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Oak Community and Seedling Response to Fire at Fort Lewis, Washington

Abstract

We evaluated effects of fire on Oregon white oak communities and regeneration at Fort Lewis, Washington. Oak stands burned by prescribed fires over the period 1994-1999 were evaluated for tree damage, mortality, and canopy tree resprouting. Neither single nor double fires had a large effect on basal area, but double fires significantly reduced oak density. Basal sprouting of oaks was related more to stand basal area reduction and crown damage than to bole damage. Small mammals preyed heavily on acorns exposed on the ground. Acorns buried in previously charred microsites in the field had higher emergence than ash treatment or the unburned control. Greenhouse studies showed little effect of soil heating prior to sowing on oak seedling survival, cover, height, or mass at the end of one growing season. Treatments with added ash reduced oak survival, cover, and height. Cover and mass of competing plants was also reduced with ash addition. Scot's broom density declined from the control with added ash, but increased in heated soils. Nutrient analyses of oak seedlings showed little interpretable effect of heat or ash treatments. Fire is important in the dynamics of oak communities, but appears not to play an obligate role in seedling recruitment.

Introduction

Oaks and oak woodlands fostered by Native American burning were once widespread in the Pacific Northwest (Taylor and Boss 1975, Boyd 1986). During the 20th century, fire exclusion, urban development, and other stresses have resulted in loss of woodland. Partial to complete conversion to conifers has occurred for Oregon white oak (*Quercus garryana*) and in general for North America oaks (Abrams et al. 1995, Robinson et al. 1995). The spatial pattern and abundance of acorns are of critical importance to many wildlife species that reside in the temperate forests of North America (McShea and Healy 2002). Renewed interest in the importance of oak-dominated communities has led to restoration efforts designed to encourage oaks and discourage both native and alien competing vegetation (e.g., The Nature Conservancy 1995, Thurston County Parks and Recreation and The Nature Conservancy 2001).

The relation of Oregon white oak and fire is critical to any restoration effort, but fire as a process will operate in altered ecosystems. Tree overstories are denser than historically and more dominated by conifers. The shrub layer is denser and may contain aggressive alien species such as Scot's broom (*Cytisus scoparius*). The herb layer may be dominated by alien species, many of them annual or rhizomatous, which may alter the potential for oaks to regenerate from seed. Herbaceous competition may limit the establishment of oaks in unburned substrates (Adams et al. 1992, Gordon and Rice 2000). Clearly, the reintroduction of fire demands a thorough knowledge of how fire will affect each of these vegetation layers, and how the vegetation layers will interact.

Oregon white oak has one of the greatest latitudinal ranges of the Pacific Coast oaks, and is the only native oak in Washington and British Columbia (Stein 1990). Four major oak-dominated communities exist locally in western Washington: riparian/wetlands, savannas, woodlands, and an oak/conifer mix generally along the ecotone between conifer forest and prairie (Stein 1990). Much of the current oak habitat is an ecotonal fringe between conifer forest and open prairie. Because ecotones are sensitive to climatic change (Brubaker 1988), projected climate changes might significantly influence future oak habitat. Douglas-fir (*Pseudotsuga menziesii*) encroachment is currently a major threat (Carey and Harrington 1999, Thysell and Carey 2001, Peterson and Hammer 2001, Foster and Shaff 2003). Intense fires in multi-layered Douglas-fir forest with dense shrub layers can topkill mature oaks and trigger a high density, small diameter oak sprout response after the fire.

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Most oak species tolerate low- to moderate-intensity fire when mature (Horney et al. 2002, Healy and McShea 2002, Harrington and Kallas 2002. When oaks are small, or when fires are of high intensity, topkill may occur and crown or bole resprouting will occur (Fry 2002). Acorn production can also be reduced for a time, although levels above control may occur 6-10 yr later (Peter and Harrington 2002). In blue oak stands in California, fire was associated with successful regeneration of sapling oaks into the overstory (McClaran and Bartolome 1989, Mensing 1992), but more recent research suggests the effect may be generally negative (Bartolome et al. 2002, Swiecki and Bernhardt 2002). Fires topkill saplings and leave the resulting sprouts vulnerable to small mammal and deer browsing. This effect, of course, may be interpreted as positive or negative from a management standpoint depending upon whether or not regeneration is desired. Higher intensity fires may result in bole and crown damage to existing oaks (Dunn 1998). Crown damage appears to be more important than bole damage for initiating a sprouting response in blue and valley oak (*Q. lobata*) in California (Fry 2002).

