



Post-fire survival and regeneration of *Eucalyptus globulus* in forest plantations in Portugal



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ABSTRACT

Eucalyptus globulus is one of the most important pulpwood plantation species in the world, and nowadays it is present in most continents. Some of the regions where *E. globulus* plantations have been expanding have a high incidence of wildfires; therefore, knowing the factors affecting the fire resistance and resilience of this species is particularly important for forest management. This is the case of Portugal, where nearly 1.4 million ha of land burned in the last decade and where *E. globulus* has become the most widespread tree species. In this paper we assessed the short-term post-fire responses of *E. globulus* trees in four sites affected by wildfires, and investigated their potential relationships with fire severity descriptors and with tree and stand characteristics. One year after fire, individual tree mortality was low (3.9%) but most trees (79.2%) were top-killed (i.e. had stem mortality). Both post-fire tree mortality and top-kill increased with fire severity (expressed by maximum char height and/or char severity rating). Moreover, top-kill was positively related with vegetation cover and the proportion of pine trees in the stand, and was negatively related with tree diameter and the proportion of other broadleaved trees in the stand. The most common post-fire regeneration type among the sampled trees was basal resprouting (89.2%), though 20.9% had epicormic resprouting. The number of basal resprouts increased with char height, top-kill and diameter of the parent tree, and decreased with slope. In terms of post-fire growth, the height of the dominant resprout increased with the number of resprouts and with char severity, while it decreased in drier southern aspects. Results showed that *E. globulus* is a fire-resilient species with a very high probability of surviving fire; however, in forest plantations where trees are usually felled in short rotations (thus with limited size), individuals have a high probability of being top-killed. The presented models may be useful to help managers on the assessment of post-fire production losses and regeneration potential in *E. globulus* plantations.

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1. Introduction

Eucalypts are native to Australasia but some species have been widely planted in many countries, mainly because of their fast growth, wood characteristics and ability to withstand dry and low nutrient conditions (Florence, 1996). One of these species, *Eucalyptus globulus* Labill. (Tasmanian blue gum), is nowadays one of the most important pulpwood plantation species in the world, having great economic importance (Potts, 2004). This eucalypt is native to south-eastern Australia (Tasmania and southern Victoria; Dutkowski and Potts, 1999) and was introduced in all continents except Antarctica (in Europe introduction occurred more than 150 years ago; Goes, 1977). In 2004 there were estimated to be over 2.5 million hectares of *E. globulus* planted

worldwide, with the main concentration of plantations occurring in the Iberian Peninsula (Potts et al., 2004). According to the Portuguese Forest Inventory, *E. globulus* is now the most widespread tree species representing 26% (812 000 ha) of the total forest cover (ICNF, 2013). In Portugal this species is cultivated through a coppice system (10–12 year rotations) and the wood is almost exclusively sold to pulp mills which in turn supply papermaking industries in different parts of the world; however, rotation cycle and main uses varies among countries (e.g. Pohjonen and Pukkala, 1990).

Some of the regions where *E. globulus* has been expanding also present a high incidence of wildfires. This is the case of Portugal and Spain in the Iberian Peninsula; in Portugal alone nearly 1.4 million ha of land burned in the last decade (JRC, 2012). Moreover, the perspectives under a climate change scenario indicate a very significant increase of the annual burned area in these and other countries (Flannigan et al., 2009; Amatulli et al., 2013). Planted stands dominated by *E. globulus* are known for being highly

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fire-prone in comparison to other forest systems (Nunes et al., 2005; Moreira et al., 2009b; Silva et al., 2009; Fernandes et al., 2011; Xanthopoulos et al., 2012). Therefore the impact of wildfires on *E. globulus* plantations is an important issue to address, both from economic and ecologic perspectives.

Most eucalypt species in their native range are subject to fires and many have characteristics indicative of adaptation to a particular regime of fire intensity, frequency and season (Florence, 1996; Gill, 1997). However, mortality and regeneration type of eucalypt species are known to be quite variable (Gill, 1997). Although various studies assessed the post-fire responses of several eucalypt species (e.g. Strasser et al., 1996; Vivian et al., 2008; Waters et al., 2010), there are still many (including *E. globulus*) for which post-fire responses remain poorly known; furthermore, very few studies investigated eucalypt responses in forest plantations beyond their native range.

Whether trees survive or die after fire and the type and extent of recovery, will depend on the type and extent of damage (e.g. Gill, 1997). Post fire tree responses may vary with fire behaviour characteristics as these are directly related with the level of tree damage. Fire behaviour variables like fire intensity or flame height are a direct consequence of surface and crown fuels (Van Wagner, 1977; Rothermel, 1983); therefore the assessment of fuel-related variables like shrub cover and tree cover can be of interest for the establishment of relationships with tree responses (e.g. Moreira et al., 2007). Additionally, topographic conditions, such as slope and aspect, have a direct influence on fire behaviour (Rothermel, 1983), but also on the vegetative conditions of each tree and surrounding vegetation, particularly in Mediterranean-type ecosystems (Kutiel and Lavee, 1999; Sternberg and Shoshany, 2001; Catry et al. 2009). Post-fire tree responses may also vary with species (which possess different regeneration and fire-resistance traits), individual tree characteristics important for fire resistance or avoidance (e.g. size, bark thickness), tree physiological condition when the fire occurs (e.g. availability of energy reserves to fund regrowth), and management factors (Whelan, 1995; DeBano et al., 1998; Catry et al., 2013).

Although several eucalypt species are sensitive to fire and are killed after full crown scorch (depending on seed for regeneration; classified as obligate seeders), the vast majority are fire-resistant and will recover from damages by vegetative regeneration (classified as resprouters) (Florence, 1996; Strasser et al., 1996; Gill, 1997; Burrows, 2013; Clarke et al., 2013). Indeed, less than 10% of the more than 900 eucalypt taxa have been classified as obligate seeders (Nicolle, 2006). The principal mechanisms of recovery in fire-resistant eucalypt species are resprouting from epicormic strands (i.e. regeneration from meristem strips, usually extending from the inner to outer bark on aboveground branches and stems, which produce buds), and/or from basal buds (i.e. regeneration from a lignotuber or the root collar, at or just below soil level) (Gill, 1997; Waters et al., 2010; Burrows, 2002, 2013).

