Global sensitivity-based modelling approach to identify suitable Eucalyptus traits for adaptation to climate variability and change

Elvis Felipe Elli¹,* , Neil Huth², Paulo Cesar Sentelhas ¹,* , Rafaela Lorenzato Carneiro³ and Clayton Alcarde Alvares⁴

¹Department of Biosystems Engineering, ‘Luiz de Queiroz’ College of Agriculture (ESALQ), University of São Paulo (USP), Piracicaba, SP 13418-900, Brazil
²CSIRO, Toowoomba, QLD 4350, Australia
³Forestry Science and Research Institute (IPEF), Piracicaba, SP 13415-000, Brazil
⁴Suzano SA Company, Limeira, SP 13473-762, Brazil
*Corresponding authors’ e-mail addresses: elvisfelipeelli@usp.br; pcsentel.esalq@usp.br

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ABSTRACT

Eucalyptus-breeding efforts have been made to identify clones of superior performance for growth and yield and how they will interact with global climate changes. This study performs a global sensitivity analysis for assessing the impact of genetic traits on Eucalyptus yield across contrasting environments in Brazil under present and future climate scenarios. The APSIM Next Generation Eucalyptus model was used to perform the simulations of stemwood biomass (t ha⁻¹) for 7-year rotations across 23 locations in Brazil. Projections for the period from 2020 to 2049 using three global circulation models under intermediate (RCP4.5) and high (RCP8.5) greenhouse gas emission scenarios were performed. The Morris sensitivity method was used to perform a global sensitivity analysis to identify the influence of plant traits on stemwood biomass. Traits for radiation use efficiency, leaf partitioning, canopy light capture and fine root partitioning were the most important, impacting the Eucalyptus yield substantially in all environments under the present climate. Some of the traits targeted now by breeders for current climate will remain important under future climates. However, breeding should place a greater emphasis on photosynthetic temperature response for Eucalyptus in some regions. Global sensitivity analysis was found to be a powerful tool for identifying suitable Eucalyptus traits for adaptation to climate variability and change. This approach can improve breeding strategies by better understanding the gene × environment interactions for forest productivity.

KEYWORDS: APSIM Eucalyptus model; biomass partitioning; extinction coefficient; Morris method; photosynthetic temperature response; radiation use efficiency.

I. INTRODUCTION

Eucalyptus is the most planted hardwood genus in the world and its cultivation provides renewable resources for pulp and paper production, lumber industry, beekeeping, firewood and charcoal (Albaugh et al. 2017; IBÁ 2019). Eucalyptus productivity may be affected by spatial and temporal climate variability as well as climate change (Stape et al. 2010; Campoe et al. 2016; Binkley et al. 2017). High-yield results are obtained from the combination of highly productive genotypes, adequate weather conditions and optimum or near-optimum forestry management. Uncertainty in the environment hampers yield
improvement. *Eucalyptus*-breeding efforts have been made to identify superior clones in terms of growth and yield (Nunes et al. 2002) and how they interact with the soil, climate and forestry management. In this context, process-based simulation models are promising tools to evaluate the effects of Genotype, Environment and Management interactions (\(G \times E \times M\)) on crop productivity (Landsberg et al. 2003; Ewert et al. 2015; Cooper et al. 2020).

Different approaches to evaluate traits and for crop design using crop models were proposed to deal with climate variability in current and future climates (Messina et al. 2011, 2020; Cooper et al. 2020; Hammer et al. 2020). In this paper, we explore a methodology based on global sensitivity analyses. The sensitivity analysis can be either local or global. In the first, the local response of the outputs is investigated by changes in a single parameter, holding all other parameters fixed. In the global sensitivity analysis, simultaneous changes in all the studied parameters are considered over their suitable ranges, and interactions between parameters are taken into account (Saltelli et al. 1999). There are different methods to assess global sensitivity analysis, including variance-based methods such as the Fourier amplitude sensitivity test—FAST (Cukier et al. 1973), Sobol’ (Sobol’ 1993), Extended-FAST (Saltelli et al. 1999) and screening-based methods such as Morris (Morris 1991). The Morris method calculates the global main effect (elementary effect, \(\mu^*\)) of a parameter by averaging a number of local-based measures for different points in the parameter space (Saltelli et al. 2008). This is a widely used and robust method that requires relatively smaller computational costs compared to other methods (Campolongo et al. 2007).

The global sensitivity analysis has been widely applied to various crops, such as wheat (Casadebaig et al. 2016), sugarcane (Sexton et al. 2017), oil palm (Pardon et al. 2017) and cotton (Pathak et al. 2007). Locatelli et al. (2017) successfully used the ForestGALES model for assessing wind risk to *Eucalyptus globulus* stands by a Sobol’ SA in one environment in North Spain. Nevertheless, there is a lack of studies on the use of global sensitivity analysis to identify suitable *Eucalyptus* genetic traits under contrasting climate conditions, including the effects of spatial and temporal climate variability and change. This approach is of high importance, useful and innovative for *Eucalyptus* breeding and management purposes. In this context, the following hypothesis was raised: a global sensitivity analysis is a useful tool to identify suitable traits for *Eucalyptus* adaptation to climate variability and change. Therefore, the aim of this study was to perform a global sensitivity analysis for assessing the impact of different genetic traits on *Eucalyptus* yield across 23 contrasting environments in Brazil under present and future climate scenarios.

