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Assessing drought-driven mortality trees with physiological process-based models



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ARTICLE INFO

Article history: Received 29 February 2016 Received in revised form 23 June 2016 Accepted 29 August 2016

Keywords: Ecophysiology Process-based model Mortality Carbon starvation Xylem embolism Abies alba Drought Mediterranean forest

ABSTRACT

(1) This study describes how physiological process-based models can be used to assess the mortality risk of forest trees under global change. (2) Using the CASTANEA model, we simulated the development over time of tree functioning with different ontogenetic and phenotypic characteristics (age, diameter, Leaf Area Index, leaf traits) and growing in different site conditions (elevation, soil water content). Based on this set of simulations, we determined the carbon and hydraulic physiological thresholds associated with tree mortality that best reproduce the observed mortality rate. (3) We tested this methodology on a long-lasting and patchy drought-induced mortality event of silver fir (*Abies alba* Mill.) in South-Eastern France. (4) We found that tree mortality was not caused by a massive summer xylem embolism, but rather by depletion in carbon reserves probably associated with bark beetle attacks. Simulation outputs also revealed that trees with high diameter and Leaf Area Index and growing on shallower soils were more prone to die. (5) This study highlighted that physiological process-based models can be of high interest to determine the factors predisposing and inducing tree death.

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1. Introduction

The anthropogenic influence on the earth's climate will be substantial by end of this century (Vitousek et al., 1997). The extreme scenario predicts up to a six degrees increase in southern Europe during the summer months combined with a 25% decrease in precipitation (IPCC, 2014). Such scenario would correspond to an upward shift of climatic niches of almost 1000 m along elevation gradients and would strongly affect tree species vegetation belts (Randin et al., 2009). In fact, many of the trees alive today will probably experience drought and temperature levels outside the range to which they are adapted (Allen et al., 2015). Trees are keystone species in many terrestrial ecosystems, and the legacy of tree mortality on forest dynamics, structure and functions can persist for a long time (e.g., Goetz et al., 2012). Consequently, it is important to correctly understand the ecological mechanisms leading to tree mortality and project the future mortality risk under climate change (e.g., Breshears et al., 2005; Adams et al., 2009; Trumbore et al., 2015).

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Although a variety of stress and disturbances may predispose and trigger tree mortality (e.g., shading, wind-throws, wildfires, pests, frosts, or floodings), drought-induced mortality represents one major cause of the recent widespread increases in number of tree mortality events (Allen et al., 2010; Allen et al., 2015; Hartmann, 2015). Mortality caused by drought is also expected to increase in the future due to the projected rise in temperature and decrease in precipitation in certain regions (IPCC, 2014; Allen et al., 2015; Anderegg et al., 2012). As drought can occur at various spatial and temporal (i.e., duration and frequency) scales with different severities, and interact with many other mortality agents, it is important to better understand the complexity of the drought-induced mortality process. Moreover, drought increases the vulnerability of forest stands to fire (Westerling et al., 2006; Brando et al., 2014) and reduces the resistance of trees to pest attacks, especially from bark beetles (Netherer et al., 2015). Despite the recent wealth of ecophysiological research on this process (e.g., McDowell et al., 2011), the physiological mechanisms leading to tree mortality, when drought increases in intensity and duration, i.e. carbon starvation or hydraulic failure, are still under debate (e.g., Hartmann, 2015). A decrease in soil water content and/or an increase in air vapour pressure deficit increase the tension in the soil-to-leaf water continuum, that potentially leads to xylem embolism (i.e., the formation of vapour cavities in the xylem caus-

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ing water column breakage; Tyree and Ewers, 1991). Trees can prevent this functional damage by closing their stomata in the early stages of drought to limit water losses (Tyree and Sperry, 1988), but to the detriment of carbon uptake. For these reasons, during a longlasting drought, these trees face a sort of cornelian dilemma to die either by xylem embolism and/or by carbon starvation (McDowell et al., 2008).

On one hand, the risk of xylem embolism might be important for many tree species as the hydraulic safety margin, i.e., the difference between minimal leaf water potential and xylem potential leading to cavitation, is low for many species across biomes (Choat et al., 2012). However, embolism leads to tree death only when xylem conductivity loss is above 80–90% for angiosperms (Urli et al., 2013) and 50% for gymnosperms (Brodribb and Cochard, 2009). These values are quite high because trees can recover their conductivity thanks to their potential capacity to refill embolized xylem conduits (mainly for angiosperms; Choat et al., 2012), and by building new xylem tissues through primary and secondary growth (Brodribb et al., 2010).

