

**RESEARCH ARTICLE** 

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## Growth decline assessment in *Pinus sylvestris* L. and *Pinus nigra* Arnold. forests by using 3-PG model

Rafael M. Navarro-Cerrillo<sup>1</sup>, Jesús Beira<sup>1</sup>, Juan Suarez<sup>2</sup>, Georgios Xenakis<sup>2</sup>, Raúl Sánchez-Salguero<sup>1</sup> and Rocío Hernández-Clemente<sup>1</sup>

<sup>1</sup>Depto. Ingeniería Forestal, Grupo de Evaluación y Restauración de Sistemas Agrícolas y Forestales - DendrodatLab-TreeSatLab. Universidad de Córdoba. Campus de Rabanales, Crta. IV, km. 396, 14071 Córdoba. Spain. <sup>2</sup>Forest Research Agency of the Forestry Commission, Northern Research Station, Roslin, Midlothian, EH25 9SY, UK

#### Abstract

Aim of the study: We assessed the ability of the 3-PG process-based model to accurately predict growth of *Pinus sylvestris* and *P. nigra* plantations across a range of sites, showing declining growth trends, in southern Spain.

Area of study: The study area is located in "Sierra de Los Filabres" (Almería).

*Material and methods:* The model was modified in fifteen parameters to predict diameter (DBH, cm), basal area increment (BAI, cm<sup>2</sup> yr<sup>-1</sup>) and leaf area index (LAI, m<sup>2</sup> m<sup>-2</sup>) in healthy trees and trees showing declining growth. We assumed that a set of specific physiological parameters (stem partitioning ratio-*pFS*<sub>20</sub>, maximum litterfall rate- $\gamma_{Fx}$ , maximum canopy conductance- $g_{Cx}$ , specific leaf area for mature aged stands- $\sigma_I$ , age at which specific leaf area =  $\frac{1}{2}(\sigma_0 + \sigma_1)$ , age at full canopy cover- $t_c$ , and canopy boundary layer conductance- $g_B$ ) included in 3-PG would be suitable for predicting growth decline related to climate conditions. The calibrated model was evaluated using dendrochronological and LAI data obtained from plots.

*Main results:* Observed and simulated DBH showed a high correlation ( $R^2 > 0.99$ ) between modelled and measured values for both species. In contrast, modelled and observed BAI showed lower correlation ( $R^2 < 0.68$ ). Sensitivity analysis on 3-PG outputs showed that the foliage parameters - maximum litterfall rate, maximum canopy conductance, specific leaf area for mature aged stands, age at which specific leaf area, and age at full canopy cover - were important for DBH and BAI predictions under drought stress.

*Research highlights:* Our overall results indicated that the 3-PG model could predict growth response of pine plantations to climatic stress with desirable accuracy in southern Spain by using readily available soil and climatic data with physiological parameters derived from experiments.

Keywords: Hybrid process model; forest management models; growth prediction; *Pinus* spp.; Parameterization; forest decline. Citation: Navarro-Cerrillo, R.M., Beira, J., Suarez, J., Xenakis, G., Sánchez-Salguero, R., Hernández-Clemente, R. (2016). Growth decline assessment in *Pinus sylvestris* L. and *Pinus nigra* Arnold. forests by using 3-PG model. Forest Systems, Volume

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Correspondence should be addressed to Rafael M Navarro Cerrillo: rmnavarro@uco.es

Supplementary material: Table S1 and Figures S1, S2 and S3 accompany the paper on FS's website.

## Introduction

Climate warming may increase the frequency and magnitude of extreme climatic events such as droughts (Allen *et al.*, 2010). Extreme drought events strongly affect the physiological functioning of forests, and an increase of their intensity and severity will negatively affect tree growth and vigour in sites where these are strongly limited by water availability (Breshears *et al.*) 2009; Allen *et al.*, 2010). Warming-induced forest decline (*sensu* Mueller-Dombois, 1993) in droughtstressed sites is usually linked to defoliation and selective mortality of trees of some species (McDowell *et al.*, 2008) with significant impacts in climatic-droughtinduced mortality of pine forests (Sánchez-Salguero *et al.*, 2012a). It is expected that southern populations of species sensitive to water stress like Scots pine (*Pinus sylvestris* L.) and Black pine (*Pinus nigra* Arnold), will be especially susceptible to greater climate stress due to temperature rise. Scots pine has its western boundary limit in the Iberian Peninsula. Southern European populations of these species persist, forming relict populations, in areas that provide a cool, moist habitat, such as high-elevation Mediterranean mountains (Costa, 2005) Moreover, those plantations have shown a high mortality under severe drought periods as 1983, 1990–1995, 1999 and 2005 (Sánchez-Salguero *et al.*, 2013).

Forest mortality and decline processes have been related to stand density and lack of adequate silvicultural practices (Sánchez-Salguero *et al.*, 2012b). Such plantations have been shown to be a high risk of dying under severe drought periods as 1990–1995, 1999 and 2005 (Sánchez-Salguero *et al.*, 2013).

Forest decline in extensive pine areas of Spain has become one of the most serious ecological problems In the Iberian Peninsula, the first signs of forest decay in natural tree populations, associated with climate, were detected in its Mediterranean area (SE, NE) at the beginning of the 1990's (Peñuelas & Filella, 2001). Since 2001, extensive decline of whole stands over several hundred hectares has been reported in the Spanish southern mountains (Navarro-Cerrillo *et al.*, 2007; Sánchez-Salguero *et al.*, 2012a). The absence of any pathogens and the coincidence with extreme climatic drought events, especially in the 1990–1995, 1999 and 2005 periods, suggested that the decline was caused by climate change (Allen *et al.*, 2010).

A number of studies have suggested that declining growth in Mediterranean pines is associated with rapid defoliation (Breda et al., 2006), which is related to changes in leaf conductance, and water and nutrient availability (Dobbertin, 2005). Periods of low water availability and high temperatures that limit physiological processes are likely to be of major importance, limiting trees' photosynthetic activity and growth (Breshears et al., 2009; Galiano et al., 2011; Williams et al., 2013). Therefore, understanding the limits of stress tolerance associated with forest decline processes is critical for predicting physiological responses under the current changing global climatic conditions, and for ensuring that successful forest management strategies can be developed (Sánchez-Salguero et al., 2013; Guada et al. 2016).

Several empirical modelling studies in Mediterranean areas have previously related forest decline and tree mortality to site characteristics, physicochemical soil properties, climatic conditions, and species genotype (Fontes *et al.*, 2010), through the construction of site index curves in the classical form, nonlinear models including soil and site attributes (Sánchez-Salguero *et al.*, 2012b; 2013), and the use of biophysical site index models (Ung *et al.*, 2001). However, efforts at physiological modelling of forest decline in relation to the effects of silviculture on Mediterranean pine and the impact of global change on forest in general are scarce (Fontes *et al.*, 2010; Medlyn *et al.*, 2011). Process-based stand growth simulation models, based on available empirical data or known physiological processes, or both, have been developed to improve our understanding of forest behaviour on the basis of descriptions of plant-soil and carbon-nutrient-water interactions. Such models can be useful tools for long-term predictions of tree growth and yield, especially under adaptive management and climate (Landsberg *et al.*, 2001).

One of the most widely used process-based models is the 3-PG (Physiological Principles Predicting Growth) dynamic, process-based model developed by Landsberg & Waring (1997). This model predicts net primary productivity (NPP), the partitioning of biomass to leaves and aboveground woody biomass, roots, and transpiration of plantations or even aged relatively homogenous naturally regenerated stands on a monthly time step (Landsberg & Sands, 2010). 3-PG model can also perform basic silvicultural treatments such as thinning; defoliation and fertilization. It provides a suite of outputs more relevant to forest management (e.g., stand volume, diameter at breast height and mean stand height). Thus, its ability to accurately predict plantation productivity and assess the effects produced by changes in environmental condition or silvicultural treatments can be a useful tool for both scientists and managers (Almeida et al., 2004; Stape et al., 2004; Fontes et al., 2010; Gonzalez-Benecke et al., 2014).