2. MATERIALS AND METHODS

2.1. Study environments

The simulations were performed for 23 *Eucalyptus* producing locations in Brazil (Fig. 1 and Supporting Information—Table S1). The weather data (maximum, minimum and mean temperatures, solar radiation, rainfall, relative humidity and wind speed) were obtained from daily gridded meteorological data (Xavier et al. 2016). The effects of temporal climate variability on *Eucalyptus* yield were assessed from a period from 1980 to 2008, assuming a *Eucalyptus* rotation of 7 years. A planting date of 15 February was assumed to be indicative for all locations. The soil types (first-order) were reported from forestry companies with experimental areas in each studied location. The soil profile required in the APSIM model was built based on pedotransfer functions fitted for Brazilian soils, RadamBrasil (1974) and Wise (Batjes 2009) databases. An effective root depth of 3 m was considered for all locations according to the findings of Christina et al. (2017) and Pinheiro et al. (2019), except for sites 8, 11 and 14, where some changes were made according to site-specific empirical evidence. Soil profile information for all locations are presented in Supporting Information—Table S2. Further information on the methodological procedures for building the soil profiles can be found in Ellì et al. (2020a). No nutrient limitations were considered during the simulations.

2.2. Process-based simulation model and CO₂ fertilization functions

The APSIM Next Generation *Eucalyptus* model was used to perform the simulations of stemwood biomass (\(\text{t ha}^{-1}\)) at 7 years, which is a common rotation period for *Eucalyptus* plantations in Brazil (McMahon et al. 2019; Ellì et al. 2020b). This model was validated against measured *Eucalyptus* yield data from plots in all sites presented in Fig. 1 (Ellì et al. 2020a), which were conducted under optimum or near-optimum forest management. Model parameters for a highly productive and homeostatic Brazilian clone of *Eucalyptus urophylla* with suitability to a wide range of environments were used. Results of the Model performance (\(R^2 = 0.89, \text{Willmott Agreement Index} = 0.97, \text{Nash–Sutcliffe efficiency index} = 0.88\)) suggest good skill in simulating *Eucalyptus* productivity for various climates and soil types across Brazil, indicating the model is suitable for the purpose of the present study.

The APSIM Next Generation *Eucalyptus* model takes into account the modelling structure from APSIM-Growth model (Huth et al. 2001), but having the possibility of modifications through the Plant Modelling Framework (PMF), a software that allows models to be adjusted and improved in the APSIM platform (Brown et al. 2014). Daily biomass production is calculated from daily intercepted solar radiation and radiation use efficiency (RUE). Radiation use efficiency is affected by soil and climatic factors. Interception of solar radiation is calculated assuming an exponential light extinction coefficient. A general approach of this model is:

\[
\Delta G = R_{\text{int}} \times \varepsilon \times \min(F_T, F_P, F_N, F_{\text{VPD}}) \times F_W \times F_{\text{CO}_2}
\]

where \(\Delta G\) is the daily growth; \(R_{\text{int}}\) the daily intercepted solar radiation; \(\varepsilon\) the radiation use efficiency (\(\text{g MJ}^{-1}\) of global solar radiation); and \(F_T, F_P, F_N, F_{\text{VPD}}, F_W\) and \(F_{\text{CO}_2}\) the growth modifiers to account for the effects of air temperature, frost, nitrogen, vapor pressure deficit (VPD), water supply and atmospheric CO₂ concentration.

The APSIM Next Generation *Eucalyptus* model includes five submodels related to different tree components: leaf, branch, stem, coarse root and fine root. Potential biomass production is modelled by the leaf submodel. Biomass is partitioned to the different organs according to tree size, environmental stresses and species-specific parametrizations. Leaf area growth is obtained from leaf growth and specific leaf area. Different soil layers are considered to describe the
vertical distribution of various soil processes. Available water of each layer depends on the progress of the extraction front to greater depths. The potential water uptake is calculated using the product of the available water in the layer and a factor that controls the rate of extraction—KL (Robertson et al. 1993a, b). When plant water absorption is lower than the plant demand, reductions in growth rate are considered by water deficit. Full model documentation is available at https://www.apsim.info/.

Fertilization effects of CO₂ enrichment were proposed for the APSIM Next Generation Eucalyptus model in the present study. Increases in CO₂ concentration impact forest growth by changes in RUE, stomatal conductance (SC) and specific leaf area. Radiation use efficiency and SC responses to CO₂ enrichment are based on Reyenga et al. (1999) approach for a C₃ plant. To consider the CO₂ effects on RUE and interactions with temperature, APSIM Next Generation Eucalyptus model scales RUE by the ratio \( \Phi_p \) of the light-limited photosynthetic response to increased CO₂ (Reyenga et al. 1999; O’Leary et al. 2015), which is calculated by the following expression:

\[
\Phi_p = \frac{(CO_2 - \Gamma)(350 + 2\Gamma)}{(CO_2 + 2\Gamma)(350 - \Gamma)}
\]  

where \( \Gamma \) is the temperature-dependent CO₂ compensation point, which is calculated by:

Figure 1. Locations for long-term yield simulations and sensitivity analyses and their respective Köppen climate classification in Brazil (map adapted from Alvares et al. 2013). The description of map codes and further information on the characteristics of each location are presented in Supporting Information—Table S1.
\[ \Gamma = \frac{(163 - T_{\text{mean}})}{(5 - 0.1 \times T_{\text{mean}})} \]  

where \( T_{\text{mean}} \) is the mean daily temperature (°C).