Seedling establishment is enhanced by acorn burial (Fuchs et al. 2000), and shading may increase early survival (Papanikolas 1997). Mature oaks are not shade-tolerant (Kertis 1986, Sugihara and Reed 1987), so that the importance of shaded reproduction is open to question. Corvids and rodents are the primary acorn dispersal agents, moving acorns away from established trees and burying them (Fuchs 1998, Vander Wall 2001). The use of acorns by mast-eating rodents has direct effects on small mammal populations (McShea 2000), and Wolff (1996) suggests that acorns act as a keystone resource in forests containing oaks because of their large effect on small mammal prey populations. Initial growth of seedlings is entirely below ground, with top growth beginning only after an extensive root system is in place (Vander Wall 2001). Annual grasses competing for available moisture (Adams et al. 1992, Gordon and Rice 2000) have negatively impacted regeneration of blue oak (*Quercus douglasii*). Changes in oak woodland herbaceous dominance from native to alien, and from perennial to annual (Kavanaugh 1992), may affect Oregon white oak regeneration.

Historically, fires were frequent in oak woodlands and forests across North America (McShea and Healy 2002). McShea and Healy (2002) note that from an ecosystem management perspective, fire is the most important, and the most difficult, disturbance factor to replicate, and emphasize the importance of controlled fire in the preservation of oak communities. Yet fire, like all disturbances, is multi-faceted: it may be applied at a range of frequencies, intensities, seasons, and extents (White and Pickett 1985). There appears to be some consensus that managed fire can help conserve existing oak overstories, encourage oak regeneration where it is desirable, encourage other native vegetation, and reduce competing alien species.

The purposes of this study were to evaluate the effects of past prescribed fires on the community structure of oak forests, and to investigate potential mechanisms of fire on oak seedling establishment and growth with field and greenhouse studies.

Methods

Field and Laboratory Methods

The research was conducted at Fort Lewis, Washington, a U.S. Army installation 15 km south of Tacoma. Various Army training exercises have resulted in wildland fires repeatedly burning some areas of the Fort. Prescribed fire has been used to reduce wildland fire risks and as an ecological restoration tool. These latter fires are the focus of this research. Eleven independent prescribed fire sites burned from 1994-1999 were selected for evaluation. Although detailed fire behavior information was not available for each burn, fire severity could be inferred from crown scorch on trees. The sample included all sites that were either an oak woodland or conifer fringe that had burned recently enough that tree mortality could be reconstructed. Four early season sites (burned February-April), four late season sites (burned August-October), and three double burn sites (burned twice in the period), were chosen from the available set of sites.

Two to eight circular 0.15 ha plots, depending on burn size, were randomly selected at each site using a 50-m grid in the summer of 2000. All trees in the plot >50 cm dbh were sampled. Trees 10.1-50 cm dbh were sampled in a 0.07 ha circular subplot centered within the larger plot. Trees

0.1-10 cm dbh were sampled in five randomly placed 0.02 ha circular subplots within the larger plots, and trees (seedlings) less than 0.1 cm dbh were sampled in 0.01 ha circular subplots centered within the 0.02 ha subplots. Tree species, condition (live or dead), height, and dbh were recorded for each tree. Oak seedlings were also counted under the canopies of trees >50 cm dbh, and seedling density was estimated as the product of seedlings per tree and large trees per ha. We classified oaks as sprouts if they were connected to boles, attached to burned stubs, or had emerged from pre-existing roots. Otherwise they were considered seedlings.

Percent crown scorch, percent bole damage, and basal sprouting response were measured on oaks. Percent crown scorch was ocularly estimated as the volumetric proportion of the crown killed, and was identified by the presence of dead branches or epicormic sprouting. Percent bole damage measurements were restricted to trees >10 cm dbh. We measured bole circumference at the base of the tree (C1) and at the tip of the scar (C2), and the length of the scar (h). The surface area (SA) of the bole within the height zone affected by the scar was calculated as

$$SA_{bole} = h*([C1 + C2]/2)$$

The geometric shape of the fire scar was determined and the area of the scar was calculated. Percent bole damage within the height zone of the scar was then calculated as

$$\text{Percent Bole Damage} = (1 - [SA_{bole} - SA_{scar}]/SA_{bole})*100$$

Basal sprouting response was identified as the number of basal sprouts within 20 cm of the bole. A model was developed to predict basal sprouting response using site means as inputs. Independent variables were percent of crown scorch (by volume), change in basal area, tree height, tree diameter, and percent bole damage. Crown scorch was arcsine transformed for normality and sprout response was transformed with natural logarithm.

