

# A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (*Quercus suber* L.) trees in Southern Portugal

Francisco Moreira · Filipe Catry · Inês Duarte ·  
Vanda Acácio · Joaquim Sande Silva

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**Abstract** The sprouting response types of 1,151 cork oak (*Quercus suber*) trees one and half years after a wildfire in southern Portugal were characterised. It was hypothesised that different response types should occur according to the following conceptual model: an increased level of damage (fire severity) on a sprouting tree that suffered a crown fire was expected to be reflected in a sequence of four alternative events, namely (a) resprouting exclusively from crown, (b) simultaneous resprouting from crown and base, (c) resprouting exclusively from base and (d) plant death. To assess whether the level of expected damage was influenced by the level of protection from disturbance, we explored the relationships between response types and tree size, bark thickness and cork stripping, using an information-theoretic approach. The more common response type was crown resprouting (68.8% of the trees), followed by plant death (15.8%), simultaneous resprouting from crown and base (10.1%) and basal resprouting (5.3%). In agreement with the conceptual model, trees which probably suffered a higher level of damage by fire (larger trees with thinner bark; exploited for cork) died or resprouted exclusively

from base. On the other hand, trees that were well protected (smaller trees with thicker bark not exploited for cork) were able to rebuild their canopy through crown resprouting. Simultaneous resprouting from the crown and base was determined mainly by tree size, and it was more common in smaller trees.

**Keywords** Apical dominance · Mediterranean · Model · Mortality · Resource allocation · Resprouting · Severity

## Introduction

Resprouting is an efficient mechanism through which many plants from the Mediterranean region recover above-ground biomass after they have suffered total crown consumption from a wildfire (Whelan 1995; Bond and van Wilgen 1996; Keeley 2006). Sprouting shoots can originate from dormant buds located above ground (axillary, branch epicormic or stem epicormic) or from the base of the plant (i.e. from the collar, roots or underground stems) (Bond and van Wilgen 1996; Miller 2000; Del Tredici 2001). Hereafter, these two sprouting modes will be referred to as ‘crown’ and ‘basal’ sprouting (Bond and van Wilgen 1996).

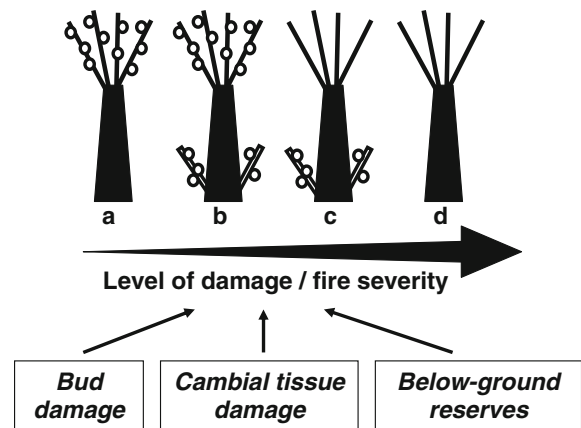
Bellingham and Sparrow (2000) presented a general model of resprouting responses as a function of increasing disturbance severity (severity defined as

F. Moreira (✉) · F. Catry · I. Duarte · V. Acácio ·  
J. S. Silva

Centro de Ecologia Aplicada “Prof. Baeta Neves”,  
Instituto Superior de Agronomia, Universidade Técnica  
de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal  
e-mail: fmoreira@isa.utl.pt

a measure of a plant's perception of a disturbance event). This gradient of increasing severity was expected to create a sequence of hierarchical regenerative responses ranging from crown (e.g. axillary and branch epicormic) to basal sprouting, where the loss of one type of tissue (e.g. in twig) induces a regenerative response from the next level of hierarchy (e.g. twig axil on the branch) (Bellingham and Sparrow 2000). In their model, disturbance severity is expressed as proportion of above-ground biomass lost (Bellingham and Sparrow 2000). For one particular type of disturbance, wildfires, and in particular crown fires, often all the canopy foliage, buds and twigs are consumed (crown consumption). When this happens, severity will depend mainly on the fire intensity and the level of fire-protection mechanisms at the individual level (e.g. Bond and van Wilgen 1996). Although the hierarchical nature of sprouting responses presented in Bellingham and Sparrow's model could also be expected in this situation, the fact that in a few studies sprouting responses at different hierarchical levels were simultaneously registered in the same individual plant (Trollope 1984, current study) suggests that the factors underlying response types will be more complex than just above-ground biomass lost.

