Trees (2011) 25:679–688
DOI 10.1007/s00468-011-0545-y

ORIGINAL PAPER

Effects of prescribed burning on leaves and flowering of *Quercus garryana*

David H. Peter · James K. Agee · Douglas G. Sprugel

Received: 1 August 2010 / Revised: 17 January 2011 / Accepted: 20 January 2011 / Published online: 13 February 2011

Abstract Many woodland understories are managed with prescribed fire. While prescribed burns intended to manipulate understory vegetation and fuels usually do not cause excessive tree mortality, sublethal canopy damage may occur and can affect tree vigor and reproductive output. We monitored *Quercus garryana* trees in western Washington, USA with multiple canopy thermocouples during three prescribed burns. Peak temperatures recorded in tree canopies ranged from 36 to 649°C. We assessed leaf damage immediately after burning, and flower, leaf and acorn production in the following year in the vicinity of each thermocouple. Leaf scorch first occurred with peak thermocouple temperatures around 45°C, was variable up to 75°C, but above 75°C all leaves were killed. Buds, including their reproductive and leaf organs were more resistant to heat damage than leaves, but leaf scorch had predictive value in forecasting bud organ damage. Staminate and pistillate inflorescences and acorn production per bud decreased and bud mortality increased with maximum thermocouple temperature. In two burns where the highest peak temperatures reached 137°C, there was no difference in leaf production between burned and control plots in the spring following burning. However, no staminate or pistillate inflorescences were produced when thermocouple peak temperatures went above 55 or 68°C, respectively. While heat damage to bud organs was detected, production of reproductive organs was also curtailed at temperatures lower than could reasonably be attributed to heat damage. Thus, it is probable that some other fire-related factor, possibly smoke, was also involved.

Keywords *Quercus garryana* · Oregon white oak · Prescribed fire · Fire effects · Buds · Foliage

Communicated by L. Gratani.

D. H. Peter (✉)
Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512-9191, USA
e-mail: dpeter@fs.fed.us

J. K. Agee · D. G. Sprugel
School of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195, USA

Introduction

Prescribed fire is a useful tool for control of woody vegetation in western Washington *Quercus garryana* Douglas ex. Hook. var. garryana (Oregon white oak) woodlands, which originally had mostly graminoid dominated understories due to frequent burning by Native Americans (Habeck 1961; Taylor and Boss 1975; White 1980; Agee 1993; Boyd 1999; Leopold and Boyd 1999). Grass fires move rapidly, doing little damage to oak trees protected by mature bark (Agee 1993). Without fire, the understory changes from grass to shrub domination and conifers increasingly dominate the overstory (Agee 1993). Oregon white oak does not survive in the shade of taller conifers (McCulloch 1940; Silen 1958; Stein 1990), but many shrubs do, which can result in greater fuel loading, longer flame lengths, and higher temperatures when burned. Thus, there is greater potential for crown damage as woody vegetation increases. However, little is actually known about how fires affect Oregon white oak canopies. White oaks initiate floral and vegetative primordia in buds 1 year prior to flowering (Johnson and Shifley 2002; Peter 2006). Thus, floral, leaf and vegetative primordia that are present in the buds are vulnerable to damage during summer fires.

In fires, heating occurs with rapidly fluctuating pulses of hot gasses against a background of fluctuating radiant heat. Flame temperatures have been measured at 600–1,093°C (Dickinson and Johnson 2001; Agee 1993; Martin et al. 1969; Hare 1961). Due to turbulent mixing with cooler air, temperatures cool rapidly with height, so maximum temperatures in an Appalachian hardwood fire that were 600–1,000°C near the ground were only 200°C at 1.5 m and 100°C at 2.6 m (Nelson and Simms 1914). In addition, even though temperatures exceeded 316°C at 0.5 m and 232°C at 1.5 m in a Florida oak scrub fire (Abrahamson and Abrahamson 1996), 31% of the area failed to exceed 66°C. It is apparent that temperature and heat exposure vary substantially in fires, but even if the fire environment is extreme near the ground, tree canopy environments above the fire may be quite different. Thus, to predict fire effects on trees it is important to understand the tolerance of the more exposed and vulnerable tissues (leaves and buds) to fire.

Tissue and cell necrosis occurs at exponentially increasing rates as temperatures rise (Dickinson and Johnson 2001; Peter et al 2009). Temperatures of 50–55°C induce tissue damage or death in plants (Larcher 1983; Seidel 1986; Colombo and Timmer 1992; Kolb and Robberecht 1996; Levitt 1956). Lower temperatures (35–45°C) adversely affect important physiological functions and can be lethal if sustained (Taiz and Zeiger 1998; Levitt 1956; Thimann and Kaufman 1958).

Effects of fire on flowering and acorn production in oaks have received little study. Sugihara and Reed (1987) found more than half of acorns on the ground after a light grass fire failed to germinate, but little canopy damage occurred and acorns in the trees were unaffected. Abrahamson and Layne (2002) found that acorn production in two shrubby species of Florida oaks returned to normal in the second season after burning. Oaks recover from extensive bud mortality with epicormic sprouting and epicormic buds do not have floral primordia (Wilson and Kelty 1994; Fontaine et al. 1998). The first buds with floral primordia were produced at the end of the first growing season producing the first acorn crop at the end of the second season.

Prescribed burning is commonly carried out with little lasting canopy damage. We asked if there were less obvious consequences of burning in terms of reproduction. Because there is greater regularity in flowering than in acorn production (Johnson and Shifley 2002), we assessed fire damage and mortality at the bud and leaf level, with the objective of relating these findings to acorn production. We were not specifically interested in the temperatures that cause tissue damage as those are better studied under laboratory conditions, and even carefully controlled prescribed burns are highly complex heating events. Rather, we describe the thermal environments around leaves and buds, and the underlying fire and fuel conditions that cause canopy damage including that which was not visibly obvious. We asked if flowering, acorn, and leaf production were affected in *Quercus garryana* canopies exposed to low severity surface and understory fires (Agee 1993) and what fire intensities might cause such damage. We also asked what heating conditions produced visible leaf damage and if visible leaf damage had value in predicting bud damage.