Seedling experiments in the field were begun in two autumn periods. Acorns were collected in 1999 and 2000, float tested (Olson 1974) and inspected for filbert weevil (*Curculio occidentalis*) or filbertworm (*Melissopus latiferreanus*) damage (Furniss and Carolin 1977). Only acorns that passed the float and insect infestation tests, and had begun germination, were used for the experiments. In the first experiment oak logs were placed in a prescribed burn unit so that planting sites of recently created ash, char, and unburned areas could be selected. Ash sites were identified by the presence of complete combustion and white ash, while blackened areas indicated incomplete combustion of grass, shrub, or litter and were called char. Two hundred acorns were planted on the surface of each substrate and protected with a 2 cm Vexar tubing mesh stapled to the ground. Because acorns fall from the tree after the summer fire season, acorns were placed in field and greenhouse studies after ash or heating were applied. A second experiment was conducted 1 yr later in a different management unit. Fifty-two acorns were planted at 2 cm depth in each of the three substrates created by uneven burning of another prescribed fire. Half were protected by 6 mm mesh hardware cloth shaped in a cone for animal exclusion. Acorns were examined at the end of 6 mo to determine predation, mortality, and emergence.

A greenhouse study was designed to evaluate the effect of soil heating, ash addition, and presence of competitor species on acorn survival and growth. The experiment lasted January-September 2000. Dependent variables included oak survival, height, and percent cover, and density and mass of competitor species, including Scot's broom. Four independent treatments with two levels each were applied before germinated acorns were planted in pots containing Fort Lewis Spanaway soil sieved to 1 cm to remove the largest rocks and gravel. The treatments were: weeding competitors weekly (weeding), soil heating to 60°C for 10 min prior to planting (heating), and the addition of a surficial 2 cm dry ash layer created from oak logs. The 60°C treatment was chosen to have a biotic effect but little effect on volatilizing organic matter (Agee 1993). A control accompanied each treatment (no weeding, no heating, no ash addition). Each treatment and control was replicated in a randomized block design with 25 blocks and 2 replications per block for a sample size of 400 pots. Pots were periodically watered, and measurements at the end of the experiment are reported here. In September, 8-12 seedlings (foliage, stem, plus roots) from each treatment cell were dried, ground in a 20-mesh Wiley mill, and composited for elemental analysis by the Analytical Laboratory, College of Forest Resources, University of Washington.

Statistical Analysis

Basal sprouting response was the only community-level overstory response (density and basal area) subjected to statistical analysis. Independent sample t-tests were used to compare all variable means (dbh, height, crown scorch, and bole damage) between oaks that sprouted and those that had no sprouting response. All percent data were arcsine square root transformed to normalize the data (Zar 1999). Mean values per site were compared across sites using one-way ANOVA (Zar 1999). Games and Howell post hoc testing (a modification of Tukey's honestly significant difference testing) was used to reduce the probability of Type I error without reducing power (Toothacker 1993). A standard regression model was used to fit mean basal sprouting response transformed with a natural logarithm to four potential predictor variables measured at the stand level as means: dbh, percent bole damage, percent crown scorch volume, and basal area change, with transformations as defined above. Forward stepwise regression was applied with $P<0.05$ required for inclusion.

Logistic regression was used to evaluate the effects of substrate and exclosures on planted acorns. Three substrate types were investigated: control, char (incomplete combustion) and ash (complete combustion). Exclusion was categorized as either caged or not caged. Logistic regression was used to test categorical response variables against categorical predictor variables. Wald statistics tested independent variable significance.

The greenhouse studies used a three-factor (weeding, heating, and ash addition), randomized complete block ANOVA with 25 blocks and 2 replicates per block. The design was unbalanced because of mortality of some seedlings during the experiment. A total of 8-12 seedlings per treatment within block were randomly chosen for mass and nutrient analysis. An unbalanced, three-factor, randomized block MANOVA was used because more than one nutrient was being analyzed for each sample.