The 3-PG model has been used for a wide variety of applications, including analysis of *Pinus sylvestris* (Landsberg *et al.*, 2005; Xenakis *et al.*, 2008) and *Pinus nigra* (Patenaude *et al.*, 2008). These studies showed that when calibrated the 3-PG model can produce realistic estimates of growth on sites with similar soil moisture and climatic conditions. Since the model includes physiological information related to the ecology and growth of species subject to forest decline it should be possible to use it as a tool to analyse the processes involved in that decline.

In this study we hypothesize that observed growth reduction of Scots pine and Black pine plantations in Southern Spain is a result of rapid defoliation after an extreme drought event and a concomitant reduction in leaf conductance, which reduces photosynthetic capacity and slows the recovery of growth after drought stress. We considered that we could use 3-PG to understand the physiological limitations (e.g., stomata conductance) associated with susceptibility to drought. To test our hypothesis we used the 3-PG model to predict growth of sample plots established in these pine plantations. Some of the plots were healthy and some showed declining growth associated with climatic drought stress. We i) parameterized 3-PG to predict growth in healthy trees and trees showing growth decline ii) identified the set of physiological parameters needed to describe decline processes and, iii) assessed whether that set of physiological parameters enabled us to predict the effects of adaptive silviculture to reduce forest decline impact.

## Materials and methods

#### Study area

The study area is located in "Sierra de Los Filabres" (37° 22' N, 2° 50' W, between 1300 and 2186 m.a.s.l) (hereafter abbreviated as Filabres) (Fig. S1 [supplementary]). Mean annual precipitation is 320 mm, temperatures are moderately mild (13.1°C, 1000 m a.s.l) for the 1940–2007 period with several drought events during this period (1990-1995, 1999, 2005; see more details in Sánchez-Salguero et al. 2012a). Soils are developed on schists and quartzites and they have a loam and silty loam texture (average composition 30-35% sand, 40-45% silt, 15-20% clay). Soil depth is 45-150 cm and available soil water content between 100 and 150 mm. Soil information was obtained from soil cartography at 1:100.000 scale (Aguilar et al., 1987). This information was used to estimate plot soil data as well as a test soil pit (Rosa et al., 1984) located in the study area. Dominant soils are xerorthents regosols and topography is characterized by steep slopes (>35%) (Aguilar et al., 1987). The forest area is dominated by Pinus sylvestris L. (hereafter as Scots pine; covering 7507 ha) and Pinus nigra Arn. subsp. salzmannii (Dunal) (hereafter as Black pine, covering 5900 ha) plantations. There are a reduced areas of native pine stands (Navarro-Cerrillo et al., 2007). Plantations were established using subsoiling as ground preparation between 1970 and 1976), but 1973 (Scots pine) and 1976 (Black pine) were selected as reference years. The planting density was 2000 trees ha<sup>-1</sup> and the current density ranges between 900 to 1000 trees ha<sup>-1</sup>. Basal area range from 20.73  $m^2 ha^{-1}$  to 26.37  $m^2 ha^{-1}$ (Sánchez-Salguero et al. 2012a; Table S1 [supplementary]).

### **Field data collection**

A stratified sampling was carried out on the basis of species and the degree of decline across the whole area

of the plantations (Dobbertin & Brang, 2001). Accordingly, 9 plots of Scots pine and 9 plots of Black pine were established in July 2009 (Fig. S1 [supplementary]). Crown defoliation status was estimated according to ICP forests' crown defoliation guide, aggregated at two different decline classes: class 1 (slightly declining trees and trees without evident defoliation <50%), and class 2 (declining trees 50-70%) (Dobbertin, 2005; Sánchez-Salguero et al., 2012 a, b). This assumption was supported by physiological data since stomatal conductance and water potential were significantly lower in defoliated than in non-defoliated trees in both species (Hernandez-Clemente et al., 2011). In each plot, all the trees with a diameter at breast height (1.3 m above ground level, dbh) greater than or equal to 10 cm were measured in circular plots with a radius of 15 m (706 m<sup>2</sup>). For every tree in each sample plot, two dbh measurements were taken at right angles with a tree calliper. Total tree height was measured with a Vertex III hypsometer (Table 1).

Dominant trees of each plot were selected based on diameter at breast height (DBH)  $\geq 20$  cm and age  $\geq 30$ years, and a total of 45 trees were harvested. One wood disk per tree ca 5 cm of thick was cut at 1.30 m of tree height. After an acclimation period of 4 weeks in a chamber at 25-30 °C, the wood discs were sanded with progressively finer grades of sandpaper until the wood anatomical elements were visible in transverse section and then scanned at 3200 dpi using an Epson Perfection V750 Pro scanner<sup>©</sup> (Seiko Epson Corp., Nagano, Japan). Tree-ring width was measured to the nearest 0.01 mm along the two radii of each section using WinDendro<sup>©</sup> (Regents Instruments, Quebec, Canada). Tree-ring series were dated following standard procedures (Stokes & Smiley, 1996). In order to detect dating and measurement errors, width series were checked with COFECHA software (Grissino-Mayer, 2001). We did not detrend chronologies to filter out eventual decrease of increment with age (age trend) since this operation could partly remove growth signal related to more short-term changes in trees' crown status (for further information see Sánchez-Salguero et al., 2012a). For the 3PG model of Basal Area Increment (hereafter abbreviated as BAI), we converted tree-ring width into basal-area increment, overcoming the problem of declining growth in bigger trees, using the formula (BAI  $=\pi (R_t^2 - R_{t-1}^2)$  where R is the radius of the tree and t is the year of tree-ring formation. To obtain values of overbark diameter and its evolution over time, a fixed ratio of bark thickness to diameter was considered.

The diurnal time course of stomatal conductance to water vapour (gL, CIRAS–1 instrument, PP Systems, Hitchin Herts, UK; every 90 min between 06.00 and 19.00 h (26<sup>th</sup> July 2009) xylem water potential ( $\Psi$ )

