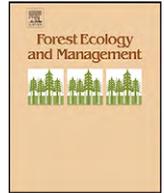Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Post-fire tree mortality in mixed forests of central Portugal

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ABSTRACT

Wildfires are a recurrent disturbance in the Mediterranean Basin. However, managers from this region are confronted with a lack of information on the effects of fire on most woody species, which is required for defining sustainable forest management strategies. Following a large wildfire in central Portugal (2003), we surveyed the area during the first year and assessed the vegetative condition of 1040 burned trees from 11 different species. Among those trees, 755 individuals were selected and monitored annually for 4 years. At the end of the study, almost all the broadleaved trees survived, while most coniferous died. In spite of the low mortality observed in broadleaves, most were top-killed and regenerated only from basal resprouts, which implies a slow recovering process. *Quercus suber*, however, showed vigorous post-fire crown resprouting and was the most resilient species. We fitted logistic regression models to predict the probability of individual tree mortality and top-kill from fire injury indicators and tree characteristics. Besides the differences between the two main functional groups (coniferous, broadleaved), bole char height and crown volume scorched or consumed were important predictors of tree responses. Additionally, the main factor determining crown mortality on broadleaved species was bark thickness. The selected models performed well when tested with independent data obtained on four other wildfires. These models have several potential applications and can be useful to managers making pre-fire or post-fire decisions in mixed forest stands in the western Mediterranean Basin.

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1. Introduction

Wildfires are a recurrent disturbance in the Mediterranean Basin. Prediction of post-fire tree mortality and top-kill (i.e., crown mortality) is essential to plan logging or to evaluate recovery options (e.g. reforestation, wildlife habitat, soil erosion) in burned areas (Ryan and Reinhardt, 1988; Regelbrugge and Conard, 1993). However, authorities and managers from the Mediterranean Basin confront with a lack of published information on the effects of wildfire on most woody species (e.g. Ordóñez et al., 2005), and especially on broadleaved ones. Even for European pines, which are relatively well studied, recent reviews indicate that most studies are based in low-intensity dormant season burns and only reflect short-term (1–2 years post-fire) mortality (Fernandes and Rigolot, 2007; Fernandes et al., 2008).

Much of the variation in plant response to burning can be attributed to varying sensitivity to heat of the different tissues and species. The time required to kill plant tissue decreases exponen-tially with the exposure time to a given temperature (Bond and van Wilgen, 1994). Tree resistance to fire depends largely on the presence of morphological traits that protects critical tissues and on the food reserves for successful recovery (Whelan, 1995; DeBano et al., 1998). The tissues important for post-fire recovery can be protected from lethal temperatures in several ways; for instance, cambium and stem buds may be protected from radiant heat by a thick bark, while below-ground stems and buds may be shielded by the overlaying soil (Whelan, 1995; DeBano et al., 1998). Fire injury on trees includes crown-kill, bole-kill and root-kill, crown damage being the most readily observed whereas root injury is seldom quantified. Variables such as bole char height and the percentage of crown scorched or consumed are often used as tree-level fire injury descriptors (e.g. Peterson, 1985; Stephens and Finney, 2002).

Crown injury has been identified as the primary cause of post-fire mortality in most conifers (e.g. Ryan and Reinhardt, 1988; Rigolot, 2004) but the response to defoliation by fire varies considerably among species. Many species are extremely sensitive and are killed if defoliation is above some threshold value, while others although completely defoliated will regenerate the crown by issuing shoots from epicormic (Bond and van Wilgen, 1994) or leaf buds (e.g. Thies et al., 2006).

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Bole damage consists of injury to phloem, cambium, or functional xylem (Ryan, 1998), and has been correlated with tree mortality and top-kill through the use of parameters like bark thickness, bole diameter, bole char height or char depth (Regelbrugge and Conard, 1993; Hély et al., 2003; McHugh and Kolb, 2003). Bark thickness has been a widely employed morphological variable to account for fire resistance (Peterson and Ryan, 1986; Pausas, 1997; Rigolot, 2004), as small differences in bark thickness produce large differences in fire resistance (Bond and van Wilgen, 1994; Moreira et al., 2007). The time taken for cambial cells to reach lethal temperature is a function of both bark thickness and thermal properties of the bark, although the former plays a more important role (Hare, 1965; Peterson and Ryan, 1986).

Post-fire tree survival and regeneration capacity are mainly influenced by factors related to both fire injury and individual tree characteristics, although additional factors of stress in the pre and post-fire environment like drought, herbivory or pests can also be relevant (Whelan, 1995; DeBano et al., 1998; Miller, 2000; McHugh and Kolb, 2003; Dylan et al., 2006).

In this paper we hypothesize that the most important factors determining the initial and delayed tree mortality and top-kill in Mediterranean mixed forests are fire injury, and bark thickness or tree size; because closely related species tend to share similar traits, we also predict that the differences within taxonomic group (coniferous, broadleaved) will be lower than between groups. Higher mortality is expected in trees apparently more injured by fire, on smaller or thinner barked individuals, and in coniferous rather than in broadleaved species, because most species from the former group are not able to resprout when the entire canopy is burned. Ungulate herbivory is also hypothesized to be an additional factor of stress affecting delayed mortality in top-killed broadleaves. A large wildfire which occurred in 2003 in a mixed forest of central-west Portugal provided an opportunity to evaluate these hypotheses in a range of tree species affected by the same fire and under similar ecological conditions. The study includes species for which there was no previous information on post-fire responses.

