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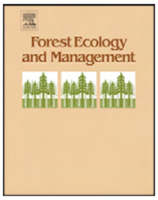

Review

Fire resistance of European pines

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ABSTRACT

Pine resistance to low- to moderate-intensity fire arises from traits (namely related to tissue insulation from heat) that enable tree survival. Predictive models of the likelihood of tree mortality after fire are quite valuable to assist decision-making after wildfire and to plan prescribed burning. Data and models pertaining to the survival of European pines following fire are reviewed. The type and quality of the current information on fire resistance of the various European species is quite variable. Data from low-intensity fire experiments or regimes is comparatively abundant for *Pinus pinaster* and *Pinus sylvestris*, while tree survival after wildfire has been modelled for *Pinus pinea* and *Pinus halepensis*. *P. pinaster* and *P. pinea*, and *Pinus canariensis* in special, are better equipped to survive fire, but low-intensity fire is tolerated even by species often referred to as fire-sensitive (*P. halepensis* and *Pinus radiata*). The relative fire resistance of European pine species is assessed on the basis of (i) morphological and experimental data, and (ii) mortality modelling that considers fire behaviour. Limitations of these approaches to rate fire resistance are discussed, and the current knowledge gaps are indicated.

Contents

1. Introduction

Disturbance by wildland fire plays a prominent role in the ecology of pine ecosystems. Pine strategies to cope with fire can assist either species persistence (by sexual reproduction) or individual survival (Keeley and Zedler, 1998). Agee (1998) combined the fire severity concept with life-history characteristics

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(Rowe, 1983) to categorize and describe the range of plant responses in fire-prone environments. Pines under a low-severity fire regime are typically fire resisters, possessing traits that enable survival to low- to moderate-intensity fire: tissue insulation from lethal temperature provided by thick bark, large and protected buds, relatively thick needles, deep rooting habit, and a crown structure favourable to heat dissipation and hence less crown scorch. Self-pruning and lower branch shedding due to competition or fire contribute to crown fire avoidance. High-severity fire regimes are characterized by stand-replacement events, and the corresponding pine species are fire evaders that store a canopy seed bank in serotinous cones, or fire endurers that recover after the disturbance by sprouting. Moderate or mixed-severity (Brown, 2000) fire regimes correspond to diverse or combined fire response strategies.

Tree mortality can directly arise from various amounts of fire-caused injury to crown (foliage and buds), vascular or root tissues, either solely or in combination. Tree size can exert an important influence on the likelihood of tree death after fire. Larger trees should be able to survive more intense fires (Ryan and Reinhardt, 1988; Beverly and Martell, 2003; Kobziar et al., 2006) mainly because of thicker bark and higher position of the foliage. Tree mortality modelling combines morphological descriptors of the trees with fire damage measurements, indirectly by considering variables related to fire behaviour or directly by observing tissue damage (Fowler and Sieg, 2004). Because tree mortality is a binary variable (trees either live or die) it is well suited to be modelled as a probability by using logistic regression analysis. The extent of crown scorch, crown consumption, or both, is included as an independent variable in most tree mortality models, in relation either to crown volume (Ryan et al., 1988; McHugh and Kolb, 2003) or to crown length (Wyant et al., 1986). The height, percentage or severity of bole charring are often adopted as model surrogates for cambium death (Ryan, 1982; Sieg et al., 2006). Fire characteristics such as fire intensity (Beverly and Martell, 2003; Kobziar et al., 2006) or forest floor consumption (Stephens and Finney, 2002; Varner et al., 2007) are less often employed as tree mortality predictors.

Pines are an important component of European forest vegetation, especially in nutrient-limited or disturbed habitats (Richardson and Rundel, 1998). The biogeography of the 13 species of native European pines is described in Barbéro et al. (1998) and Willis et al. (1998), respectively for the Mediterranean Basin and for the rest of Europe. Southern Europe pines can be divided in low- to mid-elevation species occurring predominantly along the coast and in islands (*Pinus halepensis* Mill., *Pinus brutia* Ten., *Pinus pinea* L., *Pinus pinaster* Ait., *Pinus canariensis* C. Sm.), mountain species (*Pinus nigra* Arn., *Pinus sylvestris* L.) and high-mountain species (*Pinus heldreichii* H. Christ, *Pinus uncinata* Ram.). *P. sylvestris* is widespread in northern and central Europe, but all other extra-Mediterranean pines are confined to high elevations (*Pinus cembra* L., *Pinus mugo* Turra, *Pinus peuce* Grisb., *Pinus sibirica* Du Tour). The present distribution and composition of pine forests in the Mediterranean Basin has been shaped by large-scale plantation and invasion of former agricultural land (Le Maitre, 1998), as well as by human-altered fire regimes (Richardson et al., 2007). Dense, even-aged, highly flammable stands have developed over extensive areas and burn in landscape-scale fire events (Pausas et al., 2004; Fernandes and Rigolot, 2007). Furthermore, the ability to persist after fire is threatened by increased fire recurrence and burn severity, respectively in lowland (*P. halepensis*, *P. brutia*, *P. pinaster*) and in montane (*P. nigra*, *P. sylvestris*) pine woodlands (Pausas et al., in press).

