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Climate and genotype influences on carbon fluxes and partitioning in *Eucalyptus* plantations

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ABSTRACT

Clonal plantations of *Eucalyptus* are among the most productive forests in the world, with intensification of silviculture and genetic breeding doubling the wood mean annual increments over the past four decades. The TECHS Project demonstrated that even with intensive silviculture, wood production varies by more than two-fold across environmental gradients, and growth of highly selected clones differs by more than two-fold within a site. Wood production accounts for less than half of the photosynthesis of a forest, and we tested two hypotheses about the relation between wood production and the entire carbon balance for five genotypes across four of the TECHS sites, varying in temperature and water availability. We hypothesized that the influence of the environment on carbon fluxes and partitioning related to gross primary production would be consistent across genotypes. We also hypothesized that carbon flux and partitioning would be more sensitive to water stress than temperature. Annual average temperatures ranged from 18 to 27 °C, and annual rainfall ranged from about 600 to 1500 mm yr^{-1}. Water stress was further tested by reduction in rainfall within sites using troughs to capture about 30% of incoming rain. The geographic gradient led to a six-fold range in wood net primary production during the two years of measurement (from age 1.5 to 3.5 years, the period of maximum current annual increment). Gross primary production (GPP) differed only by two-fold, highlighting very large differences among sites in partitioning: wood net primary production (NPP) accounted for 44% of GPP on sites with higher GPP, and only 34% of GPP on lower GPP sites. The average differences for wood NPP among clones was also large, with about half of the differences among clones relating to differences in GPP, and half to differences in the partitioning to wood NPP. The clones showed similar partitioning patterns across sites, supporting our first hypothesis. Differences across sites and clones in partitioning of GPP to wood NPP related inversely to belowground allocation. Belowground partitioning of carbon increased with increasing temperature and increasing water stress. Our second hypothesis was rejected, as patterns across sites related somewhat more strongly to temperature than to water stress. Overall, this ecophysiological investigation in the TECHS Project underscored the importance of understanding how carbon budgets differ across sites (even with intensive silviculture), and why clones can largely differ in wood production.

1. Introduction

The productivity of forest plantations in Brazil has increased substantially in the past fifty years. Commercial plantations became widespread in the 1960s, and collaborative research and development between universities and companies led to a 4-fold increase in growth

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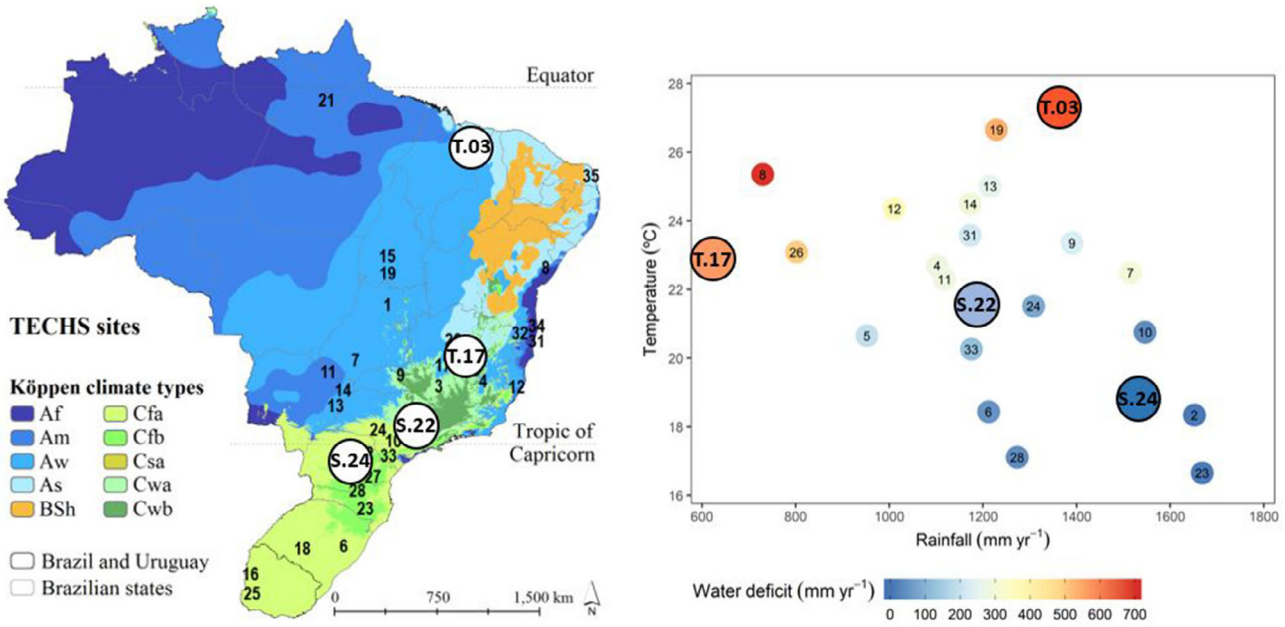

Fig. 1. Spatial distribution of the TECHS project sites and the study sites location (white circles with alphanumeric coding, T for tropical, S for subtropical and the South latitude) across the Brazilian climatic gradient (left). Rainfall, annual temperature and water deficit for all the sites, highlighting the study sites (right).

rates across several rotations. Brazilian *Eucalyptus* plantations are among the most productive forest ecosystems in the world (Binkley et al., 2017; Stape et al., 2010), and high levels of productivity depend on investments in genetic selection, soil preparation, fertilization, protection (pests and diseases) and control of competing vegetation (da Silva et al., 2019; Da Silva et al., 2019; Gonçalves et al., 2013).

The high rates of increase in *Eucalyptus* productivity in recent decades has declined, with little additional gain in the past decade (Binkley et al., 2017). One factor that limits further gains in productivity is the expansion of *Eucalyptus* plantations into regions in central, northern, and northeastern areas of Brazil, where high temperatures and droughts constrain growth. These new regions mainly show levels of abiotic and biotic stresses that limit growth to about two-thirds the levels found in more productive areas (about 40 m^3 ha^{-1} $year^{-1}$ compared with 60 m^3 ha^{-1} $year^{-1}$, Elli et al., 2020a; Gonçalves et al., 2017).