2. Methods

2.1. Study area

The study area (Tapada Nacional de Mafra, 885 ha) is a public fenced area located in central-west Portugal (western Iberian Peninsula), 8 km from the sea. Elevation ranges from 80 to 360 m and soils are predominantly humic cambisols derived from sandstone. Climate is Mediterranean, with a mean annual precipitation of 850–950 mm and a mean annual temperature ranging from 13 to 15 °C (IA, 2003). Before the fire, the vegetation was dominated mainly by forests (48%), including both broadleaved and coniferous species, and by shrublands (46%).

2.2. Sampling and measurements

In September 2003, 70% of the Tapada Nacional de Mafra burned during a large wildfire that occurred in the region. Fire weather was extreme and the crown of most trees was affected, although in different degrees. Following the fire, the study area was mapped and divided into a regular 500-m grid using a GIS (geographic information systems); 20 points (centers of each grid) were randomly selected in the burned area as starting locations for field plots. Points that fell in treeless areas were moved to the nearest burned forest stand. Each plot was about 100-m long and 20-m wide, and all the trees found within it were coded, marked and geographically located (with both GPS and terrain measurements) for monitoring in the subsequent years. Elevation, aspect and slope were derived for each tree location from a digital elevation model at 1:10,000 scale. We did not sample trees with broken stems or identified as being already dead before the fire (evaluation based e.g. on bark condition or advanced degree of decay).

The first field sampling was performed 3 months after the fire (December 2003) and included 1040 burned trees of 11 of the more representative species in the area over a range of tree sizes that were differently affected by fire (Table 1). The studied species were: *Castanea sativa* Mill. (chestnut), *Crataegus monogyna* Jacq. (weissdorn), *Eucalyptus globulus* Labill. (bluegum eucalyptus), *Fraxinus angustifolia* Vahl. (narrowleaf ash), *Olea europaea* L. var. *sylvestris* Brot. (wild olive), *Pinus pinaster* Ait. (maritime pine), *Pinus pinea* L. (stone pine), *Pistacia lentiscus* L. (evergreen pistache), *Quercus coccifera* L. (kermes oak), *Quercus faginea* Lam. ssp. *broteroi* (Portuguese oak), and *Quercus suber* L. (cork oak). All the studied broadleaved species are resprouters and the coniferous species are non-resprouters (Paula et al., 2009). Most of the studied species have a wide distribution in the Mediterranean Basin and are within their natural area of distribution, except *E. globulus* (introduced species native to southeast Australia). In the study area *C. sativa* can be also considered as an old introduction (González, 2001; Krebs et al., 2004).

Table 1
Characteristics of the trees (*n* = 1985, 11 species) used to develop and validate models to predict post-fire tree response.

Species (scientific name)	*n*	DBH (cm)		TH (m)		BT (cm)		TCD (%)		PCH (%)	
		$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Castanea sativa	30	21.0	10–38	7.5	4–11	1.2	0.6–2.1	99.7	90–100	30.9	6–75
Crataegus monogyna	133	17.8	5–41	4.0	2–8	0.9	0.4–1.6	100	100	94.9	17–100
Eucalyptus globulus	60	14.0	5–24	11.5	6–16	0.9	0.4–1.4	100	100	36.4	10–100
Fraxinus angustifolia	82	41.4	10–76	11.3	5–18	2.0	0.6–3.4	89	65–100	58.9	7–100
Olea europaea sylv.	127	21.3	5–54	4.5	2–10	1.0	0.4–1.7	100	100	98.6	25–100
Pinus pinaster	56	50.9	23–101	17.3	8–25	5.4	2.9–9.2	87.6	50–100	78.9	32–100
Pinus pinea	78	47.7	16–92	12.4	3–17	4.7	1.7–9.0	92.2	50–100	69.4	20–100
Pistacia lentiscus	113	7.8	3–20	2.4	1–5	0.5	0.2–1.1	100	100	97.2	33–100
Quercus coccifera	120	12.8	4–30	3.8	2–8	0.6	0.2–1.2	99.6	60–100	99.0	42–100
Quercus faginea	129	39.3	17–94	8.9	3–17	1.9	1.3–3.1	99.3	75–100	91.1	29–100
Quercus suber	112	47.0	15–140	8.8	3–16	4.9	1.9–14	99.3	60–100	79.9	28–100
Validation dataset											
Eucalyptus globulus	388	10.0	5–60	13.6	6–31	0.7	0.4–3.0	–	–	54.1	0–100
Pinus pinaster	397	22.7	7–49	13.7	5–25	2.8	1.2–5.9	–	–	54.1	0–100
Quercus faginea	98	17.9	10–51	8.9	4–19	1.3	1.0–2.2	–	–	58.2	0–100
Quercus suber	62	20.6	10–45	8.3	4–14	2.0	0.2–4.8	–	–	98.0	18–100

DBH, diameter at breast height; TH, total tree height; BT, bark thickness (BT for all the species but *Q. suber* is based on the equations presented in Table 2), TCD, percentage of crown volume damaged (crown scorched + crown consumed); PCH, maximum bole char height expressed as percentage of tree height; *n*, total number of sampled trees; $\bar{x}$, mean.

Table 2
Allometric relations between bark thickness (BT, cm) and diameter at breast height (DBH, cm) obtained from field measurements taken on 415 unburned trees from 10 species.