Predictive models of tree survival after fire can assist managers in making post-fire management decisions related to hazard tree removal, salvage logging, reforestation, wildlife habitat and watershed quality (Brown et al., 2003). Also, knowledge on tree resistance to low- to moderate-intensity fire is critical to the sound use of fire in forest management. However, and in spite of its potential contribution to management decisions conducive to more resilient pine forests, research on fire resistance and post-burn mortality has been limited in Europe, presumably because of the prevalence of stand-replacement fire and the incipient development of prescribed burning. Several authors (Agee, 1998; Keeley and Zedler, 1998; Climent et al., 2004; Tapias et al., 2004; Fernandes and Rigolot, 2007) describe the fire-related traits, strategies or fire regimes of European pines, including explicit comparisons with other pine species. Here we will focus on the resistance of European *Pinus* to fire, by reviewing the existing quantitative knowledge on the ability to survive fire, and then rating the fire resistance of each species.

2. Fire survival data and models for European pine species

2.1. *Pinus halepensis* and *Pinus brutia*

P. halepensis is a typical fire evader that forms highly flammable stands and as a rule is killed by wildfire (Agee, 1998; Ne'eman et al., 2004). This possibly explains the scarcity of literature on the fire resistance of *P. halepensis* (and of the closely related *P. brutia*) versus the wealth of post-fire regeneration studies.

The first experimentation with prescribed burning in the Mediterranean Basin was conducted by Liacos (1974) in *P. halepensis* and *P. brutia* in Greece. The author considered these species amenable to treatment with prescribed fire at an age of 30 years – when bark accumulation is sufficient to hamper cambium injury – and went on to develop an underburning prescription (Liacos, 1986), thereby showing how to minimize fire-induced tree mortality.

Aravanopoulos et al. (2004) refers to a surface wildfire in Greece that did not result in *P. brutia* mortality. In NE Spain after a wildfire of varying severity in a stand (DBH = 10.2 ± 7.5 cm; basal area = 21.6 m^2 ha^{-1}) composed of 20-year-old regeneration plus trees that had survived the previous fire, *P. halepensis* individuals with more than 20% of green foliage were alive less than 1 year after the fire (Pausas et al., 2003). In a naturally regenerated and open *P. halepensis* stand in SE France, Trabaud and Valina (1998) describe tree mortality 1 year after a surface wildfire ranging in flame height from 0.5 to 2.5 m. Fire damage descriptors were not measured but tree survival increased with size: all individuals with less than 5 cm ground line diameter died; 37% and 66% of the trees were alive in the 5–25 and 25–45 cm size classes, respectively; the survival rate in relation to tree height was 70% for trees with 7–10 m and 83% for trees taller than 10 m.

Ducrey et al. (1996) studied for a 7-month period the ecophysiological and growth consequences of trunk girdling by controlled heating. Cambium damage from 37% to 78% of the stem's circumference did not result in tree death, and no significant differences were found between partially burnt trees and control trees for the several parameters that were monitored.

In Italy, Lovreglio et al. (1999) studied and modelled the first post-fire year mortality of *P. halepensis* trees in three stands, respectively 15, 48 and 50 years old. Tree density and basal area varied in the ranges of 226–1500 ha^{-1} and 8.4–31.4 m^2 ha^{-1}, while individual tree DBH and bark thickness ranged from 7 to 46 cm and from 0.3 to 5 mm, respectively. The modelled likelihood of survival to fire was a combined function of stem char height (range: 0–6 m) and the % of crown length scorched (0–100%).

P. halepensis mortality was also modelled by Rigolot (2004), in a more extensive study in southern France where trees were

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Table 1
Selected logistic models for the probability of post-fire tree mortality of European pine species

Species (reference)	Model variables and coefficients			
	b_0	b_1x_1	b_2x_2	b_3x_3
Pinus halepensis (Rigolot, 2004)	2.500	−0.035 CSV	−0.057 BC	
	2.322	−0.0004 CF	0.112 DBH	−1.649 BC_{max}
Pinus pinaster (Botelho et al., 1998a)	7.390	−10.119 CSV	0.381 DBH	
	7.533	−10.662 RCS	0.264 DBH	
Pinus pinea (Rigolot, 2004)	23.006	−0.253 CSV		
	23.971	−0.236 CSV	−0.055 CSL	
	33.086	−0.312 CSV	−1.941 BC	
Pinus sylvestris (Sidoroff et al., 2007)	−1.520	−19.075 CSR	0.287 DBH	
	3.325	−18.675 CSR	3.307 BT	

All models have the form $P = [1 + \exp(b_0 + b_1x_1 + \cdots + b_kx_k)]^{-1}$. BC, bark char class (Ryan, 1983), 4 quadrants mean; BC_{max}, maximum bark char class; BT, bark thickness (cm); CF, crown factor (CSV^2); CSL, charred stem length (m), mean of the windward and leeward sides; CSR, charred stem ratio; CSV, observed proportion of crown scorch volume; DBH, diameter at breast height (cm); RCS, crown scorch ratio.

monitored for 3–5 years after wildfire. Tree dimensions varied in the ranges of 2.7–49.5 cm for DBH and 3.0–18.5 m for height and the survival rate was 31%. The visual estimation of crown scorch volume, used directly or squared (crown factor), varied in the sampled trees from nil to total, and was the most important variable in explaining the likelihood of mortality (Table 1).