Gains in productivity on stressful sites will depend on expanding knowledge on the biotic and abiotic factors limiting growth, including the range of factors influencing production ecology: canopy structure, leaf area, and light interception (de Mattos et al., 2020), water supply and tree transpiration (Hakamada et al., 2020, Hubbard et al., 2020), and the distribution of fine roots deep into the soil (Christina et al., 2011; Evangelista Silva et al., 2020; Lambais et al., 2017; Pinheiro et al., 2016). One of the most important production ecology factors in stressful sites might be the belowground allocation of photosynthates, as lower rates of stem growth might result from lower total gross primary productivity, or from differences in partitioning of photosynthates to belowground or both (Litton et al., 2007; Stape et al., 2008).

Partitioning to belowground components (coarse and fine roots, and mycorrhizae) tends to increase on stressful sites though actual flux (g m^{-2} yr^{-1}) may not increase (Litton and Giardina, 2008). This trend has been verified experimentally for *Eucalyptus* plantations by reducing stresses within sites through fertilization (Epron et al., 2012; Ryan et al., 2004) and irrigation (Stape et al., 2008), and also in mixed-species plantations with *Eucalyptus* and *Acacia* species (Epron et al., 2013; Forrester et al., 2006). Ryan et al. (2010) showed increase in wood production but no effect on partitioning belowground across four sites planted with different *Eucalyptus* clones. Campoe et al. (2012) also found no relation between gross primary productivity and partitioning belowground, despite the increase in wood production across a gradient of productivity of a *E. grandis* plantation. Responses in carbon fluxes and partitioning to increasing stresses might also vary across genotypes, and changing levels of stress within sites may not show the same pattern that develops across geographic gradients of stress (Sala et al., 2012).

Brazilian forestry companies have a large number of site-specific *Eucalyptus* clones that respond with high levels of productivity when planted in climatic regions where they were developed (Binkley et al., 2020; Gonçalves et al., 2017). However, the ability to recommend genotypes with higher tolerance to regions with soil water deficit or high temperature is limited, and currently based on empirical methods. This limitation results from the restricted knowledge about the responses of different clones when planted in climatic regions different from where they were developed. To move from the empirical to the process-based production methods, it is necessary to advance the knowledge of genotype × environment interactions. With the expansion of forest plantations in Brazil to warmer and drier regions, it is critical to understand the processes responsible for the tolerance processes of clones when planted in climatically different regions. The TECHS project was a pioneer in exploring this topic using a consistent experimental design, replicating the exact same clones across a wide range of sites (Binkley et al., 2020).

The TECHS experimental platform enabled evaluation of the effect of resource gradients (within and across sites) on the carbon fluxes and partitioning for a group of operationally used clones of *Eucalytpus*. We measured and calculated (aboveground respiration) all of the components of ecosystem carbon budgets for five of the TECHS clones across four of the sites with different climates to test two hypotheses:

1) the influence of climate on carbon flux and partitioning will be consistent across genotypes (the genotype by environment interaction will be small), and
2) water stress will influence carbon flux and partitioning more than temperature.

Table 1
Main climatic variables of the experimental sites. The sites were coded based on their climatic type (T = Tropical and S = Subtropical) and latitude (from 3°S to 24°S). See Binkley et al. (2020, 2017) for more details related to soil and climate of the sites.

Site	TECHS reference code	Latitude S	Longitude W	Altitude m	Temperature °C	Rainfall mm yr^{-1}	Water deficit mm yr^{-1}
T.03	29	3.44	43.07	81	27.3	1461	578
T.17	30	17.32	43.77	848	23.3	713	544
S.22	20	22.35	46.97	633	22.1	1097	145
S.24	22	24.23	50.53	888	19.6	1492	5

2. Methods

2.1. Experimental sites and genotypes

The study was developed using four climatically contrasting sites of the Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses (TECHS) cooperative research program (Binkley et al., 2017, 2020, Fig. 1), spanning a gradient of 800 mm in annual precipitation, 550 mm in soil water deficit and 7 °C in average annual air temperature (Table 1). Across the sites, temperature and water deficit decrease as latitude increased (R^2 = 0.69, p < 0.0001). The hottest and driest site was located at Urbano Santos-MA, a tropical region at latitude 3°S (T.03), followed by another tropical site at latitude 17°S located at Bocaiúva-MG (T.17). An intermediate site was located at Mogi-Guaçu-SP, on a transition region between tropical and subtropical climate (22°S, site S.22), with moderate temperature and water deficit. The coldest and wettest site was located at Telêmaco Borba-PR in a subtropical climate (24°S, site S.24). This geographic gradient represents important regions of the Brazilian forestry sector where most of *Eucalyptus* plantations occur (Gonçalves et al., 2017).

Meteorological information was collected with weather stations near each experimental site. Missing data due to malfunctioning of the sensors was gap-filled with different alternative sources following the methodology described by Elli et al. (2019).

Five clones were chosen to represent highly productive genotypes and drought tolerant genotypes. Clone A1 (*Eucalyptus urophylla)* is the most widely planted clone in Brazil, and A1, B2 (*E. urophylla* × *E. grandis*) and K2 (*E. saligna*) have high rates of growth under favorable environmental conditions. Clones C3 (*E. grandis* × *E. camaldulensis*) and P7 (*E. urophylla.* × *E. brassiana*) are known to be drought tolerant (Gonçalves et al., 2017).

Clones were planted at all sites in single plots of 0.2 ha with 3 × 3 m spacing (1111 trees ha^{-1}). Plots were split, with rainfall reduced by about 30% with under-canopy troughs. Planting technique followed minimum cultivation methods (Gonçalves et al., 2013), and all plots were fertilized intensively during the first year (70 kg N ha^{-1}, 45 kg P ha^{-1}, 85 kg K ha^{-1}, 500 kg Ca ha^{-1}, 90 kg Mg ha^{-1}, 40 kg S ha^{-1}, 3 kg B ha^{-1}, 1 kg Cu ha^{-1}, and 1 kg Zn ha^{-1}) to alleviate any nutrient limitation. Herbicide was used to eliminate competing vegetation prior to site preparation until canopy closure (~18 months). Leaf cutting ants (*Atta* sp. and *Acromyrmex* sp.) were controlled using sulfluramide-based baits and other occasional pests whenever necessary.