The APSIM model considers a reduction in SC with increasing CO\(_2\) levels and its interaction with enhanced RUE (\(\Phi_P\)). The SC reduction is likely to reduce water loss but maintain photosynthesis due to higher water potential and internal CO\(_2\) levels, resulting in an increased transpiration efficiency (Reyenga et al. 1999). The response of SC to increased CO\(_2\) concentration is calculated as follows:

\[ SC = \frac{\Phi_P}{RG} \]  

where \( RG \) is the relative CO\(_2\) gradient, which is obtained by:

\[ RG = \frac{(CO_2 - \Gamma)}{(350 - \Gamma)} \]  

The effects of CO\(_2\) enrichment and its interaction with temperature levels on different plant physiological features considered by the APSIM model can be seen in Supporting Information—Fig. S1. Responses of specific leaf area to increased CO\(_2\) are based on findings of Smith et al. (2012) for Eucalyptus experimental plots. A linear reduction of about 15% of specific leaf area is considered when CO\(_2\) concentration increases from 350 to 700 ppm.

### 2.3. Climate change scenarios

Climate change scenarios were generated by three Global Circulation Models (GCMs): HadGEM2-ES, GISS-E2-R and CSIRO-Mk3-6-0, which are publicly available from the Coupled Model Intercomparison Project Phase 5—CMIP5 (Taylor et al. 2012). These models were selected based on its ability to better represent the spatial and temporal distribution of rainfall in different Brazilian regions (Yin et al. 2013; Gulizia and Camilloni 2015).

The period from 2020 to 2049 (near-term) was selected to assess climate change impacts on Eucalyptus growth. This period was chosen in order to provide results that may be currently used for the planning of Eucalyptus breeding programmes for the coming decades, and then to assist in near-term management purposes. Two contrasting greenhouse gases emissions were assessed, which follow distinct representative concentration pathways (RCPs): intermediate emission scenario (RCP4.5) and high emission scenario (RCP8.5). According to Ward et al. (2011), the RCP4.5 scenario offers the best visual match to the recent studies on future fossil fuel production, while the RCP8.5 represents more extreme conditions.

The future climate data were generated from the Climate Scenario Generation Tool for R from the Agricultural Model Intercomparison and Improvement Project—AgMIP, where changes in maximum and minimum temperature and rainfall were considered (Hudson and Ruane 2013; Rosenzweig et al. 2015). The other weather variables, such as solar radiation, relative humidity and wind speed (also are required to use in the APSIM Eucalyptus model) remained unchanged. Daily weather data from 1980 to 2009 were used as the baseline. The CO\(_2\) concentrations during the simulations were 360 ppm for the baseline, 450 ppm for RCP4.5 and 480 ppm for RCP8.5. These values represent the concentration referring to the central year of the 30-year period, as recommended by AgMIP (Rosenzweig et al. 2015). Simulations for the baseline were constructed to consist of four consecutive rotations: (i) 15 February 1980 to 14 February 1987, (ii) 15 February 1987 to 14 February 1994, (iii) 15 February 1994 to 14 February 2001 and (iv) 15 February 2001 to 14 February 2008. Similarly, for climate change assessments, the following rotations were considered: (i) 15 February 2020 to 14 February 2027, (ii) 15 February 2027 to 14 February 2034, (iii) 15 February 2034 to 14 February 2041 and (iv) 15 February 2041 to 14 February 2048.

### 2.4. Parameters and outputs

The global sensitivity analysis was performed using 25 parameters of the APSIM Next Generation Eucalyptus model (Table 1). Ranges for each parameter were selected from a robust calibration of the model for different Brazilian Eucalyptus clones and environments to ensure realistic changes in magnitude. These parameters were chosen due to their ability of predicting Eucalyptus genotypes differences (Elli et al. 2020a). The effects of parameters were analysed in terms of impacts on the stemwood biomass at the seventh year of the Eucalyptus rotation.

For some age-related parameters (such as the age factor for occurrence of frost and specific leaf area), a new approach was proposed in order to consider the effects of the whole function by changing only one delta (\(\Delta\)) coefficient in each case as described below (Fig. 2). For this, some structural changes were made to the APSIM Next Generation Eucalyptus model. A delta coefficient was added as a multiplier to the x-axis of a given age-related function throughout the whole Eucalyptus rotation. Savings in execution time were gained from a reduction in the number of parameters required to evaluate any given interpolated function. For instance, the original function for specific leaf area includes 12 parameters (\(x = 0, 1, 2, 3, 4, 8, 0.015, 0.011, 0.010, 0.008, 0.007\) and 0.006). The sensitivity of the model to changes in \(x\) was evaluated using one parameter (\(\Delta\)), saving approximately 106 000 7-year simulations in the present study given the large number of environments, Eucalyptus rotations and climate scenarios assessed.

### 2.5. Global sensitivity analysis

The Morris sensitivity method (Morris 1991) was used to perform the global sensitivity analysis. This method is based on the calculation of the elementary effects of each input parameter on a given model output. The Morris method can be conceptualized as a randomized one-at-a-time (OAT) design, as it varies one factor at a time independently of the others, recording at each time the effect of this variation on the output. This procedure is repeated \(r\) times, where \(r\) is the number of trajectories to explore the variability in elementary effect across the parameter space, and generally ranges from 10 to 50 (Campolongo et al. 2007). In the present study, 15 trajectories were considered sufficient after preliminary tests for contrasting locations using up to 30 trajectories showed stable results for mean of absolute values of the elementary effects with \(r = 15\).