Methods

Study site

Data were collected from three prescribed underburns at Fort Lewis Military Installation, WA, USA (Table 1). Two burns (in August 2002) were adjacent to each other at Weir Prairie (here referred to as east and west Weir Prairie units) and one burn (in August 2003) was at 13th Division Prairie at a site here referred to as Madigan (Peter 2006). These sites are in oak stands adjacent to grassy prairies with histories of underburning. All the three burn units had about 60% tree cover of mostly Oregon white oak with a few Douglas-fir trees.

Sample tree selection

At Weir Prairie, oaks >30 cm diameter at 1.3 m were randomly selected: six trees with grassy and six trees with shrubby understories (half in the east and half in the west unit). Twelve trees with similar characteristics were randomly selected from a nearby control stand that had similar tree and vegetation characteristics. Tree understories were considered grassy if they had <30% shrub cover and were otherwise graminoid-dominated. Shrub-dominated understories had more than 30% shrub cover. At Madigan, there were three trees with shrubby and one with a grassy understory.

Temperature monitoring

Terminal buds in the outer canopy of the underburned sample trees at Weir Prairie were monitored with 191 type J iron-constantan thermocouples. The listed accuracy was ±2.2°C, but a sub-sample of 24 randomly selected thermocouples tested in a water-bath from 5 to 35°C was accurate to 0.2°C. Thirteen to seventeen thermocouples were installed in the canopy of each sample tree at Weir Prairie. One thermocouple was installed at a terminal bud cluster at the lowest canopy edge on each cardinal direction and at each 45° division. Four more were installed about 1/3 of the distance to the top of the tree from each cardinal

Table 1 Dates, times and conditions of underburning

	East Weir unit	West Weir unit	Madigan site
Date of burn	8-9-2002	8-21-2002	8-20-2003
Size of burned area (ha)	1.7	1.8	2.4
Time of lighting	12:35	13:30	10:30
End of flaming	13:05	13:55	11:05
Fire intensity (Agee 1993)	Surface	Surface-understory	Surface-understory
Approximate rate of spread (m/s)	0.02	0.03	0.04
Typical flame lengths (m)	<0.5–1.0	0.5–2	1–5
Fire residence time under a sample tree (min)	4–9	2–9	2–7
Peak canopy temperatures (°C)	45–69	36–137	171–649
Total time over 40°C (s)	0–144	0–282	17–221
Fuel moisture (10 h lag)	11%	11.5%	
Temperature at start of fire (°C)	28	21	26
Relative humidity at start (%)	52	40	52
Wind speed (km/h)	2.1–6.0	2.9–3.2	4.8–9.7
Wind direction	NNE-NW	S-SE	N-NE
Mean temp. prev. 7 days (°C)[a]	15	18	19
Total precip. prev. 7 days (cm)[a]	0.26	Trace	0.0

[a] From Olympia, WA airport weather station 15 km NW of Weir Prairie and 32 km west of Madigan (Western Region Climate Center 2004)

thermocouple and four more about 2/3 up also on cardinal directions. One thermocouple was installed at the highest point of each tree. Asymmetric canopies sometimes lacked buds at a potential thermocouple location, so no thermocouple was installed at that location leaving some trees with fewer than 17 thermocouples. Thermocouples were attached to the branch such that the tip was along side, but not in contact with the terminal bud cluster. Data recording (with a Campbell CR-10x data recorder) began prior to the burn and continued at 2 s intervals until the entire unit was burned. At Madigan, four thermocouples were installed along the lower canopy edge on open grown sides of each tree at randomly selected azimuths. The recording interval was 1 s.

We report peak canopy temperatures, which are the maximum temperatures caused by bursts of hot gasses rising turbulently through the canopy. The duration of the peak begins when the recorded temperature rises above 40°C and ends when it returns to 40°C. We refer to this entire interval as a "peak", which we describe with its maximum temperature and total duration.

Due to a data recording programming error, temperatures above 68°C were not recorded at Weir Prairie. Three canopy thermocouples (out of 191) recorded "over-limit" values. The over-limit intervals were a few seconds in duration, except for one 78 s interval. Over-limit peak temperatures were estimated from prescribed burn data obtained in the 2003 Madigan burn using some of the same thermocouples and reprogrammed data recorders (Peter 2006). Data from below 68°C up to 550°C were used to derive a linear regression of the $\log_{10}$ of peak temperature on total time under the curve above 68°C ($R^2 = 0.76$, $P < 0.01$). Data from the thermocouple with the 78 s interval was not used in statistical analyses.

Tree canopy damage assessments

Several kinds of leaf scorch were noted after burning. Light scorch appeared as small spots, patches, or whole leaves of apparently dead, drab olive-green tissues. Moderate scorch was indicated by brown leaves and extreme scorch by blackened or incinerated leaves.

Non-destructive bud sampling occurred after bud break in the year following the burn. The same buds were used to count inflorescences and leaves as they emerged in the spring. Live and total acorns produced out of these same buds were counted later in the summer. Live acorns are acorns that matured. Total acorns included live acorns, and those which had aborted, but not fallen presumably due to the droughty conditions prevalent in 2003.

Five thermal regimes were identified based on degree seconds above 40 or 50°C (Table 2) from the 191 Weir Prairie thermocouples. Degree seconds are the product of the average temperature over 40 or 50°C times the number of seconds the temperature remained above that level. Buds within a 0.5 m spherical radius of the thermocouple were considered to reside within the thermal regime of that thermocouple.

