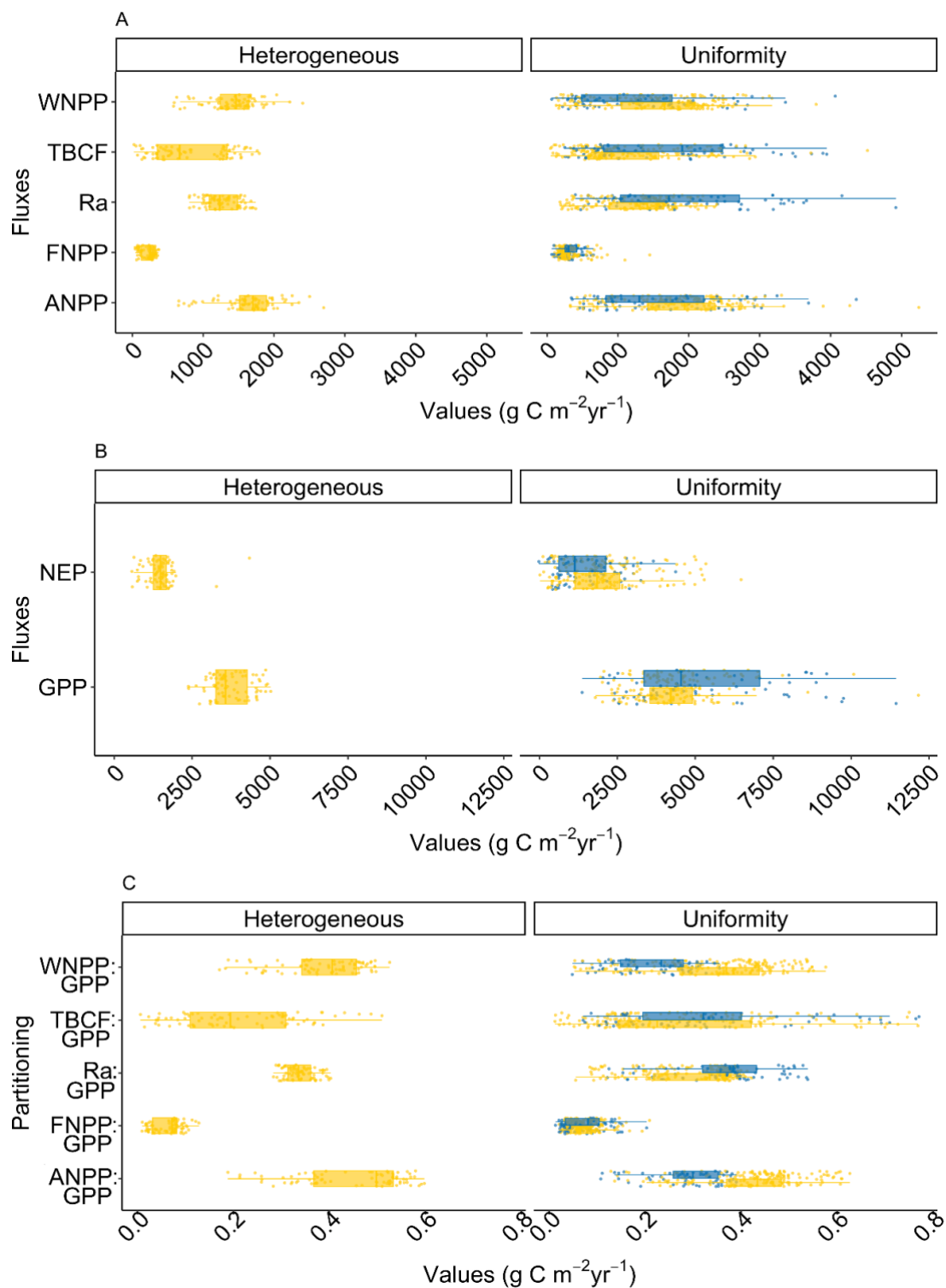
Supplementary Fig 4: (A) Range of the carbon fluxes of the different planting fertilization for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), total belowground carbon flux (TBCF), and (C) net ecosystem production (NEP), gross primary production and (GPP), and (C) partitioning values (%).



Supplementary Fig 5: (A) Range of the carbon fluxes of the different planting water availability for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), total belowground carbon flux (TBCF), and (C) net ecosystem production (NEP), gross primary production and (GPP), and (C) partitioning values (%).



Supplementary Fig 6: (A) Range of the carbon fluxes of the different planting uniformity for foliage net primary production (FNPP), wood net primary production (WNPP), aboveground tree respiration (Ra), total belowground carbon flux (TBCF), and (C) net ecosystem production (NEP), gross primary production and (GPP), and (C) partitioning values (%).



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Paper 2: Carbon partitioning as a drought-tolerance strategy in clonal *Eucalyptus* under thermal and water stress

Accept to agricultural and forest meteorology

Fernanda Leite Cunha^{1*}, Otávio Camargo Campoe^{1,2,3}, Cléber Rodrigo de Souza¹, Isaira Leite & Lopes¹, Clayton Alcarde Alvares^{2,4}, Jose Luiz Stape²

¹Department of Forestry Sciences, Federal University of Lavras (UFLA), Lavras 37200, Brazil,

²Department of Forestry Sciences, São Paulo State University “Júlio Mesquita Filho” (UNESP), Botucatu 18600, Brazil

³Institute of Forestry Research and Studies (IPEF), Piracicaba 13415, Brazil

⁴Suzano SA, Limeira 13473, Brazil

* Correspondence: fernandaleiteunha@gmail.com; Tel.: (+55-31) 99450-1613

Highlights

- 1) We provided amplitudes for C balance parameters for eco-physiological models
- 2) We elucidated the C allocation strategies for adaptation and acclimation in *Eucalyptus* plantations
- 3) Temperature is the most important variable that drives the carbon fluxes and partitioning
- 4) Fast-growing clones show 3 times higher loss in productivity with temperature rise
- 5) Drought-tolerant clones have conservative behavior in changing C partitioning

Abstract

The increase in the frequency, duration, and intensity of drought associated with climate change may alter the current productivity rates of planted forests and the risk of tree mortality associated with physiological stress. In this context, we aim to understand carbon allocation strategies in fast-growing (FG) and drought-tolerant (DT) clonal *Eucalyptus* plantations under different water and thermal stress. We used carbon balance data from two DT and three FG clones at four climatically contrasting sites, covering an area of 3,185 km in Brazil. With the aid of a generalized linear mixed model (GLMM), we observed that under extreme conditions of water and thermal stress, the clones tended to reduce gross primary production (GPP) and the partitioning of aboveground carbon, in detriment in increase in root growth. FG clones showed more significant reductions in GPP and carbon fluxes compared to DT clones, which demonstrates that FG clones are more sensitive to climate change. Our work contributes to elucidating carbon allocation strategies for the main groups of clones planted in Brazil, producing reference values that can be used in sustainable management projects and ecophysiological modeling aimed at more productive plantations that are tolerant to climatic adversity.

Keywords: Clonal groups, gross primary production, carbon sequestration, carbon allocation, climate gradients

1 Introduction

Plantation forests are reported to cover about 280 million hectares (FAO, 2022), and Brazil has approximately 8 million hectares of *Eucalyptus* plantation forests (Brazilian Tree Industry - IBÁ, 2023). *Eucalyptus* plantations that are intensively

managed to produce primary material for industry are among the forests with the highest gross primary production (GPP) worldwide (Stape et al., 2010). In recent decades, advances in silvicultural management and genetic improvements have led to maximum gains in productivity and a reduction in the length of the wood production cycle (Gonçalves et al. 2017, Elli et al. 2020). However, *Eucalyptus* plantations are highly susceptible to soil water availability and temperature variation (Queiroz et al. 2020, 2023, Martins et al. 2022).

Extreme temperature conditions and low availability of resources such as water, light, and nutrients are unfavorable for the growth and physiology of plants and can reduce their survival (Binkley et al. 2004, Stape et al. 2008, Queiroz et al. 2020). However, *Eucalyptus* species use available resources in strategic way to improve their growth and development in terms of avoiding physiological stresses and their consequences (Binkley et al. 2004, Campoe et al. 2012).

During photosynthesis, carbon dioxide (CO₂) is taken from the air and converted into non-structural carbohydrates (NSCs) that serve both as an energy carrier and as a building block for anabolic processes such as growth, defense or exchanges with other organisms (Hartmann & Trumbore, 2016). The division of the primary products of photosynthesis into different functional pools is called carbon allocation and has been the focus of studies for many decades (Litton et al. 2007, Stape et al. 2008, Ryan et al. 2010, Campoe et al. 2012, Campoe et al. 2020). These authors observed that there is a trade-off in the allocation of C between wood production and root system growth according to climate and genetic material. Under high temperatures, *Eucalyptus* species tend to allocate more C to the root system; however, some clonal groups present more efficient adaptation responses to climate variations. Therefore, understanding how plants regulate their C allocation is fundamental to understanding plant responses to environmental changes (Hartmann et al., 2020). Despite these insights, our understanding of how genetic variability influences carbon allocation strategies in *Eucalyptus* remains limited, particularly in response to temperature and water deficit gradients. While some studies have examined individual clone responses, a broader classification of clonal groups based on their physiological traits and adaptive strategies remains unexplored. This gap in knowledge hinders our ability to predict the long-term resilience and productivity of different genotypes under climate change scenarios.

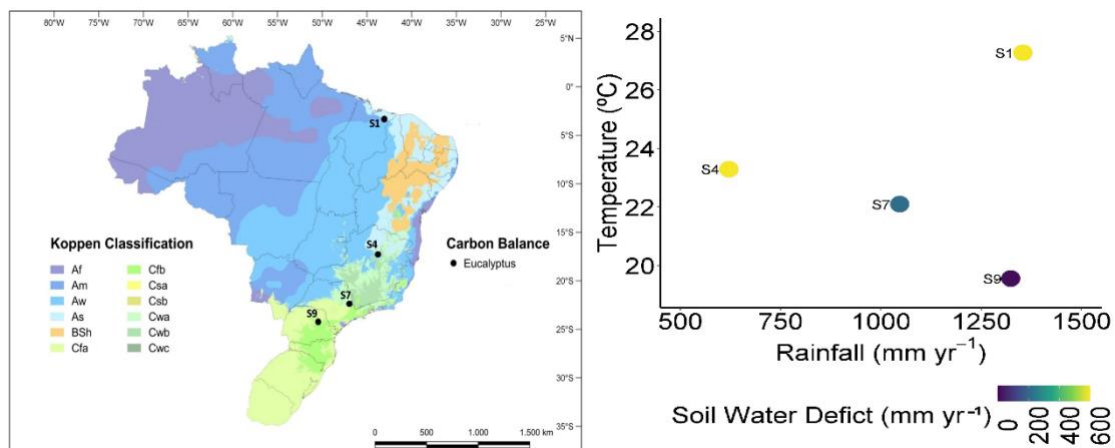
The search for suitable genotypes to be deployed under adverse environmental conditions presents a challenge for the forestry sector, and understanding the

mechanisms of climate responses according to the genetic characteristics of clones is essential to improve the understanding of the physiology of tree growth and C allocation. Unfortunately, ecophysiological studies to elucidate the growth behavior of different genetic materials are expensive and time consuming. In this context, the study of groups of clones according to their growth physiology optimizes productivity analyses and allows extrapolation to other genetic materials with similar growth characteristics. Based on the genetic materials studied across different climatic gradients in Brazil in the C balance project that is part of the experimental Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses (TECHS) cooperative research program (Campoe et al., 2020), we divided the clones based on their physiological characteristics to better understand their survival strategies under environmental stress conditions, seeking to answer the following questions: 1) Which carbon allocation strategy is adopted by drought-tolerant and fast-growing clones? 2) What is the interaction between clonal groups when submit to different temperature gradients and water deficit and 3) how does increased temperature and water deficit influence gross primary production (GPP) and carbon partitioning? We hypothesize that 1) the drought-tolerant clonal group presents greater carbon partitioning to root growth than wood production compared to fast-growing clones 2) We expect that FG are more sensitive to climate variation, while the DT clone presents less variation in C partition media, and 3) increased temperature and water deficit decrease GPP and increase C partitioning to root growth at the expense of wood production.

2 Material and Methods

2.1 Characterization of the sites

The study was developed using four climatically contrasting locations belonging to the TECHS experimental network, Cooperative Program on Clonal *Eucalyptus* Tolerance to Water and Thermal Stress (Binkley et al., 2020, Fig. 1). Sites S1 and S4 are classified as tropical sites with high water deficit (average of 516 mm year⁻¹) and average temperatures (average of 25.3 °C). Sites S7 and S9 are characterized as having a subtropical climate with low water deficit (average of 75 mm year⁻¹) and mild temperatures (average of 21.4 °C) (Table 1). The soil characteristics of each site are presented in Table 2.



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Fig. 1: Location of the studied sites along the different climatic gradients.

Table 1: Location and climatic characterization of the studied sites. Lat.: latitude; Lon.: longitude; Alt.: altitude; WD: water deficit.

Site	Location	Lat. (S)	Lon. (W)	Alt. (m)	T (°C)	Rainfall (mm yr ⁻¹)	WD (mm yr ⁻¹)
S1	Urbano Santos-Maranhã	-3.44	-43.07	81	27.3	1461	578
S4	Bocaiúva-Minas Gerais	-17.32	-43.77	848	23.3	713	544
S7	Mogi Guaçu, São Paulo	-22.35	-46.97	633	23.3	1097	145
S9	Telêmaco Borba, Paraná	-24.23	-50.53	888	19.6	1492	5

Lat.: latitude; Lon.: longitude; Alt.: altitude; WD: water deficit.

Table 2. Locations for the sites in this paper, and soil characteristics (0–40 cm depth, details for column heading are below table).

Site	Soil Order	p									
		Clay	Silt	Sand	OM	H	P	k	Ca	Mg	AWC
	m	(%)			(g L ⁻¹)	(mgL ⁻¹ _{soil})		mmol _e L ⁻³		(L m ⁻²)	
Urbano											
Santos-	Entiso					4.		1.			
Maranhão	1	9	5	87	16.0	1	0.0	4	36.5	15.5	64
Bocaiúva-	Oxiso					3.		1.			
Minas Gerais	1	76	14	10	47.5	9	2.0	6	48.5	26.5	225
Mogi Guaçu,	Oxiso	41	16	42	34.0	3.	4.5	1.	8.0	1.5	165

São Paulo	1					9		2				
Telêmaco	Oxiso							3.				
Borba, Paraná	1	56	23	21	52.0	4	3.5	8	37.5	11.0	214	

OM = Organic Matter; WSC = Water Storage Capacity; Soil order was classified according to the U.S. Taxonomy (Soil Survey Staff, 1999); Clay and sand contents were quantified using the densimeter method (Embrapa, 1997); Organic matter was determined by the Walkley-Black method (Embrapa, 1997); Extractable P, K, Ca, and Mg were extracted using ion exchange (van Raij et al., 2001); CEC refers to the cation exchange capacity; WHC (water holding capacity) was measured at a 0–2 m depth (Stape et al., 2004).

Five commercial clones were chosen to represent the productive (fast-growing) and drought-tolerant genotypes at all evaluated sites. *E. urophylla* (A1-the most widely planted clone in Brazil due to its high plasticity (Caldeira et al., 2020), B2 (*E. urophylla* x *E. grandis*), and K2 (*E. saligna*) showed high growth rates under the ambient environmental conditions. Clones C3 (*E. grandis* x *E. camaldulensis*) and P7 (*E. urophylla* x *E. brassiana*) are known to be drought-tolerant. The initial classification into "Productive" (FG) and "Drought-Tolerant" (DT) clonal groups was based on the productivity-based grouping proposed by Scolforo et al. (2019). To validate and refine this classification, we performed a Principal Component Analysis (PCA) using carbon partitioning data, which revealed a clear separation between the groups. Subsequently, an Analysis of Similarity (ANOSIM) confirmed this distinction as statistically significant ($p = 0.01$; $R = 0.75$). Moreover, the clonal groupings were further supported by ecophysiological evidence from other studies within the TECHS project, including assessments of fine root growth (Basílio et al., 2024), canopy structure (Mattos et al., 2020), carbon balance (Campoe et al., 2020), and wood physiology and anatomy (Pech, 2024; Santos et al., 2024). A description of the common ecophysiological characteristics of these clones groups is provided in Table 3. All clones were evaluated at all sites, with the exception of clone K2, which was not present at site S4.

Table 3: Ecophysiological growth characteristics of the fast-growing clone group (FG) and drought-tolerant group (DT) at the studied sites.

Characteristic	FG	DT	Reference
H (m)	24.2	22.1	Binkley et al. (2020)

DBH (cm)	16.4	14.8	Binkley et al. (2020)
Volume (m ³)	274.2	205.8	Binkley et al. (2020)
Biomass (kg tree ⁻¹)	125.2	86.5	Binkley et al. (2020)
LAI (3 yr)	3.2	2.1	Mattos et al. (2020)
Foliar Angle	37.3	68.5	Mattos et al. (2020)
SLA (cm ²)	106.0	110.5	Mattos et al. (2020)
Litterfall (g C m ⁻²)	268.7	361.1	Campoe et al. (2020)
Fine root biomass (3 yr, Mg ha ⁻¹)	5.5	7.0	Basílio et al. (2024)
Fine root deep (3 yr, m)	5.8	7.0	Basílio et al. (2024)
Stomata	Adaxial	Abaxial and adaxial	Pech (2024)
Stomata adaxial density	611.0	1109.0	Pech (2024)
Stoma width (um)	22.0	19.0	Pech (2024)
WUE	1.3	0.8	Hubbard et al. (2020)

H: Height (m); DBH: Diameter at breast height (cm); LAI: Leaf area index; SLA: Specific leaf area; WUE: Water use efficiency.

Each clone was planted in a single plot, with 8 lines $\times$ 30 trees, totaling 240 trees per plot, an area of 0.2 ha, with trees at a spacing of 3 $\times$ 3 m (1111 trees ha⁻¹). Plots were split, with rainfall reduced by about 33% in one half of the plot using under-canopy troughs as described by (Binkley et al., 2017). The experiments were planted in 2012 and were evaluated at ages 22 and 33 months. The planting technique followed minimum cultivation methods (Gonçalves et al., 2013), and all plots were fertilized intensively during the first year, and there was pest and weed control competition whenever necessary (Campoe et al., 2020).

2.2 Carbon balance

The C balance at each study site was quantified using the techniques described in Giardina & Ryan (2002) and Ryan et al. (2004). The dry masses of the branches, wood, bark, and coarse roots were fitted using the linearized model of Schumacher and Hall $\ln(\text{dry mass}) = \beta_0 + \beta_1 \times \ln(\text{diameter at breast height}) + \beta_2 \times \ln(\text{height})$, for each clone per site following the methodology presented in (Campoe et al., 2020). The models was estimated by harvesting 6 trees for each combination of clone and site (n =

24 trees/clone, total of 114 trees), at 2.5 years age, covering the range of diameter at breast height (DBH, 1.3 m above ground level).

For belowground biomass, the coarse roots (>10 cm) of 54 trees were fully excavated at sites T.17 and S.24. Each component of each tree was weighed on-site, and representative samples were dried at 65°C to a constant weight for dry mass determination. Based on climatic similarity, the equation developed for coarse roots at site S4 was applied to site S1, while the equation for site S9 was used for site S.7. All equations yielded p-values less than 0.01, and the R^2 values ranged from 0.91 to 0.99. The biomass used to adjust the equations and the performance of allometric equations can be found in Supplementary Fig. 1 and Supplementary Table 1.

The C balance was measured over 2 years and expressed as $\text{g C m}^{-2} \text{yr}^{-1}$, details of each flux methodology can be found in Table 4. Partitioning was calculated as the ratio between a specific carbon flux, i.e., wood net primary production (WNPP), foliage net primary production (FNPP), aboveground net primary production (ANPP), total belowground carbon flux (TBCF), and aboveground tree respiration (R_a), and gross primary production (GPP).

Table 4: Carbon balance variables and the methodology used in the calculations.

Variable	Definition	Methodology
		Estimated based on measurements of:
	Total	3 replicates.
TBCF	belowground C flux	1) Soil CO_2 efflux (FS), measured monthly over the study period on PVC collars using a LI-8100 device with a LI8100-103 (LI-COR, Lincoln, NE, USA). Nine PVC collars were installed in each plot, 3 positions (near the tree, between tree and middle of the row, and between these two distances), and 2) Aboveground litterfall (foliage, branches, bark, flowers, and fruits) (FA), was collected monthly, using 9 litter-traps per plot (3 positions and 3 replicates), following a similar spatial distribution of the PVC collars. Samples of each component were dried at 65°C and weighed. 3) O horizon mass change and decomposition of stumps from the previous rotation (CS). Dry mass of the O horizon was quantified at the beginning and the end of the first and

second year of the study period, using a 0.28 m² steel frame. The O horizon was sampled on 3 replicates of 3 positions per plot. Samples were dried at 65 °C until constant weight, separated into component and weighed. The estimation of the carbon flux associated with the decomposition of stumps from previous rotations was based on stump circumference measurements and dry mass equations developed by (Campoe et al., 2012).