Species	Coefficients		R^2	n	DBH range (cm)
	b_0	b_1			
Castanea sativa	0.061	0.970	0.76	41	11–49
Crataegus monogyna	0.072	0.874	0.77	40	3–42
Eucalyptus globulus	0.026	1.227	0.89	41	3–101
Fraxinus angustifolia	0.062	0.934	0.93	40	3–97
Olea europaea sylv.	0.196	0.539	0.57	42	5–56
Pinus pinaster	0.103	1.023	0.90	44	2–105
Pinus pinea	0.133	0.920	0.83	42	11–96
Pistacia lentiscus	0.022	1.410	0.69	42	3–23
Quercus coccifera	0.024	1.193	0.73	41	5–35
Quercus faginea	0.241	0.567	0.84	42	4–108

Equations have the form $BT = b_0 DBH^{b_1}$. R^2, number of sampled trees and DBH range are also shown; all the regressions are highly significant ($P < 0.001$).

For each tree we recorded diameter at breast height (DBH, measured at 1.30 m above ground to the nearest 1 cm), total tree height (TH, measured with a hypsometer to the nearest 0.5 m), and tree status (dead or alive) and resprouting type (crown, basal). Trees were considered alive whenever green foliage was present regardless of its location on the tree, and were considered top-killed if they had no green foliage in the crown but exhibited basal or root sprouts. For *Q. suber* trees we also measured the bark thickness (BT) at breast height with a bark gauge. We averaged two measurements at opposite sides of the trunk (N-S); in case of fissured bark the measurements were taken on bark "ridges" and therefore represent maximum BT. For the other 10 species, BT was not measured on burned trees because many had the bark severely affected by the fire. Alternatively we measured BT and DBH on 415 unburned trees within the study area (minimum 40 trees of different sizes per species), and derived allometric equations relating BT with DBH (Table 2, Fig. 1) to estimate BT for each burned trees (except *Q. suber*). The graphical representation of the derived allometric equations (Fig. 1) emphasizes the BT differences between the two pine species in contrast to the broadleaved species group. Among broadleaves only *Q. suber* has a thick bark comparable to the pines (see Table 1).

For each tree, the percentages of crown volume scorched (CVS) and crown volume consumed (CVC) were visually estimated to the nearest 5% with the help of binoculars. Total crown volume damaged (TCD), was then derived as TCD = CVS + CVC (McHugh and Kolb, 2003). Evidence of residual buds on branch tips was used to identify branches that supported foliage before the fire (McHugh and Kolb, 2003). Foliage scorch was defined by a change in colour as a result of the fire. Although some species initiated new foliage shortly after burning, it was easy to distinguish between pre-fire and post-fire leaves during the first months by their colour. Maximum bole char height (CH), the vertical extent of trunk blackening, was measured as an alternative indicator of fire injury. Percentage of bole char height (PCH) expressed CH in relation to total tree height. PCH was deemed considered a more reliable indicator of fire injury for some broadleaved deciduous species as at the time of the initial assessment of trees (3 months after the fire) they were unleafed, so TCD was probably overestimated.

Because of the presence of a population of wild herbivores in the area (density of 0.4 deer ha^{-1}; Nunes, 2004), constituted by *Dama dama* L. (fallow deer) and *Cervus elaphus* L. (red deer), several trees ($n = 216$; see Table 3) were protected from browsing to further evaluate potential cumulative impacts of herbivory on post-fire mortality and recovery. About half of the individuals (from seven broadleaved species) without crown sprouting but with basal regeneration were protected (in early 2004) using individual wire protectors. Thus the presence/absence of herbivory (i.e., unfenced/fenced tree) was also considered as a variable. Some species were not protected, because of (i) lack of sprouting response (*P. pinaster* and *P. pinea*), (ii) crown sprouting in all the trees (*Q. suber*), and (iii) avoidance by deer (*E. globulus*).

A second assessment of the tree status and resprouting type of the initially sampled trees ($n = 1040$) was performed 1 year after the fire. From this set, a subset of 755 individuals was assessed annually until 2007 (4 years post-fire).
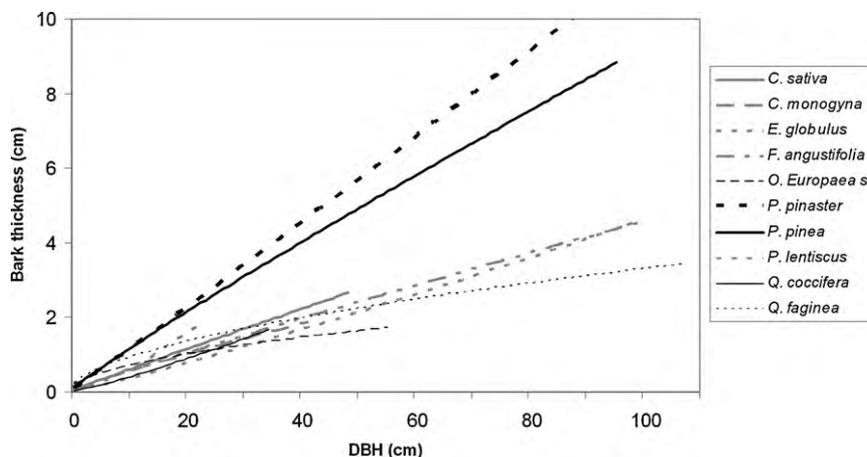

Fig. 1. Relations between bark thickness (cm) and diameter at breast height (DBH, cm) for different coniferous and broadleaved species, based on the allometric equations presented in Table 2 (Note that there are two clear groups, with conifers (*P. pinea* and *P. pinaster*, top lines) having a thicker bark).

Table 3
Observed individual tree mortality (cumulative percentage) by species in the first 4 years following Mafra wildfire (n = 755); percentage of top-killed trees (crown mortality; includes dead trees) was almost the same in the 4 years after wildfire and the values presented concern the fourth year.