In situations where wildfires caused total crown consumption in sprouting trees we allege that disturbances of differing levels of damage (severity), and corresponding sprouting responses, not necessarily organised as an hierarchical model, can still be recognised. These responses will be determined by the amount of bud damage in the twigs and branches, the level of damage to stem and root cambial tissue and the amount of below-ground reserves which determines how much carbohydrate reserves can be mobilised to rebuild the lost biomass (Chapin et al. 1990; Bond and van Wilgen 1996; Iwasa and Kubo 1997; Bellingham and Sparrow 2000) (Fig. 1). When the level of fire damage is low (e.g. caused by low fire intensity on trees with thicker bark, and where the stem cambium is not affected), the plant is expected to resprout from crown buds that survived the fire (Fig. 1a). If the level of damage is extreme (e.g. caused by high fire intensity on trees with thinner bark or where the stem cambium is damaged), the most likely outcome is plant death (Fig. 1d). At intermediate levels of severity two response types can be identified. If the level of damage is higher, all



**Fig. 1** A conceptual model of post-fire responses of a sprouting tree that suffered total crown consumption (combustion of leaves and twigs during a wildfire) in relation to a gradient of increasing level of damage/fire severity. (a) Crown sprouting, (b) simultaneous sprouting from crown and base, (c) basal sprouting, (d) plant death (for further explanations see text)

crown buds will be killed, either directly through heat or indirectly through the destruction of the vascular cambium in the stem, as the carbohydrate reserves that support sprouting are primarily stored in below-ground structures (Del Tredici 2001). Furthermore, apical dominance will be suppressed directly through bud destruction by heat or indirectly via damage to the cambium (Kozłowski 1971; Kozłowski et al. 1991; Miller 2000), and the tree is therefore expected to respond through basal resprouting (Fig. 1c). Alternatively, if the level of damage is not so severe, partial damage to the crown buds and cambium will cause weakened apical dominance (Kozłowski 1971) and at least some accessibility to below-ground reserves, thereby resulting in the simultaneous resprouting of the crown and base (Fig. 1b). Since the amount of carbohydrate, nitrogen and phosphorus resources that can be used for growth also determines the extent to which plants can resprout (Chapin et al. 1990), the observed resprouting patterns will therefore also be influenced, and plants with depleted below-ground resources may suffer higher levels of damage since they are unable to allocate enough energy to restore the lost biomass. An example of these above-mentioned four types of responses can be found in a study of *Acacia karroo* savanna by Trollope (1984), where different responses were related to tree size and fire intensity. However, no other examples were found in the literature where the

occurrence of different responses was registered and characterised for other tree species.

The cork oak *Quercus suber* L. is a very important tree species within the Mediterranean basin, both from an economic and ecological perspective (Silva and Catry 2006). The existence of a thick cork bark plays an important role in the capacity of this species to withstand the frequent occurrence of fire typical of Mediterranean climates (e.g. Pausas 1997; Moreira et al. 2007). Another feature of cork oak trees is the capacity of post-fire resprouting from the base and crown after complete defoliation, hence the species is a good model for studying the different response patterns previously described.

In general, there is little information available on the relative frequency of the different response types as well as the factors influencing these responses in cork oak. Previous studies (e.g. Cabezudo et al. 1995; Pausas 1997; Barberis et al. 2003; Catry et al. 2007; Moreira et al. 2007) focused mainly on the factors influencing post-fire survival, and showed the key role of cork stripping, cork thickness and tree size on determining oak survival. In this article, we hypothesise that these three variables also influence other post-fire response patterns (as described in Fig. 1) besides death, since they are expected to influence the level of resistance to fire and, consequently, the level of damage.