Because there were few thermocouples in regimes 1–3, buds were sampled in all of those locations. Due to the large number of thermocouples in the cool regime (regime 4), buds were sampled in 20% of those locations (locations randomly selected). In total, we sampled 90 buds for regime 1, 55 for regime 2, 80 for regime 3, 341 for regime

Table 2 Temperature regime definition and mean characteristics of the five burn regimes used to analyze bud damage in the Weir Prairie burns

Regime	Required degree seconds over		Number of thermocouples	Measured temperature (°C)			Measured degree seconds		
	50°C	40°C		Ambient	Mean maximum	Time (s) over 40°C	Over 40°C	Over 50°C	Over 60°C
1	>1,000	>2,000	4	22.87	65.84	118.3	6,825	3,952	2,637
2	>0 and <1,000	>1,000	7	21.07	52.35	43.7	2,008	297	0
3	0	>1,000	20	24.57	45.80	47.5	2,027	0	0
4	0	<1,000	32	23.73	34.68	2.0	139	0	0
5	0	0	5	26.63	28.84	0.0	0	0	0

Regime 1 hottest, *2* medium, *3* slightly raised, *4* lowest, *5* unburned control

4, and 308 for regime 5. In the control, only four thermocouples were installed in one tree. Thus, three random azimuths were chosen per tree for the sampling of buds at lower, mid and upper third crown positions. At each sample point, six buds or two branch tips (whichever provided the most buds) were evaluated.

Analysis

Trees in the east and west Weir Prairie burns were combined for a larger sample size on the basis of the similarity of the sites and the fires. Since the Madigan site was burned in a different year, under drier conditions and had larger differences in vegetation, fuel, and stand history, it was deemed inappropriate to combine this site's data with the Weir Prairie data in the same analysis.

Statistical analysis was done with SAS 8.01 software (SAS Institute, Inc. 2000) and significance was declared at $\alpha = 0.05$. For data that deviated from normality (assessed with QQ plots), a transformation was sought to normalize the data. Data that deviated from equal error variance assumptions were transformed to alleviate assumption violations, if possible (assessed with Brown and Forsythe's test of homogeneity of error variance). When suitable transformations could not be found non-parametric methods were used.

Several indicators of fire intensity were used to evaluate leaf and bud damage including the maximum temperature recorded by thermocouples, amount of time over 40°C, and degree seconds over 40°C. These indicators are closely correlated, yet none exactly measures what the others do. Degree seconds were useful because time and temperature were combined and the highest peak temperatures over 50°C are important since damage occurs rapidly at these temperatures.

To compare east and west Weir Prairie burn units in terms of fire intensity we used T tests to compare canopy temperature differences by height. To describe how fuel/vegetation characteristics affected the fire environment, we used ANOVA to compare grassy and shrubby understory composition, and temperatures in tree canopies over these understories during burning. Data used to assess fire effects including counts of leaves, inflorescences, acorns, and bud mortality were investigated with Kruskal–Wallis (KW) ANOVA as they were generally not normally distributed. In the later case, Dunn's test was used for locating differences (Zar 1999).

Linear regression was used to measure the strength of relationships and the contribution of individual variables to relationships (SAS Institute, Inc. 2000). Residual plots were examined for structure that would suggest a transformation. When non-linearity existed, transformations were attempted to linearize the response variable.

We present models to predict leaf and bud damage based on the individual thermocouples ($n = 191$), or thermocouples aggregated by 10°C peak temperature classes. Peak temperature class models predict leaf damage over six 10°C temperature classes and bud damage over five 10°C classes. These temperature classes begin at 10°C for leaf damage or 20°C for bud damage (10–20, 20–30, …, 60–70°C). Each temperature class included thermocouples whose highest temperature fell in the class range. Temperature class mean maximum recorded temperature, time above 40°C, and degree seconds above 40°C were independent variables regressed on the mean percent leaf damage by class.

Results

Stand, fire and fire effects characterization

East and west Weir Prairie unit tree cover, sample tree height and height to live crown were similar. Shrubs (most of the live understory biomass), tended to be associated with the tree canopies. The summed cover of all herb species was similar in the grassy (137%) and shrubby (117%) understories, but shrub cover varied by a factor of 5: shrubby understories (79%), grassy understories (14%). There were no significant differences in litter, coarse

woody debris, herb, live or dead shrub biomass between the east and west Weir Prairie units. At Madigan, there was significantly more dead-shrub and herb and less litter biomass than at Weir Prairie.

Conditions of burning at the three sites are compared in Table 1. Canopy temperatures were similar between the east and west burns, but variability and some peak temperatures were greater in the west burn (Fig. 1). Most buds were not exposed to especially high temperatures. Only 7% of the thermocouples recorded temperatures over 50°C and 76% of the thermocouples remained at or below 40°C. Maximum canopy temperatures from 2 to 8 m were not significantly different. Mean east burn maximum temperatures were higher than west burn temperatures at 8–10 m (41°C east, 32°C west) and 10–12 m (39°C east, 32°C west) (t tests $P < 0.01$) due in part to warmer ambient air temperature (28°C during the east burn and 21°C during the west burn). The relationship of the mean maximum temperature to canopy height was significant but weak across both Weir Prairie burns (Table 3, model 1).

Leaf damage

Leaf scorch on Weir Prairie trees was light. Total leaf scorch in the vicinity of each thermocouple was: eight trees 0–3%; one tree each: 8, 9, 12 and 15%. Leaf scorch was highly variable below peak temperatures of about 75°C, however, brief exposure to peak temperatures above 75°C were lethal to leaves and peak temperatures as low as 50°C caused damage (Fig. 2). Light scorch appeared to occur when peaks briefly spiked above 50°C or occasionally at longer exposures above 42°C. Extreme scorch occurred when peaks spiked to 500°C or 600°C.