On the other hand, the carbon starvation hypothesis is above all a theoretical consideration coming from the acquired knowledge of plant functioning (Hartmann, 2015). During a drought event, plants stop their growth before closing their stomata that paradoxically increases carbon storage and non-structural carbohydrate (NSC) concentration (Sevanto et al., 2014). Then, the reduction in Gross Primary Production (carbon uptake) due to stomata closure is stronger than the decrease in respiration and becomes not sufficient to fulfil carbon requirements for respiration, defences and reproduction leading to a decline in NSC content (McDowell et al., 2008; Sala et al., 2010). But the rhythm of these declines depends on the overall carbon economy of the plant, and the hypothetical threshold of NSC below which death occurs remains difficult to determine (McDowell et al., 2013). Indeed, plants can acclimatize their carbon economy to recurrent droughts through many mechanisms by reducing the respiratory costs or increasing the water use efficiency, e.g., via a decrease in leaf area, an increase in the thickness of leaves, or an increase in root growth (Martin-StPaul et al., 2013). In addition, the presence of pests can modify carbon allocation within a tree and often induces tree death before it reaches a threshold below which no NSC can be mobilised anymore (Herms and Mattson, 1992). For all these reasons, observations and experiments have often failed to confirm the role of carbon starvation, when observing on-going diebacks (Gruber et al., 2012; Hartmann 2015). It is unlikely that we could discover a universal NSC threshold value that could be applied across species and across a variety of ecological situations that would mimic the thresholds obtained on the percentage of conductivity loss. However, it may be possible to approximate such a NSC threshold in specific case studies, for instance through the use of physiological process-based models (e.g., McDowell et al., 2013).

model CASTANEA on a silver fir (*Abies alba* Mill.) drought-induced mortality event that occurred on Mont Ventoux, south-eastern France (Cailleret et al., 2013).

2. Materiel and methods

2.1. CASTANEA model

CASTANEA is a generic process-based model used to simulate carbon and water fluxes and tree growth in forest ecosystems (Dufrêne et al., 2005). The canopy is divided into five layers of leaves, while branches, stem, coarse and fine roots, and NSC compartments compose the rest of the tree. Photosynthesis is hourly estimated for each canopy layer using the Farquhar et al. (1980) model analytically coupled to the stomatal conductance model proposed by Ball et al. (1987) that linearly relate stomata conductance to the product of photosynthesis and relative humidity. Maintenance and growth respiration are respectively estimated proportional to the nitrogen content of the considered organs (Rvan, 1991) and from growth increment combined with a construction cost specific to the type of tissue (De Vries et al., 1974). Transpiration is also hourly calculated using the Monteith (1965) equations. The dynamics of soil water content (WC; in mm) is estimated daily using a three-layers bucket model. Soil drought drives stomata closure via a linear decrease in the Ball et al. (1987) slope, when relative soil water content is under 40% of field capacity (Sala and Tenhunen, 1996; Granier et al., 2000). More details are available in Dufrêne et al. (2005).

The model was originally developed and validated from organ to stand scales for *Fagus sylvatica* L. (Davi et al., 2005), but was also successfully applied to *Pinus sylvestris* L., *Pinus pinaster* Aiton, *Quercus ilex* L., *Quercus robur* L and *Picea abies* Karst (Davi et al., 2006b; Delpierre et al., 2012). For this study, CASTANEA was parameterized for *Abies alba* Mill. using data from the literature and *in situ* measurements (Table 1 and Table s1). We used the leaf phenology module developed for *Picea abies* Karst (Delpierre et al., 2012), while the phenology of wood growth was simulated with the same forcing model than for leaves, but with distinct parameters (F_{critWood} Stop in Table 1).

Soil water potential (Ψ_{soil} inMPa) was calculated from daily soil water content (Campbell, 1974), and leaf water potential (Ψ_{leaf}) was estimated hourly from simulated transpiration (TR in mmol m⁻² leaf s⁻¹) using one resistance ($R_{soil-leaf}$ in MPa.m⁻² s⁻¹ kg⁻¹) and one capacitance (Cap_{soil-leaf} in kg m⁻² Mpa⁻¹) along the soil-to-leaves hydraulic pathway following the model used in Loustau et al. (1998; see eq. 1). The resistance ($R_{soil-leaf}$) was assessed using sapflow measurements and midday and predawn water potentials measured in 2009 in Ventoux.

$$\Psi_{\text{leaf}}(t+1) = \Psi_{\text{soil}}(t+1) - \frac{TR}{3600} \times R_{\text{soil-leaf}} + \begin{pmatrix} \Psi_{\text{leaf}}(t) \\ \\ -\Psi_{\text{soil}}(t+1) + TR \times R_{\text{soil-leaf}} \end{pmatrix} \times \exp\left(\frac{3600}{R_{\text{soil-leaf}} \times Cap_{\text{soil-leaf}}}\right)$$
(1)

