

# "Assessing ecosystem functioning on Mediterranean forests in the context of Global Change: the case study of Mont Ventoux (France)"



Noelia López García

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# Supervised by:

Dr. Hendrik Davi. Ecologie des Forêts Méditerranéennes (INRA-PACA)

# **Co-supervised by:**

Dr. François Lefèvre. Ecologie des Forêts Méditerranéennes (INRA-PACA)

Dr. José Antonio Bonet Lledós. University of Lleida (UdL)



# University of Lleida

# School of Agrifood and Forestry Science and Engineering

Master thesis:

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"Optimism is the faith that leads to achievement. Nothing can be done without hope and confidence."

- Helen Keller -

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### Abstract

To assess the global change effects on the functioning of Mediterranean forests ecosystems, we implemented a physiologically multi-layer, process-based model (CASTANEA). The model was firstly evaluated on three Integrated Carbon Observation System (ICOS) sites by comparing measured fluxes by eddy covariance technics and simulations of Gross Primary Production (GPP), Ecosystem Respiration (Reco), and Net Ecosystem Exchange (NEE). A set of simulations have been then conducted on Mont Ventoux (South-eastern France) on nine species, which are present in Mediterranean forest ecosystems. The selected species included deciduous species (Fagus sylvatica L., Quercus pubescens Mill.), coniferous species (Pinus halepensis Mill., Pinus nigra J.F.Arnold., Pinus sylvestris L., Pinus uncinata Ramond ex DC., Abies alba Mill., Cedrus Atlantica (Manetti ex Endl.) Carrière.), and sclerophyllous evergreen species (*Quercus ilex* L.). The model was first operated by the results of the meteorological Safran-gauge-based analysis system for the period 1958 - 2016. Then, the model has been driven by two regional climate models (RCMs) for the historical period 1961-2015 and the period 2016 - 2100, following two Representative Concentration Pathway (RCP 4.5 and RCP 8.5) scenarios of the Intergovernmental Panel on Climate Change (IPCC). From 1958 to 2015, the average temperature risen by 2,8 °C and the rainfall in altitude increased by 48,88 mm. For the future projections under the RCP 4.5 and RCP 8.5 scenarios from CNRM - CM5 (RCM) the average temperature will rise by 1,28 °C and 4,52 °C respectively, and the average rainfall will increase 180,48 mm under RCPs 4.5, but it will drop by -112,24 mm under RCPs 8.5. Future predictions by HadGEM2 - ES (RCM) under RCPs 4.5 and RCPs 8.5, the temperature on average will increase by 2,85 °C and 5,79 °C respectively; likewise, the precipitation on average will drop by -142,84 mm under RCPs 4.5 and by -212,67 mm under RCPs 8.5. The ecosystem always remains carbon sink; however, the pool strength globally decreases for future projections for coniferous species and to a lesser degree for deciduous forest and sclerophyllous evergreen. Besides, we observed a substantial decrease in the NEE as well as an increase in the mortality rate under RCP 8.5 on the HadGEM2 - ES model. By contrast, implemented silviculture have a positive effect, allowing an increase in the tree-ring width, the [NSC] and finally an increment in NEE as well as a significant decrease in the mortality rate.

**Keywords:** Forest ecosystem functioning; Global change; Carbon balance; Water balance; Eco-physiological model.

### 1. Introduction

According to the Intergovernmental Panel on Climate Change (IPCC, 2013), the atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]) will increase throughout the 21<sup>st</sup> century. Due to this fact, is expected an increase in annual temperatures and based on the results of several models, also a significant decrease in summer precipitations, thereby, will trigger an increase in aridity worldwide. Under these harsh conditions, the scenarios forecast an unfavourable future for the future of Mediterranean forests, since they are currently already limited by water stress and high temperatures (Frank et al., 2015). As a positive fact, these ecosystems are already adapted to drought that can make them more resilient to climate change. In this changing frame, the ecosystem carbon balance, which could be represented through the below formula, will be directly influenced in various ways. Through NEE it can be determined if the forest ecosystem could be a source or a sink of carbon and to what degree (Le Maire et al., 2005).

Net Ecosystem Exchange (NEE) = Gross Primary Production (GPP) – (autotrophic respiration (Ra) + heterotrophic respiration (Rh)).

CO<sub>2</sub> fertilisation will drive a rise in leaf photosynthesis and, thus, GPP will undergo an increase (Davi et al., 2006). Likewise, high temperatures in spring will induce earlier leaf bud burst and flowering for deciduous species (Badeck et al., 2004), and higher photosynthesis rate for coniferous, thus, both will allow an increase in annual GPP (Davi et al., 2006). Nonetheless, high temperatures may rise autotrophic and heterotrophic respiration which will trigger a decrease in NEE (Davi et al., 2006). On the other hand, changes in rainfall patterns may arouse a decline in soil water content and, therefore, an increase in drought. Besides, high-temperatures shall increase the evaporative demand, which might drive soil water depletion, arousing a decline in photosynthesis and soil respiration rates. Likewise, ecosystem respiration would also be impacted by water availability. Although NEE dynamics depends on all these previously mentioned processes among others, it has to be taken into account that NEE could vary across time and space depending on climate and ecosystems properties (Davi et al., 2006; Figure 1). Forest productivity will also be directly affected by water stress since it is one of the environmental factor limiting plant growth.



Figure 1: Effects arising from the increase of atmospheric  $CO_2$  concentration and its influence on Carbon stockage; adapted from Davi et al., (2006).

Nowadays there are still many uncertainties and doubts about how the system performs. That is caused by its intrinsic complexity, as well as by the lack of long-term measurements along with the number of devices needed to accomplish it. Hence, it becomes necessary to develop new tools in order to facilitate the understanding of these complex processes properly, further, with the aim to integrate all previously accumulated knowledge. Despite the intricacy, ecophysiological process-based models have been designed and developed to simulate forest functioning as well as reduce uncertainty derived from complex systems.

Ecophysiological process-based models are powerful tools that are vastly valuable to simulate and predict climate changes effects over forest ecosystems as well as to estimate the impact of forest management on the ecosystem functioning (Makela et al., 2000; Morales et al., 2005). Conversely, empirical forest models are more based on substantial data sets from field measurements and experiments, but these models *per se* are not designed to predict seasonal variations in tree growth and the stand biomass increment and are less robust when used outside the range of variation for which they have been calibrated. Therefore, those models are not an appropriate tool as such to account for the effects of global climate change (Le Maire et al., 2005). Nevertheless, the use of empirical forestry knowledge coupled with ecophysiological process-based models, nowadays are the appropriated combination to build a sound approach for

modelling and foretell the evolution of forest and its productivity under changing environmental conditions. A global network (FLUXNET) long-term eddy flux stations have also been established aiming to monitor  $CO_2$ , energy and  $H_2O$  fluxes allowing to evaluate these models, ("European Fluxes Database Cluster - Sites List" 2018). Besides, several research programs, employing models as mentioned previously, have been conducted on temperate, boreal and also tropical forest to depth analysing soil organic matter dynamics and NEE of  $CO_2$ , pursuing to evaluate forest productivity as well as studying the ability of forest soils to act as a carbon sink through both aboveground and belowground litter and biomass.

Due to global change and its effects on natural systems, through this research, we desire to predict and assess impacts of past, current and future development for ecosystem functioning on "Mont Ventoux", a future Regional Natural Park in South-eastern France. Furthermore, we consider that it is essential to identify factors and mechanisms that make Mediterranean forests resilient under global change conditions. Besides, it is crucial to in-deep study and understands how these respond to different drivers of change (direct and indirect) and their interactions, at different spatiotemporal scales. Additionally, it is considered that through the implementation of forest management will help to alleviate the impact of climate change on the Mediterranean forest, to improve water balance, to foster resilience and resistance in some species, as well as, to increase productivity. Likewise, it is desirable to estimate the effects of forest management for each species and every bioclimatic stage following the below aims:

To reduce adverse effects arising from climate change

To foster an increase in timber and biomass production

To promote resilience and resistance in the remained communities facing against aridity conditions

Nowadays it is well known that changing climate will affect ecosystem functioning and, thus, forest productivity. In the same way, forest management will have to adapt to the new conditions in order to face climate change as well as to continue with sustainable production, to supply the current and future demand for wood products. Nonetheless, it is necessary to properly evaluate which would be the best choice of species, rotations, thinning schedules, harvesting operations and so forth. On the other hand, it is required to equip forest owners with proper guidance for specific circumstances derived from

climate change, along with new tools and support to incorporate new business opportunities, as well as to progress with the development of rural areas.

In order to cope against climate change along with to promote the sustainable production of the forest, it has been developed a new management strategy which aims to improve wood products in the area and to adapt forest management to changing climate conditions, as well as, to the current and future demand. To accomplish that, a few targets directly related to forest conservation and productivity within a reference scenario have been established; moreover, it has been taken into account The European Forest Sector Outlook Study II (EFSOS II) guidelines projections (FAO, 2011) of total consumption for forest wood products, as well as the yearly increase in gross domestic products (GDP) expected to 2030.

In the study area, the current consumption of wood is composed by, 60% paper and paperboard (*Pinus nigra* J.F.Arnold.), 8% saw wood (*Abies alba* Mill., *Cedrus Atlantica* (Manetti ex Endl.) Carrière.) and 32% energy (except 28% for "wood-briquette", *Quercus ilex* L., *Quercus pubescens* Mill.). In the context of the creation of the future Regional Natural Park in Ventoux, three scenarios are envisaged by researchers and foresters. In the "**business-as-usual**" scenario, according to EFSOS II guidelines projections, total consumption for wood products is expected to rise by 0.72% per year and the fuel consumption by 1.5% per year (FAO 2011).

In the scenario **promoting carbon storage within wood and soils,** we expected a slight rise in the total consumption, yet no more than in the reference scenario (respectively 0.5% and 1.2%). With this purpose, a mixed approach could be carried out. On the one hand, a few patches of old forest mainly composed by *Fagus sylvatica* L., and *Abies alba* Mill., without management or with slightly controlling located at the higher elevation and in inaccessible areas will remain for biodiversity conservation. On the other hand, it will be applied intensive management throughout pine forests to increase their productivity. Changes in the silvicultural methods were made to optimise rotation lengths and thinning schedules.

In the last scenario, **fostering wood energy**, it is expected a significant rise in local demand for fuel energy. It has been hypothesised a fuel consumption will increase by 3.5, with a rate of 6.5% per year. Along with the productivity target, natural regeneration of autochthonous tree species will be fostered except in the unexpected occurrence of massive drought-induced dieback, where pines plantation will be allowed.

The proposed management strategy is a needs assessment designed to understand the current state of forest in Mont Ventoux along with the forest industry development in the Region. Hence, it has been taken into account current and future demands, as well as the possible implementation of new policies, considering uncertainty associated with climate change.

We decided to focus on Mont Ventoux, as a case study, for being one of the Mediterranean forests with a complex ecological system. In order to accomplish that end, it has been implemented the use of future scenarios, and the eco-physiological process-based model (CASTANEA) using forest data from French National Forest Inventory (IFN) to predict the forest ecosystem functioning and ecosystem services provisioning under two different global change scenarios (RCP 4.5 and RCP 8.5).

Three questions have been addressed in this study: How will affect the increase of  $[CO_2]$ , the rise in temperature and the decrease in precipitation over ecosystems functioning? How will the different species response to face climate change? How will impact forest management on balance and fluxes of carbon and water?

# 1.1. Objectives

The primary objective of this study is to model how the effects of climate change will affect the ecosystem functioning of the Mediterranean forests on Mont Ventoux assessing how this forest will evolve under this harsh conditions throughout this century. Hence, our specific objectives are:

- Analyse the effect of climate change on forest productivity

- Evaluate the impact of climate change on individual species dynamics

- Assess the influence of forest management on reducing the climate change effects

### **1.2. Hypotheses**

Due to the increase of atmospheric  $[CO_2]$ , changes in precipitation and temperature patterns are expected to modify the annual cycle of plants activity. Therefore, we hypothesise:

I. Forest productivity will decrease at lower altitudes, where water is limiting and increase at higher altitude where the temperature is limiting (Cailleret and

Davi, 2011). As it is well known, the temperature is one of the principal drivers of several developmental processes in biology. Furthermore, water has a relevant role to play in plants productivity, as it was aforementioned. The expected increase in temperature might trigger an increment in the vegetation period length arousing -in turn- a rise in the photosynthetic rate. Besides, the expected drop in the precipitation rate and the increase of the transpiration rate due to warming will induce higher water stress and, therefore, a reduction in the photosynthesis rate, as well as a decline in the respiration rate, along with an increment in the respiration rate, which will finally provoke a decrease in the NEE.

- II. Species will be variously affected by the effects of the climate change (Davi et al., 2006b): deciduous species will benefit from the lengthening of vegetation, while evergreen sclerophyll and coniferous will suffer from an increase of respiration. Species already adapted to water stress (*Quercus ilex* L., or *Pinus halepensis* Mill.) will be less impacted than species vulnerable to drought (*Fagus sylvatica* L., or *Abies alba* Mill.).
- III. Forest management applied will help to mitigate the effects of climate change in the study area as well as to foster an increase in the resilience and resistance of remaining communities (Loustau et al., 2005).