4) Root dry mass increment (CR), were estimated using the dry mass equations (Supplementary Table 1).

5) Variation in carbon stock in the litter layer at the soil surface (CL). Was calculated based on the difference in C stocks in the soil surface litter layer, measured using the fixed depth method (0–20, 20–40, and 40–60 cm). Soil bulk density was measured with 100 cm³ steel cylinders (similar spatial distribution of the PVC collars), and C content was adjusted for bulk density and sampling depth. The TBCF (g C m⁻² year⁻¹) was calculated as follows: TBCF= FS-FA+CS+CR+CL.

WNPP	Wood net primary production	Estimated as the annual production of wood biomass, which was calculated from tree diameter measurements, for all trees and sites, using site and species-specific allometric equations (Supplementary Table 1); trees were sampled in two different years to estimate diameter changes. Clone site-specific dry mass equations were applied to the annual measurements, and then dry mass was converted into C.
FNPP	Foliage net primary production	Estimated from leaf area index (LAI), which was converted into dry mass using specific leaf area (SLA), plus foliage litterfall. The LAI was calculated using LAI-2000 Plant Canop. The SLA was calculated by measuring the area of fully developed leaf samples and drying them to determine the ratio between leaf area and dry mass.
ANPP	Aboveground	Estimated as the sum of WNPP and FNPP.

	net primary production	
Ra	Aboveground tree respiration	Aboveground autotrophic respiration (RA) was estimated using the equation $RA = ANPP \times (1 - CUE) / CUE$, where CUE (carbon use efficiency) was assumed to be constant at 0.53, as reported by (Campoe et al., 2012; Epron et al., 2012).
GPP	Gross primary production	Estimated as the sum of ANPP, TBCF, and Ra.
NEP	Net ecosystem Productivity	Estimated by subtracting the GPP from total tree respiration.

2.3 Data Analyses

To understand the effect of climate on the carbon allocation of the genotypes studied, they were grouped into drought-tolerant genetic materials, i.e., P7 and C3 (n=22 plots), and productive (fast-growing) genetic materials, i.e., A1, B2, and K2 (n=40 plots). We also grouped the sites into sites with low water deficit, i.e., S7 and S9 (n= 40 plots), and high water deficit, i.e., S1 and S4 (n = 28 plots).

We initially analyzed the effect of the interaction of each clonal group (CG) with the climate, i.e., CG vs. mean temperature (T) and CG vs. soil water deficit (WD), on the carbon flux and partitioning variables using generalized linear mixed models (GLMMs) for C fluxes (family = Gaussian) and C partitioning (family= binomial). The climate information was obtained from the Xavier et al. (2022) database, while water deficit (WD) was calculated based on the sequential scaled water balance proposed by Thornthwaite and Mather (Camargo, 1962). This method estimates potential evapotranspiration (PET) based on average monthly temperature. From PET, the water surplus and deficit for each month are calculated, considering precipitation and soil water retention capacity. The accumulated water deficit over the period of interest is obtained by summing the monthly water deficit values.

We first built a global model for each response variable in the following form: $Y \sim CG * T + CG * WD + (x|local)$. For random variables, we included x=precipitation for FNPP, ANPP, and GPP and partitioning to ANPP, TBCF, and Ra. For the other

variables, we used $x=1$. After fitting the models, we assessed multicollinearity by calculating the variance inflation factor (VIF) and checking the covariance between the variables (Supplementary Table 2).

From these global models, we obtained all submodels with combinations of uncorrelated variables ($r < |0.6|$) using the dredge function from the MuMIN R package (Bartón, 2020). The selection of the best model was made using the AICc (second-order Akaike information criterion) in relation to the best submodel with a value equal to or less than 4 (Burnham et al., 2011). We then performed multi-model inference (Burnham et al., 2011) through the model.avg function of the MuMin package (Bartón, 2020) to obtain the average coefficients of the explanatory variables and their significance. Additionally, the model was tested with the exclusion of 33% of the rainfall, but no interaction with fluxes and partitioning was found according to Campoe *et al.* (2020); therefore, we chose to remove rainfall exclusion from the model. To ensure the validity of the regression models, we first performed diagnostic checks on the residuals to assess the normality and homoscedasticity of the data. Normality of residuals was tested using the Shapiro-Wilk test, and homoscedasticity was assessed through residual plots.

When the proposed models indicated a significant effect for clone groups, Tukey's HSD test ($P < 0.05$) was applied to compare means. To further analyze the impact of climate on C fluxes and partitioning, simple regressions were fitted when the models identified a significant effect of these variables. The regression data met the assumptions of normality and homoscedasticity. The choice between a linear or logarithmic model was based on the lowest Akaike Information Criterion (AIC) value. The strength of the relationships was evaluated using the coefficient of determination (R^2) and the probability value (P-value), with a significance threshold of $P \leq 0.05$.

For each variable, we also evaluated the probability of a given observation occurring over specific ranges of possible values. For this, we extracted 1000 random samples from the dataset (with replacement), and for each sample we quantified the percentage of values of each variable present in five different classes, defined based on the average (Avg), standard deviation (Sd), minimum (Min), and maximum (Max) values: 1) Min to $\text{Avg} - 2 * \text{Sd}$; 2) $\text{Avg} - 2 * \text{Sd}$ to $\text{Avg} - 0.5 * \text{Sd}$; 3) $\text{Avg} - 0.5 * \text{Sd}$ to $\text{Avg} + 0.5 * \text{Sd}$; 4) $\text{Avg} + 0.5 * \text{Sd}$ to $\text{Avg} + 2 * \text{Sd}$; 5) $\text{Avg} + 2 * \text{Sd}$ to Max. Based on the results of the 1000 samples, for each class we quantified the average percentage of the occurrence of values for each variable, thus obtaining the probability that the value

for a variable from a random sample was contained in a particular class. All analyses were performed in R version 4.3.1 (R Core Team, 2023).

3. Results

3.1 Site and clonal group effects

Carbon flux and partitioning varied significantly between the groups of clones and between the groups of sites (Fig. 2 and 3). Drought-tolerant clones showed lower flux and partitioning to WNPP ($653 \text{ g C m}^{-2} \text{ yr}^{-1}$, 19%), which led to lower TBCF ($1761 \text{ g C m}^{-2} \text{ yr}^{-1}$, 51%), compared to productive clones, i.e., $1336 \text{ g C m}^{-2} \text{ yr}^{-1}$ (28%) and $1980 \text{ g C m}^{-2} \text{ yr}^{-1}$ (41%) for WNPP and TBCF, respectively.

The site group demonstrated greater susceptibility to environmental influence compared to the clonal group, as it presented greater GPP amplitude. Sites with high water deficit had lower fluxes and C partitioning to WNPP ($496 \text{ g C m}^{-2} \text{ yr}^{-1}$, 17%), which resulted in lower TBCF ($1637 \text{ g C m}^{-2} \text{ yr}^{-1}$, 55%), compared with sites with low water deficit, i.e., $1592 \text{ g C m}^{-2} \text{ yr}^{-1}$ (30%) and $2140 \text{ g C m}^{-2} \text{ yr}^{-1}$ (40%) for WNPP and TBCF, respectively.

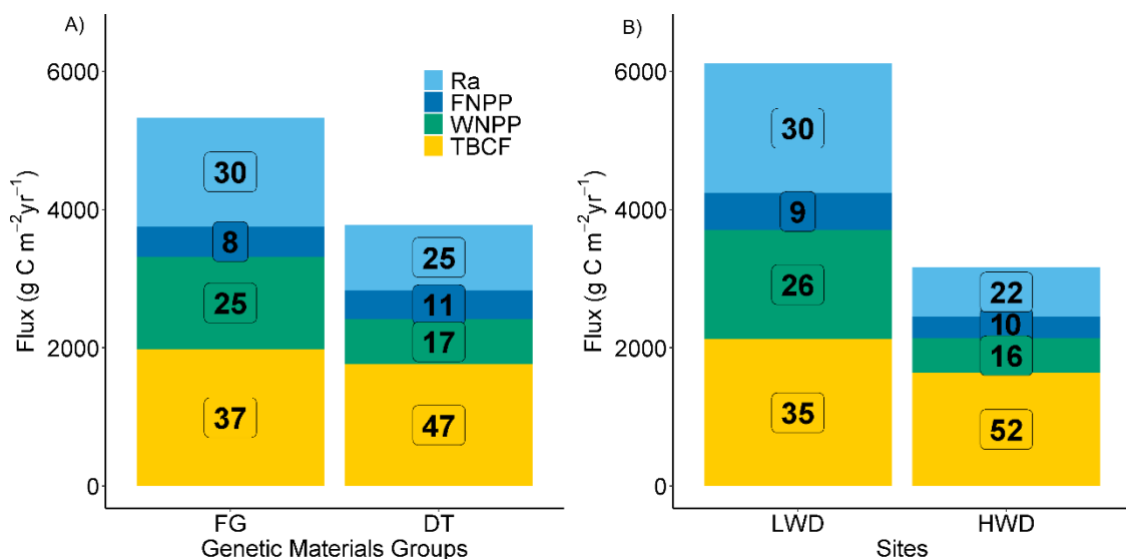


Fig. 2: Carbon fluxes for A) the fast-growing (FG) and drought-tolerant (DT) *Eucalyptus* clonal groups and B) sites with high water deficit (HWD) and low water deficit (LWD), FG clones and LWD sites had higher fluxes and wood production than DT clones and HWD sites. Partitioning (%) is numerically presented in the boxes of each bar. TBCF = total belowground carbon flux, WNPP = wood net primary production, FNPP = foliage net primary production, Ra= aboveground tree respiration.

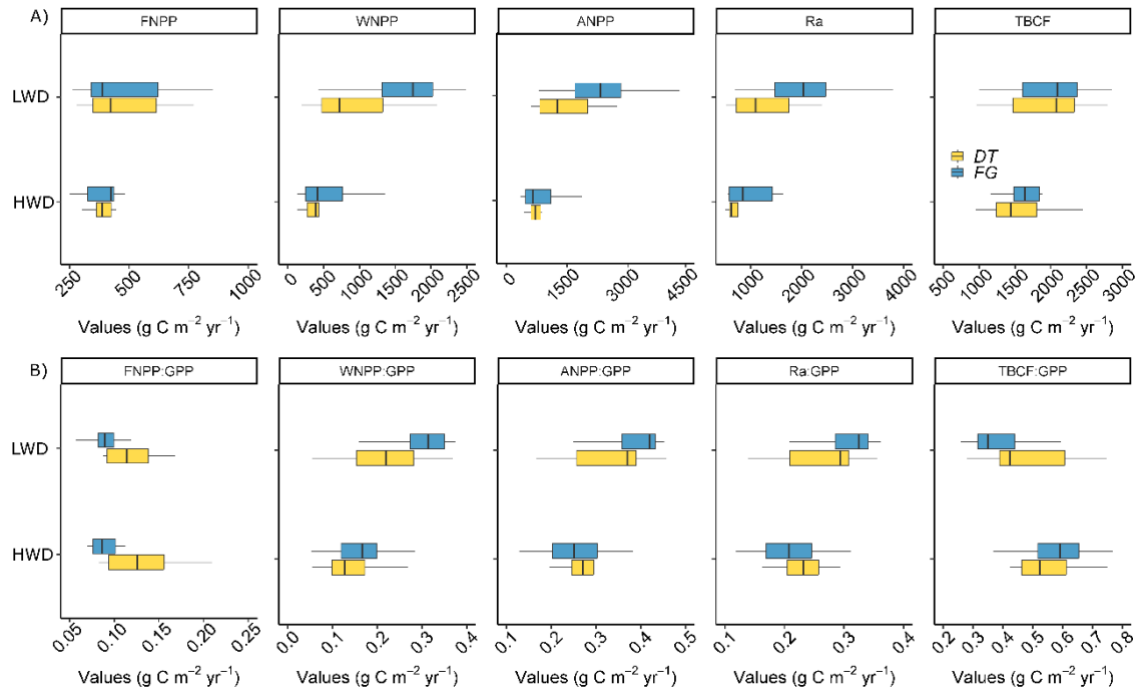


Fig. 3: Carbon fluxes for A) and partitioning B) for the fast-growing (FG- blue) and drought-tolerant (DT-yellow) *Eucalyptus* clonal groups, in sites with high water deficit (HWD) and low water deficit (LWD). FG clones and LWD sites showed higher carbon fluxes and greater wood production compared to DT clones and HWD sites. TBCF = total belowground carbon flux, WNPP = wood net primary production, FNPP = foliage net primary production, Ra= aboveground tree respiration.

3.2 Climate and genotype modeling of carbon balance in forests plantations

The main results of GLMM are in Table 5, the Categorical variables had a significant effect ($P < 0.05$) on C fluxes and partitioning. For clonal group, only FNPP and TBCF did not exhibit a significant effect. In general, we observed that the fast-growing clones presented higher means than the drought-tolerant clones (Table 6) based on the Tukey test ($P < 0.05$).

Table 5: Effect sizes (estimates) of categorical and continuous explanatory variables on carbon fluxes ($\text{g C m}^{-2} \text{ yr}^{-1}$) and carbon partitioning (ratios) based on generalized linear mixed models (GLMMs) for drought-tolerant and fast-growing *b* clonal groups (CG) in Brazil. Model selection was performed using the dredge function based on AICc. Positive estimates indicate a positive relationship between the explanatory variable and the response variable, while negative estimates indicate a negative relationship. Estimates followed by * represent statistically significant effects ($p < 0.05$), and those followed by ns indicate non-significant effects. FNPP = foliage net primary production, WNPP = wood net primary production, ANPP = aboveground net primary production, TBCF = total belowground carbon flux, Ra = aboveground tree respiration, GPP = gross primary production, NEP = net ecosystem production, T-mean = mean temperature, WD = water deficit.

Variable	Model Selection Using the Dredge Function	CG	CG*T-mean	CG*WD	T-mean	WD
FNPP	$y = \text{CG} * \text{Tmean} + \text{CG} * \text{WD} + (\text{P} \text{site})$	-38.31ns	-39.42*	-10.76ns	12.50ns	14.87ns
WNPP	$y = \text{CG} * \text{Tmean} + \text{CG} * \text{WD} + (1 \text{site})$	559.70*	-70.24*	-56.74*	67.74n	246.35ns
ANPP	$y = \text{CG} * \text{Tmean} + \text{CG} * \text{WD} + (\text{P} \text{site})$	553.00*	-414.31*	-395.53*	6.42n	270.18*
TBCF	$y = \text{CG} * \text{Tmean} + (1 \text{site})$	78.84ns	22.22ns		- 357.74*	
Ra	$y = \text{CG} * \text{Tmean} + \text{CG} * \text{WD} + (\text{P} \text{site})$	372.08*	-266.53*			
GPP	$y = \text{CG} * \text{Tmean} + \text{CG} * \text{WD} + (\text{P} \text{site})$	932.2*	-504.70*	486.9*	200.70ns	114.26ns
NEP	$y = \text{CG} * \text{Tmean} + (1 \text{site})$	828.81*	-589.56*		- 415.07ns	
FNPP:GPP	$y = \text{CG} * \text{Tmean} + (1 \text{site})$	-0.03*	-0.013*		0.41*	
WNPP:GPP	$y = \text{CG} * \text{WD} + (1 \text{site})$	0.45*		0.08ns		- 0.05*
ANPP:GPP	$y = \text{CG} * \text{Tmean} + (\text{P} \text{site})$	0.18*	-0.04*		- 0.39ns	
TBCF:GPP	$y = \text{CG} * \text{Tmean} + (\text{P} \text{site})$	-0.31*	0.20*		0.78ns	
Ra:GPP	$y = \text{CG} * \text{Tmean} + (\text{P} \text{site})$	0.18*	-0.29*		- 0.75ns	

Table 6: Averages C fluxes ($\text{g C m}^{-2} \text{ yr}^{-1}$) and partitioning (ratio) for the clonal groups-CG (fast-growing-FG and drought-tolerant-DT). We observed that fast-growing clones had greater C fluxes and higher aboveground C partitioning, which occurred at the expense of belowground partitioning. Means with different letters differ from each other based on the Tukey test ($P < 0.05$). FNPP = foliage net primary production, WNPP = wood net primary production, ANPP = aboveground net primary production, TBCF = total belowground carbon flux, Ra = aboveground tree respiration, GPP = gross primary production, NEP = net ecosystem production

CG	FNPP	WNPP	ANPP	TBCF	Ra	NEP
FG	447a	1378a	1662a	1999a	1680a	1723a
DT	417a	653b	1070b	1762a	949b	949b
CG	FNPP:GPP	WNPP:GPP	ANPP:GPP	TBCF:GPP	Ra:GPP	GPP
FG	0.09b	0.25a	0.34a	0.45b	0.20a	4871a
DT	0.13a	0.17b	0.30b	0.52a	0.18a	3781b

For the clonal group vs. mean temperature interaction, only TBCF and WNPP:GPP did not show a significant effect (Table 4). For fluxes (Fig. 4), we observed a decrease for both clonal groups with increasing temperature. In general, GPP decreased more intensely for fast-growing clones than drought-tolerant clones because of their higher slope. For partitioning (Fig. 5), in terms of FNPP:GPP, drought-tolerant clones exhibited an increase in the mean values while fast-growing clones showed no change with increasing temperature. For ANPP:GPP, both clonal groups reduced C partitioning with increasing temperature. For TBCF:GPP, the GLMM demonstrated no changes in partitioning for the drought-tolerant clones while the fast-growing clones showed an increase in partitioning with increasing temperature. However, the linear model indicated that with every one degree rise in temperature, the drought-tolerant and fast-growing clones exhibited ANPP:GPP decreases of $\sim 1\%$ and $\sim 3\%$ and TBCF:GPP increases of $\sim 2\%$ and $\sim 4\%$, respectively (Fig. 5). For respiration, fast-growing clones tended to decrease partitioning with increasing temperature, while the drought-tolerant clones tended to increase partitioning, while the drought-tolerant clones did not exhibit significant changes in their values in response to rising temperatures.

