Corrigendum

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There has been an error in citation of certain references in the Methods section, relating to the methods used to determine volume of crown scorch, bole char severity and ground char severity. The date error will cause the reader to refer to the incorrect publication in the References. The necessary corrections are:

Page 11, column 1, line 3 up, the citation 'Ryan 1982;' should be 'Ryan 1982, 1983;'.
Page 11, column 2, line 10 up, the citation 'Ryan (1982)' should be 'Ryan (1983)'.
Page 12, column 1, line 6 down, the citation 'Ryan (1982)' should be 'Ryan (1983)'.

Ryan (1982) and Ryan (1983) are both given in the References to this paper.

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Ponderosa pine mortality following fire in northern Arizona*

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Abstract. Sampling of 1367 trees was conducted in the Side wildfire (4 May 1996), Bridger-Knoll wildfire (20 June 1996) and Dauber prescribed fire (9 September 1995) in northern Arizona ponderosa pine forests (*Pinus ponderosa*). Tree mortality was assessed for 3 years after each fire. Three-year post-fire mortality was 32.4% in the Side wildfire, 18.0% in the Dauber prescribed fire, and 13.9% in the Bridger-Knoll wildfire. In the Dauber and Side fires, 95% and 94% of 3-year post-fire mortality occurred by year 2, versus 76% in the Bridger-Knoll wildfire. Compared with trees that lived for 3 years after fire, dead trees in all fires had more crown scorch, crown consumption, bole scorch, ground char, and bark beetle attacks. Logistic regression models were used to provide insight on factors associated with tree mortality after fire. A model using total crown damage by fire (scorch + consumption) and bole char severity as independent variables was the best two-variable model for predicting individual tree mortality for all fires. The amount of total crown damage associated with the onset of tree mortality decreased as bole char severity increased. Models using diameter at breast height (dbh) and crown volume damage suggested that tree mortality decreased as dbh increased in the Dauber prescribed fire where trees were smallest, and tree mortality increased as dbh increased in the Side and Bridger-Knoll wildfires where trees were largest. Moreover, a U-shaped dbh–mortality distribution for all fires suggested higher mortality for the smallest and largest trees compared with intermediate-size trees. We concluded that tree mortality is strongly influenced by interaction between crown damage and bole char severity, and differences in resistance to fire among different-sized trees can vary among sites.

Additional keywords: Pinus ponderosa; ponderosa pine; logistic regression; fire; tree mortality; mortality prediction model.

Introduction

Fire can kill a tree directly by a combination of effects on the three main tissue systems: crown, stem, and roots (Ryan 1990, 1998, 2000). Damage to these systems, either singularly or in combination, may cause mortality by adversely affecting tree physiological processes (Ryan 2000). In addition, fire may weaken a tree making it more susceptible to the attack of secondary mortality agents, such as bark beetles and pathogens (Mitchell and Martin 1980; Peterson and Arbaugh 1986; Amman and Ryan 1991; Ryan and Amman 1996; Kolb *et al.* 1998; Ryan 1998). Models that relate the probability of tree mortality to fire and tree characteristics have provided considerable insight into mechanisms of tree death after fire (e.g. Peterson and Arbaugh 1986; Ryan *et al.* 1988; Ryan and Reinhardt 1988; Saveland *et al.* 1990; Harrington 1993; Ryan 1998).

Mortality studies in ponderosa pine (*Pinus ponderosa*) and other conifer species have shown a strong positive relationship between crown damage by fire and subsequent tree mortality (Wyant *et al.* 1986; Harrington 1987, 1993; Reinhardt and Ryan 1988; Ryan and Reinhardt 1988; Ryan *et al.* 1988; Stephens 1995; Finney 1999). Crown damage has been used because it is easy to measure and crown damage directly affects whole-tree photosynthesis (Ryan 1990, 1998, 2000). Crown damage has been measured as the percentage of pre-fire live crown length or volume scorched (Herman 1954; Lynch 1959; Wagener 1961; Dieterich 1979; Wyant and Zimmerman 1983; Wyant *et al.* 1986; Harrington 1987, 1993; Potter and Foxx 1984; Reinhardt and Ryan 1988; Ryan *et al.* 1988; Stephens 1995; Finney 1999) and scorch height above ground level (Bevins 1980; Peterson 1985; Saveland *et al.* 1990). Peterson (1985) found that percentage of crown

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volume scorched was strongly related to post-fire tree mortality for Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and western red cedar (*Thuja plicata*) compared with scorch height.

Heat damage to tissues in the tree bole can contribute to tree mortality after fire (Peterson and Arbaugh 1986, 1989; Peterson and Ryan 1986; Brown and DeByle 1987). The extent of bole damage from fire primarily depends on bark thickness and the duration of exposure to lethal temperatures (Ryan 1983, 1990, 1998). Likewise, root damage from fire can contribute to tree mortality. Accurate evaluation of root damage by fire often requires root excavation (Ryan 1983; Swezy and Agee 1991). A surrogate measure of root damage by fire is the amount of charred ground (Ryan 1983; Ryan and Noste 1985; Swezy and Agee 1991). Several factors contribute to the difficulty in determining root damage by fire, such as the spatial distribution of roots, species variation in rooting depth, species successional status, soil type and moisture content, duff moisture content and flammability, and the duration of exposure to lethal temperatures (Ryan 1983, 1990, 1998).

The use of secondary agents, such as insects and fungal pathogens, in models of tree mortality after fire has been limited. Despite many reports of insect infestation of trees following fire (Morris and Mowat 1958; Miller and Keen 1960; Dieterich 1979; Mitchell and Martin 1980; Amman and Ryan 1991; Agee 1993; Ryan and Amman 1994, 1996; Rasmussen *et al.* 1996), few studies have included measures of insect infestation in tree mortality models (Peterson and Arbaugh 1986). Injuries to root systems and tree boles have been identified in lodgepole pine as entry ports for root and bole diseases following fire (Geiszler *et al.* 1980; Littke and Gara 1986).

Little information is available on factors that promote tree mortality after fire in ponderosa pine forests of the south-western United States. This region includes the largest contiguous area of ponderosa pine forests in the world in Arizona and New Mexico (Burns and Honkala 1990), and is characterized by a strongly bimodal pattern of precipitation with winter snow, extremely dry weather in spring and early summer, and intense late-summer rains that differs from the climate in other regions that support ponderosa pine forests. Logistic regression and discriminate analysis have been used to model ponderosa pine mortality after fire in California, Colorado, Idaho, Montana, and Oregon (Wyant and Zimmerman 1983; Wyant *et al.* 1986; Saveland *et al.* 1990; Swezy and Agee 1991; Harrington 1993; Regelbrugge and Conard 1993; Stephens 1995; Finney 1999). Early studies of ponderosa pine mortality after fire in northern Arizona were based on small sample sizes and a limited number of tree size classes (Herman 1950, 1954; Dieterich 1979). Harrington and Hawksworth (1990) developed a logistic regression equation for modeling ponderosa pine mortality after fire in northern Arizona, but their equation applies only to stands heavily infected with dwarf-mistletoe. Harrington's (1993) study in south-western Colorado addressed effects of season of fire, tree size, and fire damage on ponderosa pine mortality for small trees [diameter at dbh between 4 and 34 cm] with little bole scorch. Little information exists on mortality of larger trees after fire in the south-western US.

The objectives of our study were to:

(1) Describe temporal trends in ponderosa pine mortality following three fires in northern Arizona;
(2) Use logistic regression models to better understand factors associated with tree mortality; and
(3) Examine the influence of tree size on mortality after fire.

Methods

Study sites

The three fires for this study were selected based on their proximity to Flagstaff, Arizona, and season of fire occurrence. The Dauber prescribed fire was located in the Peaks Ranger District, Coconino National Forest, approximately 24 km west of Flagstaff (N3905541, E420436, UTM Zone 12, NAD27) (Fig. 1). The study site was 23.8 ha in size at an elevation range of 2225–2255 m. Aspect is generally south-southeast with slopes of 0–8%. Soils within the study area are fine, montmorillonitic Typic Argiborolls and are gravely loams derived from residuum basalt/cinder parent material (Miller *et al.* 1995). Vegetation at this site is a ponderosa pine–bunch grass type with ponderosa pine as the only tree species (USDA Forest Service 1997). Ponderosa pine in the study area ranges from 7.4 cm to 44.5 cm dbh with scattered groups and isolated old-growth trees.

The Side wildfire was also located in the Peaks Ranger District, Coconino National Forest (N3900725, E446931, UTM Zone 12, NAD27) (Fig. 1). The study site was in an 80 ha portion of the 130 ha Side wildfire at an elevation range of 2072–2195 m. Site aspect is predominately flat except where dissected by two east–west running intermittent stream courses. Soils are mixed Mollic Eutroboralfs, and are very stoney, sandy loams derived from alluvium, mixed igneous parent material (Miller *et al.* 1995). Vegetation at this site was a ponderosa pine–cliffrose type (USDA Forest Service 1997). Ponderosa pine dbh in the study area ranged between 10.2 and 91.4 cm. Unlike the Dauber prescribed fire, mature trees occurred as scattered individuals and large groups throughout the study area. The study area also included Gambel oak (*Quercus gambelii*) and alligator juniper (*Juniperus deppeana*), as well as mountain-mahogany (*Cercocarpus montanus*), cliffrose (*Purshia stansburiana*), and a variety of grasses and forbs.