The percent leaf damage by 10°C maximum peak temperature classes increased with the mean maximum temperature, mean total time above 40°C, and degree seconds over 40°C (Table 3, models 2–4). For an estimate of

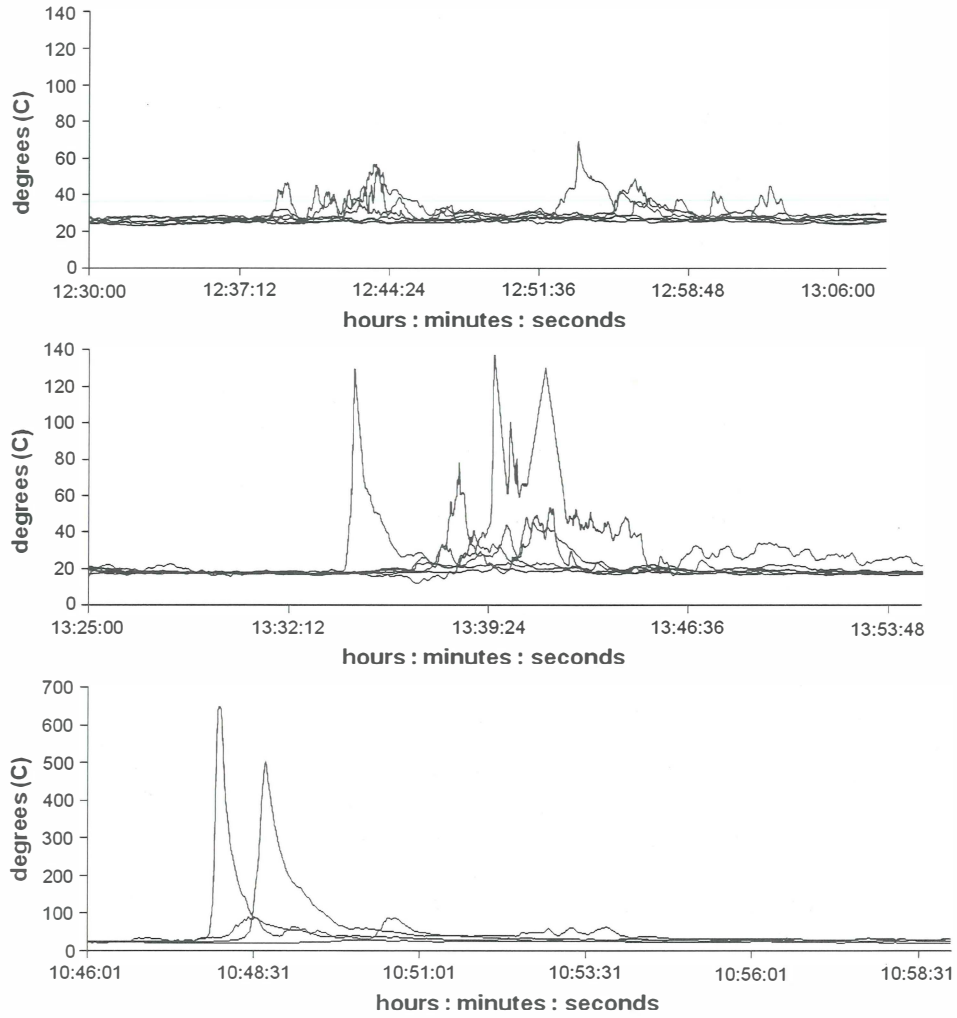

Fig. 1 High canopy temperatures from the three prescribed burns used in the study. Only thermocouples recording the highest temperature for each tree were plotted. *Top* East burn at Weir Prairie. *Middle* West burn at Weir Prairie. The thermocouple with the two highest peaks (in the center) was not used in modeling because the over-limit gap was too large to reliably estimate the peak temperature. *Bottom* Madigan burn. Note the difference in the y axis from the *top* two graphs

Table 3 Canopy damage models for the Weir Prairie data

Model	R^2	Model *P*	Intercept *P*	Variable *P*
1 log(maxtemp1) = 1.704 − 0.015 × height	0.17	<0.01	<0.01	<0.01
2 log(leafdam1) = −0.789 + 0.0374 × maxtemp2	0.98	<0.01	<0.01	<0.01
3 log(leafdam1) = −3.130 + 0.0920 × mean40	1.00	<0.01	<0.01	<0.01
4 log(leafdam1) = 0.533 + 0.0002 × degsec40	1.00	<0.01	<0.01	<0.01
5 males1 = 0.734 −0.011 × maxtemp2	0.84	0.03	0.01	0.03
6 males2 = 0.476 − 0.286 × log(leafdam2)	0.83	0.03	0.01	0.03
7 log(females) = 0.437 − 0.032 × maxtemp2	0.92	0.01	0.18	0.01
8 log(females) = −0.298 − 0.798 × log(leafdam2)	0.88	0.02	0.19	0.02
9 totacorn = 0.237 − 0.005 × maxtemp2	0.94	0.03	0.02	0.03

degsec40 Class mean of degree seconds above 40°C at 2 s intervals for 6 temperature classes, *females* mean number of pistillate inflorescences produced/bud by five temperature classes, *height* height of each canopy thermocouple in m for the east and west burns (n = 191 heights), *leafdam1* mean % of leaf damage around each thermocouple by six temperature classes, *leafdam2* mean % of leaf damage around each thermocouple by five temperature classes, *males1* mean number of males produced/bud by five temperature classes, *males2* num. of staminate inflorescences/bud in 2003 from each of five temperature classes, *maxtemp1* max. temp. for each thermocouple in the canopy of the east and west burns (n = 191 thermocouples), *maxtemp2* mean maximum temperature by 6 temperature classes over all trees (n = 12 trees), *mean40* class mean of sec. above 40°C at 2 s. intervals for six temp. classes (n = 12 trees), *totacorn* mean number of total acorns produced/bud by five temperature classes