### 2. Material and methods

#### **2.1. Site characteristics**

The Mont Ventoux (44°11'N; 5°17'E) is located in South-eastern France, 1909 m above sea level (a.s.l.) in Vaucluse department within the Provence-Alpes-Côte d'Azur region. Mont Ventoux is a calcareous mountain, which comprises five bioclimatic stages distributing in altitude from the Mediterranean (300 - 800 m), Supra-Mediterranean (600 - 1200), Mountain (1200 - 1700), Subalpine (1600 - 1800) to the Summit (1800 - 1909 m). Climate-type is the Mediterranean, characterised by rainy autumn and dry summer. The mean annual temperature has been 6.8 °C, and the annual precipitation on average was 1300 mm. (weather station of Mont Serein, 1,445 m, a.s.l., 1993–2006). According to local weather station data, precipitation increased by 48.88 mm/100 m and temperatures decreased by  $-0.65^{\circ}$ C/100 m towards higher altitudes (see Cailleret et al., 2013 for a description of local weather station). Simulations were performed along an altitudinal gradient located on both flanks, North and South of Mont Ventoux (ranging from 150 m, 450 m, 800 m, 1100 m, 1400 m and to 1750 m, where are established main species living in such place).

#### 2.1.1. Measurements for model validation

We have used three sites belonging to the ICOS network (Hesse, Font-Blanche and Puéchabon) aiming to validate the model against eddy covariance fluxes for a subset of species present on Mont Ventoux (*Fagus sylvatica* L., *Quercus ilex* L., *Pinus halepensis* Mill.).

#### 2.1.1.1. Font-Blanche site

The experimental site is located in Font-Blanche at the Department of Bouches du Rhône (13), 9 km North-East of La Ciotat (5°40'45"E, 43°14'27"N and altitude 420 m above sea level), in a mixed forest, co-dominated by the Aleppo pine (*Pinus halepensis* Mill.) and by a coppice of Holm oak (*Quercus ilex* L.), two of the most represented species in the Mediterranean region. The soil type was limestone with a high load of pebbles and a silty-clay-sand content. The area has a Mediterranean-type climate. The annual precipitation was 722 mm and an average temperature of 13.5°C (Aubagne-Les-Passons station, altitude 111 m above sea level, located 11 km West-North-West). The tower is managed by the National Institute of Agronomic Research of Avignon (Institut

National de la Recherche Agronomique). For more detailed information, ("F-ORE-T : Observatoire de Recherche En Environnement Sur Le Fonctionnement Des Écosystèmes Forestiers" 2018).

#### 2.1.1.2. The Hesse site

The experimental Euroflux site (FR02) is located in the State forest of Hesse, Eastern France (48°40' N, 7°05' E, and altitude 305 m above sea level); in a 30-year-old (in 1997) naturally regenerated beech stand (*Fagus sylvatica* L.) with very sparse understorey. The experimental plot (0,63 ha) was in the central part of a 65 ha zone composed mainly by young Beech with a density around 3480 trees ha<sup>-1</sup> and a dominant height close to 14 m. The soil type was intermediate between a luvisol and a stagnic luvisol, with a clay content ranged between 25% and 40%. The annual precipitation was 820 mm and an average temperature of 9.2°C. Three towers were established. One (18 m high) was used for eddy covariance (EC) and microclimate measurements. The two others (15 m high) were dedicated to ecophysiological measurements. For more details see (Davi et al., 2005), ("ExpeER - Hesse (France)" 2018).

# 2.1.1.3. The Puéchabon site

The experimental site is located in the Puéchabon State Forest, Southern France (43°44'N, 3°35'E, and altitude 270 m above sea level). The tower is managed by CEFE-Montpellier (Centre d'Écologie Fonctionnelle et Évolutive). The Puécharbon forest has been managed as coppice. Vegetation is largely dominated on the overstorey by *Quercus ilex* L., (90 %) and *Quercus pubescens* Mill., (10 %). Its understorey is sparse and principally composed of shrubs such as *Buxus sempervirens* L., *Phyllirea latifolia* L., *Pistacia terebinthus* L., and *Juniperus oxycedrus* L. The stand density is around 8500 trees ha<sup>-1</sup>. The soil is classified as calcareous fersiallitic with high clay content. The stone and rock fraction are about 90% across the whole-soil profile. The area has a Mediterranean climate. Rainfall occurs during autumn and winter with around 75% between September and April. The mean annual precipitation is 916 mm, and the mean annual temperature was 13.0 °C, both recorded over the 1984 – 2011 period. For more details, see (Hoff et al., 2002), ("Site Expérimental de Puéchabon" 2018).

#### 2.1.2. Meteorological data

In Ventoux, CASTANEA model was first operated by the results of the meteorological Safran-gauge-based analysis system for the period 1958 - 2015. Then, the model has been driven by two regional climate models (RCMs) for the historical period 1961-2015 and the period 2016 - 2100, following the RCP 4.5 and RCP 8.5 scenarios of the IPCC. Currently, there is a subset of four climate projections for the 21<sup>st</sup>-century build on RCPs that are used to cover a broad bandwidth of future climate evolutions (Illy et al., 2017). Concerning these two RCP scenarios used to accomplish the study, it has to be emphasised that RCP 4.5 match the most optimistic scenario while RCP 8.5 corresponds to the most pessimistic future scenario.

# 2.1.2.1. SAFRAN - Système d'Analyse Fournissant des Renseignements Atmosphériques à la Neige' (*Analysis system providing data for snow model*)

SAFRAN is a meteorological analysis system that provides atmospheric surface observations, combined with analysis of meteorological models to produce meteorological input data such as temperature, humidity, wind, precipitation solids and liquids, sunlight and infrared incident (Durand et al., 1999). Meteorological parameters are analysed every 300 m a.s.l., and finally interpolated on a regular grid (8 x 8 km). This analysis system was first developed in France to supply data in mountainous areas for avalanche hazard forecasting (Durand et al., 1999), but more recently it has developed a new tool in order to model main parts of the continental water cycle at the regional scale in France (Quintana-Seguí et al., 2008). Two points of the regular grid located in the Ventoux, one in North (point 8147) and the other in South (point 8238) aspect of the Mountain.

#### 2.1.2.2. Estimation of continuous climate gradients on Mont Ventoux

The aim was to obtain long-term meteorological data on continuous elevations located on Mont Ventoux. Measurements were taken on the ten forest sites targeted in the study with local weather stations (2007 - 2015). The minimum, maximum, and average temperatures, rainfall and relative humidity, were recorded with Prosensor HOBO Pro (RH/Temp; Onset Computer Corporation, Bourne, MA 02532, USA). Sensors were situated 1.5 m-high above the ground and were protected by a white plastic shelter to prevent any exposure to rain or to direct sunlight (Davi and Cailleret, 2017). All the regressions coefficients were used to generate daily climate data from 1959 to 2015 based on the long-term SAFRAN outputs using equations described in (Oddou-Muratorio and Davi, 2014).

#### 2.1.2.3. HadGEM2 - ES. Global Environment Model

The Hadley Centre Global Environmental Model version 2 (HadGEM2) family of the Earth system models was designed aiming at simulating and understanding the centennial scale evolution of climate including biogeochemical responses (Collins et al., 2011). The HadGEM2 family includes a coupled atmosphere-ocean configuration, with or without a vertical extension in the atmosphere to include a well-resolved stratosphere, and an Earth-System configuration which includes dynamic vegetation, ocean biology and atmospheric chemistry to characterise features of the Earth system (Martin et al., 2011), (Collins et al., 2011). Nowadays, the HadGEM2 - ES model is a useful tool to predict future climate, furthermore, provides to better understand the contributions of biogeochemical feedbacks to the future evolution of the climate system within the Earth system (Collins et al., 2011). Additional information on the model is given by Collins et al., (2011) and Martin et al., (2011).

#### 2.1.2.4. CNRM - CM5. Global Climate Model

Coupled CNRM - CM / AOGCMs - Atmosphere-Ocean General Circulation Models, have been developed by the CNRM-GAME (Centre National de Recherches Météorologiques - Groupe d'études de l'Atmosphère Météorologique) and CERFACS (Centre Européen de Recherche et de Formation Avancée). CNRM - CM5 is an Earth system model designed to make future climate projections, (Voldoire et al., 2013), which consist of several existing models designed independently and coupled through the OASIS software developed at CERFACS (Voldoire et al., 2013). CNRM-CM5 can simulate present climate and its variability on timescales ranging from months to centuries. Likewise, CNRM - CM5 is a fundamental tool which could help to improve understanding of the climate system, as well as to perform seasonal forecasts. The model allows users to simulate the historical period (1850 - present) and it performs climate change attribution studies. Furthermore, is a proper tool to simulate future climate depending on greenhouse gases scenarios. Additional information on the model can be found at ("CNRM Contribution to CMIP5" 2018) - National Centre for Meteorological Research.

#### 2.1.2.5. On the choice of the two models

To accomplish this study, we have selected the previously mentioned climates model scenarios. Being CNRM – CM5 the coldest model, that also can predict the rise in precipitation, and HadGEM2 - ES the warmest model which, likewise, can foretell a decrease in rainfall. On the other hand, both models have been interpolated on a regular grid ( $12 \times 12 \text{ km}$ ) aiming to be adjusted as regional climate models.



Change in mean surface temperature by 2080s (°C)

Figure 2: Scatter plots indicating regional average changes in mean temperature and precipitation for the European region, (McSweeney et al., 2015).

### 2.2. Model description

CASTANEA is an ecophysiological process-based model aiming to predict water and carbon flux balances in forest stands (Dufrêne et al., 2005b). Canopy is assumed to be homogeneous horizontally and is vertically subdivided into a variable number of layers, each of them with the same amount of leaf area. One averaged tree is measured as representative of the whole stand; thereby, each tree behaves as a dominant tree (i.e. any variation among trees is not consider). Mortality rate is estimated in CASTANEA from carbohydrate storage and dynamics of midday leaf potentials assuming that adult mortality is either due to carbon starvation or to hydraulic failure. Thus, neither there is any mortality due to light competition or perturbations such as storms. In CASTANEA, the tree structure is assumed as a combination of five different functional parts: stems, branches, leaves, coarse and fine roots, (Davi et al., 2005). Besides, a carbohydrate storage section is additionally included, but not physically located within the tree. The main simulated output variables are the canopy photosynthesis, maintenance and growth

respiration, growth of organs, soil heterotrophic respiration, tree transpiration, and ecosystem evapotranspiration (Davi et al., 2006).

For each canopy layer, photosynthesis is hourly or half-hourly estimated based on (Farquhar et al., 1980) model which -in turn- has been analytically coupled to the stomatal conductance model proposed by (Ball et al., 1987) that consecutively describe stomatal conductance  $(g_1)$  to the result of photosynthesis and relative humidity. Growth and maintenance respiration rates are assessed proportionately to the nitrogen content of the examined organs (Ryan, 1991) and from growth increment linked with a construction cost explicit to the tissue or organ type. (De Vries et al., 1974), (Dufrêne et al., 2005). In this study, the alive cell respiration decrease with dbh and we add an effect of drought on autotrophic respiration following the exponential equation and coefficient given by (Rodríguez-Calcerrada et al., 2014). Transpiration and evapotranspiration are also hourly calculated and are based on the big-leaf Penman-Monteith equations (Monteith, 1965). Soil water content (SWC; in mm) balance is daily assessed using a bucket with three layers (Davi et al., 2006). According to the species, soil water deplete drives stomata closure, either by a linear decrease of  $g_1$  when relative soil extractable water (SEW) is under 40% (Granier et al., 2000), or by a relationship between Soil water potential ( $\psi_{soil}$  in MPa) and  $g_1$  (Sala and Tenhunen, 1996).  $\psi_{soil}$  was calculated from daily soil water content (Campbell, 1974), and leaf water potential ( $\psi_{\text{leaf}}$ ) was estimated hourly from simulated transpiration according to Davi and Cailleret, (2017) and following the model used in Loustau et al., (1998). The resistance (R<sub>soil-leaf</sub>) was estimated employing sapflow measurements as well as midday and predawn water potentials measured previously in Mont Ventoux (Davi and Cailleret, 2017).

In the carbon allocation sub-model, which was further developed in Davi et al., (2009a), the allocation coefficients among compartments were daily calculated depending on the sink vigour and the phenology of the species (Davi and Cailleret, 2017). All phenological events were also daily assessed depending on day-degrees and day length (Davi et al., 2009a). Within the sub-model, it has been considered that throughout winter, carbon was solely distributed to reserves and fine roots (Davi and Cailleret, 2017). After the beginning of budburst, carbon was suitably redistributed firstly to the development of leaves and fine roots, and after that for wood growth (coarse roots and stems) (Davi and Cailleret, 2017). Following the methodology described in Davi et al., (2009b), the fine roots pool was calculated aiming to maintain a constant ratio between

fine roots and leaves, while the leaf sink was forced by phenology. Considering that tissue development is one of the first physiological processes hindered by drought (Körner, 2015). In this study, we further have developed the model by adding a direct effect of  $\psi_{soil}$  on wood growth and by the establishment of an external constraint, assuming no growth when the temperature is below 5°C. The allocation coefficient for coarse roots has been deduced considering a constant ratio among coarse roots and trunks (Dufrêne et al., 2005).