The Bridger-Knoll wildfire was located in the North Kaibab Ranger District, Kaibab National Forest, approximately 32 km south-southwest of Jacob Lake, Arizona (N4048518, E465706, UTM Zone 12, NAD27) (Fig. 1). This site was 6475 ha of the 21 449 ha Bridger-Knoll wildfire.

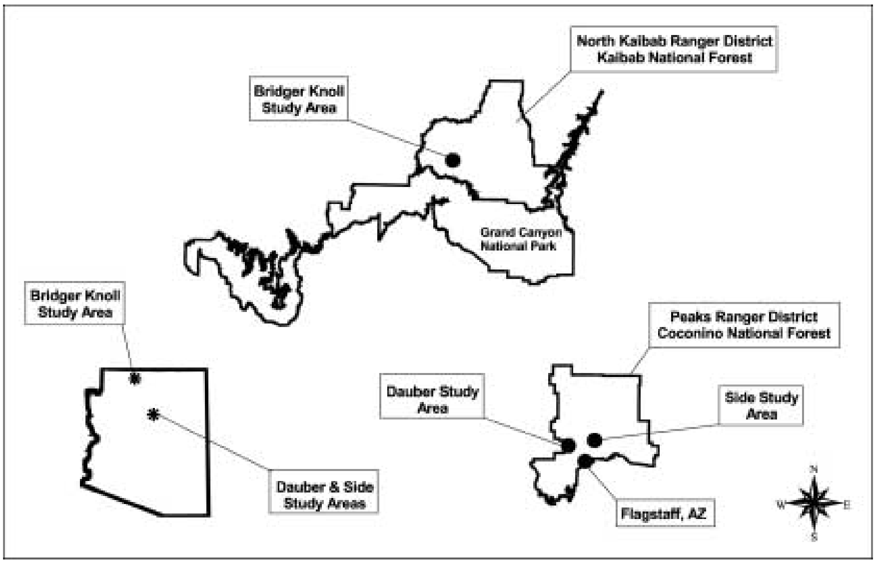

Fig. 1. Study site locations.

Elevation for the area ranged between 2134 and 2255 m. All aspects were represented and slope percent ranged between 0 and 20% in bottomland areas to over 40% on ridges. Soils are clayey-skeletal and fine montmorillonitic, Mollic Eutroboalfs, loams and gravely loams, derived from residuum limestone parent material (Brewer *et al.* 1991). Vegetation at the site was a ponderosa pine–Gambel oak type (USDA Forest Service 1997). The study area was primarily composed of ponderosa pine trees 22.9–106.2 cm dbh. Other tree species present were Gambel oak, one seed juniper (*Juniperus monosperma*), and Utah juniper (*Juniperus osteosperma*). Cliffrose, New Mexican locust (*Robinia neomexicana*), Gambel oak in shrub form, and a variety of grasses and forbs were also present in the study area.

Mean annual precipitation for the Dauber prescribed fire and Side wildfire areas is 57.9 cm with a mean annual snowfall of 276.4 cm (NOAA 1997). For the months of January and July, the mean daily minimum and maximum temperatures are −9.2°C and 5.7°C and 10.1°C and 27.7°C, respectively (NOAA 1997). Mean annual precipitation for the Bridger-Knoll wildfire area is 52.5 cm with a mean annual snowfall of 267.7 cm. For the months of January and July, the mean daily minimum and maximum temperatures are −9.1°C and 4.4°C, and 10.3°C and 26.3°C, respectively (National Climatic Data Center, station 024418, http://www.wrcc.dri.edu).

The post-fire years in our study included one extreme drought (1996), two mild droughts (1997, 1999), and one wet year (1998). Total yearly precipitation in 1996, the extreme drought, was 53% of normal. Years 1997 and 1999 were milder droughts, with similar precipitation (1997: 68% of normal; 1999: 69% of normal). Year 1998 was unusually wet; yearly precipitation was 120% of normal. These precipitation data are for Flagstaff, Arizona (National Oceanic and Atmospheric Administration, Stations 023010/03103 and 023009/9999, http://lwf.ncdc.noaa.gov/servlets/ACS), which is located close to the Dauber and Side fires. Similar trends in precipitation occurred at the site of the Bridger-Knoll wildfire.

Fire behavior and intensity

Because of the opportunistic nature of this study, direct observations of fire behavior characteristics, such as flame length, are not available. Instead, BEHAVE version 4.4 (Andrews 1986), a fire behavior prediction model, was used to predict the possible range of fire characteristics experienced across each site. We used BEHAVE to predict fire behavior in the flaming front based on the following inputs: Northern Forest Fire Laboratory (NFFL) fire behavior fuel models (Anderson 1982), percent fuel moisture content of the 1, 10, and 100 hour time lag fuels (Fosberg and Deeming 1971; Rothermel 1983), midflame windspeed (Rothermel 1983), and percent slope (Table 1). Required fuel moisture and wind data were obtained from fire records of each fire.

Fireline intensity, because of its relation to flame length, is best used to express the effects of fire on items affected by convective heating, such as foliage (Van Wagner 1973; Finney and Martin 1993). Using Agee's (1993) definitions of fire behavior based on fireline intensity (Table 1), the Dauber prescribed fire was primarily a surface fire, whereas the Side and Bridger-Knoll wildfires varied from surface fire to active crown fire. Estimated fire behavior from BEHAVE closely matched our qualitative assessments of observed burn conditions for all three fires.

The Dauber site was prescribed burned on 9 September 1995 and contained both natural and activity fuels (fuels generated as a result of logging activities). Strip ignitions designed to create head fires were initially used to ignite the

Table 1. Fuel model, fuel moisture, slope, and windspeed values used in the fire behavior model BEHAVE to predict the range of fire characteristics experienced across the study sites

Parameter	Dauber prescribed fire, Fall	Side wildfire, Spring	Bridger-Knoll wildfire, Summer
Fireline intensity (kW m^{-1})	44–234	338–3726	118–4132
Heat/unit area (kJ m^{-2})	3809–8058	5093–6260	5544–6836
Fuel model[A]	9,11	2,9	2,9
1-hour fuel moisture content (%)	9	3	2
10-hour fuel moisture content (%)	10	4	3
100-hour fuel moisture content (%)	14	5	4
1000-hour fuel moisture content (%)	18	8	6
Slope (%)	5	5	5–30
Windspeed[B] (km h^{-1})	3.2–8.0	8.0–12.9	3.2–32.2

[A] Following Anderson (1982).
[B] Midflame windspeed (Rothermel 1983).

area. Later into the ignition phase, lighting patterns were changed to create low-intensity backing fires. The 1, 10, 100, and 1000 hour time-lag moisture classes (Fosberg and Deeming 1971; Rothermel 1983) were within normal ranges for prescribed burning and winds were light (Table 1). Predicted peak fireline intensity at the Dauber site was lowest of all sites (Table 1).

The Side wildfire was a human-caused wildfire that started at approximately 1430 hours, 4 May 1996; fire danger rating for the Coconino National Forest was extreme. At the time of ignition, year-to-date precipitation was 15 cm below normal in Flagstaff, Arizona (NOAA 1997). Fuel moisture percentages for 1, 10, 100, and 1000 hour time-lag fuels were extremely low (Table 1), and fire behavior was extreme. Rates of fire spread were 0.8 km per hour with spotting 0.4 km in front of the main fire. This extreme fire behavior was primarily driven by very low fuel moisture content and wind.

The Bridger-Knoll wildfire was ignited by lightning within Grand Canyon National Park on 20 June 1996, and burned onto the North Kaibab Ranger District, Kaibab National Forest on 21 June 1996. Fire danger rating for the Kaibab National Forest at the time of ignition was extreme. As with the Side wildfire, fuel moisture percentages for 1, 10, 100, and 1000 hour time-lag fuels were extremely low (Table 1). Initial fire behavior for the Bridger-Knoll wildfire was extreme with rates of spread 0.4–0.6 km per hour and spotting 0.2 km in front of the main fire. Low fuel moisture content and wind were important drivers of fire behavior.

Sampling

Initial assessments of tree condition were completed in 1996, 5 months post-fire on the Side and Bridger-Knoll wildfires and 11 months post-fire on the Dauber prescribed fire. Trees with no foliage left (e.g. 100% consumption of foliage) were not included in the initial sampling because we assumed these trees were killed immediately by the fire front. Mortality was assessed for every tree ($n = 1367$ total) in September 1997, 1998, and 1999. Trees were recorded as dead if no green foliage was visible on the tree after 1996.