2.2. Dry mass equations

Aboveground dry mass was estimated by harvesting 6 trees for each combination of clone and site (n = 24 trees/clone, total of 114 trees). The destructive sampling was performed in July 2014 at age 2.5 years, and the sampled trees were selected to cover the range of diameter at breast height (DBH, 1.3 m above ground level). Cut trees were divided into stem wood, stem bark, branch, and foliage. 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 dried at 65 °C to a constant weight for dry mass.

Dry mass equations for above (stem, bark and branch summed) and belowground components (coarse roots) were fitted using the linearized model of Schumacher and Hall in R (R Development Core Team, 2017), as follows: $\ln(DM) = \beta0 + \beta1 \times \ln(DBH) + \beta2 \times \ln(H)$, where DM is dry mass, DBH is the diameter at breast height (cm), H is the total tree height (m); and β0, β1 and β2 are regression coefficients.

The decision to use clone- and site-specific equations was based on the need to capture the potential different behavior of carbon fluxes and partitioning of each clone at each site. Based on climatic similarity, the equation developed for coarse roots for site T.17 was used for T.03, and the equation for site S.24 was used on S.22. All equations showed p-values < 0.01 and R^2 ranged from 0.91 to 0.99. Foliage dry mass was calculated based on leaf area index measurements and specific leaf area of each clone at each site. Methodological details are further described in de Mattos et al. (2020).

2.3. Carbon fluxes and partitioning

Carbon fluxes were measured for 2 years (October 2013 to October 2015) during the phase of maximum growth in the rotations (~1.5 to 3.5 years old, Binkley et al., 2020). All dry mass increments and litterfall were converted into carbon (C) using C concentrations (0.452 g g^{-1} for coarse roots and stem, 0.424 g g^{-1} for bark, 0.453 g g^{-1} for branches, and 0.507 g g^{-1} for leaves, Campoe et al., 2012), and expressed in g of C m^{-2} $year^{-1}$.

Total belowground carbon flux (TBCF) was estimated by mass balance as described in Giardina and Ryan (2002) and Ryan et al. (2010). TBCF is estimated based on measurements of soil CO_2 efflux, aboveground litterfall (foliage, branches, bark, flowers and fruits), root dry mass increment, O horizon mass change, and decomposition of stumps from the previous rotation. Variation in soil C and losses of C through leaching or erosion were considered negligible relatively to TBCF (Giardina and Ryan, 2002) and not included. The TBCF (g C m^{-2} $year^{-1}$) was calculated as:

TBCF = (Soil C efflux) – (Aboveground litterfall mass) + (change in O horizon mass) + (change in coarse root mass) + (change in mineral soil)

Soil C efflux was measured monthly over the study period on PVC collars (20 cm in diameter) using a LI-8100 device with a LI8100-103 20 cm in diameter chamber (LI-COR, Lincoln, NE, USA). Nine PVC collars were installed in each plot distributed in 3 positions considering the distance of the trees (near the tree, between tree and middle of the row, and between these two distances). The PVC collars were positioned close to 9 different trees in each plot (3 replicates per position) at least one week before the beginning of the measurements. All the collars were inserted into the mineral soil down to a depth of 6–8 cm to ensure stability and to avoid CO_2 lateral diffusion (Davidson et al., 2002).

Litterfall was collected monthly. Foliage, flowers and fruits were collected using 9 litter-traps per plot (3 positions and 3 replicates), following a similar spatial distribution of the PVC collars. Bark and branches were collected in a ~9 m^2 area delimited between 4 trees in each plot. Samples of each component were dried at 65 °C and weighed.

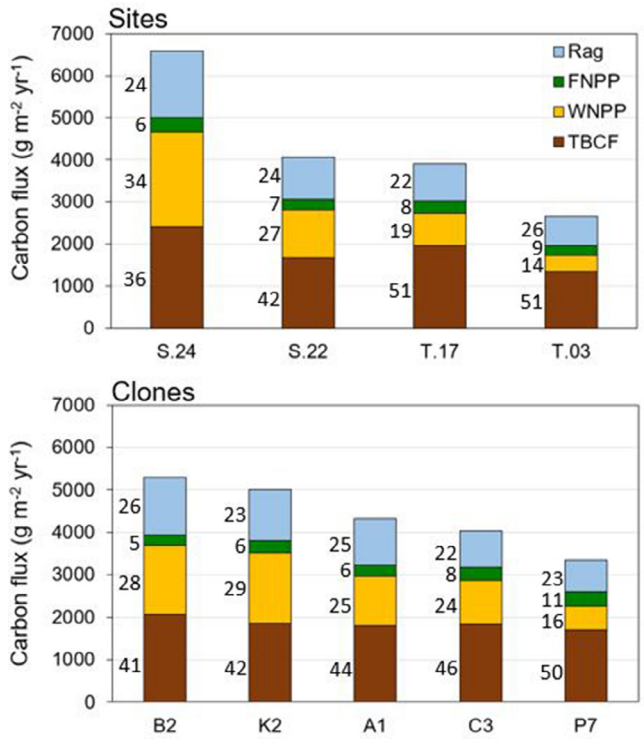

Fig. 2. Carbon fluxes for sites (averaging clones) and for clones (averaging sites). Partitioning (%) is numerically presented on the side of each bar. Rainfall reduction treatment was not significant for fluxes and partitioning ($p > 0.05$). Sites are ordered from most subtropical to most tropical, and Clones are ordered from the highest to the lowest GPP. TBCF = total belowground carbon flux, WNPP = wood net primary production, FNPP = foliage net primary production, Rag = aboveground autotrophic respiration.

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 m^2 steel frame. The O horizon was sampled on 3 replicates of 3 positions per plot (2.54 m^2 per plot), following the same spatial distribution as the PVC collars. Samples were dried at 65 °C until constant weight, separated into leaf, branch, bark and miscellaneous (flower, fruit and unidentified organic material) and weighed. Ash content analysis was performed on sub-samples, and used to correct for mineral soil contamination.

Changes in coarse root biomass (considering only roots > 1 cm in diameter) were estimated using the dry mass equations described previously. The estimation of the carbon flux associated with the decomposition of stumps from previous rotations (from 600 to 1100 stumps ha^{-1} on average) was based on stump circumference measurements and dry mass equations developed by Campoe et al. (2012).