E. globulus is known by strong resprouting capacity after disturbance, which may be explained by high epicormic bud initiation potential and the presence of a lignotuber (Burrows, 2002; Whittock et al., 2003). Although some mortality may occur in burned plantations, many trees are likely to survive by resprouting. In one of the few studies on post-fire survival of *E. globulus*, Catry et al. (2010) found 100% survival in a sample of 60 burned trees, monitored over 4 years. In another study, Marques et al. (2011) reported 47% of dead trees, but these results most likely refer to stem mortality instead of individual mortality. This is the only study to our knowledge that attempted to relate mortality with other factors, although no fire characteristics were used. However, we could not find any references for *E. globulus*, relating the different types of post-fire tree response with stand and tree characteristics, nor with fire severity descriptors.

In this paper we analyse data collected in several sites that burned in the same fire season. We aimed to: (1) characterise the post-fire responses of *E. globulus* in terms of individual tree survival and resprouting behaviour; (2) investigate through modelling which are the main fire, tree and stand characteristics influencing these responses at the tree-level. Both fire, tree and stand characteristics can be partly managed, which enables some control on mortality and regeneration of burned trees. Therefore, the identification of these factors and forecasting of tree responses may allow minimizing fire damage through adequate planning and management of *E. globulus* plantations.

2. Methods

2.1. Study sites

We used data from four different locations in central Portugal, western Mediterranean Basin (Fig. 1). Each of these locations was affected by a wildfire in the summer of 2006 (July through September; Table 1), which corresponds to the normal fire season (dry season). The climate in the four study sites is Mediterranean, with mean annual temperatures ranging from 15 to 17.5 °C and precipitation ranging from 700 to 1400 mm (IA, 2003; Table 1). Elevation ranges from 120 to 580 m.

2.2. Sampling and data collection

In the four wildfire sites we used a regular grid (300 m) of points covering the burned area and defined a circular plot (50 m radius, 7850 m²) around each point. We overlaid these plots with land cover maps (scale 1:25000) and selected those located in eucalypt areas and where no post-fire interventions occurred. In total, 22 plots were sampled (Table 1). In plots with 20 *E. globulus* trees or less, all individuals inside the plot were assessed; otherwise, we laid out up to four 50-m strip transects (20 m wide) and sampled trees (starting from north and proceeding clockwise) until obtaining 20 individuals per plot. Only trees with at least 5 cm diameter at breast height were sampled, and overall we sampled 388 *E. globulus* individuals. Data collection was performed 12–14 months after fire occurrence (12 months in all sites but Atouguia).

We recorded several tree characteristics, fire severity indicators and environmental variables (Table 2). We assessed whether each tree was dead or alive (trees were considered dead when no green foliage was present regardless of its location), and the regeneration type if alive, that is, if trees were resprouting from belowground organs (root collar or lignotuber, hereafter named basal resprouting) and/or from aboveground organs (crown or stem, hereafter named epicormic resprouting). As a result, the post-fire regeneration status of each tree (RS) was recorded as dead (no regeneration), basal resprouting only, simultaneous basal and epicormic resprouting, or epicormic resprouting only, following a decreasing gradient of fire-inflicted damage (Moreira et al., 2009a). Additionally, we classified the number of basal resprouts per tree into 5 frequency categories (0, 1–5, 6–10, 11–20, >20), and measured the height of the dominant (tallest) resprout (HDR, measured with a laser hypsometer to the nearest 0.1 m).

Tree size measurements included total tree height (*H*, measured with a laser hypsometer to the nearest 0.1 m) and diameter at breast height (DBH, measured at 1.30 m above ground level to the nearest 1 cm). Bark thickness (BT) was not measured on burned trees because the bark is often partially consumed by fire and may detach from the stem; alternatively, we measured BT and DBH on 60 nearby unburned trees (DBH range = 5.2–50.3 cm) and estimated BT for each burned tree from the derived allometric