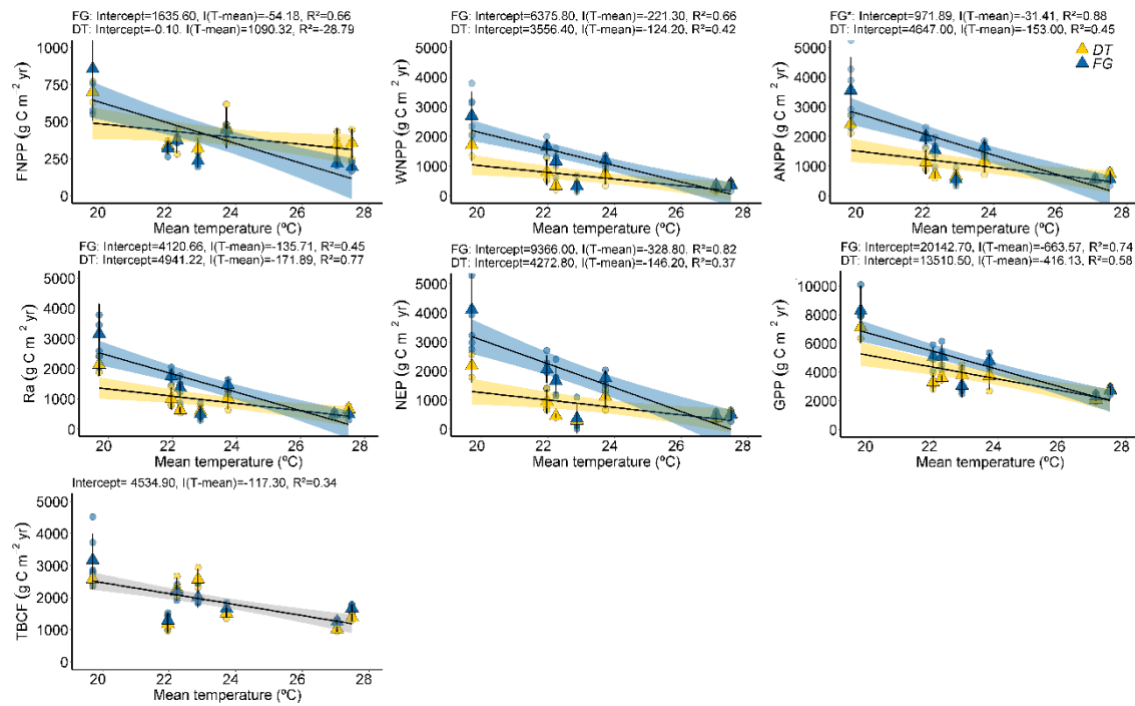


Fig. 4 The effect of the interaction between drought-tolerant (DT) (yellow) and fast-growing (FG) (blue) clonal groups with mean temperature ($^{\circ}\text{C}$) on the fluxes of foliage net primary production (FNPP), wood net primary production (WNPP), aboveground net primary production (ANPP), aboveground tree respiration (Ra), net ecosystem production (NEP), and gross primary production (GPP), and the clones mean valor of total belowground carbon flux fluxes (TBCF), obtained by GLMM. We observed that fast-growing clones had greater C fluxes, and for both groups, the fluxes decreased with increasing temperature. The circles represent the observed data, and the triangles represent the average values for each temperature point. The predictive models shown in the graphs were obtained through linear models. Models followed by * the variable y presented exponential transformation

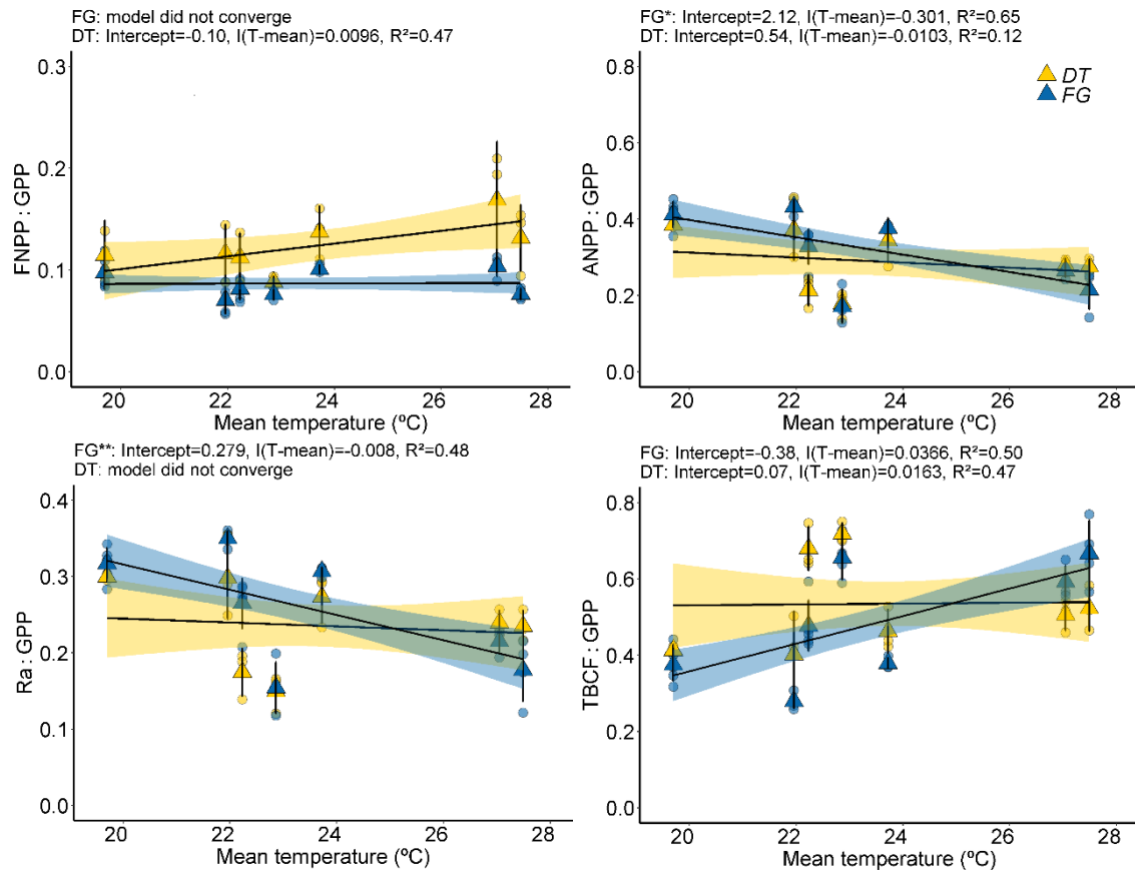


Fig. 5 The effect of the interaction between drought-tolerant (yellow) and fast-growing (blue) clonal groups and temperature (°C) on partitioning of leaf net primary production (FNPP), aboveground net primary production (ANPP), aboveground tree respiration (Ra), and bellow ground carbon flux (TBCF), obtained by GLMM. Drought-tolerant clones were more conservative in reducing C partitioning at different temperatures than fast-growing clones. As a survival strategy in locations with thermal stress, the drought-tolerant clones tended to exhibit an increase in FNPP:GPP due to the greater leaf fall from the trees. In addition, for drought-tolerant clones, high values of TBCF:GPP were retained regardless of temperature. The circles represent the observed data, and the triangles represent the average values for each temperature point. The predictive models shown in the graphs were obtained through linear models. Models followed by * the variable y presented Box–Cox transformation, ** the variable y was squared (y^2).

The interaction between clonal groups and water stress was significant only for the WNPP, ANPP, Ra, and GPP fluxes, all of which decreased with increasing water stress. Each 100 mm increase in the water deficit resulted in decreases of ~ 140 and ~ 270 g C m² yr⁻¹ for wood production and ~ 280 and ~ 552 g C m² yr⁻¹ for GPP for drought-tolerant and fast-growing clones, respectively (Fig. 6).

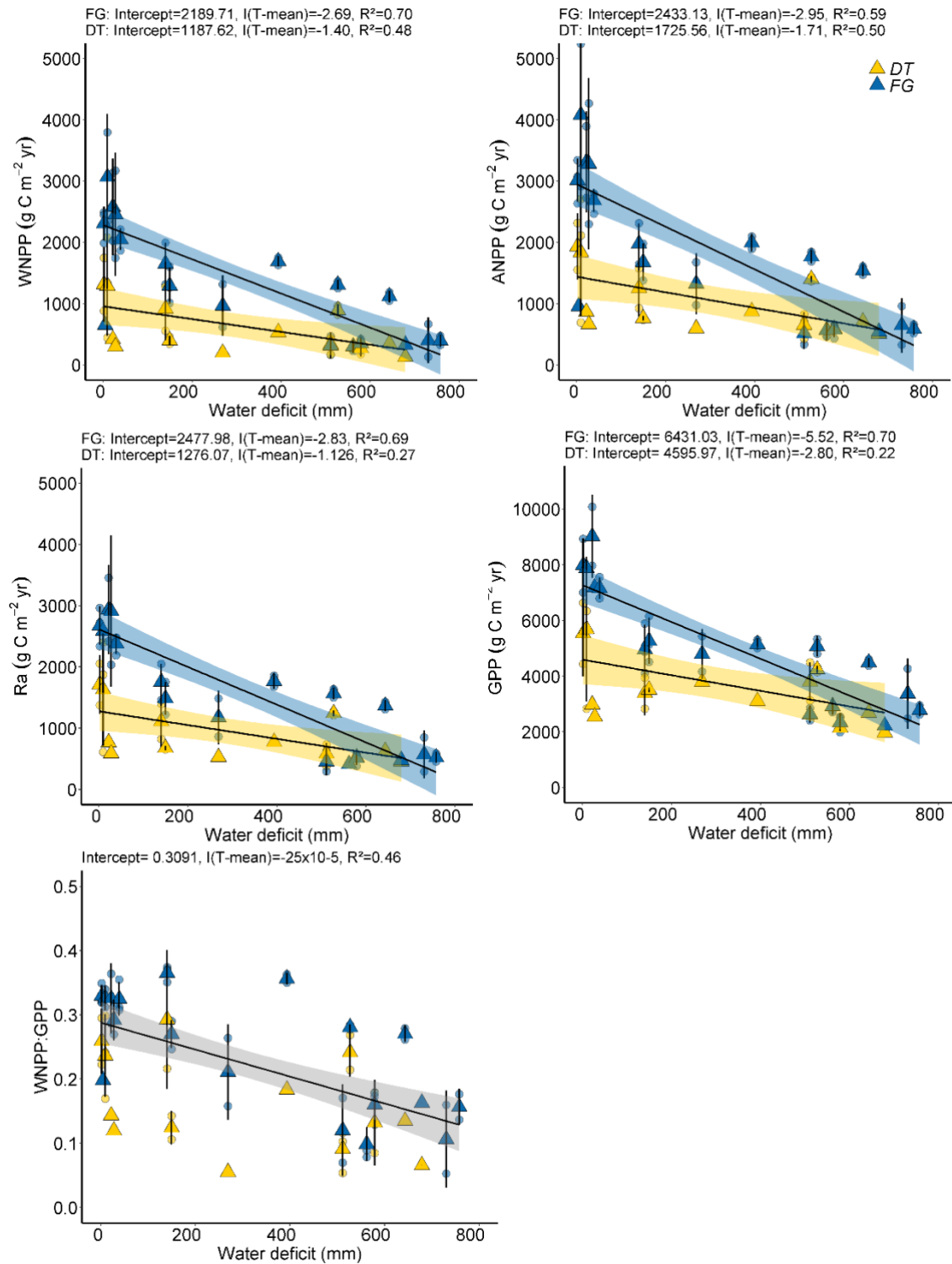


Fig. 6: The effect of the interaction between drought-tolerant (DT) (yellow) and fast-growing (FG) (blue) clonal groups with soil water deficit (mm) on wood net primary production (WNPP), aboveground net primary production (ANPP), aboveground tree respiration (Ra), gross primary production (GPP), and the clones mean value r of C partitioning (ratio) to wood net primary production (WNPP:GPP), obtained by GLMM. FG clones had higher fluxes than DT clones, and the fluxes decreased significantly with

increasing water deficit. The circles represent the observed data, and the triangles represent the average values for each temperature point. The predictive models shown in the graphs were obtained through linear models.

3.3 Carbon partitioning probability

When analyzing the partitioning probability for WNPP, we observed that the clonal groups presented antagonistic distributions, in which fast-growing clones tended to have a higher probability of occurrence (39%) of partitioning values higher than 0.3, Fig. 7. By contrast, drought-tolerant clones had a higher probability of occurrence (57%) of partitioning values between < 0.20 . Regarding the partitioning to TBCF, we observed that the clonal groups presented similar distributions; however, the fast-growing clones had a 4% of probability to have low partitioning values < 0.40 . While drought-tolerant clones had a higher probability (45%) of partitioning values < 0.40 .

Regarding FNPP:GPP, we observed that the fast-growing group presented a range of 0.05 to 0.13 while the drought-tolerant group presented a range of 0.05 to 0.23. Both clonal groups showed a higher partitioning probability for FNPP in the range of 0.09 to 0.12, than the another classes. For autotrophic respiration (Ra:GPP), both clonal groups showed higher probability of occurring in the partitioning above 0.24.

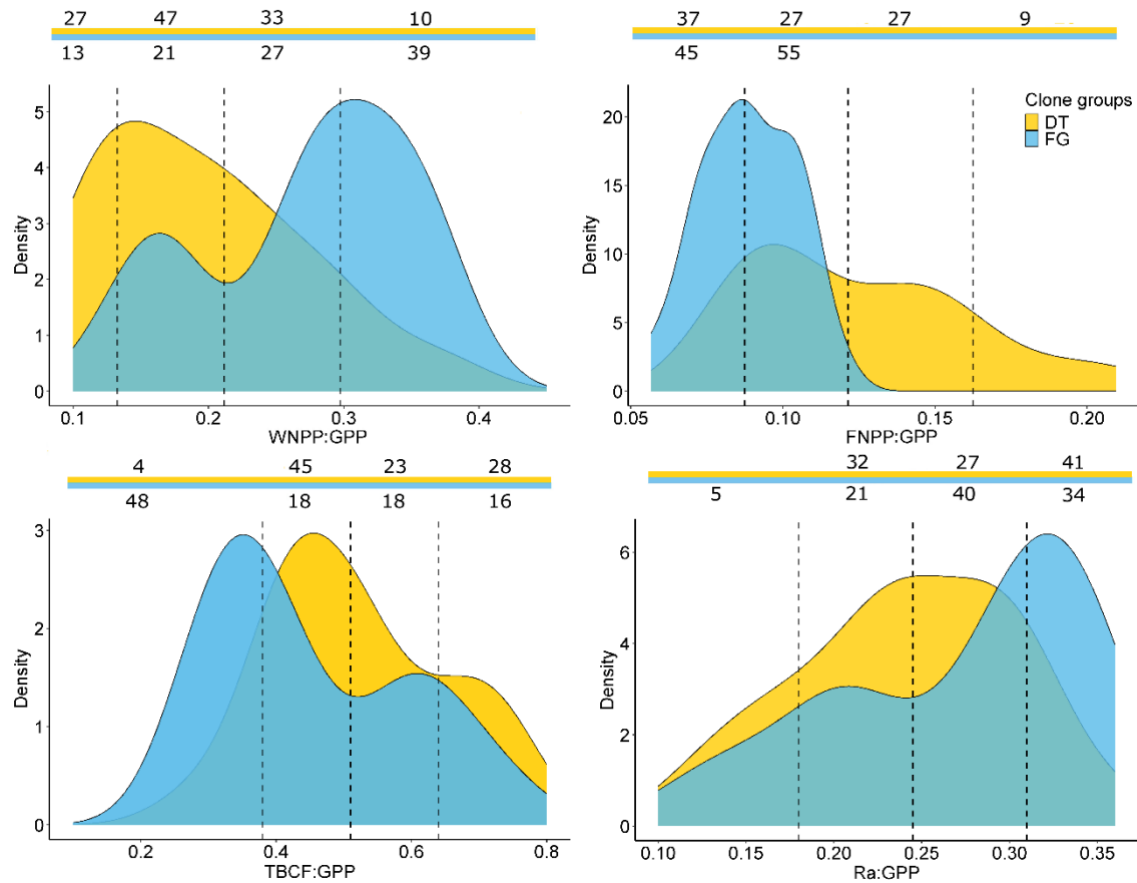


Fig. 7: Probability (%) of carbon partitioning (ratio) to wood production (WNPP:GPP), leaf production (FNPP:GPP), total aboveground respiration (Ra:GPP), and total belowground carbon flux (TBCF:GPP) in drought-tolerant (DT) clones, shown in yellow, and fast-growing (FG) clones, shown in blue, under contrasting climatic conditions in Brazil. Each break represents the carbon partitioning classes. The probability of occurrence of each partitioning proportion is indicated in the bar above the density curves, with values corresponding to each clone color. The fast-growing clones tended to have a higher probability of carbon partitioning to wood production in the higher mean classes (>0.3) and a higher probability of carbon partitioning to root production (<0.4), the opposite it is observed for drought-tolerant clones.

4 Discussion

4.1 Water stress adaptation strategies

Under stressful conditions, plants always prioritize the use of carbon for survival strategies at the expense of their biomass growth or other physiological functions that are not a priority for the immediate survival of the plant (Wiley & Helliker, 2012). The C allocation hierarchy for a tree depends on its genetic characteristics (adaptation) and its

plasticity in the face of environmental and climatic variations (acclimatization). In this context, the present work contributes to an understanding of genetic and climatic effects separately, creating opportunities to establish management strategies to mitigate the negative effect of climate on productivity.

In the present work, we observed that drought-tolerant clones had lower GPP ($\sim 3781 \text{ g C m}^{-2} \text{ year}^{-1}$) than fast-growing clones ($\sim 5332 \text{ g C m}^{-2} \text{ year}^{-1}$). In addition, the drought-tolerant clones, had greater partitioning of C to root system production (51) at the expense of wood production (19%), than fast growing clones, which led us to accept our first hypothesis. In Fig. 4, it is clear that the drought-tolerant clones did not prioritize C partitioning to wood production, allocating more energy to root production, as previously shown by Campoe et al. (2020). The lower GPP of the drought-tolerant clones can be linked to the conditions of the regions in which they developed, i.e., regions with high temperatures and water deficits. The genetic materials within a clonal group presented similar physiological and morphological characteristics, which led to distinct C partitioning patterns between the clonal groups.

The drought-tolerant clones studied exhibited lower growth and productivity across different climatic gradients in Brazil compared with the fast-growing clones (Binkley et al., 2017). This growth pattern is associated with the fact that drought-tolerant clones tend to invest more energy in water stress survival strategies than in biomass production. Different drought-tolerance mechanisms have been found for *Eucalyptus*, such as the growth pattern of the root system. For example, Basílio et al. (2024) found that drought-tolerant clones, aged three years, reached greater depths and had higher fine root biomass (means of 7 m and 7 Mg ha^{-1}) than fast-growing clones (5.8 m and 5.5 Mg ha^{-1}). We found that drought-tolerant clones exhibited approximately 10% higher TBCF values. Moreover, as shown in Figure 8, drought-tolerant clones demonstrated a 96% probability of allocating at least 40% of their carbon to root production. This strategy guarantees greater survival for these clones during the dry period, allowing greater access to deeper water reserves in the soil. Hubbard et al. (2020) found that clone C3 (drought-tolerant) had higher water use than clone A1 (fast-growing) at sites with high water deficit, which may be associated with its greater rooting depth. Clone C3 is an *E. grandis* $\times$ *E. camaldulensis* hybrid; *E. camaldulensis* originates from dry areas in Australia and depends on the deep growth of the root system to access groundwater (Dvorak, 2012; Nolan et al., 2018).

One of the ways to avoid water loss through transpiration is to reduce leaf biomass. Drought-tolerant clones have an average leaf area index (LAI) of 2.18, while fast-growing

clones have a LAI of 3.26 (Mattos et al., 2020). According to the authors, the drought-tolerant clones also have accentuated leaf angles compared to fast-growing clones, preventing direct exposure to the sun during the hottest times and periods with the greatest vapor pressure deficit. Furthermore, drought-tolerant clones have stomata on both leaf surfaces (amphistomatous), a higher density of stomata, and smaller stomata, resulting in less water loss and intensifying gas exchange in a short period (Pech). Furthermore, the leaves of the drought-tolerant clones have only palisade parenchyma, which guarantees greater protection of the leaf tissue against water loss, while the fast-growing clones have lacunose parenchyma and palisade parenchyma (Pech, 2024). In addition to the adaptive characteristics of clones in terms of water deficit conditions, they may also present certain plasticity related to their acclimatization process under different water and thermal stress conditions.

4.2 Strategies for acclimatization to water deficit

The plantations responded with a 21% reduction in GPP with increases in temperature and water deficit, with an increase in C partitioning to root system production in 27%, which led us to accept our second hypothesis. According with GLMM, we observed that there were a significant climate x genetic group interactions (Table 4).

Temperature was the main climatic variable that exhibited an interaction with the genetic groups, with a positive effect on root system growth and a negative effect on the flux of aboveground components for both clonal groups. However, the fast-growing clones had a higher slope than drought-tolerant clones, which demonstrates that they are more sensitive to changes in temperature, presenting a greater loss of productivity (three times higher) compared to the drought-tolerant clones. We observed that for each 1°C increase, the fast-growing clones reduced C partitioning to ANPP (3%) by a factor of three, which decreased TBCF (3%), compared with the drought-tolerant clones.

For FNPP:GPP, the fast-growing clones did not show significant changes, while the drought-tolerant clones exhibited an increase with an increase in the average temperature. This partitioning pattern is related to the greater loss of leaves by this group of clones, to mitigate water stress on the remaining foliage, driving the desiccation rate (Limousin et al., 2010). B silio (in prep.) recorded greater litter deposition for clone C3 (drought-tolerant) at a site with high water deficit over time compared to clone A1 (fast-growing). Trees need to invest more energy to compensate for foliage loss and maintain their metabolic regulation.

For TBCF:GPP, we observed that drought-tolerant clones were insensitive to increased temperature, while fast-growing clones showed a significant increase in TBCF:GPP. Basílio et al. (2024) found no significant change in the fine root biomass of clone C3 (drought-tolerant) at sites S30 (high water deficit) and S22 (low water deficit), with an average of 6.23 Mg ha⁻¹, while clone A1 (fast-growing) had 22% higher root biomass at the site with high water deficit.

Although the clonal groups responded differently to increasing temperatures, however, extremes temperatures tend to reduce the GPP, and the partitioning for wood production at the expense of the root system grow (Campoe et al., 2020; Litton et al., 2007). Queiroz et al. (2020, 2023) found that *Eucalyptus* plantation growth follows a bell-shaped curve, in which the ideal average temperature for fast-growing clones is around 19.6°C and for drought-tolerant clones is 21.6 °C.

At high temperatures, the decline in photosynthesis is attributed to numerous processes, including increased photorespiration, increased mitochondrial respiration, Rubisco inactivation attributed to reduced Rubisco activase activity, decreased photosystem II (PSII) activity, and damage to the thylakoid membrane, which results in a reduction in ATP synthesis (Crafts-Brandner & Salvucci 2004, Haldimann & Feller 2004, Hozain et al. 2010). Heat stress and water stress are often linked, and each tends to amplify the stress caused by the other (Choat et al., 2018). Mortality from drought is much more likely than mortality from heat stress, but the severity of drought stress and the speed of its onset increase greatly under high temperatures (McDowell 2011, Teskey et al. 2015).