For the Dauber prescribed fire, 16 plots of 0.04 ha were used to collect data on 222 trees ranging in dbh from 7.4 cm to 44.5 cm. On the Bridger-Knoll wildfire, 75 plots of 0.08 ha and 46 plots of 0.4 ha were used to collect data on 833 trees between 22.9 cm and 106.2 cm dbh. These plots were established on systematic grids using a random start, and resulted in unbiased sampling of fire-damaged trees. At the Bridger-Knoll wildfire, plots were established by Kaibab National Forest personnel for monitoring following post-fire salvage logging.

At the Side wildfire, a total of 312 trees ranging in dbh between 10.2 cm and 91.4 cm were measured. Of these trees, 241 with dbh 10.2 cm and greater were measured on 18 archaeological sites in which trees were protected from salvage logging. In order to increase the sample size of trees 45 cm dbh and larger, seven transects 20 m in width, bounded by the fire perimeter and oriented across the primary direction of the fire, were established and used to sample an additional 71 trees.

Independent variables

Sixteen tree morphological variables and measures of fire damage were assessed on all trees at each fire (Table 2). All variables were chosen *a priori* based on factors that were important in previous studies of tree mortality following fire. We (i.e. the authors) measured all variables on the Dauber prescribed fire and Side wildfire in all years. For the Bridger-Knoll wildfire, variables were measured by United States Forest Service personnel after our training. We checked year 1 measurements for accuracy on 80% of the trees on the Bridger-Knoll wildfire.

Diameter at breast height was measured from the highest ground side at 1.37 m above the forest floor to the nearest 0.10 cm. Total tree height was measured to the nearest

Table 2. Mean, standard error (SE), and range of data collected for fire-damaged ponderosa pine for three fires in northern Arizona

Data definitions: Live crown ratio (% pre-fire live crown/total tree height); crown position (0, open grown; 1, dominate; 2, co-dominate; 3, intermediate; 4, suppressed); crown scorch (% pre-fire live crown scorched); crown consumption (% pre-fire live crown consumed); total crown damage (crown scorch plus crown consumption); bole char severity rating lee side (0, none; 1, light char; 2, medium char; 3, heavy char); bole char severity rating windward side (0, none; 1, light char; 2, medium char; 3, heavy char); ground char severity rating beneath crown dripline (0, none; 1, light; 2, medium; 3, high); insect rating (0, none; 1, partial attack; 2, mass attack); weather damage (0, none; 1, wind damage portion of tree; 2, tree blown down; 3, lightning strike post-fire); logging damage (0, none; 1, cat-face from skidding operations; 2, broken top from falling operations); soil disturbance (0, none; 1, operation of skidding equipment within dripline of crown; 2, skid trail located within dripline of crown; 3, spur road located within dripline of crown)

Mode values are displayed in parentheses for crown position, bole char severity lee side, bole char severity windward side, groundchar severity, insect rating, weather damage, logging damage, and soil disturbance

Data	Dauber prescribed fire Fall (n = 222)			Side wildfire Spring (n = 312)			Bridger-Knoll wildfire Summer (n = 833)		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
dbh (cm)	24.2	0.439	7.4–44.5	40.1	1.196	10.2–91.4	51.7	0.569	22.9–106.2
Height (m)	11.6	0.172	3–16	13.2	0.306	4–27	24.5	0.216	7–43
Live crown ratio (%)	41.7	0.765	20–80	63.1	1.052	20–90	47.7	0.624	0–90
Crown position	1.7 (1.0)	0.062	1–4	1.1 (1.0)	0.055	0–4	1.8 (2.0)	0.030	0–4
Crown scorch (%)	46.0	2.233	0–100	55.3	1.781	0–100	27.2	1.068	0–100
Crown consumption (%)	0	0	0	10.3	1.165	0–90	4.3	0.552	0–90
Total crown damage (%)	46.0	2.233	0–100	65.6	1.861	0–100	31.5	1.220	0–100
Bole char, lee side (m)	3.1	0.140	0–8	6.6	0.224	0–20	7.5	0.219	0–36
Bole char, windward side (m)	0.76	0.057	0–4	3.4	0.191	0–17	3.7	0.201	0–36
Bole char severity, lee side	1.7 (2.0)	0.048	0–3	2.4 (2.0)	0.035	0–3	1.9 (2.0)	0.015	0–3
Bole char severity, windward side	1.1 (1.0)	0.059	0–3	1.8 (2.0)	0.046	0–3	1.6 (2.0)	0.024	0–3
Groundchar severity	2.3 (3.0)	0.053	0–3	2.5 (3.0)	0.039	0–3	1.9 (2.0)	0.018	0–3
Insect rating	0.14 (0.0)	0.029	0–2	0.58 (0.0)	0.044	0–2	0.21 (0.0)	0.016	0–2
Weather damage	0.11 (0.0)	0.029	0–2	0.04 (0.0)	0.018	0–3	0.02 (0.0)	0.008	0–3
Logging damage	0 (0.0)	0	0	0.03 (0.0)	0.015	0–2	0.01 (0.0)	0.004	0–2
Soil disturbance	0 (0.0)	0	0	0.05 (0.0)	0.015	0–3	0.18 (0.0)	0.017	0–3

meter with a clinometer. Pre-fire live crown ratio was ocularly reconstructed and estimated to the nearest 10% as the percentage of pre-fire total tree height occupied by live crown.

Two types of crown damage were measured directly on each tree: percent of pre-fire live crown volume scorched and percent of pre-fire live crown volume consumed. A third measure of damage, total crown damage, was derived from the previous measures (total crown damage = scorch + consumption). Estimates of crown damage were made during the initial assessment only on cloud-free days and perpendicular to the direction of the sun. Because scorch and consumption of tree crowns following wildfire is often asymmetrical, measurements from all four quadrants were used to calculate an average for the tree.

Crown scorch was ocularly estimated to the nearest 10% by observers following Peterson (1985), and was defined as the percentage of pre-fire live crown volume scorched, but not consumed by the fire (Ryan 1982; Harrington 1987). Foliage that exhibited a change in color as a result of the fire, but not consumed, was considered to be scorched. Crown consumption was ocularly estimated to the nearest 10%, and was the proportion of pre-fire live crown volume consumed by active combustion. Evidence of residual buds on branch tips was used to identify branches that supported foliage prior to the fire.

Bole char was used to estimate cambial damage from fire, and was measured two ways. First, char height above ground level was measured for each tree on the uphill, or leeward side, and on the downhill, or windward side, to the nearest meter using a tape or clinometer. Second, bole char severity was assessed using four classes (none, light char, medium char, heavy char) following criteria established by Ryan (1982). Definitions of these classes were: none: no evidence of flame contact with the bole and no charring of the bole; light: light scorch or char on edges of bark plates or where moss burned off the bole; medium: bark uniformly black with the possible exception of the inner depths of the prominent fissures, but bark character is still discernible; heavy: bark deeply charred, but not necessarily to the wood, and surface characteristics have been lost. Because cambial damage is usually greater near ground level than at breast height (Ryan 1990), bole char severity was based on the depth of bole char in the first 45.7 cm above ground.

Ground fire severity was measured under the dripline of the tree crown using four classes to indirectly measure damage to root systems (Swezy and Agee 1991). These classes followed Ryan (1982), and were defined as: none: no visible effect on soil; light: surface of litter and duff layers scorched or charred; medium: litter completely consumed and duff deeply charred or consumed, but the underlying mineral soil not visibly altered; high: litter and duff completely consumed. In addition, burned-out stump holes and the presence of consumed downed logs within the dripline were noted.

Tree crown position may be important in determining survival following fire. Thus, crown position was assessed using four classes: dominant, co-dominant, intermediate or suppressed (Smith 1986). An additional classification for open-grown trees was added to account for trees that developed without any visible interaction or competition from other trees.

Attacks of western pine beetle (*Dendroctonus brevicomis*), roundheaded pine beetle (*Dendroctonus adjunctus*), mountain pine beetle (*Dendroctonus ponderosa*), and Ips (*Ips* species) were recorded for each tree after tree death. Insect attacks were detected by inspecting for boring dust or pitch tubes. Insect species were determined by removing sections of the bark and examining gallery patterns within the first 2 m of the tree bole on dead trees (Beatty 1986). Presence or absence of wood borers (*Buprestidae* and *Cerambycidae*) was noted yearly on live and dead trees. For red turpentine beetle (*Dendroctonus valens*), the number of quadrants with pitch tubes on the bole was recorded yearly for both live and dead trees. For western pine beetle, mountain pine beetle, roundheaded pine beetle, and *Ips* species, attack level was also assessed yearly for each species. If the species was not present on the tree, a rating of none was assigned. If attacks occupied less than 75% of the tree bole circumference based on distribution of gallery patterns, a rating of partial attack was assigned. If attacks occupied greater than 75% of the tree bole circumference, a rating of mass attack was assigned.