The objectives of the present paper were to show how physiological process-based models (PBMs) that explicitly simulate water and carbon pools and fluxes in trees can help (1) to determine which process (i.e., carbon starvation or hydraulic failure) is the most involved in a given drought-induced mortality event, (2) to estimate physiological thresholds using an inverse modelling approach by comparing simulated and observed mortality rates in different environmental and biotic conditions, and (3) to hierarchize the environmental and ontogenic processes that predispose tree to death. We tested this overall approach with the process-based In the carbon allocation sub-model (Davi et al., 2009), the allocation coefficients between compartments were estimated daily depending on the sink force and the phenology constraints. During winter, carbon was only distributed to reserves and fine roots. After the initiation of budburst, carbon was first used for the development of leaves and fine roots, and then for wood growth (stem and coarse roots). The fine roots sink was calculated in order to sustain a constant ratio between fine roots and leaves, while the leaf sink was forced by phenology. Considering that tissue formation is one of the first physiological processes inhibited by drought (Körner, 2015), we also added a direct effect of Ψ_{soil} on wood growth that

Table 1

List of species-specific parameters of CASTANEA for Abies alba Mill (for equations and other parameters see Table 1 in Dufrêne et al. (2005)).

Acronym	Variable	Value and Unit			
Parameters estimated based on field measurements at Mont Ventoux					
β	ratio between V _{Cmax} and V _{Jmax}	3.2			
g _{1max}	slope of the Ball relationship	6.7			
αΝα	dependency between V _{Cmax} and leaf nitrogen	11.03 μmol CO2gN ⁻¹ s ⁻¹			
F _{critBB}	critical value of state of forcing	400 °C (cumulated °C)			
N _{Start1}	the date of onset of rest	70 days			
T ₂	base temperature for forcing budburst	1 °C			
FcritWoodStop	critical state of forcing to cessation of growth	300 (cumulated °C)			
Psapwood	proportion of sapwood	46%			
FrootstoLeaves	ratio of fine roots to leaves biomass	30%			
ψ_{wood}	Predawn potential leading to wood growth cessation	-2 Mpa			
AGaerialwood	aerial wood allocation coefficient	0.6			
aGF	height to DBH relationship (Table 3)	1.08			
bGF	height to DBH relationship (Table 3)	0.75			
CR ₁	crown ratio coefficient (Table 3)	0.3			
CR ₂	crown ratio coefficient (Table 3)	0.35			
pwood	wood density	$414 \text{kg} \text{m}^{-3}$			
b	parameter for soil water potential (Table 3)	-2.2			
RSoilToleaves	resistance to water from soil to leaves	11 MPa m ⁻² s ⁻¹ kg ⁻¹			
Parameter estimated based on literature survey					
P _{branch}	proportion of branches among aerial wood	15%			

stops growth below a certain threshold of water potential (ψ_{wood} ; Table 1).

2.2. Site characteristics

The Mont Ventoux (44°110N; 5°170E) is a calcareous mountain located in the southwestern Alps, 1909 m above sea level (a.s.l.). Rainfall increased by 14 mm/100 m and temperatures decreased by -0.71 °C/100 m towards higher elevations (Cailleret and Davi, 2011). Measurements and simulations were done along an altitudinal gradient located in the north face of Mont Ventoux (5 plots: Plot 1 at 995 m, Plot 2 at 1020 m, Plot 3 at 1117 m, Plot 4 at 1247 m and Plot 5 at 1340 m) and also along a contour line transect located at same elevation than Plot 3. Local temperature, relative humidity and precipitation were measured daily in open-forested areas nearby the five plots from 2008 to 2010 using Hobos ProV2 micro-loggers and Pendant Event data loggers connected to rainfall collectors. These data were linearly correlated to the local climatic data derived by the SAFRAN model of Météo France (Quintana-Seguí et al., 2008) for the same period, and these regressions were used to generate climate data from 1960 to 2013 based on the long-term SAFRAN outputs.

2.3. Measurements for model validation

We used both short-term ecophysiological data and long-term tree-ring data to test the accuracy of CASTANEA simulations on carbon and water fluxes on Mont Ventoux.

First, sap flux density was measured for 8 trees located on plot 2 (n = 4) and plot 5 (n = 4) in 2009, using a thermal dissipation method (Nourtier et al., 2011). Predawn and midday leaf water potentials ($\psi_{predawn}$ and ψ_{min} , respectively) were measured using a Scholander pressure chamber on branch samples of 25 trees located on these plots (more details in Nourtier et al., 2014). In April 2008, xylem vulnerability curves were constructed for branches located at the top of the canopy of 16 trees (8 per plot) using the pressurization method (Cruiziat et al., 2002) to assess the water Potential inducing 50% Loss of Conductivity (Ψ_{PLC50}).

Second, 221 dominant or codominant firs located between 1100 and 1140 m were used to validate long-term simulations of the model. Inter-annual and inter-tree variability in radial growth were analysed using classical dendrochronological approaches. Trees were sampled in 2008 with an increment borer at Diameter at Breast Height (DBH), and the cores were planned with a razor blade. Ring-widths (RW, mm per year) were measured at a precision of 0.01 mm and cross-dated using the CDendro v5.3 and CooRecorder 5.3 softwares (Cybis Elektronik & Data AB., Sweden). More details are available in Cailleret et al. (2013). We compared simulated and observed ring widths both using raw data and growth index. Growth index were estimated after detrending both the simulated and observed raw ring width chronology using modified negative exponential curve (dplR package in R).