Total mineral soil carbon was calculated using the fixed depth method from samples collected at 0–20, 20–40 and 40–60 cm layers, at the beginning and at the end of the measurements (ages 1.5 and 3.5 years). Soil bulk density was measured on samples collected using 100 cm^3 steel cylinders following a similar spatial distribution of the PVC collars. Soil C content was measured from samples collected with an auger. Soil C contents were converted to an area basis by multiplying concentrations by average bulk density and sampling depth and summing the three depths.

Wood net primary production (WNPP) was assessed as the sum of bole increment, branch and bark litterfall. Bole increment was calculated by measuring bole diameter (1.3 m above ground level) and total height (H) of all trees in October 2013, 2014 and 2015. Clone-site specific dry mass equations were applied on the annual measurements, and then converted into C. Foliage net primary production (FNPP) was assessed by the variation in leaf area index (LAI), converted into dry mass using specific leaf area (SLA), plus foliage litterfall. Methods of LAI and SLA measurements are described in de Mattos et al. (2020). Aboveground net primary production (ANPP) was estimated annually as the sum of WNPP and FNPP.

Aboveground tree respiration (Rag) was estimated as the combination of foliage dark respiration and wood CO_2 efflux, based on Ryan et al. (2009). Foliage dark respiration was calculated based on LAI measured on every site at approximately 6-months intervals following methods of de Mattos et al. (2020), with linear interpolation between LAI measurements, using the equation as follows: Foliage respiration (g C m^{-2} yr^{-1}) = 0.66 × LAI (m^2 m^{-2}). Wood C efflux was calculated based on wood net primary production (WNPP), using the equation as follows: Wood C efflux (g C m^{-2} yr^{-1}) = (0.7163 – 0.0579 × Age (in years)) × WNPP (g C m^{-2} yr^{-1}). Respiration equations were developed for 20 °C, therefore, temperature corrections were applied based on the mean annual temperature of the sites by multiplying respiration rates by 1.67 for site T.03, 1.23 for site T.17, 1.12 for site S.22, and 0.94 for site S.24 (Agren and Axelsson, 1980; Ryan et al., 2009).

Gross primary production (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.

2.4. Data analysis

Relationships between carbon fluxes and partitioning with GPP and climatic variables were evaluated using regressions. The data used to generate the regressions showed normality and variance homoscedasticity. The decision of using a linear or logarithmic relation was based on lower Akaike Information Criterion (AIC). The coefficients of determination (R^2) and probability value (p-value) were used to assess the strength of the relationships. The probability level used to determine significance was $p \leq 0.05$. All analyses were performed in R (R Development Core Team, 2017).

3. Results

Across the geographic gradient in climate, wood production (WNPP) ranged from 380 to 2260 g C m^{-2} $year^{-1}$. This 6-fold range in wood production resulted from only a 2-fold range in gross primary production (GPP, from 2660 to 6580 g C m^{-2} $year^{-1}$). The different magnitudes of ranges resulted from differences in partitioning to wood: 0.14 on low GPP sites and up to 0.34 on high GPP sites (Fig. 2).

The variation of WNPP from 550 to 1660 g C m^{-2} $year^{-1}$ resulted from roughly equal contributions of differences in GPP (~60%) and differences in partitioning to wood (~80%), though these patterns differed somewhat among clones. The most productive clone (B2) ranged from 3100 to 8200 g C m^{-2} $year^{-1}$ in GPP, with partitioning to wood ranging from 0.19 to 0.36. The least productive clone (P7) ranged from 2630 to 4400 g C m^{-2} $year^{-1}$ in GPP, with partitioning to wood ranging from 0.11 to 0.26.

The flux of carbon belowground (TBCF) differed more across sites (~80%) than across clones (~20%). Partitioning belowground also showed the same pattern ranging ~40% across sites, and ~20% across clones.

All carbon fluxes significantly increased with increasing GPP across the range of sites for all clones, however, the rate of increase was different for different components (Fig. 3). With increases in GPP, WNPP increased about twice as fast as TBCF, reflecting the shifting partitioning toward wood on more productive sites. The consistent responses among clones across the climate gradient showed minor genotypes by environments interaction, supporting the first hypothesis.

The most southern site (S.24), had very little water deficit (~15 mm yr^{-1}) and the highest production rates. The most northern site (T.03), had the highest water deficit (~700 mm yr^{-1}) and lowest production rates (Fig. 4). GPP decreased by 60% and wood production by about half from nearly zero in response to a moderate water deficit,