An overall rating of insect attack was determined for each tree by using three classes (none, partial, mass). Attacks by wood borers were not included in the overall rating because these insects generally attack only dead trees or dead sections of cambium, thus their contribution to mortality is likely small (Mitchell and Martin 1980; Rasmussen *et al.* 1996). An overall rating of mass attack was assigned if any individual insect species had this rating, or if two or more species had partial ratings. Also, a rating of partial attack was assigned if species of *Dendroctonus* or *Ips* was present with a partial attack rating.

The presence or absence of other secondary factors that may contribute to tree mortality was also recorded. Secondary factors included: weather damage, lightning damage, logging damage, and soil compaction from road building and skidding operations associated with post-fire logging operations. Lightning strikes were recorded only if the tree had been struck since the fire. Physical logging damage ('catface') was recorded if bark had been removed from greater than 50% of the tree circumference. Broken tops and limbs were also noted if they obviously resulted from felling operations. Soil disturbance was recorded if skidding equipment was operated within the dripline of the tree crown, a skid trail was created within the dripline of the crown, or if a temporary road was constructed within the dripline.

Data analysis

Mann–Whitney tests were conducted to test for differences between fire-damage and tree morphological characteristics of live and dead trees within each fire. Numbers of live and dead trees were compared by a two-dimensional contingency table using a χ^2 test to evaluate whether mortality differed among fires.

Logistic regression models were developed for each fire and for data pooled over fires using SPSS version 8.0 (SPSS, Chicago, IL, USA). For each fire, independent variables were screened for their influence on tree mortality by comparing values for dead versus live trees using two sample t-tests. Only those independent variables that differed between live and dead trees ($P \leq 0.10$) and were not strongly correlated ($r \leq 0.50$) with other independent variables were used in development of logistic regression models. Independent variables in the resulting logistic regression equations were used if significantly different from zero ($P \leq 0.10$). Model goodness of fit was assessed using graphical interpretation of each model's residuals and the -2 Log Likelihood Ratio statistic (-2LL) (Hosmer and Lemeshow 1989; Norusis 1994). The model form used to model tree mortality was:

$$P_m = 1/[1 + \exp(-(\beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n))], \quad (1)$$

where P_m is the probability of tree mortality, β_0, β_1, and β_n are regression coefficients, and X_1 and X_n are representative independent variables.

Several regression models were developed for each fire, and for data pooled over all fires following the model form of equation (1). Receiver Operating Characteristic (ROC) curves were used to compare the accuracy of different logistic regression models for each fire (Saveland and Neuenschwander 1990; Finney and Martin 1993; Regelbrugge and Conard 1993; Stephens 1995; Finney 1999). The ROC curve is a plot of the probability of a true positive prediction, or hit rate (tree is classified as dead when it is dead) versus the probability of a false positive, or false alarm rate (tree is classified dead when it is alive) by varying the decision criterion from 0 to 1 for group membership (Saveland and Neuenschwander 1990; Bradley 1996). The area under an ROC curve is equal to the probability of correctly classifying a concordant pair of observations. The ROC curve value can vary from 0.50, which is no better than chance, to 1.0, where all predictions are correct (Saveland and Neuenschwander 1990; Swets 1996). ROC values between 0.50 and 0.70 indicate low accuracy, values between 0.70 and 0.90 indicate moderate accuracy, and values greater than 0.90 indicate very high accuracy (Swets 1996). Models for each fire were ranked based on their −2 Log Likelihood ratio statistic values (−2LL), Receiver Operating Characteristic curve values (ROC), and number of independent variables.

Results

Tree characteristics by fire and mortality group

Sample trees were smaller in dbh and total height on average in the Dauber prescribed fire compared with the Side and Bridger-Knoll wildfires (Table 2). There was considerable overlap in tree size between the Side and Bridger-Knoll wildfires, but the Side wildfire had trees with dbh < 22 cm whereas the Bridger-Knoll wildfire did not (Table 2).

Live trees had larger dbh than dead trees in the Dauber prescribed fire and Side wildfire (Table 3). In contrast, dbh of live and dead trees did not differ at the Bridger-Knoll wildfire (Table 3). Plots of percent tree mortality 3-years post-fire versus dbh revealed a U-shaped distribution for all fires (Fig. 2). Percent mortality was lowest for trees with dbh between 35 and 55 cm for the Side and Bridger-Knoll wildfires and between 25 and 35 cm on the Dauber prescribed fire. Mortality was highest for the smallest trees at all fires and for trees with dbh of 75 cm at the Side and Bridger-Knoll wildfires (Fig. 2). The U-shaped mortality distribution versus dbh also occurred for data pooled over all fires (Fig. 3).

Average live crown ratio was highest on the Side wildfire, and nearly equal on the Dauber prescribed fire and Bridger-Knoll wildfire (Table 2). Live crown ratio was higher for live compared with dead trees at the Side and Bridger-Knoll wildfires, with no difference at the Dauber prescribed fire (Table 3).

Average crown position was nearly equal for trees in the Dauber prescribed fire and Bridger-Knoll wildfire at 1.7 and 1.8, respectively, indicating that the majority of trees at these sites were in the co-dominant crown class. The average crown position rating for the Side wildfire was lower at 1.1, indicating that more trees at this site were in dominant and open-grown classes. While open grown trees (rating of 0) occurred on the Side and Bridger-Knoll wildfires, none occurred at the Dauber prescribed fire (Table 2). Dead trees at the Dauber prescribed fire and Side wildfire had significantly lower crown position rating than live trees, suggesting that dead trees in these two fires were more suppressed (Table 3).

Table 3. Mean characteristics of live (L) and dead (D) ponderosa pine for three fires in northern Arizona. The P-value shows results of Mann–Whitney tests between live and dead trees

Data definitions: Live crown ratio (% pre-fire live crown/total tree height); crown position (0, open grown; 1, dominate; 2, co-dominate; 3, intermediate; 4, suppressed); crown scorch (% pre-fire live crown scorched); crown consumption (% pre-fire live crown consumed); total crown damage (crown scorch plus crown consumption); bole char severity rating lee side (0, none; 1, light char; 2, medium char; 3, heavy char); bole char severity rating windward side (0, none; 1, light char; 2, medium char; 3, heavy char); ground char severity rating beneath crown dripline (0, none; 1, light; 2, medium; 3, high); insect rating (0, none; 1, partial attack; 2, mass attack)

Mode values are displayed in parentheses for crown position, bole char severity lee side, bole char severity windward side, groundchar severity, and insect rating

Data	Tree status								
	Dauber prescribed fire Fall (n = 222)			Side wildfire Spring (n = 312)			Bridger-Knoll wildfire Summer (n = 833)		
	L	D	P-value	L	D	P-value	L	D	P-value
dbh (cm)	25.1	20.3	≤0.001	41.8	36.4	0.007	51.7	51.6	0.920
Height (m)	11.9	10.3	0.005	13.6	12.2	0.012	24.8	22.4	≤0.001
Live crown ratio (%)	41.4	42.7	0.557	66.3	56.4	≤0.001	48.2	44.6	0.079
Crown position	1.6 (1.0)	2.1 (1.0)	0.019	1.0 (1.0)	1.3 (1.0)	0.117	1.8 (2.0)	1.7 (2.0)	0.192
Crown scorch (%)	37.5	84.8	≤0.001	48.9	68.8	≤0.001	21.3	63.5	≤0.001
Crown consumption (%)	N/A	N/A	N/A	3.5	24.4	≤0.001	0.79	26.2	≤0.001
Total crown damage (%)	37.5	84.8	≤0.001	52.4	93.2	≤0.001	22.1	89.8	≤0.001
Bole char, lee side (m)	2.8	4.3	≤0.001	5.9	8.0	≤0.001	6.0	16.6	≤0.001
Bole char, windward (m)	0.64	1.3	≤0.001	2.4	5.5	≤0.001	2.1	13.1	≤0.001
Bole char severity, lee side	1.6 (2.0)	2.3 (2.0)	≤0.001	2.3 (2.0)	2.7 (3.0)	≤0.001	1.9 (2.0)	2.1 (2.0)	≤0.001
Bole char severity, windward side	0.94 (1.0)	1.9 (2.0)	≤0.001	1.6 (2.0)	2.2 (2.0)	≤0.001	1.5 (2.0)	2.0 (2.0)	≤0.001
Ground char severity	2.2 (3.0)	2.9 (3.0)	≤0.001	2.4 (3.0)	2.8 (3.0)	≤0.001	1.8 (2.0)	2.2 (2.0)	≤0.001
Insect rating	0.08 (0.0)	0.45 (0.0)	≤0.001	0.22 (0.0)	1.35 (2.0)	≤0.001	0.15 (0.0)	0.63 (0.0)	≤0.001