2.2. *Pinus radiata*

Although *P. radiata* D. Don. is a North-American species it is planted extensively in northern Spain and England. Based on fire scar and stand structure analysis, Stephens et al. (2004) argue that although usually described as a fire evader, *P. radiata* also has characteristics of a fire resister and the native populations of the species are best classified in a mixed-severity fire regime. Stephens and Libby (2006) report that Californian *P. radiata* populations historically subjected to low-intensity anthropogenic fire have thicker bark than populations that did not.

Most of the fire resistance information on *P. radiata* comes in fact from prescribed fire experimentation in the extensive plantations established in Australia. Luke and McArthur (1978) state that *P. radiata* is more vulnerable to fire than *Pinus elliotti*, *Pinus caribaea* and *P. pinaster*. Although Dawson (1982) described the species as 'very fire sensitive' and complained that it cannot be subjected to broad-scale hazard reduction burning, this assertion seems conservative in view of the knowledge currently available.

Woodman and Rawson (1982) summarize the results and conclusions of several Australian studies. Trees that after prescribed burning were scorched in more than half of the crown length reduced their diameter increment by 59% (dominant trees) and 38% (co-dominant trees) in comparison with unscorched individuals. Stem damage is restricted to small sections of trees with DBH <21 cm or bark thickness <2.5 mm and does not impact the merchantable wood volume. Low intensity wildfire (flame height <1 m but with a high-residence time) caused fire scars up to a height of 7 m and stem girdling between 22% and 46% of the circumference at stump height.

Some effort has been devoted to quantify fire damage to the trunk of *P. radiata*, which is more likely than in *P. pinaster* (de Ronde, 1982). Thomson (1978) found bole damage in 0.6% of the sampled trees, for a stand age range of 11–26 years and prescribed fires under 300 kW m^{-1} of fireline intensity. In mature trees, Burrows et al. (1989) considered stem damage unacceptable when cambium kill occurred above a 0.5-m height; the observed range of bole damage was 0–30% but it reached 60% in the presence of unusual woody fuel accumulation, in all cases without consequences to radial tree growth. Thinning slash burning with flame height <1.5 m (Billing, 1979) or fireline intensity <500 kW m^{-1} (Burrows et al., 1988) did not result in noticeable injury to the bole. Norman (1985) describes a stronger impact in stands prescribed burnt after heavy first thinning, with ca. 10% of the trees exhibiting cracks in the bark and resin exudation due to irregular fuel distribution and hence extended flame residence time (up to 4 min).

Burrows et al. (1989) report the effects of low-intensity (28–170 kW m^{-1}) prescribed fires in *P. radiata* regeneration (up to 15-m tall) underneath a mature stand of the species in Australia. 90% of the individuals taller than 1 m died when crown scorch ratio (height of crown scorch/total tree height) exceeded 0.8, but 88% survived when it was less than 0.6. In South Africa, mortality caused by prescribed burning is expected only when crown scorch reaches 90% (de Ronde, 1982).

2.3. *Pinus pinea*

Survival of *P. pinea* to fire is quite variable, but the existing data points to higher fire resistance in relation to the remaining Mediterranean Basin pines. Rodrigo et al. (2007) report a 0–100% range in individual tree survival in plots located in areas burned by high-intensity fire. Live trees were absent from 38% of the plots, while the survival rate exceeded 60% in 27% of the plots.

The tree survival rate in plots located in areas affected by high-intensity fire within a 6125 ha wildfire in Catalonia, Spain, was 13% for *P. pinea*, but zero for *P. pinaster* (Rodrigo et al., 2004). Catry et al. (2006) in CW Portugal also report higher second year post-fire survival rate for *P. pinea* (36%) than for *P. pinaster* (10%). González et al. (2007) studied tree survival to fire in the forests of Catalonia based on National Forest Inventory data from permanent plots. The data base included the pine species *P. sylvestris*, *P. pinea*, *P. halepensis*, *P. nigra* and *P. pinaster* (Table 2) and was used to develop a multi-species model for predicting the probability of a single tree surviving a fire event. The use of the model for a given tree size and

Table 2
Observed pine survival in National Forest Inventory plots burned by wildfires in Catalonia, Spain (González et al., 2007)[a]

Dominant species	Live trees proportion	Mean live trees proportion (stand level)
P. halepensis	0.50	0.55
Pinus nigra	0.67	0.58
P. pinaster	0.55	0.60
P. pinea	0.92	0.82
P. sylvestris	0.74	0.68

[a] Data from 722 plots that burned between the inventories of 1989 and 2001.

stand structure estimates that *P. pinea* is almost four times more likely to survive a fire than the other pines. González et al. (2007) reckon that an important part of the explanation for this degree of fire resistance – almost as high as for the resprouting *Quercus suber* – should be ascribed to the intensity of fuel management in *P. pinea* plantations. The results are quite representative of the fire regime and relative tree survival but unfortunately, and due to its nature, the database lacks descriptors of fire injury and burn severity.