Cork stripping is a common operation that is normally performed after the tree attains a certain circumference at breast height (70 cm in Portugal). Cork is a valuable raw material for industry and is periodically removed with an axe by manually cutting along vertical and horizontal lines on the stem and thicker branches and stripping off cork planks (Pereira and Tomé 2004). After each cork stripping, the tree has the capacity to produce new cork bark by adding new layers of cork every year (Pereira and Tomé 2004). Moreira et al. (2007) showed that unstripped trees (with unharvested virgin cork) had higher survival rates than trees that had been exploited for cork (i.e. trees debarked at least once). These authors suggested that the higher survival rates of unstripped trees may be explained by the higher insulating properties of virgin cork (for a given bark thickness) and the absence of stress caused by cork extraction. In fact, cork extraction is a disturbance that has negative effects on tree health and growth (Costa et al. 2004). Thus, stripping

probably requires a greater allocation of below-ground energy reserves that will subsequently not be available for investment in resprouting. Consequently, unstripped trees are expected to show lower levels of damage when compared to exploited trees since their buds are more protected and their below-ground reserves may be better preserved.

Cork thickness depends on the harvesting cycle and the time elapsed between harvesting events. Cork can only be harvested every 9–15 years (minimum 9 years according to Portuguese legislation), and several studies have shown that cork age (and thus thickness) is inversely related to post-fire mortality (e.g. Lamey 1893; Pampiro et al. 1992; Cabezudo et al. 1995; Pausas 1997; Barberis et al. 2003; Catry et al. 2007; Moreira et al. 2007). The thicker the bark, the lower the expected level of post-fire damage (again, buds and cambium are more protected from fire).

Barberis et al. (2003) and Moreira et al. (2007) provided evidence that trees with larger diameter at breast height (DBH) had a lower probability of survival. Possible explanation for this pattern include a likely higher amount of stripping damages, higher susceptibility to stress or diseases and higher frequency of poor management practices (e.g. deep ploughing, excessive pruning) in older trees (Costa et al. 2004; Moreira et al. 2007). A bigger tree that has suffered several damage events across its lifespan is therefore prone to higher levels of post-fire damage, mainly because of the lack of carbohydrate reserves to invest in resprouting (Iwasa and Kubo 1997).

The aim of this article is to explore the importance of tree size, bark thickness and cork stripping in determining the whole range of post-fire response types in cork oak. In particular we aimed to: (a) quantify the relative frequency of four different post-fire responses in burned cork oak trees 1.5 years after an intense wildfire and (b) explore whether stripping, bark thickness and tree size influenced each of the observed types of post-fire responses as hypothesised.

## Methods

### Study area and plot definition

The study area is located in “Serra do Caldeirão”, a mountain range in the Algarve province, southern Portugal. The climate is Mediterranean with an

average annual temperature and rainfall of 16.6°C and 900 mm, respectively. The altitude ranges from 150 to 580 m above sea level. Soils consist mainly of shallow schist lithosols that have a low fertility and are prone to erosion. The landscape is characterised by vast expanses of cork oak forests ranging from areas with high tree cover, to “montados” that have scattered trees and an understory of crops or pastures. In the 2004 summer, an intense wildfire burned ca. 25,000 ha in this region. A  $1 \times 1 \text{ km}^2$  grid of points covering part of the burned area was used to define a 50 m-radius circle (sampling plot) around each point. Plots were checked in the field for accessibility and to confirm whether they had burned and were dominated by cork oak trees. A total of 40 plots were ultimately selected. Large within-plot variability in tree size and cork age (and consequently bark thickness) was common since cork debarking was not carried out simultaneously on all individual trees (for further details see Moreira et al. 2007).

