Carbon Balance and Management

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Carbon stock, fluxes, and partitioning in *Pinus taeda* plantations are affected by genetic variation and stand density in Southeast Brazil

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Abstract

Background To understand how genetic variation among varieties and stand density affect carbon (C), we assessed C stocks, fluxes, and partitioning in *Pinus taeda* L. plantations in Southeast Brazil. We measured the annual C balance in two consecutive years (from 7 to 9 years after planting) in four different clonal varieties with distinct crown structures (C1-medium, C2-broad, C3-narrow, and C4-broad) and an OP (open-pollinated) family. From age 7 to 8 years, the C balance was assessed for all five varieties at a stand density of 1894 trees ha^{-1}. From age 8 to 9 years, the C balance was assessed for three varieties (C2, C3, and OP) at two stand densities (low density (LD): 613 trees ha^{-1} and high density (HD): 1894 trees ha^{-1}).

Results At age 7–8, the total C stock (above- and belowground plus the litter layer) among varieties ranged from 168 Mg C ha^{-1} (C3) to 186 Mg C m^{-2} (C1), with the bole as the largest pool (68%). Aboveground net primary production (ANPP) ranged from 1.9 to 3.1 kg C m^{-2} $year^{-1}$, and total belowground carbon flux (TBCF) from 2.0 to 2.9 kg C m^{-2} $year^{-1}$. The partitioning of GPP (Gross Primary Production) to ANPP and TBCF reached a maximum value of 35% and 41%, respectively. At age 8–9 years, the C stock was greater in the HD stands than in the LD stands across all varieties. Overall, C stock reached between 103.5 and 184.6 Mg C ha^{-1}. ANPP under HD was 1.9 kg C m^{-2} $year^{-1}$ compared with 0.62 kg C m^{-2} $year^{-1}$ under LD. There were no significant differences in TBCF between the HD and LD stands. The partitioning of GPP to ANPP was lower and to TBCF was higher under LD compared with HD.

Conclusion Relationship between crown structure and the C stock, fluxes, and partitioning is not clear and should be used with caution for management prescriptions related to C sequestration. Also, no differences in the bole C stock and sequestration were found across varieties within the same planting density. Finally, the genetic variation among varieties and stand density significantly affected stand productivity, with stand density showing greater effect.

Keywords Clonal plantation, Belowground allocation, Wood productivity, Genotypes, Loblolly pine

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Introduction

Carbon (C) sequestration in planted forests depends on site resources availability (e.g., sunlight, water and nutrient), the proportion of the resources captured by trees, and the efficiency with which trees utilize resources [1]. Consequently, C allocation is important in wood production, as it controls the partitioning of C fixed in photosynthesis between respiration and biomass production and the distribution of biomass between above- and belowground components [2]. Gross primary production (GPP) comprises three key components: aboveground net primary production (ANPP), aboveground autotrophic respiration (Rag), and total belowground carbon flux (TBCF) [3–5]. Approximately 30–50% of total GPP is used in the production of aboveground biomass, and the remainder is divided between belowground production (coarse roots, fine roots, and mycorrhizae) and Rag [6]. TBCF can range from 25 to 63% of GPP and is sensitive to water and nutrient availability, typically increasing under abiotic stress (e.g., soil water deficit) [7, 8]. For accurate predictions of plantation productivity across years and landscapes, understanding how C allocation responses to environmental conditions and resource availability is needed [9, 10].

Pinus taeda L., native to the United States of America (US), grows extremely well in regions outside its natural range [11]. In the US, the mean annual increment (MAI) ranges from 16 to 33 $m^3\ ha^{-1}\ year^{-1}$ [12], while in Brazil, it reaches the highest values recorded worldwide, up to 59 $m^3\ ha^{-1}\ year^{-1}$ at specific sites [11]. The rapid growth in Brazil has been attributed equally to a longer growing season (6 months in USA, compared to all year round in Brazil), higher sunlight intensity, better soils (higher clay content, organic matter and CEC), and a lack of pathogens [11]. Thus, to maintain high levels of productivity and ensure the sustainability of *Pinus* plantations, an understanding of environmental interactions with silvicultural treatments and genetic improvement is essential [13].

Forest productivity is a combination of two variables; firstly, the environment: silvicultural activities such as fertilization, competing vegetation control, irrigation, soil preparation, and planting density, as well as the selection of the best adapted genotypes to specific sites and climates, which may result in significant increases in wood production [7, 12, 14–17]. The second is genetics, as genetically improved trees, especially clones, demonstrate great potential for increasing the short-term productivity of forest plantations [18]. Such potential is mainly due to their more uniform growth and development than open-pollinated trees because of the lack of tree-to-tree genetic variation [19, 20].

Planting clones with improved genetics and defining the optimum tree density may enhances productivity and management precision. Considering that increases in C sequestration with genetically improved *P. taeda* varieties will be proportional to increases in volume or dry mass production [21], an assessment of specific ideotype characteristics, such as crown size, can be used to determine which variety will have greater biomass growth. In *P. taeda* plantations, greater stand uniformity can reduce asymmetric competition, improve light distribution, and promote more efficient use of water and nutrients, ultimately contributing to higher stand-level productivity [18, 22].

The concept of ideotypes in managed forests has been used for a long time, based on traits such as crown shape, branch characteristics (number, size, angle) and self-pruning behavior [23]. In forestry, the concept of a crown ideotype help identify consistent tree crowns patterns and their influence on intraspecific competition in forest stands [24], highlighting the importance of knowing how varieties with different crown ideotypes will respond to silvicultural treatments [25]. Therefore, ideotyping would be a useful tool to predict stand productivity and C stocks, as well as the C fluxes and partitioning responses of clones. Previous studies based on our experimental site, in comparison with two other sites in the US, showed how *P. taeda* growth is likely due to a combination of factors, including leaf area distribution, crown architecture, and site effect (heat sum) [11, 25, 26].

The aim of this study was to examine C stocks, fluxes, and partitioning to understand the differences in productivity among different *P. taeda* varieties (four clones and one open-pollinated family) at two different stand densities (613 and 1894 trees ha^{-1}) in Southeastern Brazil.

Methods

Study site

Our experimental site was established in 2011 in Paraná State, Brazil (– 26.19°S, – 49.49°W) in an area where *P. taeda* is commonly cultivated. The experiment followed a split split-plot design with three replications, encompassing two planting densities and five genetic materials (four clonal varieties and one open-pollinated family) [11, 26]. The site is located in a climatic region classified as humid subtropical without a dry season and with a temperate summer (Cfb) [27]. The historical annual (last 20 years) average temperature is 16.5 °C, and annual precipitation is 1625 mm. The site altitude is 857 m above sea level, and the soil is defined as an umbric aluminum haplic inceptisol. During the study period in 2019 and 2020, the average annual temperature was 17.3 °C and 17.0 °C and the annual rainfall was 1739 mm and 1020 mm, respectively. Weather data were collected from an automatic station monitored by the Brazilian National Institute of Meteorology (https://mapas.inmet.gov.br, Rio Negrinho

Station ID A862) located approximately 10 km from the experimental site.