Rigolot (2004) studied *P. pinea* mortality after wildfire in southern France. Tree dimensions varied in the ranges of 5.7–58.1 cm for DBH and 2.8–17.4 m for height and the survival rate was 0.61. Crown scorch volume, which varied in the sample from nil to total, was the variable that best explained mortality likelihood 3–5 years after wildfire (Table 1). According to Ryan et al. (1994) the species should be more fire resistant than *P. halepensis* owing to thicker bark for a given stem diameter and consequently improved stem insulation from heat. Also, *P. pinea* needle sensitivity to heat is less due to lower surface area-to-volume ratio: for a given exposure time *P. halepensis* needles are characterized by lower lethal temperature than *P. pinea* needles (Pageaud, 1991).

In mixed stands of *P. halepensis* and *P. pinea* the former exhibited crown scorch heights 1–5 m higher (Rigolot, 2004). According to the author this is explained by the less vulnerable needles of *P. pinea* and a crown architecture that offers increased protection of the upper crown from the heat flux. Height of crown kill and height of crown scorch are similar in *P. halepensis*, while in *P. pinea* crown scorch height often is higher than height of crown kill: buds can withstand heating below the crown scorch line, which means the scorched crown will recover partially and green-up the spring following fire (Pageaud, 1991).

2.4. *Pinus pinaster*

A relatively substantial amount of information is available on the resistance of *P. pinaster* to fire, from European, south-African and Australian sources. The available data (17 studies are synthesised in Table 3) and models are however biased towards low-intensity burning, reflecting the prevalence of a prescribed burning framework to the studies.

Keeley and Zedler (1998) associate *P. pinaster*, as well as *P. sylvestris*, to a stand-replacement fire regime, but this narrow view has been expanded and detailed by Fernandes and Rigolot (2007). *P. pinaster* stands historically subjected to surface fire (Tapias et al., 2004) with abundance of fire-scarred live trees (Vega, 2000) have been identified in Spain. Development and coexistence of fire-related traits, namely bark thickness, is highly variable between *P. pinaster* populations, which is quite obvious from Tapias et al. (2004) data. Nevertheless, bark depth can be generically classified as moderate to high and, regardless of fire intensity, mortality caused by bole injury is unlikely unless trees have DBH <20 cm or heat from extended smouldering girdles the stem base. The threshold size for tree mortality in experiments emulating prescribed fire is usually in the 5–10 cm DBH range (Table 3).

A longer exposure to a given temperature is required for *P. pinaster* needle necrosis in comparison with *P. pinea* and *P. halepensis*. Comparison of the models developed by Botelho et al. (1998a) for *P. pinaster* and by Rigolot (2004) for *P. pinea* (Table 1) indicates the two species have similar chances of surviving a given level of crown scorch, even though the underlying data were collected in quite different situations, respectively dormant season prescribed burning and summer wildfire. The large buds of *P. pinaster*, shielded by scales and by long needles, should be an important part of the explanation of why trees can endure very high levels of defoliation. Tree growth is not impaired noticeably until 25–50% of crown length is scorched, but in NW Spain high levels of mortality have been related to excessive duff consumption alone (Vega, 1988), and delayed mortality by the fungus *Leptographium* sp. after slash pile burning has also been reported in the same region (Fernández de Ana, 1982). Bark beetles can also be an important factor in delayed mortality of *P. pinaster* trees surviving wildfires (Fernández and Salgado, 1999).

2.5. *Pinus canariensis*

P. canariensis survives fire by sprouting from epicormic and root collar buds after total scorch and even crown combustion (Ceballos and Ortuño, 1951), which is explained by the huge accumulation of reserve carbohydrates in the sapwood parenchyma cells (Climent et al., 1998). Most of the features that are associated to fire resistance – thick bark, long needles, large buds, tall growth habit, self-pruning, deep rooting and longevity (Climent et al., 2004) – are also well-developed in the species.

Quantitative information on the capability of *P. canariensis* to resist fire is very scarce. Without reporting data, de Ronde (1982) and Climent et al. (2004) indicate near total survival to fire. Thick-barked populations in the Canary Islands experience more frequent and intense fires, whereas thin-barked provenances correspond to open stands with sparse understory in drier climate that experience surface fires (Climent et al., 2004). The unusual combination of resistance and recovery to fire of the species is clearly shown in Arévalo et al. (2001). Three and a half years after a wildfire, differences in pine canopy cover between an unburnt control and areas burned by a surface fire and by a crown fire were respectively 3% and 20% (windward site), and 6% and 10% (leeward site).

2.6. *Pinus nigra*

Ordóñez et al. (2005) studied *P. nigra* survival after a 15,300 ha wildfire in NE Spain. Individuals located in areas that experienced less severe fire (on green islands and near unburned edges) were monitored for 5 years. Three visually estimated crown scorch volume classes were used to describe crown damage. Survival rates of 55%, 64% and 85% were observed, respectively for small (DBH <10 cm), medium (10–20 cm DBH) and large (DBH >20 cm) trees. Almost all trees were alive when the extent of scorch was less than one-third of crown volume, while survival percentages of >80% and >60% corresponded to 1/3 to 2/3 and >2/3 of crown scorch volume, respectively.

Similar results were obtained by Rigolot (data on file) in a study of *P. nigra* mortality after a winter wildfire in a mid-high elevation (1500 m) mixed *P. nigra*–*P. sylvestris* stand in the French Southern Alps. Tree size varied in a range of 13.2–40.1 cm for DBH and 8.0–19.0 m for height. Three years after fire, survival was total when the extent of scorch was less than 2/3, and 91% for crown scorch higher than 2/3.

