

# Adapting 3-PG foliar variables to deciduous trees in response to water restriction: poplar short rotation plantations under Mediterranean conditions

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## Abstract

Poplar plantations growing in short rotation are a crucial biomass source of raw material for bioenergy and/or bioproducts, making an important contribution towards achieving a low-carbon bioeconomy. To optimize yield predictions of poplar plantations, this study aims to adapt the foliar variables of the process-based model 3-PG (Physiological Principles Predicting Growth) to a deciduous species like poplar. A total of 138 trees were sampled from a poplar plantation of the highly productive hybrid *P. x canadensis* ('AF2') over a first rotation at a planting density of 10 000 trees ha<sup>-1</sup>. Two irrigation scenarios, full soil field capacity (FC) and 50% FC, were considered to take into account the impact of climate change in the context of irrigation restrictions. Based on this information, the objectives were not only to determine the required species-specific foliar parameters but also to adapt the 3-PG model architecture to a pattern of variation along each growing season and identify the foliar parameters which present a significant response to restrictive irrigation. For this, specific leaf area (SLA) changes were modelled and the litterfall rate ( $\gamma_F$ ), and maximum canopy quantum efficiency ( $\alpha_{C_X}$ ) were calculated. SLA follows a similar dynamic in terms of water availability and year, with SLA for mature leaves being 19.9 m<sup>2</sup> kg<sup>-2</sup> and the SLA at the beginning of the growing season 10.4 m<sup>2</sup> kg<sup>-2</sup>. Leaf litter season begins in late August and lasts until early December, with 26 per cent litterfall by October. Additionally, the highly sensitive parameter  $\alpha_{C_X}$  was calibrated and a proposed value of 0.093 molC mol PAR<sup>-1</sup> was used. The validation of the proposed parameterization showed realistic estimates of the changes of leaf biomass and LAI during the growing season. These results will enable improved 3-PG-based estimations of the real variation along the growing season of variables such as Net Primary Productivity, leaf litterfall or analysis of the soil-plant nutrient cycle.

**Keywords:** poplar, 3-PG, process model, specific leaf area, litterfall, stomatal conductance

## Introduction

The Sustainable Development Goals (Baeyens and Goffin, 2015), the Paris Climate Agreement (Delbeke et al., 2019) and The Land Use and Forestry Regulation (European Commission, 2018) establish new requirements for European forests, underlining the need to mitigate climate change, commitment to deliver goods and services, create jobs and provide sustainable fuels and materials (Freer-Smith et al., 2019). Additionally, they highlight the need to support foresters by increasing awareness of the benefits to the climate of wood products, which can store carbon sequestered from the atmosphere and provide substitutes for emission-intensive materials. These different elements form part of a sustainable bio-based economy which is key to ensuring smart, green growth in Europe (European Commission (EC), 2012). In this regard, biomass plantations are expected to be a key ingredient in advancing the bioeconomy strategy (Scarlat et al., 2015).

The genus *Populus* possesses traits (abundant supply of improved genetic material largely as a result of their ease of hybridization, fast growth rates and facility for vegetative multiplication) that make it suitable for the production of biomass

under short rotation coppice (SRC) systems (Dickmann et al., 2002). Such SRC system can provide a source of raw material for bioenergy and/or bioproducts, promote employment in rural areas as well as supply environmental benefits (McEwan et al., 2020; Scarlat et al., 2015). Furthermore, these plantations make an important contribution toward achieving a low-carbon bioeconomy (Oliveira et al., 2020; Pawson et al., 2013).

However, if the desired production and associated benefits are to be achieved short rotation poplar cultivation requires a sound understanding of numerous factors influencing the cultivation. These include, for example, clonal characteristics, site conditions, change in climate and specific cultural practices (Dimitriou et al., 2009; Gielen et al., 2001; Oliveira, 2012; Pellis et al., 2004).

In ideal case, an improved understanding of above-mentioned factors and relationships should be summarized in tools that enable reliable yield predictions. Over the past decade, progress has been made as regards empirical modeling to estimate biomass from poplar SRC plantations (Di Matteo et al., 2015; Oliveira, 2019; Pérez-Cruzado et al., 2014; Vanbeveren et al., 2018), as well as other aspects regarding tree architecture, spatial distribution of leaf morphology or leaf area index (LAI). The latter is an important

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determinant of biomass production in these plantations (Broeckx et al., 2012; Casella and Sinoquet, 2003; Tripathi et al., 2018). Under a scenario of changing environmental conditions, an approach to calculate future estimates of forest growth and yield is to explicitly consider climate-sensitive forest growth models. In this context, process-based models are regarded as promising tools (Fontes et al., 2011; Nölte et al., 2020; Pretzsch et al., 2014).

The model 3-PG (Physiological Principles Predicting Growth), developed by Landsberg and Waring (1997), is a simple, process-based, stand-level model of forest growth (Sands and Landsberg, 2002). The 3-PG model has been constructed in close collaboration with intended end-users and has hence a simple, transparent structure and is therefore easy to use (Esprey et al., 2004). These characteristics increase the likelihood of its use in a management context (Landsberg and Sands, 2011) and make it a powerful tool that allows the user to set up different scenarios (Esprey et al., 2004). One challenge of the 3-PG model is that parameterization should be conducted at the species scale. 3-PG was originally developed for evergreen trees, with a monthly increment output at stand level (Landsberg and Waring, 1997). To date, few adaptations of the 3-PG model for deciduous trees have been developed, as it is necessary to consider processes specific to deciduous species that must inevitably occur, such as the fact that all the leaves must fall every year, or the monthly variations of the LAI throughout the growing season (rather than throughout the life of the plantation).

As part of estimating SRC willow productivity, Jégo et al. (2017) modified the 3-PG model to simulate annual leaf growth and fall, as well as to take litterfall into account as a function of the month, highlighting several challenges associated with predicting SRC willow productivity accurately. The challenges associated with adapting 3-PG to deciduous trees are summarized in Figure 1.

In addition to the challenges described in Figure 1, it would be of particular interest for biomass prediction in the context of global warming to introduce a modification of the 3-PG model to improve leaf cycle processes by representing changes in leaf unfolding and leaf senescence dates in relation to monthly average temperatures (Nölte et al., 2020).

There are several studies in which 3-PG is applied to deciduous trees such as willow plantations (Amichev et al., 2011; Jégo et al., 2017), subtropical mixed-species stands (Forrester and Tang, 2016), deciduous broadleaf forests dominated by the Asian white birch (Potitthep and Yasuoka, 2011) or sessile oak stands (Nölte et al., 2020). A few studies have also dealt specifically with poplar plantations (Amichev et al., 2010; Hart, 2014; Hart et al., 2015; Headlee et al., 2012; Zalesny et al., 2012). The species-specific parameters required to run the 3-PG model are often derived from literature and include the specific leaf area (SLA) and LAI-related parameters as well as the allocation parameters, which do not consider the effects of site condition on the response.

Some authors have conducted a detailed sensitivity analysis of the 3-PG model parameters to better understand them and identify those that need to be accurately determined (Esprey et al., 2004; Pérez-Cruzado et al., 2011). Parameters such as canopy quantum efficiency, maximum canopy conductance, LAI, litterfall or SLA of mature trees were identified as being highly sensitive, but information on their temporal variability is still scarce (Esprey et al., 2004; Nouvellon et al., 2010).

Detailed species-specific parameters based on observed data are key to obtaining the most accurate values for the mentioned variables and therefore achieving the full potential of the 3-PG model. In a previous paper, a detailed analysis was carried out

of the monthly change of important leaf-level variables such as the number and distribution of leaves, foliar biomass, individual and total LAI, SLA, leaf macronutrients (NPK and C) and foliar gas exchange parameters. These variables are of particular interest in the 3-PG parametrization (Fuertes et al., 2022).