To estimate stand density, average height and diameter, a few simple empirical algorithms were implemented in this version of CASTANEA, which allowed us to simulate the development of stand density. Likewise, average tree height and diameter were annually calculated. The increment of aboveground and belowground woody biomass has also been simulated by CASTANEA and distributed between branches, trunks and leaves, as a function of stand age, according to (Le Dantec et al., 2000), for the case of aboveground woody biomass. A more detailed description of CASTANEA model, including equations, is provided in Dufrêne et al., (2005).

# 2.3. Model adaptation

Previous versions of the model were fully parameterised and validated against data from beech stand (Dufrêne et al., 2005a), (Davi et al., 2005). Subsequently, new modifications of the phenology module were conducted to be used with a Mediterranean evergreen sclerophyllous (*Quercus ilex* L.) and with coniferous species (*Pinus sylvestris* L., and *Pinus pinaster* Ait.), (Davi et al., 2006). Nowadays, new improvements of the model have been carried out in order to incorporate new tree species, and a new module has been developed to include a set of silvicultural treatments to be applied at the stand level. It may be emphasised that it was the first time that CASTANEA model has simulating the evolution of annual productivity and carbon fluxes through the implementation of forest management. This new tool has provided users with the opportunity to evaluate how the forest would evolve under different climate change scenarios, considering the implementation or not of silvicultural treatments. Main silvicultural treatments were designed with aims previously mentioned in the introduction.

Additionally, the use of the RCP 4.5 and RCP 8.5 scenarios, might help to gain insights into the consequences of some silvicultural treatments choices although, these scenarios

are not meant to give prognostications of what will happen in the future, but, to provide awareness about the behaviour of the system and how climate change could influence it.

Within CASTANEA model three kinds of parameters are distinguished, (1) constant parameters through species and sites, (2) site-specific parameters and species-specific parameters. Constant parameters are listed in Dufrêne et al., (2005). The main species-specific parameters used in this study are given in Table 1.

A complete parameterisation of main species included in the study has been accomplished thanks to careful research upon material listed in the select bibliography. For some other species, for example, parameterisation of the model was given by Dufrêne et al., (2005a) for *Fagus sylvatica* L., by Davi et al., (2006) for *Quercus ilex* L., and by Davi and Cailleret, (2017) for *Abies alba* Mill.

The site-specific parameters are more related to local-scale physical or biophysical coefficients describing the vegetation and the soil. In the study, these parameters were estimated using data from the French National Inventory (IFN) as well as local data (i.e. height, diameter at breast height (dbh)). On the other hand, the leaf area index (LAI) databases employed belong to remoting sensing information from the Sentinel-2 satellite.

PARAMETERS	Species Parameters								
	Abies alba	Cedrus atlantica	Fagus sylvatica	Pinus halepensis	Pinus nigra	Pinus svlvestris	Pinus uncinata	Quercus ilex	Quercus pubescens
LEAF CONSTRUCTION COST	1.21 <sup>AV</sup>	1.21 <sup>AA</sup>	1.2 <sup>AW</sup>	1.32 <sup>A</sup>	1.32 <sup>A</sup>	1.32 <sup>A</sup>	1.32 <sup>A</sup>	1.294 <sup>AX</sup>	1.2 <sup>BB</sup>
COARSE ROOTS CONSTRUCTION COST	1.2 <sup>AV</sup>	1.2 <sup>AA</sup>	1.38 <sup>AW</sup>	1.206 BB	1.206 <sup>BB</sup>	1.206 BB	1.206 <sup>BB</sup>	1.194 <sup>AX</sup>	1.38 <sup>FS</sup>
FINE ROOTS CONSTRUCTION COST	1.28 <sup>AW</sup>	1.28 <sup>AA</sup>	1.28 <sup>AW</sup>	1.28 <sup>AW</sup>	1.28 <sup>AW</sup>	1.28 <sup>AW</sup>	1.28 <sup>AW</sup>	1.28 <sup>AX</sup>	1.28 <sup>AW</sup>
WOOD CONSTRUCTION COST	1.18 <sup>AV</sup>	1.18 <sup>AA</sup>	1.38 <sup>AW</sup>	$1.206^{B}$	1.206 <sup>B</sup>	1.206 <sup>B</sup>	1.206 <sup>B</sup>	1.194 <sup>AX</sup>	1.38 <sup>AW</sup>
RATE OF ALIVE CELLS IN STEM	0.46 <sup>AV</sup>	0.2 <sup>C</sup>	0.245 <sup>AW</sup>	$0.2^{C}$	0.24 <sup>D</sup>	0.24 <sup>D</sup>	0.24 <sup>D</sup>	0.15 <sup>CP</sup>	0.21
RATE OF ALIVE CELLS IN BRANCHES	0.46 <sup>AV</sup>	0.34 <sup>CT</sup>	0.42 <sup>AW</sup>	$0.2^{\circ}$	0.408 <sup>CT</sup>	0.408 <sup>CT</sup>	0.408 CT	0.15 <sup>CP</sup>	0.37
RATE OF ALIVE CELLS IN COARSE ROOTS	0.46 <sup>TV</sup>	0.2 <sup>TV</sup>	0.26 <sup>AW</sup>	0.2 <sup>TV</sup>	0.24 <sup>TV</sup>	0.24 <sup>TV</sup>	0.24 <sup>TV</sup>	0.1 <sup>CP</sup>	0.21 <sup>TV</sup>
INITIAL [NSC]	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.15 <sup>FV</sup>	0.2 <sup>FV</sup>
PERCENTAGE OF NITROGEN IN LEAVES	1.04 <sup>DU</sup>	1.52 <sup>DT</sup>	2.2 <sup>v</sup>	1.181 <sup>DT</sup>	1.019 <sup>E</sup>	1.33 <sup>F</sup>	1.22 <sup>G</sup>	1 <sup>DT</sup>	1.85 <sup>DT</sup>
[NITROGEN] IN COARSE ROOTS	9.40E-04 <sup>AV</sup>	9.40E-04 AA	1.60E-03 <sup>AW</sup>	1.18E-03 <sup>H</sup>	8.50E-04 <sup>G</sup>	0.001	8.50E-04 <sup>G</sup>	4.00E-03	1.20E-03
[NITROGEN] IN FINE ROOTS	8.20E-03 <sup>AV</sup>	8.20E-03 AA	0.007 <sup>AW</sup>	8.27E-03 <sup>H</sup>	8.10E-03 <sup>G</sup>	8.50E-03	8.10E-03 <sup>G</sup>	4.00E-03	9.90E-03
[NITROGEN] IN BRANCHES	4.00E-03 <sup>AV</sup>	4.00E-03 AA	5.50E-03 <sup>AW</sup>	1.18E-03 <sup>H</sup>	4.90E-03 <sup>G</sup>	1.80E-03	4.90E-03 <sup>G</sup>	4.00E-03	5.50E-03 <sup>BE</sup>
[NITROGEN] IN STEM	9.40E-04 <sup>AV</sup>	9.40E-04 AA	1.60E-03 <sup>AW</sup>	5.91E-04 <sup>H</sup>	1.42E-03 <sup>G</sup>	1.60E-03	1.42E-03 <sup>G</sup>	4.00E-03	1.20E-03
PREDAWN POTENTIAL FOR GROWTH CESSATION	-1.6 <sup>1</sup>	-21	-2.6 <sup>1</sup>	-2.21	-2.28 <sup>1</sup>	-2.1 <sup>1</sup>	-2.28 <sup>I</sup>	-3.15 <sup>1</sup>	-2.8 <sup>1</sup>
INITIAL CARBON ALLOCATION COEFFICIENT TO WOOD	0.42 <sup>BA</sup>	0.42 <sup>FV</sup>	0.1 <sup>BA</sup>	0.42 <sup>BA</sup>	0.42 <sup>BA</sup>	0.3 <sup>BA</sup>	0.42 <sup>BA</sup>	0.1 <sup>BA</sup>	0.2 <sup>BA</sup>
FINE ROOTS TURNOVER	11	1 1	11	1.51	1.5 1	1.51	1.5 1	11	1 1
RATIO BETWEEN BRANCHES AND TOTAL ABOVEGROUND BIOMASS	0.15 AV	0.15 <sup>AA</sup>	0.2 <sup>AW</sup>	0.286 <sup>K</sup>	0.286 <sup>K</sup>	0.286 <sup>K</sup>	0.268 <sup>L</sup>	0.164	0.2 <sup>FS</sup>
RATIO BETWEEN COARSE ROOTS AND TOTAL WOOD BIOMASS	0.22 <sup>AV</sup>	0.22 AA	0.2 AW	0.167 <sup>o</sup>	0.183 <sup>M</sup>	0.231 <sup>M</sup>	0.297 <sup>N</sup>	1 <sup>c</sup>	0.2 <sup>FS</sup>
RATIO BETWEEN FINE ROOTS AND LEAVES BIOMASS	0.3 <sup>AV</sup>	0.3 <sup>AA</sup>	1 <sup>AW</sup>	1.25 <sup>J. P</sup>	1.25 <sup>J. P</sup>	1.25 <sup>J. P</sup>	6.54E-01 <sup>Q</sup>	0.33 <sup>R</sup>	$1^{FS}$
BRANCHES MORTALITY	7.00E-05 <sup>FS</sup>	7.00E-05 <sup>FS</sup>	7.00E-05 <sup>AW</sup>	2.19E-04 <sup>s</sup>	1.37E-04 <sup>K</sup>	7.00E-05 <sup>K</sup>	1.37E-04 K	7.00E-05 FS	7.00E-05 FS
LEAF AREA	5.00E-04 <sup>AV</sup>	1.04E-05 <sup>T</sup>	1.80E-03 <sup>AW</sup>	1.50E-03 <sup>H</sup>	1.11E-04 <sup>E</sup>	7.05E-03 <sup>DU</sup>	1.06E-04 <sup>U</sup>	3.70E-03 <sup>BE</sup>	3.70E-03 <sup>BE</sup>
LEAF MASS PER AREA OF SUN LEAVES	292 AV	245 <sup>T</sup>	$100^{\vee}$	392 <sup>v</sup>	227 <sup>E</sup>	246.7 <sup>C</sup>	256.1 <sup>E</sup>	224 <sup>AX</sup>	93 <sup>DO</sup>