| Meaning/comments   | Name          | Units                             | Pinus sylvestris <sup>1</sup> | Pinus nigra <sup>2</sup> |
|--|---------------|-----------------------------------|-------------------------------|--------------------------|
| Allometric relationships & partitioning                      |               |                                   |                               |                          |
| Foliage:stem partitioning ratio @ D=2 cm                     | pFS2          | -                                 | 0.73                          | 0.71                     |
| Foliage:stem partitioning ratio @ D=20 cm                    | pFS20         | _                                 | 0.20                          | 0.20                     |
| Constant in the stem mass v. diam. relationship              | StemConst     | _                                 | 0.0215                        | 0.043808                 |
| Power in the stem mass v. diam. relationship                 | StemPower     | -                                 | 2.7184                        | 2.4975                   |
| Maximum fraction of NPP to roots                             | pRx           | -                                 | 0.5                           | 0.5                      |
| Minimum fraction of NPP to roots                             | pRn           | -                                 | 0.25                          | 0.25                     |
| Temperature modifier (fT)                                    |               |                                   |                               |                          |
| Minimum temperature for growth                               | Tmin          | deg. C                            | -5                            | 0                        |
| Optimum temperature for growth                               | Topt          | deg. C                            | 15                            | 15                       |
| Maximum temperature for growth                               | Tmax          | deg. C                            | 35                            | 35                       |
| Frost modifier (fFRost)                                      |               |                                   |                               |                          |
| Days production lost per frost day                           | kF            | days                              | 1                             | 1                        |
| Soil water modifier (fSW)                                    |               | 5                                 |                               |                          |
| Moisture ratio deficit for $fq = 0.5$                        | SWconst       | _                                 | 0.7                           | 0.7                      |
| Power of moisture ratio deficit                              | SWpower       | _                                 | 9                             | 9                        |
| Fortility effects  | Birpower      |                                   |                               | ,                        |
| Value of 'm' when $FR = 0$                                   | m0            |                                   | 0.015                         | 0.015                    |
| Value of 'fNutr' when $FR = 0$                               | fN0           | —                                 | 0.015                         | 0.55                     |
|  | IINO          | —                                 | 0.33                          | 0.33                     |
| Age modifier (fAge)  |               |                                   | 500                           | 100                      |
| Maximum stand age used in age modifier                       | MaxAge        | years                             | 500                           | 120                      |
| Power of relative age in function for fAge                   | nAge          | —                                 | 4                             | 4                        |
| Relative age to give $fAge = 0.5$                            | rAge          | -                                 | 0.95                          | 0.95                     |
| Litterfall & root turnover                                   |               |                                   |                               |                          |
| Maximum litterfall rate                                      | gammaFx       | 1/month                           | 0.025                         | 0.03                     |
| Litterfall rate at $t = 0$                                   | gammaF0       | 1/month                           | 0.001                         | 0.001                    |
| Age at which litterfall rate has median value                | tgammaF       | month                             | 36                            | 36                       |
| Average monthly root turnover rate                           | Rttover       | 1/month                           | 0.2                           | 0.2                      |
| Conductance  |               |                                   |                               |                          |
| Maximum canopy conductance                                   | MaxCond       | m/s                               | 0.02                          | 0.018                    |
| LAI for maximum canopy conductance                           | LAIgex        | _                                 | 3.33                          | 3.33                     |
| Defines stomatal response to VPD                             | CoeffCond     | 1/mBar                            | 0.05                          | 0.05                     |
| Canopy boundary layer conductance                            | BLcond        | m/s                               | 0.2                           | 0.2                      |
| Max. stem mass per tree @ 1000 trees/hectare                 | wSx1000       | kg/tree                           | 500                           | 500                      |
| Power in self-thinning rule                                  | thinPower     | -                                 | 1.5                           | 1.5                      |
| Fraction mean single-tree foliage biomass lost per dead tree | mF            | -                                 | 0                             | 0                        |
| Fraction mean single-tree root biomass lost per dead tree    | mR            | -                                 | 0.2                           | 0.2                      |
| Fraction mean single-tree stem biomass lost per dead tree    | mS            | -                                 | 0.2                           | 0.2                      |
| Canopy structure and processes                               |               |                                   |                               |                          |
| Specific leaf area at age 0                                  | SLA0          | m²/kg                             | 6                             | 5                        |
| Specific leaf area for mature leaves                         | SLA1          | m²/kg                             | 4                             | 4                        |
| Age at which specific leaf area = $(SLA0+SLA1)/2$            | tSLA          | years                             | 6                             | 4                        |
| Extinction coefficient for absorption of PAR by canopy       | k             | _                                 | 0.6                           | 0.5                      |
| Age at canopy cover  | fullCanAge    | years                             | 14                            | 8                        |
| Maximum proportion of rainfall evaporated from canopy        | MaxInteptn    | _                                 | 0.18                          | 0.18                     |
| LAI for maximum rainfall interception                        | LAImaxInteptn | _                                 | 5                             | 5                        |
| Canopy quantum efficiency                                    | alpha         | molC/molPAR                       | 0.05                          | 0.05                     |
| Branch and bark fraction (fracBB)                            |               |                                   |                               |                          |
| Branch and bark fraction at age 0                            | fracBB0       | _                                 | 0.15                          | 0.5                      |
| Branch and bark fraction for mature stands                   | fracBB1       | _                                 | 0.1                           | 0.1                      |
| Age at which fracBB = $(fracBB0+fracBB1)/2$                  | tBB           | years                             | 20                            | 5                        |
| Various  |               | J                                 | -                             | -                        |
| Ratio NPP/GPP  | Y             | _                                 | 0.47                          | 0.47                     |
| Basic density  | Density       | t/m <sup>3</sup>                  | 0.35                          | 0.47                     |
| Conversion factors   | Density       | v 111                             | 0.55                          | 0.75                     |
|  | 0.2           | <b>U</b> <i>I</i> /m <sup>2</sup> | 00                            | 00                       |
| Intercept of net v. solar radiation relationship             | Qa<br>Ob      | $W/m^2$                           | $-90 \\ 0.9$                  | -90                      |
| Slope of net v. solar radiation relationship                 |               | aDM/mal                           |                               | 0.9                      |
| Molecular weight of dry matter                               | gDM_mol       | gDM/mol                           | 24                            | 24                       |
| Conversion of solar radiation to PAR                         | molPAR_MJ     | mol/MJ                            | 2.3                           | 2.3                      |

 Table 1. Definitions, symbols, units, values, and sources for the parameters used in 3-PG model for Scots pine (*Pinus sylvestris* L.) and Black pine (*Pinus nigra* Arnold) in Sierra de los Filabres (Southern Spain)

<sup>1</sup>3-PG input variables from Sand & Landsberg, 2001. Bold type from this study

<sup>2</sup>3-PG input variables from Patenaude et al., 2008. Bold type from this study

(Predawn  $Y_{pd}$ , 4:00 GTM and midday  $Y_m$ , 12:00 GTM; pressure chamber, SKPM 1400, Skye Instruments, UK) were measured in five trees per plot.

In each plot, LAI was non-destructively measured using a widely used optical instrument, the Plant Canopy Analyzer LAI-2000 (LICOR Inc., Lincoln, Nebraska, USA). The LAI-2000 measurements were performed in the sample plots during July 2009 using one intercalibrated instrument for all measurements. The unit was first located in a large open area to obtain the above-canopy measurements, and immediately the instrument was carried along a plot transect (10 m) to make the below-canopy measurements. All measures were done at dawn conditions. To minimize the contribution of the understory, LAI-2000 measurements were taken at 1.5 m above the ground. LAI was calculated as the arithmetic average of four LAI measures taken along the transect. LAI measured using LAI-2000 corresponds to plant area index (PAI) including photosynthetic and non-photosynthetic components. We computed effective LAI according to the methods used in Dufrêne & Breda (1995).

# **3-PG model and site specific** parameterization

For this study, the 3-PG model was used to predict stand growth of Scots pine and Black pine plantations. The data required to run the model are organized in four categories: climate data, site-specific factors, initial conditions in the plantation and 3-PG physiological parameter relating to the species under study (Sands, 2004).

Site-specific climate data required by the model were obtained from thirty local meteorological stations with long, continuous records from the study area (distance less than 30 km in all cases) (Spanish Meteorological Agency; http://www.aemet.es/, see Sánchez-Salguero et al., 2010) including minimum, maximum, and average monthly air temperature (°C), monthly rainfall (mm), number of rain and frost days per month. Direct measurements of vapour pressure deficit (VPD, mbar) were not available from the weather station used and VPD was estimated using the equations included in the 3-PG model (Landsberg, 1986). Solar radiation data (MJ m<sup>-2</sup> day<sup>-1</sup>) were also not available from the permanent weather stations near our study sites, solar radiation was calculated using the Thornton-Running model by the software package developed by MT-CLIM for Excel, (available online: from http://www.ntsg.umt.edu/bioclimatology/mtclim). This produces solar radiation estimates based on site latitude, altitude, and daily precipitation and

minimum and maximum temperatures (Thornton & Running, 1999; Amichev *et al.*, 2011). Although the 3-PG model can be run using long-term monthly averages, we used current monthly weather data to account for drought events, in particular, during periods of relatively high mean temperature and high solar radiation that occurred during 1983, 1990–1995, 1999, 2001 and 2005. Climatic and site characteristics datasets were implemented in a Geographic Information System (GIS) environment. Spatial interpolation based on inverse distance weighting and spline, were used to predict monthly and average annual precipitation, as well as average annual, minimum and maximum temperatures with a spatial resolution of 10 m (Sánchez-Salguero *et al.*, 2013).

The soil information needed for 3-PG initialization were obtained from soil cartography at 1:100.000 scale (Aguilar *et al.*, 1987) and a test soil pit (Rosa *et al.*, 1984) located in the study area. This information was used to parameterize the available soil water (ASW), and soil texture class variables required by 3-PG (Table 1). Soil texture was described as clay loam. The range of ASW was from 100 to 150 mm. We consider previous works using empirical expressions based on some measurements of soil depth and texture which have demonstrated to be useful in some recent works with 3-PG in Spain (e.g. Pérez-Cruzado et al., 2011; Vega-Nieva et al., 2013). Fertility rating (FR) was estimated based on the best match between model predictions and the measured average stem diameter, keeping all other parameters unchanged (Sampson et al., 2006; Rodríguez-Suárez et al., 2010). In this study, low values for FR were chosen, FR = 0.55, in healthy and decline stands, because of limitations imposed by soil texture and depth.