The present study aims on adapting 3-PG foliar variables to deciduous poplar plantations over the course of the first rotation of three years of a poplar SRC plantation under two contrasting irrigation scenarios: optimal and restricted water availability. Furthermore, we propose foliar parameters for poplar short rotation plantations, which also take into consideration their differing response under a water restriction scenario. More specifically, we (i) model the change of SLA, (ii) calculate the litterfall rate ( $\gamma_f$ ) and (iii) determine the maximum canopy quantum efficiency ( $\alpha_{c,x}$ ) of poplar stands growing in an SRC plantation.

## Material and methods

### Model description

The model 3-PG (Landsberg and Waring, 1997) is a simple, process-based, stand-level model of forest growth consisting of different submodels: the assimilation of carbohydrates, the distribution of biomass among foliage, roots and stems, the determination of stem number, soil water balance, and conversion of biomass values into variables of interest to forest managers. It requires species-specific parameter values as well as site and climatic data as inputs (Sands and Landsberg, 2002). An overview of all the process models that comprise the 3-PG model and all the required species-specific parameters and their interactions within the 3-PG models is provided (Figure 2).

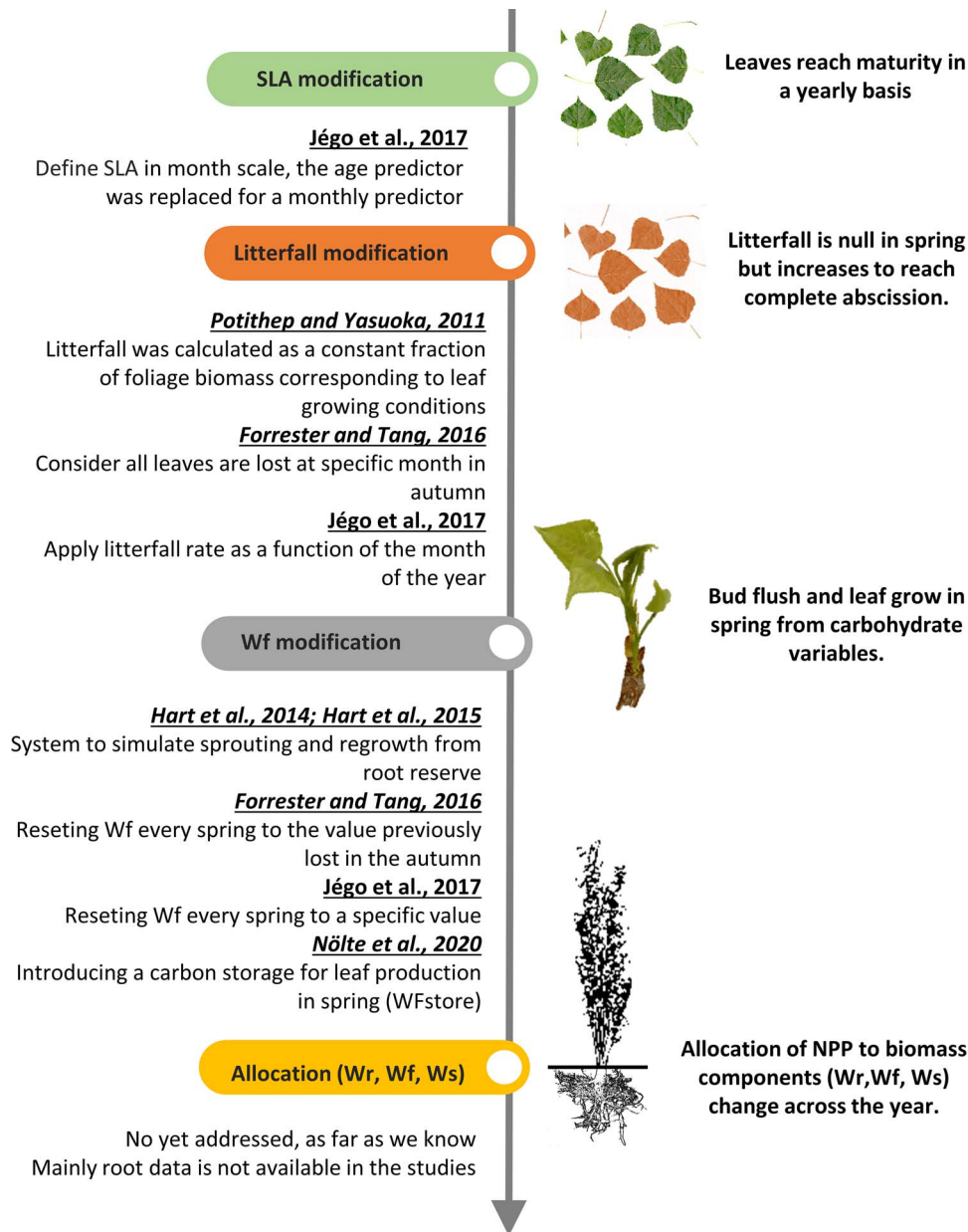
Some modifications were made to version 2.7 of the 3PGpjs Microsoft Excel spreadsheet code (Sands, 2010) to (i) take into account the monthly variation of the leaf area index (LAI) throughout the growing season (rather than throughout the life of the plantation, see section 2.5.1), (ii) simulate leaf fall every year, considering litterfall rate as a function of the month (see section 2.5.2) and (iii) simulate leaf growth every spring from 10% of the root biomass ( $\eta_r = 0.10 \text{ } ^0/1$ ), this fraction of root carbohydrates reserves will generate  $W_f$  every spring ensuring that the model will generate a LAI value to start a new growing season (Regier et al., 2010).

### Data source

Parametrization and calibration data for this study was collected from a poplar SRC plantation (SRC-trial1) established in early spring 2018 for a rotation length of three years and a planting density of 10 000 trees  $\text{ha}^{-1}$  (spacing 2 m  $\times$  0.5 m). The study site was located in central Spain (40° 27' 27" N; 3° 45' 01" W) at an elevation of 592 m a.s.l. The annual mean temperature is 14.66°C, and the annual mean precipitation is 425.5 mm. The soil has a sandy loam texture with a pH of 8.6 and 0.86 per cent organic matter.

The genotype used was 'AF2' (*Populus*  $\times$  *canadensis* Mönch), which is widely used for the production of chip biomass in the Mediterranean area (Pannacci et al., 2009; Sabatti et al., 2014). It was specifically selected as a high biomass productivity clone by the private forest nursery company Alasia Franco Vivai (Savigliano, Italy) and has shown both high adaptability and the highest biomass productivity across Spain according to results obtained from a Poplar Plot Network (PPN) under SRC management with irrigation (Sixto et al., 2015).

The outdoors plantation (SRC-trial1) was established manually using hardwood cuttings of 25 cm in length. Two neighboring



**Figure 1.** Description of the challenges associated with adapting 3-PG to deciduous trees and the solutions that have been proposed by different authors (Forrester and Tang, 2016; Hart et al., 2015; Jégo et al., 2017; Nölte et al., 2020; Potitthep and Yasuoka, 2011). NPP: net primary productivity;  $W_r$ : root biomass;  $W_f$ : leaf biomass and  $W_s$ : stem biomass.

plots were defined. The first (T1) was irrigated to field capacity. The second, adjacent plot (T2), was irrigated to 50 per cent of field capacity. Precipitation was taken into consideration when calculating irrigation doses. A total of 590 trees were planted. Each plot (T1 and T2) consisted of five single rows with a total of 295 trees per plot, including inner and outer border rows to minimize border effects.