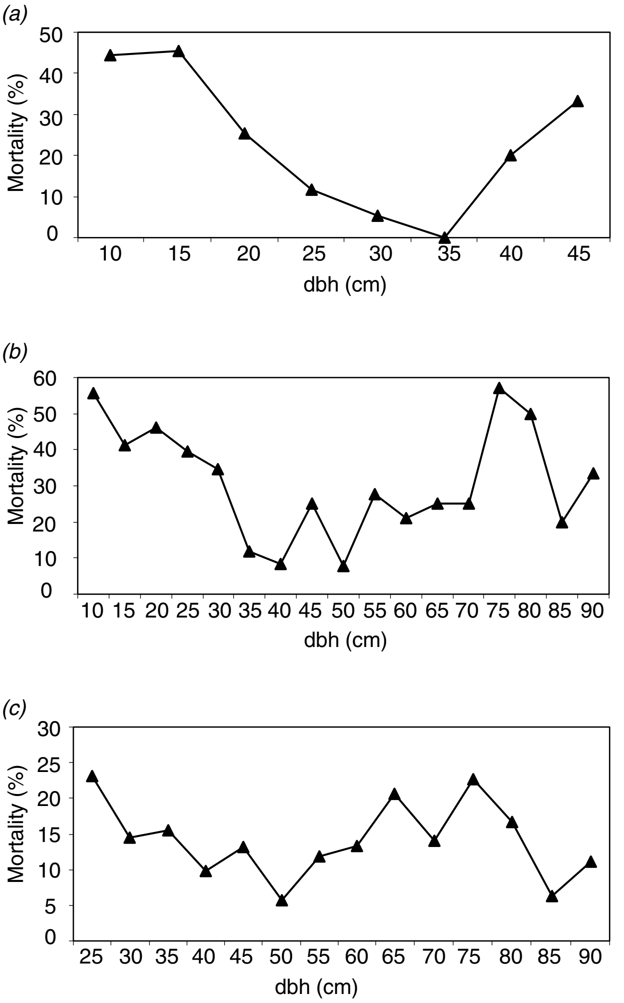

Fig. 2. Observed percent mortality of ponderosa pine 3 years after fire by 5 cm dbh class for three fires in northern Arizona. Sample size range for each dbh class was 3–71 for the Dauber prescribed fire (*a*), 3–48 for the Side wildfire (*b*), and 9–109 for the Bridger-Knoll wildfire (*c*). Data are not shown for dbh classes with <3 trees.

In contrast, crown position did not differ between live and dead trees at the Bridger-Knoll wildfire (Table 3).

Average crown scorch was lowest on the Bridger-Knoll wildfire (27.2%), intermediate on the Dauber prescribed fire (46.0%), and highest on the Side wildfire (55.3%) (Table 2). For all fires, live trees had significantly less crown scorch than dead trees (Table 3). Crown scorch of dead trees was highest on the Dauber prescribed fire (84.8%), with similar levels at the Side and Bridger-Knoll wildfires (68.8% and 63.5%, respectively) (Table 3).

Crown consumption occurred only on the Side and Bridger-Knoll wildfires, and was lower on the Bridger-Knoll wildfire (4.3%) than the Side wildfire (10.3%) (Table 2). Crown consumption on dead trees was nearly equal in the Side and Bridger-Knoll wildfires, and was significantly greater than consumption of live trees at both fires (Table 3). Over

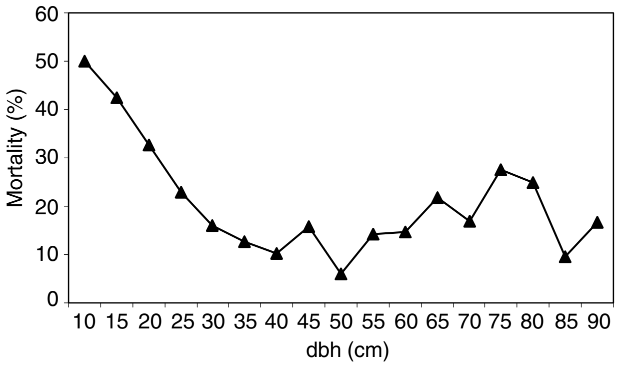

Fig. 3. Observed percent mortality of ponderosa pine 3 years after fire by 5 cm dbh class for data combined over three fires in northern Arizona. Data are not shown for dbh classes with <3 trees.

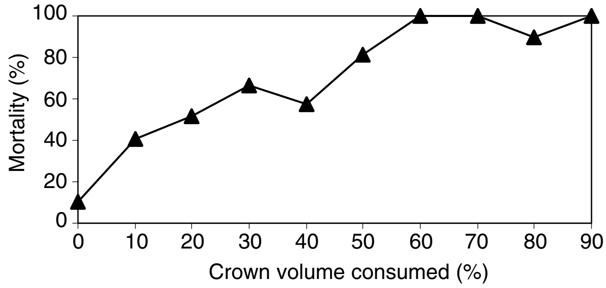

Fig. 4. Observed percent mortality of ponderosa pine 3 years after fire by crown volume consumed for the Side and Bridger-Knoll wildfires in northern Arizona.

half of all dead trees in the Side (55.4%) and Bridger-Knoll (54.3%) wildfires had some crown consumption. While some live trees on both fires experienced consumption, the vast majority of live trees in both fires did not (82.9% Side wildfire; 96% Bridger-Knoll wildfire). Tree mortality was 67% at 30% crown consumption, and 100% at 60% crown consumption (Fig. 4).

Average total crown damage was lowest on the Bridger-Knoll wildfire (31.5%), intermediate on the Dauber prescribed fire (46.0%), and greatest on the Side wildfire (65.6%) (Table 2). For all three fires, total crown damage on live trees was significantly lower compared with dead trees (Table 3). Total crown damage of dead trees was nearly equal across all three fires and ranged from a low of 84.8% on the Dauber prescribed fire to a high of 93.2% on the Side wildfire (Table 3). Total crown damage of live trees was variable among fires, and was greatest on the Side wildfire (52.4%), intermediate on the Dauber prescribed fire (37.5%), and lowest on the Bridger-Knoll wildfire (22.1%) (Table 3). The level of crown damage where tree mortality started was also variable across fires (Fig. 5). However, mortality increased sharply at all fires when total crown damage was 80% or more (Fig. 5).

Windward and leeside bole char varied between the Dauber prescribed fire and the Side and Bridger-Knoll

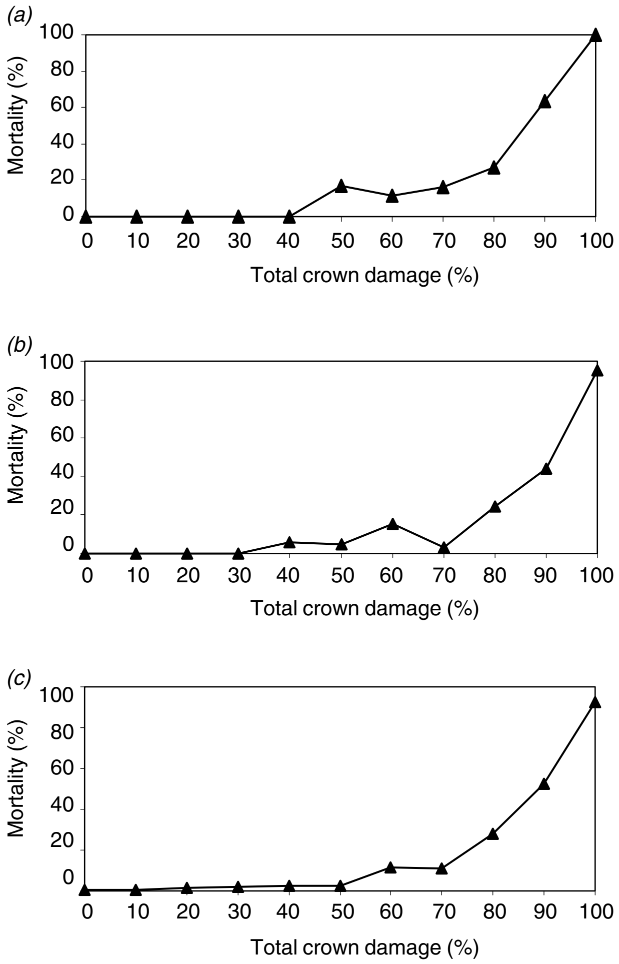

Fig. 5. Observed percent mortality of ponderosa pine 3 years after fire by total crown damage (scorch + consumption) for three fires in northern Arizona. Dauber prescribed fire (*a*), Side wildfire (*b*), and Bridger-Knoll wildfire (*c*).