Experimental design

Details of the experiment were presented by [11]. The experiment was established as a split-plot design with three replicates, where main plots were planted in blocks at two stand densities, 613 stems ha^{-1} (low density, LD; spacing 2.4 × 6.8 m) and 1894 stems ha^{-1} (high density, HD; spacing 2.4 × 2.2 m), in an intensive silvicultural treatment. This treatment ensured no nutrient limitations due to balanced macro- and micronutrient fertilization at planting and post-planting stages (including 150 kg ha^{-1} of triple superphosphate and lime). Competing vegetation was controlled at site preparation using a glyphosate-based product (1.5 kg ha^{-1}). Additional spot spraying and mowing were performed as needed, which ensured an almost nonexistent understory vegetation by year seven. Ant control was carried out during the early years using granulated formicide [26, 28]. The split plot consisted of the four clonal varieties (C1, C2, C3, and C4) and an open-pollinated (OP) family, providing a range in crown ideotypes [23, 24] to examine the silvicultural and stand density effects on ideotype growth (Fig. 1). The varieties were classified by crown ideotype as follows: C1-medium, C2-broad, C3-narrow, and C4-broad, as well as OP-open pollinated, which was classified as having a medium to broad crown size.

Measurements of the C stock, GPP, ANPP, TBCF, Rag, and NPP were performed for two consecutive growing seasons, from 7 to 8 and from 8 to 9 years after planting. During the first year, we measured all clones and the OP family at high stand density under high silviculture to evaluate the effect of crown size on the stock, fluxes, and partitioning of C. In the second year, we measured the broad and narrow clones and the OP trees at both planting densities (LD and HD) to compare the most contrasting crown sizes to examine potential genetic-by-density interactions. Each treatment plot consisted of 9 × 9 trees, and the measurement plot had 25 trees (5 × 5). The 9 × 9

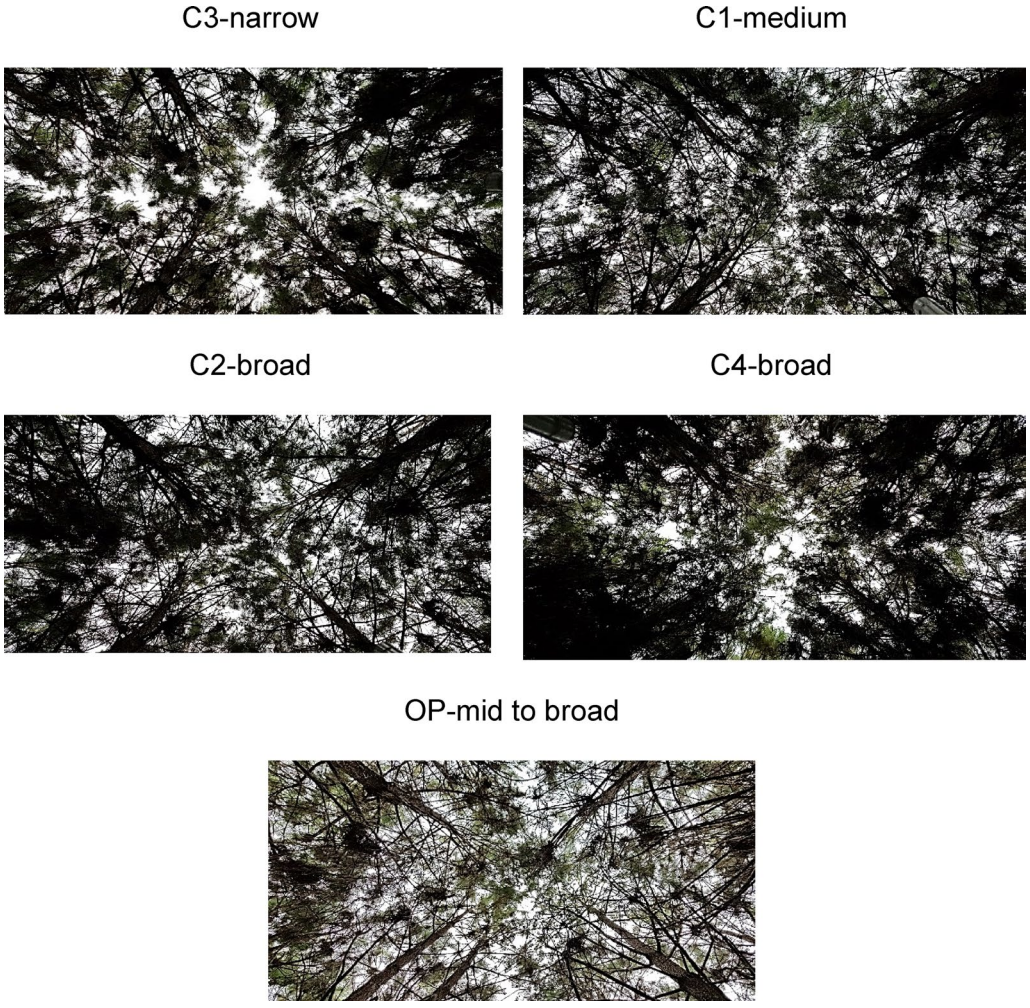

Fig. 1 Canopy photos of different *Pinus taeda* varieties in the high-density stands (1894 stems ha^{-1}) 8 years after planting

treatment plot size was 1322 m^2 and 428 m^2 for the low and high density, respectively, and the corresponding measurement plots were 408 m^2 and 132 m^2.

Dry mass equations

Diameter over-bark at breast height (DBH – 1.3 m above ground level) and total height (H) were measured for all live trees (the whole site) annually from year 4. Individual tree volume was calculated from diameter at breast height and height using an equation presented by [29]. Individual tree volume and basal area were summed by plot and scaled to a hectare basis [11] and subsequently used in regression equations (see additional supporting files – Table S1). In the 2017 winter season, a total of 12 trees (covering the 2017 DBH distribution) were destructively harvested to determine the above- and belowground biomasses across the range in tree height and diameter in the intensive silvicultural treatments, LD and HD plots, and C3 and OP varieties; these varieties were initially selected because they represented contrasting crown length and width among all genetic varieties based on annual measurements of all trees. Cut trees were divided into the bole (wood + bark), living branches, and foliage. For belowground biomass, the coarse roots (diameter >2 mm) were excavated from a one-meter square centered on the stump at the base of each tree. We quantified coarse roots outside the square meter at the base of the tree by excavating a trench 50 × 50 cm to a depth of 50 cm. The coarse roots from the base of the tree and the trench were scaled appropriately and summed as the coarse root biomass. The total fresh weight of the aboveground components was measured on-site, and 300 g of branches and foliage (on every third of the crown height) were collected and dried at 65 °C to a constant weight to determine the dry mass. These values of humidity percentage were then used to convert fresh weight to a dry weight. Soil was washed from the coarse root material before the roots were weighed. See [11, 26] for more details.