2.4. Simulation set-up

We accounted for the diversity in environmental, ontogenetic and phenotypic characteristics among trees, and consequently for the spatio-temporal diversity in the mortality process (Fig. 1). Tree vulnerability to drought varies within a population according to: (1) the microclimate; (2) the micro-topographic and –edaphic conditions; (3) the stand structure; (4) tree size; (5) tree-specific functional traits. The originality of our work is to explicitly consider all these sources of variability to simulate spatial and temporal changes in annual mortality rates at the population level (Meir et al., 2015).

Consequently, CASTANEA was used to simulate the carbon and water fluxes and pools from 1960 to 2013 for 500 trees growing along an altitudinal gradient located in the north face of Mont Ventoux (100 trees in 5 plots: plot 1 at 995 m, plot 2 at 1020 m, plot 3 at 1117 m, plot 4 at 1247 m and plot 5 at 1340m). 100 trees were also simulated along a contour line transect located at same elevation than plot 3 (named hereafter CLT). For each simulated tree, seven input variables age, DBH, Leaf Area Index (LAI), Clumping Factor (CF), Water Holding Capacity (WHC), Leaf Nitrogen Content (LNC), and Leaf Mass per Area (LMA) were randomly selected within normal distributions fitted to field observations (Fig. 2, Table S3, see Appendix A for a complete description of the field measurements). LMA, LAI, CF and WHC did not significantly change with elevation (p>0.05) and we therefore use the same normal distributions for all the plots. In contrast, LNC significantly increased with elevation in 2007 and in 2009 (p < 0.05), and plot-specific distributions were used. Tree age and DBH followed a bimodal distribution; thus, we simulated trees from two age classes, centred on the first and third quartiles in 1960, i.e., 15 and 105 years old.



Fig 1. Presentation of the overall workflow.

2.5. Data and simulated proxies of mortality

Two kinds of data were used to estimate tree mortality rate at the stand scale. First, annual mortality rates until 2008 were determined for 221 dominant or codominant firs located in CLT. and 94 dominant or codominant firs located in the plots 1-5. Based on tree-ring data, the year of death of dead trees was determined as the date of the outermost ring. The crown condition of these trees was also assessed through the visual analysis of crown defoliation and chlorosis at the end of August in 2008 (hereafter 'crown condition' dataset). Second. diameter and status (alive or not) of all trees (height >30 cm) within all plots were measured in 2008 ('forest inventory' dataset). The 'crown condition' dataset gave a good indication of the temporal dynamics of mortality rate, but only for dominant trees that may be outside of the studied plots. The 'forest inventory' dataset was exhaustive and thus provides some insights on the spatial heterogeneity in mortality rates, but includes dominated trees whose physiology was probably less well simulated by CASTANEA.

The temporal and spatial variability in observed mortality rates were compared to mortality rates simulated using six proxies *a priori* related to tree vitality and mortality risk: The Non Structural Carbohydrates concentration [NSC] ($g_C g_C^{-1}$), the NSC biomass ($g_C m^{-2} year^{-1}$), the Net Primary Productivity (NPP; gross primary productivity minus autotrophic respiration; $g_C m^{-2} year^{-1}$), the ring width, (RW, mm), a Water Stress Index (WSI = annual sum of daily simulated soil water potential; MPa), and the minimal leaf water potential (Ψ_{min} ; MPa). For each proxy, we determined the threshold that minimized the average of the Root Mean Square Errors (RMSE) calculated between simulated and observed mortality rates in 2008 on both datasets, considering all elevations.

Then, these proxies were compared in terms of their (1) performance by calculating the correlation coefficient between observed and simulated (using the obtained threshold) mortality rates across elevations in Plot 1 to Plot 5 and across years in CLT, and (2) ecophysiological significance. For instance, to test the hydraulic failure hypothesis, we compared the ψ_{min} threshold with the measured $\Psi_{PLC50}.$

3. Results

3.1. Model evaluation

The model CASTANEA accurately simulated the seasonal dynamics of sap flow during the growing season (Figs. 3a and 3b, r = 0.58 and 0.47 for the plots 5 and 2, respectively), even though the transpiration during the summer was slightly overestimated at the plot 2. It also adequately reproduced (i) the daily variations in drought intensity, i.e., the simulated soil water potential followed the observations for the two plots (r = 0.89 and 0.88 for the plots 5 and 2, respectively), and (ii) the stronger drought intensity in 2009 at low elevation (Fig. 3c and 3d). Finally, over the longer-term, the model was able to reproduce the inter-annual variations in tree RW (Fig. 4, r = 0.82) and in growth index (r = 0.62). The simulated tree RW did not significantly differ in average from the measurements (t-test, p-value = 0.65). The variation in RW among trees was partly captured, but CASTANEA simulated a decrease in inter-tree variability over time (p < 0.01), while an increase was observed with tree-ring data (Figure s2).