Pimont and Rigolot (2005) observed in Corsica, France, that *P. nigra* is more vulnerable to fire than *P. pinaster*, especially at higher fire intensities. However, the species is able to persist through a surface fire regime over several centuries, as testified by a relict and multi-aged forest in eastern Spain (Fulé et al., 2008).

2.7. *Pinus sylvestris*

P. sylvestris is classified by Agee (1998) in the moderate-severity fire regime, which is coherent with the wide geographical distribution and environmental variation under which the species can be found. Granström (2001) categorizes *P. sylvestris* trees as moderately fire resistant and able to survive several low-intensity

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Table 3
A summary of data from studies on the post-fire mortality and growth of *P. pinaster*

Reference, location, time since fire	Stand age	DBH (cm), height (m)	Season or month of fire	Fireline intensity (kW m^{-1})	Crown scorch ratio	Mortality (%), DBH threshold (cm)	Mortality by size class	Effect on diameter growth
Peet and McCormick (1971), SW Australia, 2 years		13–23, –	Winter	32, 38				=
McCormick (1976), SW Australia, 3 years	17	–, 12.8			0.50–0.75			↓ (2 years)
McCormick (1976), SW Australia, 5 years	38	–, 14.0			0.5 m green tip			↓ (3 years)
					1.5 m green tip			↓ (3 years)
					3 m green tip			=
Vega (1978),[a] NW Spain, 5 months	9–11	4.7, –	March	60–170		41, –	<5 cm = 52%, 5–10 cm = 15%	
de Ronde (1983), S Africa, 2 years					0.5[b] to >0.9			↓ (2 years)
Rego (1986), N Portugal, 2–6 years	27–60	18.3–31.4, –	Autumn, spring	0.8–2 m (flame height)				=
Rego et al. (1988), N Portugal, n.a.	20	2–27, –	February			–, 10	2.5 cm = 50%, 7.5 cm = 16%	=
Vega (1988), NW Spain, 7 years	–		March–April					
Duff reduction <25%[c]		17.3–27.0, 10.7–16.5		92–309[d]	0–0.34	0–7,[e] –		↓ (*n* = 1), = (*n* = 5)
Duff reduction 25–50%		21.0–23.0, 12.0–13.2		88–372[d]	0–0.19	15–80,[e] –		↓ (*n* = 4), = (*n* = 2)
Rego et al. (1993), N Portugal, 2 years	30 and 33	14.6–20.6, 13.1–17.3	December	50–101	0	0, –		=
Botelho et al. (1998a), N and C Portugal, 2 years	10–18	2.9–12.3, 2.7–10.1	November –March	85–854	0.17–0.81	1.5–59.1, 15	<2.5 cm = 75%, 5 cm = 24%, 10 cm = 4%, 15 cm = 1%	↑ (scorch <25%), ↓ (scorch >25%)
Botelho et al. (1998b, 1998c), N Portugal, 3 years	18 and 20	2.7–17.2, 2.9–9.2	February	44–2369[f]	0.43 (0–1)[f]	20, 7		=
Silva (1997), N Portugal, n.a.	10	3.6–16.0, –				0, –		
Vega et al. (1998), NW Spain, 2 years	17 and 19	9.2–39.6, 5.8–15.5		92–5443	0–0.84	0, –		
Burrows et al. (2000), SW Australia, 3 months	30–44	22.5–51.3, 16.2–23.3	Summer (December)	1500–18,000	0.06–0.95	7–91,[g] –		
						0–46,[h] –		
Rigolot (2000), SE France, 1 year	15	3.3, 4	March	20–51	0.36–0.40	<1–43, 3		
			May	21	0.84	80, 6		
Fernandes (2002), N Portugal, 2 years	14–41	11–26, 6.1–18.3	November –June	32–3608	0–0.91	0–68, 3–17		
Fernandes et al. (2004), N Portugal, 1 year	28	12.3 and 13.4; 10.1 and 9.1	July	399 and 931	0.88 and 0.94	41 and 55, –		

[a] Scattered pines (4% of the basal area) in a *Eucalyptus globulus* stand.
[b] Described by the author as ‘heavily scorched’.
[c] Forest floor F and H layers.
[d] Estimated from crown scorch height or stem char height.
[e] Not significantly different from unburned paired plots.
[f] Tree-level variation.
[g] Induced by damage to crown.
[h] Induced by stem girdling (350 kW m^{-1}).

fires. Angelstam and Kuuluvainen (2004) describe *P. sylvestris* forest in boreal Europe dry sites as being park-like and adapted to frequent low-intensity fire that results in multi-aged stands, and state that the species is more tolerant to fire as it ages, due to increased bark thickness and crown base height. Old and thick-barked trees usually survive fire, although fire scars are common as a result of cambium damage at the base of the trunk (Parviainen, 1996). In the presence of heavy slash fuels a 16-mm bark depth was enough to decrease cambium damage to ca. 5% (Sirén, 1974).

Fire history studies reveal varying fire frequency in Fennoscandia, but low-severity fires were largely prevalent over stand replacement events. The presence of fire-scarred live trees provides evidence of the survival of *P. sylvestris* to surface fire, in Latvia (Brumelis et al., 2005), SE Norway (Groven and Niklasson, 2005), boreal Sweden (Hellberg et al., 2004), southern Finland (Wallenius et al., 2002), and NW Russia (Lehtonen and Kolström, 2000).