#### Species specific parameterization

Species-specific properties and features are controlled in the 3-PG model by different parameters grouped into five main categories: (i) biomass partitioning and turnover; (ii) growth modifiers; (iii) stem mortality and self-thinning; (iv) canopy structure and processes; and (v) wood and stand properties. We used four methods to parameterize each of the four speciesspecific sections of the model. First, we used empirical observations from permanent plots established on our study sites (Hernandez-Clemente *et al.*, 2011); second, we used Scots pine and Black pine data from the literature (Patenaude *et al.*, 2008); third, default 3-PG parameters published for Scots pine (Landsberg *et al.*, 2005) and for Black pine (Patenaude *et al.*, 2008); and fourth, we varied the remaining parameters to fit model output to DBH observations (Table 1). Twelve of the 3-PG parameters in Table 1 were parameterized using field stand observations, two with data reported in the literature, and three parameters were parameterized by fitting DBH data. We used the default 3-PG values for the remaining 31 parameters (Table 1).

The initial stem (WS), root (WR), and foliage (WF) biomass were estimated based on seedling weight and plantation density, with values of WF=0.068/0.089 tons ha<sup>-1</sup>, WR= 0.058/0.071 tons ha<sup>-1</sup>, and WS=0.041/0.050 tons ha<sup>-1</sup> for Scots pine and Black pine respectively (Montero *et al.*, 2005). Tree diameters and BAI were derived from dendrochronological data. We parameterized the 3-PG tree allometric equations using a nation-wide Scots pine and Black pine stem biomass equations (Montero *et al.*, 2005) including stem weight W<sub>s</sub> (kg) = 0.0215 \* (DBH, cm)<sup>2.7184</sup> for Scots pine (R<sup>2</sup>=0.981), and W<sub>s</sub> (kg) = 0.043808 \* (DBH, cm)<sup>2.4975</sup> for Black pine (R<sup>2</sup>=0.989).

For the simulation model with adaptive silvicultural treatments (e.g. uniform thinning), we considered a density reduction from the initial 2000 trees  $ha^{-1}$  (in 1973 or 1976) to 1400 trees  $ha^{-1}$  (in 1980) and to 1000 trees  $ha^{-1}$  (in 2003).

#### Model sensitivity analysis

Once, the model was calibrated using an initial set of parameters (Table 1) and tested against observations (healthy trees), we performed sensitivity analyses to assess the effects of defoliation on 3-PG predictions for decline areas. In order to assess the relative influence of different model parameters on model results related to forest decline (DBH and BAI), we selected seven of the 3-PG parameters, likely to be related to drought stress. These were (Table 1): stem partitioning ratio (*pFS*<sub>20</sub>), maximum litterfall rate ( $\gamma_{Fx}$ ), maximum canopy conductance  $(g_{Cx})$ , specific leaf area for mature aged stands ( $\sigma_1$ ), age at which specific leaf area =  $\frac{1}{2}$  $(\sigma_0 + \sigma_1)$ , age at full canopy cover  $(t_c)$ , and canopy boundary layer conductance  $(g_R)$ . The initial values for these parameters was based on field observations (Figs. S2 and S3 [supplementaries]). These simulations were based on empirically changes (increase and decrease) of those seven 3-PG parameter values (Table 2) after a first drought period (1983; see Sánchez-Salguero et al. 2012a). For this analysis we used a 32 year (1973– 2008) and a 29 year (1976-2008, Black pine) annual time series of DBH and BAI for Scots pine and Black pine, respectively. Finally, the 3-PG model structure

**Table 2.** Sensitivity analysis results for Scots pine and Black pine in Sierra de los Filabres (Southern Spain) shown as DBH values at age 35 yr and 32 yr respectively, produced by the 3PG model assuming 20 and 40% decrease and increase of the value of eleven 3PG model parameters

| Meaning/comments  | Name                       | -40%                 | -20%                 | +20%                 | +40%                 |
|---|----------------------------|----------------------|----------------------|----------------------|----------------------|
|   | Pinus sylvestr             | ris                  |                      |                      |                      |
| Allometric relationships & partitioning<br>Foliage:stem partitioning ratio @ D=20 cm  | pFS20                      | 16.4                 | 16.4                 | 16.4                 | 16.4                 |
| Litterfall & root turnover<br>Maximum litterfall rate   | gammaFx                    | 17.0                 | 16.8                 | 15.8                 | 15.0                 |
| <b>Conductance</b><br>Maximum canopy conductance<br>Canopy boundary layer conductance   | MaxCond<br>BLcond          | 18.5<br>15.8         | 17.3<br>16.2         | 15.6<br>16.6         | 15.0<br>16.7         |
| <b>Canopy structure and processes</b><br>Specific leaf area for mature leaves<br>Age at which specific leaf area = (SLA0+SLA1)/2<br>Age at canopy cover | SLA1<br>tSLA<br>fullCanAge | 15.0<br>15.7<br>16.5 | 15.9<br>15.8<br>16.2 | 16.7<br>16.0<br>15.4 | 17.0<br>16.0<br>14.9 |
|   | Pinus nigra                |                      |                      |                      |                      |
| Allometric relationships & partitioning<br>Foliage:stem partitioning ratio @ D=20 cm<br>Litterfall & root turnover                                      | pFS20                      | 17.0                 | 17.0                 | 17.0                 | 17.0                 |
| Maximum litterfall rate<br>Conductance  | gammaFx                    | 18.4                 | 17.8                 | 15.9                 | 14.3                 |
| Maximum canopy conductance<br>Canopy boundary layer conductance   | MaxCond<br>BLcond          | 19.4<br>16.5         | 18.1<br>16.8         | 16.4<br>17.2         | 15.7<br>17.3         |
| <b>Canopy structure and processes</b><br>Specific leaf area for mature leaves<br>Age at which specific leaf area = (SLA0+SLA1)/2                        | SLA1<br>tSLA               | 15.1<br>17.0         | 15.3<br>17.0         | 17.8<br>17.1         | 18.2<br>17.1         |
| Age at canopy cover   | fullCanAge                 | 17.4                 | 17.2                 | 16.7                 | 16.4                 |

enables to study management intervention. Therefore, it was used to evaluate the impact of different thinning intensities on Scots pine and Black pine growth. Specifically, simulations were conducted at two levels of thinning intensities (remove of 50% and 60% of trees).

The model version used in this study was the 3-PGpjs2.5 (Sands & Landsberg, 2001) which is implemented as a Microsoft Excel spreadsheet with a userinterface that facilitates data entry and interpretation of results (FS 599\_ALL EX + ANS 2015RHW.xlsm).

## Assessment of accuracy of model performance

The outputs of 3-PG include stand attributes (average stem DBH, basal area ha<sup>-1</sup>, volume ha<sup>-1</sup>, biomass ha<sup>-1</sup>, stand density and mortality) as well as physiological attributes (leaf area index, NPP, gross primary production, and transpiration). 3-PG results were validated by comparing measured and modelled data of average diameter at breast height (DBH, cm), basal area increment (BAI, cm<sup>2</sup> yr<sup>-1</sup>), and leaf area index (LAI, m<sup>2</sup> m<sup>-2</sup>) for healthy and decline conditions. We used DBH and BAI measurements from our testing data set to compute the bias of 3-PG predictions, as well as the R-square of linear regressions of predicted (dependent variable) versus observed (independent variable) data. Model error was evaluated using root mean squared error (RMSE) (Willmott, 1981).

### Results

# Estimation of diameter at breast height growth on healthy trees

Nominal values applied for the calibration of the 3-PG model are included in Table 1 such as: site specific functions, and climate data from the plantation under study. Based on this model, we predicted mean diameter at breast height (DBH, cm), basal area increment (BAI, cm<sup>2</sup> yr<sup>-1</sup>) and leaf area index (LAI, m<sup>2</sup> m<sup>-2</sup>) for Scots pine and Black pine trees and we compared these results with field observations from permanent plots. This analysis was done to establish a performance baseline of 3-PG for plantations of Scots pine and Black pine growth predictions.