Species	Cumulative mortality (%)				Top-killed (%)	n (P)
	1st year	2nd year	3rd year	4th year		
Castanea sativa	20	40	80	83	83	30 (0)
Crataegus monogyna	0	0	7	7	93	75 (46)
Eucalyptus globulus	0	0	0	0	100	60 (0)
Fraxinus angustifolia	0	0	0	0	15	62 (10)
Olea europaea sylvestris	0	0	0	0	97	78 (44)
Pinus pinaster	84	88	95	95	95	56 (0)
Pinus pinea	77	82	85	85	85	78 (0)
Pistacia lentiscus	0	0	0	0	100	71 (34)
Quercus coccifera	0	0	10	10	99	67 (26)
Quercus faginea	2	3	3	14	89	89 (56)
Quercus suber	1	1	1	1	1	89 (0)

n (P), total number of trees monitored during the 4-year period (number of trees protected from deer browsing).

2.3. Data analysis

The probability of individual tree mortality and crown mortality (top-kill) 1 and 4 years after fire were modelled by using binary logistic regression (Hosmer and Lemeshow, 1989). All the previously mentioned variables, including some interactions, were tested as independent variables. Since resistance to cambium injury increases with the square of bark thickness (Peterson and Ryan, 1986; Rego and Rigolot, 1990), fire injury resistance is expected to increase roughly with the square of stem diameter (Ryan, 1998), thus both BT^2 and DBH^2 were also tested as independent variables. Squared PCH and CVS were also included, as some authors recognized their non-linear influence on tree survival (Peterson and Ryan, 1986; Ryan and Reinhardt, 1988). The independent variables were selected by forward stepwise selection, and were included in each model only when statistically significant ($P < 0.05$). When correlation between two variables was higher than 0.5, only one of them was used in the model. The most correlated pairs of variables ($r > |0.5|$; Pearson correlation coefficient) were: DBH with BT ($r = 0.86$), DBH with TH ($r = 0.68$), CVS with CVC ($r = −0.84$), CVC with TCD ($r = 0.64$), and CH with TH ($r = 0.63$). Comparisons between treatments (e.g. protected vs. non-protected trees) were based on Chi-square statistics (Sokal and Rohlf, 1987). All the analyses were carried out using SPSS software (SPSS, 2006).

2.4. Model evaluation

The overall model significance was assessed through the Chi-square goodness-of-fit omnibus test. Model performance was assessed by calculating the area under the receiver operating characteristics (ROC) curve (Hosmer and Lemeshow, 1989). The ROC method has advantages in assessing model performance in a threshold-independent fashion, being independent of prevalence (e.g. Manel et al., 2001). Area under the curve (AUC) values of 0.5–0.7 are usually taken to indicate low accuracy, values of 0.7–0.9 indicate useful applications and values above 0.9 indicate high accuracy (Swets, 1988). Models with different combinations of variables were also compared using the Akaike Information Criterion (AIC) (Burnham and Anderson, 2003), and the one with lowest AIC considered the most parsimonious. Several models were tested using the available variables, but only the more parsimonious ones are presented.

In the validation phase (see next section), the model predictive ability was also quantified through cross-classification tables, which are based on the comparison of observed and predicted events. For this purpose, a range of cut-off-points were used to convert event probability (mortality or top-kill) to dichotomous (presence/absence) data in order to define optimal cut-off point.

Although a cut-off-point value of 0.5 is often used, this threshold can be modified according to data specificities or user's needs (e.g. Thies et al., 2006). The dataset was used to construct classification tables for different cut-off-points, helping defining optimal values. The optimal cut-off point corresponds to the value where both sensitivity and specificity reach the same proportion, which in our case was 0.6 and 0.7.

2.5. Model validation

Models were validated through an independent dataset, constituted by pooling information from 4 different 2006 wildfires that occurred in central-west Portugal, collected in another study (70–110 km far from the Mafra site; Tujeira and Morgado, 2007). Porto-de-Mós wildfire occurred in Leiria district and burned about 3400 ha. Agroal, Atouguia and Vale Florido wildfires occurred in Santarém district and burned about 380, 280 and 250 ha, respectively. The altitude in the burned sites ranges from 80 to 600 m and the soils are predominantly rhodo-chromic luvisols and calcic cambisols. Climate is Mediterranean, with a mean annual precipitation of 700–1600 mm, mean annual temperature ranging from 15 to 17.5 °C (IA, 2003).

The dataset included 945 trees of four species monitored in the Mafra wildfire (*P. pinaster*, *E. globulus*, *Q. faginea* and *Q. suber*). The assessment of post-fire tree status (alive or dead) was performed only once and simultaneously with the assessment of the remaining tree and fire data (about 1 year following wildfire occurrence). The field methods used in these fires (details are given by Tujeira and Morgado, 2007) were similar to those described for the Mafra wildfire, except that crown volume damage (CSV, CVC, TCD) was not assessed because it was not possible to accurately estimate it 1 year after the fire. Bark thickness was calculated using the same allometric equations (Table 2).

3. Results

3.1. Tree responses

Most broadleaved trees survived the first post-fire year, while most conifers died (Table 3). Only 11% of the pine trees were alive by the end of the study period (5% in *P. pinaster* and 15% in *P. pinea*). In contrast, 92% of the broadleaved trees were still alive by the end of the study period. Four years after wildfire, 5 of the 9 monitored broadleaved species had some mortality (ranging from 1% to 14%), but only *C. sativa* presented very high mortality (83%). In spite of the low mortality observed in most broadleaved trees, the majority were top-killed and regenerated only from the base of the trunk or roots. The remarkable excep-

Table 4
Logistic regression models to predict post-fire tree mortality. Models based on data from 11 species ($n = 1040$ trees for the first-year models, and $n = 755$ for the fourth-year model).