Several studies on *P. sylvestris* post-burn mortality highlight the importance of tree size to withstand surface fire. A survival rate of 20% after wildfire, shifted towards larger trees, is reported by Kolström and Kellomäki (1993). In a 43-year-old stand in Germany, Schmidt et al. (2004) have observed mortality in the smaller diameter individuals and equated the effect of a low-intensity surface fire to a thinning from below. Bruce and Servant (2003) report on experiments in mature stands in Scotland: more than half of the crown was scorched in 18% of the trees but no mortality was observed 1 year after the fires.

Wirth et al. (1999) worked in central Siberia and found that fire killed all trees (DBH $<$10 cm) in a 18-year-old patch, but none of the individuals in a contiguous 235-year-old stand (DBH range of 10–50 cm). In a 39-year-old stand the number of live trees exceeded the number of dead trees only for Trees 6-m high and taller, and the fire had a strong thinning effect, reducing stand density by 86%. Surviving fire-scarred individuals were significantly lower in diameter than unaffected trees 31 years after fire, indicating growth suppression by the fire. Wirth et al. (1999) conclude that trees younger than 20 years are killed by any fire, selective mortality occurs in 20–100-year-old stands without modifying stand structure, and tree survival is near total in stands older than 100 years.

Somewhat different results were obtained by the FIRESCAN Science Team (1996) in the Bor Forest Island, also in central Siberia, owing to the different nature of the event, a stand-replacement large-scale fire experiment. Tree survival was almost nil over 82% of the area. In a surface fire affected stand (mean DBH = 15 cm), 75% of the individuals died in the first post-fire year, and nearly all trees with DBH $<$12 cm were completely scorched and died, but survival in the 20–24 cm DBH class was above 85%. Additional mortality was expected, given the high level of insect infestation among the surviving trees.

In northern Sweden Linder et al. (1998) studied the mortality induced to a multi-aged stand by a prescribed fire that generally did not exceed a fireline intensity of 700 kW m^{-1}. Mortality was strongly size-dependent among the smaller individuals, decreasing from almost 100% (DBH $<$2 cm) to ca. 20% (DBH 10–12 cm). For larger trees mortality decreased until a minimum of 1.5% in the 40–50 cm DBH class, but trees with DBH $\geq$ 50 cm suffered a 20% mortality rate, due to burn out of open scars from past fires.

Sidoroff et al. (2007) modelled *P. sylvestris* mortality with data from 11 even-aged plantations from southern Finland, with ranges of 30–45 years for stand age, 588–2200 ha^{-1} for tree density, 11–20 m for dominant height, 11–23 cm for DBH, 0.4–1.2 cm for bark thickness, and 0.5–1.3 m for flame height. Small-sized trees were far more affected 1 year after fire, with a 70% mortality rate in the 5–7 cm class but 20% only in the 7–9 cm class. Survival was very high beyond a DBH of 15 cm, a height of 13 m and a bark thickness of 0.6 cm, as well as below a charred stem ratio of 0.12. Mortality was associated to higher levels of burn severity in the forest floor. The authors present models for the probability of tree mortality that combine charred stem ratio with DBH or with bark thickness (Table 1). Crown damage and apparent root damage were almost non-existent and thus stem damage was assumed as the cause of mortality.

In the Mediterranean context, *P. sylvestris* post-fire mortality was monitored by Rigolot (data on file) after a winter fire in a mid-high elevation (1500 m) mixed *P. nigra*–*P. sylvestris* stand in southern France. Tree dimensions varied in a range of 13.0–42.0 cm for DBH and 7.7–19.6 m for height. Three years after fire, survival was total when the extent of scorch was less than 2/3 and survival was 70% when crown scorch was $>$2/3. Detailed analysis showed a similar fire resistance of both species after this specific fire event.

3. The relative fire resistance of European pine species

Based on the available information we now propose a fire resistance rating for the European species of *Pinus* (Fig. 1). The classification is almost entirely derived from quantitative data (see the sources in Fig. 1 legend), thus minimizing subjective judgement, and combines the likelihoods of cambium kill and crown kill. Resistance to cambium kill was a function of normalized bark thickness, which was calculated as the percentage of tree radius occupied by bark (at 1.3 m). Resistance to crown kill reflects bud tolerance to heating (inferred from bud width), bud shielding from heat provided by needles, and time-temperature thresholds for needle and bud necrosis. For *P. pinea* two ratings were produced, respectively *pinea* 1 and *pinea* 2 in Fig. 1. *Pinea 2* accommodates the canopy architecture effect mentioned by Rigolot (2004) and is consistent with the empirical observations previously mentioned (Rodrigo et al., 2004; Catry et al., 2006; González et al., 2007).