Table 1 Leaf area index (LAI) of different *Pinus taeda* varieties under contrasting stand densities

Density	Variety	Leaf area index (m^2 m^{-2})		
		7.3 years (2018)	8.3 years (2019)	8.9 years (2020)
High	C1	6.2	7.0	6.0
High	C2	6.1	6.2	4.9
High	C3	6.0	5.7	5.9
High	C4	8.2	7.9	6.3
High	OP	6.7	6.7	5.2
Low	C2	4.2	5.0	4.8
Low	C3	3.9	4.0	4.7
Low	OP	5.0	5.5	4.8

This data permitted those authors to develop site- and treatment-specific individual tree foliage, branch, bole, and coarse root regression equations following the method developed by [12]. These equations were developed for C3 and OP varieties under intensive silviculture treatment at the two stand densities, i.e., 613 (LD) and 1894 (HD) stems ha^{-1} [11]., Therefore, we applied the C3 biomass regression equations for clones C1, C2 and C4 to calculate their biomass. The [12] method guarantees the additivity of components, so for an individual tree, the sum of the component masses provides an estimate of the total tree mass, which is not necessarily the case when individual component regression equations are used. The method also accounts for correlations among the equations and the heteroscedasticity inherent in biomass relationships. We used tree diameter at breast height, total height, and the length of the live crown as our primary independent variables and included adjustments for site, silviculture, variety, and stand density for each of the primary independent variables. If an adjustment term for a given independent variable was not significant in a regression, the term was not included. Site, silviculture, variety, and stand density were significant in the final models. Finally, the litterfall C concentration was estimated from composited litterfall. Samples from all components were analyzed using a LECO 1000 CN analyzer (Leco Corp. St. Joseph, MI, USA).

Leaf area index

Leaf area index (LAI) was measured using a LICOR LAI-2000 or LAI-2200 Plant Canopy Analyzer with a 10° view cap, which estimates projected LAI. Off-peak leaf area index measurements were collected in August 2018 and July 2019 using the LAI-2000, with one sensor set up in an open area outside the plots and ten below-canopy readings taken per plot. Peak LAI measurements were collected in March 2020 using the LAI-2200 model; a two-sensor setup was used where above-canopy light was measured at the same time as the below-canopy measurements were taken. Ten parallel points were measured per plot (Table 1).

Carbon fluxes and partitioning

Carbon fluxes were measured in two consecutive growing seasons (September 2018 to October 2020), i.e., years 7 to 8 and 8 to 9. We assessed the C fluxes and partitioning in HD plots among the varieties (C3, C1, C2, C4, and OP) in the first year and the effect of the two different stand densities (HD and LD) on C balance for a subset of these varieties (C3, C2, and OP) in the second year. All annual dry mass increments and monthly litterfall collections were converted into C using their carbon content after CNH laboratory composition analysis and expressed as g C m^{-2} $year^{-1}$.

Aboveground autotrophic respiration (Rag) was estimated as a constant fraction of the aboveground net primary production (ANPP), following the methodology of [2], which uses the concept of carbon use efficiency, known as CUE; Therefore, we assumed a CUE value of 0.47 for all varieties because the CUE of *P. taeda* did not vary with silvicultural treatment [17, 30]. Some studies in which the autotrophic respiration of *P. taeda* and *Pinus radiata* was directly measured revealed values between 0.42 and 0.52 supporting this approach [4, 6, 17, 31–33]. Equation for Rag:

$$\mathrm{Rag} = \mathrm{ANPP} \times \left(\frac{1 - \mathrm{CUE}}{\mathrm{CUE}}\right)$$

The total belowground carbon flux (TBCF) was estimated using the mass balance methodology described by [5, 21] as the sum of the soil CO_2 efflux, aboveground litterfall (foliage, branches, bark, and cones), root dry mass increment, and the change in the mass of the O horizon (forest floor). Erosion or losses of C by leaching and the decomposition of stumps from previous rotations are considered negligible for TBCF [5] and were not included in the calculations. In addition, the variation in soil C allocation was not included since its variation during different rotations does not represent important changes [34]. The TBCF (g C m^{-2} $year^{-1}$) was calculated following [35]:

TBCF = (Soil C efflux) − (aboveground litterfall mass) + (the change in the mass of the O horizon) + (the change in the coarse root mass).

Soil C efflux (Fs) was measured monthly during the study period using PVC collars (20 cm in diameter) and an SRC-1 chamber (PPSystem, Haverhill, MA, USA) coupled to a portable infrared gas analyzer (EGM-4) and presented on an annual basis (g C m^2 y^{-1}). Eight PVC collars were installed in each plot in two locations, near the tree and in the middle of the inter-row, with four replicates. All collars were inserted into the mineral soil to a depth of 5–7 cm to ensure stability and to prevent lateral CO_2 diffusion [36].

Litterfall was collected monthly using three randomly located litter traps per plot. Each litter trap (2 mm mesh plastic net) was placed 30 cm above ground and covered all the area among four trees. In the HD plots, this area was ~4.9 m^2 at each location, and in the LD plots, the area was ~13.9 m^2. Foliage and branches were collected and dried at 65 °C to a constant weight. Cones and bark in the litter traps were included with branch material.

The dry mass of the O horizon was quantified at the beginning and at the end of the first (age 8) and second (age 9) years of the study period using a 0.25 m^2 steel frame. The sampling was performed immediately adjacent to a random trunk or in the mid-row, with two replicate per position to sum to a 1 m^2. The O horizon samples consisted of only *P. taeda* material because competing vegetation was controlled until canopy closure. All samples were dried at 65 °C until constant weight, separated into leaves, branches, bark, and cones, and weighed. Ash content analysis was performed on subsamples and was used to correct for mineral soil contamination. Subsamples were analyzed to determine the dry weight C content percentages, and the values were summed to calculate the annual accumulation of litterfall and the litter layer.

Changes in coarse root biomass (only roots >2 mm in diameter) were estimated for each year using the dry mass equations. The change in mineral soil organic matter was disregarded for the period of the study as the change in this soil C stock over short time intervals is very small compared with other carbon inputs and outputs [3, 34, 37].