PARAMETERS	Abies alba	Cedrus	Fagus	Pinus	Pinus nigra	Pinus	Pinus	Quercus ilex	Quercus
EXTINCTION COEFFICIENT OF LEAF	7.29E-02 <sup>BU</sup>	atlantica 7.29E-02 <sup>AA</sup>	sylvatica 0.187 <sup>C</sup>	halepensis 0.076 <sup>C</sup>	0.076 <sup>°</sup>	sylvestris 5.79E-02 <sup>C</sup>	uncinata 0.076 <sup>C</sup>	0.14 <sup>C</sup>	pubescens 0.187 <sup>C</sup>
MASS PER AREA WITHIN THE CANOPY LEAF ANGLE	40 <sup>AV</sup>	40 <sup>AA</sup>	24 <sup>AW</sup>	48 <sup>H</sup>	48 <sup>H</sup>	51 <sup>AX</sup>	48 <sup>H</sup>	30 <sup>AX</sup>	33.15 <sup>BE</sup>
BRANCHES ANGLE	8.7 <sup>AV</sup>	8.7 <sup>AA</sup>	45 <sup>AW</sup>	10	68.23 <sup>X</sup>	10 AX	68.23	40 <sup>AX</sup>	45 <sup>FS</sup>
SLOPE OF THE CROWN AREA TO DBH	8.15E-02 <sup>C</sup>	8.04E-02 <sup>Y</sup>	0.108 <sup>C</sup>	8.52E-02 <sup>C</sup>	8.31E-02 <sup>Z</sup>	7.43E-02 <sup>z</sup>	4.35E-02 <sup>BC</sup>	0.119 <sup>C</sup>	0.187 <sup>AB</sup>
RELATION INTERCEPT OF THE CROWN AREA TO	0.695 <sup>C</sup>	0.628 <sup>Y</sup>	1.04 <sup>C</sup>	0.231 <sup>C</sup>	0.919 <sup>Z</sup>	1.35 <sup>Z</sup>	0.731 <sup>BC</sup>	0.781 <sup>C</sup>	-1.61 <sup>AB</sup>
DBH RELATION SLOPE OF THE HEIGHT-DBH	1.4 <sup>CV</sup>	4.36 <sup>CV</sup>	1.75 <sup>CV</sup>	2.554 <sup>AS</sup>	2.49 <sup>CV</sup>	2.17 <sup>CV</sup>	1.23 <sup>CV</sup>	1.79 <sup>AS</sup>	0.711 <sup>AB</sup>
RELATIONSHIP POWER COEFFICIENT OF THE HEIGHT-	0.751 <sup>CV</sup>	0.365 <sup>AC</sup>	0.665 <sup>CV</sup>	0.45 <sup>AS</sup>	0.385 <sup>CV</sup>	0.515 <sup>CV</sup>	0.726 <sup>CV</sup>	0.505 <sup>AS</sup>	0.867 AB
DBH RELATIONSHIP FORM COEFFICIENT OF STEM	0.52 <sup>AE</sup>	0.41 <sup>AF</sup>	0.515 <sup>AE</sup>	0.522 <sup>AE</sup>	0.498 <sup>AE</sup>	0.473 <sup>AE</sup>	0.541 <sup>AE</sup>	0.62 <sup>AE</sup>	0.5 <sup>AE</sup>
WOOD DENSITY	414 <sup>AV</sup>	545.2 <sup>AG</sup>	764 <sup>BC</sup>	545 <sup>°</sup>	481 <sup>AH</sup>	493 <sup>DU</sup>	502 <sup>AI</sup>	613 <sup>DU</sup>	550 <sup>DU</sup>
CANOPY CLUMPING COEFFICIENT	0.46 <sup>DU</sup>	0.46 <sup>AA</sup>	0.79 AW	0.58 <sup>PN</sup>	0.58 <sup>DU</sup>	0.47 <sup>C</sup>	0.43 <sup>C</sup>	0.4 <sup>AX</sup>	0.59 <sup>FS</sup>
WOOD REFLECTANCE IN PIR DOMAIN	0.3 <sup>cv</sup>	0.5 <sup>AJ</sup>	0.39 <sup>AW</sup>	0.3 <sup>AJ</sup>	0.3 <sup>AJ</sup>	0.33 <sup>AJ</sup>	0.33 <sup>AJ</sup>	0.39 <sup>BB</sup>	0.39 <sup>FS</sup>
WOOD REFLECTANCE IN PAIR DOMAIN	0.15 <sup>CV</sup>	0.1 <sup>AJ</sup>	0.16 <sup>AW</sup>	0.1 <sup>AJ</sup>	0.1 <sup>AJ</sup>	0.153 <sup>AJ</sup>	0.153 <sup>AJ</sup>	0.15 <sup>BB</sup>	0.16 <sup>FS</sup>
LEAF REFLECTANCE IN PIR DOMAIN	0.33 <sup>CV</sup>	0.427 <sup>AJ</sup>	0.34 AW	0.36 <sup>AJ</sup>	0.36 <sup>AJ</sup>	0.2593 <sup>AJ</sup>	0.2593 <sup>AJ</sup>	0.3 <sup>BB</sup>	0.32 <sup>FS</sup>
LEAF TRANSMITTANCE IN PIR DOMAIN	0.225 <sup>CV</sup>	0.4 <sup>AJ</sup>	0.388 AW	0.375 <sup>AJ</sup>	0.375 <sup>AJ</sup>	0.1883 <sup>AJ</sup>	0.1883 <sup>AJ</sup>	0.388 <sup>BB</sup>	0.26 <sup>FS</sup>
LEAF REFLECTANCE IN PAR DOMAIN	0.09 <sup>CV</sup>	0.05 <sup>AJ</sup>	0.057 <sup>AW</sup>	5.86E-02 <sup>AJ</sup>	5.86E-02 <sup>AJ</sup>	0.0553 <sup>AJ</sup>	0.0553 <sup>AJ</sup>	$0.085^{BB}$	0.05 <sup>FS</sup>
LEAF TRANSMITTANCE IN PAR DOMAIN	0.045 <sup>CV</sup>	0.04 <sup>AJ</sup>	0.048	0.04 <sup>AJ</sup>	0.04 <sup>AJ</sup>	0.0053 <sup>AJ</sup>	0.0053 <sup>AJ</sup>	0.1 <sup>BB</sup>	0.11 <sup>FS</sup>
WATER STORAGE CAPACITY PER UNIT OF LEAF AREA	0.4 <sup>C-V</sup>	0.4 <sup>AA</sup>	0.3 <sup>AK</sup>	0.208 <sup>AL</sup>	0.119 <sup>AL</sup>	0.208 <sup>AL</sup>	0.208 <sup>AL</sup>	0.2 <sup>AX</sup>	0.2
WATER STORAGE CAPACITY PER UNIT OF BARK AREA	0.32 <sup>CV</sup>	0.32 AA	0.3 <sup>AW</sup>	1.95 <sup>AL</sup>	1.83 <sup>AL</sup>	1.95 <sup>AL</sup>	1.95 <sup>AL</sup>	0.2 <sup>AX</sup>	0.3 <sup>FS</sup>
SLOPE OF THE WATER INTERCEPTION COEFFICIENT	0.85 <sup>CV</sup>	0.85	0.85 <sup>AW</sup>	2.7	2.7	2.7 <sup>AM</sup>	2.7	2.3 <sup>AX</sup>	0.85 <sup>FS</sup>
INTERCEPT OF THE WATER INTERCEPTION COEFFICIENT	1.5 <sup>CV</sup>	1.5 <sup>AA</sup>	1.9 <sup>AW</sup>	1.5 <sup>AA</sup>	1.5 <sup>AA</sup>	1.9 <sup>FS</sup>	1.9 <sup>FS</sup>	1.9 <sup>AX</sup>	1.9 <sup>FS</sup>
RATIO BETWEEN STEM FLOW AND THROUGH FALL	0.35 <sup>FS</sup>	0.35 <sup>FS</sup>	0.35 <sup>AW</sup>	$0.09^{\text{AM}}$	0.09 <sup>AM</sup>	0.09 <sup>AM</sup>	0.09 <sup>AM</sup>	0.35 <sup>FS</sup>	0.35 <sup>FS</sup>
PARAMETERS	Abies alba	Cedrus atlantica	Fagus sylvatica	Pinus halepensis	Pinus nigra	Pinus sylvestris	Pinus uncinata	Quercus ilex	Quercus pubescens
PARAMETERS INTERCEPT OF BALL AND BERRY RELATION	0.001 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup>	sylvatica 0.001 <sup>AW</sup>	halepensis 0.001 <sup>AN</sup>	0.001 <sup>AN</sup>	sylvestris 0.00 <sup>AN</sup>	<b>uncinata</b> 0.001 <sup>AN</sup>	0.005	pubescens 0.001
INTERCEPT OF BALL AND BERRY	0.001 <sup>AV</sup> 6.7 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup>	0.005 10.07 <sup>CP</sup>	pubescens 0.001 9.27 <sup>BD</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA	0.001 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup>	sylvatica 0.001 <sup>AW</sup>	halepensis 0.001 <sup>AN</sup>	0.001 <sup>AN</sup>	sylvestris 0.00 <sup>AN</sup>	<b>uncinata</b> 0.001 <sup>AN</sup>	0.005	pubescens 0.001
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO	0.001 <sup>AV</sup> 6.7 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup>	0.005 10.07 <sup>CP</sup>	pubescens 0.001 9.27 <sup>BD</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50%	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN YCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE LUCTRON	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.67 <sup>DU</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.92 <sup>AG</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.261 <sup>DU</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN VCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE QUANTUM RESPONSE OF THE ELECTRON TRANSPORT RATE BASE TEMPERATURE FOR FORCING	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.67 <sup>DU</sup> 18 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup> 10.47 <sup>AO</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup> 26 <sup>BA</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup> 20.8 <sup>AR</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.92 <sup>AG</sup> 13.4 <sup>BC</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup> 16.5 <sup>AG</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN VCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE QUANTUM RESPONSE OF THE QUANTUM RESPONSE OF THE LLECTRON TRANSPORT RATE BASE TEMPERATURE FOR FORCING BUDBURST	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.67 <sup>DU</sup> 18 <sup>AV</sup> 0.7 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup> 10.47 <sup>AO</sup> 0.7 <sup>AA</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup> 26 <sup>BA</sup> 0.7 <sup>AX</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup> 20.8 <sup>AR</sup> 0.7 <sup>FS</sup>	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> -2.92 <sup>AG</sup> 13.4 <sup>BC</sup> 0.7 <sup>PS</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup> 16.5 <sup>AG</sup> 0.57 <sup>AX</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup> 0.9 <sup>AP</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup> 0.7 <sup>AX</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup> 0.7 <sup>BF</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN VCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE QUANTUM RESPONSE OF THE ELECTRON TRANSPORT RATE BASE TEMPERATURE FOR FORCING BUDBURST BASE TEMPERATURE FOR LEAF GROWTH BASE TEMPERATURE FOR FORCING	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.67 <sup>DU</sup> 18 <sup>AV</sup> 0.7 <sup>AV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup> 10.47 <sup>AO</sup> 0.7 <sup>AA</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup> 26 <sup>BA</sup> 0.7 <sup>AX</sup> 0 <sup>CV</sup> 0 <sup>CV</sup> 20 <sup>CV</sup>	halepensis 0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup> 20.8 <sup>AR</sup> 0.7 <sup>FS</sup> 3.5	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.92 <sup>AG</sup> 13.4 <sup>BC</sup> 0.7 <sup>PS</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup> 16.5 <sup>AG</sup> 0.57 <sup>AX</sup> 0. <sup>AX</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup> 0.9 <sup>AP</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup> 0.7 <sup>AX</sup> 0 <sup>C</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup> 0.7 <sup>BF</sup> 3.5
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN VCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE LUCTRON TRANSPORT RATE BASE TEMPERATURE FOR FORCING BUDBURST BASE TEMPERATURE FOR LEAF GROWTH	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.67 <sup>DU</sup> 18 <sup>AV</sup> 0.7 <sup>AV</sup> 1 <sup>CV</sup> 0 <sup>CV</sup> 20 <sup>CV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup> 10.47 <sup>AO</sup> 0.7 <sup>AA</sup> 1 <sup>AA</sup> 0 <sup>AA</sup> 20 <sup>AA</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup> 26 <sup>BA</sup> 0.7 <sup>AX</sup> 0 <sup>CV</sup> 0 <sup>CV</sup> 20 <sup>CV</sup>	halepensis           0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup> 20.8 <sup>AR</sup> 0.7 <sup>FS</sup> 3.5           0	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.92 <sup>AG</sup> 13.4 <sup>BC</sup> 0.7 <sup>FS</sup> 0 <sup>PS</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup> 16.5 <sup>AG</sup> 0.57 <sup>AX</sup> 0 <sup>AX</sup> 0 <sup>AX</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup> 0.9 <sup>AP</sup> 0. <sup>98</sup> 0 <sup>PS</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup> 0.7 <sup>AX</sup> 0 <sup>C</sup> 11 <sup>C</sup> 20 <sup>AX</sup>	pubescens         0.001           9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup> 0.7 <sup>BF</sup> 3.5         11 <sup>C</sup> 20 <sup>QI</sup> -2.0 <sup>QI</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN VCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE QUANTUM RESPONSE OF THE ELECTRON TRANSPORT RATE BASE TEMPERATURE FOR FORCING BUDBURST BASE TEMPERATURE FOR LEAF GROWTH BASE TEMPERATURE FOR LEAF GROWTH BASE TEMPERATURE FOR FORCING LEAF FALL	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.67 <sup>DU</sup> 18 <sup>AV</sup> 0.7 <sup>AV</sup> 1 <sup>CV</sup> 0 <sup>CV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup> 10.47 <sup>AO</sup> 0.7 <sup>AA</sup> 1 <sup>AA</sup> 0 <sup>AA</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup> 26 <sup>BA</sup> 0.7 <sup>AX</sup> 0. <sup>CV</sup> 0 <sup>CV</sup> 20 <sup>CV</sup> 20 <sup>CV</sup> 20 <sup>CV</sup>	halepensis           0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup> 20.8 <sup>AR</sup> 0.7 <sup>FS</sup> 3.5           0           20	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.92 <sup>AG</sup> 13.4 <sup>BC</sup> 0.7 <sup>FS</sup> 0 <sup>PS</sup> 0 <sup>PS</sup> 0 <sup>PS</sup> 1 <sup>PS</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup> 16.5 <sup>AG</sup> 0.57 <sup>AX</sup> 0 <sup>AX</sup> 0 <sup>AX</sup> 0 <sup>AX</sup> 0 <sup>AX</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup> 0.9 <sup>AP</sup> 0. <sup>PS</sup> 0 <sup>PS</sup> 0 <sup>PS</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup> 0.7 <sup>AX</sup> 0 <sup>C</sup> 11 <sup>C</sup>	pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup> 0.7 <sup>BF</sup> 3.5 11 <sup>C</sup>
INTERCEPT OF BALL AND BERRY RELATION SLOPE OF BALL AND BERRY RELATION ROOTS TO LEAVES RESISTANCE TO FLOW TRANSPORT PER AREA SAPWOOD BASIS CAPACITANCE OF TRUNK WATER POTENTIAL INDUCING 50% LOSS OF CONDUCTIVITY DEPENDENCY BETWEEN VCMAX AND LEAF NITROGEN DENSITY CURVATURE OF THE LECTRON TRANSPORT RATE BASE TEMPERATURE FOR FORCING BUDBURST BASE TEMPERATURE FOR FORCING BASE TEMPERATURE FOR FORCING LEAF FALL DATE OF ONSET OF REST DATE OF ONSET OF AGEING CRITICAL VALUE OF STATE OF FORCING (FROM QUESCENCE TO	0.001 <sup>AV</sup> 6.7 <sup>AV</sup> 2.87E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 4.67 <sup>DU</sup> 18 <sup>AV</sup> 0.7 <sup>AV</sup> 1 <sup>CV</sup> 0 <sup>CV</sup> 20 <sup>CV</sup> 70 <sup>CV</sup>	atlantica 0.001 <sup>BC</sup> 10.5 <sup>AO</sup> 2.87E+04 <sup>AA</sup> 0.04 <sup>Y</sup> -5.482 <sup>AG</sup> 10.47 <sup>AO</sup> 0.7 <sup>AA</sup> 1 <sup>AA</sup> 0 <sup>AA</sup> 20 <sup>AA</sup> 70 <sup>AA</sup>	sylvatica 0.001 <sup>AW</sup> 11.8 <sup>AW</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.175 <sup>DU</sup> 26 <sup>BA</sup> 0.7 <sup>AX</sup> 0 <sup>CV</sup> 0 <sup>CV</sup> 20 <sup>CV</sup>	halepensis           0.001 <sup>AN</sup> 12.5 <sup>C</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> 51 <sup>AG</sup> 20.8 <sup>AR</sup> 0.7 <sup>FS</sup> 3.5           0           20           1	0.001 <sup>AN</sup> 10 <sup>BC</sup> 4.50E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.92 <sup>AG</sup> 13.4 <sup>BC</sup> 0.7 <sup>FS</sup> 0 <sup>PS</sup> 0 <sup>PS</sup>	sylvestris 0.00 <sup>AN</sup> 5.7 <sup>AN</sup> 1.79E+04 <sup>AQ</sup> 0.04 <sup>Y</sup> -3.2 <sup>AG</sup> 16.5 <sup>AG</sup> 0.57 <sup>AX</sup> 0 <sup>AX</sup> 0 <sup>AX</sup>	uncinata 0.001 <sup>AN</sup> 5.4 <sup>AP</sup> 1.79E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -4.18 <sup>AG</sup> 25.6 <sup>AP</sup> 0.9 <sup>AP</sup> 0.9 <sup>AP</sup> 0 <sup>PS</sup> 0 <sup>PS</sup> 0 <sup>PS</sup> 0 <sup>PS</sup>	0.005 10.07 <sup>CP</sup> 3.18E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -3.261 <sup>DU</sup> 22 <sup>AX</sup> 0.7 <sup>AX</sup> 0 <sup>C</sup> 11 <sup>C</sup> 20 <sup>AX</sup> 48 <sup>AX</sup>	Pubescens 0.001 9.27 <sup>BD</sup> 1.15E+04 <sup>CM</sup> 0.04 <sup>Y</sup> -2.475 <sup>DU</sup> 27 <sup>BF</sup> 0.7 <sup>BF</sup> 3.5 11 <sup>C</sup> 20 <sup>QI</sup> 48 <sup>QI</sup> 213 <sup>QI</sup> 600 <sup>QI</sup>
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PARAMETERS	Abies alba	Cedrus atlantica	Fagus sylvatica	Pinus halepensis	Pinus nigra	Pinus sylvestris	Pinus uncinata	Quercus ilex	Quercus pubescens	
CRITICAL VALUE OF STATE OF FORCING FROM NSTART2 TO END OF WOOD GROWTH	300 <sup>cv</sup>	300 <sup>AA</sup>	60 <sup>CV</sup>	na	150	150	150	300 <sup>CP</sup>	100 <sup>co</sup>	
MAXIMUM NEEDLE OR LEAVES LIFESPAN	11	3	1	3	3	3	3	3	1	
NSC BIOMASS ABOVE WHICH SEEDS ARE PRODUCED	200 <sup> CV</sup>	200 <sup>CV</sup>	100 <sup>CV</sup>	200	200	200	200	250 <sup>CP</sup>	250 <sup>QI</sup>	
[NSC] UNDER WHICH TREE DIE	0.028 <sup>TS</sup>	0.049 TS	0.053 TS	0.095 TS	0.056 TS	0.055 TS	0.063 TS	0.11 TS	0.037 TS	
CARBON COST TO PRODUCE ONE SEED	0.08	5.63E-02	0.45	1.28E-01 <sup>AT</sup>	2.76E-02 <sup>E</sup>	4.88E-03 <sup>E</sup>	6.75E-03 <sup>AI</sup>	1.92E+09 <sup>E</sup>	2.115 <sup>AU</sup>	
RATE OF CARBON ALLOCATED TO SEED PRODUCTION AT THE END OF THE YEAR	1 <sup>cv</sup>	0.08 <sup>CV</sup>	0.03 <sup>cv</sup>	0.15	0.15	0.15	0.15	0.5	0.005	
A. Villar & Merino		N. R. Ruiz-P	einado et al.,	<b>Y.</b> L	ousteau 1988		AM. Ausse	nac 1969		
B. J. Rodríguez-Calcerrada	2011			<b>Z.</b> C	ondes et Sterba 20	005	AO. Ladjal et al., 2005			
<b>C.</b> Davi et al., 2008	(1981)	O. Jackson a	nd Chittendon	BC. Ameztegui et al., 2012			AP. Fernadez et Fleck 2015			
<b>D</b> . Glavan et al., 2012			18	AQ. Irvin et al., 1998						
<b>G</b> . Dawes et al., 2016		<ul><li>Q. Hagdorn et al., 2013</li><li>R. Lopez 2001 &amp; Rambal 2004</li></ul>		AD. Serrano et al. 2005		<ul> <li>AR. Calibrated from H. Davi and G. Simioni database</li> <li>AT. Moya et al. 2017</li> </ul>				
H. Simioni et al., 2016				AE. Deleuze 2015 AF. Courbet 1991						
I. Martin et al., 2017										
J. Santantonio and Grad	ce	S. Vennetier.		AH.	<b>AH.</b> Oliva et al., 2006			AU. Landergotta et al 2012		
(1987)		(80 % in 10 years) <b>T.</b> Matteo et al., 2012		AL.	<b>AI.</b> Tapias et al., 2004 <b>AJ.</b> Williams et al., 1991		AV Davi et Cailleret (2017)			
K. Snowdon and Benso	on			AI			AW Dufrên			
(1992)		U. Boratyńska e	et al 2000		Aussenac 1968		AX Davi et	al. (2006)		
L. Lin et yang 2003		W. Falge epicea	1					et al. 2006		
M. Halle & Nicole		X. Cetin 2016		AL. Llorens & Gallart 2000						
BB Ourcival 1999		FV fixed value		TS o	btain using this st	udy	<b>CT</b> calculated from trunk value using a ratio of 1.7		k	
BC calculated from		AA like Abies a	lba		Calibrated on	data on				
Lebourgeois 1998		FS like Fagus sy	lvatica	Font	-Blanche site		<b>DU</b> Databas	e URFM		
<b>BD</b> Average value from Ball & Berry (1987)		PS like Pinus sy	like Pinus sylvestris data		Ventoux		DT Database TRY			
<b>BE</b> Davi (2000)		PN like Pinus ni	igra		Calibrated on O3F	IP data	DR.Databas stands PS04		or	
BF from Damesin & Rambal		QI like Quercus	ilex		CM calibrated on Pmin data		DM. Databa			
1998		TL as trunk valu	ue	com	calculated from c position see Dut 2005)					