3.2. Which threshold best predicts tree mortality?

The simulations show an increase of water stress index and a decrease in GPP, NPP, NSC biomass and RW between 2001 and 2005 (Fig. 5), while observed mortality rates have started to increase since 2002 (Fig. 6). For each of the six proxies tested, we estimated the threshold that leads to an average cumulative mortality rate of 8.8% in 2008 on plots 1–5 based on observations (Table 2). The obtained thresholds are: 2% for [NSC], 48 g_C m⁻² for NSC biomass, 260 g_C m⁻² year⁻¹ for NPP, 0.51 mm for RWI, –226 MPa for WSI, and –3.41 MPa for ψ_{min} (Table 3). Most of these proxies partly reproduced the observed increase in mortality rates from high to low elevations (from 0.5% to 23% using inventory data in 2007, and from



Fig. 2. Observed (black) and simulated (grey) distribution of the input variables that vary in the simulation experiment: Age and Diameter at breast height (DBH in cm) in two age classes (see text), Leaf Area Index (LAI in $m^2 m^{-2}$), Water Holding Capacity (WHC in mm), Leaf Mass per Area of sunlit leaves (LMA g_C m^{-2}), Nitrogen content per mass unit (LNC in%). For age distribution, if we divided the observed population in two populations using the median (>30 years and <30 years), the obtained distributions are normal for old trees (shapiro test, p-value = 2.6e-07) and almost normal for the young trees (Shapiro test, p-value = 0.076).

Table 2

Cumulative mortality rates in 2008 observed at Mont Ventoux using the 'forest inventory' and 'crown condition' datasets and simulated by CASTANEA assuming a NSC concentration threshold of 2.1% of alive biomass.

	Elevation	Inventory 2008	Crown condition 2008	Simulated from [NSC] 2008
Plot 1	995	0.23	0.09	0.23
Plot 2	1020	0.13	0.23	0.06
Plot 3	1147	0.02	0.03	0.12
CLT plots	1100 and 1140 m	0.25	0.30	
Plot 4	1247	0.04	0.1	0.02
Plot 5	1340	0.005	0	0.02

0% to 23% using health survey of adult trees in 2008; Table 3); however, WSI and [NSC] perform the best, and NPP and ψ_{min} the worst (Table 3). [NSC] seemed to be a better proxy to predict the variability in mortality rate among stands, and also its temporal dynamics. The model that used [NSC] threshold was the only one whose simulated



Fig. 3. Simulated (lines) and observed (open circle) seasonal dynamics in sap flow (TRmax; relative values to the maximal hourly transpiration; a, b), predawn water potential ($\psi_{predawn}$; in MPa; c, d) in plot 5 (1340m; a, c) and plot 2 (1020m; b, d) in 2009. Climatic diagrams of the year 2009 were also represented for both plots revealing monthly changes in rainfall (Rain; e) and mean temperatures (T_{mean}; f). The grey error bars and polygons represent the variability in measurements and among simulations, respectively.

Table 3

Thresholds of different proxies obtained by minimizing the difference between observed and simulated average mortality rates on the five plots. Coefficient of correlation between observed and simulated mortality rates across elevations ($r_{elevation}$). Coefficient of correlation between observed and simulated mortality rates across years (r_{time}).

Proxy	Value of threshold	r _{elevation}	r _{time}
[NSC]	0.021	0.47	0.23
Biomass NSC	52.00	0.44	0.10
NPP	259.69	0.32	-0.26
Ring Width	0.514	0.45	-0.43
WSI	-224.88	0.51	0.00
Ψmin	-3.41	0.31	-0.34

annual mortality rates across years were positively correlated with the observed ones (Table 3, Fig. 6), which could be related with the overall decrease in simulated [NSC] since 2003, especially in plots 1–3 (Fig. 5), However, using this proxy as single predicting variable was not sufficient to account for any lag effects, as the model predicted tree death only between 2002 and 2005, while the observed annual mortality rates were maximal in 2006 and 2007 (Fig. 6).