#### Tree variables

Individual tree evaluation in the plots took place between December 2005 and April 2006, approximately 1.5 years after the fire. Trees were assessed along four 50-m strip transects departing from the plot centres at right angles. Given the very high density of young trees in many plots, only trees larger than ca. 9 cm DBH were measured. Approximately 30 trees per plot were assessed (mean  $\pm$  s.e. of  $28.8 \pm 0.51$ , range = 14–30,  $n = 40$ ) yielding a total of 1,151 individuals. For each tree, several variables were measured (see Moreira et al. 2007 for details); however, for the purposes of this article only the following variables are presented: (a) tree size (DBH, cm), taken as the average of two measurements at 1.3 m above ground level, (b) bark thickness (average thickness, cm) at breast height, calculated from four measurements using a bark gauge and (c) presence/absence of cork stripping in order to distinguish unstripped trees with virgin cork from exploited trees where cork debarking (stripping) had occurred at least once. The types of post-fire responses were also assessed and classified into four mutually exclusive categories: (a) dead trees (no resprouting from the base or crown), (b) trees that resprouted exclusively from the crown, (c) trees that resprouted exclusively

from the base (thus with a dead stem) and (d) trees that resprouted from both the crown and base.

#### Data analysis

To examine the influence of tree variables on post-fire response types, an information theoretic approach was used based on the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ) (Burnham and Anderson 2002). This approach starts with the formulation of a series of models that rely on an understanding of the system being studied, followed by an assessment of how different putative models compare to the reality (Rushton et al. 2004). The suite of candidate models is compared using  $AIC_c$ , and the smaller the  $AIC_c$  value the better the model fits the data.

Each of the four response types was modelled separately using a binary variable taking the value 1 for the specific response type and 0 for the remaining types. A generalised linear model with binomial error structure and a logit link function (McCullagh and Nelder 1989) was used to test a group of biologically plausible models, including separate models for each of the three variables (stripping, bark thickness, DBH) assumed to be biologically significant, and all possible combinations of these variables. Two interaction terms were also added to this list of variables: stripping  $\times$  bark thickness, as previous analyses showed that we could expect different responses, for a given bark thickness, of unstripped or exploited trees (Moreira et al. 2007); and stripping  $\times$  DBH, as the effects of tree size could also vary according to stripping status. This yielded four groups (one group per response type) of 27 models each, resulting from all combinations of these five variables. The smaller  $AIC_c$  among the models in each group was used to identify the more parsimonious model (Burnham and Anderson 2002) for each response type.

The fit and predictive performance of the models with smaller  $AIC_c$  was evaluated through the likelihood ratio statistic (full model  $\chi^2$ ) and by calculating the area under the receiver operating characteristics (ROC) curve (Saveland and Neueschwander 1990; Pearce and Ferrier 2000). This has the advantage of assessing model performance in a threshold-independent fashion, being independent of the prevalence of the several response types. The AUC varies between 0.5 (no discrimination ability) to 1 (perfect discrimination ability) (Pearce and Ferrier 2000). Usually,

AUC values of 0.5–0.7 are taken to indicate low accuracy, values of 0.7–0.9 indicate useful applications and values above 0.9 indicate high accuracy (Swets 1988). The calculation of the AUC and standard error was based on a non-parametric assumption. For a better visualization of the expected probabilities of the fitted models, data from bark thickness and tree size were grouped into classes. The former was divided into three classes:  $\leq 2$  cm (33.8% of the trees), 2–4 cm (54.4%) and  $> 4$  cm (11.8%). Tree size was also divided into three DBH categories:  $\leq 20$  cm (28.8% of the trees), 20–40 cm (58.5%) and  $> 40$  cm (12.7%).

There was no correlation between bark thickness and DBH ( $r = 0.021$ ,  $n = 1151$ ,  $P = 0.487$ ). However, exploited trees ( $n = 859$ ) had significantly larger DBH than unstripped ones ( $n = 292$ ) (mean  $\pm$  s.e. of  $30.7 \pm 0.406$  cm and  $16.5 \pm 0.253$  cm, respectively,  $t$ -test,  $t = 29.6$ ,  $P < 0.001$ ), and had a slightly thinner bark (mean  $\pm$  s.e. of  $2.39 \pm 1.289$  cm and  $2.93 \pm 0.835$ , respectively,  $t$ -test,  $t = 8.1$ ,  $P < 0.001$ ).