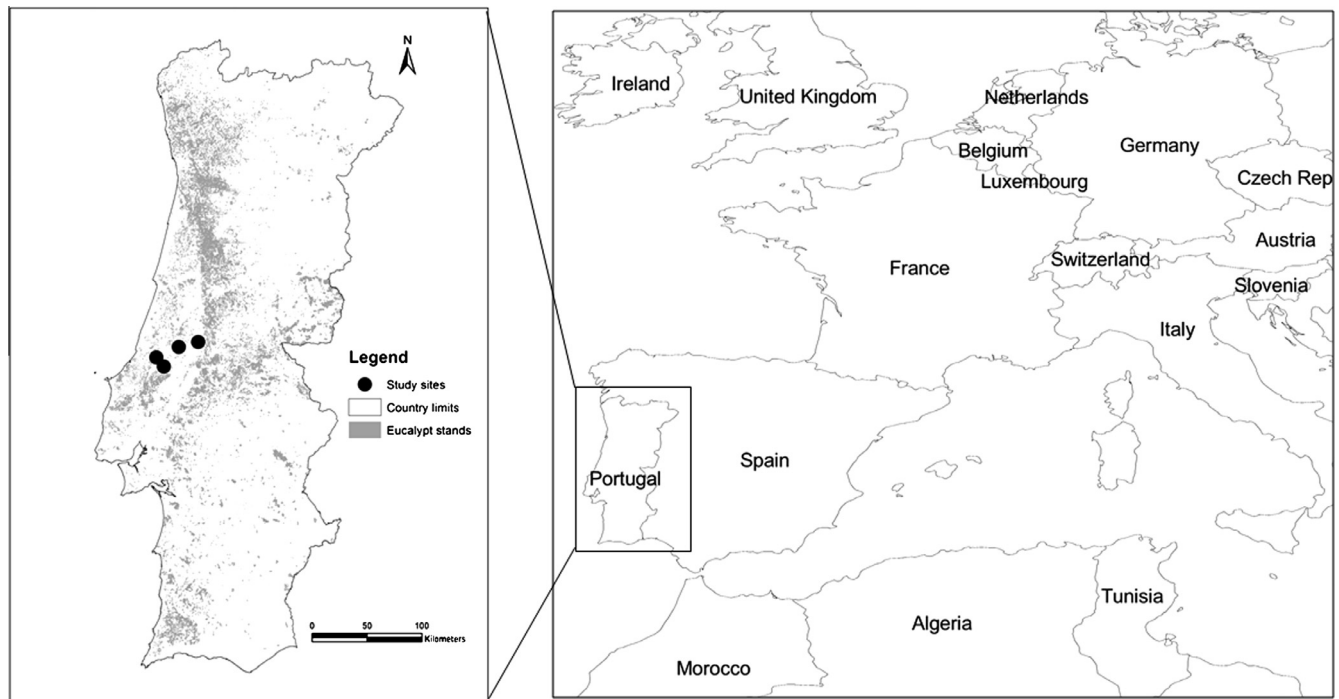


Fig. 1. General location of Portugal (right) and location of the four study sites (left; black dots represent the study sites and grey polygons represent major eucalypt plantations).

Table 1
List of the four study sites.

Site name	<i>n</i> Trees	<i>n</i> Plots	Fire date	Burned area (ha)
Agroal	90	5	September 2006	375
Atouguia	92	5	July 2006	261
P. Mós	123	8	August 2006	2964
V. Florido	83	4	August 2006	252

n Trees, number of sampled trees; *n* plots, number of established plots.

equation ($BT = 0.093 * DBH^{0.732}$; $R^2 = 0.854$). Bark thickness measurements (to the nearest 0.1 cm) were performed at 1.30 m with

a bark gauge, and represent the average of two measurements at opposite sides of the trunk.

We also assessed two commonly used indicators of fire severity and potential tree injury (Woolley et al., 2012; Thies and Westlind, 2012): the proportion of maximum tree height charred (PCH) and bole char severity (CS). First, the maximum bole char height (the vertical extent of blackening of the outer bark) was measured in each tree (CH, measured with a laser hypsometer to the nearest 0.1 m); then, we calculated the proportion of maximum bole char height (PCH) as CH relative to total tree height. Second, bole char severity (CS) was assessed and classified in four categories

Table 2
Summary of the variables assessed in four wildfires and used for modelling.

Variable (code)	Units	Type ^h	Level	Mean (SD)	Range
Tree regeneration status (RS)	4 cat. ^a	R, E	Tree	–	–
Number of basal resprouts (NBR)	5 cat. ^b	R, E	Tree	2.15 (1.3)	0–4
Height of the dominant basal resprout (HDR)	m	R	Tree	3.3 (1.1)	0.5–7.1
Diameter at breast height (DBH)	cm	E	Tree	10.0 (6.5)	5–60
Tree height (H)	m	E	Tree	13.6 (5.2)	6–31
Bark thickness (BT)	cm	E	Tree	0.5 (0.2)	0.3–1.9
Percentage of char height (PCH)	%	E	Tree	54.1 (37.8)	1–100
Char severity rating (CS)	3 cat. ^c	E	Tree	2.0 (0.4)	1–3
First rotation (FR)	2 cat. ^d	E	Tree	0.47 (0.5)	0–1
Tree cover (TC)	3 cat. ^e	E	Transect	52.8 (15.8)	12.5–87.5
Shrub cover (SC)	5 cat. ^f	E	Transect	28.1 (24.4)	2.5–87.5
Location in southern aspects (SA)	2 cat. ^g	E	Transect	0.4 (0.5)	0–1
Slope (SL)	%	E	Transect	15.4 (9.7)	0.0–30.6
Percentage of pine trees (PP)	%	E	Plot	14	0–95
Percentage of other tree species (PO)	%	E	Plot	10	0–97

^a Tree regeneration status (R), 4 categories: dead, basal resprouting only, simultaneous basal and epicormic resprouting, or epicormic resprouting only.

^b Number of basal resprouts (NR), 4 ordered categories: 0 (0 resprouts), 1 (1–5), 2 (6–10), 3 (11–20), 4 (>20).

^c Char severity rating (CS), 3 ordered categories: 1 (light), 2 (medium), or 3 (heavy).

^d First rotation (FR), 2 categories: 1 (yes), or 0 (no).

^e Tree cover (TC), 3 ordered categories: <25%, 25–75%, or >75%.

^f Shrub cover (SC), 5 ordered categories: <5%, 5–25%, 25–50%, 50–75%, or >75%.

^g Location in southern aspects (SA), 2 categories: 1 (yes), or 0 (no).

^h Type: variable used in the models as response (R) and/or explanatory (E).

following criteria established by Ryan (1982). Definitions of these classes were: none: no evidence of flame contact with the bole and no charring; light: bark partially charred; medium: bark uniformly black, but bark character is still discernible; heavy: bark deeply charred, but not necessarily to the wood, with loss of bark superficial characteristics. Because cambial damage is usually greater near ground level than at breast height, bole char severity was based on the depth of bole char in the first 50 cm above ground (McHugh and Kolb, 2003).

In addition we recorded whether each individual tree was in the first rotation or not (FR; i.e. originating directly from seed and never harvested before, or from resprout origin). Typically, trees in the first rotation have a single stem and their age is lower than 12 years, while the others are multi-stemmed and older. In the case of multi-stemmed individuals, tree characteristics (namely size and bark thickness) and char severity refer to the largest stem. Tree post-fire responses refer to a given individual, regardless the number of stems it possesses (e.g. a tree is considered to be dead only if all stems are dead).