The total number of model simulations is given by \(r(n + 1)\), where \(n\) is the total number of studied parameters. In the present study, 25 genetic parameters were considered, then \(15(25 + 1) = 390\) 7-year simulations were performed in each environment and considering only one 7-year
Table 1. Description and ranges of the parameters (Elli et al. 2020a) used to perform the global sensitivity analysis of the APSIM Next Generation *Eucalyptus* model. For some of the parameters presented, x- and y-axis are required to make the parameter response curve. *SA = sensitivity analysis.*

| Parameters                                      | Functions and units | x- or y-axis used in the SA | Abbreviation | Lower limit | Upper limit |
|-------------------------------------------------|---------------------|-----------------------------|--------------|-------------|-------------|
| Radiation use efficiency                        | g MJ⁻¹              | –                           | RUE          | 1.30        | 1.69        |
| Light extinction coefficient of seedlings       | –                   | –                           | Ky           | 0.25        | 0.38        |
| Light extinction coefficient of mature trees    | –                   | –                           | Km           | 0.45        | 0.61        |
| Photosynthesis modifier for temperature (FT)    | x: temperature (°C) | x                           | FT_1         | 6.00        | 10.00       |
|                                                 | y: FT               |                             | FT_2         | 17.00       | 19.00       |
|                                                 |                     |                             | FT_3         | 22.00       | 24.00       |
|                                                 |                     |                             | FT_4         | 38.00       | 40.00       |
| Photosynthesis modifier for frost (FF)          | x: minimum temperature (°C) | y                       | FFrost_1     | 0.80        | 1.00        |
|                                                 | y: FF               |                             | FFrost_2     | 0.00        | 0.50        |
| Stem senescence rate for frost (SSRF)           | x: minimum temperature (°C) | y                       | MFrost_1     | 0.00        | 0.20        |
|                                                 | y: SSRF             |                             | MFrost_2     | 0.00        | 1.00        |
|                                                 |                     |                             | MFrost_3     | 0.50        | 1.00        |
| Age factor for occurrence of frost (AFOC)       | x: age (years)      | x                           | AgeFrost     | 0.80        | 1.20        |
|                                                 | y: AFOC             |                             |              |             |             |
| Stem partitioning fraction (SPF)                 | x: individual tree weight (g m⁻²) | y                       | Stem_Part_1  | 0.15        | 0.20        |
|                                                 | y: SPF              |                             | Stem_Part_2  | 0.30        | 0.40        |
|                                                 |                     |                             | Stem_Part_3  | 0.37        | 0.64        |
| Branch partitioning fraction                    | –                   | y                           | Branch_Part  | 0.08        | 0.12        |
| Leaf partitioning fraction (LPF)                 | x: individual tree weight (g m⁻²) | y                       | Leaf_Part_1  | 0.14        | 0.28        |
|                                                 | y: LPF              |                             | Leaf_Part_2  | 0.10        | 0.24        |
|                                                 |                     |                             | Leaf_Part_3  | 0.09        | 0.20        |
| Coarse root partitioning fraction (CRPF)        | x: individual tree weight (g m⁻²) | y                       | CRoot_Part_1 | 0.01        | 0.03        |
|                                                 | y: CRPF             |                             | CRoot_Part_2 | 0.03        | 0.10        |
|                                                 |                     |                             | CRoot_Part_3 | 0.04        | 0.10        |
| Fine root partitioning fraction                 | –                   | y                           | FRoot_Part   | 0.24        | 0.35        |
| Specific leaf area (SLA)                        | x: Age (years)      | x                           | SLA          | 0.80        | 1.20        |
|                                                 | y: SLA (m² g⁻¹)     |                             |              |             |             |
3. RESULTS

3.1. Influential traits under present climates

Radiation use efficiency, Km, Ky, FT_3 and parameters related to biomass partitioning (Leaf_Part_1, Leaf_Part_3 and FRoot_Part) were the most influential parameters in most locations under the present climate conditions (Fig. 3 and Supporting Information—Fig. S2), indicating that these parameters substantially affect stemwood biomass regardless of the environmental conditions. Parameters related to frost effects (mainly AgeFrost and MFrost_2) were influential for predicted yield only at locations in Southern Brazil where night-time temperatures are lower. In general, traits related to leaf partitioning (Leaf_Part_1 and Leaf_Part_3) presented the highest levels of interaction with other parameters and/or non-linearity effects for most locations as shown by the highest values of σ.

3.2. Temporal climate variability affecting the level of influence of Eucalyptus traits

The value of μ* was affected by the temporal climate variability as indicated by its variation across the different 7-year Eucalyptus rotations (Fig. 4 and Supporting Information—Fig. S3). For instance, the μ* for RUE in Otacílio Costa, SC (23-KLO) was higher during the first two rotations (75.9 and 76.4 t ha⁻¹ for 1980–87 and 1987–94, respectively), compared to the results found for subsequent rotations (63.7 and 64.4, respectively). On the other hand, effects of AgeFrost were lower during the first two rotations (0 and 2.0 t ha⁻¹ for 1980–87 and 1987–94, respectively) compared to the next rotations (1994–2001 and 2001–08), when the parameter values were, respectively, 23.8 and 33.4 t ha⁻¹. Temporal variations were also observed for Leaf_Part_1 at Inhambupe, BA (08-COP), Botucatu, SP (10-DUB), Mogi Guaçu, SP (20-IPB) and Telêmaco Borba, PR (22-KLT) and for Leaf_Part_3 at Botucatu, SP (10-DUB), Chapadão do Sul, MS (11-FCB), and Buri, SP (33-DUR).