Concerning the results that would support or contradict the hydraulic failure hypothesis, we did not find any significant difference of measured vulnerability to xylem embolism between the trees located on plot 2 ($\Psi_{PLC50} = -4.92$ MPa) and plot 5 ($\Psi_{PLC50} = -4.41$ MPa), or between trees with high crown defoliation rate (>20%; $\Psi_{PLC50} = -4.85 \pm 0.28$ MPa) and healthy ones



Fig. 4. Comparison between averaged and standard deviation simulated (lines and grey area) and observed (black dots and vertical error bars) inter-annual dynamics of tree-ring width in CLT stands (1100m) from 1970 to 2010. In the top-right block, the black line is the y = x line and the blue one represents the linear regression fitted to the data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

 $(\Psi_{PLC50}$ = -4.41 ± 0.32 MPa). In 2008, the Ψ_{min} recorded in plots 2 and 5 were -2.03 MPa and 1.97 MPa, respectively. At these potentials, the loss of xylem conductivity was lower than 10%. Finally, the Ψ_{min} threshold that reproduced the average mortality rate was much higher than the measured Ψ_{PLC50} (-3.41 MPa; leads to 20% of conductivity loss) and the mortality events simulated with this threshold occurred in 2000 that fully contradict the measurements (Fig. 6).

Considering that mortality was most likely caused by low [NSC], the model that simulated tree death based on this proxy predicted that mortality mainly affected old trees (>140 years old; p < 0.001) located at low elevations (plots 1 and 2; p < 0.001) and on shallower soils (WHC < 40 mm; p < 0.001). These dead trees had higher individual LAI (p < 0.001) and reduced recent RW (p < 0.001) than living ones; and surprisingly, they also had a higher LMA (p < 0.001) and water use efficiency (p < 0.001), while their LNC did not significantly differ (data not shown).

4. Discussion

4.1. On the use of physiological process-based models to simulate tree mortality

The development of a physiological predictor of tree mortality is fundamental to improve the simulation of this process, and consequently improve our ability to predict vegetation dynamics (Meir et al., 2015). In most Dynamic Global Vegetation Models (DGVM), the loss of biomass through mortality is modelled very simply. Mortality formulations range from fixed carbon turnover rates (Delbart et al., 2010), to approaches where mortality is related to growth efficiency or negative carbon balance (e.g., Steinkamp and Hickler, 2015), including age-dependent or size-dependent mortality functions (Galbraith et al., 2010; Manusch et al., 2012). However, such approaches do not adequately predict observations of droughtinduced tree mortality (Powell et al., 2013) revealing the need for an explicit and interactive consideration of both hydraulic architecture and carbon allocation processes to simulate mortality (Xu et al., 2013; Mencuccini et al., 2015). For instance, in the hydraulic model developed by Martinez-Vilalta et al. (2002), the mortality

mechanism was based on a carbon balance approach as mortality occurred when a plant exceeded a critical time with less than 5% of the original leaf area. On the other hand, Tague et al. (2013) used a relatively simple NSC-based model (i.e., ratio NSC/Net Primary Productivity) to estimate ponderosa pine vulnerability to drought.

Some PBMs now include state-of-the-art representations of the internal hydraulic and NSC dynamics of woody plants allowing for multi-model comparisons of physiological processes involved in drought-induced mortality. Recently, McDowell et al. (2013) compared simulations from six PBMs (FINNSIM, the Sperry model, TREES, MuSICA, ED(X) and CLM (ED)) on a mortality event of Pinus edulis and Juniperus monosperma in Southern USA. All their simulations predicted that the mortality of both species was caused by both hydraulic failure and carbon starvation. They also found that the time spent with severe hydraulic failure and carbon starvation is a better predictor of mortality than absolute thresholds per se. A main strength of their study is the use of several PBMs on both isohydric and anisohydric, but a drawback was the lack of consideration of the spatial variability in tree and soil characteristics. At some sites, drought-induced mortality can be patchy in space and time as trees do not share the exact same environment (soil, topography or elevation; e.g., Nourtier et al., 2014) and/or because of a different genetic and ontogenic background. Following the recommendations of Meir et al. (2015), the present study explicitly considered all these sources of variability to simulate an averaged mortality rate at the population level. This original approach was also helpful to analyse how mortality probability vary across elevation and among trees depending on their age/size, stand density, and soil characteristics.

4.2. Probable causes of Abies alba mortality on Mont Ventoux

The modelling approach used in this study provided new insights on the physiological causes of the massive mortality event of *Abies alba* that occurred on Mont Ventoux since 2002 (43% of mortality in some plots). This mortality was most likely not exclusively due to massive xylem cavitation, since minimum leaf water potential was not low enough to produce significant losses of hydraulic conductivity (PLC < 10% at $\Psi_{min} = -2$ MPa), but rather to



Fig. 5. (a) Average Gross Primary Production (GPP in $g_C m^{-2}_{soil}$ year⁻¹), (b) Autotrophic respiration (R_{veg} in $g_C m^{-2}_{soil}$ year⁻¹) (c) Ring Width (rw in mm year⁻¹), (d) Net Primary Productivity ($g_C m^{-2}_{soil}$ year⁻¹), (e) Evapotranspiration (ETR in mm.year⁻¹ the sum of transpiration, plus free evaporation when canopy is wet), (f) Water Stress Index (WSI in MPa: cumulated daily soil water potentials), (g) NSC biomass (NSC in $g_C m^{-2}_{soil}$ year⁻¹) and (h) minimal leaf water potential (Ψ_{min} in MPa) simulated between 1960 and 2013 at the five plots (red 995 m, orange 1020 m, green 1147 m, magenta 1247 m and blue 1340 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a combination of partial xylem embolism, carbon starvation, and attacks by pathogens.