For the interaction between the clonal groups and the water deficit, we observed that the drought-tolerant clones presented lower C fluxes, and under the most extreme conditions (water deficit between 600 and 800 mm), the clonal groups tended to present similar C fluxes. According to Kozłowski and Pallardy (2002), a slow increase in stress can induce a physiological adjustment that protects plants from the growth inhibition and/or injury that follows when environmental stress is abruptly imposed. We observed that water stress affected only C partitioning (Fig. 5); each 100 mm increase in the water deficit decreased the ANPP by ~171 and ~295 g C cm⁻² yr⁻¹ for the drought-tolerant and fast-growing clones, respectively. Campoe et al. (2020) also found a small influence of water deficit on C balance compared to temperature. These results indicate that clonal groups respond differently to water stress, suggesting that carbon partitioning strategies may be a key factor in determining survival and productivity under drought conditions.

Fast-growing clones exhibit varying degrees of plasticity in carbon partitioning, allowing them to adjust their allocation between wood production and root growth in response to environmental stress. For example, Clone A1, classified as highly productive and plastic (Scolforo et al., 2019), reduces carbon allocation to wood while increasing root investment under stressful conditions (Campoe et al., 2020). However, even in plastic genotypes, high-intensity stress can significantly reduce productivity and survival. Despite these general patterns, carbon partitioning strategies can vary within the same clonal group. For instance, Clone B2, another highly productive genotype, maintains high wood allocation regardless of climatic conditions (Campoe et al., 2020). As a result, when exposed to thermal and water stress, it exhibited high mortality rates (Binkley et al., 2020). This highlights the trade-off between growth and stress tolerance: while some clones can temporarily shift allocation strategies to withstand drought, others may prioritize productivity at the cost of survival. These findings emphasize the importance of genetic selection strategies in forestry, particularly for regions with high water deficits, where efficient breeding programs are crucial to ensuring minimum productivity thresholds and plantation viability under climate stress. Beyond differences in carbon allocation, drought tolerance also involves physiological and morphological adjustments that directly impact gas exchange, defense mechanisms, and overall carbon fluxes.

In adaptive responses to water stress, plants invest in morphological or physiological changes and defense processes, which consequently reduce C fluxes and GPP, as these processes are expensive for the plant because defense compounds are rich in C (Chaves et al. 2002, Bilgin et al. 2010). There is a reduction in CO₂ diffusion due to the closure of stomata, resulting in a lower rate of net C assimilation (Hummel et al., 2010). Controlling stomatal opening is one of the main defense mechanisms to reduce water loss by plants. (Santos et al., 2024) found that clone C3 (drought-tolerant) has greater stomatal opening compared to that of A1 (fast-growing), indicating that fast-growing clones have greater susceptibility to climate change, as observed in Figs 5, 6, and 7. Pech (2020) found for the same clones that when subjected to a 33% reduction in rainwater, trees increased stomatal density compared to those in locations without rain exclusion. Clones also change their water use pattern; at high water deficit sites, they show lower water use compared to those at low water deficit sites (Hubbard et al., 2020). At intermediate levels of drought stress, plants reduce growth and increase carbon partitioning for their defense system (Herms & Mattson 1992, Stamp 2003, Navarro et al. 2008). However, when the metabolic demand of a plant is greater than the reserves of non-structural C and C from photosynthesis, the plant

collapses, increasing its vulnerability to pests and diseases, and may die (McDowell, 2011).

Climate studies predict future increases in drought events and their intensity in the tropics, which will impact water use and the productivity of forestry plantations. Binkley et al. (2020) found 15% lower wood biomass at sites with high water deficit compared to sites with low water deficit. We observed that plantations prioritize the allocation of C belowground at the expense of wood production at locations with high water deficit. One of the greatest contributions of this work is the delivery of valuable information about the C partitioning strategy of two clonal groups of *Eucalyptus*. With the data presented, we can state that there is a large trade-off between productivity and drought-tolerance mechanisms. Furthermore, drought-tolerant clones showed less influence of climate variables on C balance compared to fast-growing clones. Within this context, it is necessary to investigate the behavior of ecophysiological variables for each clonal group under different silvicultural management options to achieve better plantation productivity. This information is timely to guide the understanding of drought-tolerance mechanisms and establish more sustainable and efficient management of forest plantations, in addition to enabling the more efficient use of ecophysiological models and the development of genetic improvement programs along different climate gradients.

5. Conclusion

Drought-tolerant clones had lower GPP and higher C investment belowground than aboveground for wood growth compared to fast-growing clones. The clones at sites with lower soil water deficit had higher carbon fluxes and higher investment in wood production. Temperature was distinguished as the most important climate variable in changes in carbon fluxes and partitioning. For fast-growing clones, there was a three-fold reduction in carbon partitioning to wood production compared to drought-tolerant clones.

For both clonal groups under optimal climatic conditions, there was an increase in partitioning to wood production. However, we observed that drought-tolerant clones showed a more conservative behavior in changing their carbon allocation patterns. We did not find significant changes in carbon partitioning belowground, which is one of the main strategies of the drought-tolerant group for survival in locations with climatic stresses. Furthermore, as a way of reporting leaf losses caused by climatic stresses, drought-tolerant clones increased partitioning to FNPP.

6 Acknowledgments

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7 Supplementary materials

Supplementary Table 1: Estimates for the intercept and the slope coefficient, as well as the p-values for the intercept and the slope, providing a deeper insight into the fit of the adjusted models ($\ln(y) = \beta_0 + \beta_1 * \ln(D2H)$) for each site and clone analyzed.

Component	Site	Clone	Intercept	Slope	RSE	R ²	Model (p- value)	Intercept (p- value)	Slope (p- value)
Steam Biomass	S7	A1	4.94	0.99	0.05	0.99	0.00	0.00	0.00
Steam Biomass	S7	B2	5.16	1.20	0.11	0.94	0.00	0.00	0.00
Steam Biomass	S7	C3	4.69	0.86	0.04	0.98	0.00	0.00	0.00
Steam Biomass	S7	K2	4.91	0.97	0.08	0.98	0.00	0.00	0.00
Steam Biomass	S7	P7	4.34	0.68	0.11	0.83	0.01	0.00	0.01
Steam Biomass	S9	A1	4.82	0.87	0.04	0.98	0.00	0.00	0.00
Steam Biomass	S9	B2	4.79	0.88	0.03	0.99	0.00	0.00	0.00
Steam Biomass	S9	C3	4.56	0.80	0.03	0.96	0.00	0.00	0.00
Steam Biomass	S9	K2	4.95	1.01	0.04	0.99	0.00	0.00	0.00
Steam Biomass	S9	P7	5.05	0.99	0.04	0.97	0.00	0.00	0.00
Steam Biomass	S1	A1	4.80	1.03	0.11	0.97	0.00	0.00	0.00
Steam Biomass	S1	B2	4.63	0.95	0.07	0.99	0.00	0.00	0.00
Steam Biomass	S1	C3	4.89	1.03	0.04	1.00	0.00	0.00	0.00
Steam Biomass	S1	K2	4.81	1.04	0.07	0.98	0.00	0.00	0.00
Steam Biomass	S1	P7	3.97	0.56	0.08	0.86	0.01	0.00	0.01
Steam Biomass	S4	A1	4.61	0.84	0.04	0.98	0.00	0.00	0.00
Steam Biomass	S4	B2	4.84	0.94	0.08	0.97	0.00	0.00	0.00
Steam Biomass	S4	C3	4.69	0.91	0.08	0.97	0.00	0.00	0.00

Steam Biomass	S4	P7	4.84	0.89	0.08	0.96	0.00	0.00	0.00
Bark biomas	S7	A1	2.79	1.01	0.05	0.99	0.00	0.00	0.00
Bark biomas	S7	B2	2.71	1.16	0.12	0.93	0.00	0.00	0.00
Bark biomas	S7	C3	2.44	0.82	0.06	0.95	0.00	0.00	0.00
Bark biomas	S7	K2	2.69	0.97	0.05	0.99	0.00	0.00	0.00
Bark biomas	S7	P7	2.23	0.70	0.06	0.95	0.00	0.00	0.00
Bark biomas	S9	A1	2.61	0.87	0.04	0.98	0.00	0.00	0.00
Bark biomas	S9	B2	2.59	0.88	0.03	0.99	0.00	0.00	0.00
Bark biomas	S9	C3	2.35	0.80	0.03	0.96	0.00	0.00	0.00
Bark biomas	S9	K2	2.74	1.01	0.04	0.99	0.00	0.00	0.00
Bark biomas	S9	P7	2.84	0.99	0.04	0.97	0.00	0.00	0.00
Bark biomas	S1	A1	2.59	1.03	0.11	0.97	0.00	0.00	0.00
Bark biomas	S1	B2	2.42	0.95	0.07	0.99	0.00	0.00	0.00
Bark biomas	S1	C3	2.68	1.03	0.04	1.00	0.00	0.00	0.00
Bark biomas	S1	K2	2.60	1.04	0.07	0.98	0.00	0.00	0.00
Bark biomas	S1	P7	1.77	0.56	0.08	0.86	0.01	0.00	0.01
Bark biomas	S4	A1	2.70	0.86	0.03	0.99	0.00	0.00	0.00
Bark biomas	S4	B2	2.20	0.81	0.21	0.79	0.01	0.00	0.01
Bark biomas	S4	C3	2.51	0.87	0.07	0.98	0.00	0.00	0.00
Bark biomas	S4	P7	2.64	0.70	0.07	0.96	0.00	0.00	0.00
Dead/live									
Branch biomass	S7	A1	3.03	0.82	0.26	0.69	0.03	0.00	0.03
Dead/live									
Branch biomass	S7	B2	3.09	0.93	0.12	0.89	0.00	0.00	0.00
Dead/live									
Branch biomass	S7	C3	2.89	0.75	0.20	0.57	0.05	0.00	0.05
Dead/live									
Branch biomass	S7	K2	3.61	0.99	0.22	0.88	0.00	0.00	0.00
Dead/live	S7	P7	3.13	0.72	0.12	0.82	0.01	0.00	0.01

Branch									
biomass									
Dead/live									
Branch	S9	A1	3.65	0.61	0.15	0.61	0.04	0.00	0.04
biomass									
Dead/live									
Branch	S9	B2	4.30	1.57	0.15	0.89	0.00	0.00	0.00
biomass									
Dead/live									
Branch	S9	C3	3.20	0.73	0.10	0.56	0.05	0.00	0.05
biomass									
Dead/live									
Branch	S9	K2	4.07	1.12	0.30	0.54	0.06	0.00	0.06
biomass									
Dead/live									
Branch	S9	P7	3.62	0.75	0.10	0.74	0.02	0.00	0.02
biomass									
Dead/live									
Branch	S1	A1	3.38	1.20	0.16	0.95	0.00	0.00	0.00
biomass									
Dead/live									
Branch	S1	B2	2.28	0.69	0.19	0.89	0.00	0.00	0.00
biomass									
Dead/live									
Branch	S1	C3	3.40	0.84	0.24	0.82	0.01	0.00	0.01
biomass									
Dead/live									
Branch	S1	K2	4.13	1.24	0.16	0.93	0.00	0.00	0.00
biomass									
Dead/live									
Branch	S1	P7	3.01	0.74	0.07	0.94	0.00	0.00	0.00
biomass									
Dead/live	S4	A1	4.73	2.01	0.11	0.98	0.00	0.00	0.00

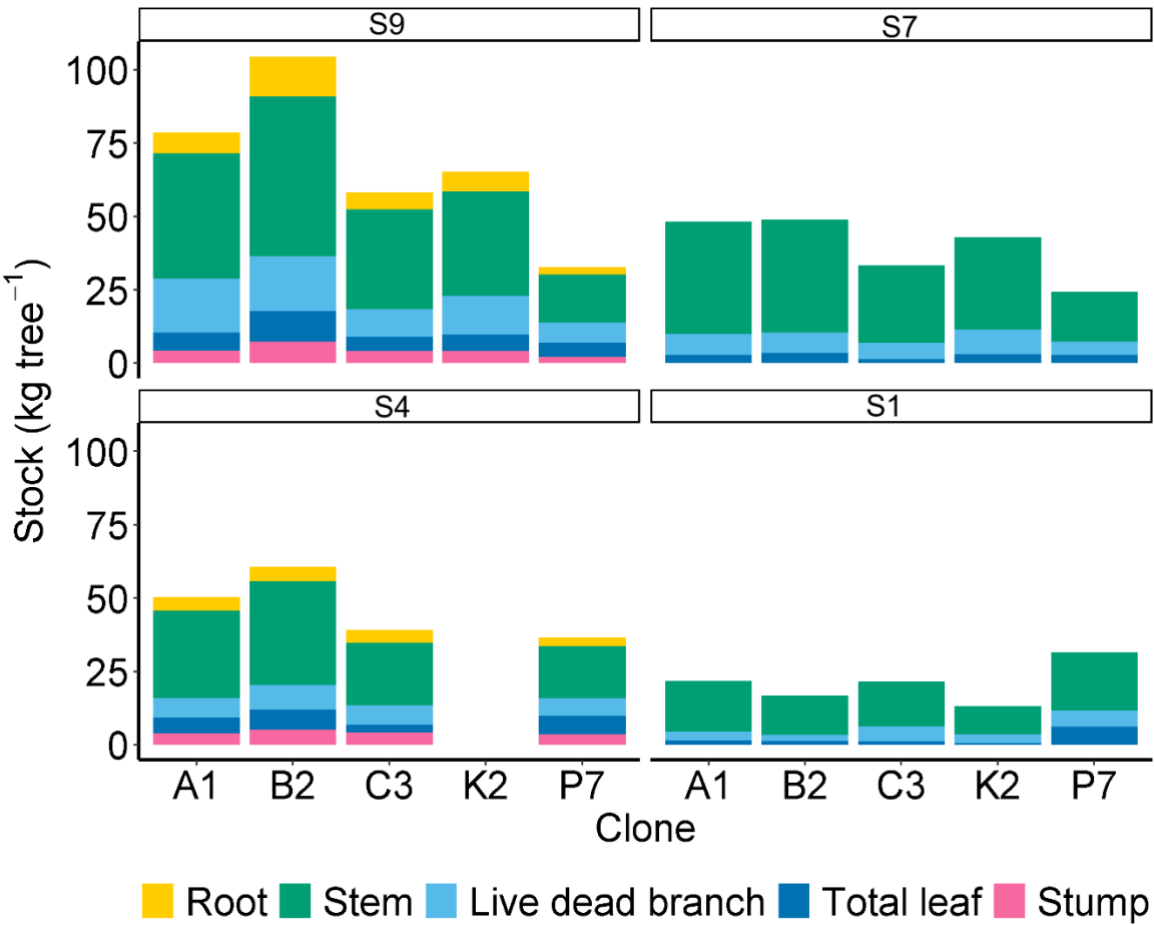
Total leaf biomass	S1	B2	2.65	1.19	0.44	0.81	0.01	0.01	0.01
Total leaf biomass	S1	C3	2.34	1.10	0.18	0.93	0.00	0.00	0.00
Total leaf biomass	S1	K2	1.87	1.09	0.20	0.86	0.00	0.02	0.00
Total leaf biomass	S1	P7	3.98	1.26	0.09	0.96	0.00	0.00	0.00
Total leaf biomass	S4	A1	3.46	1.26	0.15	0.90	0.00	0.00	0.00
Total leaf biomass	S4	B2	3.38	1.13	0.26	0.84	0.01	0.00	0.01
Total leaf biomass	S4	C3	2.78	1.05	0.12	0.95	0.00	0.00	0.00
Total leaf biomass	S4	P7	3.52	0.76	0.06	0.97	0.00	0.00	0.00
Roots+Stump Biomass	S9	A1	4.18	1.46	0.10	0.96	0.00	0.00	0.00
Roots+Stump Biomass	S9	B2	4.41	1.54	0.19	0.82	0.01	0.00	0.01
Roots+Stump Biomass	S9	C3	3.33	0.81	0.02	0.98	0.00	0.00	0.00
Roots+Stump Biomass	S9	K2	3.81	1.05	0.19	0.74	0.02	0.00	0.02
Roots+Stump Biomass	S9	P7	4.24	1.18	0.12	0.84	0.01	0.00	0.01
Roots+Stump Biomass	S4	A1	3.56	0.98	0.14	0.85	0.01	0.00	0.01
Roots+Stump Biomass	S4	B2	3.60	0.95	0.22	0.84	0.01	0.00	0.01
Roots+Stump Biomass	S4	C3	4.11	1.11	0.10	0.97	0.00	0.00	0.00
Roots+Stump Biomass	S4	P7	3.15	0.58	0.11	0.85	0.01	0.00	0.01

Biomass

Supplementary table 2: Generalized Variance Inflation Factor for the GLMM models for the variables

Flux/Partitioning	Variable	Generalized Variance Inflation Factor
FNPP	GE	1.05
	WD	3.19
	Tmean	2.72
	GE:Tmean	3.83
	GE:WD	3.32
WNPP	GE	2.99
	WD	7.10
	Tmean	4.67
	GE:Tmean	11.15
	GE:WD	12.82
ANPP	GE	4.15
	WD	1.06
	Tmean	3.66
	GE:Tmean	4.06
	GE:WD	3.56
Ra	GE	1.02
	WD	3.58
	Tmean	3.38
	GE:Tmean	4.27
	GE:WD	4.08
TBCF	GE	1.01
	WD	3.56
	Tmean	3.34
	GE:Tmean	4.35
	GE:WD	4.14
GPP	GE	2.95
	WD	1.03
	Tmean	2.45
	GE:Tmean	4.07
	GE:WD	3.47
NEP	GE	1.83
	dh	3.91
	tmean	4.42
	GE:dh	7.48
	GE:tmean	8.37
FNPP:GPP	GE	1.72
	WD	1.16
	Tmean	1.20
	GE:Tmean	3.53
	GE:WD	3.11
WNPP:GPP	GE	1.02
	WD	7.76

ANPP:GPP	Tmean	7.72
	GE:Tmean	8.05
	GE:WD	8.00
	GE	1.77
	WD	1.07
	Tmean	1.65
Ra:GPP	GE:Tmean	4.05
	GE:WD	3.90
	GE	1.23
	WD	1.07
TBCF:GPP	Tmean	1.10
	GE:Tmean	3.76
	GE:WD	3.61
	GE	1.02
	WD	1.30
TBCF:GPP	Tmean	1.19
	GE:Tmean	3.36
	GE:WD	3.24
	GE	1.02



Supplementary Fig. 1 Biomass stock of different plant components (root + stump, stem, live and dead branch, and total leaf) for the clones studied across various sites. Each

component is represented by separate colars bars, with data presented for individual clone trees in their respective sites. The biomass stock values are provided in kg dry weight. Note: Based on climatic similarity, the equation developed for coarse roots and stump at site S4 was applied to site S1, while the equation for site S9 was used for site S.7. All equations yielded p-values less than 0.01, and the R^2 values ranged from 0.91 to 0.99.

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Paper 3: Life cycle assessment of paper products from *Eucalyptus* forests in Brazil

The paper was formatted according to the guidelines of the journal carbon balance and management

Fernanda Leite Cunha¹, Otávio Camargo Campoe¹, Sarah Pulls², Justin Backer², Rachel Cook¹, José Leonardo Gonçalves³, Timothy Albaugh⁴, Rafael Rubilar⁵

¹Department of Forestry Sciences, Federal University of Lavras (UFLA), Lavras 37200, Brazil,

²Cooperativa de Productividad Forestal, Departamento de Silvicultura, Facultad de Ciencias Forestales, Universidad de Concepción, Victoria 631, Casilla 160-C, Concepción 4070386, Chile

³Institute of Forestry Research and Studies (IPEF), Piracicaba 13415, Brazil

⁴Department of Forest Resources and Environmental Conservation, Virginia Polytechnic Institute and State University, Cheatham Hall, Blacksburg, VA 24061, USA

⁵ Cooperativa de Productividad Forestal, Departamento de Silvicultura, Facultad de Ciencias Forestales, Universidad de Concepción, Victoria 631, Casilla 160-C, Concepción 4070386, Chile

* Correspondence: fernandaleitecunha@gmail.com; Tel.: (+55-31) 99450-1613

Highlights

- 1) ForestWise model simulates carbon flows in forest plantations over a 18-year cycle
- 2) Products store 12.7 MtC at year 0
- 3) Paper and cellulose products represent an important carbon pool
- 4) Manufacturing emits over 90% of total GHG across the product life cycle

Abstract

Background

Planted forests are increasingly recognized for their role in climate change mitigation, not only through carbon sequestration during forest growth but also via long-term storage in harvested wood products (HWPs). However, few studies have modeled the life cycle carbon balance of tropical plantations using region-specific data.

Results

We adapted a carbon model originally developed for U.S. *Pinus* plantations to simulate the life cycle of *Eucalyptus*-based paper products in Brazil. The model incorporates life cycle assessment (LCA) elements in five stages: (1) silviculture (2) harvest, (3) transport, (4) milling and postmill manufacturing (industry), (5) use and recycling, and (6) emission. Simulations over 18 years using dry biomass inputs from pulp companies revealed that HWPs store 12.7 MtC at market entry. Considering recycling, paper products have a maximum lifespan of 15 years. Simulations over 18 years using dry biomass inputs from pulp companies revealed that a positive net carbon balance is only achieved when industrial emissions are excluded or forest biomass is included.