3.3. Climate change projections and their impacts on Eucalyptus yield

According to the climate change projections from three global circulation models for the period from 2020 to 2049, the annual mean air temperature is expected to increase at all assessed locations (Fig. 5 and Supporting Information—Table S3). The overall increases in air temperature for RCP4.5 and RCP8.5 will be, respectively, 1.3 °C and 1.6 °C, in relation to the baseline period from 1980 to 2009. Annual rainfall projections vary according to the region. In general, North and Northeast Brazil are predicted to experience decreases in annual rainfall, while the South region may have annual rainfall increase. The Midwest and Southeast regions showed no clear trends for annual rainfall. Eucalyptus yield forecasts indicate a likely increase for most locations evaluated, except for tropical locations, such as Peixe, TO, for RCP8.5, and Inocência, MS, for both RCPs 4.5 and 8.5, where current mean annual temperatures are higher (24.6 °C and 27.1 °C, respectively). The average yield increment obtained for future climates was 8 % for RCP4.5, ranging from –3 to 21 %, and 9 % for RCP8.5, ranging from –3 to 24 %.

3.4. Influential traits under future climate scenarios

Radiation use efficiency, Km, Ky, FT_3 and parameters related to biomass partitioning remained the most influential parameters in most locations under climate change scenarios (Fig. 6 and Supporting Information—Fig. S4). An increased influence was observed for parameters related to the effect of temperature on photosynthesis. FT_4 became one of the five most important parameters in tropical locations.
such as Bom Despacho, MG (03-AMB), Chapadão do Sul, MS (11-FCB), Peixe, TO (19-GMR) and Coração de Jesus, MG (26-PLA). FT_3 increased its relative level of importance under climate change scenarios. For instance, under present climate, FT_3 was the fifth most influential trait in Três Lagoas, MS (13-FIT), with a μ* of 21.9 t ha⁻¹, while under the RCP8.5, it was the second most important, with a μ* of 57.0 t ha⁻¹. Similar patterns were obtained when RCP4.5 was assessed [see Supporting Information—Fig. S5].

3.5. General ranking of influential traits under present and future climate scenarios

Considering all locations and 7-year rotations for Eucalyptus production, RUE, Leaf_Part_1, Km, Ky and FRoot_Part were the five most influential traits (median of μ* above 20 t ha⁻¹) for the present climate (Fig. 7). About half of the assessed parameters (13 of the 25) had little impact on yield (median of μ* below 1 t ha⁻¹). Leaf_Part_1, Ky, Leaf_Part_3, RUE and Km were the five parameters with the highest interaction and/or non-linearity effects, with a median of σ above 6.0 t ha⁻¹. Again, 13 of the 25 parameters presented low levels of interaction and/or non-linearity effects (median of σ below 1 t ha⁻¹). When the future climate scenarios were assessed (RCP4.5 and 8.5), RUE, Leaf_Part_1, FT_3, Km and Ky were the five most influential parameters for both RCPs, with a median of μ* above 30 t ha⁻¹. Leaf_Part_1, Ky, RUE, Leaf_Part_3, Km and FT_3 were the parameters with the highest interaction level with other parameters and/or non-linearity effects (median of σ above 10.0 t ha⁻¹) for both RCPs.
3.6. Spatial climate variability, climate change and their interaction with influential traits

Existing spatial climate variability in Brazil affected the level of influence of some *Eucalyptus* traits (Fig. 8). In the present analysis, $\mu^*$ was divided by the stemwood biomass of each location (normalized $\mu^*$), in order to better compare sites and climate scenarios. For present climate conditions, no clear regional trends were observed, mainly for RUE and FRoot_Part. On average, the normalized $\mu^*$ for FT_3 was higher in Northeast (0.31), North (0.15) and Midwest (0.14) regions, than in the South (0.08) and Southeast (0.09) regions. Km presented the highest values of normalized $\mu^*$ (>0.2) at Inhambupe, BA (08-COP), and Bom Despacho (04-CEB), Coração de Jesus (26-PLA) and Bocaiuva (30-VMT), all in the state of Minas Gerais.

The level of influence of RUE, FT_3, Km and FRoot_Part on *Eucalyptus* yield showed a tendency to increase under future climates (Fig. 8). Relative increments in the level of influence for such parameters was higher in South and Southeast than in the other regions of the country. At a national level, the normalized $\mu^*$ of FT_3, RUE, FRoot_Part and Km, respectively, increases by 127 %, 21 %, 8 % and 3 %, under the RCP8.5, in relation to the baseline. On the other hand, frost-related traits were less influential on *Eucalyptus* yield in the subtropical sites under future climate scenarios. On average, the normalized $\mu^*$ of AgeFrost was 50 % and 11 % lower in the states of Rio Grande do Sul and Santa Catarina, respectively, under the RCP8.5, in relation to the baseline. On the other hand, frost-related traits were less influential on *Eucalyptus* yield in the subtropical sites under future climate scenarios. On average, the normalized $\mu^*$ of AgeFrost was 50 % and 11 % lower in the states of Rio Grande do Sul and Santa Catarina, respectively, under the RCP8.5. For MFrost_2, the normalized $\mu^*$ decreased 50 % in the state of Santa Catarina and become null in the states of Rio Grande do Sul and Paraná, under the RCP8.5 (data not presented in the spatial overview in Fig. 8).
4. DISCUSSION