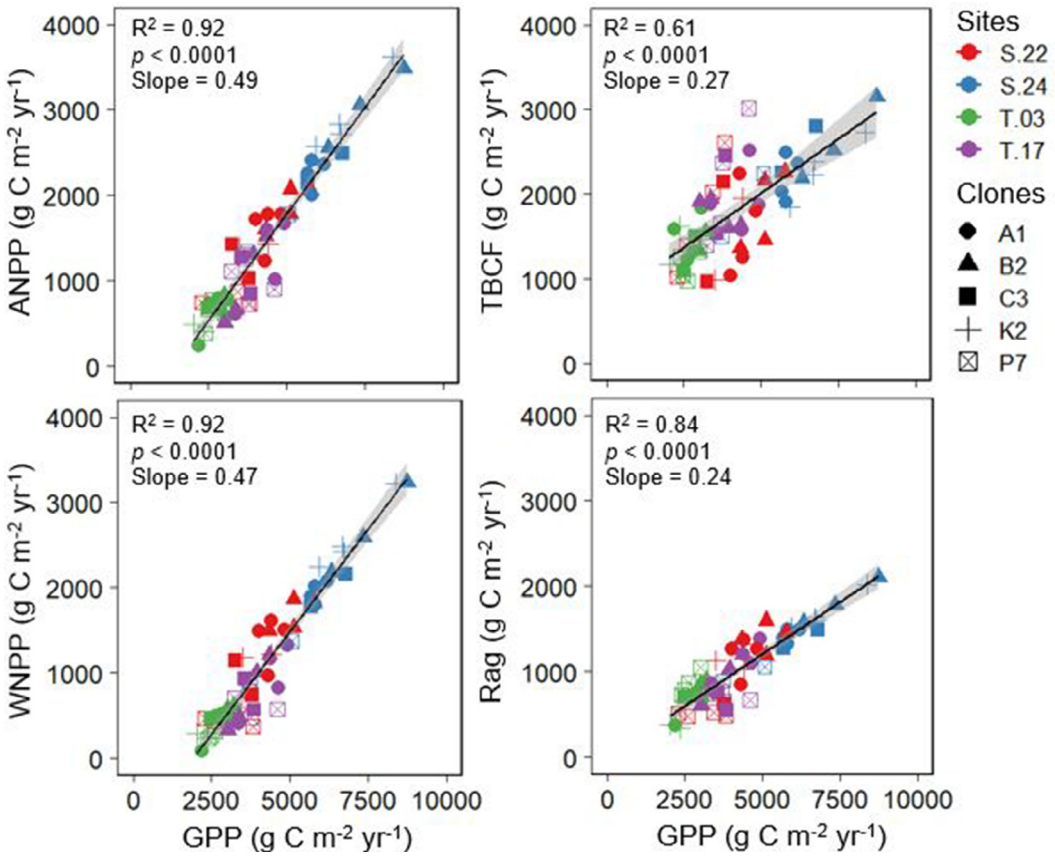

Fig. 3. Aboveground net primary production (ANPP), wood net primary production (WNPP), total belowground carbon flux (TBCF) and aboveground respiration (Rag) showed significant linear relation with gross primary production (GPP). Each entry denotes one treatment (full rain or reduced rain) for each clone at each site for each year. Shaded regions on regression lines represent the standard error.

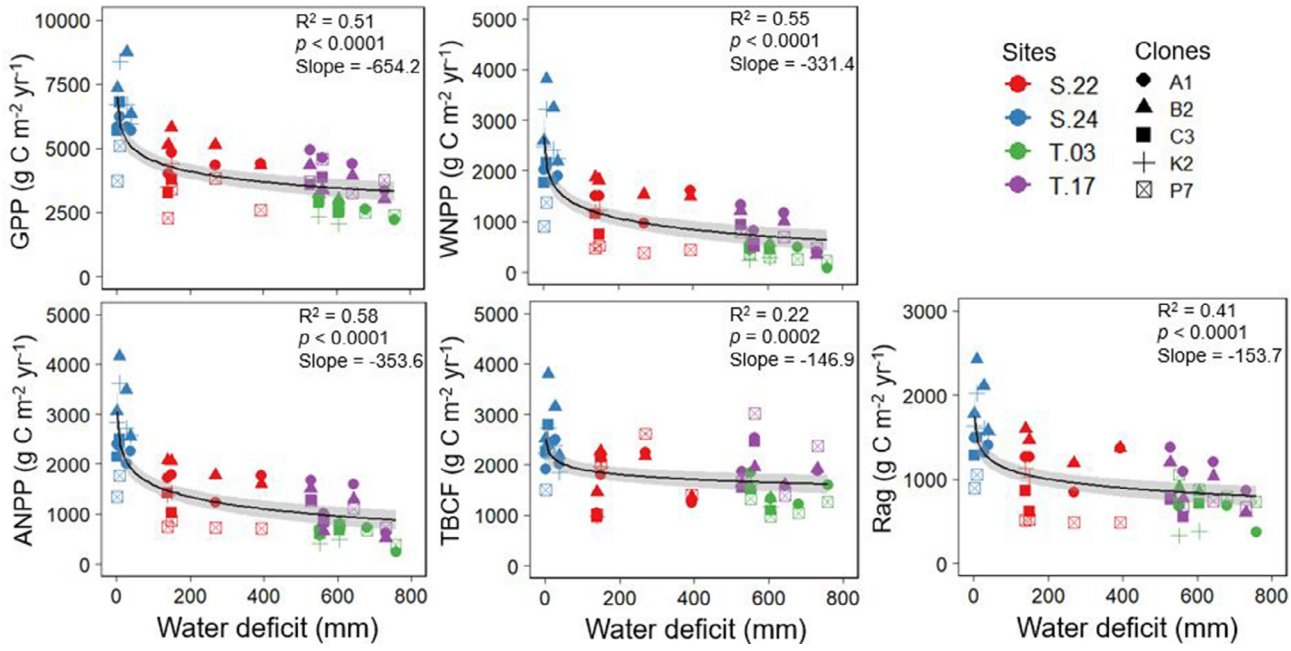

Fig. 4. All carbon fluxes (Gross primary production – GPP, Aboveground net primary production – ANPP, Wood net primary production – WNPP, Total belowground carbon flux – TBCF, Aboveground respiration – Rag) decreased with increasing soil water deficit. Adding in the effect of temperature did not improve the fit with the data. Each entry denotes one treatment (full rain or reduced rain) for each clone at each site for each year. Shaded regions on regression lines represent the standard error.