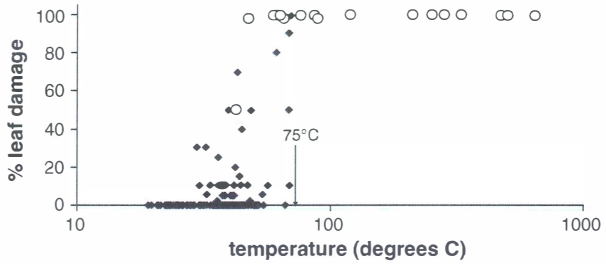

Fig. 2 Peak temperatures associated with leaf kill within a 0.5 m radius of each thermocouple. *Black diamonds* are from Weir Prairie; *open circles* are from Madigan

damage threshold conditions, these models predict 5% leaf damage at a mean maximum temperature of 40°C (2), 19 s over 40°C (3) or 830° s above 40°C (4). The same equations predict complete leaf mortality at (respectively), a mean maximum temperature of 75°C, 134 s over 40°C or 7,335° s over 40°C.

The nature of canopy heating over grassy and shrubby understories differed. Shrubby understories raised canopy temperatures for longer periods, while grassy understories produced short, hot, spikes in canopy temperatures. Thermocouples in trees over shrubby understories had significantly higher mean maximum temperatures (grassy = 36°C, shrubby = 40°C), degree seconds over 40°C (grassy = 416, shrubby = 893), and more time over 40°C (grassy = 9 s, shrubby = 16 s) than trees with grassy understories. However, the means of temperatures over 50°C where most leaf damage occurred (60°C over grassy and 53°C over shrubby understories) were also significantly different. Trees with grassy understories also had significantly more leaf damage and bud mortality than trees with shrubby understories (Table 4).

Bud damage

Little effect on spring leaf production was detected at Weir Prairie. Some leaves were produced from buds in the vicinity of nearly every Weir Prairie thermocouple. There was no difference in the number of leaves produced per bud between the hottest temperature regime and the control (Table 5).

The control produced more staminate inflorescences than any other regime (Table 5). No staminate inflorescences were produced in the vicinity of thermocouples that peaked above 55°C or with more than 3,280° s exposure above 40°C in the highest recorded peak. The mean number of staminate inflorescences per bud decreased with maximum thermocouple temperature (Table 3, model 5). In addition, leaf scorch has predictive value in forecasting reproductive damage. Model 6 (Table 3) predicts that the number of staminate inflorescences produced will go to 0 at around 50% leaf kill.

The control produced significantly more pistillate inflorescences than any other regime (Table 5). No pistillate inflorescences were produced in the vicinity of thermocouples that peaked above 68°C or had a peak with more than 3,201° s exposure above 40°C. Pistillate inflorescences per bud decreased with increasing temperature (Table 3, model 7). Leaf scorch also had predictive value in forecasting pistillate inflorescence production. Model 8 (Table 3) predicts that pistillate inflorescences will decrease as leaf mortality increases, but some pistillate

Table 4 Comparison of mean leaf damage, bud organ production and mortality between six trees with shrubby and six trees with grassy understories at Weir Prairie

Understory	*n*	% leaf damage	Staminate infl./bud	Pistillate infl./bud	Leaves/bud	% dead buds	Total acorns
Grassy	97	7.5	0.3	0.1	3.9	0.2	0.0
Shrubby	93	1.0	0.2	0.1	4.1	0.1	0.0
KW *P*		<0.01	0.06	0.38	0.72	0.04	0.38

Leaf damage includes the % of leaf surface area damaged within a 0.5 m spherical radius of the thermocouple. Counts of primordia and leaves/bud and dead buds are based on buds within a 0.5 m spherical radius of each thermocouple

Table 5 Mean number of organs produced by live buds in 2003 (post fire year 1) at Weir Prairie by thermal regime

Regime	*n*	Staminate inflor.	Pistillate inflor.	Emerging leaves	Live acorns	Total acorns	% dead buds
1 Hottest	59	0a	0.03a	5.34bc	0	0a	34c
2 Hot	37	0.08a	0.08a	3.95a	0	0a	33bc
3 Warm	72	0.21a	0.13a	4.88ab	0	0.01a	10a
4 Cool	267	0.27a	0.11a	5.16b	0.01	0.02a	21ab
5 Unburned	248	1.16b	0.69b	5.96c	0.05	0.21b	20ab
KW *P*		<0.01	<0.01	<0.01	0.02	<0.01	<0.01

The *n* in this data set includes only live buds (total buds sampled minus dead buds). Different letters in columns indicate statistically different groups (Dunn test $\alpha = 0.05$)

inflorescences may still be produced when 100% of the leaves are killed.

Total acorn production in the unburned control (regime 5) was significantly greater than in any other regime (Table 5). The mean total number of acorns per bud decreased with increasing maximum temperature (Table 3, model 9). The summer of 2003 was very dry which may be why most acorns aborted before maturing resulting in a smaller sample size of live acorns. Live acorns followed a similar overall pattern as was found for total acorns. No live acorns were produced in thermal regimes 1–3, but a few were produced in regimes 4 and 5 (Table 5). KW ANOVA indicated significant differences existed among live acorns by thermal regime, but a Dunn test failed to locate the differences.

Obvious bud mortality appeared when most or all leaves near a bud were killed, but some live buds were still found even then. Elsewhere, buds in these circumstances have been observed to open in the weeks following the fire, producing a late summer or fall flush of leaves (Peter 2006). In this study, however, extensive leaf kill only occurred on two Madigan trees where much extreme scorch and bud mortality also occurred. The two hottest regimes at Weir Prairie had more bud mortality than the three coolest regimes (Table 5). There were no thermocouple locations with 100% bud survival where thermocouples peaked above 50°C or had 5,002° s over 40°C in the highest peak.