Conclusions

Our findings emphasize the strategic role of HWPs in carbon storage. Recycling improvements, longer product lifespans, and more efficient industrial practices can significantly increase carbon retention. These strategies are essential to enhance the forest sector's contribution to climate mitigation and should be incorporated into national carbon policies.

Keywords: Harvested wood products, Life cycle assessment, Carbon storage, Climate mitigation.

1 Introduction

Forests are recognized as essential players in the global carbon cycle, capturing and storing approximately 30% of annual anthropogenic CO₂ emissions, equivalent to 8.8 Pg CO₂e yr⁻¹ [1]. In addition to native forests, productive planted forests have been recognized for their climate mitigation potential [2]. In Brazil, *Eucalyptus* and *Pinus* plantations cover 9.93 million hectares and store approximately 1.82 Gt CO₂e annually [3]. In 2015, 335 megatons of CO₂ were stored annually in harvested wood products (HWPs), and it is estimated that by 2030, this capacity will increase to 441 megatons [4]. Although the increase in the HWP carbon pool is smaller than that in the forest carbon pool, its role in mitigating global warming should not be overlooked [5].

HWP refers to products made from wood such as sawn timber, panels, paper, cellulose, coal, among others [6,7]. which can contribute to carbon stock and emissions,

from this raw material production phase, through the industry until its end of life [8]. The Intergovernmental Panel on Climate Change (IPCC) first recognized the carbon storage potential of HWPs in its 1996 Guidelines [9], which were later revised in the 2006 Guidelines and the 2013 Supplementary Methods [9,10]. Within this context, HWP carbon was accepted as part of a country's greenhouse gas (GHG) reduction contributions at the 17th Conference of the Parties (COP17) [11,12]. The United States Environmental Protection Agency (EPA) also adopted a methodology [6] for estimating harvested wood product stocks in national greenhouse gas inventories [8,13].

Many scientific papers have focused on the potential of forests and HWPs to reduce greenhouse gas (GHG) emissions [7,14–18]. The contribution of carbon storage in HWPs appears to be small compared with that in temperate forest carbon pools [19]. HWPs derived from *Pinus taeda* harvested across the southern United States store 29.7 MtC in the year they enter the market (year 0), 15.2 MtC after 10 years, and 11.4 MtC after 120 years in use and in landfills [11]. Thus, even though their potential is often marginalized, HWPs play a crucial role in limiting GHG emissions [20,21]. Pulp-based products also present a potentially promising substitution effect by avoiding GHG emissions, such as carton beverage packaging [7], which has a lower climate impact than do functionally equivalent products such as glass bottles or polyethylene terephthalate (PET) bottles [22–24]. Additionally, the lifespan of HWPs can be extended through the production of more durable products or recycling, thereby delaying emissions for many years [25].

Processed wood products play a crucial role in climate mitigation strategies in the forestry sector, alongside sustainable management practices [26]. However, to fully understand the contribution of these products to carbon sequestration, we need to use methodologies that include the production, use, cascade use and end-of-life phases of these products. [27–29]. Life cycle assessment (LCA) is an efficient and validated tool for investigating the sustainability of different products, from their production to their end of life [15].

Pulp production has grown globally, [30] and Brazil stands out as one of the world leaders in the production and export of these products originating from highly productive *Eucalyptus* and *Pinus* plantations [3]. The high productivity of *Eucalyptus* plantations in Brazil ($33 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$), combined with the vast extension of planted areas (~10 million ha), may represent a large carbon reservoir. Therefore, this study aims to model the life cycle of pulp and paper products, quantifying their carbon storage potential and associated

GHG emissions. Our approach considers the entire process, from the harvesting of *Eucalyptus* forests to the cradle-to-use perspective, enabling a detailed analysis over different time horizons. Our specific objectives are (1) to improve the pulp and paper products life cycle model [11] and adapt its settings to reflect Brazilian forest conditions and production systems and (2) to provide a comprehensive analysis of the carbon fluxes of pulp and paper products derived from *Eucalyptus* plantations in Brazil, assessing their contribution to atmospheric carbon removal. Our hypothesis is that the Brazilian forestry sector plays a strategic but underestimated role in global climate mitigation, contributing significantly to sustainability goals and the development of nature-based solutions.

2 Metodology

2.1 Database

To model the life cycle of paper and pulp products in Brazil, we used data provided by the Brazilian Tree Industry [31]. The *Eucalyptus* planted area for paper and pulp production totaled 2.8 million hectares (36% of the national planted area), with minimum, mean, and maximum annual increments of 20, 33.7, and 41.1 m³ yr⁻¹, respectively. The states with the largest planted areas are Minas Gerais (~792 thousand ha), Mato Grosso do Sul (~478 thousand ha), and São Paulo (~359 thousand ha) (Fig. 1 A). To estimate aboveground green biomass, we used the annual productivity values [31] (minimum: 20, average: 33.7, and maximum: 41.1 m³ ha⁻¹ yr⁻¹), and assumed a wood density of 0.44 g cm⁻³ for *Eucalyptus* [32]. Biomass was calculated as the product of volume and density (biomass = volume × density), considering only the biomass from the harvest year as inputs in the model.

To model the data in the Life Cycle Assessment model, we used results from the TECHS experimental network, the Cooperative Program on Clonal *Eucalyptus* Tolerance to Water and Thermal Stress [33] (Fig. 1B). These data were used to estimate the necessary input variables for the model, specifically (1) the *k* factor, related to the decomposition rate (described in detail in Section 2.2.1), and (2) the biomass produced per hectare, based on empirical data from the TECHS experimental network.

To model both forest biomass and biomass in paper products, we used 11 locations from the TECHS, associated with pulp- and paper-producing companies in Brazil and located in the main producing states: Minas Gerais, Mato Grosso do Sul, São Paulo, and Paraná (Table 1). The climatic description of each site can be found in Supplementary Table 1. The experiments were planted in 2012, and each clone was planted in a single plot, with 8 lines × 30 trees in an area of 0.2

ha, with trees spaced 3×3 m (1111 trees ha^{-1}). The planting technique followed minimum cultivation methods [34], all plots were fertilized intensively during the first year, and there was pest and weed control competition whenever necessary [35]. To represent the forest growth biomass, we used the clone *Eucalyptus urophylla* (A1, the most widely planted clone in Brazil due to its high plasticity). For the analysis, we used only plots in which the amount of rainfall was not reduced [33].

The diameter at breast height (DBH, 1.3 m above ground level), total height (H), and live crown depth of all trees and sites were measured every 6 months. Stem wood biomass was estimated via allometric equations developed from destructive sampling of 6 trees per clone. The sampled trees were selected to cover the range of DBHs. After harvesting, the DBH and total height (H) were measured. Stem wood was separated from the other components of the tree and weighed onsite individually, and representative samples were collected and dried at 65°C to a constant weight for dry mass determination. The dry masses of the branches, wood, bark, and coarse roots were fitted using the linearized model of Schumacher and Hall $\ln(\text{dry mass}) = \beta_0 + \beta_1 \times \ln(\text{diameter at breast height}) + \beta_2 \times \ln(\text{height})$ for each clone per site following the methodology presented in [35].

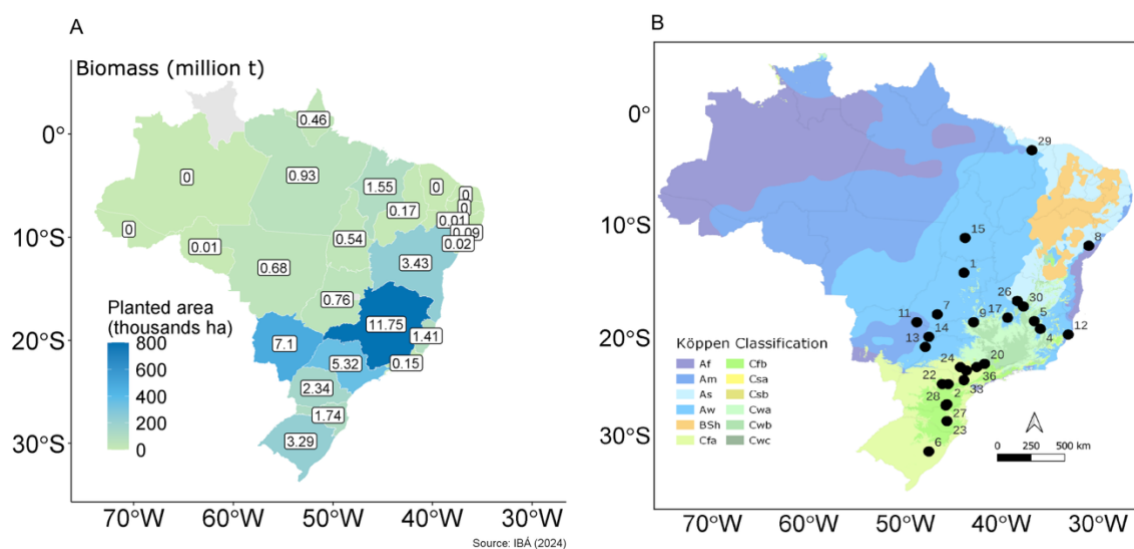


Fig. 1: A) *Eucalyptus* planted area destined for cellulose production in Brazil. The color of each state represents the planted area, with green indicating smaller areas, blue representing larger areas, and gray indicating that the state does not have any *Eucalyptus* plantations. The label within each state indicates the corresponding biomass produced in that region (million t). B) Location of TECHS site in Brazil.

Table 1: Dry biomass productivity (t ha^{-1}) over time at representative TECHS sites of major Brazilian pulp producers.

State	Site	City	Years
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			1	2	3	4	5	6
MG	S4	Belo Oriente	10.8	32.0	53.4	62.3	84.6	114.3
	S5	Guanhães	6.7	28.1	62.1	88.7	117.4	136.1
SP	S20	Mogi Guaçu	8.4	38.6	58.4	80.0	120.1	139.5
	S24	Borebi	10.1	42.6	63.4	73.6	112.4	138.6
	S33	Buri	7.0	42.6	60.3	79.4	111.0	135.8
MS	S11	Chapadão do Sul	13.4	31.9	57.2	97.6	133.9	144.3
	S13	Três Lagoas	13.5	33.9	64.4	82.0	112.4	144.3
	S14	Inocência	4.2	26.4	62.1	88.9	116.5	140.0
PR	S2	Arapoti	16.0	21.3	60.2	115.4	128.4	151.7
	S22	Telêmaco Borba	14.0	30.3	66.1	117.0	138.5	170.2
	S27	Antônio Olinto	2.2	5.6	39.1	71.2	93.7	161.0

2.2 Model Description

For this study, we adapt the Loblolly Wood Inventory, Storage, and Emissions (LobWise) model [11], to reflect the characteristics of *Eucalyptus* plantations and pulp and paper production systems in Brazil. Given the structural changes in model assumptions, and input data required to represent Brazilian forestry conditions, particularly those specific to *Eucalyptus*-based systems, we rename the adapted version as ForestWise (Forest Inventory, Storage, and Emissions), to reflect its broader applicability beyond *Pinus*.

The model uses elements of an attributional life cycle assessment (LCA) approach to create a framework, using R version 4.3.1 [36]. In this study, the functional unit is defined as t C (tonne of carbon). The system boundary follows a cradle-to-use perspective, encompassing the main stages from forest establishment to the industrial gate. To provide a more comprehensive view of carbon dynamics, the model traces wood product carbon through six processes: (1) silviculture, (2) harvest, (3) transport, (4) milling and postmill manufacturing (industry), (5) use and recycling, and (6) emissions (Fig. 2). The framework accepts input data as either total values or diameter-based data, measured in volume (m³) or dry biomass (tons). It generates various outputs, including the carbon stored in different uses at any point in time, and fossil fuel emissions associated with the production of harvested wood products (HWPs). For this analysis, we used total dry biomass as the input, since *Eucalyptus* plantations in Brazil typically have uniform characteristics, eliminating the need for diameter class-based inputs. All available parameters for *Eucalyptus*

plantations in Brazil were adapted to the model, regardless of where the products are consumed. It assumes that exported products are consumed similarly to domestic products. The framework produces 18 years of outputs after the initial harvest simulating tree years of consecutive harvests, considering six years of rotations [3]. The year 0 is considered the time at which the wood products enter the market; thus, we do not account for cumulative storage or emissions from an existing wood product stock. The methodologies used in each stage of the model and the new cycles added to adapt the Brazilian conditions are described below:

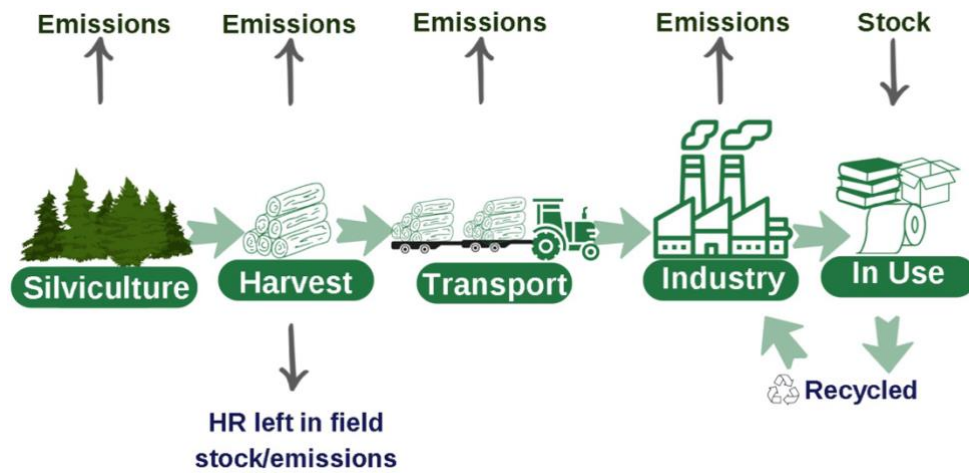


Fig. 2: System boundary and modeling projects performed by the ForestWise model simplified for pulp and paper production in Brazil

2.2.1 Harvest residue stock and emissions

In Brazil, 14% of harvest residues in *Eucalyptus* plantations, such as bark, leaves, and branches are left in the field (Leite & Lopes et al., in prep.) and decompose over time. Thus, only the timber logs are transported to the factory for processing. To estimate the total aboveground biomass, we applied the *Eucalyptus* aboveground biomass expansion factor (BEF), Brazil average of 1.2, and the root-to-shoot ratio (R), Brazil average of 0.28, multiplying it by [37] biomass of branches, leaves, and bark was then calculated by subtracting the wood biomass from the total aboveground biomass.

Litter decomposition coefficient

To assess plant material decomposition over time, data were collected from 27 experimental sites of the TECHS project (Supplementary Table 1). In 2014, when the plantations were approximately 12 months old, 135 cylindrical wood samples ($25 \times 25 \times 250$ mm) with an initial average biomass of 70 g, from clone *Eucalyptus urophylla* (A1).

em each sample was tagged with an aluminum label to prevent its loss after 2 to 3 years of intense decomposition in tropical soils. The samples were buried vertically in the soil. Each sample was firmly inserted into the ground using a metal rod of the same dimensions and placed 40 cm away from the nearest tree along the planting row. The top of each sample was positioned 15 cm below the soil surface. Border areas of the plots were avoided, as they could be used for biomass assessments. Every 12 months postburial, one sample was excavated; its length and diameter were measured using a metric ruler and caliper, respectively, and its volume was calculated using the cylinder volume formula. Each sample was then dried in a forced-air oven for 3 days until a constant weight was achieved, and the dry weight was recorded. Finally, the biomass was determined using the equation $\text{biomass} = \text{volume} \times \text{density}$, with a density of 0.45 g cm^{-3} . We used the initial and final biomass of each sample to estimate the decomposition rate (k). Consequently, each site yielded five k values corresponding to different years of data collection. The data were fitted to a first-order exponential decay model, Equation 1 [38].

Equation 1: $k = (\ln(y/y_0))/t$

where k is the decay coefficient, y is the remaining dry matter after time t (in years), and y_0 is the initial dry matter input.

Stepwise multiple regression equations were fitted using k as the dependent variable and the following independent variables: soil properties, i.e., sand, silt, and clay contents, along with pH, provided by each company according to the physical and chemical soil analyses described in the Embrapa Manual of Soil Analysis Methods [39]; and climatic variables, i.e., minimum, maximum, and mean temperatures; precipitation; and relative humidity, obtained from [40]. Using the adjusted coefficient of determination ($R^2=52\%$), the root mean squared error (RSME=0.16) and the mean absolute percentage error (MAPE=34%), we select the model (Equation 2, Supplementary Fig. 1).

Equation 2: $k = 1.0199713 + 0.025766 * \text{latitude}$

Litter decompositions

On average, 14% of harvest residues remain in the field in Brazil (Leite & Lopes et al., in prep.). To reduce the estimation error of litter decomposition over time at the state level, the model incorporated state-level data and used the latitude corresponding to the highest plantation density, as obtained from MapBiomass [41]. Litter decomposition was

modeled for each state using a first-order decay equation (Equation 3), where the decomposition constant (k) was incorporated into the calculation, as described by [38]. The biomass decomposed and emitted as biogenic carbon into the atmosphere was determined by subtracting the final biomass (y) from the initial biomass (y_0).

Equation 3: $y = y_0 * e^{(-k \cdot t)}$

where k is the decay coefficient, y is the remaining dry matter after time t (in years), and y_0 is the initial dry matter input.

2.2.2 Milling for primary, second use and recycled

In the milling process, whole logs undergo a series of transformations to produce primary products. First, the inputs are converted into tC for the pulp product. Mill residues, fine residues (sawdust and undersized wood chips), are removed from the log on the basis of mill efficiency (Supplementary Table 2), leaving the primary products. These residues are then combusted, releasing biogenic carbon emissions. Thus, the emissions resulting from the combustion of mill residues (representing 5% of the input biomass, Supplementary Table 2) were not explicitly included in the ForestWise model to avoid overestimating total emissions. This approach prevents double counting, as the emission factors based on life cycle inventory (LCI) data already account for the total energy used in pulp and paper production, including the energy generated from internal biomass combustion.

Primary products are converted into secondary products (card paper, sanitary products, packaging, print and write, and miscellaneous paper products) on the basis of national production averages (

Supplementary Table 3) [31]. All paper products can be recycled within the framework, except for sanitary products [42]. An individual paper product can be recycled only into the same product [11] and can be recycled only a limited number of times (

Supplementary Table 4) [42].

After year 0, the remaining secondary product carbon transitions out of use according to Weibull distribution functions (**Error! Reference source not found.**). The

functions use 2.63 as a shape factor (k) (EPA, 2020) and estimate modes unique to each product according to the literature to calculate the scale factor ($\lambda=1.19$) (**Error! Reference source not found.**) [11,43].

$$\text{Equation 4: } f(x) = C - C (1 - e^{(-x/\lambda)^k})$$

$$\text{Equation 5: } \lambda = \text{mode}/(1-1/k)^{1/k}$$

where C is the carbon in products that enter the market, x is the time since harvest in years, k is the shape factor, λ is the scale factor, mode is an approximation of the product's lifespan, and $f(x)$ is the carbon remaining in use at year x .

2.2.3 Emissions

To estimate greenhouse gas (GHG) emissions from forestry, Harvest and transport operations, we used data from a technical inventory conducted by the Brazilian Institute for Forest Research and Studies (IPEF) in collaboration with major pulp and paper companies (Gonçalves et al., in prep.). The inventory covers three main operational phases: silviculture, harvest, and transport.

Silviculture, Harvest, and Transport Emissions

The inventory considered both fuel consumption and the embodied energy in the machinery and inputs used in each phase. Embodied energy in machinery refers to the energy required to manufacture, maintain, and depreciate equipment over its useful life. This value was allocated per hectare based on machine mass, operational field capacity (ha h^{-1}), and total lifetime hours [44]. The degree of machinery energy depreciation was calculated according to **Error! Reference source not found.** Diesel consumption per activity (L ha^{-1}) was estimated according to Equation [44].

$$\text{Equation 6 : } D = \text{EMM} * \text{Mass} / (\text{UL} * \text{Fc})$$

where D is the depreciation (MJ ha^{-1}); EEM is the embodied energy of machinery (MJ kg^{-1}); Mass is the machine mass (kg); UL is the machine useful lifetime (h); and Fc is the operational field capacity of a specific mechanized operation (ha h^{-1}).

$$\text{Equation 7: } \text{Fc} = \text{Cf} * \text{TP} * \text{TO}$$

The energy required to produce diesel was considered to be 35.86 MJ L^{-1} [45], and this value was used to extrapolate the total energy demand and convert it to kg C ha^{-1} .

Five key activities were evaluated in the silviculture phase: (1) soil preparation, (2) planting and replanting, (3) fertilizer application (liming, planting, and cover), (4) weed control, and (5) ant control. Emissions from forest inputs were calculated by multiplying the amount used per hectare by their respective energy coefficients (MJ unit⁻¹) [44].