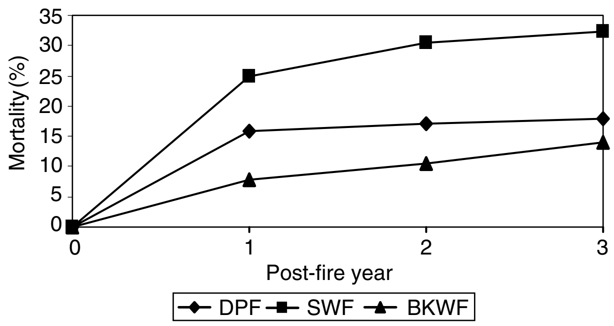

Fig. 6. Observed 3-year post-fire cumulative mortality (%) of ponderosa pine for three fires in northern Arizona. DPF, Dauber prescribed fire; SWF, Side wildfire; BKWF, Bridger-Knoll wildfire.

wildfires, with the lowest bole char height on the Dauber prescribed fire (Table 2). Average bole char height was similar on the Side and Bridger-Knoll wildfires (Table 2). However, variation in bole char height among trees was highest at the Bridger-Knoll wildfire (0–36 m), intermediate at the Side wildfire (0–20 m), and lowest at the Dauber prescribed fire (0–8 m) (Table 2). For all fires, both windward and leeside bole char height were lower for live versus dead trees (Table 3). Bole char severity ratings (lee and windward sides) were highest on the Side wildfire, intermediate on the Bridger-Knoll wildfire, and lowest on the Dauber prescribed fire (Table 2). For all fires, both measures of bole char severity were significantly greater for dead than live trees (Table 3). Average ground char rating was greatest at the Side wildfire, intermediate at the Dauber prescribed fire, and lowest at the Bridger-Knoll wildfire (Table 2). For all fires, live trees had significantly less ground char than dead trees (Table 3).

Insect activity on trees at the Side wildfire was 2.8 times higher than at the Bridger-Knoll wildfire, and over four times higher than at the Dauber prescribed fire (Table 2). Across all fires, live trees had a significantly lower insect rating than dead trees (Table 3). Insect rating for the Side wildfire was also highest among sites for both live and dead trees; the rating for dead trees at the Side wildfire was two to three times higher than the Bridger-Knoll wildfire and Dauber prescribed fire (Table 3).

Very few dead trees suffered logging damage or soil disturbance on the Side and Bridger-Knoll wildfires. For the Side wildfire, 98% of the dead trees had no logging damage and 97% of the dead trees had no soil disturbance. On the Bridger-Knoll wildfire none of the dead trees had logging damage, and 71.5% had no soil disturbance. Salvage logging did not occur on the Dauber prescribed fire.

Differences in tree mortality among fires and years

Mortality differed significantly ($P \leq 0.001$) among fires based on a Pearson χ^2 distribution test with two degrees of freedom. Three years after fire, mortality was much higher at the Side wildfire (32.4%) than at the Bridger-Knoll wildfire (13.9%) and Dauber prescribed fire (18.0%) (Fig. 6). Percentage change in mortality between years 1 and 3 after fire varied from 13.9% at the Dauber prescribed fire, 29.6% at the Side wildfire, to 75.9% at the Bridger-Knoll wildfire. For the Dauber prescribed fire and Side wildfire, 95% and 94% of 3-year post-fire mortality occurred by the end of the second year. In contrast, only 76% of 3-year post-fire mortality occurred by the end of the second year in the Bridger-Knoll wildfire. Thus, tree mortality appears to have stabilized after year 2 post-fire at the Dauber prescribed fire and Side wildfire, but not at the Bridger-Knoll wildfire (Fig. 6).

Mortality models

Multivariate logistic regression models were developed for each fire and the combined data set to model individual tree

Table 4. Logistic regression coefficients (±1 standard error), −2 Log Likelihood ratio statistic (−2LL), and receiver operating characteristic curve value (ROC) for selected ponderosa pine mortality prediction equations following fire in northern Arizona for the Dauber prescribed fire (Fall), Side wildfire (Spring), Bridger-Knoll wildfire (Summer), and combined data set

All model coefficients are significantly different from zero at $P \leq 0.10$ except those indicated by an asterisk (*). Pm, = predicted probability of mortality; β_0 = intercept, β_n = model coefficients; TCD, total crown damage (scorch + consumption) (0–100); CHUPS, bole char severity rating leeward side (0, none; 1, light char; 2, medium char; 3, heavy char); DBH, diameter at breast height (cm)

	Model form: $Pm = 1/[1 + \exp(-(\beta_0 + \beta_1\text{TCD} + \beta_2\text{CHUPS}))]$				
	β_0	β_1	β_2	−2LL	ROC
Dauber prescribed fire	-13.0829 ± 2.1830	0.1107 ± 0.0201	1.8879 ± 0.5011	97.97	0.94
Side wildfire	-13.6452 ± 1.8584	0.1268 ± 0.0179	0.9914 ± 0.3115	206.76	0.93
Bridger-Knoll wildfire	-9.9728 ± 1.7900	0.0852 ± 0.0084	1.3421 ± 0.7507	281.59	0.96
Combined data Set	-9.7149 ± 0.0070	0.0921 ± 0.2029	0.8082 ± 0.7649	609.96	0.95
	Model form: $Pm = 1/[1 + \exp(-(\beta_0 + \beta_3\text{DBH} + \beta_4\text{TCD}))]$				
	β_0	β_3	β_4	−2LL	ROC
Dauber prescribed fire	-6.1425 ± 1.7209	$-0.0648^* \pm 0.0408$	0.0912 ± 0.0171	113.32	0.92
Side wildfire	-14.8856 ± 2.1338	0.0348 ± 0.0106	0.1554 ± 0.0216	204.96	0.93
Bridger-Knoll wildfire	-8.2851 ± 0.9354	0.0169 ± 0.0087	0.0875 ± 0.0086	281.16	0.96
Combined data set	-8.7456 ± 0.6729	0.0128 ± 0.0050	0.0960 ± 0.0070	619.97	0.95

mortality. For all fires and the combined data set, models using three to five variables (not including intercept) provided little improvement in prediction over models using two variables based on ROC and −2LL values. Selected two-variable models are shown in Table 4.

For the Dauber prescribed fire, the model using total crown damage (TCD) and bole char severity on the leeward side (CHUPS) as independent variables was the best two-variable model for this data set (Table 4). Modeled probability of mortality increased as CHUPS and TCD increased (Fig. 7). Moreover, high levels of CHUPS reduced levels of TCD associated with the onset of tree mortality. A model combining TCD and dbh, the most common set of independent variables in other ponderosa pine mortality studies (Harrington and Hawksworth 1990; Saveland *et al.* 1990; Harrington 1993; Stephens 1995), was not optimal based on its high −2LL value (113.32) (Table 4). Also, the dbh coefficient for this model was not significant ($P = 0.113$). This model predicted higher probability of mortality for smaller diameter trees at equal levels of crown damage for the Dauber prescribed fire (Fig. 8).

At the Side wildfire, the model using TCD and CHUPS as independent variables was again the best two-variable model (Table 4). Consistent with the Dauber prescribed fire, predicted tree mortality increased as CHUPS and TCD increased at the Side wildfire (Fig. 7). The model using TCD and DBH as independent variables predicted higher rates of mortality for larger trees than smaller trees at equivalent levels of crown damage (Fig. 8). A second model using squared terms for TCD and dbh predicted 100% mortality for all trees with dbh $\geq$ 70 cm regardless of the level of crown damage.

For the Bridger-Knoll wildfire, the preferred model again used TCD and CHUPS as independent variables (Table 4), and consistent with the other fires, predicted an increase in tree mortality as TCD and CHUPS increased (Fig. 7). Similar to the Side wildfire, the model using TCD and dbh predicted that larger trees had a higher probability of mortality than smaller trees at equivalent levels of crown damage for the Bridger-Knoll wildfire (Fig. 8).

For data pooled over all fires, models were developed with and without season of fire occurrence as a categorical value. Based on −2LL and ROC values, models without season performed better and are easier to use because of a smaller number of variables. Consistent with the analyses of data from individual fires, the model using TCD and CHUPS as independent variables (Table 4) performed well and predicted an increasing probability of mortality as both measures of fire damage increased (Fig. 9). A model using dbh and TCD for the combined data predicted higher mortality of large versus small trees at equivalent levels of crown damage (Fig. 9).

We also used logistic regression models to understand factors causing the U-shaped pattern of tree mortality versus tree dbh (Figs 2 and 3). Initially, we ran logistic regression models for three dbh classes (small–high mortality, medium–low mortality, large–high mortality) for each fire. Small sample size for some dbh classes within individual fires limited this approach. Consequently, we ran logistic regression models on data pooled over all fires for the following dbh classes (Fig. 3): small trees, 10–20 cm (high mortality), medium-sized trees, 30–50 cm (low mortality), and large trees, 65–80 cm (high mortality). The two factors most strongly associated with