Since not all the plots were pure eucalypt stands, we counted the number of trees of each species and calculated at the plot-level: (i) the proportion of pine trees (PP; *Pinus pinaster*); and (ii) the proportion of other non-eucalypt broadleaved trees (PO). Total tree cover (TC) and shrub cover (SC) prior to fire were visually estimated at the transect-level during field assessments (based on the amount and size of burned tree and shrub remains and on resprouting vegetation) and with the help of aerial photographs taken before the fire. Tree cover was estimated using three categories (<25%, 25–75%, >75%) and shrub cover according to five categories (<5%, 5–25, 25–50%, 50–75%, >75%). We also assessed the topographic conditions in each transect, namely the dominant slope (SL, measured with a hypsometer to the nearest 1%) and aspect (8 categories); aspect was later simplified as a binary variable named southern aspects (SA; i.e., taking the value 1 for southern exposures S, SE or SW, which are drier conditions in the study area, and 0 for the remaining). The values for the plot and transect variables (Table 2) were used to characterise all trees in a given plot or transect.

2.3. Data analysis

The main data analysis was performed using generalized linear mixed-effects models (GLMM) (Bates et al., 2009; Zuur et al., 2009). As dependent variables we used the following post-fire tree responses: (i) individual mortality, i.e., mortality of all above-ground and belowground organs (tree death), (ii) top-kill (TK), i.e., death of all the aboveground biomass (thus including both live trees with basal resprouting only and dead trees), (iii) basal resprouting only, (iv) epicormic resprouting only, (v) number of basal resprouts (NBR), and (vi) height of the dominant basal resprout (HDR). Variables (i) to (iv) were treated as binary (i.e., yes/no), and variables (v) and (vi) were treated as continuous. These post-fire responses were examined in relation to the different independent (explanatory) variables collected at the tree-, transect- and plot-level (Table 2). For modelling purposes the categorical variables FR and SA were treated as binary (i.e., yes/no), while the ordinal variables (TC, SC and CS) were treated as continuous: TC and SC were coded according to the midpoint of the respective categories; CS was coded as 1 (light), 2 (medium) and 3 (heavy), as there were no trees with the “none” category.

All the mixed models were fitted in R (R Development Core Team, 2010) using the function *glmer* of the *lme4* package (binomial and gaussian families for binary and continuous responses, respectively; Bates et al., 2009), with wildfire site as a random effect. For each response variable assessed we started with a model including all explanatory variables and we used backward

elimination to select the most important ones (Zuur et al., 2009). Model selection was performed by removing in each step the variable that explained less deviance, until all remaining variables in the model were significant ($p < 0.05$). Correlation between pairs of variables was checked using the Pearson correlation coefficient (between continuous variables) and the point biserial correlation (between continuous and dichotomous variables); when presenting a magnitude greater than ± 0.6 , only one variable was used in the model in order to avoid collinearity (Zuur et al., 2009).

The Nagelkerke pseudo- R^2 (Nagelkerke, 1991) was used as an indicator of the proportion of variance explained by the models. Additionally, in the mortality and top-kill models (binary response variables), model performance was assessed by calculating the area under the receiver operating characteristics (ROC) curve (Hosmer and Lemeshow, 2000; Pearce and Ferrier, 2000). The ROC method has advantages in assessing model performance in a threshold-independent fashion, being independent of prevalence (Manel et al., 2001). Usually area under curve (AUC) values of 0.7–0.9 indicate useful applications and values above 0.9 indicate high accuracy (Swets, 1988).

3. Results

3.1. Mortality and top-kill

Our sampling captured a range of individual tree characteristics, as well as varying levels of fire severity (Table 2). Overall, 96.1% of the trees assessed regenerated vegetatively and were alive 1 year after the fire. Despite the low (3.9%) post-fire mortality, most (79.2%) sampled trees were top-killed (i.e., had stem death), while the remaining resprouted from epicormic (aerial) buds (Fig. 2).

Model results show that post-fire tree mortality increased with char severity (CS); however, model performance was relatively poor (ROC = 0.77, $R^2 = 0.08$; Table 3). In contrast, the best model for predicting tree top-kill performed very well (Table 4). The proportion of maximum char height (PCH), char severity (CS), tree cover (TC), shrub cover (SC) and the proportion of pine trees (PP), all increased the probability of eucalypt top-kill, while tree diameter (DBH) and the proportion of other broadleaved tree species (PO) had a negative effect on top-kill. The ROC curve indicated 95% concordance between predicted probabilities and observed outcomes; the explained variance of this model was 59% (Table 4).

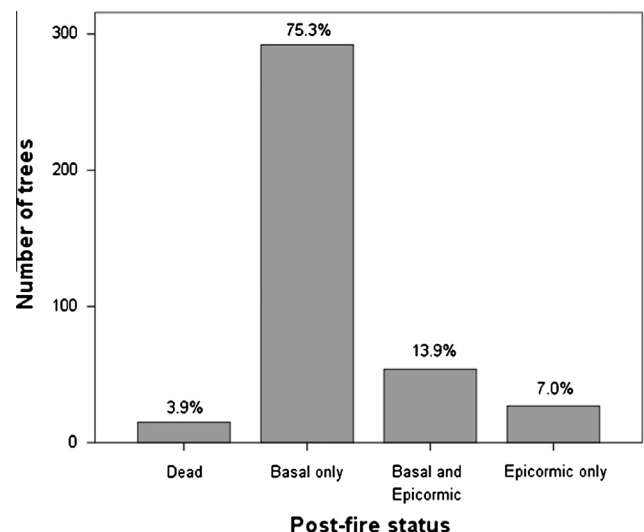


Fig. 2. Post-fire regeneration status of 388 *E. globulus* trees sampled in four wildfire sites.

Table 3
Generalized linear mixed model to predict the probability of *E. globulus* mortality (M) 1 year after fire.