Table 1: Main species-specific parameters implemented throughout the accomplished study.

### 2.4. Model validation

#### 2.4.1. Eddy covariance data set

Database employed belong to the EUROFLUX network (Hesse, Font-Blanche and Puéchabon).  $CO_2$  and  $H_2O$  fluxes were monitored in meteorological towers using the eddy covariance method to measure and calculate vertical turbulent fluxes within atmospheric boundary layers. More detailed information can be found in Leuning and Moncrieff, (1990), Aubinet et al., (1999). Concerning the site's information, all details can be found in Granier et al., (1999) for Hesse and Reichstein, (2003) for Puéchabon.

#### 2.4.2. The model simulations and result analysis

In order to analyse the accuracy and completeness of the model in predicting water and carbon balances among different forests, the simulations were compared and contrasted to eddy covariance data measurements. In the correlative relationship with the eddy covariance data, it was widely further evaluated the daily NEE, the GPP ( $gCm^{-2}_{soil}$  day<sup>-1</sup>), as well as the ecosystem respiration (Reco) and the evapotranspiration (ETR). Fully comparisons have been accomplished employing valid CO<sub>2</sub> and H<sub>2</sub>O fluxes from

1997 to 2013 for Hesse. In Font-Blanche we used data from 2009 to 2017. For Puéchabon available data utilised for performed comparisons belong to the period from 2007 to 2013.

### 2.5.Risk of mortality

Risk of mortality by carbon starvation and hydraulic failure were assessed according to Davi and Cailleret, (2017). For this purpose, we simulated [NSC] and midday leaf water potential between 2000 and 2015 using SAFRAN climate data. Hydraulic failure is computed when midday leaf water potential drops below species P50 (leaf water potentials below which 50% of conductivity loss occurs). Threshold of mortality on [NSC] is estimated by fitting the threshold to minimise the difference among simulated and measured annual mortality rate once the hydraulics failure was computed. The mortality measurements come from the French National Inventory on Alpes de Haute Provence department. Concerning hydraulic failure mortality, it seems that is underestimated following this procedure, and a comparison with Sur-Eau model (Martin-StPaul et al., 2017) is currently made in order to include it in a future publication. The results on mortality are, therefore, to be used with cautiousness.

# **2.6.** Analysis of the climate change trends

#### 2.6.1. Methodological data simulations

The climate simulations have been performed through the implementation of SAFRAN meteorological analysis system for the period 1958-2015. Afterwards, simulations have been driven by two regional climate models (RCMs), HadGEM2 - ES and CNRM - CM5 for the period 1961-2015 and 2016-2100 following the RCP 4.5 and RCP 8.5 climate change scenarios of the IPCC. The results of both regional climate models were evaluated by comparison among with measured meteorological data belonging to SAFRAN system.

#### 2.6.2. Long-term simulations of fluxes

An overall of 27216 simulations have been executed from 1958 to 2100 on the Mont Ventoux, described previously. Likewise, simulations were divided into two periods of time, comprising the past period since 1958 to 2015, past modelled by climate model and future from 2016 to 2100. Complete future simulations were conducted under the two different climates scenarios following RCP 4.5 and RCP 8.5 of IPCC. Apart from

the above, to accomplish all the simulations, the following inputs were taken into consideration:

- Nine representative forest tree species established in the study area have been considered, distinguishing among deciduous species (*Fagus sylvatica* L., *Quercus pubescens* Mill.), coniferous species (*Pinus halepensis* Mill., *Pinus nigra* J.F.Arnold., *Pinus sylvestris* L., *Pinus uncinata* Ramond ex DC., *Abies alba* Mill., *Cedrus Atlantica* (Manetti ex Endl.) Carrière., and sclerophyllous evergreen species (*Quercus ilex* L.).
- Three depths of soils have been considered in order to evaluate the effects of the quantity of water in the soil available to plants, through the relative extractable water (REW) coefficient.
- Two distinct leave area index (LAI) has been considered, specifying between open and closed canopy. In these simulations, no effect of drought on LAI is considered.
- Three different age classes among species were also assumed within simulations.

Finally, simulations were performed along an altitudinal gradient located on both flanks, North and South of Mont Ventoux (ranging from 150 m, 450 m, 800 m, 1100 m, 1400 m and to 1750 m). In order to be more accurate when evaluating where is established each species across altitude on Mont Ventoux. It has been determined altitudinal ranges to classify and modelling each species according to its elevation and orientation. Similarly, we launched simulations considering two sylvicultural management options, with and without silvicultural treatments.

Smaniag	Elevation (m)			
Species	North	South		
Abies alba Mill	1000 - 1600	-		
Cedrus Atlantica (Manetti ex Endl.) Carrière	300 - 1000	300 - 1200		
Fagus sylvatica L	1000 - 1600	1200 - 1750		
Pinus halepensis Mill	0 - 800	0 - 600		
Pinus nigra J.F.Arnold	1000 - 1600	1200 - 1750		
Pinus sylvestris L	300 - 1600	300 - 1700		
Pinus uncinata Ramond ex DC	1000 - 1600	1200 - 1750		
Quercus ilex L	0 - 1000	0 - 1200		
Quercus pubescens Mill	0 - 1200	0 - 1400		

Table 2: Established altitudinal ranges to classify each species according to its elevation and orientation.

The significance of the trends was tested with linear regression equations as well as with the analysis of the variance (ANOVA) and quantified over two periods: 1958 - 2015 and 2016 - 2100.

#### 2.6.3. Set of simulations accomplished according to objectives

One of our objectives is to analyse effects of climate change on forest productivity as well as to evaluate the influence of forest management on reducing such effects derived from climate change. To separately evaluate these effects, in order to test the hypothesis mentioned previously, we designed two sets of simulations. The first set is a base simulation launched for each species, includes all the effects evaluated in the study such as (I) climate change using historical data and according to the different RCPs, (II) altitudinal gradient effect, (III) exposition effect, differentiating among flanks, north and south (IV) soil water content, (V) canopy openness, (VI) stand age and finally (VII) species composition. The second set is equal to the first set, except with the difference that silvicultural treatments among species have been included.