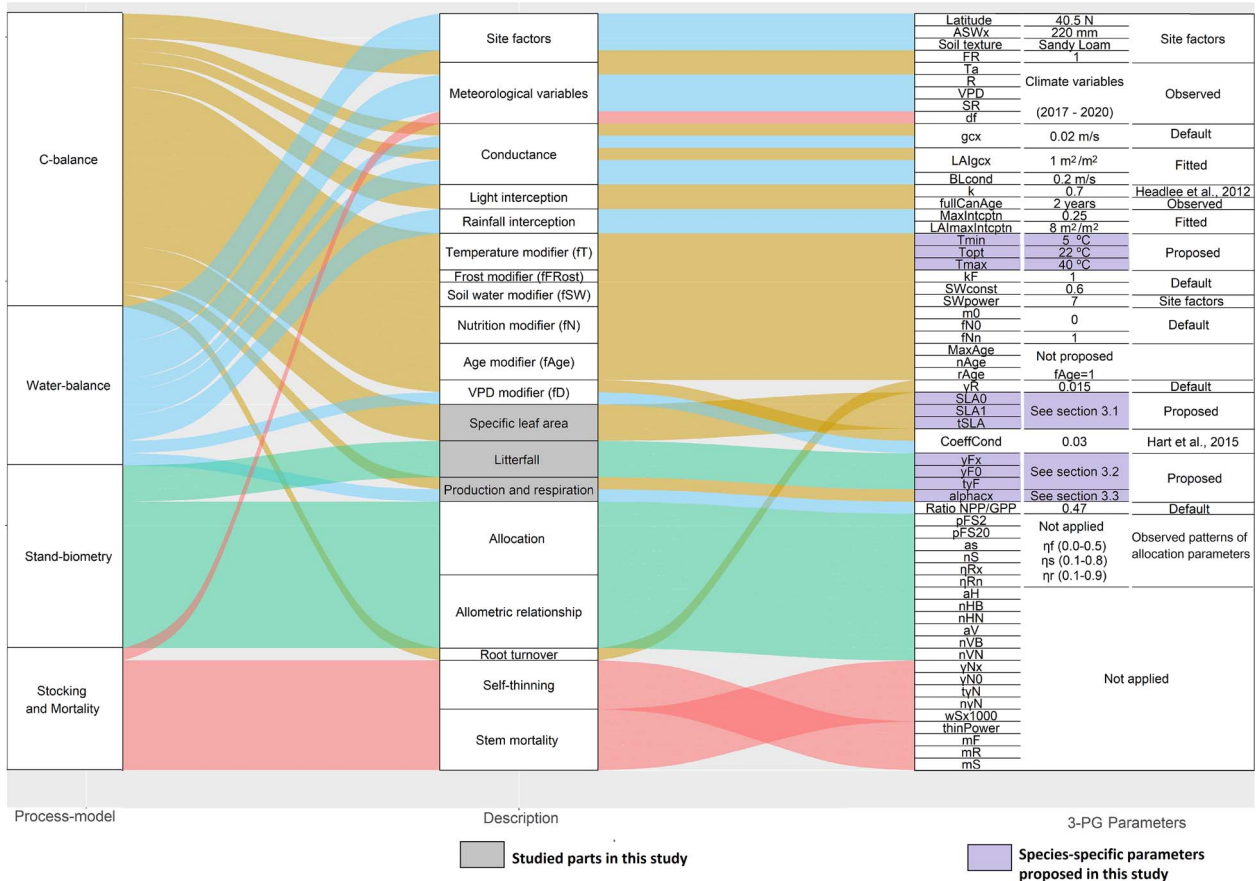
A drip irrigation system was used from May to October every year over the whole rotation period. Moisture in both plots was monitored using moisture sensors (SM200 Delta-T). Weed competition was avoided over all three years. Fertilization was not applied.

Every month, on the  $21st \pm 3$  days, during the three growing seasons of the first rotation (from April to November), three trees (sampling group) per water scenario (T1 and T2) were harvested, measured and destructively sampled. The data set collected was

from 138 measured trees out of 590 at the end of the first rotation (no sample in April in the first year).

Validation data for this study was collected from an adjacent poplar SRC plantation (SRC-trial2) established a year earlier than the SRC-trial1 for a rotation length of three years (2017–2019) and a planting density of  $10\,000$  trees  $ha^{-1}$  (spacing  $2\text{ m} \times 0.5\text{ m}$ ) and a planting density of 10 000 trees  $ha^{-1}$  (spacing  $2\text{ m} \times 0.5\text{ m}$ ) planted with 20–30 cm long hardwood cuttings in 30 L pots filled with the same soil layer and buried in the ground to simulate, as far as possible, the management conditions of a real plantation. Pots were used in this trial to study below-ground biomass in subsequent studies. The SRC-trial2 was irrigated to FC using drip irrigation system from May to October every year over the whole rotation period.

As part of this study, additional data from the PPN was used to support all parameters estimated, including gas exchange measurements, thus giving a broader perspective of the response in



**Figure 2.** The flow diagram shows the process models that comprise the 3-PG model on the left, the description of the variables is shown in the center and all the required species-specific 3-PG parameters are shown on the right. The description of the variables, the symbols and names used to abbreviate the parameters are based on the data from Sands (2001).  $\eta_f$ ,  $\eta_s$  and  $\eta_r$ : leaf, stem and roots allocation rates ( $l/1$ ).

the Mediterranean area. The inclusion of the data from the PPN, which comprises 350 plots in 98 trials located at 30 different sites under Mediterranean conditions, means that the results will be more representative of the overall response under Mediterranean conditions in comparison to using data from only one specific trial. A detailed description of the PPN can be found in Sixto et al. (2013, 2015).

### 3-PG model inputs

The 3-PG model was run to validate the foliar parameterization proposed, comparing the predictions based on the parameterization identified in this study with the observed values of leaf biomass and LAI recorded for the SRC-trial2. Data for initializing the simulation, such as observed initial stem and foliage biomass, were 1 and 2.5 g tree<sup>-1</sup>, respectively, and observed initial root biomass was 13 g tree<sup>-1</sup>. The observed pattern of variation of allocation parameters in SRC-trial1 for T1 was applied. We have considered the fertility rate (FR) as 1, since no nutrient limitation was observed restricting poplar growth and considered a value of 2 years for the Full Canopy Age parameter, following the procedure of Forrester et al. (2014, equation 11). For the third year in the validation data, the value of FR was set as 0.7 because the trees were growing in pots, which clearly reduced the volume explored by the roots in relation to the SRC-trial1. In addition, site-specific input data and climate data were needed. Air temperature minimum (T<sub>min</sub>, °C), maximum (T<sub>max</sub>, °C) and mean temperature (T<sub>m</sub>, °C), as well as air humidity (H<sub>r</sub>, %), were taken from an

experimental weather station 500 m from the study site. Data on solar radiation, precipitation and frost days were obtained from the Spanish Meteorological Service (AEMET) database for a station located 2.1 km away.

### Adapting age-dependent variables. Foliar parameters

Some variables in 3-PG are age dependent and are given by empirical relationships whose parameters are species specific (Sands, 2004). As regards the foliar fraction, variables such as the SLA ( $\sigma_{(t)}$ ) and the litterfall rate ( $\gamma_f$ ) must be adapted to the fact that poplars are deciduous species in order to estimate the species-specific parameters associated with these variables on a monthly basis. The age predictor was replaced by a monthly predictor, the growth season month (equations 2 and 3).

On the left side of the flow diagram (Figure 2), we highlight the adaptations made in this study and the species-specific parameters studied.

Users can enter species-specific values for up to 60 parameters describing tree physiology and allometric growth relationships. Our study focused on the foliar part of the 3-PG model, proposing most of the leaf parameters from observed data. The remaining parameters were estimated values from previously published research on hybrid poplars, assumed values based on expert knowledge or best-fit of the model and default 3-PG values were used for the remaining parameters (Figure 2).