	Coefficients	χ^2	P-value
β_0	-7.068 ± 1.378	–	–
CS	1.779 ± 0.583	9.120	0.003

Model coefficients (\pm standard error): β_0 , intercept; CS, char severity rating (cat.). Result of the likelihood ratio test (χ^2 and respective P-value). Model fit: area under ROC curve = 0.77; Nagelkerke R^2 = 0.08.

Table 4
Generalized linear mixed models to predict the probability of *E. globulus* top-kill (TK) 1 year after fire. Both the selected model (above) and an alternative (simpler) model (below) are presented.

	Coefficients	χ^2	P-value
<i>Selected model</i>			
β_0	-3.827 ± 1.374	–	–
DBH	-0.315 ± 0.048	88.942	<0.001
TC	0.109 ± 0.024	22.803	<0.001
PP	0.088 ± 0.637	21.333	<0.001
PO	-0.055 ± 0.015	14.885	<0.001
PCH	0.024 ± 0.007	13.159	<0.001
SC	0.020 ± 0.009	5.116	0.024
CS	0.834 ± 0.392	4.155	0.042
<i>Alternative model</i>			
β_0	2.838 ± 0.731	–	–
DBH	-0.224 ± 0.035	64.281	<0.001
PCH	0.033 ± 0.007	35.046	<0.001

Model coefficients (\pm standard error): β_0 , intercept; DBH, diameter at breast height (cm); TC, tree cover (%); PP, percentage of pine trees in the plot (%); PO, percentage of other species in the plot (%); PCH, maximum char height expressed as percentage of tree height (%); SC, shrub cover (%); CS, char severity rating (cat.). Results of the likelihood ratio test (χ^2 and respective P-value) to evaluate the importance of each variable (variables are ordered by decreasing order of importance). Model fit: Selected model: area under ROC curve = 0.95; Nagelkerke R^2 = 0.59; Alternative model: ROC = 0.93; R^2 = 0.50.

A simpler model with just two variables (DBH and PCH), still showed very good accuracy (ROC = 0.93; R^2 = 0.50), and is presented as an alternative (Table 4, Fig. 3).

Specific models to predict basal resprouting only and epicormic resprouting only (see Fig. 2) were also developed and performed

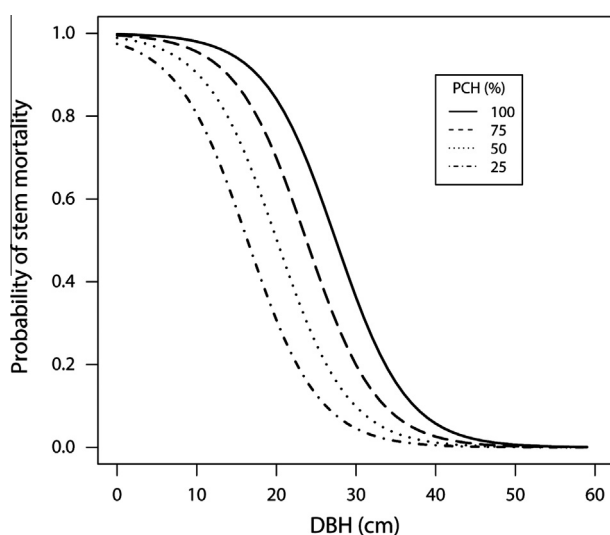


Fig. 3. Predicted probability of post-fire top-kill (stem mortality) for *E. globulus* trees as a function of diameter at 1.30 m (DBH) and fire severity (expressed by the proportion of maximum char height, PCH). This alternative simpler model with only two variables still showed very good performance (see Table 4).

well. Basal resprouting increased with PCH and decreased with DBH, while epicormic resprouting decreased with both PCH and CS (Table 5). There was a nearly significant ($P = 0.061$) positive effect of DBH in the epicormic resprouting model.

3.2. Number and growth of basal resprouts

Overall, 89.2% of eucalypt trees had post-fire basal regeneration, with varying number of resprouts (Fig. 4). Model results (Table 6) show that the number of basal resprouts per tree increased with char height (PCH) and parent tree diameter (DBH), was higher in top-killed individuals (TK), and decreased with slope (SL). Although we found these four variables to significantly influence the number of resprouts, the explained variance was not high ($R^2 = 0.11$; Table 6). Char height (PCH) was the most important variable affecting the number of basal resprouts, while the remaining three variables accounted for little additional explained variance (about 2%).

The growth of basal resprouts was remarkably fast and one year after fire the mean height of the dominant resprout (3.3 m) was already nearly 25% of the mean pre-fire tree height (13.6 m; Table 2, Fig. 5). The height of the dominant basal resprout (HDR) was positively related with the number of resprouts (NBR) and with char severity (CS); additionally HDR was lower in southern aspects (SA) (see Table 7).

4. Discussion

4.1. Mortality and top-kill

One year after fire, the large majority (96.1%) of eucalypt trees were still alive, although most (79.2%) were top-killed. We found that the probability of individual tree mortality significantly increased with fire severity (expressed by CS). None of the other variables assessed affected tree mortality. Although the ROC analysis indicated the usefulness of a model with only one predictor, the explained variance was quite low. The usually low fire-induced individual tree mortality observed in most temperate broadleaved species makes it difficult to establish relationships with potential explanatory variables, and several other studies found similar difficulties (Stephens and Finney, 2002; Franklin et al., 2006; Catry et al., 2010). In contrast, the developed models for predicting tree top-kill showed very good performance, and we could find significant relationships between top-kill and several explanatory variables. The most important predictors of *E. globulus* top-kill were the tree morphological traits, namely DBH and BT (which were not used simultaneously to avoid collinearity). These two variables were highly correlated ($r = 0.99$) as expected, and both decreased tree vulnerability to fire. In general, using BT instead of DBH resulted in slightly better model performance, suggesting that BT may be the main morphological trait conferring resistance to top-kill; however, since differences were small and DBH is usually more easily available, we opted to present the models with this variable. Tree height (H) was also highly correlated with BT ($r = 0.76$) and DBH ($r = 0.73$), but showed considerably lower performance. Bark thickness has been shown to have an important influence on fire-induced responses of several broadleaved species worldwide, including eucalypt trees (Catry et al., 2010; Lawes et al., 2011; Brando et al., 2012). Bark can protect the tree vascular cambium and epicormic strands or buds from lethal temperatures during a fire, and small differences in BT have been reported to produce large differences in fire resistance and resilience to fire (Bond and Van Wilgen, 1996; Catry et al., 2012; Catry et al., 2013). Like BT, DBH has also been shown to increase fire resistance in several tree species (e.g. Woolley et al., 2012), including eucalypts (Catry et al.,