All significant effects are defined at $P<0.05$, with P values shown only for significant results.

Results

Community-Level Responses to Fire

The prescribed fires studied at Fort Lewis had little effect on overstory structure. In stands where basal area averaged 18.1 m^2 ha^{-1}, early and late season burns reduced basal area 0.7 m^2 ha^{-1} and 0.6 m^2 ha^{-1}, while repeat burns reduced basal area 2.1 m^2 ha^{-1}. Tree mortality (including topkill for oaks) was concentrated in the small size classes, as density reductions were much larger than basal area reductions. Mortality or topkill in early and late season burns was similar at 94 and 91 stems ha^{-1}, while mortality in repeat burns averaged 523 stems ha^{-1} (Figure 1). Due to substantial variance within each burn site and between individual burns

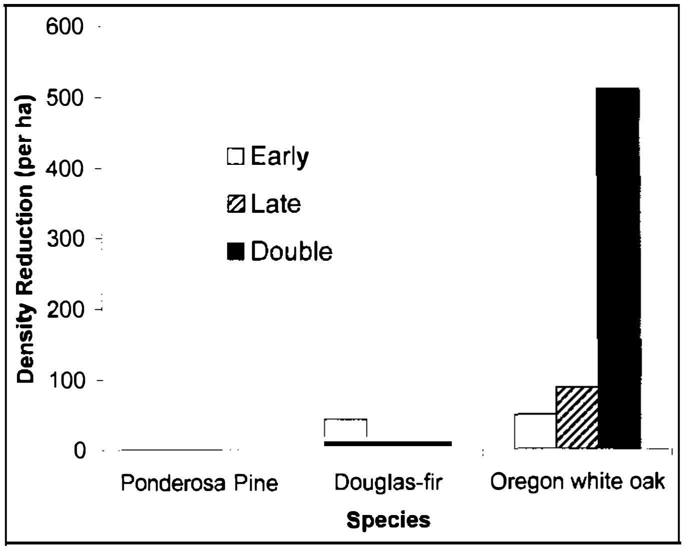

Figure 1. Tree density reduction in prescribed fires at Fort Lewis, 1994-1999. Early = late winter or spring burns, Late summer to fall burns, Double = two fires of any season.

within seasonal and repeat categories, none of these differences was tested for significance. Most of the mortality or topkill was in the smallest size class (0.1-10 cm dbh) and in Oregon white oak, as it was the pre-burn dominant tree species in the stands.

Oak Sprouting Responses

At our 11 sites, 39% of the 874 oaks of breast height or greater exhibited some form of sprouting response after prescribed fire. Sprouters were on average 9 cm in diameter smaller, 3.5 m shorter, and had about twice as much crown scorch by volume (all $P<0.001$) than non-sprouters. Bole damage was not significantly different between the two groups. Site means were used to develop a model for sprouting response ($r^2 = 0.96$):

$$\mathrm{Ln}\,(\text{mean sprout} + 1) = -.069 + 0.15\,\Delta BA + 2.09\,\sin^{-1}\sqrt{\text{scorch}}$$

Where:

$\mathrm{Ln}\,(\text{mean sprout} + 1)$ = natural logarithm of mean sprouts per tree per site

ΔBA = change in site basal area ($m^2\ ha^{-1}$) after burning

$\sin^{-1}\sqrt{\text{scorch}}$ = arcsine of the square root of crown scorch volume

The model suggests that at the site level, individual tree dimensions such as height and diameter are not as important as the effects of fire, indexed by change in basal area and percent crown scorch. Of the fire variables, only bole damage was not a significant contributor to the model.

Oak Seedling and Acorn Responses

Tree regeneration after these burns was abundant. Oak seedlings colonized the burned sites, but response was variable across sites. Seedlings colonized 7 of 11 burns. Two sites had no regeneration from either seedlings or sprouts. Douglas-fir and oak seedlings were abundant, but oak sprouts outnumbered oak seedlings about 4 to 1 (Figure 2). More than 96% of the regeneration occurred under the canopy of existing trees. Most of the oak regeneration (>75%) occurred under the canopy of >50 cm dbh Douglas-firs.