ANPP was estimated annually as the sum of the wood net primary production (WNPP) and foliage net primary production (FNPP). FNPP was assessed by the variation in leaf area index (LAI), converted into dry mass using specific leaf area (SLA), plus foliage litterfall. SLA was estimated for each treatment using the method presented by [26].

WNPP was calculated as the sum of the bole increment, branch and bark litterfall. Bole increment was calculated by measuring DBH and H of all trees in October 2018, July 2019, and July 2020.

GPP was calculated as the sum of ANPP, TBCF, and Rag. Partitioning was calculated as the ratio between a specific carbon flux (WNPP, ANPP, TCBF, and Rag) and GPP.

Net ecosystem productivity (NEP)

Ecosystem respiration (Re) was calculated as the sum of Rag and Fs.

Net ecosystem productivity was calculated as follows:

$$\mathrm{NEP} = \mathrm{GPP} - \mathrm{RE}$$

Data analyses

Analysis of variance was applied to all C fluxes with variety and density treated as fixed effects. To evaluate the relationships between C fluxes and GPP partitioning, the coefficient of determination (R^2) and significance value (p) were examined; where factors were significant, differences were tested by Tukey's separation of means for the C stock. We tested GPP and partitioning for interactions and main effects. All analyses were performed in R (ExpDes.pt_1.2.0), and the significance value was $p \leq 0.05$ for all tests with $n = 3$ (three plots or replicates). The average values of the C stock, fluxes and partitioning were calculated to allow comparisons between densities and within

a density among the varieties. These values were also averaged and compared between the age of 8 and 9 years for each variety grown at HD.

Results

Carbon stocks of the five varieties at high stand density

The total C stock at age 8 years ranged from 163 to 186 Mg C ha^{-1} (Table 2). The largest aboveground component was the bole, which ranged from 113 Mg C ha^{-1} (OP) to 124 Mg C ha^{-1} (C1), and coarse roots ranged from 27.7 Mg C ha^{-1} for C3 to 33 Mg C ha^{-1} for C1. The mean percentage of the total C stock across all varieties was 68, 17, 6.5, 6.1, and 1.6% for the bole, coarse roots, branches, foliage, and forest floor (litter layer), respectively. The bole and branches were the only biomass components that did not differ among the varieties. The total C stock of C1 differed from that of the C3 and C4 varieties, driven mostly by the higher foliage and coarse root biomasses.

Table 2 Carbon stock (Mg C ha^{-1}) of each component of different *Pinus taeda* varieties at age 8 years under high density (HD)

Component	Variety				
	C3	C1	C2	C4	OP
Foliage	8.7 (0.10) b	12.3 (0.31) a	10.0 (0.32) ab	10.5 (0.29) ab	10.8 (0.66) ab
Branches	10.3 (0.89) a	14.1 (1.16) a	9.8 (0.15) a	10.0 (0.47) a	11.2 (0.87) a
Bole	113.9 (1.03) a	124.3 (3.54) a	115.7 (3.74) a	111.5 (2.80) a	113.3 (6.44) a
Coarse roots	27.7 (0.10) b	33.0 (0.79) a	28.3 (0.88) ab	28.7 (0.74) ab	29.4 (1.2) ab
Litter layer					
Foliage	2.5 (0.05) b	2.4 (0.08) b	2.9 (0.02) a	2.5 (0.05) b	3.1 (0.03) a
Branches	0.1 (0.02) c	0.1 (0.02) c	0.3 (0.02) ab	0.2 (0.02) b	0.3 (0.04) a
Total	163.1 (1.69) b	186.2 (5.57) a	167.0 (4.97) ab	163.3 (3.94) b	168.1 (7.93) ab

Varieties are shown from the narrow to the broad crown ideotypes. Values in parentheses represent the standard error ($n=3$). Different letters within a row indicate differences among varieties for a particular component based on Tukey's test ($p=0.05$)

Gross primary productivity (GPP) and carbon partitioning among the five varieties at the high stand density

Gross primary productivity at age 8 years ranged from 6.02 to 8.83 kg C m^{-2} $year^{-1}$, with no significant difference among varieties. TBCF ranged from 2.03 kg C m^{-2} $year^{-1}$ for C4 to 2.85 kg C m^{-2} $year^{-1}$ for C3. The greatest differences in ANPP and Rag were observed between C1 and OP, i.e., 3.14 kg C m^{-2} $year^{-1}$ (C1) and 1.85 kg C m^{-2} $year^{-1}$ (OP) for ANPP and 3.54 kg C m^{-2} $year^{-1}$ (C1) and 2.09 kg C m^{-2} $year^{-1}$ (OP) for Rag (Fig. 2, see also Table S2 in the additional supporting files). TBCF was the only C flux that differed between at least two varieties (C3 and C4), driven primarily by the higher Fs in C3. Only C3 exhibited an increase in the litter layer along the two measurements (e.g. at the beginning and end of that year), and even though this variety had the lowest coarse root production (see additional supporting files

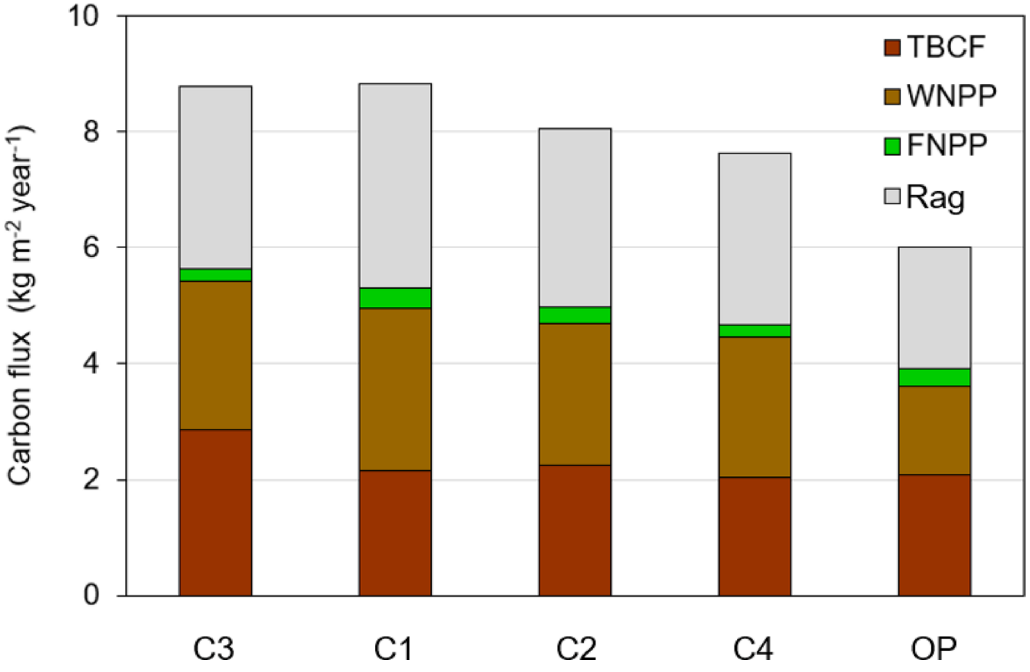

Fig. 2 Carbon fluxes in different *Pinus taeda* varieties at age 8 years growing at high planting density. TBCF = carbon flux to soil; WNPP = wood net primary productivity; FNPP = foliage net primary production; Rag = aboveground autotrophic respiration