Model	Years since fire	Coefficients					Model χ^2	d.f.	P-value	AUC	AIC	R^2
		b_0	b_1	b_2	b_3	b_4						
M1	1	−7.151	6.657	0.028	–	–	506.95	2	<0.001	0.935	−434.9	0.77
M2	1	−12.901	7.121	–	0.083	–	526.21	2	<0.001	0.958	−396.4	0.80
M3	1	−10.551	8.717	0.052	–	7.330	563.84	3	<0.001	0.981	−319.2	0.83
M4	4	−5.494	5.818	0.027	–	6.350	490.23	3	<0.001	0.923	−617.4	0.73

Model coefficients: b_0, constant; coefficients for the following variables: b_1 for species group (takes value 1 if species is coniferous, and 0 otherwise); b_2 for PCH (maximum bole char height expressed as percentage of tree height); b_3 for TCD (percentage of crown volume damaged); b_4 for *Castanea sativa* (takes value 1 if species is *C. sativa*, and 0 otherwise); model χ^2, full model goodness-of-fit statistic; d.f., degrees of freedom; P-value, significance level; AUC, area under ROC curve; AIC, akaike information criteria; R^2, Nagelkerke R^2.

tion was *Q. suber* for which none of the surviving individuals were top-killed.

Most conifer mortality occurred within the first year following wildfire, and only an additional 9% died in the three subsequent years. In contrast, most (82%) mortality on broadleaved trees occurred after the first year (Table 3).

3.2. Mortality models

Species group, bole char height and crown volume damaged were the most important variables influencing the probability of initial and delayed tree mortality (Table 4). The two fire injury indicators (PCH and TCD) were positively associated to tree mortality. Coniferous showed significantly higher mortality than broadleaved species. *C. sativa* suffered significantly greater mortality (not shown) than any of the remaining broadleaved species and thus a model differentiating this species was also included (Table 4). The ROC curves indicated that all the selected models perform very well, with 92–98% concordance between predicted probabilities and observed outcomes.

We selected model M1 to be used in the validation phase, because TCD was not available on the validation subset and *C. sativa* species was not present. The full model goodness-of-fit test showed adequate fit of model M1 to the data. This model indicates that probability of mortality increases with char height, but the likelihood for broadleaved species survival is high and almost insensitive to this fire injury descriptor (Fig. 2).

The area under the ROC curve (AUC) of the M1 validated model was 0.956, indicating a very good model performance, with close agreement between predicted and observed status 1 year following wildfires. The global accuracy (using a 0.6 probability threshold) was 93.2%. For the validation dataset, 91.9% of the trees predicted to die were in fact dead 1 year following fire, and 93.8% of the trees were correctly predicted to survive (user's accuracy, Table 5; commission errors represent the incorrect predictions). On the other hand 86.4% of the observed dead trees were predicted to die by the model and 96.4% of the observed living trees were predicted to be alive (producer's accuracy, Table 5; omission errors represent the percentage of observed dead or alive trees that were not predicted by the model).
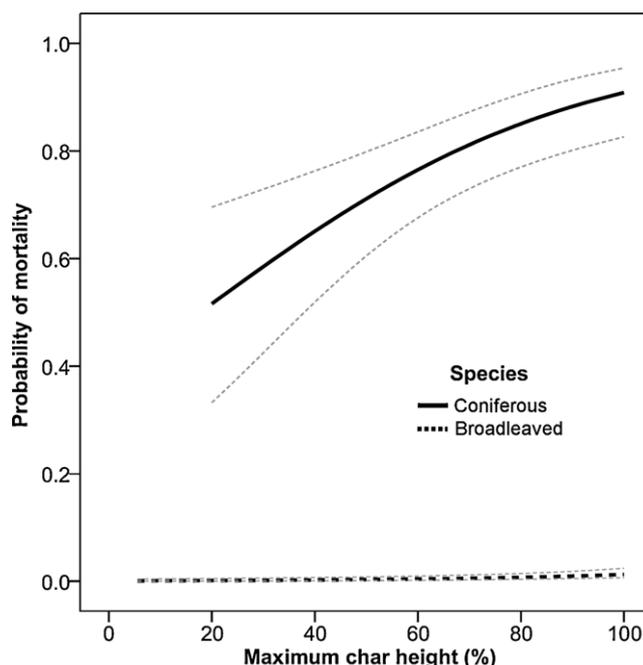

Fig. 2. Probability of individual tree mortality (with 95% confidence intervals) 1 year following wildfire as a function of PCH (maximum bole char height expressed as percentage of tree height) for the two species group considered (coniferous vs. broaleaved trees).

Additionally we tested different model fitting possibilities to predict delayed conifer mortality over the entire study period, using species as an additional variable (Mafra fire). The best model for conifers included one indicator of fire injury and a term for tree species (Table 6). As for the global mortality models, the fire injury descriptors were positively associated with the probability of mortality, but in this case TCD was a better predictor of mortality than PCH. The species term was also significant in such a way that the probability of survival was higher for *P. pinea* (Fig. 3).

For the delayed mortality of broadleaves, only the species factor showed to be significant. *C. sativa*, *Q. coccifera*, and *Q. faginea* were

Table 5
Cross-classification table presenting the predicted and observed tree mortality. Based on a validation dataset of 945 trees from 4 species (using a 0.6 probability threshold).