Vulnerability to cavitation varied among trees, and even if in average maximum PLC was most likely lower than 50%, partial losses of conductivity caused by drought may explain model overestimation of transpiration some trees for instance in plot 2 (see Nourtier et al., 2014). The long-lasting drought process that occurred from 2000 to 2014 with recurrent dry periods (Fig. 5f) may have led to a continuous decline of NSC especially at low elevation. Tree mortality was probably not caused by complete NSC depletion, since the threshold of NSC that best predicts the observed mortality rates was above zero (2% of the NSC contain in the aerial biomass). This result is in line with recent studies suggesting that tree death from carbon starvation may not occur (Hartmann, 2015; Körner, 2015) since trees need a given amount of NSC to maintain osmoregulation and to mobilize and transport carbon reserves to the phloem (Dietze et al., 2014; Sevanto et al., 2014). However, the decline in NSC over time seemed to be a good proxy for predicting



Fig. 6. Observed and simulated relative frequency of years of tree death in the 'crown condition' dataset in CLT plots (grey histograms) and in plot 3 (coloured lines; same elevation than CLT plots), respectively. Different proxies were used to simulate tree death: The Non Structural Carbohydrates concentration [NSC] ($g_C g_C^{-1}$), the NSC biomass ($g_C m^{-2}$.year⁻¹), the Net Primary Productivity (NPP; gross primary productivity minus autotrophic respiration; $g_C m^{-2}$.year⁻¹), the ring width, (RW, mm), a Water Stress Index (WSI = annual sum of daily simulated soil water potential; MPa), and the minimal leaf water potential (Ψ_{min} ; MPa).

mortality (McDowell et al., 2013). The decrease in NSC, mainly simulated for old/big trees with large LAI, may have weakened trees by decreasing their capacity to face pest attacks (see Martínez-Vilalta, 2014), which was especially problematic at low elevation where the bark beetle population was highly abundant (Durand-Gillmann et al., 2014).

Process-based models can also be useful to disentangle the respective roles of the different factors that predisposed tree mortality. By simulating the functions and development of trees with different structure and growing in different stand types, we showed that stands with high LAI are more prone to dieback (Bréda et al., 2006). Respiration costs rise with the increase in LAI, and are not fully compensated by additional photosynthesis because of the non-linear relationship between LAI and photosynthesis, and because of higher transpiration, and thus water stress. Higher LAI is likely to lead to mortality also because of the higher rates of transpiration that increase drought risk. Mortality rates were also higher on shallower soils where water capacity is limited, because stomata closure occurred earlier and [NSC] reached therefore lower values. This result was in line with a previous study in which we found a negative relationship between WHC and Abies alba mortality rate at three sites in South-Eastern France (including Mont Ventoux; Cailleret et al., 2013). However, it partially contradicts another study carried out on the CLT transect in which we observed that mortality occurred in patches with deeper soils (Nourtier et al., 2014). Two reasons can explain these contradictory results. First, trees growing on shallower sites may have developed lower LAI and higher investment to roots (Bréda et al., 2006) that were not considered in this version of CASTANEA (but see Davi et al., 2009). Second, trees are able to use water from the deep soil from one to five meters (Nourtier et al., 2014; Barbeta et al., 2015) and shallower soils can also be located above subsoil with more water resources (see Nourtier et al., 2014). Finally, leaf nitrogen content had no effect on tree mortality, while trees with higher LMA were more prone to die. Both results indicated that (i) higher leaf-scale photosynthetic capacity may not be an appropriate strategy to prevent death from depletion in NSC, (ii) the higher simulated leaf water use efficiency due to higher LMA (higher ratio photosynthesis/transpiration) may be offset by the high cost of growth and maintenance of thick needles, and thus (iii) the inappropriate use of LMA to predict drought tolerance (Maréchaux et al., 2015).

4.3. Advantages and limitations of the CASTANEA model

Although CASTANEA was first developed to assess carbon and water fluxes of temperate deciduous tree species (Dufrêne et al., 2005; Davi et al., 2005), it has successfully been applied to evergreen coniferous trees (Davi et al., 2006a,b; Delpierre et al., 2012). The photosynthesis sub-model was also able to reproduce the edaphic and atmospheric drought in a Mediterranean context (Davi et al., 2006a,b). On the Mont Ventoux, the model was able to reproduce the temporal dynamics of soil water dynamics during a dry year, but underestimated the impact of summer drought on transpiration at one site (plot 2). As already discussed in Nourtier et al. (2014), this may be due to the post-effects of previous droughts (partial embolism or fine roots mortality), which were not considered in this model version (see above).