### Temporal change in specific leaf area ( $\sigma_{(t)}$ )

In order to obtain real values for SLA throughout the rotation, 138 subsamples of 50 mature, randomly selected leaves ( $ss_{50}$ ) from different parts of the crown of 3 representative trees per month and water scenario (T1 and T2) were fresh scanned during the first rotation to calculate the green leaf area of  $ss_{50}$ , in  $cm^2$ , using the ImageJ software (Abràmoff et al., 2004). The leaves were then dried at  $60^\circ C$  in a forced air oven to constant dry mass to obtain their individual dry weight using a balance (EU-C 7500PQ) with an accuracy of 0.1 g to calculate the dry leaf biomass of the subsample  $W_{fss50}$  ( $kg\ tree^{-1}$ ).

The total leaf area measured for 50 random leaves per tree, associated with its dry mass, is the specific leaf area, SLA ( $m^2\ kg^{-1}$ ), according to equation (1):

$$SLA = \frac{\text{Leaf area}_{ss50}}{W_{fss50}} \quad (1)$$

where SLA is the specific leaf area ( $m^2\ kg^{-1}$ ), leaf area $_{ss50}$  is the leaf area of the subsample of 50 leaves per tree ( $m^2\ tree^{-1}$ ) and  $W_{fss50}$  is the dry-leaf biomass of the subsample per tree ( $kg\ tree^{-1}$ ).

SLA is a function of the growing season month ( $t$ , months), which describes the monthly change in SLA, and is given by the empirical relationship (Sands and Landsberg, 2002):

$$\sigma_{(t)} = \sigma_0 + (\sigma_1 - \sigma_0) e^{-(\ln 2) * \left(\frac{t}{t_r}\right)^2} \quad (2)$$

where  $\sigma_0$  is the SLA at the beginning of the growing season ( $m^2\ kg^{-2}$ ),  $\sigma_1$  is the SLA of mature leaves before complete abscission ( $m^2\ kg^{-2}$ ),  $t$  is the growing season month (with  $t=1$  for the first month showing leaves) and  $t_r$  is the month of the growing season at which SLA reaches its median value.

### Temporal change in the litterfall rate ( $\gamma_F$ )

The temporal change in litterfall rate ( $\gamma_F$ ) was calculated based on monthly changes in the total number of leaves ( $n_l$ ) present on the tree. During the three years of the rotation, all leaves were counted from the bottom to the top of all stools, obtaining the total amount of leaves per month and sampled tree (three trees per month and water scenarios T1 and T2).

We predicted the monthly theoretical  $n_l$  trend along the growing season (month) for both water scenarios (T1 and T2) using the best equation to fit our experimental data based on 170 observations. Quadratic models (equation 3) were fitted using the statistical programme R (R Core Team, 2019):

$$n_l = a * t^2 + b * t \quad (3)$$

where  $n_l$  is the number of leaves and  $t$  is the growing season month.

Litterfall rates were then derived from the variation in leaf number by calculating on a monthly time step the percentage of leaves that were abscised in that month with respect to the previous number of leaves present on the trees, as is the usual procedure in the 3-PG model (Landsberg and Waring, 1997). This means that the litterfall rate of the last month in which leaves are observed on the trees is necessarily equal to 100 per cent.

### Canopy conductance

In the field, stomatal conductance rarely operates at absolute maximum (Körner, 1995; Schulze et al., 1994). The absolute maximum stomatal conductance ( $g_s$ ) achievable in the field occurs when species-specific plant growth conditions are

optimum (Murray et al., 2019). To estimate the maximum canopy quantum efficiency ( $\alpha_{cx}$ ), two additional data sets were used:

- i) D1: data from the PPN under SRC management with irrigation, and
- ii) D2: data from experimental trials in a greenhouse under controlled temperature ( $25 \pm 3^\circ C$  max. and  $10 \pm 3^\circ C$  min.) and relative air humidity ( $\approx 70\%$ ). Plants were regularly well watered.

Both data sets include different genotypes belonging to different hybrid groups of the *Populus* genus and autochthonous clones *P. alba* L. originally from Spain. The data sets (D1 ( $n=138$ ) and D2 ( $n=509$ )) were selected to capture as much variability as possible within the constraints of the study. However, we are aware that it may still not have fully captured the maximum canopy quantum efficiency  $\alpha_{cx}$ .

### Gas exchange measurements

The stomatal conductance ( $g_s$ ,  $mol\ m^{-2}\ s^{-1}$ ), photosynthetic assimilation rate ( $A$ ,  $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ ), leaf temperature ( $T_l$ ,  $^\circ C$ ) and photosynthetically active radiation (PAR,  $\mu mol\ s^{-1}\ m^{-2}$ ) were sampled throughout the growing seasons during the months from April to September in the field (D1) and in the greenhouse from May to July. Gas exchange measurements were taken between 9 and 11 a.m. in both data sets (D1 and D2) on two fully expanded mature leaves per tree from the top of the canopy. A portable photosynthesis system (LCPro+ with Broad Head, ADC BioScientific Ltd., Hoddesdon, UK) was used. The data were used in the parameterization procedure.

### Statistical analyses

#### Model evaluation

To evaluate the goodness of fit of the models, we used the proportion of variance explained by the models (pseudo coefficient of determination,  $pse-R^2$ ) and the root of mean square error (RMSE):

$$pse-R^2 = R^2_{y\hat{y}i} \quad (4)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n}} \quad (5)$$

where  $R^2_{y\hat{y}i}$  is the correlation coefficient for a linear regression between the observed and the predicted values of the dependent variable (Ryan, 2008),  $y_i$  is the observed value,  $\hat{y}_i$  is the estimated value and  $n$  is the number of data used in the fitting.

The effect of scenarios T1 and T2 on the different variables over the three growing seasons was analyzed using analysis of variance ANOVA (generalized linear model procedure, GLM). Prior to the ANOVA, when normality was not fulfilled, data were transformed using the Box-Cox procedure.

All the analyses and graphing were performed using the R program (R Core Team, 2019), and the level of significance was set to a  $P$ -value  $< 0.05$  for all the analyses.

#### Model evaluation between irrigation scenarios

To compare the differences in the SLA models between scenarios (T1 and T2), the nonlinear extra sum of square method was used (Bates and Watts, 1988, pp. 103–104). This method was used to determine the simplest model to fit a data set adequately (Corral-Rivas et al., 2007; Huang et al., 2000). The method requires the fitting of full and reduced models. For the variables as a function of the length of the growing season, the full model corresponds to

**Table 1.** F-test of the water scenario differences for the SLA as a function of the length of the growing season models

	SSE	DF	n	F-value
Full model	879.93	122	128	1.756
Reduced model	843.50	125	128	

SSE: error sum of squares; DF: degrees of freedom; n: number of observations. The F-value is calculated according to equation (10). Significant F-values if  $F > F_{\text{critical}}$  at  $\alpha = 0.05$ .

different sets of parameters for the two water scenarios (T1 and T2) and is obtained by expanding each parameter by including an associated parameter and a dummy variable to differentiate the water scenarios. The reduced model corresponds to the same set of parameters for both scenarios.

The appropriate test statistic uses the following expression (Bates and Watts, 1988):

$$F = \frac{(SSE_R - SSE_F) / (df_R - df_F)}{SSE_F / df_F} \quad (6)$$

where  $SSE_R$  is the error sum of squares of the reduced model,  $SSE_F$  is the error sum of squares of the full model, and  $df_R$  and  $df_F$  are the degrees of freedom of the full and reduced models, respectively. The nonlinear extra sum of squares follows an F-distribution.

The reduced model is accepted at the specified  $\alpha = 0.05$ , if

$F > F_{\text{critical}}(1-\alpha; df_R - df_F, df_F)$ , reject  $H_0$ , separate models are required for separate scenarios; and if

$F \leq F_{\text{critical}}(1-\alpha; df_R - df_F, df_F)$ , accept  $H_0$ , the reduced model is appropriate for combined scenarios.