#### 2.6.4. How climate effects modify fundamental methods in CASTANEA

Some effects have an impact on the model in various ways. For instance, the rise of  $[CO_2]$  directly influences photosynthesis evoking an increase in its rate what, therefore, decline the stomatal conductance due to the coupling of the photosynthesis model (Farquhar et al., 1980) and the conductance model (Ball et al., 1987). Furthermore, modelled photosynthesis is similarly sensitive to the relative humidity and global radiation (Davi et al., 2006). According to Bernacchi et al., (2001) the rise in temperature alters photosynthesis and prompt both, autotrophic and heterotrophic respiration, based on  $Q_{10}$  relationships which depend on the tree species and the type of

respiration (autotrophic or heterotrophic). Moreover, changes in the temperature may also trigger variations on the phenology depending on the degree of days. To conclude, it has to be emphasised that within the model, the precipitation has a direct influence on water stress, thus, regulate the degree and the length of the water stress, which -in turnshas an impact on stomatal conductance, photosynthesis and soil heterotrophic respiration, but the increase of  $CO_2$  also increases the Water Use Efficiency (WUE).

# 3. Results

### 3.1. Comparison with eddy covariance measurements

Comparison between averaged daily fluxes simulated by CASTANEA model and measured by eddy covariance technics are showed for species *Quercus ilex* L., and *Pinus halepensis* Mill., in Font-Blanche site, (Fig. 3), while comparisons regarding *Fagus sylvatica* L., in Hesse site, are shown in Fig. 4. Finally, comparisons for species *Quercus ilex* L., and *Pinus halepensis* Mill., in Puéchabon site are exposed in Fig. 5.



# Font-Blanche

Figure 3: Evaluation of the model predictions in Font-Blanche site, where *Quercus ilex* L., and *Pinus halepensis* Mill., are the dominant tree species. Left: measured vs simulated averaged Net Ecosystem Exchange (NEE), Ecosystem Respiration (Reco) and Growth Primary Production (GPP) in (gC m<sup>-2</sup> days<sup>-1</sup>). Right: measured vs simulated fitted linear regression coefficient of Net Ecosystem Exchange (NEE), Ecosystem Respiration (Reco) and GPP (gC m<sup>-2</sup> days<sup>-1</sup>).

In the Font-Blanche site for *Quercus ilex* L., and *Pinus halepensis* Mill., the model reproduces very well the seasonal pattern (r=0.95), with a tendency to overestimated the NEE during summer and in autumn when the drought period ends. Moreover, the model tends to slightly underestimate NEE at the end of spring. By contrast, the model mildly overestimates photosynthesis at the end of spring as well as at the end of summer and beginning of autumn. Concerning ecosystem respiration in Font-Blanche, the model tends to overestimate respiration in spring and during autumn.

In the Hesse site where *Fagus sylvatica* L., is the main representative species, the model reproduces very well the seasonal pattern (r=-0.96), with a slight tendency to overestimate NEE at the spring as well as at the end of summer. Regarding photosynthesis, the model reproduces a slight tendency to overestimate its rate during spring and autumn, as well as underestimated briefly at the end of autumn. On the contrary, the model underestimates ecosystem respiration through spring and lightly in the autumn. Concerning evapotranspiration, the model showed a tendency to overestimate its rate during summer and in the autumn, when the drought period ends.

For *Quercus ilex* L., stand at Puéchabon, the model provides a seasonal pattern (r=0.9), with a tendency to overestimate NEE during spring and slightly during summer and at the beginning of autumn due to a tendency to underestimate the ecosystem respiration at spring and also during summer and beginning of autumn.

When data from the study sites were integrated yearly, it was presumed that NEE had been overestimated in overall either for conifers species and broadleaf species. Additionally, data vary among sites, being the estimations documented, (122.40 in gC.m<sup>-2</sup>.year<sup>-1</sup>) for *Quercus ilex* L., in Puéchabon, (-62,68 in gC.m<sup>-2</sup> year<sup>-1</sup>) for *Quercus ilex* L., and *Pinus halepensis* Mill., in Font-Blanche and (87.58 gC.m<sup>-2</sup>.year<sup>-1</sup>) for *Fagus sylvatica* L., in Hesse site. In the annual estimations for the photosynthesis, the model displayed an overestimation in Font-Blanche (31.76 in gC. m<sup>-2</sup>.year<sup>-1</sup>), Puéchabon (60.22 in gC.m<sup>-2</sup>.year<sup>-1</sup> and Hesse (2.22 gC.m<sup>-2</sup>.year<sup>-1</sup>) for *Fagus sylvatica* L.





Figure 4: Evaluation of the model predictions in Hesse site, where *Fagus sylvatica* L., is the dominant tree species. Left: measured vs simulated Net Ecosystem Exchange (NEE), Ecosystem Respiration (Reco) in (gC m<sup>-2</sup> days<sup>-1</sup>), Growth Primary Production (GPP) in (gC m<sup>-2</sup> days<sup>-1</sup>) and Evapotranspiration (ETR) in (mm days<sup>-1</sup>). Right: measured vs simulated fitted linear regression coefficient of NEE, Reco in (gC m<sup>-2</sup> days<sup>-1</sup>), GPP in (gC m<sup>-2</sup> days<sup>-1</sup>) and Evapotranspiration (ETR) in (mm days<sup>-1</sup>).

# Puéchabon



Figure 5: Evaluation of the model predictions in Puéchabon site, where *Quercus ilex* L., and *Pinus halepensis* Mill., are the dominant tree species. Left: measured vs simulated Net Ecosystem Exchange (NEE) in (gC m<sup>-2</sup> days<sup>-1</sup>), Ecosystem Respiration (Reco) in (gC m<sup>-2</sup> days<sup>-1</sup>) and Growth Primary Production GPP in (gC m<sup>-2</sup> days<sup>-1</sup>). Right: measured vs simulated fitted linear regression coefficient of NEE (gC m<sup>-2</sup> days<sup>-1</sup>), Reco (gC m<sup>-2</sup> days<sup>-1</sup>) and GPP (gC m<sup>-2</sup> days<sup>-1</sup>).

In regards to Ecosystem Respiration (Reco), the model tends to underestimate in overall for Puéchabon and Hesse sites, being data reported for Reco (-62.18 gC.m<sup>-2</sup>.year<sup>-1</sup>) in Puéchabon and (-85.25 gC.m<sup>-2</sup>.year<sup>-1</sup>) in Hesse. By contrast, we overestimated it (94.46 gC.m<sup>-2</sup>.year<sup>-1</sup>), in Font-Blanche site.

Concerning evapotranspiration (ETR; mm year<sup>-1</sup>) annual estimations, the model tends to underestimate in overall for Puéchabon (-4.22 mm.year<sup>-1</sup>) and Font-Blanche sites (-26.87 mm year<sup>-1</sup>), being data reported respectively. By contrast, the model also has overestimated measurements in Hesse site, in which annual data displayed (89.06 mm.year<sup>-1</sup>) for ETR.

To conclude, it has to be emphasised that despite some mild underestimations and overestimations, the model CASTANEA accurately has simulated the seasonal dynamics of NEE, GPP, Ecosystem Respiration and Evapotranspiration in the ICOS sites evaluated.

### **3.2. Simulation of climate evolution**

Tables 3 and 4 show the meteorological trends in the temperature and precipitation measurements through the past by SAFRAN system and predictions for the future by the two climatic models utilised in the study to assess trends variations over time. From 1958 to 2016, the average temperature risen by 1,62 °C and the rainfall in altitude increased by 48.88 mm.

	(	Climate model scenar	Average	Average	
Past		Temperature (°C 100 year <sup>-1</sup> )	Precipitation (mm 100 year <sup>-1</sup> )	temperature °C 100 year <sup>-1</sup>	precipitation mm 100 year <sup>-1</sup>
CAEDAN	North	3,333	257,358	2.8016	246.4454
SAFRAN	South	2,271	235,532	2,0010	240,4434

Table 3: Meteorological trends simulated between 1958 and 2016 for the Mont Ventoux.

For the future projections, from 2016 to 2100, under the RCP 4.5 and RCP 8.5 scenarios from CNRM – CM5 the average temperature rise by 1,28 °C and 4,52 °C respectively (Fig. 6), and the average rainfall increase 180,48 mm under the RCP 4.5 scenario, but it will drop on average -112,24 mm under the RCP 8.5 scenario. Concerning future predictions under the RCP 4.5 and RCP 8.5 scenarios from HadGEM2 – ES, the temperature on average increase by 2,85 °C and 5,79 °C respectively (Fig. 6); likewise, the precipitation on average drop by -142,84 mm under RCPs 4.5 and by -212,67 mm under RCPs 8.5. Hence, we can conclude that predictions displayed from both climatic models under the RCP 8.5 scenario are the most extremes and, thus, we will have negatives effects on the ecosystem functioning. With the purpose of assessing impacts over the ecosystem due to the expected harsh climate conditions, the significance has been evaluated for climate type effects over each species as well as through an altitudinal gradient and considering or not the implementation of silvicultural management among species.

Climate model scenarios						
Past		Temperature (°C 100 year <sup>-1</sup> )	Precipitation (mm 100 year <sup>-1</sup> )			
	North	3,333	257,358			
SAFRAN	South	2,271	235,532			
Future		No	orth			
CNRM - CM5	RCP 4.5	1,311	219,230			
CINKIVI - CIVIS	RCP 8.5	4,511	-112,794			
HadGEM2 – ES	RCP 4.5	2,854	-175,349			
HadGEMI2 – ES	RCP 8.5	5,819	-257,301			
Future		So	uth			
CNRM - CM5	RCP 4.5	1,240	210,473			
CINKIM - CIVIS	RCP 8.5	4,526	-154,448			
HodCEM2 ES	RCP 4,5	2,837	-164,752			
HadGEM2 – ES	RCP 8,5	5,761	-249,063			

Table 4: Meteorological trends simulated between 1958 and 2100 for the Mont Ventoux in which negative values referred to a decrease in temperature or precipitation rates, as well as positive values, correspond to increases in temperature and precipitations rates.



Figure 6: CASTANEA model predictions comparison among the means temperature rates in altitude (at 800 m, a.s.l. and 1400 m, a.s.l.) across the time under different climate change scenarios following RCP 8.5 and RCP 4.5.

#### **3.3. Effect of climate change**

The effect of climate change can be analyzed by comparing the simulations carried out under the different scenarios or by observing within a scenario the temporal evolutions. When comparing historical and future simulations, NEE decreases in all scenarios except CNRM – CM5 RCP 8.5 (Figure 7 (up)). Note that the simulated NEE is much

lower using SAFRAN data (past) than with the modelled climate under historical conditions. By contrast, wood growth increase in all scenarios under climatic change (Figure 7 (bottom)). Regarding temporal trends within a scenario (Figure 8), the NEE increases when using the SAFRAN data, and the mortality rate has decreased; while water stress has increased (WSI is even more negative when the stress is intense). In the future, we observe a decrease in the NEE and an increase in the mortality extreme in the RCPs 8.5 of the HadGEM2 - ES model.



Figure 7: Effects of climate change on forest productivity. Up: Results from the simulation of Net Ecosystem Exchange (NEE) in (gC m<sup>-2</sup> year<sup>-1</sup>) under various climate change models, following the RCP 4.5 and RCP 8.5 scenarios of the IPCC. Bottom: Results of wood growth in  $(m^3 ha^{-1} year^{-1})$  under different climate change scenarios.


Figure 8: Evaluation of trends across time under climate change scenarios of (Upper left) Net Ecosystem Exchange (NEE) in (gC  $m^{-2}$  year<sup>-1</sup>), (Upper right) Non-structural carbohydrates concentration [NSC] (gCgC<sup>-1</sup>), (Bottom right) Water Stress Index (WSI; MPa), and, (Bottom left) Mortality rate due to [NSC] (gC gC<sup>-1</sup>).

#### **3.4.Effect of altitude**

When testing the effect of altitude on forest functioning among all species (Fig. 9), results from the simulations show in the past a tendency of a lower NEE in the high altitudes. On the contrary, the reported simulations showed a greater NEE in low altitudes despite water constraint. It also has been registered an increase in the Gross Primary Production (GPP) (gC.m<sup>-2</sup>.year<sup>-1</sup>) and Ecosystem Respiration (Reco) in (gC.m<sup>-2</sup>.year<sup>-1</sup>) in altitude, presenting both substantial rates at higher elevations (1750 - 1909 m, a.s.l.).



Figure 9: Altitude effects on forest productivity for all the considered species. Evaluation of (Bottom right) Net Ecosystem Exchange (NEE) in (gC m<sup>-2</sup> year<sup>-1</sup>), (Bottom left) Net Primary Production in (gC m<sup>-2</sup> year<sup>-1</sup>), (Upper right) Ecosystem Respiration (Reco) in (gC m<sup>-2</sup> days<sup>-1</sup>), and, (Upper left) Growth Primary Production GPP in (gC m<sup>-2</sup> days<sup>-1</sup>) simulated through an altitudinal gradient ranging from 150 to 1750 m, a.s.l.