Harvest and transport emissions were based on a six-year rotation with an average productivity of 40 m³ ha⁻¹ year⁻¹. Two mechanization scenarios were considered: (1) Harvester (CAT 320) + forwarder and (2) Feller-buncher + skidder, with productivities of 20, 65 m³ ha⁻¹ and 112, 100 m³ ha⁻¹, respectively. For transport, we assumed the use of a 66 m³ tritrem truck over a 150 km average distance.

Product end-of-life and carbon dynamics

Emissions associated with log acquisition, including silviculture; harvesting operations; log transportation from the harvest site to the mill; and the production of primary products from logs at the mill, were calculated on the basis of the type and quantity of primary product produced. These emissions are reported in tCO₂eq and are not distinguished among different greenhouse gases. The emission factors used are based on LCA studies of each product (Supplementary Table).

We assumed that all forestry emissions occurred in the year of harvest to simplify graphical representation and data modeling. To calculate the emissions from silviculture, harvest, transport and pulp and paper production, we multiply the carbon content of the biomass by the corresponding parameter in Supplementary Table . The production emission factors used are based on LCA studies of each product. All emission parameters consider the use of fossil fuels, chemicals, and energy. Emissions are reported in tCO₂e and are not distinguished between different greenhouse gases (i.e., only scope 1 emissions). Fossil fuel emissions for postmill activities (e.g., recycling, postmilling transportation, etc.) are not included.

To account for the varying levels of the emissions that occur from different log type mixes, the amount of GHG remaining in the atmosphere after the initial pulse emission in the harvest year was calculated according to the revised version of the Bern carbon cycle model, as reported in the 5th Assessment Report of the IPCC (**Error! Reference source not found.**) [10]

Equation 8: $C_{CO2}(t) = a_0 + \sum_k a_k e^{-t/a_k}$

2.3 ForestWise data analyses

We applied three different approaches to analyze the data. In the first approach, we calculated the total carbon stock and emissions over the 120-year period. To assess the net carbon accumulation over time, we integrated the carbon stock and emission curves using the trapz function from the pracma package in R (Borchers et al. 2019). The net carbon stock was obtained by subtracting total emissions from total carbon storage, allowing us to quantify carbon retention throughout the study period. Additionally, we evaluated two different consumption scenarios: (i) total cellulose and paper consumption in Brazil and (ii) a scenario where only 20% of the production is consumed, as suggested by [31]. This comparison helps to understand how different consumption levels influence long-term carbon storage and emissions.

In the second approach, we modeled a scenario of annual harvests over a 120-year period, assuming that 469,517 ha were harvested each year. This value was obtained by dividing the total planted area in Brazil by the average rotation length (6 years), ensuring that the same area is harvested every year throughout the simulation period. This approach enables a cumulative analysis of the carbon balance strategy, integrating the carbon stock and emissions from each harvest on an annual basis. To ensure the consistency of the simulations, we assumed that both forest productivity and market production and consumption dynamics remained constant, simplifying the analysis. In this process, we overlapped the carbon stocks and emissions from each harvest and summed these values per year to obtain the total carbon stock and emissions. To calculate the net carbon balance, we applied the integration of carbon storage as described in the first approach. Additionally, we considered three different productivity scenarios: the minimum mean annual increment-MAI ($20.0 \text{ m}^3 \text{ yr}^{-1}$), average MAI ($33.7 \text{ m}^3 \text{ yr}^{-1}$), and maximum MAI ($41.1 \text{ m}^3 \text{ yr}^{-1}$), to assess the carbon storage potential of pulp and paper products over time. To determine the carbon balance (stock minus emissions) over the study period, we replicated the same methodology applied in the first approach.

Since incorporating biomass production into the ForestWise model while considering the national production of planted forests was not feasible because of the lack of spatialized data on the planted areas of forestry companies in Brazil, we adopted a third approach aimed at understanding the total potential of carbon storage and emissions in the planting of one hectare of *Eucalyptus* for pulp and paper production over 120 years. To achieve this goal, we integrated the carbon stocks from above- and belowground biomass of *Eucalyptus* plantations established in the main cellulose-producing states in Brazil, Minas Gerais, Mato Grosso do Sul, São Paulo and Paraná. To estimate the productivity per hectare, we selected the TECHS sites located in each state where the pulp-producing companies operate (Table 1). We used the average green biomass at six years of age, obtained per hectare, as an input for ForestWise. We applied a six-year planting cycle, assuming

that the forest was harvested and immediately replanted in the same year, with no intervals between cycles. Additionally, we considered that wood-derived products entered use in the same year as the harvest. To calculate the net carbon balance, we applied the integration of carbon storage as described in the first approach. For better data interpretation, we also analyzed the carbon balance at intervals of 0–15, 16–30, 31–60, and 61–120 years.

3 Results

In 2023, Brazil produced approximately 21.3 million tons of short-fiber pulp, of which 4.26 million tons were consumed by the domestic market (Fig. 3 A and C). Under the simulated scenario of total raw material consumption within Brazil, the estimated carbon content allocated to different product categories was as follows: approximately 5.12 million tC for packaging, 1.83 million tC for printing and writing paper, 1.19 million tC for sanitary paper products, 0.54 million tC for cardboard, and 0.45 million tC for miscellaneous paper products (Fig. 3 B). The estimated product lifespans for these categories were 16 years for packaging, 16 years for printing and writing paper, 4 years for sanitary paper products, 15 years for cardboard, and 10 years for miscellaneous products (Fig. 3 B and D).

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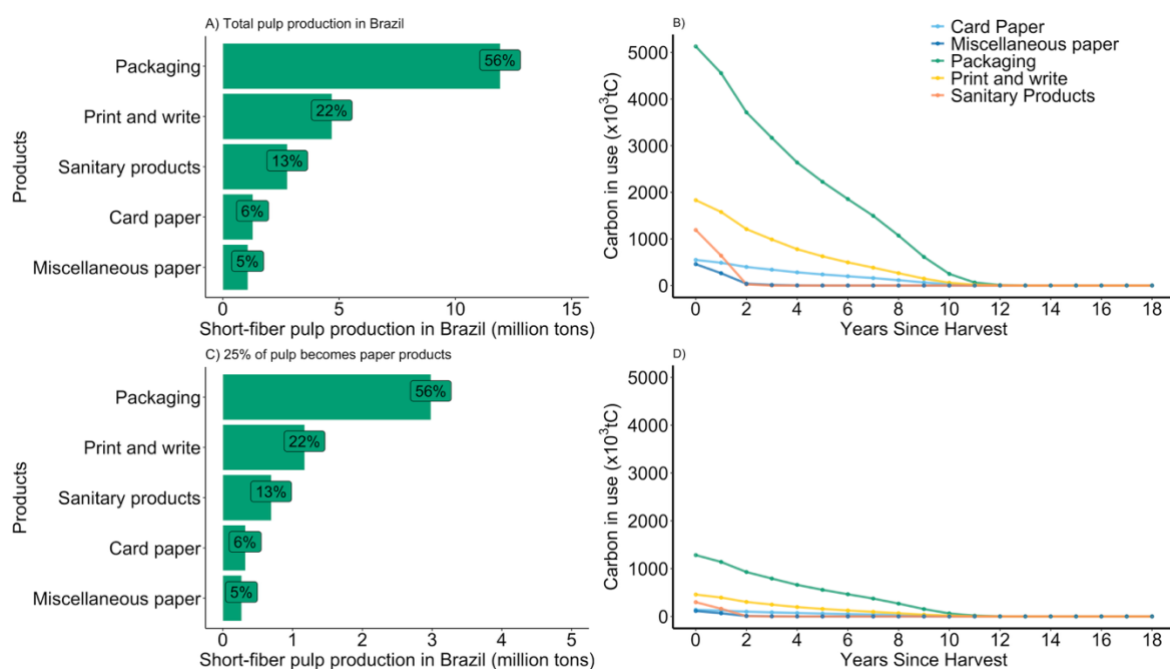


Fig. 3: Total production of short-fiber pulp and paper in Brazil as reported by the Brazilian Tree Industry [31](A); the lifespan of paper products modeled using ForestWise (B); final paper products produced in Brazil (25%) (C); and the lifespan of paper products modeled using ForestWise for domestic pulp and paper consumption (D).

We estimate that harvested wood products (HWPs) from *Eucalyptus* store 12.7 million tC in the year they enter the market (year 0), 4.2 million tC after 5 years, and 0.3 million tC after 11 years, both in use and harvest residue left in the field (Fig. 4A). The contributions of paper products vary between 73-93%, and the residue left in the field varies between 8-31%. Carbon emissions in the year paper products entered the market were 26 MtCO₂, after 10 years emissions had decreased to 19 MtCO₂ and after 18 years they had reduced to 14 MtCO₂ (Fig. 4B). The main source of carbon emissions is the industrial production of pulp and paper, contributing 84-92% of total emissions during the 18 years.

When considering only the emissions associated with forest management operations (Fig. 4D), from stand establishment to harvest, the largest contribution was attributed to silvicultural activities (43%), followed by transport (40%) and harvesting operations (17%) (Fig. 4C). Among the silvicultural components, fertilization was the main contributor (50%), followed by weed control (33%), soil preparation (7%), ant control (6%), and planting/replanting (4%).

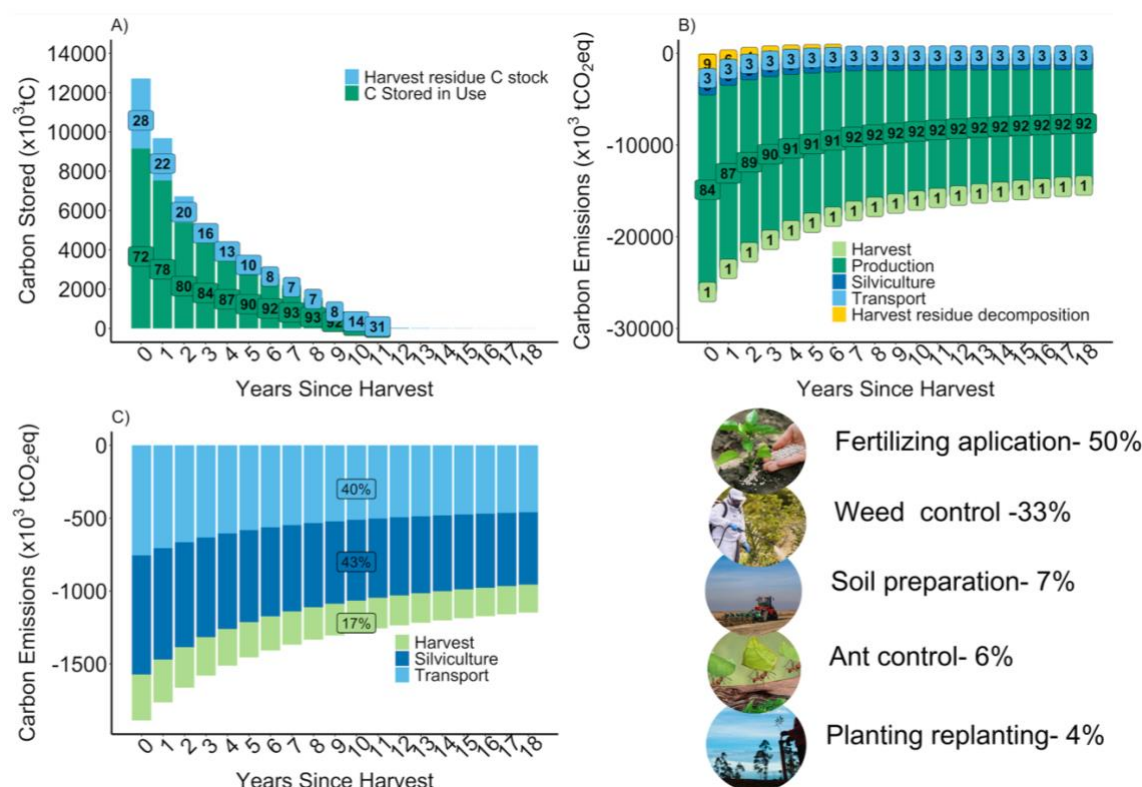


Fig. 4: ForestWise outputs for one harvest: A) Carbon stock stored in paper and pulp products (dark green), forest harvest residues left in the field (light blue) B) Greenhouse gas (GHG) emission pulses (t CO₂ eq) by type and source: fossil fuel use, chemicals, and energy associated with silviculture (dark blue), harvesting (light green), transportation (light blue), and industrial production activities (dark green), as well as emissions from the decomposition of harvest residues left in the field (yellow). C) Emission contribution from forest management only, from planting to harvest. The contribution of each type of stock and emission, expressed as a percentage, is shown in the labels within the graphs.

3.1 Carbon budget: balance between stocks and emissions

Over the 18-year simulation conducted using the ForestWise model and assuming full consumption of pulp and paper products within the Brazilian market, the net carbon balance, calculated as the difference between carbon stocks and emissions was negative (-152 million tCO₂eq) (Fig. 5A). The net balance was positive until year 3 (23 million tCO₂eq). Under the scenario of the final paper produced in Brazil, the net carbon accumulation was estimated at -38 million tCO₂eq (Fig. 5B). When industrial emissions from pulp and paper production are excluded (Fig. 5C–D), the total carbon balance becomes positive for the total pulp production (152 million tCO₂eq) and for final paper products produced in Brazil (36 million tCO₂eq). However, after year

10, due to the end-of-life phase of pulp and paper products, the balance turns negative, reaching -8 and -2 million tCO_2eq , respectively.

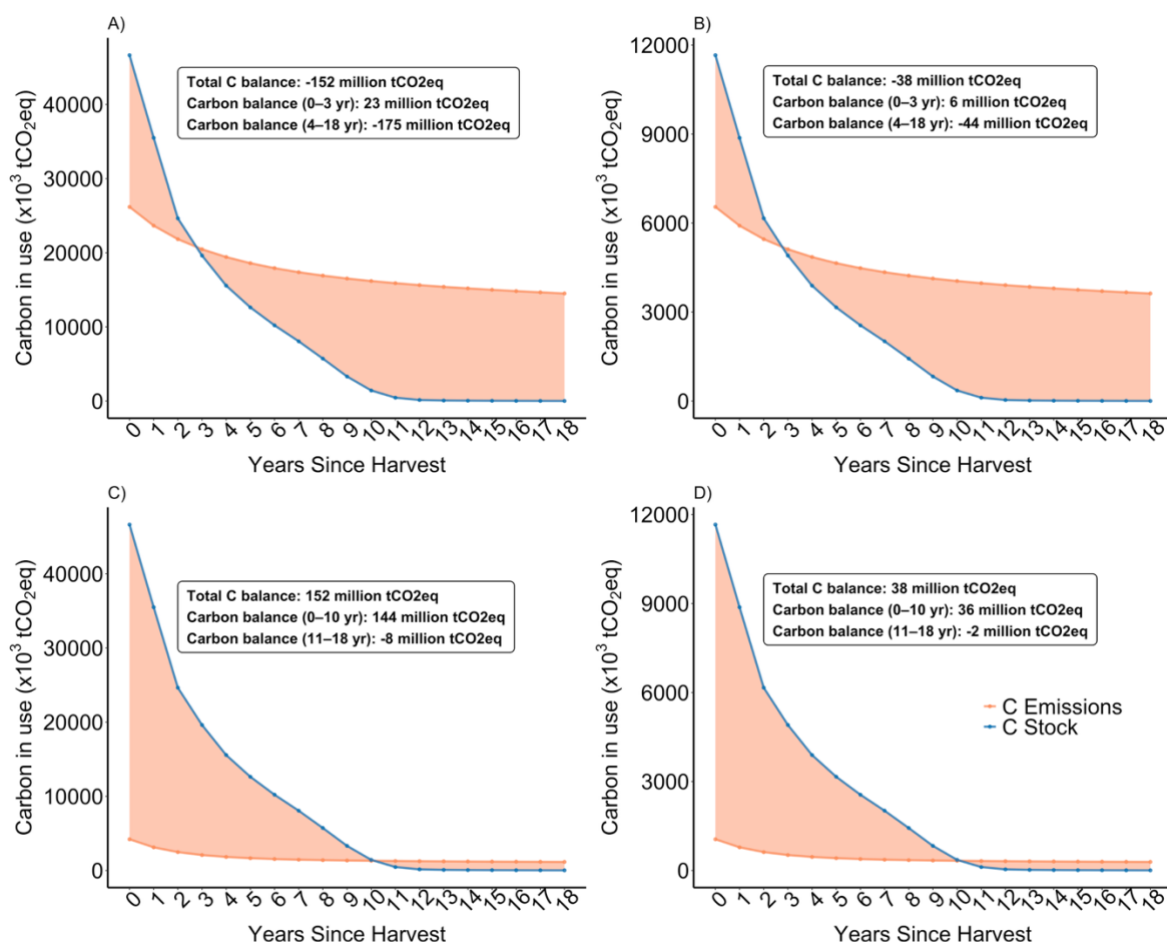


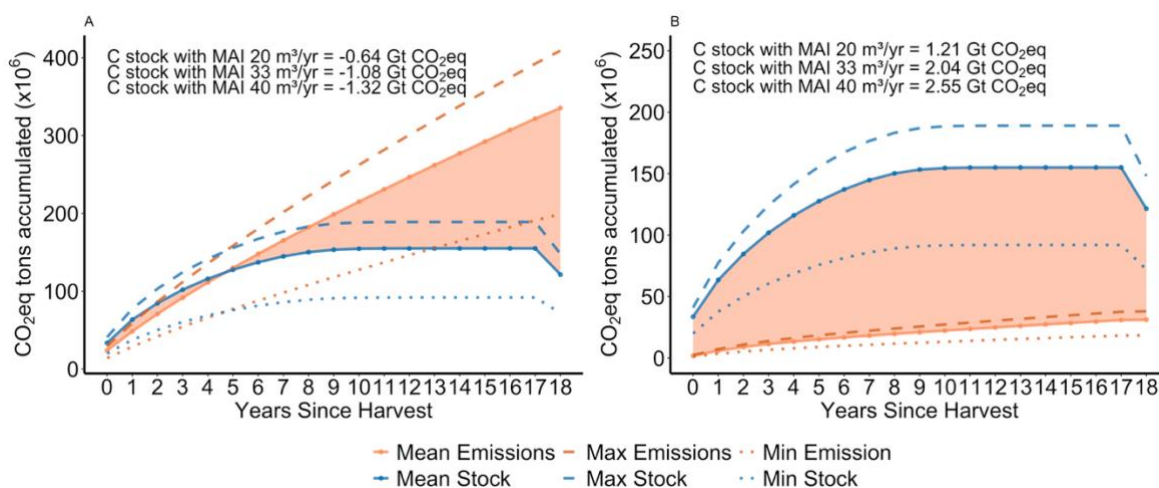
Fig. 5: Carbon emissions and stock associated with the life cycle of pulp and paper products over 120 years in Brazil. The panels represent (A) total pulp production and (B) final paper products produced in Brazil (25%). Carbon stocks are shown in blue, and emissions are shown in orange. The shaded area illustrates the net carbon balance between emissions and stock accumulation over time.

3.2 Life cycle of paper products over 18 annual harvests

We observed a continuous increase in carbon stocks and emissions over time, driven by cumulative paper production across 18 harvest cycles (Fig. 6A–B). In the scenario including all stages up to industrial production (Fig. 6A), total accumulated carbon stock was negative, for all productivity scenarios (minimum, mean and maximum) - 0.64, -1.08, -1.32 Gt CO_2eq , respectively. When emissions from industrial production are excluded (Fig. 6B), the carbon balance become positive 1.21, 2.04 and 2.55 Gt CO_2eq , respectively. The contributions of each component to carbon stocks (paper in use, and

harvest residues left on site) and emissions (fossil fuel emissions, and decomposition of harvest residues) are detailed in Supplementary Figure 2.

Fig. 6: Carbon emissions and carbon stocks associated with the life cycle of pulp and paper products over 120 annual harvest cycles in Brazil. The analysis considers three productivity scenarios based on mean annual increment (MAI): minimum ($20 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$), average ($33 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$), and maximum ($40 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$), represented by dotted, solid, and dashed lines, respectively. Carbon stocks are shown in blue, and emissions are shown in orange. The shaded area illustrates the net carbon balance between emissions and stock accumulation over time.