Radiation use efficiency and traits relating to canopy light interception (Km, Ky), temperature effects on photosynthesis (FT_3) and biomass partitioning (Leaf_Part_1, Leaf_Part_3 and FRoot_Part) were the most influential in most Brazilian locations under present climate. Whilst this is the first application of global sensitivity analysis for the simulation of Eucalyptus traits under present and future climate scenarios, previous studies in other crops have found similar results. Casadebaig et al. (2016) performed a global sensitivity analysis using the APSIM-Wheat model and the Morris method in four environments in Australia and found that radiation use efficiency (y_rue), extinction coefficient (y_extinct_coef), thermal time (tt_end_of_juvenile) and traits related to biomass partitioning (y_frac_leaf and y_frac_pod) were among the most influential traits to this crop. Sexton et al. (2017) used the APSIM-Sugar model to perform a global sensitivity analysis in two Australian environments, and found that RUE, number of green leaves (green_leaf_no) and root conductance (K_r) were the most influential traits in both environments.

The results of the present study are also supported by other studies in the literature, showing that RUE is an important trait affecting Eucalyptus yield (Binkley et al. 2010; le Maire et al. 2013), which indicates that special attention should be given to such trait in the breeding programmes. Plant architecture and leaf area distribution are also important features affecting the amount of light absorbed (Larsen and Kershaw 1996) and therefore Eucalyptus productivity, which justifies the high levels of influence of Km and Ky on...
Eucalyptus stemwood biomass found in the present study. Similarly, Mattos et al. (2020) evaluated the wood growth, canopy structure and light use efficiency in 18 Eucalyptus clones in Brazil and found that leaf angle distribution may be an important factor that affects the amount of intercepted solar radiation and, consequently, Eucalyptus productivity.

FT_3 was among the most influential parameters in all assessed locations in the present study. This parameter defines photosynthetic responses to temperature in the APSIM Next Generation Eucalyptus model. Our results suggest the use of genotypes with suitable cardinal temperatures for a given environment may substantially increase stemwood yield. This is supported by findings of Binkley et al. (2017), who evaluated the yield of 18 Eucalyptus clones across 27 locations in Brazil and found different patterns of yield response among the clones to mean annual temperature and annual rainfall. These authors also concluded that overall patterns of stem production varied strongly among clones within sites and across them.

Leaf_Part_1 was the most influential parameter related to biomass partitioning and presented the highest levels of parameter interaction for most locations. The results in the present study agree with those of Campoe et al. (2012), who evaluated stand-level patterns of carbon fluxes and partitioning in Eucalyptus grandis plantations in Brazil, and found that carbon partitioning to the leaf was significantly correlated with gross primary production.

Figure 6. Level of influence ($\mu^*$) and level of interaction and/or non-linearity ($\sigma$) of 25 parameters of the APSIM Next Generation Eucalyptus model to estimate stem biomass for six producing locations with contrasting environmental conditions in Brazil, for the future climate (2020–2049), under a high emission scenario (RCP8.5), considering the average of three global circulation models. Titles given for individual graphs indicate location codes (01-ANG = Niquelândia, GO; 08-COP = Inhambupe, BA; 11-FCB = Chapadão do Sul, MS; 19-GMR = Peixe, TO; 23-KLO = Otacílio Costa, SC; and 30-VMT = Bocaíva, MG). Text labels with parameter names for individual graphs indicate the five highest values of $\mu^*$. Plots for all locations are presented in Supporting Information—Fig. S4.
Figure 7. Level of influence ($\mu^*$) and level of interaction and/or non-linearity ($\sigma$) of 25 parameters of the APSIM Next Generation Eucalyptus model to estimate stem biomass for the baseline period (A and B), and from the average of three global circulation models, considering the future period from 2020 to 2049, under intermediate (RCP4.5—C and D) and high (RCP8.5—E and F) emission scenarios. All Eucalyptus rotations and environments were considered. Parameters were sorted in descending order according to the median.
Similarly, Forrester et al. (2012) found that periodic annual volume increment was strongly correlated with leaf area index (LAI) in *Eucalyptus nitens* plantations in Australia. Whilst a reduction of the leaf partitioning may increase the amount of biomass partitioned to the stem, it may also decrease the forest growth rate due to reduced photosynthesis. However, partitioning patterns also may be affected by biotic and abiotic factors, silvicultural management practices as well as the responsiveness of a given genotype to environmental stresses.

Variations in $\mu^*$ among the different simulated rotations were found. This suggests the temporal climate variability affects the influence of some traits on *Eucalyptus* yield. This highlights the need to consider not only large-scale spatial variability when evaluating potential traits, but also the impact of seasonal climate variability at each location and the need for repeated sampling of climate records when undertaking sensitivity analyses. These results are supported by Sexton et al. (2017), who identified an inter-annual variability in sensitivity indexes on sugarcane biomass and sucrose yield using the APSIM-Sugar model.