Figure 1 shows the comparison between observed and simulated values of DBH growth for healthy trees of Scots pine plantation during a 35-year period (1973– 2008 years). Predicted DBH was in near perfect agreement with observed measurements. At age 32, the Scots pine stand had a mean DBH of 16.0 cm while the model

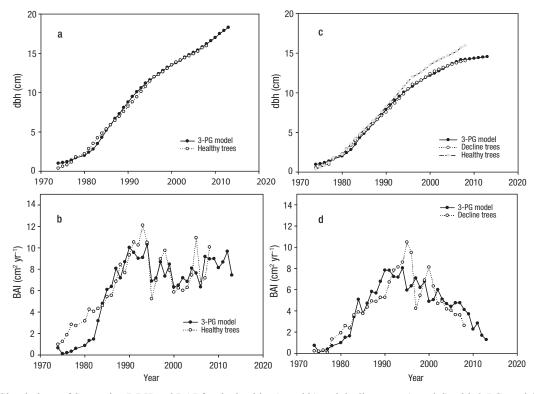


Figure 1. Simulations of Scots pine DBH and BAI for the healthy (a and b) and decline trees (c and d) with 3-PG model using local specific functions and the parameters suggested by Sands & Landsberg (2001) (Table 1).

predicted 16.2 cm. A good correlation between measured and estimated DBH data was obtained, with an  $R^2$  higher than 0.99, and an RMSE of 0.33 cm (Fig. 3a).

Regarding BAI, there was a lower agreement between observed and simulated values (Fig. 1b). The 3-PG model tended to underestimate tree BAI at younger stand ages during the early development stage (15 years old) due to the higher variation of our BAI observations (Fig. 1b). However, the large differences between modelled and observed data during early stand development had largely disappeared by middle-age period (13 years old). Overall, there was poor correspondence between modelled and observed BAI with a lower regression R-square values ( $R^2 = 0.83$ , RMSE = 1.54) (Fig. 3b).

Figure 2 shows the comparison between observed and simulated values of DBH growth for Black pine during a 32-year period (1976–2008). As with the results obtained for Scots pine, predicted DBH was in very good agreement with observed measurements in Black pine (means DBH=15.5 cm while the model predicted 15.9 cm). The regression between modelled and observed DBH, had an  $R^2$  higher than 0.99 and an RMSE of 0.35 cm (Fig. 3c). There was a lower agreement between observed and simulated values for BAI (Fig. 2d). The 3-PG model tended to underestimate tree BAI at younger stand ages for the early development stage (7 years old) due to the higher variation of our BAI observations (Fig. 2d). However, the large differences between modelled and observed during early stand development were more marked by middle-age period (10 years old). There was a low correspondence between modelled and observed BAI ( $R^2 = 0.68$ , RMSE = 1.52) (Fig. 3d).

# **3-PG model sensitivity analysis to simulate forest decline trees**

In order to identify the relative influence of different model variables on the ability to predict results for forest decline trees (DBH and BAI), field data were used to fit site specific empirical functions. These simulations were based on changes either positive or negative of seven 3-PG parameter values (Table 2) after a first drought period (1983).

Our sensitivity analysis results indicated that the most pronounced effects on DBH predictions for decline trees could be due to parameterizing the foliage: stem partitioning ratio (*pFS*<sub>20</sub>), maximum litterfall rate ( $\gamma_{Fx}$ ), maximum canopy conductance ( $g_{Cx}$ ), specific leaf area for mature aged stands ( $\sigma_1$ ), age at which specific leaf area =  $\frac{1}{2}$  ( $\sigma_0 + \sigma_1$ ), age at full canopy cover ( $t_c$ ), and canopy boundary layer conductance ( $g_B$ ) (Table 2).

By using this new set of parameters related to decline process (Table 3), estimations were able to ap-

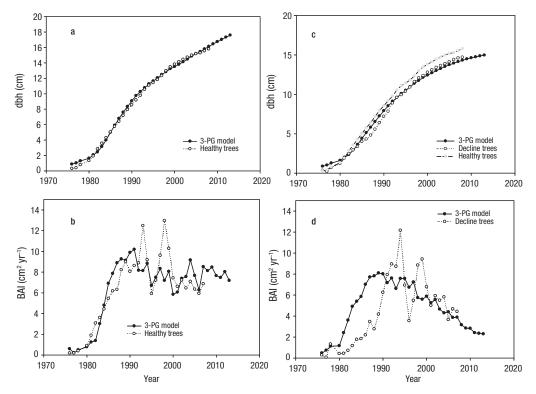
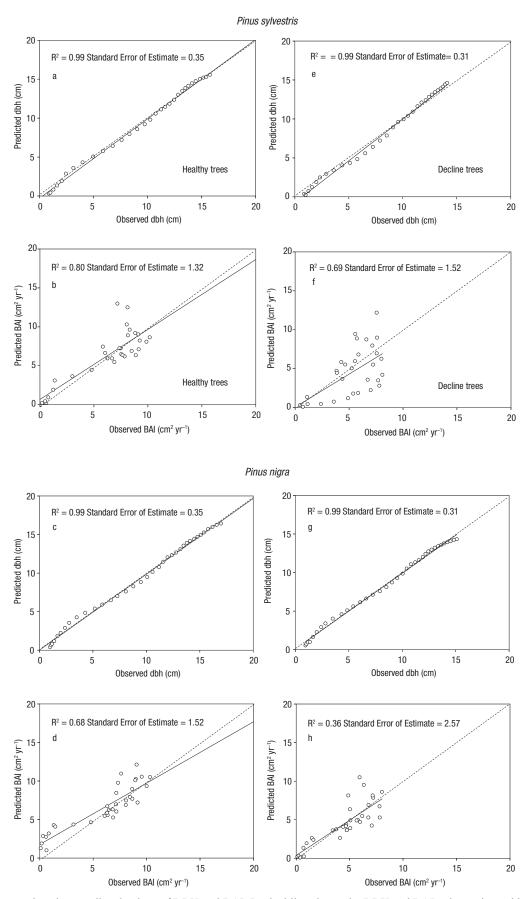


Figure 2. Simulations of Black pine DBH and BAI for the healthy (a and b) and decline trees (c and d) with 3-PG model using local specific functions and the parameters suggested by Patenaude *et al.* (2008) (Table 1).



**Figure 3.** Observed against predicted values of DBH and BAI. Dashed line shows the DBH and BAI value estimated by the model from the standard 3-PG model parameters for healthy and decline trees (Tables 1 and 2). Dotted line 1:1.

| Meaning/comments  | Name                       | Units                                | Pinus sylvestris | Pinus nigra    |
|---|----------------------------|--------------------------------------|------------------|----------------|
| Allometric relationships & partitioning<br>Foliage:stem partitioning ratio @ D=20 cm  | pFS20                      | -                                    | 0.16             | 0.16           |
| Litterfall & root turnover<br>Maximum litterfall rate   | gammaFx                    | 1/month                              | 0.03             | 0.035          |
| <b>Conductance</b><br>Maximum canopy conductance<br>Canopy boundary layer conductance   | MaxCond<br>BLcond          | m/s<br>m/s                           | 0.025<br>0.15    | 0.020<br>0.2   |
| <b>Canopy structure and processes</b><br>Specific leaf area for mature leaves<br>Age at which specific leaf area = (SLA0+SLA1)/2<br>Age at canopy cover | SLA1<br>tSLA<br>fullCanAge | m <sup>2</sup> /kg<br>years<br>years | 3<br>4<br>14     | 3.8<br>4<br>10 |

**Table 3.** Values for the parameters used in 3-PG model for Scots pine (*Pinus sylvestris* L.) and Black pine (*Pinus nigra* Arnold) in Sierra de los Filabres (Southern Spain) related to decline process under stress conditions

propriately predict the DBH of decline trees during the 1983–2008 periods for both species (Figs. 1c and 2c). At age 32, the Scots pine stand had 14.1 cm while the model predicted 14.4 cm, and Black pine stand had 14.2 cm while the model predicted 14.2 cm. Model estimates were highly correlated with observed measurements with slopes near unity with an  $R^2$  of 0.99, and an RMSE of 0.31 cm (Figs. 3c, 2 g, 3g). On decline trees, 3-PG predicted BAI values showed a lower correlation with field data (Figs. 1d, 2d, 3f and 3h) ( $R^2$  = 0.69, RMSE = 1.84 cm<sup>2</sup> yr<sup>-1</sup>, and  $R^2$  = 0.36, RMSE = 2.57 cm<sup>2</sup> yr<sup>-1</sup> respectively).