The fire resistance rating in Fig. 1 is not capable of identifying and combining the relative contribution of crown and cambium kill to tree mortality. Empirical models for the likelihood of pine survival or death should result in a sounder classification of

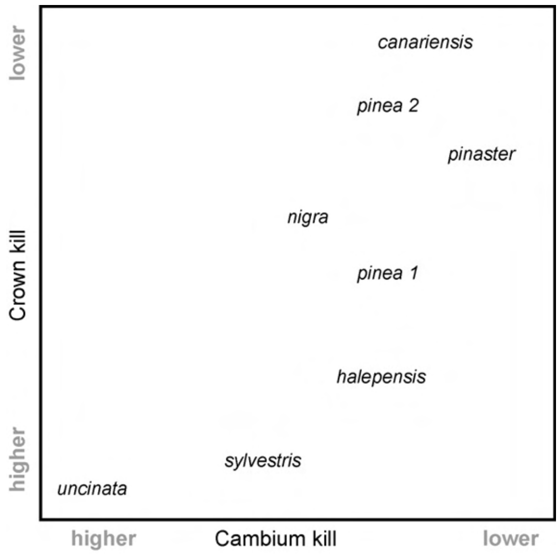

Fig. 1. Fire resistance rating of European pine species, based on morphological traits and lethal heating experiments. Information sources: de Ronde (1982), Alexandrian and Rigolot (1992), Duhoux (1994), Ryan et al. (1994), Keeley and Zedler (1998), Jackson et al. (1999), Burrows et al. (2000), Rigolot (2004), and Tapias et al. (2004).

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Table 4
Application to European pines of the conifer mortality model of Peterson and Ryan (1986)

Species	Cambium kill			Crown kill			P_m
	NBT	BT (cm)	τ_c (min)	T_L (°C)	h_k (m)	c_k	
Pinus uncinata	0.074	0.6	0.9	60	6.9	0.97	0.99
Pinus radiata	0.140	1.1	3.2	60	6.9	0.97	0.93
P. sylvestris	0.150	1.1	3.7	60	6.9	0.97	0.92
P. nigra	0.182	1.4	5.4	65	6.1	0.91	0.64
P. halepensis /P. brutia	0.200	1.5	6.5	60	6.9	0.97	0.85
P. pinea	0.200	1.5	6.5	70	5.4	0.84	0.35
P. pinaster	0.245	1.8	9.8	70	5.4	0.84	0.20

NBT, normalized bark thickness, the ratio of bark thickness to stem radius; BT, bark thickness; τ_c, critical time for cambium kill; T_L, lethal bud kill temperature; h_k, height of crown kill; c_k, fraction of crown volume killed; P_m, probability of tree mortality. Fireline intensity, tree diameter, height and crown length, and ambient air temperature, were kept constant, respectively at 400 kW m^{-1}, 15 cm, 8 m, 6.5 m, and 25 °C to calculate P_m.

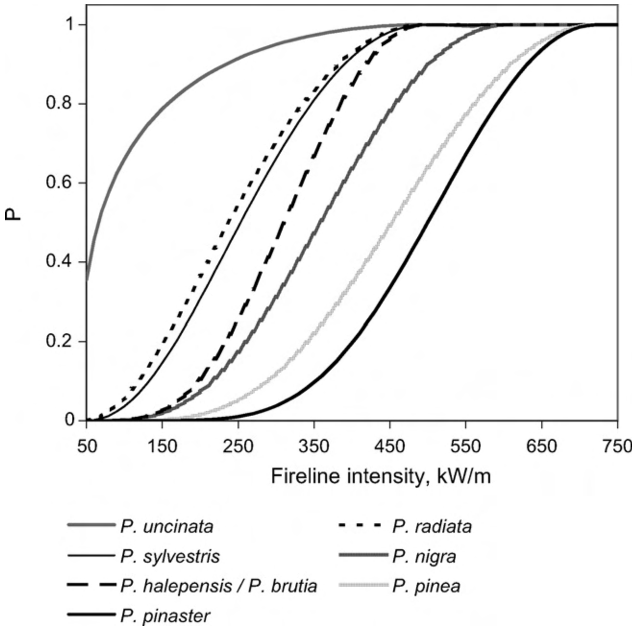

Fig. 2. Probability of post-fire tree mortality for different European pines calculated as per Peterson and Ryan (1986) for a range of hypothetical fireline intensities. A 8-m tall tree, with a crown length of 6.5 m and a diameter of 15 cm was assumed.

resistance to fire, but are not available for all species and are not directly comparable (see Table 1). Recent advances in the physical understanding of thermal injury (Bova and Dickinson, 2005; Michaletz and Johnson, 2006a) did not materialize in convenient models. A feasible alternative is the conceptual approach of Peterson and Ryan (1986) to fire-induced conifer mortality, which calculates the probability of mortality from crown kill fraction (c_k), critical time for cambium kill (τ_c) and duration of lethal bole heating (τ_L). Height of crown kill (h_k), tree height and crown length determine c_k, while the former is a function of fireline intensity, ambient air temperature (T_A), wind speed and the temperature threshold for bud necrosis (T_L). Bark thickness determines τ_c. The model of Peterson and Ryan (1986) integrates heat transfer principles and provides broad resolution estimates of post-fire mortality for a variety of conifers, and as such it can be generalized to distinguish fire resistance between species.