## Results and discussion

### Specific leaf area

No significant differences in SLA were observed between the water scenarios T1 and T2 over the 3 years of the rotation ( $P$ -value = 0.607, 0.249 and 0.647, respectively). Based on our observations, SLA follows a similar trend in each year of the rotation. Our results are in agreement with those of other authors who found no effect of water availability on SLA in hybrid clones *Populus × euramericana* (Marron et al., 2002; Monclus et al., 2009).

Temporal changes in SLA are described in Figure 3. The model (equation 2) was fitted based on observed SLA values ( $n = 128$  trees) per month and water scenario T1 and T2 (Sands and Landsberg, 2002).

Results of the nonlinear extra sum of squares method are shown in Table 1. The calculated F-value for full and reduced SLA models is 1.756, which is lower than the  $F_{\text{critical}}$  value at  $\alpha = 0.05$  (2.677). Therefore,  $H_0$  is accepted, suggesting that the reduced model is appropriate for combined scenarios. Estimated coefficients and fit statistics of the model that describe the temporal change in SLA are given in Table 2.

The results revealed that the SLA for mature leaves ( $\sigma_1$ ) was  $10.4 \text{ m}^2 \text{ kg}^{-2}$ , and the SLA at the beginning of the growing season ( $\sigma_0$ ) was  $19.9 \text{ m}^2 \text{ kg}^{-2}$ . The month of the growing season at which SLA has a median value ( $t_\sigma$ ) was 1.4, with all estimated parameters being significant ( $P$ -value  $< 0.001$ ), Table 2.

Our results show that  $\sigma_0$  and  $\sigma_1$  were in the same range as those values given in the literature by Headlee et al. (2012) in their study of hybrid poplar as a short rotation woody crop in the North Central USA,  $\sigma_0 = 19$  and  $\sigma_1 = 10 \text{ m}^2 \text{ kg}^{-2}$ . Other authors considered both parameters with the same values  $\sigma_1 = \sigma_0 =$

$10.8 \text{ m}^2 \text{ kg}^{-2}$  (Amichev et al., 2010), which in the case of poplar in SRC,  $\sigma_0$  and  $\sigma_1$  vary markedly from young to mature leaves. Here, we observed a declining trend over the life span of the leaf, starting with high SLA values of  $20.31 \pm 1.92 \text{ m}^2 \text{ kg}^{-2}$  for the first leaves to  $11.24 \pm 3.16 \text{ m}^2 \text{ kg}^{-2}$  at the end of the growing season, coinciding with the leaf fall (Table 3). Our results showed high variability in the first months of the growing season, probably because of the strong morphological changes that occur at that stage.

For a model such as 3-PG, which calculates growth on the basis of intercepted radiation, the relationship between leaf area and foliage mass is of central importance (Feikema et al., 2010). The 3-PG output prediction is highly sensitive to SLA-related parameters (Esprey et al., 2004; Nouvellon et al., 2010; Pérez-Cruzado et al., 2011), and detailed information on SLA, designed specifically to obtain  $\sigma_1$ ,  $\sigma_0$  and  $t_\sigma$  values, is still scarce for poplar plantations. To date, other authors have used SLA values from the literature to predict growth and yield of poplar plantations using the 3-PG model (Amichev et al., 2010; Hart et al., 2015; Headlee et al., 2012) as well as for deciduous trees in general (Jégo et al., 2017; Nölte et al., 2020; Potitthep and Yasuoka, 2011). This study presents specific parameters for poplar SRC that were not previously available.

The latest approaches for adapting 3-PG to deciduous species have also addressed the optimization of the values of  $\sigma_1$ ,  $\sigma_0$  and  $t_\sigma$ , seeking to minimize the differences between the predicted and measured leaf area index (Jégo et al., 2017). The values obtained by these authors in the case of willows in short rotation in Canada are in the same range as the values observed in this study.

### Litterfall rate ( $\gamma_F$ )

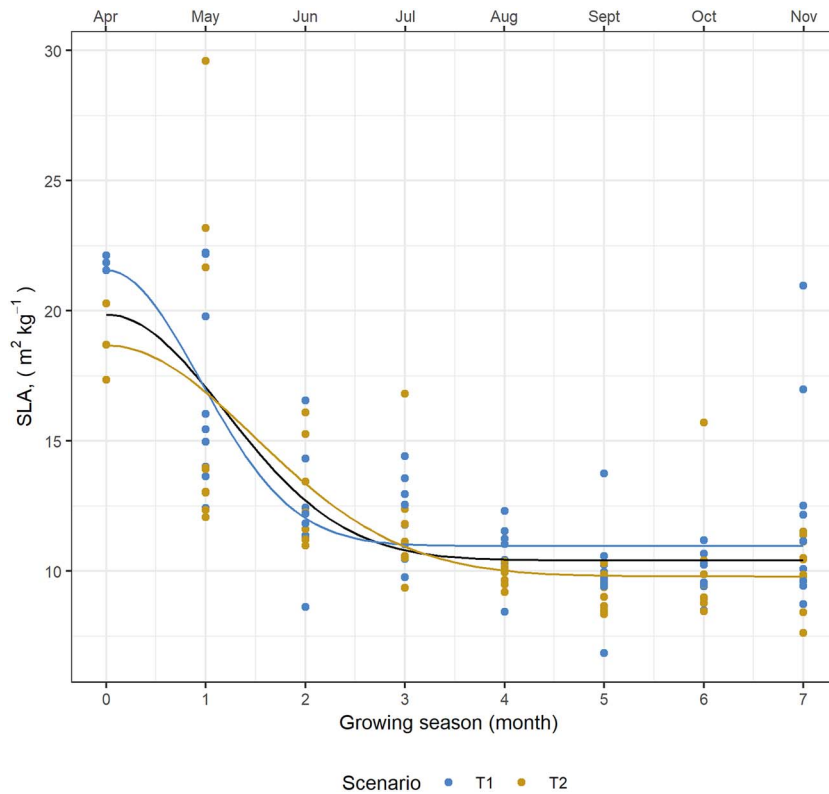
The relationships between the number of leaves and time course over the growing season for both water scenarios (T1 and T2) are shown in Figure 4 as obtained for quadratic models (equation 3). The equations considered achieved convergence, and all estimated parameters  $a$  and  $b$  were significant ( $P$ -value  $< 0.001$ ) (Table 4).

Although both scenarios had roughly the same number of leaves during this first year, the water restriction applied in this study, led to a clear reduction in the number of leaves in year 2 and 3 (Figure 4). Many agronomic practices, including irrigation, affect the number, size and display of leaves (Nelson et al., 1981), water availability being one of the core factor affecting poplar foliage production and distribution (Cocozza et al., 2010; Fuertes et al., 2022; Gaudillere, 1989).

Sands and Landsberg (2002) recommended that further development (of 3-PG) should consider environmental effects on litterfall, such as water stress. Our results showed that litterfall varies seasonally, with no significant response to the irrigation regimes applied in this study (T2),  $P$ -value = 0.94, 0.98 and 0.94, respectively. However,  $\gamma_F$  varies markedly during leaf fall, starting in August with very small percentages of  $0.704 \pm 0.97$  per cent to reach the maximum litterfall rate of 100 per cent in early December under the scenario without water restriction (T1), although it should be noted that leaf fall started a month later under the restricted water scenario (T2), as shown in Table 5.

Based on these observations, litterfall rate for very young stands at the beginning of the growing season ( $\gamma_{F0}$ ) was zero, and the calendar month in which the litterfall rate presented a median value ( $t_{\gamma_F}$ ) was mid-October, which, in terms of the growing season month, is  $t_{\gamma_F} = 6.5$  (Figure 5).