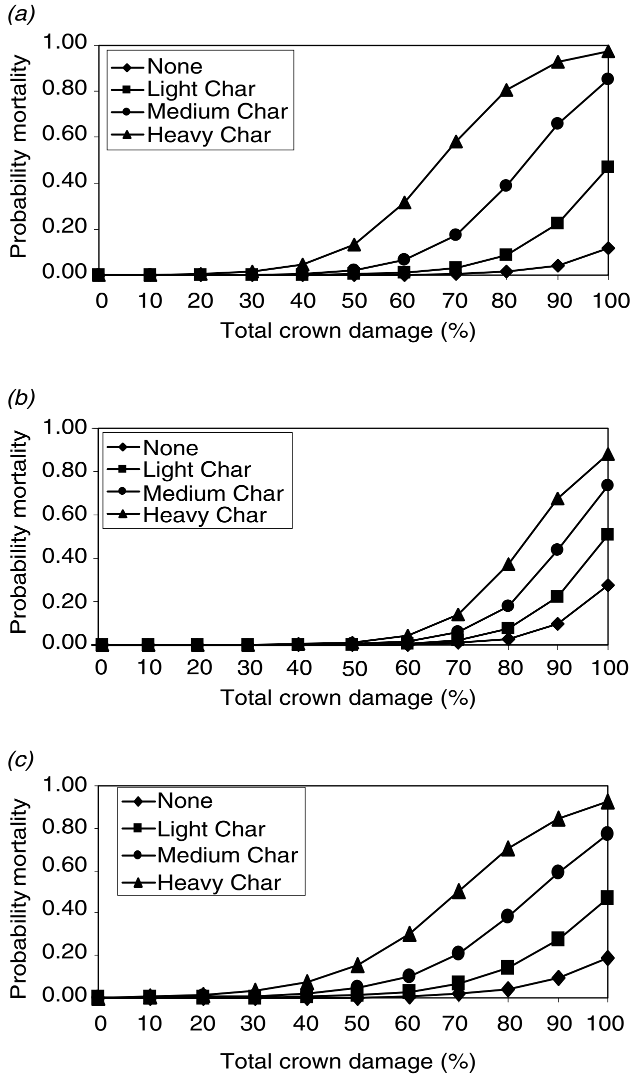

Fig. 7. Distribution of predicted probability of ponderosa pine mortality for logistic regression models using total crown damage and bole char severity rating leeward side (CHUPS) (none, light char, medium char, heavy char) for three fires in northern Arizona. Dauber prescribed fire (*a*), Side wildfire (*b*), and Bridger-Knoll wildfire (*c*). See Table 4 for model form.

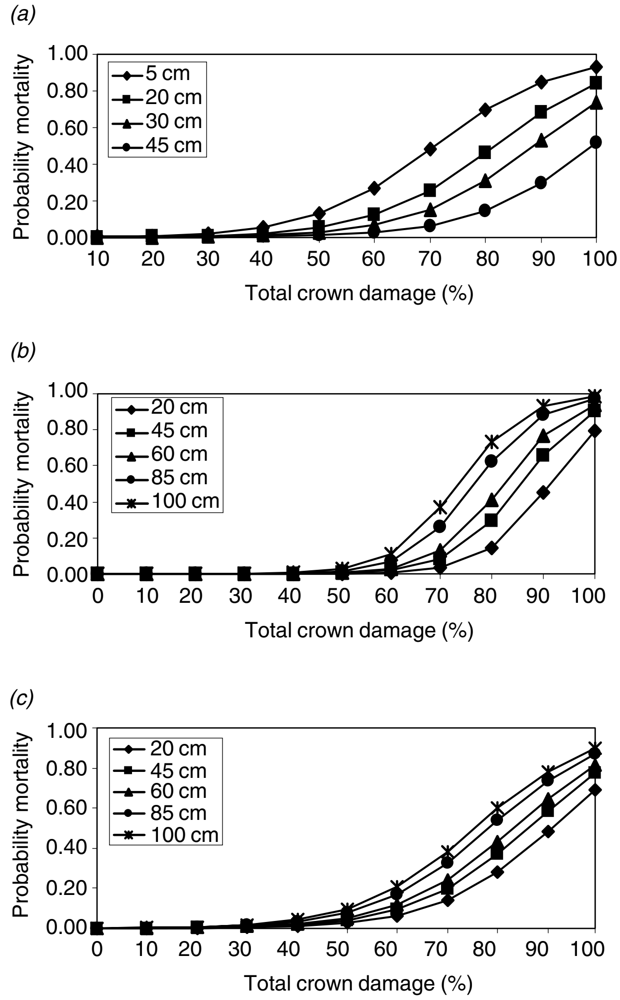

Fig. 8. Distribution of predicted probability of ponderosa pine mortality for logistic regression models using total crown damage and diameter at breast height (dbh) for three fires in northern Arizona. Dauber prescribed fire (*a*), Side wildfire (*b*), and Bridger-Knoll wildfire (*c*). See Table 4 for model form.

tree mortality for small trees were bole char severity on the windward side ($P < 0.001$) and insect rating ($P = 0.001$); mortality was positively related to these factors. In contrast, the two factors most strongly associated with tree mortality for medium (30–50 cm dbh) and large (65–80 cm dbh) trees were total crown damage ($P < 0.001$) and insect rating ($P < 0.001$); mortality was positively related to these factors. Total crown damage was also significantly ($P = 0.001$) related to mortality of small trees, but it was the fourth most important factor. Thus, we found evidence that bole char was a more important cause of mortality for small trees, and that crown damage was a stronger cause of mortality for medium-sized and large trees.

Discussion

For all fires, models of tree mortality using dbh and total crown damage were developed similar to other studies (Harrington and Hawksworth 1990; Saveland *et al.* 1990; Harrington 1993; Stephens 1995). Other studies have used dbh to predict bark thickness, which was used in combination with crown scorch to predict tree mortality (Reinhardt and Ryan 1988; Ryan and Reinhardt 1988; Finney 1999). The coefficients for bark thickness and dbh in such models are usually negative, which indicates a lower probability of mortality for larger trees. However, in the Side wildfire, Bridger-Knoll wildfire, and combined data over all fires, models using dbh and total crown damage resulted in a positive dbh coefficient, suggesting higher probability of mortality for larger than smaller trees at a similar level of crown damage (Figs 8 and 9). This is contrary to other studies

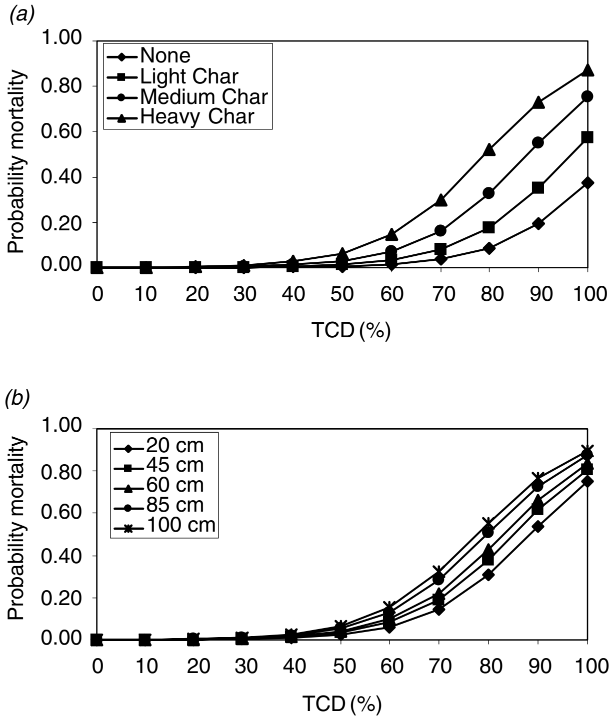

Fig. 9. Distribution of predicted probability of ponderosa pine mortality for logistic regression models using total crown damage (TCD) and bole char severity rating leeward side (CHUPS) (none, light char, medium char, heavy char) (*a*), and total crown damage (TCD) and diameter at breast height (DBH) (*b*) for data combined over three fires in northern Arizona. See Table 4 for model form.

in ponderosa pine where dbh (not bark thickness) was used as an independent variable with a measure of crown damage (Saveland *et al.* 1990; Harrington 1993; Stephens 1995). Only the Dauber prescribed fire, where trees were smallest of all fires, produced a model with a negative coefficient for dbh and a lower probability of mortality for larger trees (Fig. 8).

We were concerned about the suitability of our models that included dbh as an independent variable because the predicted mortality trend with dbh did not reflect the observed U-shaped dbh–mortality distributions and, in some cases, dbh was not a statistically significant variable. Diameter may not be an appropriate predictor of tree mortality because of the combinations of fire behavior, tree morphology, tree size, and tree phenology that occurred in our study. Likewise, other investigators also have found dbh to be weakly related to tree mortality prediction functions after fire for: western larch (*Larix occidentalis*), sugar pine (*Pinus lambertiana*), pignon pine (*Pinus pinea*), ponderosa pine, and giant sequoia (*Sequoiadendron giganteum*) (Lambert and Stohlgren 1988; Swezy and Agee 1991; Ryan *et al.* 1994; Stephens 1995; Mutch and Parsons 1998). In these studies, other tree damage or fire behavior variables were better predictors of tree mortality than dbh.

Where dbh was an important predictor of tree mortality after fire in ponderosa pine, dbh ranged between 5 and 70 cm (Saveland *et al.* 1990; Harrington 1993; Stephens 1995; Finney 1999). Interestingly, this dbh range is close to the range at the Dauber prescribed fire, where the dbh coefficient was negative showing lower probability of mortality for larger trees. Thus at the Dauber site, larger trees likely had a lower probability of mortality because of thicker bark and perhaps higher vigor than smaller trees (Peterson and Ryan 1986; Reinhardt and Ryan 1988; Ryan and Reinhardt 1988; Ryan 1998). Also, our logistic regression models for data pooled over all fires suggested that bole scorch is a more important source of mortality for small tree versus large trees. This result is likely due to the thin bark of small trees.