A modelling scenario where equally sized trees of different species are exposed to the same low-intensity fire is better suited to differentiate fire resistance levels, because the inter-specific range in mortality probability will decrease as fire behaviour increases. Accordingly, we apply Peterson and Ryan's model by setting fireline intensity to 400 kW m^{-1} and τ_L to 1 min, which corresponds to a mild surface fire where glowing combustion and the consumption of coarse woody fuels are insignificant. The calculation of h_k is for T_A = 25 °C and with Eq. (10) in van Wagner (1973), i.e. excluding the effect of wind speed on crown scorch height. Tree diameter, height and crown length are fixed, respectively at 15 cm, 8 m and 6.5 m for all species. As a consequence, variation in the probability of mortality among species is exclusively determined by bark thickness and T_L (60, 65 or 70 °C), which were compiled or inferred from de Ronde (1982), Alexandrian and Rigolot (1992), Ryan et al. (1994), Keeley and Zedler (1998), Jackson et al. (1999), Burrows et al. (2000) and Tapias et al. (2004). Table 4 presents the data and results of applying the model of Peterson and Ryan (1986) to European pines, this time excluding *P. canariensis* because of its resprouting habit, while Fig. 2 displays the full spectrum of mortality likelihood as a function of fireline intensity. The fire resistance ranking of species that this modelling exercise produces is nearly the same as in Fig. 1.

Both classifications of the fire resistance degree suffer from readily apparent limitations:

1. The insulating capacity of bark depends also of its structure, composition and density, although these variables influence is minor in comparison to bark thickness (Hengst and Dawson, 1994; van Mantgem and Schwarz, 2003).
2. The possible range in tree size of each species, and thus the variations in bark thickness (dictating insulation) and in crown base height and total height (determining the distance from the heat source) is not considered.
3. The variability in bark thickness along the length of the bole is also overlooked. The stem base often is proportionally more protected from thermal injury, i.e. the ratio of bark depth to stem radius decreases with height in the bole, namely in *P. pinea* and *P. halepensis* (Pageaud, 1991), *P. pinaster* and *P. radiata* (de Ronde, 1982), and *P. nigra* (Fernandes, data on file), especially in smaller trees, e.g. *P. radiata* (Jackson et al., 1999).
4. The structural arrangement of canopy foliage affects heat transfer by convection (Michaletz and Johnson, 2006b).
5. As in other approaches, the contributions to mortality of stem girdling by smouldering combustion and of root damage are ignored.

The fire environment – fuels, topography and weather – can easily override a fire resistance classification, thus minimizing the relevance of the above limitations, or, on the contrary, can emphasise the different species ability to resist fire. This implies that the proposed classification should not be dissociated from the fire environment context. A stand-replacement effect will result if a species deemed fire-resistant is affected by a high-intensity fire, whether the cause is crown scorch or combustion, long-lasting smouldering that completely girdles the stem base, or a combination of both. From the management point of view this emphasizes the importance of controlling fuels in stands of highly flammable species (*P. pinaster*, *P. halepensis*, *P. radiata*): if the available fuel load is reduced, the fire weather threshold for survival of a given size individual will increase and trees will tolerate fires under drier and windier conditions. The issue of fuel management will be less critical for species whose fuel complex and/or in-stand microclimate tend to create a milder fire environment, e.g. *P. sylvestris*. Apparently less defended species can therefore cope with fire better than would be expected from

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their degree of physical resistance (e.g. Table 2). Fire behaviour simulations for typical fire environment scenarios are useful to refine the fire resistance classification. Rodriguez-Trejo and Fulé (2003) suggest basing fire management in pine stands upon a site-specific and species-specific understanding of the ecological role of fire.

4. Conclusion

The heterogeneity of fire severity in the landscape implies that fire damage to trees depends of complex interactions. Pine species and size obviously matter, but will be less relevant to individual survival as the fire environment increases in severity. In the end, the level of injury and mortality for a given pine species is a combined outcome of fire behaviour, tree size and stand structure. As a result, the fire resistance rating developed in this study is more useful and makes more sense for prescribed burning conditions and, more generally, for low- to moderate-intensity surface fires. Nevertheless, a fire resistance classification – especially if supported by sound models based on physical principles and better knowledge of the physiological response – enables comparison between species. Assessments of this type would hardly be achieved alone by the use of empirical data obtained after fire events.

The existing data and studies indicate that all European pine species can resist fire, but their degree of resistance (the fire intensity they can tolerate) is variable. *P. canariensis*, *P. pinea* and *P. pinaster* are the most fire-resistant species, and even evader pines regarded as fire-sensitive like *P. halepensis* and *P. radiata* are able to survive low-intensity fire. Quantitative information on resistance to fire is absent from the literature for high-elevation pines.

Our review also made evident the current knowledge gaps. Most studies are based on low-intensity fire experiments and their results reflect post-burn survival on the short-term. Moreover, many of them have been conducted out of the wildfire season and the physiological response, soil moisture content and subsequent root damage, and post-fire biotic interferences, can be very different from those occurring after wildfire. This imposes limitations on the scope of the currently available models of post-burn tree mortality/survival. Fire injury and burn severity quantitative data are scant for many species and not always available together with tree survival data, because some of the studies targeted other research objectives or were opportunistic. Finally, the interaction between fire and biotic agents of damage and mortality, fire effects on tree growth, and the role of fire recurrence are still largely unexplored subjects. Future experimentation should strive to consider as much as possible the physical and biological processes involved in fire injury and tree death in order to add generality to the developed models.

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