	Observed status			User's accuracy	Commission error
	Dead	Alive	Total		
Predicted status					
Dead	261	23	284	91.9%	8.1%
Alive	41	620	661	93.8%	6.2%
Total	302	643	945		
Producer's accuracy	86.4%	96.4%		Global accuracy	93.2%
Omission error	13.6%	3.6%			

Table 6
Logistic regression model to predict delayed (4 years after fire) mortality of *P. pinaster* and *P. pinea*. Variables are ordered by their decreasing importance on tree survival ($n = 134$).

Effect	Variables	Coefficient	SE	Wald χ^2	d.f.	*P*-value
b_0	Constant	−7.152	1.928	13.766	1	<0.001
b_1	TCD	0.150	0.033	20.560	1	<0.001
b_2	Species	−3.979	1.230	10.470	1	<0.001

Coefficients: TCD, percentage of crown volume damaged (crown scorched + crown consumed); species takes the value 1 for predicting *P. pinea* mortality and 0 for *P. pinaster*; SE, standard error; Wald χ^2, Wald Chi-square statistic; d.f., degrees of freedom; *P*-value, significance level; full model χ^2, 46.33 ($P < 0.001$); area under ROC curve, 0.924 ($P < 0.001$).

the only broadleaved species with a significant mortality, and so we fitted individual models for these species. For *Q. faginea*, none of the variables measured was a significant predictor of mortality. The only variable related with *C. sativa* mortality was DBH, and the relationship was negative (model $\chi^2 = 6.218$, $P = 0.013$; AUC = 0.800, $P = 0.037$). For *Q. coccifera* only the variable protected vs. unprotected was selected in the models (model $\chi^2 = 7.387$, $P = 0.007$; AUC = 0.717, $P = 0.062$). Concerning ungulate herbivory, and besides the logistic models, significant differences between trees protected from browsing and non-protected trees were observed in *C. monogyna* ($\chi^2 = 8.036$, $P = 0.0046$) and in *Q. coccifera* ($\chi^2 = 4.957$, $P = 0.0260$).

3.3. Top-kill models

Bark thickness and char height were the most important variables affecting the probability of tree top-kill, and their influence was highly significant ($P < 0.001$; Table 7). The probability of top-kill increased with decreasing bark thickness and with increasing fire injury (Fig. 4), as it was previously hypothesized. Few differences exist between top-kill models concerning 1-year or 4-years after fire, and both showed good performance (Table 7). As with mortality, very few broadleaves (only 5%) had delayed top-kill.

The TK1 model (Tables 7 and 8) was selected for the validation phase. The validation dataset was constituted by 548 trees from three broadleaved species (403 were top-killed), monitored in four different wildfires. The model showed good performance, with AUC of 0.931. Cross-classification table evaluation showed a global accuracy of 85.4% (using a 0.7 probability threshold). Within this sample, 89.7% of the trees were correctly predicted to be top-killed 1 year following fire, and 73.0% were correctly predicted to regenerate from the crown.

4. Discussion

4.1. General response patterns

Most coniferous trees died as a consequence of the fire while the majority of broadleaved trees survived. Pine mortality was above 85%, and ranged from 55% to 92% for the validation data set. However, pine mortality can be highly variable, ranging from 0% to 100% depending of fire characteristics and tree size (e.g. Fernandes et al., 2008). For most conifers, including our two pine species, top-kill equals individual tree mortality, because they lack the ability to sprout from basal buds.

Variations in mortality can also occur in broadleaved species, although survival is often much higher than for conifers (e.g. Franklin et al., 2006; Quevedo et al., 2007). In the Mafra study area only 1% of all the broadleaved trees were dead 1 year after fire, and this number increased to 8% by the end of the 4-year study period. These values are close to the 1-year mortality found in the validation dataset (3%). Despite the generally low mortality observed in broadleaves, most were top-killed and regenerated only from basal sprouts, meaning that several years or even decades are required until the trees reach the pre-fire size.
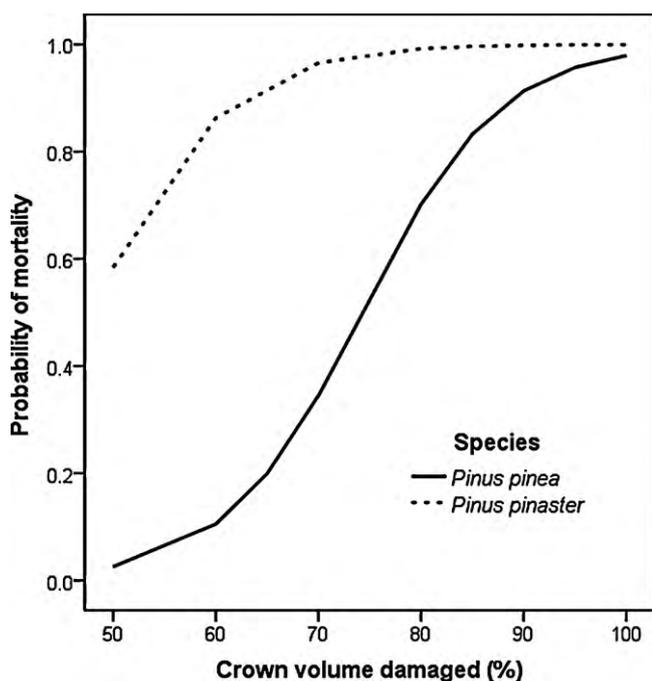