- Table S2), it also had the highest Fs. Litterfall differed between C2 and OP compared with C1 and C3; however, there was no difference between C4 and the C3 crown ideotype.

Rag typically represented the greatest proportion of GPP, ranging from 31% (OP) to 39% (C1 and C4) (Fig. 3). TBCF varied among the varieties; OP allocated the greatest proportion of GPP to TBCF. All the varieties were C sinks. NEP ranged from 1.73 to 3.10 g C m^{-2} $year^{-1}$, with no significant difference among the varieties ($p = 0.576$). Carbon partitioning did not differ among the varieties, although GPP distributed to WNPP ranged from 22% for OP to 32% for C4. C1 had the highest ANPP: GPP ratio (0.3), and OP had the highest TBCF: GPP ratio (0.4), which were also not statistically different.

Carbon stocks of three varieties at high and low stand densities

At age 9 years, the HD treatment had a higher total C stock than the LD treatment (Table 3). In some cases, nearly 40% more C stock was contained in the tree components under HD compared with LD. The foliage, bole, litter layer, and total C stock differed among the varieties under LD compared with only the litter layer under HD.

On average, the total C stock across the varieties under HD was 183 Mg C ha^{-1}, which was 40% higher than that under LD (111 Mg C ha^{-1}). There were significant differences in the total C stock between C2 and C3 and OP under LD, whereas under HD the varieties showed similar total C stocks, characterizing a genotype × density (G × D) interaction (Table 3).

The mean C stock of each component under LD was 67.7 Mg C ha^{-1} for the bole, 14.8 Mg C ha^{-1} for branches, 6.8 Mg C ha^{-1} for foliage, and 19.0 Mg C ha^{-1} for coarse roots. The mean C stock of each component under HD was 127.5 Mg C ha^{-1} for the bole, 11.0 Mg C ha^{-1} for branches, 10.1 Mg C ha^{-1} for foliage, and 30.7 Mg C ha^{-1} for coarse roots. On a percentage basis, the C stocks of the bole, foliage, and coarse roots under HD were 47%, 33%, and 38% greater, respectively, than those under LD. The living branch C stock under HD was 26% lower than that under LD.

Gross primary productivity and carbon partitioning among three varieties at two stand densities

For all varieties, there was no difference between the stand densities for TBCF, foliage production, the soil C flux, and the litter layer (see additional supporting files - Table S3). C3 had greater coarse root production than the other varieties under HD ($p < 0.001$).

All combinations of variety and stand density were C sinks at 9 years. C2 and C3 had higher NEP under HD compared with LD. There were no significant differences in NEP among the varieties for a given stand density. The average NEP across the varieties under LD was 0.52 kg C m^{-2} $year^{-1}$, which was 73% lower than that under HD (1.94 kg C m^{-2} $year^{-1}$).

Overall, ANPP was consistently higher under HD than under LD regardless of the variety (Fig. 4). The mean

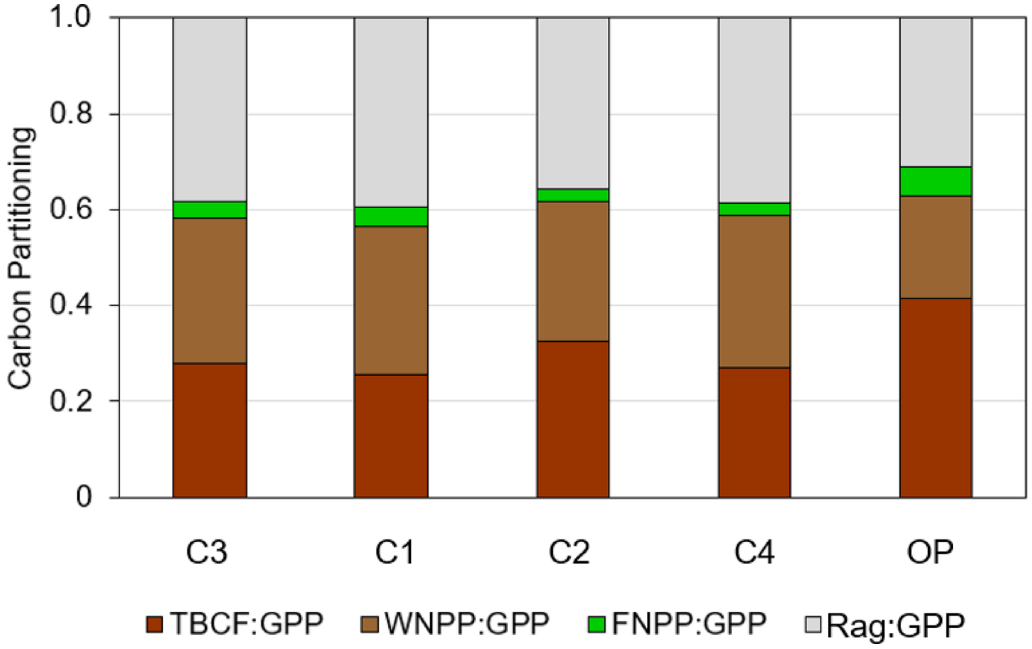

Fig. 3 Partitioning of the gross primary production of *Pinus taeda* varieties at age 8 years growing at high planting density. ANPP = Aboveground net primary production; Rag = Aboveground autotrophic respiration; TBCF = carbon flux to soil; GPP = gross primary production; WNPP = wood net primary production

Table 3 Carbon stock (Mg C ha^{-1}) of each component of different *Pinus taeda* varieties at age 9 years growing under contrasting planting densities