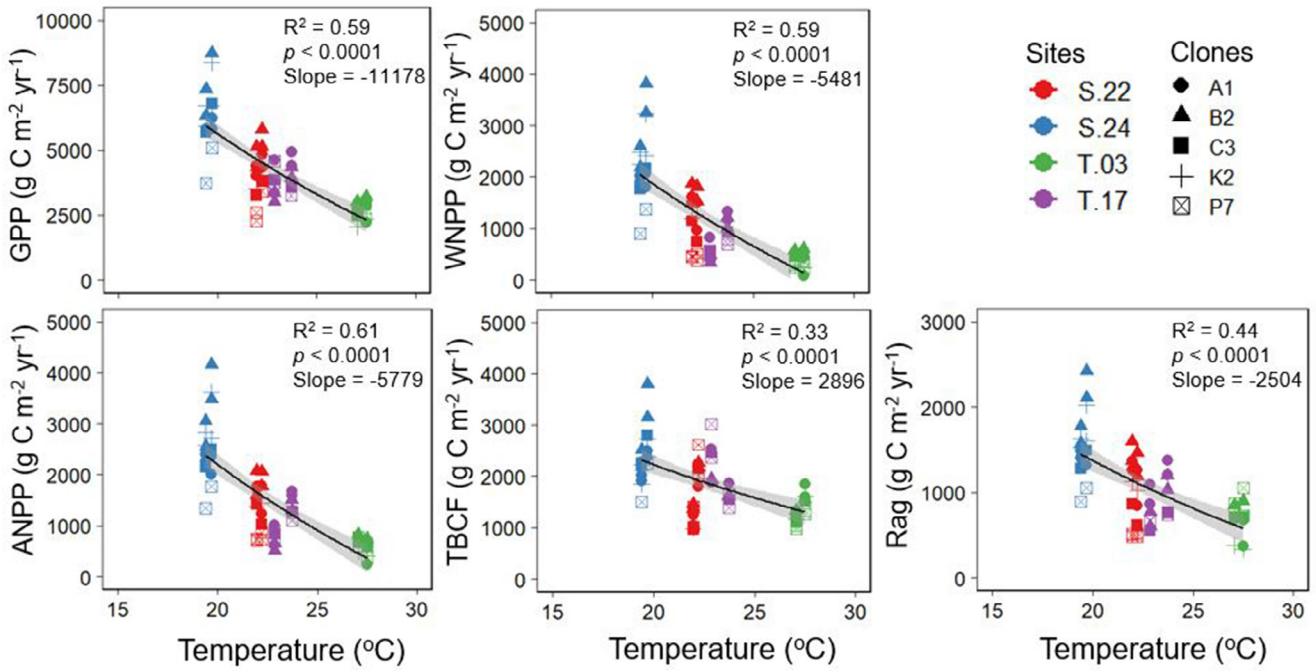

Fig. 5. All carbon fluxes (Gross primary production – GPP, Aboveground net primary production – ANPP, Wood net primary production – WNPP, Total belowground carbon flux – TBCF, Aboveground respiration – Rag) decreased with increasing mean annual temperature. Each entry denotes one treatment (full rain or reduced rain) for each clone at each site for each year. Shaded regions on regression lines represent the standard error.

with a change rate of about 290 g C m^{-2} yr^{-1} per 100 mm of water deficit for GPP and 350 g C m^{-2} yr^{-1} for wood production. Further increases in water deficit had smaller effects, on the order of 60 g C m^{-2} yr^{-1} per 100 mm of water deficit for GPP and 70 g C m^{-2} yr^{-1} for wood production (1.4 Mg ha^{-1} yr^{-1}). Water deficit also reduced fluxes belowground (TBCF), but to a lesser extent (Fig. 4). Across the full range of water deficit, TBCF showed a reduction of 90 g C m^{-2} yr^{-1} per 100 mm.

Our second hypothesis was that water deficits would have a stronger effect on production than temperature. Contrary to the hypothesis, the relationship with temperature was statistically stronger (higher R^2 and AIC 6–10 units lower, Fig. 5). Similar to the pattern for water deficit, site S.24, the most southern site, showed the lowest mean annual temperature (~20 °C) and the highest production rates, contrastingly S.03, the most northern site, showed highest mean annual temperature (~28 °C) and lowest production rates (Fig. 5).

Wood production reduced 90% across the range of temperature, decreasing 240 g C m^{-2} yr^{-1} (4.8 Mg ha^{-1} yr^{-1}) for every additional 1 °C, with the rate 490 g C m^{-2} yr^{-1} for GPP. Increase in temperature also reduced TBCF, at a rate of 127 g C m^{-2} yr^{-1} for every additional 1 °C.

Partitioning to WNPP increased and to TBCF decreased with increasing GPP (Fig. 6). Overall partitioning to aboveground respiration (foliage and wood) showing no particular trend.

Carbon partitioning shifted from aboveground to belowground with increasing temperature or water deficit (Fig. 7). For every 100 mm of additional water deficit or additional 1 °C in temperature, partitioning to wood production declined and partitioning to belowground increased by approximately 15%.

Partitioning to wood production was more sensitive to climatic and genotypic variation than partitioning belowground. Across sites for all clones, partitioning to wood was smaller but covered a wider range (from 0.11 to 0.37), compared to the partitioning belowground (from 0.33 to 0.63).

4. Discussion

The TECHS experimental platform was pioneer in exploring the influence of climate on carbon fluxes and partitioning, replicating the same five contrasting *Eucalyptus* clones across a significant gradient of water availability and temperature.

The climatic gradient across the sites significantly affected carbon partitioning (Fig. 2). Averaging across the five clones, the most southern site, mild temperature and high rainfall (S.24, Fig. 1 and table 1) showed that a similar fraction of GPP was partitioned to WNPP and to TBCF (~35%). Conversely, the most northern site, warmest with high water deficit (T.03, Fig. 1 and Table 1) showed the most divergence in partitioning pattern between WNPP and TCBF (~15% and ~50%). These patterns are consistent with the relations among resource availability and carbon fluxes and partitioning (Binkley et al., 2004; Ryan et al., 2008). In less stressful environments, where *Eucalyptus* species have more access to growth resource (e.g. soil water availability), carbon uptake and partitioning to woody tissues increase. In stressful environments, carbon uptake decreases and partitioning belowground increases. The results suggest that the limited access to resources indices the trees to invest higher proportions to belowground processes, specially production of fine roots to reach pools of resources in the soil to match the demand. This is not a particular trend for *Eucalyptus* plantations, as these patterns are consistent for different tree species across a wide range of environments (Litton et al., 2007).

Fluxes and partitioning for the clones (averaging across sites) showed consistent patterns with the region they were genetically developed (Fig. 2). For example, B2 showed the smallest TBCF (~40% of GPP) and largest WNPP (~30%), and P7 showed the largest TCBF (~50%) and smallest WNPP (~15%). They were selected in climatically contrasting regions of Brazil. B2 was selected on a region with lower and fairly constant temperature, and a well distributed and high rainfall regime, and this clone invested less in TBCF and more in wood production. P7 had the opposite behavior. It was developed in a region with high temperature and limited soil water availability, and this clone had a high investment in TBCF at the expense of wood production, perhaps to be able to reach deeper soil layers for water resources. These