Table 5

Generalized linear mixed models to predict two types of *E. globulus* resprouting: (1) Basal resprouting only (above), and (2) epicormic resprouting only (below).

Resprouting type	Coefficients	χ^2	P-value
<i>Basal only</i>			
β_0	2.017 ± 0.544	–	–
DBH	–0.195 ± 0.032	55.886	<0.001
PCH	0.028 ± 0.005	34.576	<0.001
<i>Epicormic only</i>			
β_0	2.247 ± 1.004	–	–
PCH	–0.086 ± 0.038	17.575	<0.001
CS	–1.828 ± 0.609	10.491	0.001

Model coefficients (±standard error): β_0 , intercept; DBH, diameter at breast height (cm); PCH, maximum char height expressed as percentage of tree height (%); CS, char severity rating (cat.). Results of the likelihood ratio test (χ^2 and respective P-value) to evaluate the importance of each variable (variables are ordered by decreasing order of importance). Model fit: Basal resprouting model: Area under ROC curve = 0.89; Nagelkerke R^2 = 0.44; Epicormic resprouting model: ROC = 0.96; R^2 = 0.50.

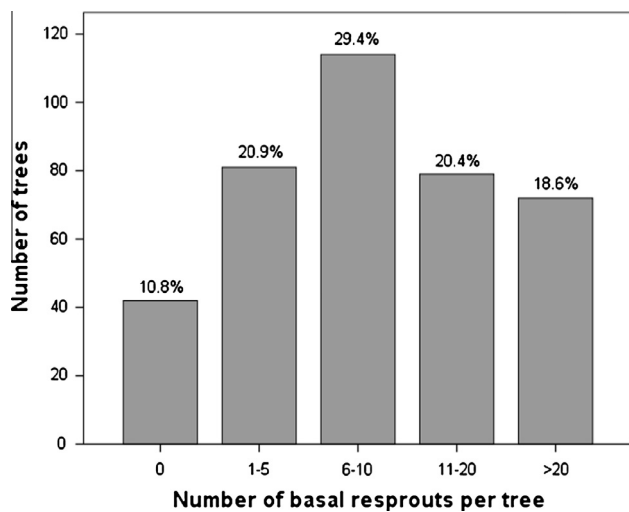


Fig. 4. Number (classes) of post-fire basal resprouts on 388 *E. globulus* trees.

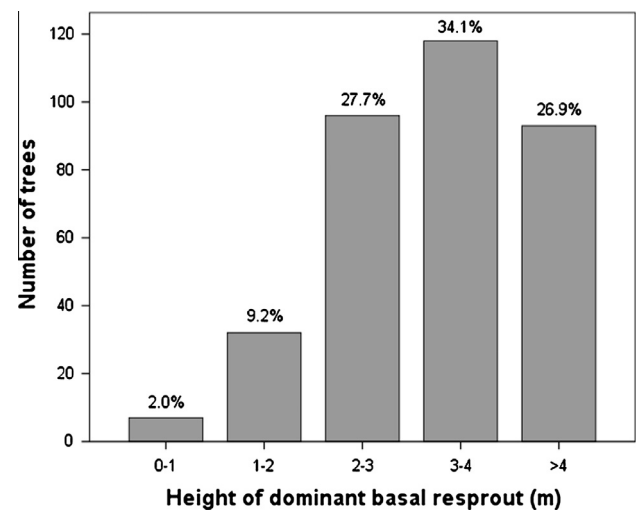


Fig. 5. Classes of height of the dominant basal resprout for 346 *E. globulus* trees with basal regeneration.

Table 6

Generalized linear mixed model to predict the number of basal resprouts per tree (NBR) 1 year after fire.

	Coefficients	χ^2	P-value
β_0	1.371 ± 0.316	–	–
PCH	0.013 ± 0.002	43.778	<0.001
SL	–0.041 ± 0.010	15.862	<0.001
DBH	0.031 ± 0.011	7.6028	0.006
TK (yes)	0.482 ± 0.185	6.9723	0.008

Model coefficients (±standard error): β_0 , intercept; PCH, maximum char height expressed as percentage of tree height (%); SL, slope (%); DBH, diameter at breast height (cm); TK, top-killed tree (yes vs. no). Result of the likelihood ratio test (χ^2 and respective P-value) to evaluate the importance of each variable (variables are ordered by decreasing order of importance). Model fit: Nagelkerke R^2 = 0.11.

Table 7

Generalized linear mixed model to predict the height of the dominant basal resprout (HDR) 1 year after fire.

	Coefficients	χ^2	P-value
β_0	2.010 ± 0.403	–	–
NBR	0.314 ± 0.050	37.328	<0.001
SA	–0.271 ± 0.118	5.455	0.020
CS	0.341 ± 0.143	5.348	0.021

Model coefficients (±standard error): β_0 , intercept; NBR, number of basal resprouts (categories); SA, location in southern aspects (yes vs. no); CS, char severity rating (categories). Result of the likelihood ratio test (χ^2 and respective P-value) to evaluate the importance of each variable (variables are ordered by decreasing order of importance). Model fit: Nagelkerke R^2 = 0.11.