Variety	LD	HD	LD	HD	LD	HD
	C2	C2	C3	C3	OP	OP
Foliage	7.6 (0.3) Aa	10.2 (0.3) Aa	5.7 (0.1) Bb	9.6 (0.1) Aa	7.3 (0.05) Ba	10.8 (0.6) Aa
p-value	Varieties = 0.005		Planting density = < 0.001		Varieties × planting density = 0.286	
Branches	16.0 (0.2) Aa	10.1 (0.04) Ba	15.0 (1.5) Aa	11.1(0.4) Aa	13.5 (1.0) Aa	12.2 (0.8) Aa
p-value	Varieties = 0.965		Planting density = < 0.001		Varieties × planting density = 0.142	
Bole	74.5 (2.3) Ba	126.6 (3.8) Aa	62.7 (1.0) Bb	129.4 (0.9) Aa	66.0 (0.9) Bb	126.6 (4.4) Aa
p-value	Varieties = 0.324		Planting density = < 0.001		Varieties × planting density = 0.118	
Coarse roots	20.2 (0.6) Ba	29.8 (0.8) Aa	18.1 (0.2) Ba	31.6 (0.2) Aa	18.9 (0.1) Ba	30.7 (1.3) Aa
p-value	Varieties = 0.956		Planting density = < 0.001		Varieties × planting density = 0.110	
Litter layer						
Foliage	2.2 (0.1) Ba	3.4 (0.1) Aab	1.8 (0.1) Bb	2.5 (0.1) Ab	2.4 (0.1) Aa	3.6 (0.2) Aa
p-value>	Varieties = < 0.001		Planting density = < 0.001		Varieties × planting density = 0.220	
Branches	0.3 (0.02) Ba	0.6 (0.04) Aab	0.2 (0.01) Bb	0.4 (0.04) Ab	0.3 (0.004) Ba	0.7 (0.1) Aa
p-value	Varieties = < 0.001		Planting density = < 0.001		Varieties × planting density = 0.068	
Total	120.8 (3.3) Ba	180.7 (4.7) Aa	103.5 (1.9) Bb	184.6 (1.0) Aa	108.4 (2.0) Bb	184.6 (6.5) Aa

Values in parentheses represent the standard error ($n = 3$). Values followed by the same uppercase letter do not differ significantly between planting densities within the same variety. Values followed by the same lowercase letter do not differ significantly among varieties under the same planting density. Comparisons were performed under the condition that the interaction between variety and planting density was not significant ($p > 0.05$)

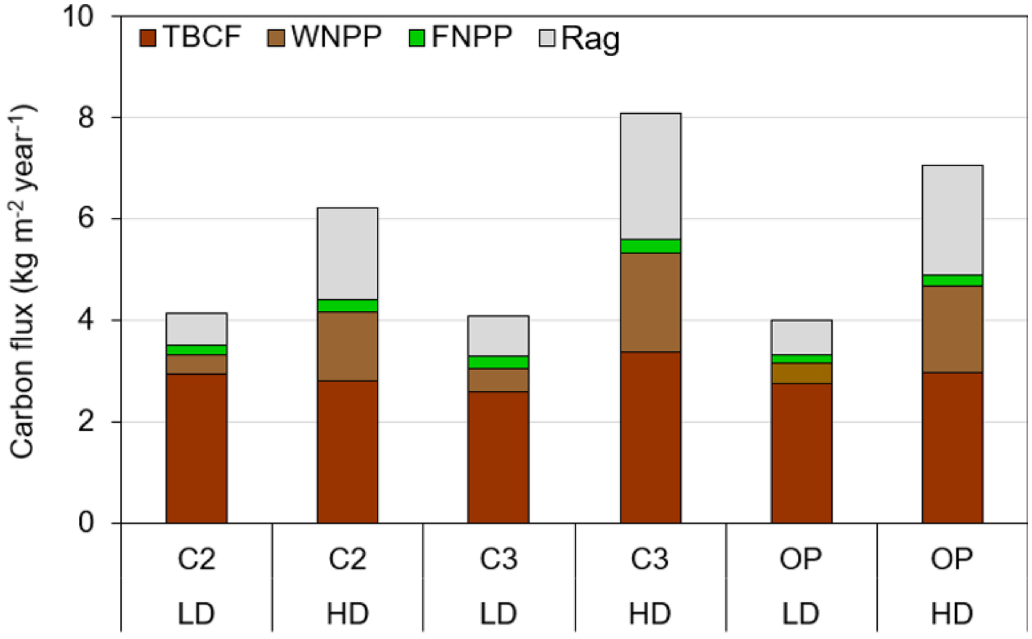

Fig. 4 Distribution of C fluxes in different *Pinus taeda* varieties at age 9 years growing under contrasting planting densities. The data are presented in the order shown to highlight the differences due to stand density for a particular variety. TBCF = carbon flux to soil; WNPP = wood net primary productivity; FNPP = Foliage net primary production; Rag = Aboveground autotrophic respiration

WNPP under LD was 0.36 kg C m^{-2} $year^{-1}$, which was 77% lower than that under HD (1.54 kg C m^{-2} $year^{-1}$). The mean ANPP under LD was 0.62 kg C m^{-2} $year^{-1}$, which was 67% lower than that under HD (1.9 kg C m^{-2} $year^{-1}$). In addition, the mean Rag under LD was 0.69 kg C m^{-2} $year^{-1}$, which was 67% lower than that under HD (2.16 kg C m^{-2} $year^{-1}$). There was no significant difference in TBCF between HD (3.05 kg C m^{-2} $year^{-1}$) and LD (2.76 kg C m^{-2} $year^{-1}$).

The C fluxes of the varieties were similar under HD and LD (see additional supporting files - Table S3). There were no differences among the varieties for any flux measured, but litterfall and coarse root production varied.

C partitioning to WNPP differed between densities for C2 and C3. Under HD, the WNPP: GPP ratio of C2 reached 22% compared with only 9% under LD, whereas for C3, the ratio reached 24% under HD and only 10% under LD (Fig. 5). ANPP, TBCF, and Rag differed between