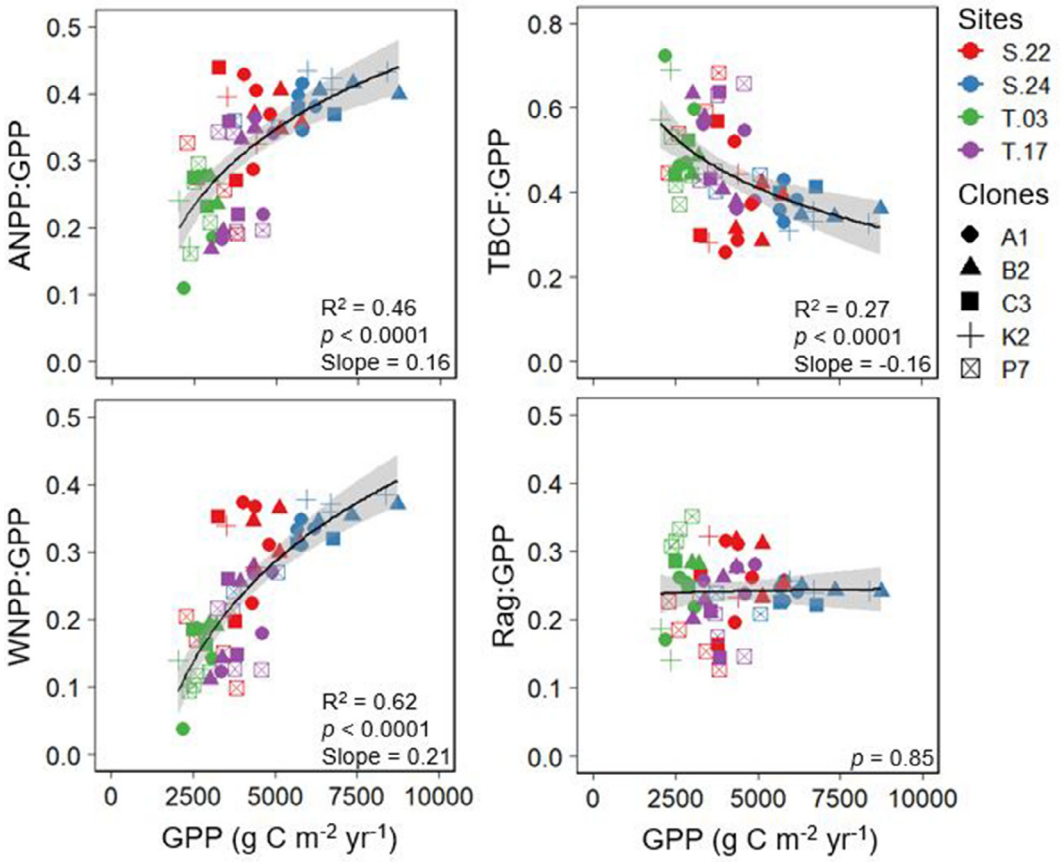

Fig. 6. Partitioning to aboveground net primary production (ANPP) and to wood net primary production (WNPP) increased, to total belowground carbon flux (TBCF) decreased, and to aboveground respiration (Ra) was constant with increasing gross primary production (GPP). Each entry denotes one treatment (full rain or reduced rain) for each clone at each site for each year. Shaded regions on regression lines represent the standard error.

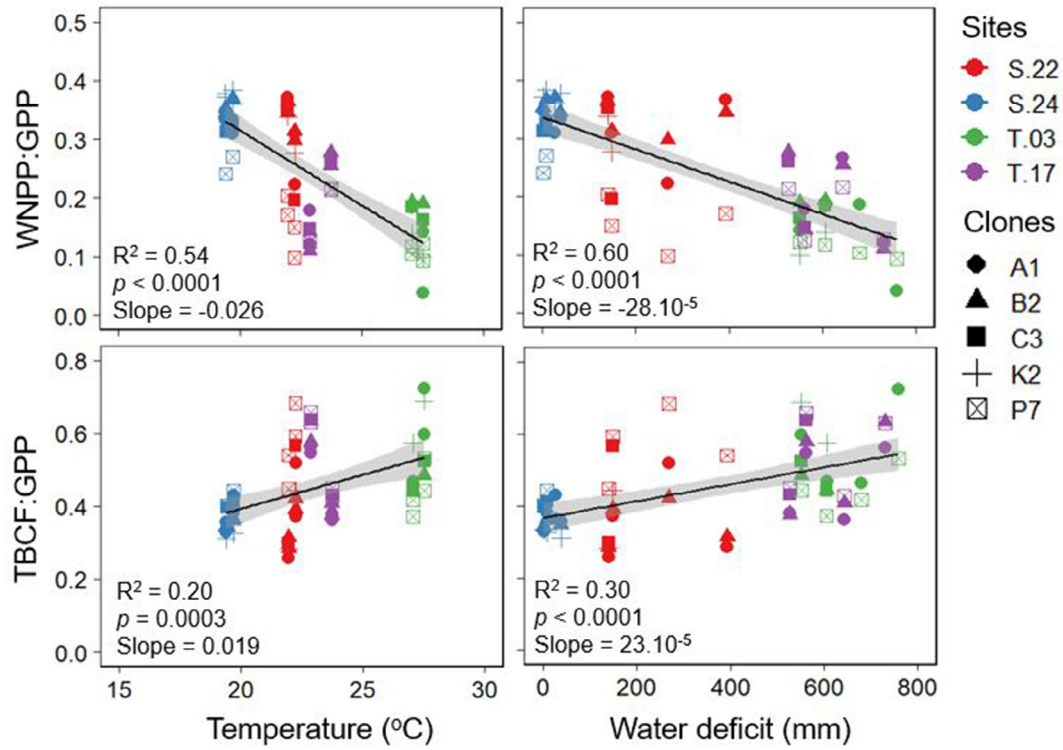

Fig. 7. Wood production partitioning (WNPP:GPP) decreased and belowground partitioning (TBCF:GPP) increased with increasing mean annual temperature or soil water deficit. Each entry denotes one treatment (full rain or reduced rain) for each clone at each site for each year. Shaded regions on regression lines represent the standard error.

two clones are good examples of contrasting behavior, where P7 showed a strong stability in for its fluxes and partitioning across sites, compared to clone B2 which showed a significant adaptability to express its potential production under specific climatic conditions (de Araujo et al., 2019). How much of the carbon fluxes and partitioning of a clone are controlled by genetics and how much by environment? Would a clone that was selected for a dry environment maintain high TBCF flux and partitioning in a wet climate? Our results show that both genetic differences and plasticity within a genotype occur—specificities for different clones will be explored in a future study. The lack of a controlled experimental design like TECHS project, with measurements of carbon balance of the exact same five clones replicated across four sites prevents comparisons with other studies. Most of the results with complete carbon balance measurements either have same species across sites or different species on a single site.