2010; Marques et al., 2011); however, it is not always obvious if this relationship is solely a result of the strong positive correlation between DBH and BT, or if it can be also a consequence of other factors, such as the lower probability of larger stems to be lethally damaged around the entire circumference (Gutsell and Johnson, 1996). Additionally, previous studies suggested that the epicormic structure of small-diameter eucalypt stems are in transition from axillary buds and meristems to fully developed epicormic strands (Burrows, 2000; Waters et al., 2010), which may be also a reason for lower epicormic resprouting potential of smaller trees. Other authors remarked that species like eucalypts or individuals within a species that tend to produce developed epicormic structures and retain persistent meristems may increase their epicormic potential over time as they grow (Meier et al., 2012). Our results

clearly show that the probability of fire-induced tree top-kill sharply decreases with increasing DBH (or BT). Furthermore the presented model suggests that the probability of top-kill will be less than 50% when DBH exceeds 30 cm, regardless of char height; however, since our sample included a small number of these large trees (because they are seldom found in eucalypt plantations; Table 2), these results should be confirmed in future studies.

In addition to morphological traits, the two fire severity indicators and four variables reflecting the stand structure and composition also influenced the probability of top-kill. Both the proportion of maximum char height (PHC) and bole char severity (CS) increased the likelihood of eucalypt top-kill, as expected. Char height correlates with flame height or fire intensity (e.g. Finney and Martin, 1993) and is one of the most widely used fire severity

indicators, indirectly providing information on possible injury to cambial tissue or foliage (Regelbrugge and Conard, 1993; Thies et al., 2006; Woolley et al., 2012; Catry et al., 2013). On the other hand, char severity rating has also been used as an indicator of possible cambial damage from lethal heating, and may reflect differences in the fire residence time and energy released at the base of the tree (McHugh and Kolb, 2003; Woolley et al., 2012). The two fire severity indicators showed very low correlation ($r = 0.19$) and our results suggest that they are both useful and can be used complementarily to predict top-kill (and epicormic resprouting only).

Among the variables reflecting the forest stand structure and composition, total tree cover (TC), shrub cover (SC) and the proportion of pine trees (PP), all had a positive effect on eucalypt top-kill, while the proportion of other broadleaved tree species in the stand (PO) had a negative influence. The relationship between tree cover and top-kill may be explained by the higher crown bulk density of denser stands, which may sustain higher-intensity fires (Van Wagner, 1977) and therefore increase top-kill. Also crown fire spread is more likely in dense stands if the critical surface fire intensity for crowning is attained (Cruz et al., 2005; Castedo-Dorado et al., 2012). As regards to stand composition, maritime pine (*P. pinaster*) is a flammable species (Fernandes and Rigolot, 2007) and stands are known to be highly prone to fire (Nunes et al., 2005; Fernandes, 2009; Moreira et al., 2009b). In the case of mixed eucalypt and pine stands, fire hazard may be even higher, when compared with pure stands of eucalypts or pines (Moreira et al., 2009b). As to the presence of other broadleaves, the species found in the study plots (*Quercus rotundifolia*, *Arbutus unedo*, *Q. faginea* and *Q. suber*, by decreasing order of abundance) tend to have lower flammability than *E. globulus*, and thus could have contributed to decrease fire severity and hence, top-kill. Other studies in the Mediterranean Basin have shown that the presence of hardwoods (e.g. oaks) may contribute to decrease burn probability and fire severity (González et al., 2006; Fernandes et al., 2010).

Our results suggest that all the seven variables presented in the selected model (Table 4) are useful to predict tree top-kill, and each one gives an additional contribution to the explained variance. Although using seven predictors makes the model more complex, several of these variables can be obtained quite easily. Nevertheless, our results also suggest that it is possible to maintain a very good accuracy in the predictions using only DBH and PCH as predictors.

4.2. Basal resprouting

Most *E. globulus* trees (89.2%) resprouted from basal buds and had live resprouts one year after the fire. Among these trees, nearly one third had 6–10 basal resprouts and 79.2% had less than 21 resprouts. The most important factor influencing the number of basal resprouts was PCH; trees with higher levels of PCH tended to have more basal resprouts, thus indicating that increasing PCH did not cause a major reduction in the bud bank located belowground. Soil is a good insulator, and since heat input into the soil is a small fraction of the total heat released by fire, subterranean buds are usually well protected from lethal temperatures (Bond and Van Wilgen, 1996; Florence, 1996). Although there is relatively little information about the effect of fire severity on the number of basal resprouts, previous studies showed that different tree species may respond differently to increasing fire severity (Sampaio et al., 1993; Masaka et al., 2000). For example trees from the genus *Betula*, *Caesalpinia* and *Quercus* were reported to produce more resprouts when subjected to disturbances of increasing severity (Sampaio et al., 1993; Masaka et al., 2000; Bonfil et al., 2004). Moreover, the individuals with stem mortality and showing basal resprouting only, which had higher levels of PCH and were likely more severely

damaged (e.g. Moreira et al., 2009a), tended to have more basal resprouts than those with simultaneous basal and epicormic resprouting. This may be explained by loss of apical dominance, which is mediated by hormones produced in actively growing stem tips and adjacent young leaves (Miller, 2000). Trees showing only basal resprouting are those in which all crown buds or bud producing structures were killed (either directly through heat or indirectly through the destruction of the vascular cambium in the stem); thus, the complete suppression of apical dominance in these individuals is expected to have a stronger effect in stimulating basal resprouting (Moreira et al., 2009a). On the other hand, trees showing epicormic resprouting were less affected by fire; in these cases, the presence of aboveground resprouts could cause weakened apical dominance (Kozłowski, 1971), preventing part of the bank of dormant basal buds from developing into new shoots (Miller, 2000).