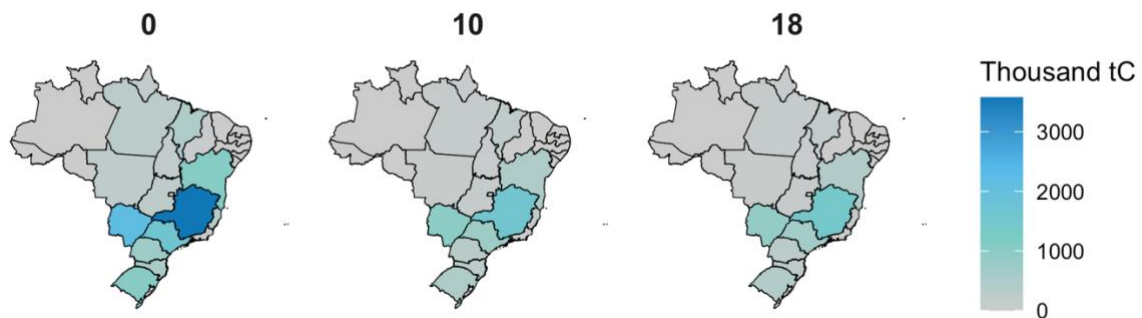


3.3 State-Level Carbon Footprint of Pulp Production in Brazil

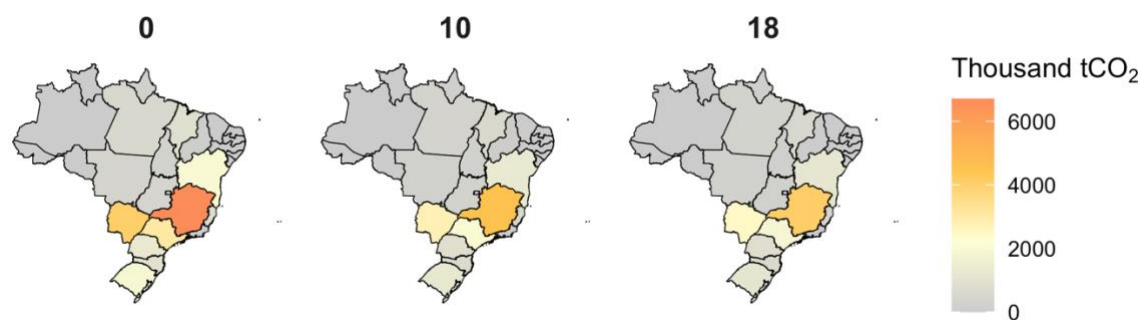
We found that carbon stocks and emissions, varied significantly between states, which reflects the productive potential of each environment and the management used (Fig. 6; Supplementary Table 6). Minas Gerais stood out as the state with the largest stock (3.58 million t C) and emissions (6.7 million t CO₂ eq) in year 0. Mato Grosso do Sul and São Paulo also made significant contributions, storing approximately 2.16 million tC and 1.62 million tC and emitting around 4 million tCO₂ and 3 million tCO₂, respectively, in year 0. In contrast, the Northern and Northeastern states, such as Rio Grande do Norte, Paraíba, Acre, Amazonas, Ceará and Pernambuco, had the lowest contributions to both stocks and carbon emissions. In year 0, its cumulative carbon stocks remained at approximately 3,000 t CO₂ eq, and emissions were insignificant compared to those of the main producing states. These spatial patterns persisted over time, with the southeastern and southern states holding the largest stocks and emissions in years 10 and 18.

Fig. 7. Carbon emissions and stock throughout the forestry production lifecycle, for the medium productivity scenario ($33 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). The values were estimated at years 0, 15, and 120 based on biomass production from *Eucalyptus* plantations and are reported by the state in Brazil, according to data from the Brazilian Tree Industry (2024).

Carbon Stock (Thousand tC)



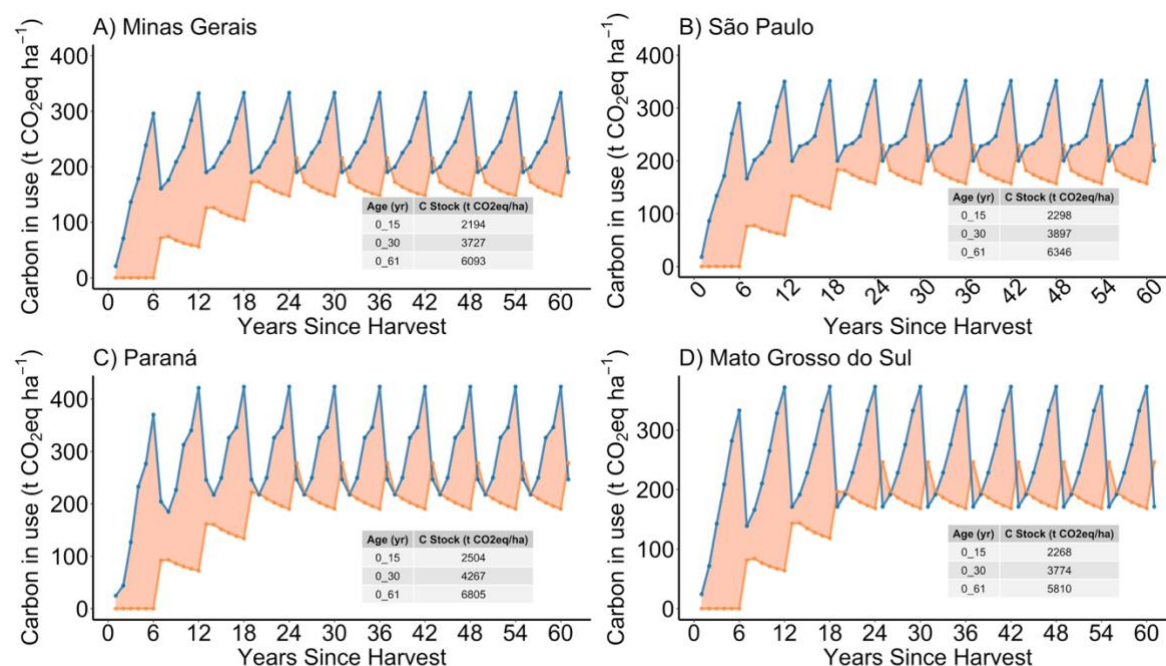
Carbon Emissions (Thousand tCO₂)



Integrating forest biomass with ForestWise model outputs demonstrated that carbon emissions and stock remained in a stadystate over time. The sawtooth pattern of the observed data reflects the six-year cycles between forest planting and harvesting. The shaded area represents the carbon balance between stock and emissions, thus, we observe that for the entire cycle, the four states presented a positive balance. Paraná presented the largest accumulated carbon stock at the end of the period, reaching $6,805 \text{ t CO}_2\text{eq ha}^{-1}$, followed by São Paulo ($6,346 \text{ t CO}_2 \text{ eq ha}^{-1}$) and Minas Gerais ($6,063 \text{ t CO}_2 \text{ eq ha}^{-1}$), Mato Grosso do Sul ($5,810 \text{ t CO}_2 \text{ eq ha}^{-1}$). These differences reflect site productivity and management practices captured in TECHS data.

Fig. 8. Cumulative carbon stock and emissions over 120 years for *Eucalyptus* plantations (1 ha) in the states of Minas Gerais, São Paulo, Mato Grosso do Sul, and Paraná. Carbon in

use (blue line) and emissions (orange line) represent the full life cycle of pulp and paper products, including silviculture, harvesting, processing, and end-of-life. The shaded area represents the net carbon balance, which is calculated as the difference between accumulated carbon stocks and emissions over time. Biomass productivity data were derived from TECHS sites associated with pulp and paper companies operating in each state.



The contribution of carbon stocks and partitioning over time reached a steady state, with the main carbon pool concentrated in forest biomass, accounting for approximately 54–57% throughout the 60-year analysis period. This was followed by carbon stored in paper products (30–60%) and harvest residues left on site (8–10%). In terms of emissions, the largest contribution came from industrial production (90–91%), followed by silvicultural and transport activities (3%), decomposition of harvest residues left in the field (2–3%), and harvesting operations (1%).

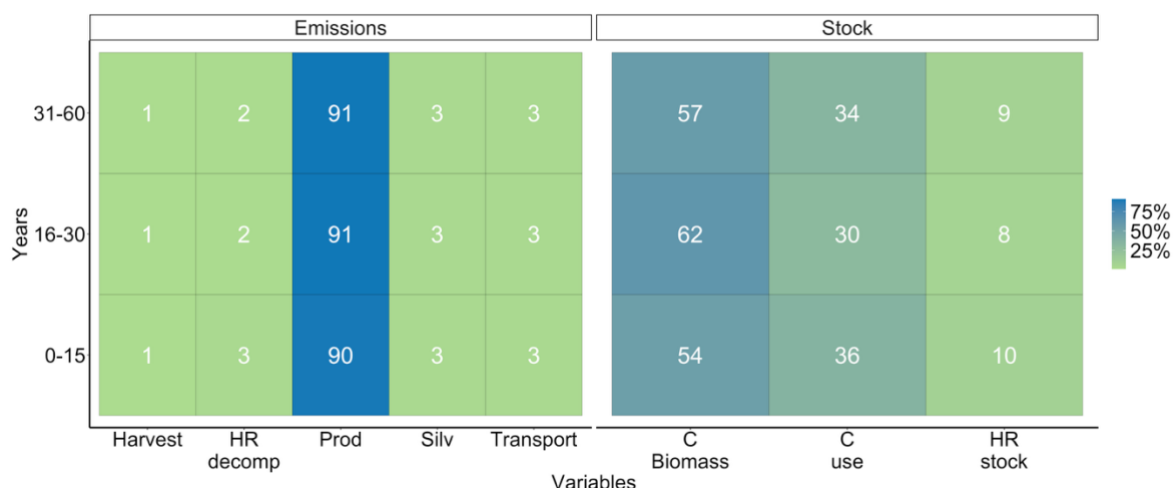


Fig. 9. Relative contributions (%) of carbon emissions and carbon stocks over 120 years of simulation for the life cycle of pulp and paper products derived from *Eucalyptus* plantations in the main productive states of Brazil, Minas Gerais, Mato Grosso do Sul, São Paulo and Paraná. Emissions include contributions from pulp and paper production (Prod), silviculture (Silv), transport, and harvest residue decomposition (HR decomp). Carbon stocks include tree biomass, paper products in use, and harvest residues.

4 Discussion

4.1 Carbon stock

The pulp and paper industry in Brazil has significant potential for carbon accumulation throughout the product life cycle. In our simulation, we estimated a carbon stock of 12.7 million tC in the year the products enter the market. For comparison, in the United States, [11] estimated an annual stock of approximately 18.9 million tC for paper products at the same stage, reflecting the country's larger planted area and domestic consumption market. Most of the literature indicates that the lifespan of paper products ranges from 1-3 years [4,9,47]. However, our results indicated that paper can reach a lifespan of 15 years due to recycling practices (

Supplementary Table 4), accounting for approximately 42% of the carbon stock during the first decade. Corrugated cardboard boxes are the most produced paper category in Brazil [31] with high recycling rates (91.4%). According to [11] the recycling rates of this

category of paper strongly influence the dynamics of stocks and carbon emissions in the ForestWise model, due to the high production rates in the American market. Therefore, despite the high recycling rates of this material in Brazil (91.4%), additional improvements in recycling processes can generate substantial gains in the carbon balance of paper-based products.

Paper recycling is declared to be a fundamental point to extend the lifespan of carbon in use, however it is important to acknowledge that the process is not always environmentally or economically viable [48]. Brazil faces problems in the recycling chain due its structural and logistical challenges, limiting the recycling potential of the industry in different regions of the country. Furthermore, the recycling chain itself can generate greenhouse gas emissions during steps such as transportation, reprocessing and material loss, environmentally offsetting part of the carbon benefits [49–51]. However, a review of life cycle assessment (LCA) studies [52] comparing different final destinations for paper products, even with emissions from recycling, found that this is environmentally preferable to incineration or landfill. Unfortunately, there is still a gap regarding the impacts and emissions on this phase of the life cycle chain of paper and pulp products, mainly aimed at the Brazilian market, which limits a comprehensive understanding of the total carbon balance of the production chain.

The harvest residues left in the field play a fundamental role in ecosystem dynamics and organic matter cycling. *Eucalyptus* plantations produced approximately 30 Mg ha⁻¹ of dry matter from harvest residues in Brazil [53]. Climatic factors, such as temperature, variation, and edaphic factors, such as physical and chemical properties of the soil, can influence the storage rates of organic matter in the soil [54]. Thus, using site-specific productivities would allow us to estimate more realistic carbon residence times, as local biomass inputs are often lower than national means, thereby improving the accuracy of carbon stock and emission predictions.

4.2 Carbon Emissions

Pulp and paper production has been identified as one of the main sources of greenhouse gas (GHG) emissions along the value chain. [11] reported that emissions from paper production are among the most sensitive parameters in ForestWise. Toilet paper (0.93 tCO₂eq t⁻¹) is the product with the highest GHG emissions, followed by card paper (0.67 tCO₂eq t⁻¹), miscellaneous paper (0.51 tCO₂eq t⁻¹), print and write (tCO₂eq t⁻¹), and packaging (0.37 tCO₂eq t⁻¹) (Supplementary Table). Although packaging has the lowest

emission factor, it contributes the most to total GHG emissions due to its large share of overall production (56%). Despite the use of LCI-based emission factors from international pulp and paper production inventories, the Brazilian sector presents important particularities related to its energy efficiency, including the intensive use of black liquor, an organic effluent generated during the pulping process, and wood residues as sources of thermal energy [55,56]. This practice reduces reliance on fossil fuels, which have a longer atmospheric lifetime, and increases the use of short-lived biogenic carbon, enhancing the sustainability of the Brazilian sector [57]. Overall, when the average emission factors for harvesting and transportation in the Brazilian industry (0.009 and 0.022 tCO₂eq t⁻¹, respectively) are lower than those reported for the U.S. industry (0.05, 0.04, and 0.41 tCO₂eq t⁻¹, respectively) [11]. Brazilian emission factors are lower due to the efficiency of forestry and high national productivity rates, with averages of 33 m³ha⁻¹year⁻¹ [31], compared with the 15–24 m³ ha⁻¹ yr⁻¹ observed in the United States [58,59]. As a result, larger volumes of biomass are harvested per hectare and transported per trip, reducing emissions per ton of processed wood and contributing to a more environmentally efficient system in Brazil.

Although the industrial phase of paper and pulp production stands out as the main source of carbon emissions, when we observe emissions from forest management in isolation (from planting to harvesting), Figure 4C, it is possible to observe opportunities to reduce carbon emissions. One example is the fertilization of plantations, which alone is responsible for more than 50% of emissions at this stage. Implementing more sustainable nutrient management strategies, such as optimized application rates, the use of organic inputs, or enhanced-efficiency fertilizers, can significantly reduce emissions without compromising productivity [73–75].

Figure 7 shows that the states with the largest planted areas of *Eucalyptus* (Minas Gerais, Mato Grosso do Sul, São Paulo, and Paraná), concentrate the highest carbon stocks and emissions, reflecting the pattern observed by [11] in the United States. The simulation of annual harvests over 60 years per hectare revealed that stored carbon exceeds cumulative emissions, with Paraná standing out (6,805 tCO₂eq). Despite having the smallest planted area among the four states (Figure 1), Paraná presented the highest net balance because of its high productivity per hectare, which is favored by climatic conditions [33,63]. Our combined analysis of ForestWise outputs and standing forest stocks revealed that biomass is the main carbon pool. This underscores the sustainability of the Brazilian forestry sector in pulp and paper production and highlights the potential of

productive forest plantations to contribute to climate change mitigation [4]. Moreover, even hardwood products with short life cycles can provide climate benefits through carbon storage, especially when properly managed [18].

4.3 Climate Contributions and Challenges of Pulp and Paper Products in Brazil

The net carbon balance of the pulp and paper life cycle is only positive when industrial emissions are excluded (152 million tCO₂eq over 18 years, Fig. 4A) or when forest biomass stocks are included (Fig. 8). According to the [31], approximately 80% of pulp and paper production is exported; however, as outlined in the IPCC Good Practice Guidance [64], only products derived from domestically sourced raw material can be accounted for in the national carbon stocks of the producing country, and the carbon contained in exported final products cannot be claimed by any nation. In this context, public policies that promote domestic industrialization, with greater value addition, could not only increase national revenue but also ensure greater climate recognition for Brazil in terms of the carbon stocks effectively generated from its planted forests.

Although temporary, the accumulation of carbon in forest biomass is significant, it is a dynamic stock that is renewed with each rotation, and which represents a large part of the contribution to the carbon stock in the first decades of the life cycle of paper products. This carbon pool is important when combining carbon stock between forest and pulp and paper products, especially when materials with a high carbon footprint and environmental impact, such as plastic, are replaced by renewable forest products with lower emissions intensity [28]. Life cycle assessment (LCA) studies on the substitution effects of plastic products with paper-based alternatives have been conducted in recent decades [65–68]. In general, replacing single-use plastics with cellulose-based products, such as cups, cutlery, and packaging, can generate significant climate benefits, particularly when the paper is produced using renewable energy and follows efficient end-of-life disposal routes [69]. However, the net substitution effect depends on variables such as product weight, type of coating, landfill decomposition, and collection system [69,70]. Thus, mitigation potential exists, but policies that promote sustainable production and proper end-of-life management are needed.

Although harvested wood products (HWPs) account for less than 1% of global GHG emissions (excluding Land use, land-use change, and forestry - LULUCF), their contribution can be significant, as evidenced by [4]. As climate frameworks move toward mandatory accounting of carbon flows from HWPs, addressing the current sequestration

gap becomes crucial [8,13]. Countries such as Canada and Sweden have already demonstrated that HWPs can offset substantial portions of industrial emissions [4]. However, according to the authors, this potential is sensitive to socioeconomic changes, such as production and consumption patterns.

This study demonstrates that pulp and paper products provide limited long-term carbon storage. However, they represent an important reservoir that helps the industrial sector maintain a positive carbon balance, especially when considered alongside forest biomass. Previous studies have shown that the primary carbon pool tends to be stored in s for extended periods (11). Therefore, we recommend that future studies adopt a cradle-to-grave life cycle inventory (LCI) approach, including end-of-life stages of pulp and paper products. The ForestWise model has proven to be a powerful tool for simulating carbon dynamics in harvested wood products, however, there are still important gaps for its full adaptation to Brazilian conditions. There is a need to develop national LCI datasets for different paper types, and to extend these studies to recycling phases. Future research should explore the climate benefits of carbon retention, assess the influence of forestry practices on the net carbon balance, and include economic analyses to support decision-making in public policies and industrial sustainability strategies.

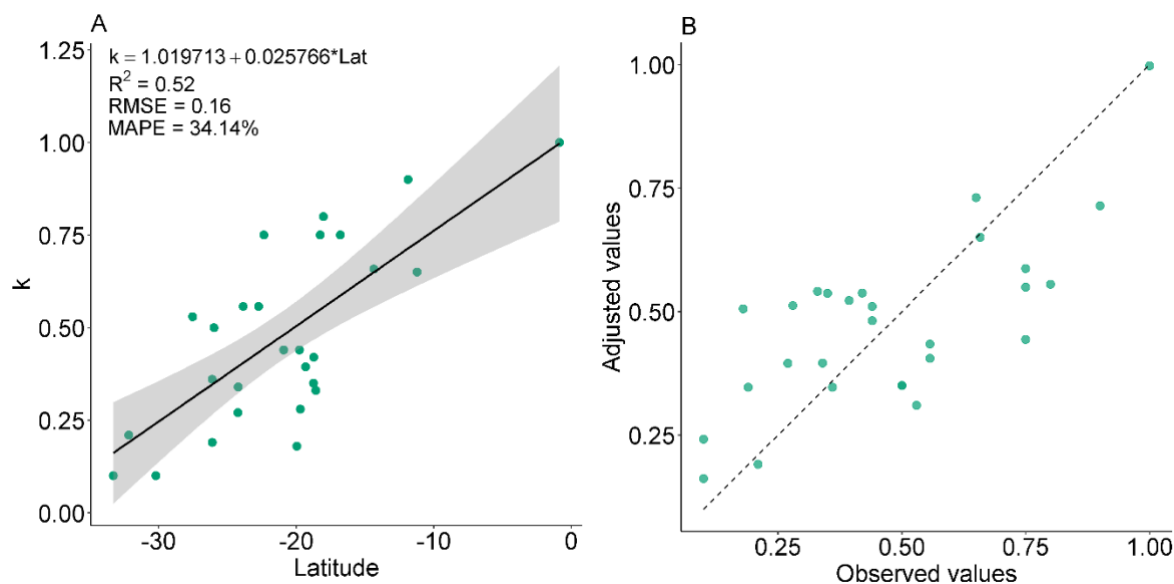
5 Conclusions

This study demonstrates the long-term climate mitigation potential of the Brazilian pulp and paper sector, although our findings reveal that the net carbon balance remains negative when total emissions are included. However, when industrial emissions are excluded, the balance becomes positive, reaching 152 million tCO₂eq over 18 years. A consistently positive balance is only achieved when forest biomass is considered, with a pronounced effect observed when accounting for the cumulative impact of successive rotations, including biomass stocks, pulp and paper products, and harvest residues left on site. For use in national emission inventories, following IPCC recommendations, only 20% of the carbon is considered to be converted into final paper products within Brazil. This means that only 38 million tCO₂eq (excluding industrial emissions) can be accounted for over the 18-year simulation period. The carbon balance quantified in this study reinforces the importance of including harvested wood products in national inventories. Accounting for these contributions is essential for corporate climate strategies and for advancing Brazil's commitment to a low-carbon economy. Recognizing the role of forest-based value chains in carbon mitigation is key to building more accurate and impactful.