In the 1999 field experiment all acorns left on the soil surface were removed or consumed within 75 days (Figure 3). Although birds were excluded by the 2 cm mesh placed around all seedlings, small mammals were able to enter and take all e acorns. Acorns in ash were not removed as quickly, but no acorns were left after 3 mo. In the 2000 experiment, where all acorns were buried, half of the acorns either died or disappeared: 25% of the total aborted, and another 25% were removed by animals (we assume they were either cached in another location or consumed). Of the remaining 50% of the planted acorns, caging had no influence on emergence, but those planted in char had significantly higher emergence ($P<0.02$) than those planted in ash or unburned soil (Figure 4). There were no differences in survival between acorns planted in char, ash, or unburned soils, and no effect of the 20 mm mesh caging placed around half of the acorns was discernible. These results should be cautiously interpreted as they come from a single prescribed fire site.

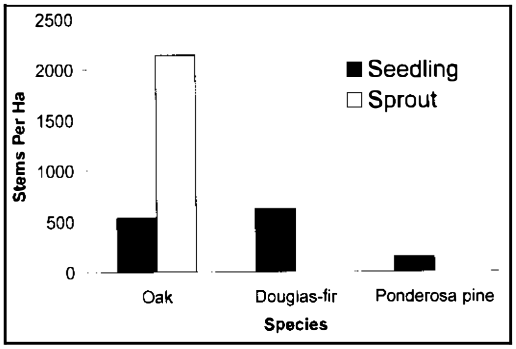

Figure 2. Regeneration of the major tree species (>0.1 cm dbh) after prescribed fires. Oaks regenerated from both sprouts and seedlings.

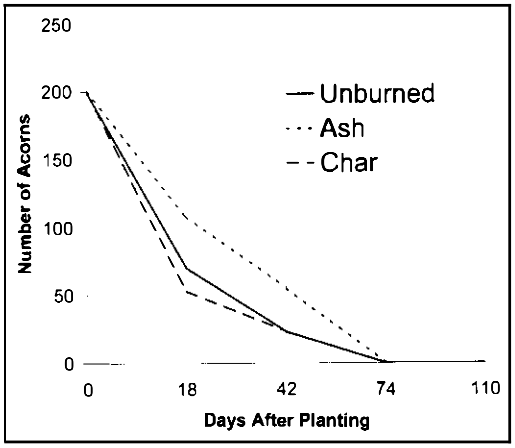

Figure 3. Decline of acorns after surface planting with 2 cm protective mesh in three substrates: unburned, ash, and char. Ash denoted areas that had complete combustion and appeared white. Char indicated areas of incomplete combustion and substantial blackening of the surface.

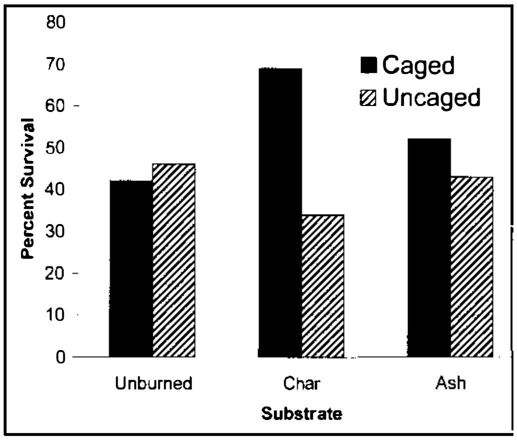

Figure 4. Percent survival of buried acorns in the second-year experiment. Acorns were either caged with 6 mm hardware cloth or left unprotected on each of three substrates: unburned, ash, and char.

The greenhouse studies with acorns showed oak seedling survival ($P<0.001$), cover ($P<0.007$), and height ($P<0.001$) were significantly less in the ash treatment (Table 1). Oak cover was significantly higher in weeded pots ($P<0.05$). Top growth was low in all treatments. Competitor cover and competitor mass (Table 2) also were less due to ash addition ($P<0.001$). Competitor stem density (Table 2) was lower in the ash addition ($P<0.001$) and heating treatments ($P<0.006$). Scot's broom density (Table 2) declined with ash ($P<0.01$), but heating significantly increased Scot's broom density ($P<0.001$). Heating and weeding had no significant effects on survival of oaks.

Elemental analysis of the oak tissue grown in the greenhouse experiments indicated few significant differences due to treatment (Table 3). Potassium and sodium were significantly lower ($P<0.03$ and $P<0.007$) in oaks grown in soils that had been heated, and calcium and magnesium were significantly lower ($P<0.05$ and $P<0.04$) in oaks grown in non-weeded plots. Boron was higher in the ash treatment ($P<0.02$) and lower in heated

TABLE 1. Response of oak seedlings to the simple effects of three factors in greenhouse tests. Means with different superscripted letters within a column by factor are significantly different. Means with no letters are not significantly different.