Figure 8. Effects of spatial climate variability on the level of influence (normalized $\mu^*$) of the following parameters: RUE (A–C); FT_3 (D–F); Km (G–I); and FRoot_Part (J–L), to estimate *Eucalyptus* stem biomass for the present (baseline) and future climates, under intermediate (RCP4.5) and high (RCP8.5) emission scenarios.
These authors also found the level of inter-annual variability varied according to the environment. The effects of temporal climate variability on $\mu^*$ of some traits found in the present study are mostly related to the inter-annual and inter-seasonal rainfall variability, mainly in the centre-north region of the country. In Southern Brazil, where meteorological frost days are frequent (Alvares et al. 2018), frost-related parameters became more important compared to the other regions. Clear differences in these parameters were found among the rotations, as can be observed in Otacílio Costa, SC, for AgeFrost (Fig. 4).

According to the climate change projections for the period 2020–49, the annual mean air temperature will increase at all assessed locations, while the future annual rainfall change will vary according to the region (Fig. 5). These results agree with those found by Bender and Sentelhas (2018) for Brazilian conditions. These authors used seven GCMs to project climate change scenarios for 31 locations in Brazil. They found that South region will mostly experience increases in annual rainfall and the North and Northeast regions will experience decreases. These authors projected mean temperature increases of 1.9 °C and 2.63 °C for RCP4.5 and 8.5, respectively, considering the future period from 2040 to 2069. These values are slightly higher than those found in the present study (1.60 °C and 1.90 °C for RCP4.5 and 8.5), which are justified by the different future periods evaluated, since we used the period from 2020 to 2049.

The Eucalyptus plantations in Brazil will experience increases in stemwood biomass in most of the locations evaluated in centre-south Brazil under future climates (Fig. 5), which is mostly explained by the increased atmospheric CO$_2$ concentration (Almeida et al. 2009). The average yield increments for RCP4.5 were 8 %, ranging from −3 to 21 %, while for RCP8.5 it was 9 %, ranging from −3 to 24 %. Similarly, Pinkard et al. (2010) assessed the Eucalyptus productivity (stemwood volume) under current and future climates from six locations in Australia, using two GCMs (CSIRO-Mk3 and Hadley-Mk2) for period from 2015 to 2044, and the process-based model CABALA (Battaglia et al. 2004). Pinkard et al. (2010) applied the A2 emission scenario to the CSIRO-Mk3 GCM, and the A1FI emission scenario to the Hadley-Mk2 GCM. The CO$_2$ concentration of 450 ppm was used for both scenarios. These authors found that average yield will increment by 20.6 %, ranging from 11.2 to 30.4 % for the scenario generated by GCM CSIROMk3-A2, and 6.9 %, ranging from −5.5 to 23.9 % when using GCM Hadley-Mk2-A1FI. On average, the yield increment found by these authors was 13.8 %, similar to the results found in the present study.

Similar results were found by Almeida et al. (2009), who used the 3PG process-based model to quantify the spatial variation of Eucalyptus productivity under climate change scenarios across about 32 million ha located near the Atlantic coast of Brazil (covering parts of the states of Espírito Santo, Bahia, Rio de Janeiro and Minas Gerais). The GCM CSIRO Mark 3.0 climate model was used to project climate changes for the 30-year period centred on 2030. The A1B emission scenario was considered, using a CO$_2$ concentration of 450 ppm. These authors suggested an average increase of 17 % in mean annual stem biomass increment, a similar result compared to our findings from the same region, which was about 15 % for RCP4.5 and 16 % for RCP8.5, considering the average of the results from Belo Oriente, MG, Guanhães, MG, and Inhambupe, BA. Eucalyptus yield forecasts indicate a likely slight decrease at the tropical locations of Peixe, TO, and Inocência, MS. The reason is that positive effects of CO$_2$ fertilization will not be able to offset the negative impacts of high temperatures and water deficit, which is consistent with the findings of Booth (2013).

Radiation use efficiency, Km, Ky and parameters related to biomass partitioning (Leaf_Part_1, Leaf_Part_3 and FRoot_Part) remained among the most influential parameters under climate change scenarios (Figs 6 and 7). On the other hand, traits related to cardinal temperatures became more important when future climates were assessed, mainly the traits FT_3 and FT_4. In this context, characterizing genotypes according to their relative leaf photosynthesis and growth rate responses to temperature changes should be an important first step, as information in the literature is in early stages of development. This may allow the selection of genetic materials with increased adaptation to thermal conditions of given environments. In Brazil, Eucalyptus plantations are expanding in tropical states such as Mato Grosso and Tocantins states, and even to equatorial zones such as Maranhão and Piauí states (Gonçalves et al. 2017). Furthermore, climate change projections indicate increases in annual mean air temperature throughout the country. Thus, breeding solutions to high-temperature tolerance assumes greater importance to avoid yield losses under warming climates (Hammer et al. 2020).

The level of interaction $(\sigma)$ for RUE increased with increasing $\mu^*$ for current climates (Fig. 3), but much more under future climates (Fig. 6). This may indicate that rising temperatures may be introducing $G \times E$ interactions due to greater atmospheric VPD. Higher forest growth rates due to enhanced RUE associated with higher evaporative demand by rising temperatures may increase water consumption and drought effects in some environments (Stape et al. 2004; Booth 2013; Battaglia and Bruce 2017; Scolforo et al. 2019; Lim et al. 2020). On the other hand, elevated CO$_2$ reduces SC, increasing transpiration efficiency and decreasing plant water use for a given amount of plant growth (Leakey et al. 2009; Lobell et al. 2015; Hammer et al. 2020). The combination of these factors along with shifts in projected rainfall will define the real effects of climate change on the forest water balance not only in the assessed regions, but also around the world.