Discussion

Bud scale insulation, bud mass, the position of primordia in buds, and the distribution of primordia in trees (Peter 2006) determine heat resistance, while heat exposure is determined by stand and burning conditions and the position in the canopy. Since the stand and burning conditions can be manipulated it should be possible to manage prescribed burns for minimum impact on the acorn crop.

This study is based on only three prescribed burns; however, the fires were typical for prescribed burning in western Washington and thus provided relevant information. All three burn units had similar climate, physical environment, stand, and fuel structure. The east and west Weir Prairie sites and burns were very similar, justifying a combined analysis. The Madigan burn was hotter than the Weir Prairie burns and caused much more canopy damage. No tree mortality occurred in any burn, and visible canopy damage was very sparse at Weir Prairie, but not at Madigan where three trees were nearly completely scorched. Even the worst damaged trees at Madigan had little bud mortality with the exception of several low branches that were extremely scorched.

Leaf damage

Leaves are the most sensitive late summer organ. While heat damage is time dependent, leaves are thin, and heat up

rapidly, making damage occur almost instantaneously. Even temperatures from 35 to 45°C can be harmful with long exposure times (Taiz and Zeiger 1998; Levitt 1956; Thimann and Kaufman 1958). For shorter exposures, most studies show leaf damage begins around 50–55°C (Levitt 1956; Hare 1961; Larcher 1983; Seidel 1986; Colombo and Timmer 1992; Kolb and Robberecht 1996). Byram (1948) suggested a lethal temperature of 46°C for southeastern pine foliage. Methven (1971) noted slight needle scorch on red and white pine seedlings with 240 s treatments briefly peaking at 50°C. In our study, leaf damage followed an exponential curve with increasing temperature as has been found by others (Dickinson and Johnson 2001). Leaf damage began when peak temperatures reached about 45°C; at 50°C about 12% of foliage was damaged, but at 67°C, half and at 75°C all foliage was killed (Table 3, model 2).

Variation in temperature between thermocouples is an important result that fits with field observations of highly variable damage. Low wind speeds allowed for mostly vertical updrafts, but even so the relationship of temperature to height was weak (Table 3, model 1). The patchy nature of damage at Weir Prairie probably reflects variability in the fuel bed and the passage through the canopy of a few especially large or hot bursts of gasses. Under these weather and fuel conditions, fires do less canopy damage the more closed the canopy is probably because these conditions suppress fine fuel production (grasses) even while encouraging coarser fuels (shrubs) (Peter 2006). However, under drier conditions, greater damage is likely with the higher fuel loadings of shrubby understories.

Internal bud damage, mortality and relationships to acorn production

Only regime 1 could have produced high enough internal bud temperatures to damage deeper tissues in *Q. garryana* buds, yet this regime occurred rarely at Weir Prairie. Microscopically observed internal bud damage that was unambiguously attributable to heat began with treatments of 60 continuous seconds at 133°C or 7,980° s, but even this treatment failed to produce a measurable effect in spring organ emergence (Peter et al. 2009). Sixty continuous seconds at 133°C is probably more extreme than what most buds experienced in the Weir Prairie fires. The hottest thermocouple at Weir Prairie was estimated to have briefly peaked at 137°C, although the total exposure over 40°C was >7,980° s. In regime 2 there were temperature spikes over 50°C, which may have affected mature leaves or outer bud tissues, but deeper, internal bud tissues would not be expected to be harmed. Regimes 3 and 4 produced peak temperatures equivalent to a hot summer day and then only for seconds to minutes. While some buds were exposed to damaging temperatures, by far most were not. Even so, there was a widespread depression of reproductive organ emergence in the following spring. Factors related to burning other than heat, perhaps smoke, may have contributed to the damage. If smoke is a factor, the method of its action is not clear, although smoke is known to affect plant physiology in multiple ways (Imanishi 1983; Keeley and Fotheringham 1998; Light et al. 2010). Alternatively, canopy damage may have caused the trees to reallocated carbon to foliar production resulting in a lower reproductive investment. However, this would not explain the loss of reproductive capacity in trees experiencing primarily regime 4 and little canopy damage.

There was a clear reduction in staminate inflorescence production with increasing levels of heat (Table 3, model 5) and no staminate inflorescences were produced from buds in the hottest thermal regime, compared to 1.16 per bud in the control. In addition, thermal environments resulting in high levels of leaf damage precluded staminate flowering (Table 3, model 6). However, the depression of inflorescence production in regime 4 was unexpected. Regime 4 had <1,000° s over 40°C and 80% of the thermocouples did not record any temperatures over 40°C. These are temperatures that this species might experience for much longer periods on multiple hot summer days. Yet, the mean production of staminate inflorescences in regime 4 was <25% of the control and not significantly different from regimes 1–3. No staminate inflorescences were produced when peaks exceeded 55°C or when peaks accrued over 3,280° s over 40°C. It is important to note that even these levels are well below the 60 s at 133°C level (7,980 deg. seconds over 40°C) where microscopically visible staminate damage was detected (Peter et al. 2009).

Thermal environments resulting in high levels of leaf damage reduced, but did not preclude, pistillate flowering at Weir Prairie. While the modeled number of staminate inflorescences per bud approached zero around 50% leaf kill (Table 3, model 6), some pistillate inflorescences (0.01 per bud) were predicted even at 100% leaf kill (Table 3, model 8) suggesting pistillate inflorescences were less vulnerable than staminate inflorescences to fire damage as was suggested by Peter et al. (2009).