Leaf area index (LAI) was predicted for both species and physiological status (Fig. 4). It was always much higher for the healthy trees than the decline trees. Predicted highest LAI value occurred between ages 16–17 (*P. sylvestris* in 1992, LAI = 1.14 m<sup>2</sup> m<sup>-2</sup>; *P. nigra* in 1989, LAI = 1.47 m<sup>2</sup> m<sup>-2</sup>). There was a substantial difference between healthy (*P. sylvestris*, LAI = 0.76 m<sup>2</sup> m<sup>-2</sup>; *P. nigra* LAI = 0.74 m<sup>2</sup> m<sup>-2</sup>) and declining trees (*P. sylvestris* LAI = 0.29 m<sup>2</sup> m<sup>-2</sup>; *P. nigra* LAI = 0.37 m<sup>2</sup> m<sup>-2</sup>), where at age 32-35 observed LAI was much lower than predicted LAI. (Fig. 4). Although we only had one year of measured LAI data for comparison purposes, the observed LAI showed a limited agreement with predicted LAI.

#### Sensitivity analysis of silvicultural treatments

Model predictions for DBH of Scots pine under two different thinning intensities (50% and 60%) were consistently higher than predicted measurements, with an estimated DBH increment of 1.3 cm after 7 years (17.4/17.6 cm versus 16.3 cm) (Fig. 5). However, predictions after thinning were relatively closer on both silvicultural treatments, with a trend indicating a larger DBH overestimation as stands aged.

### Discussion

#### **3PG-model to assess decline processes**

In this study, we applied the 3-PG model to describe the physiological process behind forest decline in pine forests (McDowell *et al.*, 2008; Williams *et al.*, 2013). Supporting our hypothesis, a comparison of the model simulations with growth measurements indicated that a fixed physiological parameter set in 3-PG was able to predict DBH, BAI and to a lesser degree LAI with reasonable accuracy under healthy and decline conditions for plantations of Scots pine and Black pine in Southern Spain. We were then able to reproduce the observed growth reduction indicated by dendrochronology data by reducing leaf conductance and the available foliage area, which lead to less photosynthetic capacity and slower recovery after a drought stress.

Previous studies have shown that 3-PG could produce accurate estimates of Scots pine and Black pine DBH and were able to simulate growth patterns under different ecological conditions (Esprey *et al.*, 2004; Landsberg *et al.*, 2005; Patenaude *et al.*, 2008; Xenakis *et al.*, 2008). Nominal values applied for this study were based on previous studies (Sands & Landsberg, 2001; Patenaude *et al.*, 2008). This paper presents a novel approach in the application of 3-PG model to accurately estimate the effects on growth of forest decline processes in pine stand based on the analysis of three parameters (DBH, BAI and LAI).

In the first approach, we modified sixteen of the 3-PG variables using field stand observations (Table 1) (Sands & Landsberg, 2001; Patenaude *et al.*, 2008). All of these parameters are directly related to photosynthesis, stomata response and carbon accumulation, as they affect foliage biomass production and litter input (Landsberg & Sands, 2010). The model was able to predict DBH with reasonable accuracy for the base-

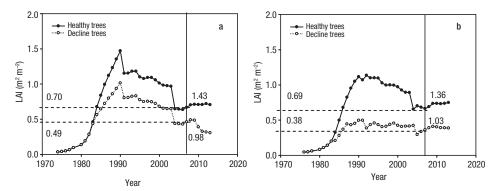


Figure 4. Simulated LAI of Scots pine (a) and Black pine (b) LAI for the healthy and decline trees with 3-PG model using local specific functions and the parameters values e presented on table 1. Modelled values (bold) and real values (italic) at 2008.

line physiological set; although, there were some systematic differences between estimated and measured values of DBH. The model tended to under-predict DBH during early stand development and then overpredict later (Figs. 1 and 2). However, the good correlations between predicted and observed data may be explained for two reasons. First, we used current monthly weather data instead of monthly average, which allowed accounting for drought and heat discrete events as previously noted on other studies (Almeida *et al.*, 2004; Bryars *et al.*, 2013).

Second, under the particular study conditions (evenage plantations, regular tree distribution, no thermal growth limitations), pine growth appears to be much more dependent on leaf area development and the quantity of intercepted solar radiation than on changes in the rates or efficiencies of specific physiological processes (Beadle *et al.*, 1985a,b,c; Samuelson *et al.*, 2004).

The accuracy of the BAI estimates was lower but varied during different stages of stand development (Fig. 3). The low model accuracy for BAI was due to poor predictions during early and late stand development. It is noteworthy that in the Filabres area, P. sylvestris grew (increased biomass) well in the wet 1970s, when conditions were much more favourable for establishment, than in the drier 1990s. In the case of Scots pine, an introduced species there, the plantations are located well beyond the natural southern boundary for the species' distribution area (Sánchez-Salguero et al., 2012a). These results are biologically reasonable and illustrated how the processes embedded in the 3-PG model controlled tree biomass production based on parameter values (Sands, 2004; Landsberg & Sands, 2010).

Once the base growth line was established, the physiological parameter set was modified to describe forest decline process (Hernández-Clemente *et al.*, 2011; Sánchez-Salguero *et al.* 2012a,b). Previous studies have established physiological parameters related

to forest decline (McDowell et al., 2008). On decline trees, values of stem partitioning ratio  $(pFS_{20})$ , maximum litterfall rate ( $\gamma_{Fx}$ ), maximum canopy conductance  $(g_{Cx})$ , specific leaf area for mature aged stands  $(\sigma_1)$ , age at which specific leaf area =  $\frac{1}{2}(\sigma_0 + \sigma_1)$ , age at full canopy cover  $(t_c)$ , and canopy boundary layer conductance  $(g_B)$  were different from those used on other simulations for pine species (Landsberg et al., 2005; Patenaude et al., 2008; van Oijen et al., 2013), and they were important for DBH and BAI predictions under drought stress (Esprey et al., 2004). However, the use of those parameters led to values which are in good agreement with field data (Figs. S2 and S3, [supplementaries]). The litterfall rate was fitted to match agerelated decline of growth observed by Sánchez-Salguero et al. (2012a), whereas values used for the specific area were 4.6 m<sup>2</sup> kg<sup>-1</sup> and 4.3 m<sup>2</sup> kg<sup>-1</sup> for Scots pine mature leaves and values of 4.2 m<sup>2</sup> kg<sup>-1</sup> and 3.5 m<sup>2</sup> kg<sup>-1</sup> for Black pine were within the lower range of those measured in England (Mencuccini & Bonosi, 2001; Patenaude et al., 2008). More restrictive physiological values (i.e., maximum canopy conductance  $(g_{Cx})$  and canopy boundary layer conductance  $(g_B)$  affecting water photosynthetic status) led to a different biomass allocation to the stem or to foliage, resulting in lower DBH and BAI estimates. On the other hand, the inaccuracy in predicting LAI in older stand ages seems to be more related to an inaccurate prediction of stem allometry or growth allocation (Fig. 4; Beadle et al., 1982); although, measured LAI data for the plots used in this study were limited. Again it is important to point out that this relationship was biologically reasonable and consisted with the processes are embedded in the 3-PG model (Landsberg et al., 2005). However, it is important to recognize that it was possible to obtain similar values with different combinations of values for the tuned parameters, suggesting that a deeper analysis, including sensitivity analysis, will be needed. The sensitivity analysis of those parameters on growth under forest decline process has demonstrated the im-

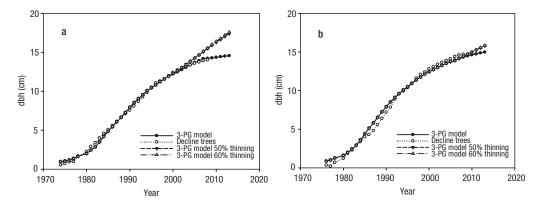


Figure 5. Simulations of Scots pine (a) and Black pine (b) DBH for the adaptive silvicultural treatments with 3PG model using local specific functions and the parameters suggested by Sands & Landsberg (2002) (Table 1).

portance of selecting an adequate physiological set value to obtain an accurate model fit under stress conditions.