Effects of the spatial climate variability on the influential level of some traits are shown in Fig. 8. No clear regional trends were observed, mainly for RUE and FRoot_Part. Besides that, no well-defined relationships between the normalized $\mu^*$ and climate variables (e.g. annual rainfall, temperature, reference evapotranspiration, CMI) were found (data not shown). This may be related, in part, to the site-specific physical and hydraulic soil properties used during the process-based simulations with soil water holding capacity highly variable among the sites (0.70–1.25 mm cm$^{-1}$).

The simulation of virtual genotypes across environments by combining modelling and global sensitivity analysis is promising for exploring $G \times E$ interactions (Casadebaig et al. 2016). In the present study, for example, we have created 390 virtual genotypes for each environment (present and future climates) by sampling the parameter space of 25 genetic traits, resulting in various potential interactions [see Supporting Information—Fig. S6]. Our results provide directions of important traits that may offer strategies for Eucalyptus adaptation to climate variability and change. Therefore, Eucalyptus straightforward research programmes, dealing together with breeding, management and ecophysiology, could give special attention to
such traits in order to select superior clones and matching them with better sites for obtaining higher sustainable productivities at the present and in the future climates.

5. CONCLUSIONS

Global sensitivity analysis was found to be a powerful tool for identifying suitable Eucalyptus traits for adaptation to climate variability and change. This approach can improve breeding strategies by better understanding the gene x environment interactions for yield. Traits for radiation use efficiency, leaf partitioning, canopy light capture and fine root partitioning were the most important, impacting the Eucalyptus yield substantially in all environments under the present climate. The Eucalyptus yield under climate change scenarios showed results in agreement with those found in the literature, giving confidence that the APSIM Next Generation Eucalyptus model is suitable to perform future climate assessments for different plant traits. Some of the traits targeted now by breeders for current climate will remain important under future climates. However, breeding should place a greater emphasis on temperature response for Eucalyptus in some regions.

SUPPORTING INFORMATION

The following additional information is available in the online version of this article—

Table S1. Locations for long-term yield simulations and sensitivity analyses and their respective soil order and summary of the weather conditions (1980 to 2009).

Table S2. Physical and hydraulic characteristics of the soil profiles used to perform the simulations of stemwood biomass with the APSIM Eucalyptus model. Abbreviations given in table header are for soil depth (Depth), soil bulk density (BD), air dry water content (Air Dry), Wilting point (LL15), drained upper limit (DUL), saturated water content (SAT), Root extraction factor (KL), Root exploration factor (XF), plant available water capacity per mm (PAWC) and per soil layer (PAWCL).

Table S3. Annual mean air temperature (Tmean), annual rainfall, and Eucalyptus yield (stem biomass at 7 years) changes for the future climate (2020-2049), according to the average of three global circulation models, for 23 locations in Brazil, considering intermediate (RCP4.5) and high (RCP8.5) emission scenarios. The period from 1980 to 2009 was used as baseline (Base).

Figure S1. Effects of CO₂ enrichment and its interaction with temperature levels on different plant physiological features.

Figure S2. Level of influence (μ*) and level of interaction and/or non-linearity (σ) of 25 parameters of the APSIM Next Generation Eucalyptus model to estimate stem biomass for 23 producing locations in Brazil, considering the period from 1980 to 2008. Text labels with parameter names for individual graphs indicate the five highest values of μ*.

Figure S3. Effects of temperature variability on the level of influence (μ*) of 25 parameters of the APSIM Next Generation Eucalyptus model to estimate stem biomass for 23 producing locations in Brazil. Titles given for individual graphs indicate location codes (Table S1).

Figure S4. Level of influence (μ*) and level of interaction and/or non-linearity (σ) of 25 parameters of the APSIM Next Generation

Eucalyptus model to estimate stem biomass for 23 locations in Brazil, for the future climate (2020-2049), under a high emission scenario (RCP8.5), considering the average of three global circulation models. Text labels with parameter names for individual graphs indicate the five highest values of μ*.

Figure S5. Level of influence (μ*) and level of interaction and/or non-linearity (σ) of 25 parameters of the APSIM Next Generation Eucalyptus model to estimate stem biomass for 23 locations in Brazil, for the future climate (2020-2049), under an intermediate emission scenario (RCP4.5), considering the average of three global circulation models. Text labels with parameter names for individual graphs indicate the five highest values of μ*.

Figure S6. Example of exploring G x E landscape using 390 Eucalyptus virtual genotypes (coloured lines) across the environments, considering the present climate and the simulated seven-year rotation from 15 February 2001 to 14 February 2008.

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CONFLICT OF INTEREST

None declared.

CONTRIBUTIONS BY THE AUTHORS

E. F. E. contributed to conceptualization, validation, formal analysis, writing – original draft, project administration. N. H. contributed to conceptualization, software, writing – review & editing, supervision, methodology. P. C. S. contributed to writing – review & editing, supervision, project administration, funding acquisition. R. L. C. contributed to resources. C. A. A. contributed to writing – review & editing, methodology, resources.

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