Nevertheless, these trends vary when testing different climate model scenarios as could be seen in (Fig. 10(up)). When comparing among past and future, even though trends of NEE are increasing softly in altitude, the higher rates of NEE remains more meaningful at low and middle altitudes than at high elevations.

The capability of species to succeed under extreme climate conditions was evaluated accomplishing simulations of the Non-Structural Carbohydrates concentration [NSC] in  $(gC gC^{-1})$ . Results from past simulations (Fig. 10 (bottom)) have described a reasonable increase in the quantity of [NSC] from low altitudes (150 - 800 m), to high elevations (1100 - 1750 m). On the other hand, results from simulations analysing climate change scenarios have shown a meaningful increase of [NSC] at higher altitudes (1400 and 1750 m, a.s.l.) than at lower (below 800 m, a.s.l.). We assume that this effect might be due to species as well as to the climatic conditions at those elevations.



Figure 10: Effects of climate change on forest productivity. Up: Results from the simulation of Net Ecosystem Exchange (NEE) in (gC m<sup>-2</sup> year<sup>-1</sup>) under various climate changes scenarios simulated from 150 to 1750 (m). Bottom: Results of Non-Structural Carbohydrates concentration [NSC] in (gC gC<sup>-1</sup>) in altitude (m) under different climate change scenarios.

## **3.5.Effect of climate change on individual species dynamics**

Evergreen species presented a higher GPP index, since they profit from all the year to photosynthesise, except *Pinus nigra* J. F. Arnold. Nevertheless, Reco is also more significant for evergreen species. NEE is higher for two contrasted species: *Quercus ilex* L., and *Abies alba* Mill., (Figure 11).



Figure 11: Evaluation of Net Ecosystem Exchange (NEE) in (gC m<sup>-2</sup> year<sup>-1</sup>), Ecosystem Respiration (Reco) in (gC m<sup>-2</sup> year<sup>-1</sup>), Growth Primary Production GPP in (gC m<sup>-2</sup> year<sup>-1</sup>) and Ring Width in (mm) simulated to each species.

In order to achieve species mortality risk, the temporal and spatial variability within observed mortality rates were correlated to mortality rates simulated using a set of factors that previously related to tree vitality, vulnerability and mortality risk. These proxies are, the Non-Structural Carbohydrates concentration [NSC] ( $gCgC^{-1}$ ), the NSC biomass ( $gCm^{-2}year^{-1}$ ), a Water Stress Index (WSI = annual sum of daily simulated soil water potential; MPa), and the Percent Loss of Hydraulic Conductivity (PLC; %). According to simulations results, (Fig. 12), Quercus ilex L., and Pinus uncinata Ramond ex DC., are showing thus a low-risk mortality rate. Alternatively, species as Pinus sylvestris L., Pinus nigra J. F. Arnold., Quercus pubescens Mill., Fagus sylvatica L., and Pinus halepensis Mill., presented a rise in risk of mortality rate due to its registered low [NSC] index, as well as, to the critical PLC rate recorded mainly by Pinus nigra J. F. Arnold., and Ouercus pubescens Mill., following by Fagus sylvatica L., Pinus halepensis Mill., and Pinus sylvestris L., although in a minor extent. When comparing among species, on overall, it can be assumed that simulations have documented a better performance by deciduous species than by sclerophyllous species and coniferous species. Furthermore, Fagus sylvatica L., presented a lower photosynthetic rate as well as low respiration rate. Nevertheless, although some species as Quercus ilex L., and Pinus halepensis Mill., have been suffered an increase in their respiration rates, similarly are better adapted to drought conditions, for this reason, will be less impacted than species vulnerable to drought as Abies alba Mill., or Fagus sylvatica L., among others.



Figure 12: Evaluation of Water Stress Index (WSI; MPa), Non-Structural Carbohydrates concentration [NSC]  $(gCgC^{-1})$ , NSC biomass  $(gCm^{-2}year^{-1})$  and the Percent Loss of Hydraulic Conductivity (PLC; %) simulated to assess species mortality risk.

# 3.6.Effect of forest management on reducing the climate change effects

One aim of silvicultural treatments was to foster resilience and resistance to the forests in order to face against the impacts of climate change. Firstly, the effects of climate change on the ecosystem functioning was evaluated by species across time, taking into consideration the implementation of a set of silvicultural treatments calculated previously for each species and estimated under two different climate change scenarios following RCPs 4.5 and 8.5 of the IPCC. Results derived from simulations (Fig. 13) have confirmed that after conducted silvicultural treatments, in overall, the ecosystem suffers at the beginning a decrease in the amount of the stand volume due to the extractions performed. Therefore, that will allow to remaining trees to increase its diameter at breast height (dbh) throughout time, as well as to a reduction in the competency index among trees, provoking a final increase of the NEE.



Figure 13: Evaluation of simulated Net Ecosystem Exchange (NEE) in (gC  $m^{-2}$  year<sup>-1</sup>), the stand volume (Vha;  $m^{-3}$  ha<sup>-1</sup> year<sup>-1</sup>) and mortality rate due to Non-Structural Carbohydrates concentration [NSC] (%) trends assessed by species with and without silvicultural managements.

Furthermore, recorded results after implemented silvicultural treatments have verified a substantial decrease in the mortality ratio (Fig. 13), being *Quercus ilex* L., the species which benefited most from applied silviculture following by *Pinus halepensis* Mill.,

*Cedrus Atlantica* (Manetti ex Endl.) Carrière., and *Fagus sylvatica* L., By contrast, *Pinus nigra* J. F. Arnold., is the species which be adversely affected by applying silviculture following by *Abies alba* Mill., *Pinus sylvestris* L., *Pinus uncinata* Ramond ex DC., and *Quercus pubescens* Mill., which do not have experienced significant changes after implemented silviculture (Fig. 13).

Results displayed from conducted simulations (Fig. 14), when analysing all species together, suggested in overall, a decrease in the stand volume after implemented silviculture as well as an increase in the tree-ring width, the non-structural carbohydrates concentration [NSC] and finally an increment in the Net Ecosystem Exchange rate (NEE). Representing a significant correlation among the NEE, silviculture implemented and all species together.



Figure 14: Evaluation of simulated, (Bottom left) Net Ecosystem Exchange (NEE) in (gC m<sup>-2</sup> year<sup>-1</sup>), (Upper left) the Stand Volume (Vha; m<sup>-3</sup> ha<sup>-1</sup> year<sup>-1</sup>), (Bottom right) Non-Structural Carbohydrates concentration [NSC] (gCgC<sup>-1</sup>) and, (Upper right) Ring Width in (RW; mm year<sup>-1</sup>) simulated to all species together, whit and without implemented silviculture.

#### 4. Discussion

### 4.1. Analysis of the model

Mediterranean forests are of crucial ecological and economic importance in the South of Europe, although there is still a significant degree of uncertainty over how climate change will impact the services provided by such ecosystems. In order to predict the effects of climate change alongside to try to fill current knowledge gaps due to forest ecosystem complexity, it is become essential to develop powerful operational models which may have both, empirical and causal components at the same level (Makela et al., 2000). CASTANEA is an ecophysiological process-based model which may be coupled with empirical data models to assess forest ecosystem functioning. The model was tested in previous studies in Hesse, Bray, Puéchabon, Fontainebleau, Loobos, (Dufrêne et al., 2005; Davi et al., 2006) as well as on Mont Ventoux (Davi and Cailleret, 2017). In this study, it has been evaluated its performance over a broader range of tree species as well as across three different climate models throughout time.

Regarding yearly simulations, in overall, there is a soft systematic overestimation of NEE within the three ICOS sites evaluated. To what concern the total photosynthetically fixed carbon (GPP), there is a mild trend to overestimate for the three species. Concerning ecosystem respiration and total evapotranspiration, the model showed a faint tendency to also underestimated for *Fagus sylvatica* L., stands and the *Quercus ilex* L., as well as to overestimate for *Pinus halepensis* Mill.

On the other hand, the seasonal pattern of NEE was not accurately recorded, specifically in the summer and autumn for the *Quercus ilex* L., and *Pinus halepensis* Mill., stands. That fact could be due to the delay effects of drought on photosynthetic parameters in Font-Blanche or respiration in Puéchabon. For *Fagus sylvatica* L., stands, the model underestimated NEE, especially during spring and summer. That fact is undoubtedly due to a lack of accuracy in phenology (budburst) or owing to lag effects of spring frost damage. As instructed in previous studies, *Fagus sylvatica* L., is more sensitive than other tree species to the late spring frost events, however, circumvents this sensitivity by late budburst dates (Príncipe et al., 2017). On the other hand, and regarding response to frost, Sakai and Larcher, (1987) found lower resistance in juvenile than adult individuals of *Quercus ilex* L. Nevertheless and according to Kramer and Kozlowski, (1979) and Neilson and Wullstein, (1983), leaves frost damage may be partially compensated for by refoliation, either from activation of latent buds or development of adventitious buds. Consequently, it has to be emphasised that refoliation is, costly in requiring additional resources and time, thus reducing the length of the growing season and, therefore, the tree-ring width growth (Augspurger, 2009).

Concerning the water balance, the model has shown an overestimation of ETR higher than measured data by eddy covariance technique. That overestimation on evapotranspiration during the water stress period might probably underestimate the water use efficiency (WUE), which would be defined as the ratio between daily photosynthesis (GPP) and daily transpiration (TR) which is well correlated with measured sapflow. Finally, it has to be emphasised that despite some mild underestimations and overestimations, the model CASTANEA accurately has simulated the seasonal as well as the yearly dynamics of NEE, GPP, Ecosystem Respiration and Evapotranspiration across time under different climate change scenarios. Hence, we are confident about the reliability of our results.

## 4.2. Effects of climate change on forest ecosystem considering altitude

The capability of the forest to store carbon has been evaluated since 1958 to 2100 aiming to analyse the impact of climate change on forest productivity considering two different climatic models following RCP 4.5 and RCP 8.5 of IPCC, across an altitudinal gradient and including the dominant tree species existing in such area. According to simulations results, in the past, the carbon gain rate within the ecosystem is more significant at low altitude than at high elevation. Although at low altitudes, water availability and temperatures are constraining factors for forest yield, we assumed that this augmentation effect on NEE is due to species effects living at these low altitudes. Amongst all these species, we may find Quercus ilex L., and Pinus halepensis Mill., which are well adapted to drought conditions registering a soft growth, occasionally, even during summer and winter like in the case of Pinus halepensis Mill., if climate conditions are favourable. Coomes and Allen, (2007) reported a drop in potential growth index in altitude due to low temperatures and a shorter growing season. Despite, in their study water limitation was not a significant constraint on low elevation sites as on Mont Ventoux case. According to Cailleret and Davi, (2011), in the Mediterranean areas, where summer drought is the primary growth restricting factor, trees at low

elevations may be more constrained than those on upper altitudes due to the positive effect of altitude on water availability: less evaporation and more precipitation.

Nevertheless, past simulations on Mont Ventoux have reported a greater carbon gain rate at lower altitudes than at high elevations. When considering future simulations, the carbon storage patterns showed a significant drop across altitude as in Cailleret and Davi, (2011).

In contrast, *Fagus sylvatica* L., reported a positive growth rate effect due to May temperatures at high altitudes. Which would confirm that temperatures at the beginning of growing season are more significant for cambial activity and timber production than summer rainfall (Cailleret and Davi, 2011). Likewise, the most significant levels of NEE have been recorded under both evaluated RCP scenarios of the climate model HadGEM2 - ES at low altitudes, which could be due to the  $CO_2$  fertilisation which generally enhances the total photosynthetically fixed carbon (GPP). Alternatively, the rise in temperature could lead to a higher photosynthetic rate on coniferous, allowing an increase in the annual GPP. Besides, high spring temperatures may prompt earlier budburst for deciduous species allowing, therefore, a rise in the total annual GPP (Badeck et al., 2004; Davi et al., 2006).

Nonetheless, the predicted rise in the temperature leads an increase in the autotrophic and heterotrophic respiration rate which prompts a drop in the NEE. Furthermore, changes in rainfall patterns may induce an increase in the evaporative demand and, an increment of soil drought, a fact which incites a decrease of photosynthesis and soil respiration generating, therefore, a reduction in the ecosystem carbon gain (Davi et al., 2006). Hence, the  $CO_2$  fertilisation effect might be counteracted throughout time due to the rise of aridity and the increase in the maintenance respiration (Nadal-Sala et al., 2017).