Pistillate inflorescence production also showed strong relationships to maximum temperature (Table 3, model 7). Pistillate inflorescences were only produced when the highest peak temperature over 40°C was under 68°C and the area under the peak included no more than 3,201° s. These levels (68°C and 3,201° s) are still well below the levels found by Peter et al. (2009) to produce visible damage.

The only significant difference in pistillate inflorescence production among temperature regimes was between the unburned control and regimes 1–4. The control produced

almost six times more inflorescences than the coolest burn regimes. Again, it seems unlikely that heat was solely responsible in the case of the coolest burn regime (regime 4) since it had <1,000° s over 40°C and many thermocouples remained below 40°C.

Unlike with inflorescences, there was no clear pattern among temperature regimes for leaf production. The data offers no explanation although it might be hypothesized that leaf primordia are relatively resistant to heat and/or smoke. In some cases, leaves were produced even when peak temperatures reached 129°C and 6,133° s over 40°C under the highest peak. While these conditions are hotter than for staminate and pistillate inflorescences they are similar to conditions that only just produced consistent microscopically visible damage, but that failed to produce measurable differences during spring bud break (Peter et al. 2009). Apparently, leaf primordia were not affected by the fires in the same way or to the same degree as inflorescences, a phenomenon also observed after hot water treatments applied to dormant raspberry buds (Rantanen and Palonen 2010).

The hottest temperature regime resulted in significantly more bud mortality than the three coolest regimes (3–5). Thus, heat was a factor in causing bud mortality, but Peter et al. (2009) predict little mortality with the exposures attained at Weir Prairie. The conditions at Weir Prairie under which staminate and pistillate inflorescences were consistently produced were also the conditions where bud survival approached 100%. Thus bud mortality began with conditions severe enough to damage the largest (staminate) or deeper (pistillate) floral primordia, but some buds survived to produce leaves in much more extreme conditions, suggesting that leaf primordia are hardier or other factors affected floral, but not leaf primordia.

Although 2003 was a generally poor crop year (Peter and Harrington 2009), acorn production was negatively related to maximum temperature (Table 3, model 9). Since staminate primordia are the most vulnerable bud organs to heat damage, the contribution of underburned trees to pollination may be reduced in the following year. This might have fruit production implications for large wildfires, but probably not for small prescribed burns where adequate pollen supply from nearby unburned trees would be available.

Pistillate flowering is important to acorn crop size, but many factors that occur after flowering also affect crop size (Cecich and Sullivan 1999; Neilson and Wullstein 1980; Peter et al. 2009). Due to heavy abortion of acorns in late July, probably in response to drought, the difference in live acorn counts between the control and the burn regimes was not clear, but a total count of live and dead acorns mirrored floral production results. The control produced significantly more inflorescences and total acorns than any other regime and the two hottest regimes produced the fewest pistillate inflorescences and no acorns at all. The only burned regime that produced any live acorns was the coolest one (regime 4).

Height relationships to canopy damage

Height relationships to canopy temperature are the basis for crown scorch models (Van Wagner 1973; Peterson and Ryan 1986), but the relationship of maximum temperature to individual thermocouple height was weak at Weir Prairie (Table 3, model 1; $R^2 = 0.17$). This probably reflects turbulent breakup of weak convection plumes from the low-intensity fire line.

The Peterson and Ryan (1986) model for, large budded conifers, predicts bud mortality with growing season exposures of 65°C for 1 min (degree seconds equivalent to regime 2). This is similar to exposures that caused bud damage to *Q. garryana*, but not appreciable bud mortality (Peter et al. 2009). In the Weir Prairie prescribed fires about one third of the oak buds in regime 2 died, but even this level of mortality suggests oak crowns should survive hotter fires than conifers of similar height. Thus, while Oregon white oak leaves are killed easily, its buds are very resistant to heat rendering leaf scorch height or volume in Oregon white oak a less useful predictor of tree mortality than in conifers.

Conclusions

Leaf damage began with exposures to temperatures higher than 42°C, followed an exponentially increasing curve with temperature until all leaves died even with brief exposures of 75°C. While leaf damage occurred at much lower temperatures than bud damage, it had predictive value for flowering in the following spring.

Underburning can reduce spring flower and fruit production even when buds are not killed. We found evidence that heat was one cause of bud damage. For example, there were strong negative relationships between production of bud organs and maximum temperature. However, floral primordia were also damaged at lower exposures of heat than was found to cause bud damage in carefully controlled experiments using just heat (Peter et al. 2009). Therefore, while heat from prescribed burns of the intensities that we used caused limited reproductive damage, we hypothesize that another fire related factor, possibly a component of smoke, enhanced damage to floral primordia.

Acknowledgments We would like to thank the Fort Lewis Forestry Department for financial and logistical support in carrying out this study; in particular we thank former head Forester Gary McCausland and Ecologist Jeff Foster. We especially thank Joe Reasoner of Fort

Lewis Forestry for his expert help in conducting the prescribed burns for this study. We also wish to thank Connie Harrington and David Peterson of the USFS PNW Research Station for their help, advice and review of all parts of this study and two anonymous reviewers for their constructive suggestions. Finally we wish to thank PNW Research Station crew members Marty Acker, Melissa Borsting, Doug Waldren and others for their expert assistance.