## Results

### Response types

For the 1,151 sampled trees, the most common response type was resprouting exclusively from crown (68.8%,  $n = 792$  trees), followed by death (15.8%,  $n = 182$ ), simultaneous resprouting from the crown and base (10.1%,  $n = 116$ ) and lastly, resprouting exclusively from the base (5.3%,  $n = 61$ ).

**Table 1** Generalized linear models with the lowest AIC<sub>c</sub> among the set of models compared, for each of the four post-fire response types in cork oak (death, resprouting exclusively from crown, resprouting exclusively from base, resprouting from both crown and base).

Variable	Death	Base only	Crown and base	Crown only
Stripping	1.645 $\pm$ 0.280	2.955 $\pm$ 0.440		-1.464 $\pm$ 0.278
Bark thickness				
DBH	0.031 $\pm$ 0.007		-0.055 $\pm$ 0.012	
Stripping $\times$ bark thickness	-0.688 $\pm$ 0.086	-1.272 $\pm$ 0.182		0.809 $\pm$ 0.075
Stripping $\times$ DBH				-0.016 $\pm$ 0.007
Constant	-2.722 $\pm$ 0.229	-3.570 $\pm$ 0.358	-0.842 $\pm$ 0.283	0.940 $\pm$ 0.130
Model $\chi^2$	101.95	81.03	27.79	153.65
AUC	0.71 $\pm$ 0.022	0.82 $\pm$ 0.026	0.64 $\pm$ 0.026	0.70 $\pm$ 0.017

The variables entering each model (linear predictor), their coefficients ( $\pm$ s.e.), the model  $\chi^2$  and the area under the ROC curve (AUC  $\pm$  s.e.) are shown for each response type. See Fig. 2 for model visualization. All model  $\chi^2$ , variable coefficients and AUC values are significant ( $P < 0.05$ )

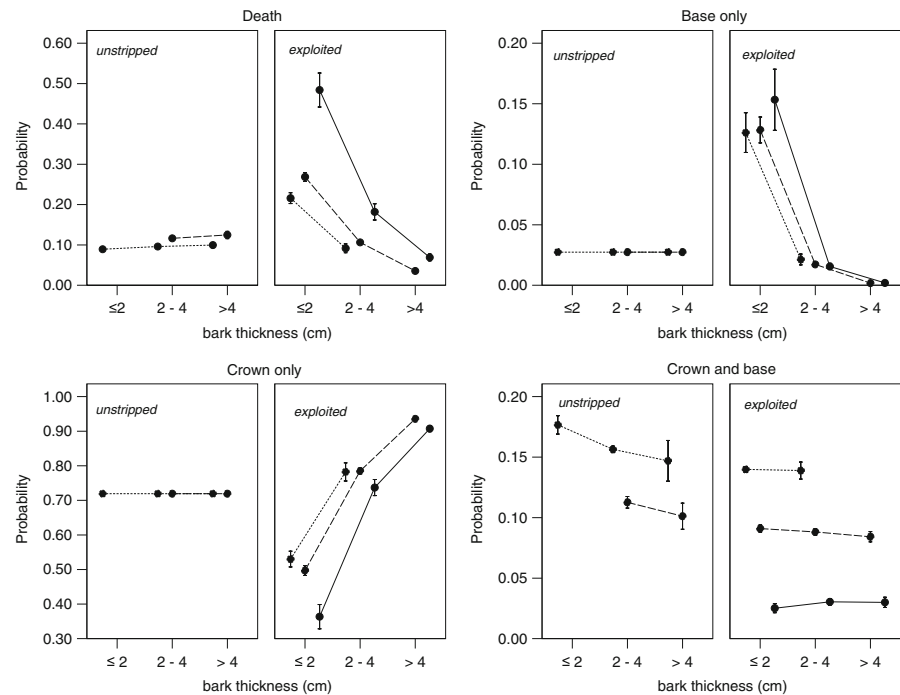
### Influence of predictor variables on response types