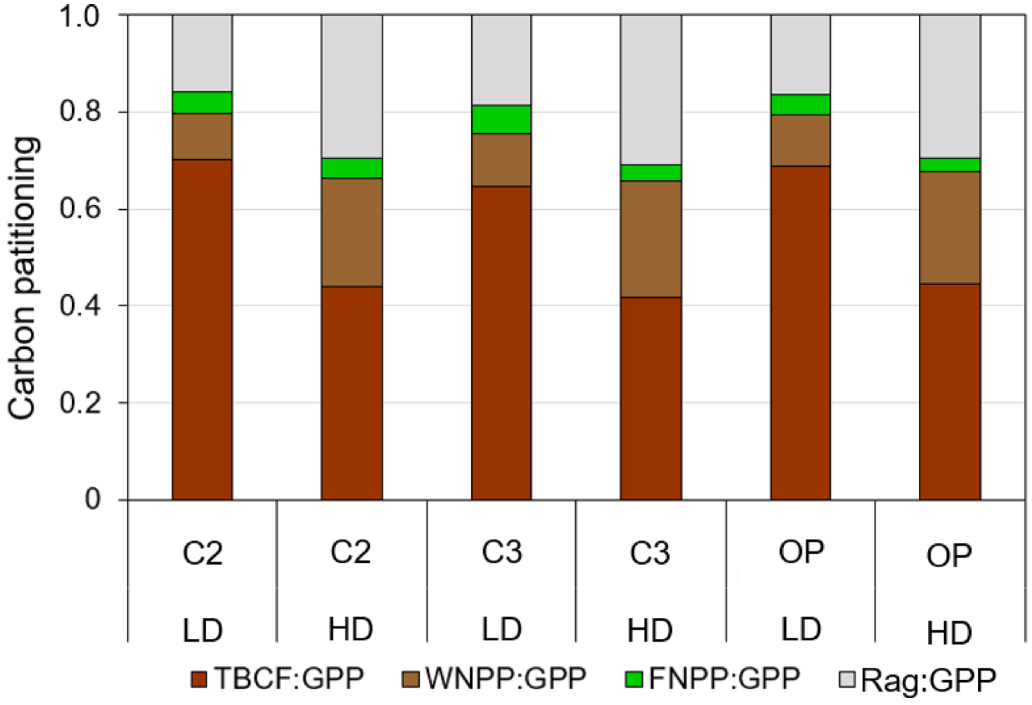

Fig. 5 Partitioning of the gross primary production of *Pinus taeda* varieties at age 9 years growing under contrasting planting densities. ANPP = Aboveground net primary production; Rag = Aboveground autotrophic respiration; TBCF = carbon flux to soil; GPP = gross primary production; WNPP = wood net primary production

densities for broad (ANPP was 26% under HD compared with 14% under LD; TBCF was 70% under HD compared with 44% under LD; Rag was 29% under HD compared with 16% under LD (Fig. 4).

More than a 2-fold increase was found in the GPP distribution to WNPP under HD compared with LD, in addition to a notable decrease in the TBCF: GPP ratio from HD to LD. Decreases under HD vs. LD of 37%, 35.5%, and 34.7% in the TBCF: GPP ratio were observed for C2, C3, and OP, respectively. The distribution of GPP to ANPP (FNPP: GPP + WNPP: GPP) was 46.1%, 37.0%, and 42.3% lower under LD compared with HD for C2, C3, and OP, respectively.

Discussion

Globally, *Pinus* plantation are managed primarily for timber production due to the species' fast growth and the great economic value. Our findings show that *Pinus taeda* acts as a strong carbon sink across different varieties and planting densities, with great C accumulation in the bole, the commercially most value component. Despite genetic and morphological differences among the varieties (mainly crown size), the bole carbon stock did not differ significantly across varieties. This pattern reinforces the idea that differences in total C stock among varieties are likely driven by variations in other components, such as coarse roots, foliage, and litterfall, rather than the stem. Finally, the greater increment of wood volume for some varieties may be more related to wood density than to bole carbon stocks.

Carbon stock

The C stocks calculated in this study confirm that *P. taeda* plantations in Brazil are some of the most productive *P. taeda* plantations worldwide [7]. We found a poor relationship between the crown structure of the varieties and the C stock, fluxes, and partitioning. C1 under HD had the highest C stock, i.e., 186.2 Mg C ha^{-1} at age 8 years. At age 9 years, the total C stock differed between the stand densities; the highest values were obtained for C3 and OP under HD, i.e., 184.6 Mg C ha^{-1}, which is higher than that obtained in a fertilized and irrigated *P. taeda* plantation in Brazil, i.e., 86 Mg C ha^{-1} at age 8.4 years [38]. Similarly, the C stocks measured in this study were greater than the 72 Mg C ha^{-1} reported by [14] for 6-year-old stands in Georgia, USA, and the 33 Mg C ha^{-1} reported by [17] for 12-year-old stands in North Carolina, USA, all in the same species.

We found no clear pattern indicating that a broader crown will lead to a larger C stock; however, the difference could be explained by differential growth at an early stage of stand development due to crown ideotype. These results may be due to sensitivity to competition, mainly sunlight, even with genetically related materials [28, 39]. Although some clonal varieties showed increased GPP compared to OP, no significant differences were found in

WNPP or bole biomass across varieties. This finding suggests that, even with the morphological or physiological differences, clones do not completely outperform the OP in terms of wood volume. The distinct variation in GPP as well the C allocation patterns indicate a potential for improvement. Overall, the results point out the need and importance of continued genetic improvement focused not only in the total productivity, but also on traits that drive the timber yield.

Most importantly, our results suggest that changes in canopy width across varieties are at least partially associated with biomass partitioning and stand-level total production. Tree density differences caused large changes in C stocks, fluxes, and partitioning. TBCF was constant across the three varieties and two stand densities measured at age 8–9 years; however, the partitioning of GPP changed dramatically. The fraction of TBCF relative to GPP at the low stand density was higher than that at the high stand density (67% compared with 43%), while ANPP at the low stand density received a lower fraction of GPP than that at the high stand density (15% compared with 27%). Overall, under low-density stands, the reduced competition for resources such as water, light, and nutrients may lead to decreased aboveground growth demands and a shift in C allocation priorities [8, 40–42]. This shift suggests a potential physiological strategy, in which trees maintain root activity and soil interactions as a survival mechanism [8, 40–42].

The foliage, coarse root, and litterfall C stocks can differ among varieties even though the bole and branch C stocks are similar [18]. In addition, we showed that the varieties that produced large amounts of foliage and branches also tended to show a large amount of these materials in the litter layer, suggesting a direct relationship between the productivity and litter deposition. Furthermore, the variety with the highest overall total C stock also had consistently lower partitioning to coarse root production and higher partitioning to aboveground WNPP and FNPP. Finally, the good site quality in terms of resources availability may drive both biomass production and the decomposition rates, which are a particular aspect of each ecosystem, the variety and its residuals quality.

At age 9 years, the HD treatment resulted in 39% higher total C stock per hectare on average compared with LD. This difference was expected as the aboveground biomass was higher under HD, given that more trees were planted per unit area. The result show that LD does not reach the supporting capacity of the site after 9 years [43–45].

Stand density had a substantial impact on biomass production through stand growth, as shown by the significant effect of planting density on the C stocks of all components. In addition, density affected the litterfall amount, i.e., HD resulted in a higher O horizon dry mass.