According to other authors, leaf litter production for dense stands of hybrid poplars in Wisconsin started in mid-June and



**Figure 3.** SLA ( $\text{m}^2 \text{kg}^{-2}$ ) development over the growing season (month) for the three years of the first rotation and two water scenarios (T1: optimal scenario, irrigated to field capacity (FC); T2: restricted scenario, irrigated to 50 per cent FC). The black solid line corresponds to all data including both scenarios of the first rotation (3 years).

**Table 2.** Parameter estimates and goodness-of-fit statistics for SLA as a function of the length of the growing season model with the equation

Equation (2)	$\sigma(t) = \sigma_0 + (\sigma_1 - \sigma_0) e^{-(\ln 2) * (\frac{t}{t_\sigma})^2}$								
Year	Scenario	Estimate	Std. Error	t-value	Pr(> t )	RMSE	pse-R <sup>2</sup>	DF	
1, 2, 3	T1 and T2	$\sigma_0$	19.863	0.865	22.972	<0.001	2.622	0.541	125
		$\sigma_1$	10.413	0.304	34.238	<0.001			
		$t_\sigma$	1.402	0.152	9.212	<0.001			

T1: Optimal scenario, irrigated to field capacity (FC); T2: restricted scenario, irrigated to 50 per cent FC;  $\sigma_0$  is SLA at the beginning of the growing season ( $\text{m}^2 \text{kg}^{-2}$ );  $\sigma_1$  is SLA of mature leaves ( $\text{m}^2 \text{kg}^{-2}$ );  $t_\sigma$  is the month of the growing season in which SLA has median value; Std.Error: standard error; RMSE: root of mean square error; pse-R<sup>2</sup>: pseudo coefficient of determination; DF: degrees of freedom.

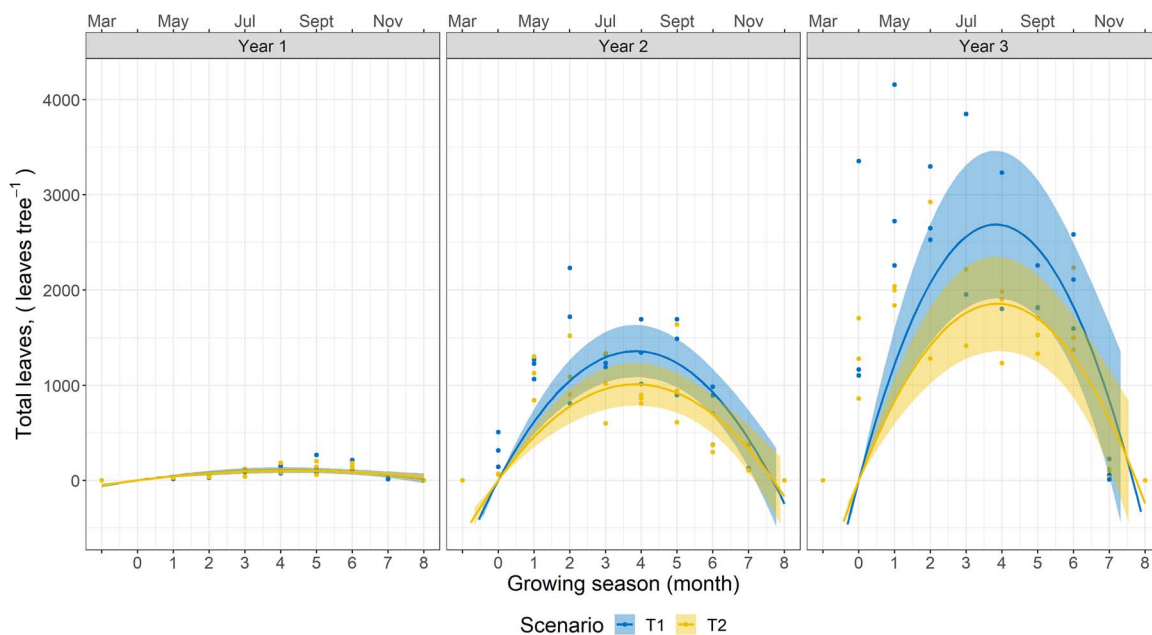
**Table 3.** Monthly SLA ( $\text{m}^2 \text{kg}^{-2}$ ) values, mean  $\pm$  SD values per growing season (month) of both water scenarios (T1 and T2)

Growing season (month)	SLA ( $\text{m}^2 \text{kg}^{-2}$ )
April	20.31 $\pm$ 1.92
May	16.86 $\pm$ 5.00
June	12.46 $\pm$ 2.05
July	11.93 $\pm$ 1.88
August	10.28 $\pm$ 0.90
September	9.54 $\pm$ 1.37
October	9.88 $\pm$ 1.64
November	11.24 $\pm$ 3.16

peaked in October, while in northern Wisconsin maximum leaf fall occurred in late October or early November (Zavitkovski, 1981). Another study of an SRC stand of hybrid poplars located in north-west France revealed litterfall began in July and continued

until the end of November (Berthelot et al., 2000). In Spain, other authors have reported that leaf fall in short rotation plantations usually begins in mid-July and usually continues until the end of November (Pérez et al., 2021). The results obtained under Mediterranean conditions agree with those of this study, indicating that genotype and climate could affect litterfall patterns.

Previous studies applying 3-PG to deciduous trees have used values from the literature for  $\gamma_{F0}$  and  $t_{\gamma F}$  in order to predict yield (Amichev et al., 2011; Forrester and Tang, 2016; Nölte et al., 2020; Potitph and Yasuoka, 2011), and the same approach was used in studies specifically focusing on poplar plantations (Amichev et al., 2010; Hart, 2014; Hart et al., 2015; Headlee et al., 2012; Zalesny et al., 2012). In these studies, the common fitted value for the  $\gamma_{F0}$  parameter was close to zero, which is in line with our observations. In the case of the  $t_{\gamma F}$  parameters, it was difficult to compare values with those of other studies due to differences in rotation lengths, plantation densities, genotype or climate conditions.



**Figure 4.** Development of the total number of leaves (leaves tree<sup>-1</sup>) over the growing season (month) for both water scenarios (T1: optimal scenario, irrigated to field capacity (FC); T2: restricted scenario, irrigated to 50 per cent FC). Shaded areas correspond to the 95 per cent confidence interval.

**Table 4.** Estimated parameters and goodness-of-fit statistics for the total number of leaves ( $N_l$ ) model as a function of the length of the growing season using equation (3)

Equation (3)	$N_l = a * t^2 + b * t$		Estimate	Std. Error	t-value	Pr(> t )	RMSE	pse-R <sup>2</sup>	DF
Year 1	T1	a	-5.99	1.298	-4.615	<0.001	52.666	0.42	25
		b	50.567	8.493	5.954	<0.001			
	T2	a	-5.66	1.156	-4.893	<0.001	46.910	0.44	25
		b	48.5	7.565	6.411	<0.001			
Year 2	T1	a	-92.43	11.54	-8.007	<0.001	470.127	0.66	28
		b	708.72	75.51	9.385	<0.001			
	T2	a	-68.39	9.446	-7.240	<0.001	384.696	0.59	28
		b	525.76	61.792	8.509	<0.001			
Year 3	T1	a	-183.29	32.11	-5.709	<0.001	1231.638	0.46	26
		b	1403.63	213.07	6.588	<0.001			
	T2	a	-123.44	20.69	-5.965	<0.001	797.64	0.51	26
		b	956.85	136.58	7.006	<0.001			

T1: optimal scenario, irrigated to field capacity (FC); T2: restricted scenario, irrigated to 50 per cent FC; Std.Error: standard error; RMSE: root of mean square error; pse-R<sup>2</sup>: pseudo coefficient of determination; DF: degrees of freedom; t: growing season month.