The more parsimonious model for tree death, among the set of models compared, is shown in Table 1 and Fig. 2. The probability of a tree dying increased if it had been exploited and had a larger DBH. Bark thickness was also a key variable but only if trees were exploited, in this case the probability of death increased as bark thickness decreased. Similarly to death, the model with the lowest AIC for resprouting only from base showed that this response type was also more likely in stripped trees (Table 1; Fig. 2). Bark thickness was an important variable in the case of stripped trees, and was negatively correlated to basal resprouting probability. The more parsimonious model for simultaneous resprouting from the base and crown (Table 1; Fig. 2) included only DBH, with larger trees being less likely to show this response type. Finally, resprouting exclusively from the crown was more likely in unstripped trees (Table 1; Fig. 2). For stripped trees, this resprouting type increased with bark thickness and decreased with DBH. Overall, model performance was low to moderate with AUC values ranging from 0.64 to 0.82.

## Discussion

Differences in sprouting behaviour are important for understanding vegetation dynamics, extinction risks for threatened species and for defining management regimes for woody plants (Bond and Midgley 2003).

**Fig. 2** Mean ( $\pm 95\%$  confidence intervals) of the predicted probability of each response type (dead, base only, crown and base, crown only), according to the GLM models shown in Table 1, for each combination of bark thickness and DBH classes. Unstripped and exploited trees correspond, respectively, to the left and right panels. The three DBH classes are shown by different line styles (—:  $>40$  cm, - - - : 20–40 cm, .....:  $<20$  cm)



Bellingham and Sparrow's (2000) model of resprouting response as a function of increasing disturbance severity assumes a hierarchical sequence of regenerative responses that depends on the proportion of the above-ground biomass lost. Here, a conceptual model is presented (Fig. 1) which can be applied to situations where a specific disturbance (fire) caused crown consumption on a tree with resprouting abilities. In this situation, different levels of damage are expected to create a sequence of response types where the hierarchical nature of sprouting type is not necessarily followed. These damage levels are assumed to be determined by the amount of damage to buds and cambial tissue, and by the available below-ground reserves that can be used to rebuild the lost biomass (e.g. Bond and van Wilgen 1996). Different levels of damage will cause four different types of post-fire responses that were identified in cork oaks in southern Portugal, 1.5 years after being burned in an intense wildfire. The majority of trees (ca. 70%) resprouted exclusively from the crown, which is expected to correspond to the lower level of damage. The second most common response category was death (16% of the trees), which corresponds to the highest level of damage. Response types expected to correspond to intermediate damage levels were less

common: simultaneous resprouting of the crown and base was the third most common response type (10% of the trees), whereas the least common response type was resprouting only from the base (i.e. stem death) (5% of the trees).

The relationship between the expected level of damage and the degree to which a tree is protected from disturbance was also addressed. The focus was on three variables previously known to have an important impact on cork oak post-fire survival, namely cork stripping, bark thickness and tree size.

It was hypothesised that stripping would be a strong determinant of the expected level of post-fire damage to trees, since the process of extracting highly insulating virgin cork for the first time initialises major periodic stresses across the life span of a tree (e.g. Natividade 1950; Costa et al. 2004; Moreira et al. 2007). This is consistent with the result that stripping is positively correlated with the likelihood of response types with higher levels of damage (i.e. dead trees and resprouting from base), and was negatively related to the probability of crown resprouting (corresponding to lower levels of damage).

Bark thickness is a well-known determinant of post-fire survival in cork oak (e.g. Cabezudo et al.