The wide range of climate and genotypes studied provides values for the current biological limits of carbon partitioning to above and belowground components, at least for *Eucalyptus* plantations. Partitioning to wood production ranged from ~0.10 to ~0.40 and to TBCF from ~0.30 to ~0.70. These values are key parameters for process-based models of forest productivity, and using biologically possible values are crucial for accurate predictions. Elli et al. (2020b), using a sensitivity analysis to identify the most important parameters to assess climate change impacts on *Eucalyptus* plantations, found that partitioning parameters are mandatory for accurate production estimation. Caldeira et al. (2020), using 3-PG, successfully calculated productivity of *Eucalyptus urophylla* plantations in Brazil by using the partitioning parameters calculated for this current study.

Absolute values of GPP, WNPP and TBCF are higher, mainly at site S.24, however, partitioning ranges are within the expected values under field conditions (Campoe et al., 2012; Litton et al., 2007; Ryan et al., 2010; Stape et al., 2008). These analyses show that to increase current levels of productivity, increasing carbon uptake may be more fruitful than extending the boundaries of partitioning.

Rainfall correlation with carbon fluxes and partitioning was not as significant as soil water deficit. Soil water deficit was a better predictor, decreasing all carbon fluxes, while increasing partitioning to TBCF (Figs. 4 and 7). Binkley et al. (2017) also found that water deficit was a better predictor for wood productivity across the TECHS sites, compared to rainfall. The lack of a strong correlation between rainfall and productivity may be related to a more than 3-fold variation in water holding capacity of the sites, ranging from 65 to 225 l m^{-2}.

The hypothesis that soil water deficit would have a stronger effect on fluxes and partitioning, compared to temperature, was not supported. The relationship with temperature was equal or stronger (Figs. 5 and 7). In addition to the direct negative impact on photosynthetic processes (Aspinwall et al., 2016; Drake et al., 2016), temperature also increases vapor pressure deficit and consequently evaporation, reducing soil water availability (Grossiord et al., 2020). Warmer temperatures also reduce cell division, which will directly reduce growth in tropical trees (Way and Oren, 2010), and indirectly feedback through sink limitation to reduce photosynthesis. Soil water deficit and temperature were individually strongly correlated with carbon fluxes and partitioning, but the combination of both did not improve prediction capacity.

Increase in temperature decreased all carbon fluxes among the study sites (Fig. 5), however (Litton and Giardina, 2008) showed an increase in all carbon fluxes with increasing temperature. Most of their study sites showed mean annual temperature from −5 to 20 °C, and our sites ranged approximately from 20 to 28 °C. These opposite trends may represent a turning point for carbon fluxes, showing a bell-shaped curve around 20 °C. Queiroz et al. (2020) evaluating wood growth of several *Eucalyptus* clones, at sites ranging mean annual temperature from ~15 to ~30 °C, found an optimal growth rate of around 20 °C, decreasing for higher or lower temperature.

Clones may show similar gross primary production but different wood production due to different carbon partitioning patterns. High wood production is a combined result of higher photosynthesis (GPP) and increased carbon partitioning to WNPP (Ryan et al., 2010). Clones with high rates of wood production generally partition less carbon belowground, and may face physiological dysfunction and mortality on sites with intense and prolonged droughts (Blackman et al., 2017). However, higher partitioning belowground provides more tolerance to soil water stress, but also leads to a decrease in wood production.

One of the strategies to cope with soil water deficit is to increase belowground carbon fluxes, mainly root development, to better explore available soil water and reach deeper layers. Lambais et al. (2017) showed that the majority of *Eucalyptus grandis* fine roots are distributed over the first two meters, and that some may reach deep soil layers (deeper than 10 m) to access stored water. Christina et al. (2017), studying the same *E. grandis* stand showed that fine roots, especially those distributed on deep layers of the soil during prolonged droughts, are very important to maintain water supply to physiological processes during dry periods. Our results show that as soil water deficit increases across sites, clones significantly increased carbon partitioning to belowground processes by ~45%.

However, clones with higher partitioning to TBCF also show high rates of water use. Hubbard et al. (2020), studying the same clones and sites as the present study found that clone C3, known as a drought tolerant clone, used as much or more water than A1, a high productivity clone. Since clone C3 has higher TBCF, it explores more soil volume and has access to water in deeper soil layers during dry periods that other non-drought tolerant clones are not.

Implications for the predictions of climate change on productivity of *Eucalyptus* plantations are clear. Some predictions for the tropical regions of plantations in Brazil suggest both reduction in rainfall volume and also increase in temperature (Chou et al., 2014). If confirmed, it has the potential to negatively impact *Eucalyptus* plantations by both reducing photosynthesis and also increasing partitioning belowground. Therefore, actually apply these new information related to the responses of *Eucalyptus* clones to climate will mandatory to sustain the current levels of productivity in Brazil.

Understanding the balance between carbon fluxes and partitioning to above and belowground components provides i) new insights for breeding programs aiming selection of clones to dry regions; ii) zoning optimization of *Eucalyptus* genotypes across regions with different climatic conditions to increase wood productivity.

CRediT authorship contribution statement

Otávio C. Campoe: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing - original draft, Writing - review & editing. **Clayton A. Alvares:** Data curation, Formal analysis, Visualization, Writing - review & editing. **Rafaela L. Carneiro:** Data curation, Project administration, Writing - review & editing. **Dan Binkley:** Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing - original draft, Writing - review & editing. **Michael G. Ryan:** Funding acquisition, Investigation, Methodology, Writing - review & editing. **Robert M. Hubbard:** Methodology, Visualization, Writing - original draft, Writing - review & editing. **James Stahl:** Investigation, Writing - review & editing. **Gabriela Moreira:** Investigation, Writing - review & editing. **Luiz Fabiano Moraes:** Investigation, Writing - review & editing. **José Luiz Stape:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The work has not been published elsewhere, and is not under

consideration by any other journal. We declare no personal or financial interests that could conflict and bias the science of our paper.

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