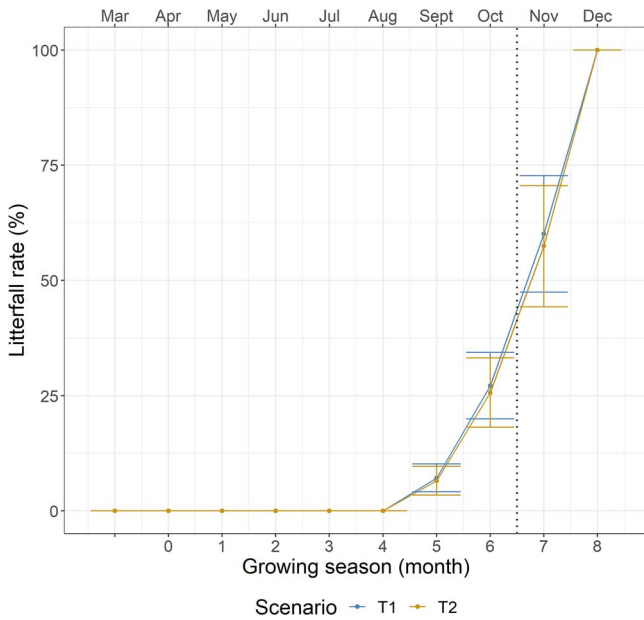
**Table 5.** Monthly mean  $\pm$  SD litterfall rate (%) during the first rotation: optimal (T1) and restrictive (T2) water scenarios

	Scenario	Growing season (month)					
		Jan-Jul	Aug	Sep	Oct	Nov	Dec
Litterfall rate (%)	T1	0	0.704 $\pm$ 0.97	7.15 $\pm$ 3.01	27.17 $\pm$ 7.22	60.05 $\pm$ 12.64	100
	T2	0	0	6.52 $\pm$ 3.13	25.66 $\pm$ 7.52	57.40 $\pm$ 13.16	100
	T1 and T2	0	0.32 $\pm$ 0.74	6.84 $\pm$ 2.99	26.42 $\pm$ 7.19	58.73 $\pm$ 12.59	100

T1: optimal scenario, irrigated to field capacity (FC); T2: restricted scenario, irrigated to 50 per cent FC. T1 and T2 correspond to all data including both scenarios.

In relation to leaf fall, some authors applying the 3-PG model for deciduous trees considered null litterfall during the growing season, arguing that litterfall of deciduous tree species is negligible during that period (Nölte et al., 2020). This may be the case under other climatic conditions where growing seasons are shorter. However, under Mediterranean conditions the growing season generally lasts from late March to late November, with the

months of active tree growth being from June to September. Small rates of litterfall (although not negligible) were even observed in the mid growing season (June to September). Sands and Landsberg (2002) recommended that monthly litterfall rates should ideally be site-dependent, other authors also highlighting variations in litterfall depending on local conditions (Pérez-Cruzado et al., 2011). However, in studies where litterfall data were not available,



**Figure 5.** Monthly litterfall rate ( $\gamma_f$ ) per growing season for both water scenarios (T1: optimal scenario, irrigated to field capacity (FC); T2: restricted scenario, irrigated to 50 per cent FC). Vertical dotted line shows when litterfall rate reaches a median value.

default values were applied (Hart *et al.*, 2015; Headlee *et al.*, 2012).

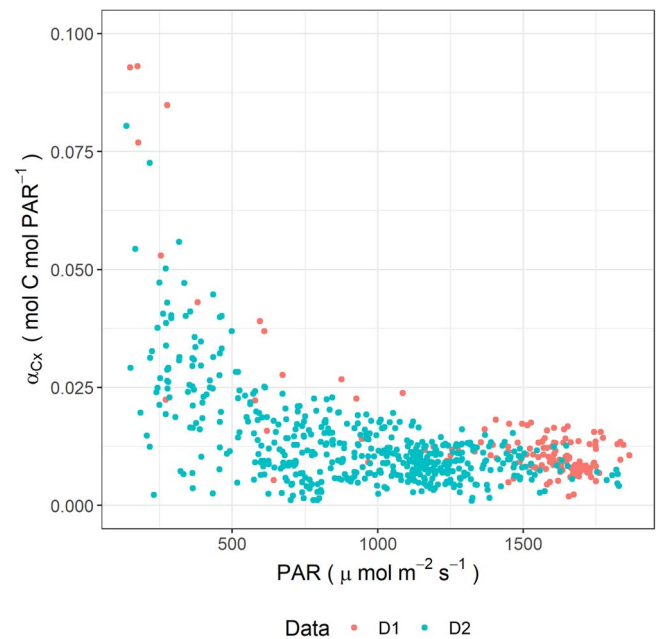
### Maximum canopy quantum efficiency ( $\alpha_{C_x}$ )

Experimental poplar-specific values ( $n=647$ ) for  $\alpha_{C_x}$  are shown in Figure 6 for two different data sets (D1: field conditions in the Mediterranean, and D2: controlled conditions). Both experiments show maximum photosynthetic rates ranging from 0.05 to 0.093 mol C mol PAR<sup>-1</sup> in the case of D1 and from 0.05 to 0.08 mol C mol PAR<sup>-1</sup> in D2, as shown in Figure 6.

While the number of observations in D2 is such that it allows for a more comprehensive representation of the data, D1 is limited due to the fact that it is a field experiment, so the range of PAR measurements is more restricted. Despite this limitation, both data sets still obtain very high  $\alpha_{C_x}$  values at low PAR (around 250  $\mu\text{mol s}^{-1} \text{m}^{-2}$ ). The value of  $\alpha_{C_x}$  that best fits our observed and modelled data was 0.09 mol C mol PAR<sup>-1</sup>.

The maximum canopy quantum efficiency ( $\alpha_{C_x}$ ) is considered to be among the six most important 3-PG parameters explaining growth differences. A sensitivity analysis performed on these parameters pointed to important changes in the predictions (Esprey *et al.*, 2004; Forrester and Tang, 2016; Pérez-Cruzado *et al.*, 2011). Almeida *et al.* (2004) observed that all biomass pools were highly sensitive to maximum canopy quantum efficiency. Furthermore, the 3-PG outputs also showed sensitivity to maximum canopy conductance, and the above-mentioned studies highlighting the importance of these two parameters in the accuracy of the 3-PG predictions.

Waring *et al.* (1995), recommended the use of cuvette gas-exchange measurements in the upper, most active canopy strata in order to accurately estimate the maximum quantum efficiency. Our data show a considerable range of solar radiation from 130 up to 1800  $\mu\text{mol s}^{-1} \text{m}^{-2}$ . Nevertheless, we acknowledge that the study may not have captured the maximum parameter value due to certain experimental limitations such as measuring at specific times of day to ensure adequate temperature, solar radiation,



**Figure 6.** The maximum canopy quantum efficiency ( $\alpha_{C_x}$ ) for both data sets (D1: field conditions; D2: controlled conditions).