Concerning the Non-Structural Carbohydrates concentration [NSC], there is a mild increase at low elevation and a more significant raise at high altitudes, while in middle elevations, this rate was lower when compared with simulated trends at low and high altitudes. We assumed that this effect also is due to species-specific living there and even by climate conditions at such height (1100 m). The future trends of [NSC] patterns show an increment across altitude, which may be due to the present species effects and even to the favourable climate conditions, being [NSC] higher in the larger altitude areas. At low altitudes in which the climate conditions are critical, the quantity of

[NSC] is more limited. During drought episode, plants stop their growth before closing stomata what contradictorily prompts an increment of carbon storage as well as in the [NSC] quantity (Sevanto et al., 2014; Davi and Cailleret, 2017). Subsequently, when the decline in Gross Primary Production (carbon uptake) as a consequence of stomata closure is more significant than the drop in respiration and, therefore, becomes not sufficient to satisfy carbon requirements for respiration, defences and reproduction prompt to a decline in NSC content (McDowell et al., 2011; Sala et al., 2010; Davi and Cailleret, 2017). Indeed, plants may become accustomed to recurrent droughts and acclimate their carbon economy through many mechanisms by reducing the respiratory costs or improving the water use efficiency (Martin-StPaul et al., 2013) such as is the *Quercus ilex* L., case.

As we previously hypothesised that, "forest productivity would decrease at lower elevations, where water is limiting and increase at higher altitude where the temperature is limiting" (Cailleret and Davi, 2011). According to CASTANEA predictions, we must reject the hypothesis (I) since the data do not support it. To conclude, we can confirm:

- Forest productivity increases at low elevations and decreases at high altitude.

- Considering both RCP scenarios, productivity trends rise softly in elevation but do not drop at low altitudes, due to the  $CO_2$  fertilisation effect.

Consequently, both, climate and species have a meaningful effect on the forest productivity.

### 4.3. Impact of climate change on individual species dynamics

Through this approach, we pursued to analyse how plants might act under extreme climates with the objective to assess how vulnerability and mortality likelihood vary across elevation and among trees species depending on their age/size, stands density and soil characteristics. This modelling approach also aims to provide new insights into the physiological causes of mortality as well as on the capability of some species to overcome extended extreme events prompted by climate change. In order to accomplish this approach, the NEE, the Reco, the GPP and the capability to enlarge RW were evaluated and simulated for each species. Furthermore, the [NSC], the WSI and the PLC, were estimated to assess vulnerability and mortality rate according to Davi and Cailleret, (2017) methodology.

When comparing among species, simulations have displayed significant growth in the capability of the ecosystem to uptake carbon by broadleaved species which might be due to the lengthened of the vegetative period in species such as Fagus sylvatica L., as well as due to the resilience of sclerophyllous evergreen species like *Ouercus ilex* L., which are well adapted to extreme conditions. Some authors agree that at high elevations, changes in late budbursts date might avoid frosts damage probabilities as well as in competitiveness, thereby altering Fagus sylvatica L., vitality (Cailleret and Davi, 2011; Príncipe et al., 2017). Furthermore, Dittmar et al., (2006), Awaya et al., (2009) and Príncipe et al., (2017) have reported almost a complete recovery of radial increment as well as and net primary production in most of the Fagus sylvatica L., Fagus crenata Blume., trees in subsequent years following a late frost event. Suggesting that possibly, beech assures next year's growth potential by storing photosynthetic products in the later part of the growing season, rather than using the assimilates during the current year's growth (Larcher, 2003). Hence, and according to aforementioned authors, we may emphasise that frost resilience of growth in *Fagus sylvatica* L., is very high, as growth one and two years after the spring frost event returned to pre-frost growth rates.

According to previous studies results, in Mediterranean areas, high temperatures may prompt an increase in the potential evapotranspiration, thereby arousing a reduction of soil water reserves, with the consequent adverse effect on growth (Moreno et al., 2005; Condés and García-Robredo, 2012). By contrast, in the boreal and temperate forest, high temperatures might leads to a significant and positive influence on growth (Bergh et al., 2003; Matala et al., 2005; Laubhann et al., 2009; Condés and García-Robredo, 2012). Therefore, it could be confirmed that precipitation is the most important climatic factor in the Mediterranean area, having a direct influence on growth and in the survival of the coniferous species as *Abies alba* Mill., *Pinus uncinata* Ramond ex DC., and *Pinus sylvestris* L., among others. (Condés and García-Robredo, 2012).

Similarly, some authors agree that vegetative phenology in the Mediterranean area mainly depends on seasonality in water availability which could have a direct influence on the mass of foliage, and therefore, light interception and transpiration, fact, which might result in a growth drop (Vicente-Serrano et al., 2010; Condés and García-Robredo, 2012). Besides, the same authors, Vicente-Serrano et al., (2010); Condés and García-Robredo, (2012), found in previous studies, that due to future predictions of

warming and declining precipitation, shall rise the stress conditions, thereby affecting coniferous forests in the Mediterranean region, which is in agreement with the result indicated by CASTANEA model. Hence, results revealed that coniferous species are vulnerable to extreme environmental conditions; likewise, some coniferous species such as Pinus uncinata Ramond ex DC., Cedrus Atlantica (Manetti ex Endl.) Carrière., Abies alba Mill., and Pinus sylvestris L., could be even more susceptible than deciduous and sclerophyllous evergreen species to store carbon and overcome extended drought events, suggesting, that these last species are more efficient and resilient than coniferous previously mentioned. According to Galiano et al., (2010) sclerophyllous evergreen species as Quercus ilex L., have developed greater resilience to the increase of aridity than those of coniferous species as Pinus sylvestris L. Similarly, in a study under moderate climate change conditions, Nadal-Sala et al., (2017) have pointed that Pinus sylvestris L., and Quercus ilex L., stands suffered severe restrictions in their growth and capacity to carbon gain. Nevertheless, Quercus ilex L., increased its growth and its carbon stock under conditions of extreme climate change while Pinus sylvestris L., experienced a decrease in its capacity for growth and carbon storage at the end of the considered study period due to severe environmental constraints.

On the other hand, evaluated annual carbohydrate storage rate displayed a decrease in simulated NEE alongside with a drop of [NSC] and Minimal NSC content (BSSmin), what might induce an increase in the mortality rate by depletion in NSC. Given the preceding, when comparing mortality rate among species considering both climate models and RCPs, simulated results (Fig. 15), revealed that the most vulnerable species to experience death by starvation under the influence of HadGEM2 - ES, following RCP 8.5 and 4.5 scenarios, respectively are, *Pinus uncinata* Ramond ex DC., *Pinus sylvestris* L., *Cedrus Atlantica* (Manetti ex Endl.) Carrière., *Abies alba* Mill., *Fagus sylvatica* L., *Pinus nigra* J.F.Arnold., *Quercus pubescens* Mill., and to a lesser proportion are *Quercus ilex* L., and *Pinus halepensis* Mill.



Figure 15: Analysis of Non-Structural Carbohydrates ( $gCgC^{-1}$ ) rate simulated aiming to assess species mortality by NSC depletion under different climate change scenarios (type).

To conclude, by correlating mortality rates aroused by CRNM - CM5 climatic scenario, under RCP 8.5 scenario, surprisingly mortality patterns considerably drop as can be seen in Figure 15, what implies that species such as *Pinus sylvestris* L., *Cedrus Atlantica* (Manetti ex Endl.) Carrière., *Pinus nigra* J.F.Arnold., and *Quercus pubescens* Mill., have registered a mortality rate by starvation lesser than the displayed rate displayed by CRNM - CM5 under RCP 4.5. Therefore, we assume that this effect might be due to the CO<sub>2</sub> fertilisation effect.

Concerning the hypothesis (II) "Species will be variously affected by the effects of the climate change (Davi et al., 2006b): deciduous species will benefit from the lengthening of vegetation, while evergreen sclerophyll and coniferous will suffer from an increase of respiration. Species already adapted to water stress (*Quercus ilex* L., or *Pinus halepensis* Mill.) will be less impacted than species vulnerable to drought (*Fagus sylvatica* L., or *Abies alba* Mill.)". To conclude and after evaluating the impact of climate change on individual species dynamics, we may confirm that both, measured and simulated data are generally supported the second hypothesis.

# 4.4. Influence of forest management on mitigating climate change effects

Silvicultural treatments were simulated primarily to foster resilience and resistance to the forest with the principal aim to face against impacts of climate change. Effects of climate change on the ecosystem functioning were evaluated, by species across time, considering the implementation of a set of silvicultural treatments previously calculated for each species aiming to increase the growth, health and value of the remaining ones. Simulation results when applied silviculture treatments revealed a trend to decrease stand volume in a short time. Consequently, the remaining trees may enlarge the dbh, and thus, the RW alongside to the enhancement of the capability to augment the [NSC] as well as the NEE fluxes within the ecosystem. Suggesting that silviculture treatments lead to a positive effect on reducing drought and fire vulnerability as well as to enhance tree growth and carbon sequestration. Alternatively, other thinning experiments have reported a reduction on tree-to-tree competition for resources leading -in turns- has improved tree growth, survival or fruit production as well as others forest functions such as carbon gain (Olivar et al., 2014; Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011; de las Heras et al., 2013; Vilà-Cabrera et al., 2018). Besides, results have confirmed a decline in the rate of mortality prompted by depletion of [NSC] on the species, being Quercus ilex L., the species which benefited the most from applied silviculture following by Pinus halepensis Mill., Cedrus Atlantica (Manetti ex Endl.) Carrière., and Fagus sylvatica L. By contrast, Pinus nigra J. F. Arnold., is the species which be adversely affected by applying silviculture operations following by Abies alba Mill., Pinus sylvestris L., Pinus uncinata Ramond ex DC., and Quercus pubescens Mill., which do not have practised significant changes after implemented silviculture. Hence, our results show that management strategies are reasonably good at achieving the adaptation objectives for which they were designed.

Regarding the hypothesis (III) "Forest management applied will help to mitigate the effects of climate change in the study area as well as to foster an increase in the resilience and resistance of remaining communities" (Loustau et al., 2005). To conclude and after evaluating the influence of forest management on attenuating climate change effects, we may confirm that the data measured and simulated are in general supported the third hypothesis. Due to the increase in the non-structural carbohydrates concentration [NSC] as well as due to the ability of remained trees to enlarge the tree-

ring width in (mm) and in the capability of the ecosystem in sequestering carbon, the system becomes more resilient, thereby, being more resistant and presenting more plasticity to overcome harsh conditions derived from climate change.

## 4.5. Model limitations

CASTANEA model allows simulating carbon, energy and water fluxes in monospecific forests, under changing environmental conditions. What makes it a powerful tool to evaluate climate changes effects on forest ecosystems under varying conditions. Nevertheless, the model still presents some ambiguities which make it weak. For this reason, nowadays is still under revision and innovation.

Regarding limitations, for example, CASTANEA model is not allowed to estimate mixed forest stands as well as uneven-aged stands. Consequently, forest on Mont Ventoux was evaluated as an even-aged monospecific forest.

In the same way, there is some uncertainty due to the high number of parameters that the model needs to properly evaluate species functioning further, as well as due to the lack of some of these parameters as a result of the complex physiology of species. Additionally, there is some uncertainty due to the complexity as well as of the unknown of the state of art of edaphic composition of soils on Mont Ventoux. Concerning mortality rate, nowadays the model cannot predict mortality rate due to competition as well as death due to disturbances like snowstorm or windstorm among others.

Although all the above, we are confident about the reliability of our results, since CASTANEA model has successfully been applied to deciduous, sclerophyllous evergreen and conifer tree species. In this study, for example, the photosynthesis sub-model was also able to simulate the edaphic and atmospheric drought in a Mediterranean environment. Besides, the model successfully reproduced the year-to-year variation in RW as well as to accurately simulate NSC dynamics alongside GPP, NPP, Reco and NEE fluxes within the ecosystem.

### 5. Conclusions

Effects of climate change were analysed by comparing historical and future conducted simulations under different scenarios and models. The test suggested that NEE decreases in all scenarios except upon CNRM - CM5 under RCP 8.5. On the other hand, the growth of wood increase in all RCPs, but concerning temporal trends, during the past, mortality rate decreased; nevertheless, NEE rose as well as the water stress. By contrast, in the future, a fall of NEE and an increase in the mortality rate especially under the RCPs 8.5 of the HadGEM2 - ES model will occur. Considering the elevation effect, we show that the NEE tend to decrease across altitude in the past. Similarly, in the future, the model has predicted a drop in the rate of NEE in altitude despite water constraint. Besides, the model has simulated a drop in the rate of NPP. On the contrary, results from simulations analysing all climate change scenarios have revealed a meaningful increase of [NSC] at higher altitudes than at lower. Suggesting, therefore, that this effect might be due to species as well as to the climatic conditions at these elevations. Our findings verified that the ecosystem in the future would remain carbon sinks; though, the pool strength globally will decrease across altitude and thus, among species.

One of the primary objectives of the present analysis was to understand simulated vegetation dynamics through predictions from ecophysiological process-based models, under different climate models and scenarios. To what concern all the above, we are convinced that our correlating approach between observed mortality index at the population level and the simulated carbon and water fluxes, growth, NSC content, and mortality probability for nine trees species through the implementation of CASTANEA, provide valuable insights to understand forest mortality processes better and predict them under a changing climate.

Finally, to foster resilience and resistance of the forest facing against the impacts of climate change, we decided to implement a set of silvicultural treatments. Results from silviculture operations suggested an improvement in the capability of the ecosystem to store carbon as well as a substantial decrease in the mortality rate, being the most benefited species those that are well adapted to extreme drought conditions, which already is one of the ambitions of the implemented silvicultural measure, the improvement of the stand stability against drought.

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