1995; Pausas 1997; Barberis et al. 2003; Catry et al. 2007; Moreira et al. 2007). Insulating capacity increases with bark thickness (Dickinson and Johnson 2001), thereby providing a higher level of protection to both the buds and the living tissues in the vascular cambium from which resprouting closely depends. As expected, the thicker the bark the lower the probability of a greater level of damage (expressed in the negative correlation of this variable with dead and basal resprouting probability), and the higher the probability of a low level of damage (expressed in the positive correlation with crown resprouting probability). However, the effect of bark thickness on post-fire responses is expressed only in exploited trees, suggesting that trees with virgin cork have an additional degree of protection that appears independent of bark thickness, as previously discussed in Moreira et al. (2007).

The relationship between tree size (DBH) and level of protection from fire was hypothesised to be related to the amount of damage and to the availability of below-ground carbohydrate reserves that may be allocated to resprouting. To be able to sprout and support regrowth, a plant needs surviving meristems and stored carbohydrate reserves (Iwasa and Kubo 1997; Bond and Midgley 2001). Older plants should have larger below-ground reserves (Gurvich et al. 2005) and consequently a higher capacity to mobilise reserves in response to disturbance (Bellingham and Sparrow 2000). For example, Malanson and Trabaud (1988) found that a 9-year-old *Q. coccifera* resprouted more vigorously than a 3-year-old, presumably because the latter had less developed below-ground reserves. Other empirical studies, however, suggest that resprouting ability declines with age and that below-ground carbohydrate storage in larger trees may be invested in survival rather than growth (Bond and van Wilgen 1996; Bond and Midgley 2001). In the case of cork oak, once cork exploitation has begun, the older (and therefore larger) trees have probably experienced a higher number of stripping events and poor management practices (e.g. deep ploughing or excessive canopy pruning) (Natividade 1950; Costa et al. 2004; Silva and Catry 2006). Therefore, if below ground reserves are allocated to recover from damages accumulated across the plant's lifespan, they will be diverted from resprouting (Bellingham and Sparrow 2000; Chapin et al. 1990). Reduced vigour and

survivorship of resprouting shrubs have been related to increasing disturbance frequency due to the impossibility of rebuilding or maintaining energy reserves in storage organs between consecutive disturbances (Bellingham and Sparrow 2000). Thus, it was hypothesised that bigger trees would be prone to higher levels of damage, and this was consistent with the fact that DBH was positively correlated with the likelihood of death, particularly in exploited trees. Bigger trees were also less likely to resprout from the crown, which also indicated a higher level of damage, and of simultaneous resprouting from the crown and base.

The fact that the models obtained had moderate predictive performance suggests that other variables, which may not be directly related to tree features, also contribute to the level of damage suffered by each individual. If these other factors had been taken into account, they would probably explain a larger proportion of variability in the observed patterns. For example, Moreira et al. (2007) showed that variables related to stand structure (e.g. tree density or understory vegetation height) and topographic location (slope and aspect) as well as indicators of fire severity (e.g. charring height) were significant predictors of cork oak mortality in the same study area. Other factors known to influence post-fire sprouting responses include site quality (López Soria and Castell 1992), disturbance frequency (Bond and Midgley 2001), fire season (Konstantidinis et al. 2006) and the existence of herbivory (Moreno and Oechel 1991).

The expected probabilities of the different response type models reflected the relative frequency of these types in the field. Thus, the more likely response type (the one with higher expected probability) for all possible combinations of stripping status, cork thickness and bark thickness was resprouting from crown. The only exception was when trees were exploited, had a very thin bark (<2 cm) and were very big (>40 cm DBH). This corresponds to the higher level of damage in our model, which is consistent with the fact that death was the most likely outcome (Fig. 2).

In summary, the influence of the studied variables on the post-fire response patterns of cork oak after fire were in agreement with the hypothesis that different levels of damage (and corresponding response types) may be found in sprouting trees where all the crown

was destroyed by wildfire. We provided evidence that four different response types may occur, and that these are influenced by stripping status, bark thickness and tree size, which are probably related to the level of protection of buds and cambial tissue, and to the amount of below ground reserves available for the plant to invest in resprouting.

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