Although contrary to most studies of conifers (Bevins 1980; Wyant *et al.* 1986; Reinhardt and Ryan 1988; Ryan and Reinhardt 1988; Saveland *et al.* 1990; Harrington 1993; Regelbrugge and Conard 1993; Stephens 1995), the U-shaped dbh–mortality distribution present at all fires in our study has also been reported in two other studies of ponderosa pine (Swezy and Agee 1991; Finney 1999). This trend has also been reported for Scots pine (*Pinus sylvestris*) following prescribed burning in northern Sweden (Linder *et al.* 1998). What reasons may account for the U-shaped dbh–mortality distribution and higher levels of mortality in larger trees after fire? First, large trees may have previous fire scars, lightning scars, and damage from insects and fungi that enable fire to extend deeper into the cambium as well as higher up the bole causing higher levels of crown damage (Weaver 1943; Linder *et al.* 1998). Second, large trees may have higher fuel loads at their base and thus experience hotter root or cambial temperatures than small trees (Sackett and Haase 1998; Finney 1999). Third, large old trees may have low amounts of carbohydrate available to replace or repair damaged tissues because of high respiration rate, low photosynthetic rate, or large carbon allocation to roots and mycorrhizae (Ryan 1990; Ryan *et al.* 1997; Finney 1999). Fourth, large trees with thick phloem may be a better food source for phloem feeding insects such as bark beetles that can cause tree mortality (Finney 1999). Our logistic regression models suggested higher tree mortality for larger than smaller trees at a given level of total crown damage under the fire behavior and intensity that occurred at the Side and Bridger-Knoll wildfires. This is consistent with the idea that the largest trees are physiologically disadvantaged to survive heavy crown damage by fire.

Our results are similar to other studies of ponderosa pine that have documented increased tree mortality with increasing crown scorch or damage (Herman 1954; Lynch 1959; Dieterich 1979; Potter and Foxx 1984; Wyant *et al.* 1986; Harrington 1987, 1993; Reinhardt and Ryan 1988; Ryan and Reinhardt 1988). In our study the threshold level of total crown damage (scorch + consumption) at which ponderosa pine mortality began (70%) was fairly consistent among fires; mortality sharply increasing when total crown damage was

80% or more. For ponderosa pine, this threshold has been quite variable in different studies: 60% crown scorch for a summer wildfire in Arizona (Herman 1954), 67% for a fall prescribed fire in Arizona (Davis *et al.* 1968), 90% crown scorch for both dormant and growing season prescribed fires in south-western Colorado (Harrington 1993), 90% crown scorch for a summer wildfire in Washington State (Lynch 1959), and 100% crown scorch for a June wildfire in New Mexico (Potter and Foxx 1984). Moreover, less crown scorch or damage has been reported to kill ponderosa pine in growing season fires compared with dormant season fires (Dieterich 1979; Harrington 1993).

We found distinct differences in cumulative tree mortality after 3 years among the three fires in our study. Many factors could cause such differences, including variations in tree physiological activity, carbohydrate storage, growth phenology, as well as differences in site quality, tree size, tree vigor, fire intensity, and fire behavior. Tree mortality three years post-fire was highest on the Side wildfire (32.4%) that occurred in early May prior to budbreak, lower on the Dauber prescribed fire (18.0%, early September), and lowest on the Bridger-Knoll wildfire (13.9%, late June). Swezy and Agee (1991) also found higher ponderosa pine mortality following a late June versus a September prescribed fire.

What factors may explain the difference in cumulative tree mortality among fires in our study? First, the ranking of tree mortality by fire corresponds to the ranking of tree damage; crown scorch, crown consumption, total crown damage (scorch + consumption), and ground char severity were highest in the Side wildfire, followed by the Dauber prescribed fire and the Bridger-Knoll wildfire. Thus, we believe that differences in the level of fire damage to trees, and perhaps insect infestation levels, among our sites offer the simplest explanation for seasonal differences in tree mortality.

Factors unique to the Side wildfire may have led to high rates of tree mortality. The Side wildfire occurred in early May before budburst, but during the period when root growth is often occurring for ponderosa pine in northern Arizona (Schubert 1974). Large reductions in fine root biomass after spring fires have been reported for ponderosa pine (Grier 1989; Swezy and Agee 1991). Also, low duff and soil moisture may have contributed to tree mortality at the Side wildfire. The Side wildfire occurred during an extreme drought, and soils at this site are well drained because of their coarse texture. Dry soils and possibly low duff moisture on this site may have caused deeper heating of the soil profile, and consequently more root and cambial damage than at the other fires (Ryan and Frandsen 1991; Hartford and Frandsen 1992; Sackett and Haase 1998). Because spring root production for ponderosa pine is important in facilitating water and nutrient uptake, loss of fine root biomass due to fire under extreme drought conditions may have negatively affected nutrient and water uptake, photosynthesis, carbohydrate storage, and thus tree survival.

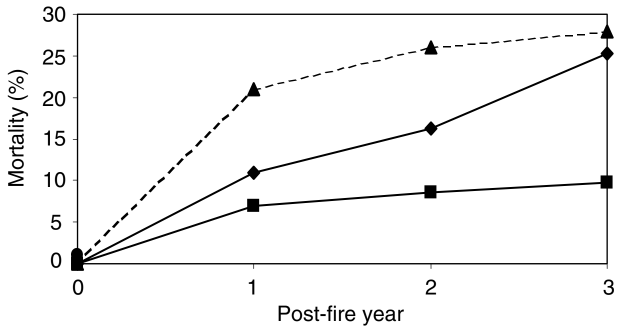

Fig. 10. Percent cumulative ponderosa pine mortality for three post-fire years for the Bridger-Knoll wildfire (solid lines). Data for a summer prescribed fire from Harrington (1993) are represented by dashed line. For the Bridger-Knoll wildfire, squares represent lightly burned areas; diamonds represent severely burned areas.

Harrington (1993) concluded that ponderosa pine trees damaged by fire during the summer prior to bud set when root and diameter growth are still active are most susceptible to mortality. However, in our study, trees on the summer Bridger-Knoll wildfire suffered the lowest mortality among all fires. Three-year post-fire mortality on the Bridger-Knoll wildfire (13.9%) was almost half the 3-year post-fire mortality (28%) reported by Harrington (1993) for a summer prescribed fire in south-western Colorado. Lower than expected tree mortality on the Bridger-Knoll wildfire may be explained by low levels of fire damage or favorable site conditions. However, another explanation is that tree mortality in large trees may occur over time periods longer than 3-years post-fire. On the Willis wildfire on the North Kaibab Ranger District in Arizona (June of 1987), tree mortality did not stabilize until 6 years post-fire (Dave Steffenson, personal communication). Sackett and Haase (1998) reported that mortality of old-growth ponderosa pine in a long-term prescribed fire study in northern Arizona did not appear until several years post-fire and continues 20 years after the initial burning took place. Consistent with these findings, mortality on the Bridger-Knoll wildfire increased between years 2 and 3 post-fire, with only 76% of 3-year post-fire mortality occurring in year 2. Thus, tree mortality caused by the summer Bridger-Knoll wildfire may continue in the future.

Data collected on the Bridger-Knoll wildfire can be separated based on fire severity into areas that burned severely and areas that burned less severely. Forty-eight percent of total mortality on the Bridger-Knoll wildfire occurred in the severe burn areas, yet these areas account for only 26.5% of the sampled area. Interestingly, year 3 mortality rates in severely burned areas of the Bridger-Knoll wildfire are comparable to those for the summer prescribed fire in Harrington's (1993) study (Fig. 10). Thus, the difference in year 3 mortality of ponderosa pine for summer fires in our study and Harrington (1993) may have resulted from spatial variation in fire severity on the Bridger-Knoll wildfire, and differences in tree size and site conditions between studies, as well as latent mortality of old trees from cambial and or root damage (Ryan and Frandsen 1991; Swezy and Agee 1991; Sackett and Haase 1998) in our study.

Conclusions

This study highlights many of the problems of opportunistic fire studies. The lack of pre-fire data on fuels and direct measurements of fuel consumption and fire intensity at the plot or tree level required us to infer these characteristics using other models or by retrospective observations. While difficult, future research in this area should attempt to include more accurate measures of fuel consumption and fire behavior. Future research should also examine the effect of spring fires on ponderosa pine mortality in the south-western US, as mortality can be high at this time of the year, especially during droughts.

We found that logistic regression models using total crown damage (scorch + consumption) and bole char severity as independent variables adequately modeled ponderosa pine mortality following three fires that occurred on different sites and in different seasons in northern Arizona. The amount of total crown damage associated with the onset of tree mortality decreased as bole char severity increased. A U-shape dbh–mortality distribution occurred at all three fires, suggesting higher mortality in the smallest and largest trees compared with medium size trees.

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