References

Abrahamson WG, Abrahamson JR (1996) Effects of a low-intensity winter fire on long-unburned Florida sand pine scrub. Nat Area J 16:171–183

Abrahamson WG, Layne JN (2002) Post-fire recovery of acorn production by four oak species in southern ridge sandhill association in south-central Florida. Am J Bot 89:119–123

Agee JK (1993) Fire ecology of Pacific Northwest forests. Island Press, Washington, DC

Boyd R (1999) Introduction: basic issues. In: Boyd R (ed) Indians, fire and the land in the Pacific Northwest. Oregon State University Press, Corvallis, pp 1–30

Byram GM (1948) Vegetation temperatures and fire damage in southern pines. Fire Control Notes 9:34–36

Cecich RA, Sullivan NH (1999) Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*. Can J For Res 29:1817–1823

Colombo SJ, Timmer VR (1992) Limits of tolerance to high temperatures causing direct and indirect damage to black spruce. Tree Physiol 11:95–104

Dickinson MB, Johnson EA (2001) Fire effects on trees. In: Johnson EA, Miyanishi K (eds) Forest fires. Behavior and ecological effects. Academic Press, New York, pp 477–525

Fontaine F, Druelle JL, Clement C, Burrus M, Audran JC (1998) Ontogeny of proventitious epicormic buds in *Quercus petraea*. I. In the 5 years following initiation. Trees 13:54–62

Habeck JR (1961) The original vegetation of the mid-Willamette Valley, Oregon. Northwest Sci 35:65–77

Hare RC (1961) Heat effects on living plants. USDA Forest Service Occasional Paper 183, Southern For Exp Station, New Orleans, LA

Imanishi H (1983) Effects of exposure of bulbs to smoke and ethylene on flowering of *Narcissus tazetta* cultivar 'grand soleil d'or'. Sci Hortic 21:173–180

Johnson PS, Shifley SR (2002) The ecology and silviculture of oaks. CABI Publishing, New York

Keeley JE, Fotheringham CJ (1998) Mechanism of smoke-induced seed germination in a post-fire chaparral annual. J Ecol 86:27–36

Kolb PF, Robberecht R (1996) High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. Tree Physiol 16:665–672

Larcher W (1983) Physiological plant ecology, 2nd edn. Springer, New York

Leopold EB, Boyd R (1999) An ecological history of old prairie areas in southwestern Washington. In: Boyd R (ed) Indians, fire and the land in the Pacific Northwest. Oregon State University Press, Corvallis, pp 139–163

Levitt J (1956) The hardiness of plants. Academic Press, New York

Light ME, Burger BV, Staerk D, Kohout L, Van Staden J (2010) Butenolides from plant-derived smoke: natural plant-growth regulators with antagonistic actions on seed germination. J Nat Prod 73:267–269

Martin RE, Cushwa CT, Miller RL (1969) Fire as a physical factor in wildland management. In: Proceedings of the 8th annual tall timbers fire ecology conference, Tall Timbers Research Station, Tallahassee, FL, pp 271–288

McCulloch WF (1940) Oregon oak—tree of conflict. Am Forests 46:264–266 and 286–288

Methven IR (1971) Prescribed fire, crown scorch and mortality: field and laboratory studies on red and white pine. Dept. of the Environment, Canadian Forest Service, Petawawa Forest Exp. Sta. Inf. Report PS-X-31, Chalk River, Ontario

Neilson RP, Wullstein LH (1980) Catkin freezing and acorn production in gambel oak in Utah, 1978. Am J Bot 67:426–428

Nelson RM, Simms IH (1914) A method for measuring experimental forest fire temperatures. J For 32:488–490

Peter DH (2006) Effects of underburning on Oregon white oak reproductive capacity. Dissertation. University of Washington

Peter DH, Harrington CA (2009) Synchronicity and geographic variation in Oregon White Oak acorn production in the Pacific Northwest. Northwest Sci 83:117–130

Peter DH, Agee JK, Sprugel DG (2009) Bud damage from controlled heat treatments in *Quercus garryana*. Trees 23:381–390

Peterson DL, Ryan KC (1986) Modeling post-fire conifer mortality for long-range planning. Environ Manag 19:797–808

Rantanen M, Palonen P (2010) Hot water treatment released endodormancy but reduced number of flowers in potted red raspberry plants. Hortscience 45:894–898

SAS Institute Inc (2000) The SAS System for Windows, version 8.01. Cary, NC

Seidel KW (1986) Tolerance of seedlings of ponderosa pine, Douglas-fir, grand fir, and Engelmann spruce for high temperatures. Northwest Sci 60:1–7

Silen RR (1958) Silvical characteristics of Oregon white oak. USDA forest service silvical series 10, Pacific Northwest Forest Range Experiment Station, Portland, OR

Stein WI (1990) *Quercus garryana* Dougl. ex Hook. Oregon white oak. In: Burns RM, Honkala BH (tech coord) Silvics of North America: hardwoods USDA agricultural handbook no 654. USDA For Serv, Washington, DC, pp 650–660

Sugihara NG, Reed LJ (1987) Vegetation ecology of the Bald Hills oak woodlands of Redwood National Park. USDI National Park Service, Redwood National Park technical report no. 21, South Operations Center, Orick, CA

Taiz L, Zeiger E (1998) Plant Physiology, 2nd edn. Sinauer and Associates, Inc, Publishers, Sunderland

Taylor RJ, Boss TR (1975) Biosystematics of *Quercus garryana* in relation to its distribution in the State of Washington. Northwest Sci 49:49–57

Thimann KV, Kaufman D (1958) Cytoplasmic streaming in the cambium of white pine. In: Thimann KV, Critchfield WB, Zimmermann HH (eds) The physiology of forest trees; a symposium held at the Harvard forest. Ronald Press Company, New York, pp 479–492

Van Wagner CE (1973) Height of crown scorch in forest fires. Can J For Res 3:373–378

Western Regional Climate Center (2004) Olympia WSO AP, Washington Climate Summaries. Desert Research Institute, Reno, NE. http://www.wrcc.dri.edu. Accessed 15 Decr 2004

White R (1980) Land use, environment, and social change: the shaping of Island County, Washington. University of Washington Press, Seattle

Wilson B, Kelty MJ (1994) Characteristics of shoot growth from the bud bank in black oak. Can J For Res 24:149–153

Zar JH (1999) Biostatistical Analysis, 4th edn. Prentice Hall, Upper Saddle River