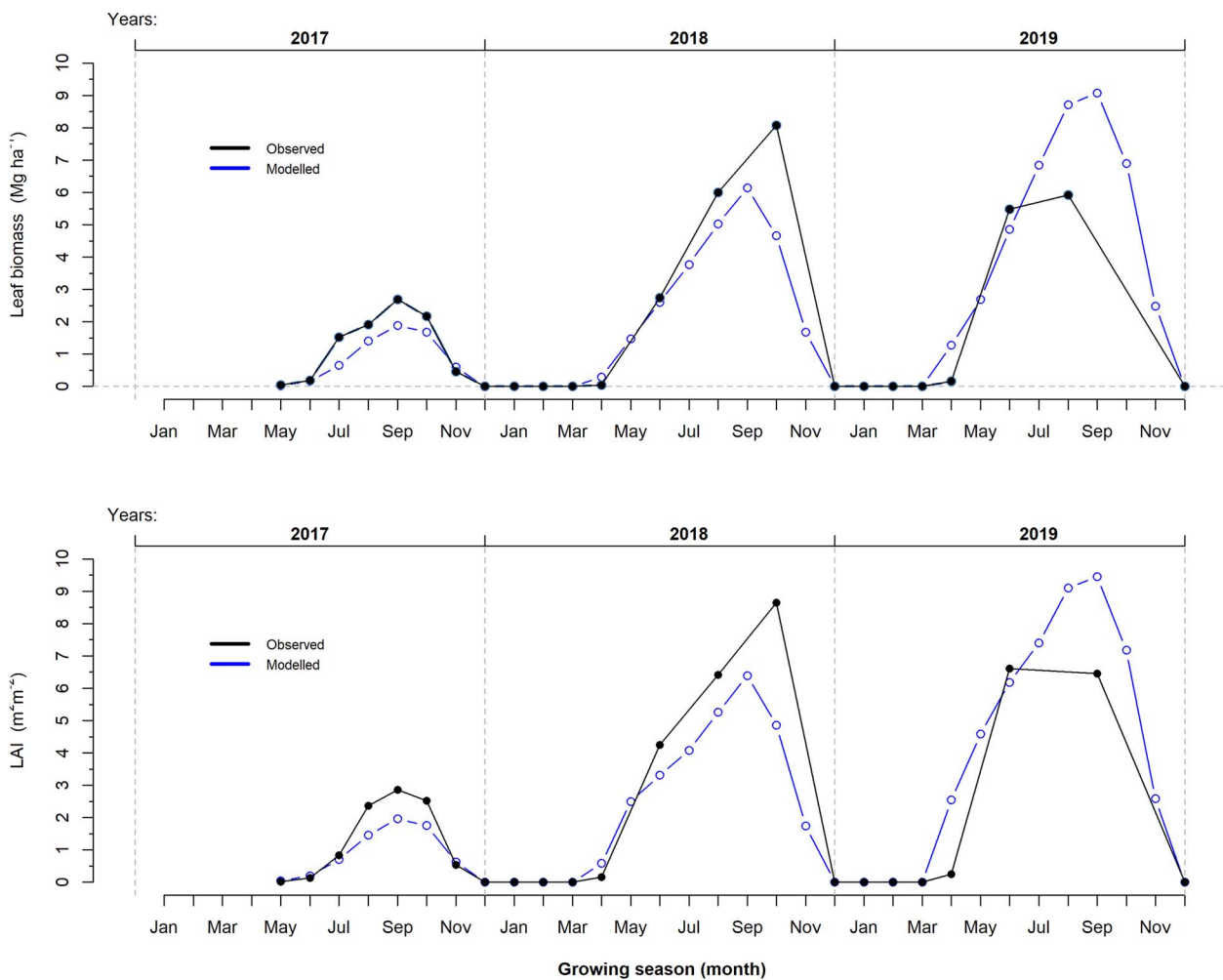
irrigation and humidity levels to simulate optimal plant growth conditions.

Previous studies concerning poplar biomass predictions using the 3-PG model used values taken from the literature of 0.08 mol C mol PAR<sup>-1</sup> for  $\alpha_{C_x}$  (Hart, 2014; Headlee *et al.*, 2012; Zalesny *et al.*, 2012). However, Hart *et al.* 2015 varied the  $\alpha_{C_x}$  parameter used among the different poplar clones studied, proposing 0.11 mol C mol PAR<sup>-1</sup> (Raspalje), 0.09 mol C mol PAR<sup>-1</sup> (Beaupre), 0.08 mol C mol PAR<sup>-1</sup> (Fritzi) and 0.06 mol C mol PAR<sup>-1</sup> (Robusta), (2015). Our results show that the maximum  $\alpha_{C_x}$  observed for the D1 dataset was 0.093 mol C mol PAR<sup>-1</sup> and for the D2 dataset it was 0.08 mol C mol PAR<sup>-1</sup>, which is in line with the values used in other studies for poplar plantations.

### 3-PG model performance

Based on the parameterization changes proposed for the 3-PG, we compared the predicted leaf biomass  $W_f$  and LAI with those observed in the SRC-trial2 (Figure 7). Results of the bias and RMSE for both variables on a yearly basis and for the whole period of three years are presented in Table 6. The predicted values are realistic and fit well with the observed values. In the third year, however, the pot effect resulted in a decrease in foliar biomass compared to the second year, which was difficult to simulate. It was in fact observed that the volume of soil explored by the roots in the SRC-trial1 in the field was 35% larger than the volume of pots in the SRC-trial2.

The proposed parameterization related to SLA and litterfall rate variables allows realistic estimates of the changes during the growing season of leaf biomass and LAI. This allows null values for both variables during the dormancy months. Moreover, as LAI varies on a monthly basis, the predictions of GPP (gross primary productivity) and, eventually, NPP would be much more realistic on a monthly basis, since the 3-PG model is based on the leaf surface interception of photosynthetically active radiation. The pattern of peaking and decreasing foliar biomass and LAI, which is an effect of the decrease in foliar biomass allocation and increase in litterfall along the growing season, is also well resolved with



**Figure 7.** Observed vs. modeled data points of leaf biomass ( $\text{Mg ha}^{-1}$ ) and LAI ( $\text{m}^2 \text{m}^{-2}$ ) for the validation data with 3-PG model using the proposed parametrization.

**Table 6.** Model performance indicators for evaluating the model's ability to predict leaf biomass and LAI with the validation data

		Rotation (years)			Total
		2017	2018	2019	
Leaf biomass ( $\text{Mg ha}^{-1}$ )	RMSE	0.525	1.781	1.772	1.31
	Bias	0.370	1.069	-1.096	0.256
LAI ( $\text{m}^2 \text{m}^{-2}$ )	RMSE	0.531	1.447	1.437	1.206
	Bias	0.316	0.946	-0.696	0.136

RSME = root of mean square error. Bias = average of observed - predicted.

the parameterization proposed. This allows realistic predictions of foliar litterfall and thus of patterns of nutrient contributions to soil via senescent leaves.

## Conclusions

Adapting the 3-PG model architecture to SRC deciduous poplar plantations, as well as employing species-specific parameters based on observed data, is key to provide the most accurate estimates and realizing the full potential of the 3-PG model. Furthermore, it is of particular interest to take into account the poplar plantation response to irrigation restriction in the context

of climate change. No significant differences in SLA and litterfall rates were found between water scenarios T1 and T2, the trend being similar over the 3 years of the first rotation and the resulting parameters could be applied to both irrigation scenarios T1 and T2. The SLA variation for deciduous species can be modelled on a monthly scale over the course of the growing season. Values for fully developed leaves from  $19.9 \text{ m}^2 \text{kg}^{-2}$  at the beginning of the growing season to  $10.4 \text{ m}^2 \text{kg}^{-2}$  after only 3 months of growth were found for both irrigation scenarios T1 and T2.

Monthly litterfall rates for poplar leaves should be taken into account, as non-zero litterfall rates were found as soon as late August and lasted until early December. Additionally, the highly sensitive parameter  $\alpha_{Cx}$  reaches an observed maximum  $\alpha_{Cx}$  of  $0.093 \text{ molC mol PAR}^{-1}$ , which allows us to gain an insight into this highly sensitive parameter, bearing in mind the lack of observed values for these plantation systems.

The proposed parameterization matched well with leaf biomass and LAI prediction in the validation data set. The patterns of monthly change of both variables along the growing season show a late maximum for both variables in September–October and a sustained reduction till December. Null values are predicted by 3-PG with the parameterization proposed for 4 months. The results are useful to provide realistic predictions of leaf litterfall and nutrient contributions to soil via senescent leaves.

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## Conflict of interest statement

None declared.

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## Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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