Carbon fluxes and partitioning

The stands had already reached canopy closure at the start of this study, and although genotypes had different crown size, LAI, and foliage biomass, the ANPP did not differ among the varieties. GPP partitioning to each component of the forest ecosystem (FNPP, WNPP, Rag, and TBFC) did not differ among the varieties at age 8 years, and except for C2, there were no significant differences between planting densities at 9 years. However, the constant C flux to TBCF and aboveground respiration as well as different amounts of C partitioning across varieties and tree densities are factors that contribute to the decline in aboveground wood production with stand age as reported by [46].

Total GPP was strongly influenced by the difference in TBCF among the varieties in the first assessment year. In the second year of assessment, under different densities, ANPP differed for C2 and C3, and likely OP, whereas TBCF remained the same for each variety. C partitioning did not differ among the varieties at age 8 years and differed only for some fluxes in C2 between densities at age 9 years. This lack of differences suggests that the varieties may had different C partitioning ranges during the early years of development (3–5 years after planting), which resulted in differences in the total C stock at the time of assessment.

In the first measurement year, the average ANPP across the varieties was 26.3 Mg C ha^{-1} $year^{-1}$, and in the second year, the average ANPP across the varieties under LD and HD was 6.2 and 19.0 Mg C ha^{-1} $year^{-1}$, respectively. [38] assessed the C stocks in similar aged *P. taeda* plantations in Brazil under a fertilization–irrigation treatment and reported an ANPP value of 8.9 Mg C ha^{-1} $year^{-1}$; [17] measured ANPP in 12-year-old plantations of the same species in NC, USA, i.e., 8.4 Mg C ha^{-1} $year^{-1}$; and [47] reported an ANPP value of 8.8 Mg C ha^{-1} $year^{-1}$ for a 9-year-old plantation and 9.9 Mg C ha^{-1} $year^{-1}$ for the same plantation that was remeasured at age 24 years. Our ANPP range is higher than that reported in other studies, mainly in the high-density stand. The greater aboveground C allocation observed in our site may be related to the outstanding edaphoclimatic conditions in southern Brazil, which enhanced the species growth [11, 22, 29, 48]. Also, the intensive silviculture practices favor the resources availability and reduce competition, which may drive greater ANPP [22, 48]. Overall, *P. taeda* greater growth in Brazil is associated to the lack of pathogens, longer growing season, higher sunlight intensity, better soils (higher clay content, organic matter and CEC), stand density and genotype [11, 28, 29, 48].

Aboveground autotrophic respiration accounted for an average of 38% of the GPP across the varieties in the first year of this study (age 8 years) at the same stand density. In the second year (age 9 years), the average ANPP

of the GPP was 17% under LD and 30% under HD [17]. reported that autotrophic respiration (Ra) was 58% of GPP, like other studies in conifers where Rag was one of the largest components of the C balance [31, 49]. In these systems, foliage respiration was the largest component of autotrophic respiration. Conversely, in the current study, WNPP was the main GPP component. This result provides important insight into why *P. taeda* can grow more rapidly in Brazil than in its native range, as losses due to Rag are lower than those in other parts of the world.

The belowground allocation of GPP is one of the most important production ecology factors, and lower rates of bole growth might result from differences in the partitioning of GPP belowground, from lower total GPP, or from both responses under water-stress conditions [7, 9] [38]. evaluated C flux over two consecutive years and found a decrease from 22.0 to 13.2 Mg C ha^{-1} $year^{-1}$ for TBCF and decreases in all C fluxes due to lower total GPP during the second year, which may have been associated with longer periods of eater deficit and higher vapor pressure deficit (VPD).

Our TBCF values are relatively high compared with estimates from the literature, e.g., values of 13.7–17.8 Mg C ha^{-1} $year^{-1}$ were reported in FL, USA [50] and of 7.0–8.9 Mg C ha^{-1} $year^{-1}$ in NC, USA [17] at age 12 years for both studies. This difference may be due to the high overall NPP achieved in this plantation [51, 52]. Furthermore, in both years, TBCF was the main flux component of GPP, similar to the findings in other studies [9, 53, 54]. TBCF was mainly affected by soil CO_2 efflux, whereas litterfall was not as important. This finding agrees with the results presented by [3, 36], who stated that TBCF is usually two times the aboveground litterfall in mature forests. The relatively high soil CO_2 efflux observed in our study could be related to the higher annual rainfall and temperature at this site compared with the natural range of *P. taeda* in southeastern USA.

Ecosystem respiration (Re, the sum of Rag and soil CO_2 efflux) was 67% of GPP during the first year (8 years after planting). During the second year (9 years after planting), this value reached 87% under LD and 73% under HD. These results are similar to those reported for mid-rotation *P. taeda* plantations [55] and greater than those (47–66%) reported by [17]. Our Re values are like those measured in temperate [49] and coniferous forests in North America and Europe [56].

NEP under LD (5.2 Mg C ha^{-1} $year^{-1}$ on average at age 9 years) was fairly similar to the value reported for 12-year-old fertilized *P. taeda* stands, i.e., 6.4 Mg C ha^{-1} $year^{-1}$, by [17] and that for an 8-year-old stand, i.e., 1.3 Mg C ha^{-1} $year^{-1}$, by [57]. Other studies where pine forests had positive NEP had similar values (3.6 Mg C ha^{-1} $year^{-1}$ for *P. ponderosa* [49]; 5.0 and 7.2 Mg C ha^{-1} $year^{-1}$ for *P. radiata* [58]. NEP under HD was nearly triple that under LD at the same age.

Conclusions

There was no difference between crown structure (ideotype) and the C stock, fluxes, and partitioning, indicating that ideotype should not be used for management prescriptions related to C stocks and sequestration in *P. taeda* plantations. Also, no differences in the bole C stock and sequestration were found across varieties within the same planting density, which is a key finding considering its implications for volume production and economic returns. In contrast, genetic variation among varieties and stand density significantly affect C stocks and sequestration, with stand density playing a stronger role. To maximize C stock and sequestration in *P. taeda* plantations in Brazil recommendation of site-specific varieties and stand density must be addressed. To achieve this purpose, robust experiments focusing on the relationship between resources availability -such as water and nutrients – and C dynamics must be replicated and distributed across the soil and climatic range of interest.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13021-025-00372-7.

Supplementary Material 1

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Author contributions

OC: Conceptualization, Supervision, Funding acquisition, Methodology Visualization, Writing – review & editing. NC: Writing – review & editing. GR: Data curation, Visualization, Writing – original draft. TA: Data curation, Conceptualization, Methodology, Writing. RC: Supervision, Funding acquisition, Review. RR: Supervision, Funding acquisition, Review. DC: Supervision, Funding acquisition, Review. CA: Supervision, Review. CM: Methodology, Review.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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