#### Silvicultural treatments

On the adaptive silviculture treatments, the model tended to show a similar increase of DBH during post thinning stand development (Fig. 5) for both thinning levels. The average variation of DBH growth 10 years after thinning was estimated as 2.6 cm higher than the current stand. This inter-rotation analysis highlighted the strong influence of management practices on pine forest growth and drought adaptation (Fontes et al., 2010). The increase in the model DBH growth estimation could be due to water availability related to tree density (Martín-Benito et al., 2010), effects on stem C allocation (Oleksyn et al., 1999), and reduction of the ratio of foliage: stem biomass following severe thinning (Vanninen et al., 1996). However, it has been suggested that silviculture has little effect on stem allometry (Retzlaff et al., 2001). Since there are few empirical estimates of the impact of silvicultural treatments on forest decline response (Millar et al., 2007; Sánchez-Salguero et al., 2012b, 2013), field data of foliage and stem partitioning coefficients from component growth, litterfall, and stem mortality should be collected.

## Conclusions

Our results indicated that, once parameterized, the 3-PG model using a commonly available soil and climatic data as well as experimental physiological parameters can predict the growth responses of pine plantations to climatic stress with useful accuracy in southern Spain. Growth response variables such as DBH and BAI were accurately estimated using the standard 3-PG parameters, but other variables, such as LAI, showed a lower agreement between predicted data and field values. The sensitivity analysis of physiological parameters related to water status and conductance shows their importance to estimate the physiological response of pine plantations to extreme climatic events. The results of this preliminary study indicate the model can be used to evaluate the impact of adaptive silviculture to mitigate decline processes at rear edge forests. Some future works might look at climatic and edaphic gradients within this area using a GIS approach such as Almeida et al. (2010). Because water limitation is possibly behind forest decline in these forests, some focus could be put into the measurement and mapping of Available Soil Water along topographic gradients in the area.

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## References

- Aguilar J, Simón M, Fernández J, García I, Milán JM, 1987. Mapa de Suelos. E 1: 100.000. Fiñana. Hoja 1012. LUCDEME. ICONA. Universidad de Granada. Madrid, Spain.
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, Mc-Dowell N, Vennetier M, Kitzberger T, Rigling A, Bres-

hears DD *et al.*, 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecol Manag 259: 660-684. http://dx.doi.org/10.1016/j.foreco.2009.09.001.

- Almeida AC, Landsberg JJ, Sands PJ, 2004. Parameterisation of 3-PG model for fast-growing *Eucalyptus grandis* plantations. Forest Ecol Manag 193: 179-195. http://dx.doi. org/10.1016/j.foreco.2004.01.029.
- Almeida AC, Siggins A, Batista TR, Beadle C, Fonseca S, Loos R, 2010. Mapping the effect of spatial and temporal variation in climate and soils on Eucalyptus plantation production with 3-PG, a process-based growth model. Forest Ecol Manag 259: 1730-1740. http://dx.doi. org/10.1016/j.foreco.2009.10.008.
- Amichev BY, Hangs RD, van Rees KC, 2011. A novel approach to simulate growth of multi-stem willow in bioenergy production systems with a simple process-based model (3PG). Biomass Bioenerg 35(1): 473-488. http://dx.doi.org/10.1016/j.biombioe.2010.09.007.
- Beadle CL, Talbot H, Jarvis PG, 1982. Canopy structure and leaf-area index in a mature Scots pine forest. Forestry, 55: 105-123. http://dx.doi.org/10.1093/forestry/55.2.105.
- Beadle CL, Neilson RE, Talbot H, Jarvis PG, 1985a. Stomatal conductance and photosynthesis in a mature Scots pine forest 1 Diurnal, seasonal and spatial variation in shoots. J App Ecol 22: 557-571. http://dx.doi.org/10.2307/2403185.
- Beadle CL, Jarvis PG, Talbot H, Neilson RE, 1985b. Stomatal conductance and photosynthesis in a mature Scots pine forest 2 Dependence on environmental variables of single shoots. J App Ecol 22: 573-586. http://dx.doi. org/10.2307/2403186.
- Beadle CL, Talbot H, Neilson RE, Jarvis PG, 1985c. Stomatal conductance and photosynthesis in a mature Scots pine forest 3 Variation in canopy conductance and canopy photosynthesis. J App Ecol 22: 587-595. http://dx.doi. org/10.2307/2403187.
- Breda N, Huc R, Granier A, Dreyer E, 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63: 625-644. http:// dx.doi.org/10.1051/forest:2006042.
- Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT, 2009. Tree dieoff in response to global-change type drought: Mortality insights from a decade of plant water-potential measurements. Frontiers Ecol Environ 7: 185-189. http://dx.doi. org/10.1890/080016.
- Bryars C, Maier C, Zhao D, Kane M, Borders B, Will R, Teskey R, 2013. Fixed physiological parameters in the 3-PG model produced accurate estimates of loblolly pine growth on sites in different geographic regions. Forest Ecol Manag 289: 501-514. http://dx.doi.org/10.1016/j. foreco.2012.09.031.
- Costa M, 2005. Los bosques ibéricos: una interpretación geobotánica. Ed. Planeta, Madrid.
- Dobbertin M, 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. Eur J For Res 124: 319-333. http://dx.doi.org/10.1007/s10342-005-0085-3.

- Dobbertin M, Brang P, 2001. Crown defoliation improves tree mortality models. For Ecol Manag 141: 271-84.
- Dufrêne E, Bréda N, 1995. Estimation of deciduous forest leaf area index using direct and indirect methods. Oecologia, 104(2): 156-162. http://dx.doi.org/10.1007/ BF00328580.
- Esprey LJ, Sands PJ, Smith CW, 2004. Understanding 3-PG using a sensitivity analysis. Forest Ecol Manag 193 :235–250. http://dx.doi.org/10.1016/j.foreco.2004.01.032.
- Fontes L, Bontemps JD, Bugmann H, van Oijen M, Gracia C, Kramer K, Lindner M, Rötzer T, Skovsgaard JP, 2010. Models for supporting forest management in a changing environment. Forest Systems 19: 8–29.
- Galiano L, Martínez-Vilalta J, Lloret F, 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 year after a drought episode. New Phytol 190: 750-759. http://dx.doi.org/10.1111/j.1469-8137.2010.03628.x.
- Gonzalez-Benecke CA, Jokela EJ, Cropper WP, Bracho R, Leduc DJ, 2014. Parameterization of the 3PG model for *Pinus elliottii* stands using alternative methods to estimate fertility rating, biomass partitioning and canopy closure. Forest Ecol Manag 327: 55-75. http://dx.doi.org/10.1016/j. foreco.2014.04.030.
- Grissino-Mayer HD, 2001. Evaluating crossdating, accuracy: a manual and tutorial for the computer program COFE-CHA. Tree-Ring Res 57: 205–221.
- Guada G, Camarero JJ, Sánchez-Salguero R, Navarro Cerrillo RM, 2016. Limited growth recovery after droughtinduced forest dieback in very defoliated trees of two pine species. Front Plant Sci, 7: 418. http://dx.doi.org/10.3389/ fpls.2016.00418.
- Hernandez-Clemente R, Navarro-Cerrillo RM, Suarez L, Morales F, Zarco-Tejada PJ, 2011. Assessing structural effects on PRI for stress detection in conifer forests. Remote Sens Environ 115: 2360–2375. http://dx.doi. org/10.1016/j.rse.2011.04.036.
- Landsberg JJ, 1986. Physiological ecology of forest production. Academic Press, London, UK.
- Landsberg JJ, Johnsen KH, Albaugh TJ, Allen L, McKeand SE, 2001. Applying 3-PG, a simple process-based model designed to produce practical results, to data from Loblolly pine experiments. For Sci 47: 43-51.
- Landsberg JJ, Waring RH, 1997. A generalized model of forest productivity using simplified concepts of radiation - use efficiency, carbon balance and partitioning. Forest Ecol Manag 95: 209–228. http://dx.doi.org/10.1016/ S0378-1127(97)00026-1.
- Landsberg JJ, Mäkelä A, Sievänen R, Kukkola M, 2005. Analysis of biomass accumulation and stem size distributions over long period in managed stands of *Pinus* sylvestris in Finland using the 3-PG model. Tree Physiol 25: 781-792. http://dx.doi.org/10.1093/treephys/25.7.781.
- Landsberg JJ, Sands P, 2010. Physiological ecology of forest production: principles, processes and models. Vol. 4. Academic Press.
- Martín-Benito D, del Río M, Heinrich I, Helle G, Cañellas I, 2010. Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* affores-

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tation. Forest Ecol Manag 259: 967-975. http://dx.doi. org/10.1016/j.foreco.2009.12.001.