The model successfully reproduced the year-to-year variation in RW. Few PBMs simulating carbon and water fluxes have also been tested against long-term growth data (but see Guillemot et al., 2014), and the determination coefficient obtained in this study ($r^2 = 0.7$) was higher than the ones obtained by Misson et al. (2004) for Quercus petraea Matt. ($r^2 = 0.44$) and Pinus halepensis Mill. ($r^2 = 0.67$), by Gaucherel et al. (2008; $r^2 = 0.37$) and Touchan et al. (2012; r²⁼0.58) for Pinus halepensis Mill., and by Li et al. $(2014; r^{2=}0.21)$ for Pinus koraiensis. The good agreement between observed and simulated RW for Abies alba Mill. on Mont Ventoux was probably due to (i) the high number of trees used to derive the RW reference chronology (n = 221), (ii) the ability of CASTANEA to accurately simulate NSC dynamics (Davi et al., 2009), and (iii) the recent improvements of the carbon allocation module. In addition to the accurate simulation of transpiration and soil water content, the present version of CASTANEA was also able to simulate Ψ_{min} using a simple resistance and a capacitance between soil and leaves. This simple equation was good enough to accurately simulate Ψ_{\min} and $\Psi_{predawn}$ temporal dynamics. One main shortcoming of this study may be the lack of in situ NSC data. Nevertheless, considering the large variability in NSC measured among laboratories (Quentin et al., 2015) and the comparable NSC content on Abies

alba simulated by CASTANEA (averaged 7% and 5% of the aerial woody biomass in spring and summer respectively) and measured by Hoch et al. (2003), we are confident about the reliability of our results. Similarly, competition between trees was not considered in this simulation study, but mainly because dead trees did not show higher competition intensity than surviving ones on Mont Ventoux (Cailleret et al., 2013).

4.4. Towards a better simulation of tree mortality by process-based models

Improving the reliability of tree mortality functions in PBMs is a key challenge nowadays to reduce the uncertainty of their projections into the future (Friend et al., 2014), especially in a climate change context. First, it is necessary to better couple hydraulic architecture with the stomata conductance. This coupled model would properly simulate the decrease in conductivity, when leaf and branches water potential exceed certain thresholds, calibrated using vulnerability curves to xylem embolism (Mackay et al., 2015). This complete schema would better reproduce the impact of drought on branch and leaf mortality (Martinez-Vilalta et al., 2002), and thus on foliage biomass. Moreover, photosynthesis was found to decrease more than could be explained by the reduction stomata conductance, implying a decline in apparent carboxylation capacity (Zhou et al., 2013). It will be necessary to also represent non-stomatal limitation to photosynthesis during drought to better simulate drought-induced mortality.

Second, to simulate seasonal and annual post-drought effects (i.e., drought legacies), a more accurate carbon allocation model has to be built (Anderegg et al., 2015). Models that consider both changes in hydraulic architecture and carbon allocation over time are rare as they usually focused on one or the other compartment (e.g. Ogle and Pacala, 2009 for carbon allocation). This work represents one of the first attempts in this direction. For instance, recent studies on carbon source-sink relationships indicate that the direct effects of the environment (drought and temperature) on cell division and growth must be included to better simulate growth of the different organs (Lempereur et al., 2015; Guillemot et al., 2015), especially to account for the intra-annual variations (Schiestl-Aalto et al., 2015). This version of CASTANEA already included a direct effect of drought on wood growth and the initiation and end of wood growth was simulated depending on temperature. However, it did not consider the direct effect of summer and winter daily temperatures on growth rate of wood and fine roots (Mao et al., 2013), respectively.

Despite these shortcomings, we are convinced that our approach that compare the observed mortality rate at the population level and the simulated carbon and water fluxes, growth, NSC content, and mortality probability for a large diversity of trees, is promising. Applying this approach on many other cases of drought-induced dieback will provide useful insights to better understand forest mortality processes and predict them under a changing climate.

Acknowledgement

We wish to thank N. Mariotte, W. Brunetto, F. Courdier, O. Ambrosio and A. Jouinaud for their contribution to field measurements and dendrochronological analyses. We especially thank Alexandre Bosc for the development of hydraulic component of the model; Guillaume Carton, Roland Huc and Marie Nourtier for hydraulic and sapflow measurements; Günter Hoch for providing NSC data on silver fir stem and branches; Nicolas Delpierre for the phenology module he developed for coniferous species; Rebecca S. Snell for her careful correction of the English language and Nicolas Martin for their advises. The French Research National Agency (ANR) and INRA supported research funding in the frame of the DRYADE project (ANR-06-VULN-004) and this work was also supported by the metaprogramme Adaptation of Agriculture and Forests to Climate Change (AAFCC) of the French National Institute for Agricultural Research (INRA).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2016. 08.019.

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