Fig. 3. Probability of mortality for *Pinus pinea* and *P. pinaster* 4 years following fire, as a function of the percentage of crown volume damaged (TCD).
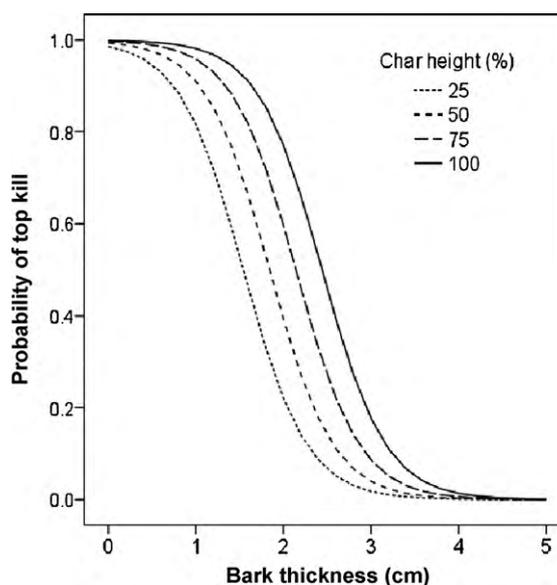

Fig. 4. Probability of top-kill (crown mortality) following wildfire on broadleaved species, as a function of bark thickness (cm) and PCH (maximum bole char height expressed as percentage of tree height).

Table 7
Models to predict top-kill on 9 broadleaved species 1 and 4 years after Mafra wildfire (n = 906 trees for the first year model, and n = 621 for the fourth year model).

Model	Years since fire	Coefficients			Model χ^2	d.f.	P-value	AUC	AIC	R^2
		b_0	b_1	b_2						
TK1	1	2.793	−2.613	0.027	597.26	2	<0.001	0.931	−1010.5	0.69
TK2	4	3.415	−2.750	0.033	437.14	2	<0.001	0.949	−557.8	0.74

Coefficients: b_0, constant; b_1, bark thickness (cm); b_2, PCH (maximum bole char height expressed as percentage of tree height); model χ^2, full model goodness-of-fit statistic, d.f., degrees of freedom; P-value, significance level; AUC, area under ROC curve; AIC, Akaike information criteria; R^2, Nagelkerke R^2.

4.2. Factors affecting mortality and top-kill

Besides the differences between the two main taxonomic groups (gymnosperms, angiosperms), fire injury indicators (crown volume scorched or consumed and bole char height) were major factors affecting post-fire mortality of coniferous and top-kill of broadleaved species (e.g. Ryan and Reinhardt, 1988; Hély et al., 2003; Thies et al., 2006; Fernandes et al., 2008). Both CH and PCH were significant predictors of mortality and top-kill, although PCH understandably performed slightly better than CH. Char height was effectively employed as a tree mortality predictor but it does not necessarily quantify fire injury, especially as bark depth increases. Also, bole char height varies with factors other than fire intensity (Gutsell and Johnson, 1996), namely with tree diameter, hence decreasing its adequacy as a predictive variable. Direct cambium examination should predict bole damage better (Ryan and Reinhardt, 1988), however, a direct cambium assessment is less expedite and would have induced further injury to the burned trees (e.g. Thies et al., 2006).

In the case of conifers, crown volume damaged was the most important factor determining mortality. Sieg et al. (2006) found that including CVS and CVC separately in a mortality model for *Pinus ponderosa* resulted in greater predictive ability than considering TCD, but in our study the two models performed similarly. The mortality model for conifers suggests that for the same level of crown injury *P. pinaster* is more susceptible than *P. pinea*. Other studies also point to higher fire resistance of *P. pinea* in relation to *P. pinaster* and to other Mediterranean pines (Rigolot, 2004; González et al., 2007). Since these two species have similar bark thickness, we hypothesize that the higher *P. pinaster* mortality might be due to differences in crown architecture and to differences in susceptibility to insect attacks. Concerning crown architecture there are substantial differences between the two species, with *P. pinea* having the upper crown better protected from the heat flux (Rigolot, 2004; Fernandes et al., 2008). Concerning susceptibility to insect attacks, it is known that bark beetles can reach epidemic levels after fires and Vasconcelos et al. (2003) showed that *Tomicus* spp. in Portugal preferably attacks *P. pinaster* in comparison with *P. pinea*. In our study area trees from both pine species presented signs of bark beetle attacks, but no measurements were made, thus hindering any additional conclusion.

Because most of the Mafra study area was severely affected by wildfire, all the sampled pines had at least 50% of crown volume damaged, thus the presented model applies only to situations where at least half of the crown has been affected. For *P. pinea* this is not a limiting factor because the threshold level of TCD at which

P. pinea mortality began was 50%. However, for the same level of crown damage *P. pinaster* is predicted to have about 60% mortality, thus, the TCD-based models have a limited value for predicting mortality in low-injured trees; in those cases, it will probably be better to use the global mortality model based on PCH instead of TCD.

Contrarily to conifers, none of the fire injury indicators was related to broadleaves mortality, which is consistent with other authors' findings (Stephens and Finney, 2002; Franklin et al., 2006). As broadleaves (resprouters) have buds located below ground, which are generally well protected from heat by the overlaying soil, the more commonly used fire injury indicators (related with crown and stem injury, but not with root injury) are more likely to be poorly or unrelated with the capacity of basal resprouting and survival. The usually low mortality rates of broadleaved species also contribute to the difficulty of fitting predictive models. However, we successfully developed models of top-kill suggesting a positive relation with PCH and a strong negative relation with BT.