Model results also showed that the number of basal resprouts decreased with slope and increased with parent tree DBH, although these factors explained little additional variability. Steeper slopes tend to retain less water, to be more susceptible to soil erosion and nutrient loss, and therefore soils in these slopes are usually thinner and less productive (e.g. Shakesby, 2011); these harsher conditions could reduce tree vigour and consequently their ability to produce and maintain viable resprouts. On the other hand the positive effect of DBH on the number of resprouts, may be explained by the presence of a larger bud bank and more belowground reserves in larger individuals (e.g. Bonfil et al., 2004; Quevedo et al., 2007), and by increased bud protection by bark thickness (e.g. Bond and Van Wilgen, 1996; Lawes et al., 2011). These results are in agreement with several studies of other tree species (e.g. Ross et al., 1986; Bonfil et al., 2004; Matula et al., 2012), although in other cases a negative relation was observed (e.g. Kauppi et al., 1988; Johansson, 2008). Indeed resprouting ability may vary with species and ontogenetic stage (Del Tredici, 2001; Vesk, 2006). Tree size is often positively related to age, but in coppice systems, like those of *E. globulus*, it is not possible to relate them without knowing the number of times each individual has been coppiced. Nevertheless, *E. globulus* is known to maintain its resprouting ability during several decades (e.g. Burns and Honkala, 1990), and Florence (1996) reported that in the case of eucalypts, where the tree is young enough to maintain its resprouting vigour, there may be a direct positive relationship between the number of resprouts and the diameter of the stump, which is consistent with our results.

The post-fire growth of the basal resprouts also ranged widely among trees, but in most cases (61%) the dominant resprout was more than three meters high (Fig. 3). The fast growth of the resprouts is due to the high growth capacity of this eucalypt species and because they are linked to a large and well established root system (Skolmen and Ledig, 1990). The four studied wildfire sites burned in summer 2006, and tree assessment took place 12–14 months after fire, thus the resprouts grew under relatively similar conditions, particularly in terms of time since fire (76% of all trees were assessed 12 months after fire). Three of the variables assessed (NBR, SA and CS) had a significant influence on the height of the dominant resprout (Table 7). The more important one was the number of basal resprouts, which had a positive effect on the height of the tallest resprout. This might be directly related to competition between basal resprouts for light, which lead the dominant one to grow taller, or the number of resprouts could be an indirect indicator of the carbohydrate reserves available in parent trees, since such reserves have been shown to positively affect both the number and growth of resprouts (Walters et al., 2005). Although contradictory reports exist in the literature, other authors found a significant positive relationship between the number of resprouts and the height of the dominant resprout

in several broadleaved species (Masaka et al., 2004; Imanishi et al., 2010).

We also found that the height of the dominant basal resprout was lower in trees growing in southern aspects. In the Mediterranean Basin, south-facing slopes receive higher solar radiation, which increase temperature and reduce water availability to plants (Kutiel and Lavee, 1999; Sternberg and Shoshany, 2001). These unfavourable drier conditions are likely the reason for the smaller growth of resprouts in southern aspects (Konstantinidis et al., 2006). Results also suggest that the height of the dominant resprout increased with CS; a possible explanation to this could be that basal resprouts may have benefited from the lower competition for resources at the tree and/or at the site level, due to lower levels of epicormic resprouting and higher levels of understory elimination (Clarke et al., 2013; Quevedo et al., 2013).

Although we found several variables to significantly affect both the number of basal resprouts and the height of the dominant resprout, the variability explained by the models was not high (Tables 6 and 7). Basal regeneration of *E. globulus* could be more affected by other factors such as individual tree carbohydrate reserve pools and genotypic variation (Walters et al., 2005), and also by differences in the environmental conditions of the micro-site and site quality (Malanson and Trabaud, 1988; Espelta et al., 2003; Gracia and Retana, 2004). For example concerning tree reserves, Walters et al. (2005) found that *E. obliqua* plants with larger carbohydrate reserve pools prior to disturbance (associated with larger lignotubers), supported production of a greater number of resprouts of greater total biomass than plants with smaller reserves. In our study the size of the parent tree at the time of the fire (indicated by DBH or H) was weakly but positively related with the number of basal resprouts, but it did not influence the height of the dominant resprout. In undisturbed forests, larger individuals are often more vigorous and are expected to have larger pools of carbohydrate reserves, thus it could be also expected that their resprouts would grow taller; however, in a coppice system where trees are regularly felled, in most cases tree size *per se* cannot be directly related to tree age or vigour. Thus, knowing the age of the trees (for example by knowing the number of previous coppicing rotations), could potentially be useful information for predicting post-fire resprouting intensity and growth. Other variables such as the disturbance history of individual plants (e.g. previous fires or extreme drought; López et al., 2009), the number of pre-fire stems in each stump (Johnson, 1975; Ducrey and Turrel, 1992), the source provenance of the planted trees (Walters et al., 2005) or site characteristics, such as soil depth (López-Soria and Castell, 1992), could possibly improve our ability to predict tree responses to fire.

4.3. Management implications

Understanding how trees respond to fire and which are the factors driving such responses is important for assisting pre- and post-fire management decisions, particularly in ecosystems where fire is a recurrent disturbance. The presented models may be useful to help managers in the assessment of post-fire production losses and regeneration potential in *E. globulus* plantations. They may also be useful to help estimating the fire effects on carbon stocks, on soil erosion, or as guidance to prescribed burning operations.

In general, all management actions contributing to decrease fire intensity and severity in *E. globulus* stands (e.g. reflected by a reduction of char height or char depth) will likely increase the probability of tree and stem survival. Our results specifically suggest that reducing vegetation cover, reducing the proportion of pine trees and increasing the proportion of other (less flammable) broadleaved trees may contribute to decrease the probability of top-kill. Results also suggest that post-fire basal resprouting tend to be less vigorous under harsher topographic conditions (namely

steeper terrains and southern aspects), thus managers may want to consider avoiding them (e.g. when planning new plantations), in order to increase resilience to fire.

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