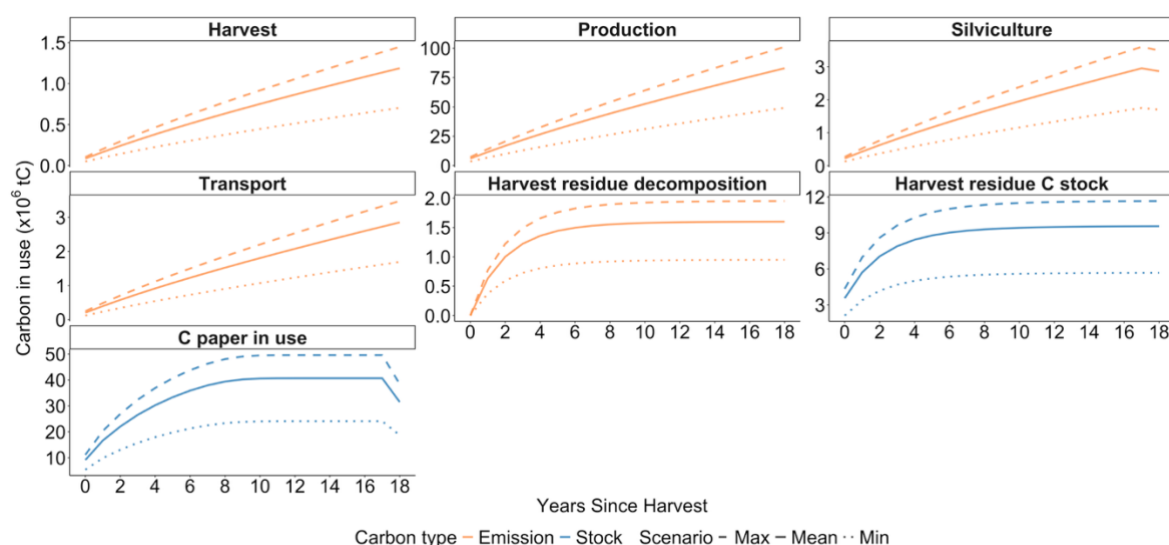
6 Acknowledgments

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7 Supplementary materials



Supplementary Fig. 1: (a) relationship between the decomposition constant (k) of harvest residues and latitude, with a fitted linear regression line and 95% confidence interval. (b) comparison between the observed and predicted values based on the linear model ($k = 1.019713 + 0.025766 \times \text{latitude}$). The model had an R^2 of 0.52, a root mean square error (RMSE) of 0.16, and a mean absolute percentage error (MAPE) of 34.14%. The data were obtained from experimental sites of the techs project (tolerance of *Eucalyptus* clones to hydric, thermal and biotic stresses).



Supplementary Fig. 2: Carbon stock and emission components associated with the life cycle of pulp and paper products over 120 annual harvests in Brazil. The panels show individual contributions to total carbon stocks (top row: harvest residue C stock, and C stored in C in paper in use) and carbon emissions (bottom row: decomposition of harvest residues, silviculture, harvest, transport and production emissions). The solid lines represent the average productivity scenario ($\text{MAI} = 33 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$), whereas the dashed and dotted lines indicate the maximum ($40 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) and minimum ($20 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) scenarios, respectively.

Supplementary Table 1: Climate characteristics of the 27 TECHS sites used to calibrate the decomposition coefficient (k)

Site	Lat	Lon	Alt (m)	Tmean (°C)	Tmax (°C)	Tmin (°C)	RH (%)	P (mm)	CAD (mm)	Sand (%)	Silte (%)	Clay (%)	pH
6	-30.2	-51.6	150	20.4	25.9	16.4	74	1805	1.7	27	19	54	3.7
23	-27.5	-50.1	870	17.4	22.7	12.0	82	2055	1.9	43	28	29	3.9
28	-26.1	-50.2	812	18.5	23.6	13.3	78	1487	1.8	60	24	16	3.8
31	-26.1	-50.2	200	23.9	28.2	19.5	76	982	1.8	25	3	73	4.1
27	-26.0	-50.1	916	19.0	24.8	13.1	76	1487	1.8	14	5	81	3.9
30	-26.0	-50.1	848	22.4	28.7	16.0	62	507	1.8	76	14	10	3.9
22	-24.2	-50.5	888	19.8	23.9	15.6	77	1554	1.7	56	23	21	4.0
2	-24.2	-50.0	770	19.0	23.2	14.7	73	1495	1.7	71	22	7	4.1
33	-23.9	-48.7	695	21.0	26.0	16.0	72	1357	1.5	52	20	28	4.3
24	-22.7	-49.0	656	21.4	28.4	14.4	69	1701	1.4	8	3	89	4.6
20	-22.4	-47.0	633	23.1	29.7	16.4	62	1224	1.4	41	16	42	4.1

13	-20.9	-51.9	361	26.5	32.7	20.3	63	1155	1.1	14	9	77	4.0
14	-20.0	-51.6	480	24.6	30.8	18.3	69	1392	1.1	10	8	82	4.1
12	-19.8	-40.1	36	25.2	29.8	20.6	72	832	1.6	30	12	58	4.0
3	-19.7	-45.4	727	22.8	28.7	16.9	64	946	1.5	79	19	2	4.4
4	-19.3	-42.4	243	23.6	28.5	18.7	68	964	1.7	59	10	31	4.0
9	-18.7	-47.9	969	21.8	26.8	16.7	66	1412	1.7	80	9	11	3.9
11	-18.7	-52.6	783	23.7	29.1	18.2	66	1290	1.3	15	9	76	4.3
5	-18.6	-42.9	873	21.8	27.4	16.1	68	932	1.7	44	13	43	3.9
17	-18.3	-45.1	806	22.9	28.7	17.0	62	792	1.3	14	5	81	4.1
7	-18.0	-50.9	681	24.0	30.2	17.8	62	1628	1.5	6	5	89	4.5
26	-16.8	-44.3	926	23.3	29.4	17.2	64	477	1.3	35	6	59	3.9
1	-14.3	-48.7	545	25.5	31.4	19.6	61	1321	1.8	39	18	43	4.2
8	-11.9	-38.4	218	25.3	30.0	20.6	70	896	1.4	18	7	75	4.1
15	-11.2	-48.6	255	27.0	33.3	20.6	66	1204	1.5	10	8	82	4.2
29	-3.4	-44.3	81	28.0	32.7	23.2	72	1560	1.8	9	5	87	4.1

Tmean = mean annual air temperature; Tmax = average maximum air temperature; Tmin = average minimum air temperature; RH = average relative humidity; P = total precipitation; CAD = available water capacity.

Supplementary Table 2: Residue utilization in product production: chipping efficiency, carbon distribution in products and residues

Pulpwood	Portion	Source
Wood used	0.95	[71]
Undersized wood chips - burned	0.05	[71]
Fine residue used	0.00	[34]
Bark used	0.00	[34]
Coarse residue used	0.00	[34]

Supplementary Table 3: National production averages for paper products in Brazil according to Brazilian tree industry-IBÁ (2024)

Paper and Paper Products	Portion (%)	Description
Card paper	0.06	Paperboard used in cards, covers, folders, and other

graphic applications.

Sanitary Products	0.12	Tissue paper used in toilet paper, napkins, paper towels, and facial tissues.
Packaging	0.55	Corrugated board, paper bags, and other paper-based packaging materials.
Print and write	0.22	Uncoated and coated papers for books, notebooks, magazines, and office use.
Miscellaneous Paper Products	0.05	Specialty papers including filter paper, wallpaper, and other niche products.

Supplementary Table 4: Recycling parameters.

Recycling (as same product)	Portion (%)	Source
Portion of Card Paper recycled as Card Paper	0.42	[42]
Number of times Card Paper are recycled	5	[11]
Portion of sanitary products recycled as sanitary products	0	[42]
Number of times sanitary products are recycled	0	[42]
Portion of packaging recycled as packaging	0.914	[42]
Number of packaging is recycled	5	[11]
Portion of Print and write recycled as Print and write	0.66	[31]
Number of times Print and write are recycled	5	[11]
Portion of miscellaneous paper products recycled as miscellaneous paper products	0.081	[42]
Number of times miscellaneous paper is recycled	5	[11]

Supplementary Table 5: Chemical and fossil fuel emissions from harvest, transportation, production and silviculture processes.

Stage	Product	Factor (t CO ₂ emitted/	Source
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t CO ₂ final product)			
Silviculture	Card paper	0.0244	IPEF (2023)
	Sanitary Products	0.0244	IPEF (2023)
	Packaging	0.0244	IPEF (2023)
	Print and write	0.0244	IPEF (2023)
	Miscellaneous Paper	0.0244	IPEF (2023)
Extraction	Card paper	0.0094	IPEF (2023)
	Sanitary Products	0.0094	IPEF (2023)
	Packaging	0.0094	IPEF (2023)
	Print and write	0.0094	IPEF (2023)
	Miscellaneous Paper	0.0094	IPEF (2023)
Transportation	Card paper	0.0225	IPEF (2023)
	Sanitary Products	0.0225	IPEF (2023)
	Packaging	0.0225	IPEF (2023)
	Print and write	0.0225	IPEF (2023)
	Miscellaneous Paper	0.0225	IPEF (2023)
Production	Card paper	0.6764	[72]
	Sanitary Products	0.9382	[73]
	Packaging	0.3763	[74]
	Print and write	0.4362	[75]
	Miscellaneous Paper	0.5138	[73]

Supplementary Table 6: Carbon emissions and stock associated with the life cycle of pulp and paper products over 18 years

Estado	Yr	Stock (t C)		Emissions (t C)				
		Paper in use	HR	HR decomposition	Harvet	Silviculture	Transport	Production
AC	0-5	98.1	19.4	-4.6	-1.3	-3.4	-3.2	-92.0
AC	0-10	21.2	0.2	-0.1	-0.9	-2.3	-2.1	-62.5
AC	0-11	0.3	0.0	0.0	-1.3	-3.3	-3.1	-89.4
AL	0-5	72348.8	10756.4	-3468.7	-971.9	-2526.8	-2332.5	-67882.1
AL	0-10	15618.3	5.5	-6.2	-659.6	-1714.9	-1583.0	-46069.3
AL	0-11	217.5	0.0	0.0	-943.9	-2454.2	-2265.4	-65930.7
AM	0-5	1663.2	290.5	-79.2	-22.3	-58.1	-53.6	-1560.5
AM	0-10	359.0	1.0	-0.7	-15.2	-39.4	-36.4	-1059.1
AM	0-11	5.0	0.0	0.0	-21.7	-56.4	-52.1	-1515.6
AP	0-5	364136.6	60738.0	-17381.6	-4891.5	-12717.8	-11739.5	-341655.5
AP	0-10	78607.9	135.1	-107.4	-3319.7	-8631.1	-7967.2	-231870.1
AP	0-11	1094.6	0.8	-0.7	-4750.8	-12352.2	-11402.0	-331833.6
BA	0-5	2742534.7	656469.0	-123849.7	-36840.6	-95785.6	-88417.4	-2573215.6
BA	0-10	592044.3	21746.9	-7404.5	-25002.5	-65006.4	-60005.9	-1746355.1
BA	0-11	8243.8	1367.6	-465.6	-35781.5	-93031.9	-85875.6	-2499241.0
CE	0-5	332.6	58.8	-15.8	-4.5	-11.6	-10.7	-312.1
CE	0-10	71.8	0.2	-0.2	-3.0	-7.9	-7.3	-211.8
CE	0-11	1.0	0.0	0.0	-4.3	-11.3	-10.4	-303.1
ES	0-5	1125622.5	276021.4	-50467.0	-15120.5	-39313.4	-36289.3	-1056128.6
ES	0-10	242993.6	10371.1	-3357.7	-10261.8	-26680.7	-24628.3	-716759.1
ES	0-11	3383.5	729.5	-236.2	-14685.9	-38183.2	-35246.1	-1025767.1
GO	0-5	610604.6	149819.1	-27371.3	-8202.3	-21325.9	-19685.5	-572906.9
GO	0-10	131814.2	5646.3	-1825.8	-5566.6	-14473.2	-13359.9	-388812.7
GO	0-11	1835.4	398.3	-128.8	-7966.5	-20712.9	-19119.6	-556437.0
MA	0-5	1237056.3	215686.7	-58880.3	-16617.4	-43205.3	-39881.8	-1160682.7

MA	0-10	267049.4	754.6	-531.2	-11277.7	-29322.0	-27066.5	-787716.4
MA	0-11	3718.5	6.9	-4.8	-16139.7	-41963.3	-38735.3	-1127315.5
MG	0-5	9383603.4	2285481.9	-421587.4	-126050.4	-327731.0	-302520.9	-8804276.6
MG	0-10	2025684.2	82929.7	-27230.5	-85546.2	-222420.0	-205310.8	-5975167.4
MG	0-11	28206.3	5654.9	-1856.8	-122426.7	-318309.4	-293824.1	-8551171.9
MS	0-5	5668208.2	1472661.6	-249169.0	-76141.3	-197967.4	-182739.1	-5318263.2
MS	0-10	1223623.7	73549.2	-21121.1	-51674.6	-134353.8	-124018.9	-3609327.0
MS	0-11	17038.1	6680.6	-1918.5	-73952.4	-192276.2	-177485.8	-5165374.2
MT	0-5	546111.1	123374.1	-25035.0	-7335.9	-19073.4	-17606.2	-512395.2
MT	0-10	117891.7	2965.0	-1140.5	-4978.7	-12944.5	-11948.8	-347745.4
MT	0-11	1641.6	140.5	-54.0	-7125.0	-18525.1	-17100.1	-497664.9
PA	0-5	746837.0	126506.3	-35616.9	-10032.3	-26084.0	-24077.5	-700728.6
PA	0-10	161223.3	331.3	-252.2	-6808.6	-17702.3	-16340.6	-475561.0
PA	0-11	2244.9	2.4	-1.8	-9743.9	-25334.1	-23385.3	-680584.1
PB	0-5	609.8	113.7	-28.9	-8.2	-21.3	-19.7	-572.2
PB	0-10	131.6	0.7	-0.4	-5.6	-14.5	-13.3	-388.3
PB	0-11	1.8	0.0	0.0	-8.0	-20.7	-19.1	-555.7
PE	0-5	5497.1	1046.7	-259.5	-73.8	-192.0	-177.2	-5157.7
PE	0-10	1186.7	7.9	-4.5	-50.1	-130.3	-120.3	-3500.3
PE	0-11	16.5	0.1	-0.1	-71.7	-186.5	-172.1	-5009.4
PI	0-5	136731.4	27214.2	-6417.5	-1836.7	-4775.5	-4408.1	-128289.9
PI	0-10	29516.9	287.8	-146.4	-1246.5	-3241.0	-2991.6	-87066.0
PI	0-11	411.0	6.7	-3.4	-1783.9	-4638.2	-4281.4	-124601.8
PR	0-5	1870966.9	569280.9	-76244.4	-25132.8	-65345.2	-60318.7	-1755456.8
PR	0-10	403894.7	56010.9	-11554.9	-17056.8	-44347.6	-40936.3	-1191369.7
PR	0-11	5624.0	9516.0	-1963.1	-24410.3	-63466.7	-58584.6	-1704991.0
RJ	0-5	121327.7	33276.5	-5217.2	-1629.8	-4237.5	-3911.5	-113837.1
RJ	0-10	26191.6	2128.4	-546.3	-1106.1	-2875.8	-2654.6	-77257.5

RJ	0-11	364.7	242.2	-62.2	-1582.9	-4115.7	-3799.1	-110564.6
RN	0-5	187.6	34.1	-8.9	-2.5	-6.6	-6.0	-176.1
RN	0-10	40.5	0.2	-0.1	-1.7	-4.4	-4.1	-119.5
RN	0-11	0.6	0.0	0.0	-2.4	-6.4	-5.9	-171.0
RO	0-5	11036.8	2134.0	-520.0	-148.3	-385.5	-355.8	-10355.4
RO	0-10	2382.6	18.2	-9.9	-100.6	-261.6	-241.5	-7027.8
RO	0-11	33.2	0.4	-0.2	-144.0	-374.4	-345.6	-10057.7
RS	0-5	2631152.1	1006161.3	-88121.6	-35344.4	-91895.4	-84826.5	-2468709.5
RS	0-10	567999.6	219555.9	-26674.3	-23987.1	-62366.3	-57568.9	-1675430.4
RS	0-11	7909.0	81224.6	-9868.2	-34328.3	-89253.6	-82387.9	-2397739.2
SC	0-5	1390829.1	466768.6	-52938.8	-18683.1	-48576.0	-44839.4	-1304961.8
SC	0-10	300245.0	66060.3	-10986.3	-12679.6	-32966.9	-30431.0	-885633.8
SC	0-11	4180.7	15902.0	-2644.6	-18146.0	-47179.5	-43550.3	-1267446.8
SE	0-5	16649.0	3374.1	-779.3	-223.6	-581.5	-536.8	-15621.1
SE	0-10	3594.1	40.6	-19.8	-151.8	-394.6	-364.3	-10601.5
SE	0-11	50.0	1.1	-0.5	-217.2	-564.8	-521.3	-15172.0
SP	0-5	4254115.8	1215903.1	-179419.5	-57145.7	-148578.9	-137149.8	-3991474.3
SP	0-10	918356.7	92868.6	-21871.2	-38782.9	-100835.5	-93078.9	-2708879.8
SP	0-11	12787.5	12447.7	-2931.5	-55502.9	-144307.6	-133207.0	-3876727.7
TO	0-5	433389.4	88158.4	-20275.1	-5821.7	-15136.5	-13972.2	-406632.7
TO	0-10	93557.9	1088.5	-526.7	-3951.0	-10272.7	-9482.4	-275968.0
TO	0-11	1302.7	28.9	-14.0	-5654.4	-14701.4	-13570.5	-394942.8

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THESIS CONCLUSIONS

This dissertation investigates the carbon balance of Brazilian forest plantations through an integrative approach that combines ecophysiological experiments with life cycle assessment (LCA) modeling, focusing on *Eucalyptus* and *Pinus* species. The results offer new perspectives on how carbon is distributed within trees, how different genetic materials respond to environmental and management conditions, and the potential of these systems to contribute to climate change mitigation.

In the first study, we observed that maximum temperature and planting density emerged as the main limiting factors for productivity, directly influencing carbon fluxes and their allocation among plant components. In denser stands and in environments with greater thermal and water stress, trees tended to allocate more carbon to their root systems at the expense of aboveground growth. Understanding these responses, especially in the most commercially used clones, is essential for guiding adaptive forest management strategies in the face of climate change.

Overall, average NEP values indicated that, even under different climatic conditions, *Eucalyptus* and *Pinus* plantations in Brazil maintain a positive carbon balance, acting as important carbon sinks. *Pinus* plantations aged between 6 and 9 years showed the highest absolute NEP values. Regions with fewer climatic constraints also showed higher NEP. These findings highlight the role of planted forests in Brazil as valuable allies in addressing the climate crisis.

The second study aimed to compare fast-growing (FG) *Eucalyptus* clones with more drought-tolerant (DT) ones. As expected, DT clones showed lower gross and net primary productivity (GPP and NEP). However, they maintained remarkable stability in carbon fluxes and allocation patterns, even under varying environmental conditions, demonstrating greater resilience. FG clones, while more productive in optimal conditions, proved more vulnerable to high temperatures and water scarcity, reducing carbon allocation to wood production. These results illustrate a classic trade-off: grow fast or endure stress? This balance between productivity and resilience underscores the importance of breeding programs that focus not only on yield but also on the long-term stability of genetic materials in a changing climate.

In the third study, the ForestWise model was used to simulate the life cycle of pulp and paper products over an 18-year horizon. Although these products are mostly short-lived, lasting

up to 15 years when recycled, a substantial portion of their carbon is retained throughout the value chain, especially when considering successive rotations and the accumulation of carbon in forest biomass, paper products, and residues left on site. The analysis showed that, when excluding industrial emissions or including forest biomass, the Brazilian pulp and paper sector can achieve a positive net carbon balance.

In terms of emissions, the industrial phase represents the main hotspot, accounting for over 90% of total emissions. Within forest operations, fertilization (50%) and weed control (33%) are the primary contributors to silvicultural emissions. Strategies such as technological innovation, the use of bio-based inputs, and regenerative practices show great potential to reduce emissions while maintaining or even improving productivity.

Taken together, the results of this research reinforce the tremendous potential of Brazilian planted forests, especially when paired with low-carbon industrial practices, to contribute to climate neutrality goals. Measures that enhance carbon sequestration or reduce emissions are urgently needed to slow the effects of climate change. Furthermore, companies committed to sustainable practices can gain a competitive advantage in increasingly demanding markets. Advancing toward a more sustainable forest sector requires an integrated approach, combining ecophysiological knowledge, climate-resilient genetic materials, and low-emission value chains. The insights generated through this research provide a solid foundation to support this transition and to maximize the environmental, economic, and social contributions of Brazilian planted forests in a global context.