- McDowell NG, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.*, 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178: 719-739. http:// dx.doi.org/10.1111/j.1469-8137.2008.02436.x.
- Medlyn BE, Duursma RA, Zeppel MJB, 2011. Forest productivity under climate change: a checklist for evaluating model studies. Wiley Interdisciplinary Reviews: Climate Change 2: 332-355. http://dx.doi.org/10.1002/wcc.108.
- Mencuccini M, Bonosi L, 2001. Leaf/sapwood area ratios in Scots pine show acclimation across Europe. Can J For Res 31: 442-456. http://dx.doi.org/10.1139/x00-173.
- Millar CI, Stephenson NL, Stephens SL, 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecology Applications 17: 2145–2151. http://dx.doi.org/10.1890/06-1715.1.
- Montero G, Ruiz-Peinado R, Muñoz M, 2005. Producción de biomasa y fijación de CO2 por los bosques españoles. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, España.
- Mueller-Dombois D, 1993. Biotic Impoverishment and Climate Change: Global Causes of Forest Decline? In Mueller-Dombois, D and Reinhard F.H. Professor. Forest Decline in the Atlantic and Pacific Region, pp 339-348.
- Navarro-Cerrillo RM, Varo MA, Lanjeri S, Hernández Clemente R, 2007. Cartografía de defoliación en los pinares de pino silvestre (*Pinus sylvestris* L.) y pino salgareño (*Pinus nigra* Arn.) en la Sierra de los Filabres. Ecosistemas 16: 163-171.
- Oleksyn J, Reich PB, Chalupka W, Tjoelker MG, 1999. Differential above- and below-ground biomass accumulation of European *Pinus sylvestris* populations in a 12-year-old provenance experiment. Scan J For Res 14: 7-17. http:// dx.doi.org/10.1080/02827589908540804.
- Patenaude G, Milne R, van Oijen M, Rowland CS, Hill RA, 2008. Integrating remote sensing datasets into ecological modelling: a Bayesian approach. Int J Remote Sens 29(5): 1295-1315. http://dx.doi.org/10.1080/01431160701736414.
- Peñuelas J, Filella I, 2001. Responses to a warming world. Science, 294(5543): 793-795. http://dx.doi.org/10.1126/ science.1066860.
- Pérez Cruzado C, Muñoz Sáez F, Basurco F, Riesco G, Rodríguez Soalleiro R, 2011. Combining empirical models and the process-based model 3-PG to predict *Eucalyptus nitens* plantation growth in Spain. Forest Ecol Manag 262 (6): 1067-1077. http://dx.doi.org/10.1016/j.foreco.2011.05.045.
- Retzlaff WA, Handest JA, O'Malley DM, McKeand SE, Topa MA, 2001. Whole-tree biomass and carbon allocation of juvenile trees of loblolly pine (*Pinus taeda*): influence of genetics and fertilization. Can J For Res 31(6): 960-970. http://dx.doi.org/10.1139/cjfr-31-6-960.
- Rodríguez-Suárez JA, Soto B, Iglesias ML, Diaz-Fierros F, 2010. Application of the 3PG forest growth model to a *Eucalyptus globulus* plantation in Northwest Spain. Eur

J Forest Res 129(4): 573-583. http://dx.doi.org/10.1007/ s10342-010-0355-6.

- Rosa D, Baños Moreno C, Mudarra Gómez JL, Barahona E, Moreira Madueño JM, Gago R, Ramos A, 1984. Catálogo de suelos de Andalucía. Junta de Andalucía, Sevilla, España.
- Sampson DA, Waring RH, Maier CA, Gough CM, Ducey MJ, Johnsen KH, 2006. Fertilization effects on forest carbon storage and exchange, and net primary production: A new hybrid process model for stand management. Forest Ecol Manag 221: 91-109. http://dx.doi.org/10.1016/j. foreco.2005.09.010.
- Samuelson LJ, Johnsen K, Stokes T, 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. Forest Ecol Manag 192: 59-70. http://dx.doi.org/10.1016/j. foreco.2004.01.005.
- Sánchez-Salguero R, Navarro-Cerrillo RM, Camarero JJ, Fernández-Cancio Á, 2010. Drought-induced growth decline of Aleppo and maritime pine forests in southeastern Spain. Forest Systems, 19: 458-470. http://dx.doi. org/10.5424/fs/2010193-9131.
- Sánchez-Salguero R, Navarro-Cerrillo RM, Camarero JJ, Fernández-Cancio A, 2012 a. Selective drought-induced decline of pine species in southeastern Spain. Climatic Change 113: 767-785. http://dx.doi.org/10.1007/s10584-011-0372-6.
- Sánchez-Salguero R, Navarro-Cerrillo RM, Swetnam TW, Zavala MA, 2012 b. Is drought the main decline factor at the rear edge of Europe? The case of southern Iberian pine plantations. Forest Ecol Manag 271: 158-169. http://dx. doi.org/10.1016/j.foreco.2012.01.040.
- Sánchez-Salguero R, Camarero J, Dobbertin M, Fernández-Cancio A., Vilà-Cabrera A., Manzanedo R, Zavala M, Navarro-Cerrillo RM, 2013. Contrasting vulnerability and resilience to drought-induced decline of densely planted vs. natural rear-edge *Pinus nigra* forests, Forest Ecol Manag 15: 956-967. http://dx.doi.org/10.1016/j.foreco.2013.09.050.
- Sands PJ, 2004. Adaptation of 3-PG to novel species: guidelines for data collection and parameter assignment. Technical Report. No. 141, CSIRO, CRC Sustainable Production Forestry, Hobart.
- Sands PJ, Landsberg JJ, 2001. 3-PGpjs: a user interface for 3-PG, a forest growth model. Version IDs 3-PGpjs 2 beta. CSIRO.
- Stape JL, Ryan M, Binkley D, 2004. Testing the utility of the 3-PG model for growth of *Eucalyptus grandis* x uro-phylla with natural and manipulated supplies of water and nutrients. Forest Ecol Manag 193: 219–234. http://dx.doi. org/10.1016/j.foreco.2004.01.031.
- Stokes MA, Smiley TL, 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson, Arizona, USA.
- Thornton PE, Running SW, 1999. An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. Agr Forest Meteorol 93: 211–228. http://dx.doi.org/10.1016/ S0168-1923(98)00126-9.

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- Ung CH, Bernier PY, Raulier F, Fournier RA, Lambert MC, Régnière J, 2001. Biophysical site indices for shade tolerant and intolerant boreal species. Forest Sci 47: 83-95.
- van Oijen M, Reyer C, Bohn F, Cameron D, Deckmyn G, Flechsig M, Härkönen S, Hartig F, Huth A, Kiviste A *et al.*, 2013. Bayesian calibration, comparison and averaging of six forest models, using data from Scots pine stands across Europe. Forest Ecol Manag 289: 255–268. http:// dx.doi.org/10.1016/j.foreco.2012.09.043.
- Vanninen P, Ylitalo H, Sievänen R, Mäkelä A, 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L). Trees-Struct Funct 10: 231–238. http://dx.doi.org/10.1007/bf02185674.
- Vega-Nieva DJ; Tomé M; Tomé J; Fontes L; Soares P; Ortiz L; Basurco F; Rodríguez-Soalleiro R, 2013. Developing a general method for the estimation of fertility rating

parameter of the 3-PG model: Application in *Eucalyptus globulus* plantations in Northwestern Spain. Can J For Res 43: 627-636. http://dx.doi.org/10.1139/cjfr-2012-0491.

- Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD, 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3: 292–297. http://dx.doi. org/10.1038/nclimate1693.
- Willmott CJ, 1981. On the validation of models Physiographic Plant Geography 2: 184-194.
- Xenakis G, Ray D, Mencuccini M, 2008. Sensitivity and uncertainty from a coupled 3-PG and soil organic matter decomposition model. Ecol Model 219: 1-16. http://dx.doi. org/10.1016/j.ecolmodel.2008.07.020.