Bark thickness (BT) did not significantly affect individual tree mortality but it was the most important factor in predicting top-kill in broadleaves. In other studies, *Q. suber* post-fire mortality has been shown to be much variable, mainly as a function of bark thickness (e.g. Silva and Catry, 2006; Moreira et al., 2007). However, this species is a very special case because regular bark extraction for cork production (Aronson et al., 2009) makes this species particularly vulnerable to fire after debarking (Pausas, 1997; Catry et al., 2009). On the other hand this species is recognized as the only European tree with above ground sprouting capability when the canopy is entirely burned (Pausas, 1997). In our study *Q. suber* was by far the most resilient to fire, as 99% of all the trees resprouted from the crown, most likely because trees had not been debarked in the last decades. Concerning *F. angustifolia*, the low crown mortality observed (15%) is probably due to the lower fire injury experienced, mainly due to their thicker bark, higher average height, and lower fire intensity, because most trees were located near streams or paths with lower fuel load. In our models, DBH and TH were also significant predictors of top-kill, but using these variables instead of BT resulted in lower predictive ability. Considering that BT is usually highly correlated with DBH and with TH, our results are consistent with other studies that also reported these variables as good predictors of crown mortality (e.g. Regelbrugge and Conard, 1993; Hély et al., 2003).

Besides fire injury indicators and the tree individual characteristics mentioned, there are other factors that can also determine the ability of post-fire trees survival such as herbivory, weather conditions and tree vigour (e.g. Ryan and Reinhardt, 1988; Whelan,

Table 8
Selected model (TK1) to predict broadleaves top-kill 1 year after wildfire.

Effect	Variables	Coefficient	SE	Wald χ^2	d.f.	P-value
b_0	Intercept	2.793	0.366	58.318	1	<0.001
b_1	BT	−2.613	0.200	170.063	1	<0.001
b_2	PCH	0.027	0.004	52.120	1	<0.001

Coefficients: BT, bark thickness (cm); PCH, maximum bole char height expressed as percentage of tree height; SE, standard error, Wald χ^2, Wald Chi-square statistic; d.f., degrees of freedom; P-value, significance level; full model χ^2, 597.26 (P<0.001); area under ROC curve, 0.931 (P<0.001).

1995). In this study we hypothesized that ungulate herbivory could be an additional factor influencing the delayed mortality of top-killed broadleaves, because a regular consumption of basal sprouts would maintain the leaf area at low levels, hindering the adequate functioning of vital physiological processes (e.g. Canham et al., 1999). In fact, by the third year, cumulative impacts of deer on tree survival were apparent in *C. monogyna* and *Q. coccifera*. All the dead *Q. coccifera* individuals had been browsed, and browsed *C. monogyna* trees experienced three times more mortality than unbrowsed individuals. In spite of the high resistance of resprouting species to repeated disturbances (Espelta et al., 2006), and although this effect killed only a small proportion of trees and was not observed in all the broadleaved species, it is possible that the persistence of ungulate consumption will increase mortality in the future.

Weather conditions could also represent a cumulative factor of stress contributing to the observed delayed mortality. In 2005 the Portuguese mainland suffered the worst drought in the last 60 years (INAG, 2005). This can potentially explain the increased number of dead trees observed between 2005 and 2006, when some mortality occurred for the first time on *C. monogyna* and *Q. coccifera* (7% and 10%, respectively), and doubled in *C. sativa* (from 40% to 80%). These results emphasize the importance of understanding the interaction between fire and climate for predicting ecosystem responses and specifically the role of heat waves in increasing tree mortality.

C. sativa showed very high fire sensitivity (83% mortality) compared to the other broadleaved resprouters. We could not found any reference concerning the post-fire resistance of *C. sativa* that would enable some comparison. Given that this species is outside of its natural area (e.g. Capelo and Catry, 2007), it remains to explore to what extent this sensivity is inherent to the species or it is due to local conditions.

Some factors that can affect post-fire tree mortality are not accounted for by our models, such as insect or disease incidence. However our models may implicitly reflect the interactions between fire injury and insect or disease incidence, as both of them were present in several sampled trees. Despite these additional sources of variation, model performance was good, and the presented equations should be useful for the modeling and management of fire-injured stands.

4.3. Implications for management

The presented models perform similarly to other published models for different species and geographical locations (e.g. Regelbrugge and Conard, 1993; Rigolot, 2004; Hély et al., 2003; McHugh and Kolb, 2003; Hood et al., 2007). They were validated using independent datasets from other locations, suggesting some degree of applicability outside the study area.

Knowledge of fire effects on trees is valuable both for controlling fire injury and for predicting its consequences. The presented logistic regression equations rely on readily obtainable data, and are applicable over a wide range of tree sizes and species, and in a variety of stand conditions suffering moderate to severe burning. These models have several potential applications and can be useful to managers making pre-fire or post-fire decisions in mixed forest stands in the western Mediterranean Basin, where the studied species are present. They may be used for example when selecting species for reforestation, privileging the ones that are more fire-resistant (e.g. Pausas et al., 2004). They may also be used following fire, either to assess the probability of mortality or top-kill of individual trees when developing salvage guidelines, or to assess potential stand damages and economical losses when considering different management alternatives. These predictions can for example provide a better idea on how exposed the burned areas will be in terms of soil erosion, or the impacts on wildlife habitat. Managers should also be aware of the importance of herbivory

in post-fire restoration. For most forest species, the presence of either wild or domestic herbivores can have a negative impact on the post-fire recovery, even if not killing the trees, hindering the natural regrowth.

Acknowledgements

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