Treatment	Survival (%)	Cover (%)	Height (cm)	Mass (g)
Ash	20.0^a	4.19^a	1.16^a	0.53
No ash	36.5^b	7.14^b	2.42^b	0.52
Heat	28.0	6.44	1.62	0.57
No heat	28.5	4.89	2.00	0.48
Weeding	31.0	6.76^a	1.81	0.60
No weeding	25.5	4.57^b	1.95	0.44

TABLE 2. Response of oak competitor plants in non-weeded pots to ash and heat. The stem density of all species includes Scot's broom. Means with different superscripted letters within a column by response variable are significantly different. Means with no letters are not significantly different.

Response variable	Cover (%)	Mass (g)	All species	Scot's broom
All competitor species				
Ash	43.0^a	7.5^a	-	-
No ash	84.0^b	33.0^b	-	-
Heat	65.5	17.0	-	-
No heat	61.5	23.5	-	-
Stem density per pot				
Ash	-	-	8.5^a	4.0^a
No ash	-	-	49.5^b	10.5^b
Heat	-	-	33.5^a	11.0^a
No heat	-	-	49.5^b	3.5^b

TABLE 3. Nutrient content (mg g^{-1}) of oak seedlings in factorial greenhouse tests. Element means with different superscripted letters within a treatment are significantly different. Means with no letters are not significantly different.

Element	Ash	No ash	Heat	No heat	Weeding	No weeding
Potassium	10.11	4.19	4.78^a	8.60^b	7.27	6.42
Calcium	7.26	6.75	6.48	7.41	7.81^a	6.17^b
Magnesium	1.34	1.39	1.39	1.35	1.55^a	1.19^b
Sulfur	1.00	0.88	0.92	0.94	0.96	0.91
Sodium	0.98	0.97	0.84^a	1.09^b	1.02	0.92
Phosphorus	0.94	0.90	0.91	0.92	0.92	0.92
Nitrogen	0.26	0.23	0.25	0.24	0.24	0.25
Boron	0.03^a	0.02^b	0.02^a	0.03^b	0.02	0.02

soil ($P< 0.03$), although the absolute differences were small. Phosphorus showed a significant interaction ($P< 0.02$) between weeding and heating, and concentrations were higher in heated pots when they were weeded than without weeding.

Discussion

Char, but not ash, appeared to have a positive influence on emergence (Figure 4). This result was partly consistent with previous observations of seedling recruitment in heavily burned, ashy microsites, and oak sprouts in charred areas (Agee 1993). Black char may encourage soil warming in late winter and stimulate oak sprouting (Agee 1993). Our data suggest that much of the seedling regeneration occurred under the canopy of trees where herbs would often be more sparse, rather than in the open where competition from herbs would be more severe. Severely burned open microsites may still be important for oak establishment, but most of the regeneration in our study occurred under tree canopies.

Our seedling experiments did not show a strong obligate relationship between fire and successful oak seedling establishment. There was little or no effect of soil heating on oak survival, cover, height, or mass (Table 1). Ash decreased seedling survival, cover, and height. The high pH of ash slows elongation of oak seedling radicles (Henig-Sever et al. 1996). It was not surprising that the weeding of competitors increased the cover of oak in our greenhouse studies, or that heating the soil (Table 2) increased the density of Scot's broom and decreased the herbaceous seed bank (Calvo et al. 1999, Agee 1996a). However, we were experimenting in recently mixed soil where all plants had to germinate from seed, and there was no pre-existing herb or shrub cover. In prairies, savannas, and woodlands, sprouting perennial grasses, many of them alien, will provide competition not seen in our experiments. Low-intensity burning increases both native and alien herbaceous seed germination over control plots (MacDougall 2002).

The significant results of the seedling nutrient analyses (Table 3) are difficult to interpret. Ash appeared to have little effect on oak tissue nutrient concentrations. There are no obvious reasons why potassium and sodium were lower in heated oils, as they would not volatilize at the relatively w temperatures (60°C) we used. It might be that as monovalent cations they were leached through the pots, but we did not measure nutrient movement. Similarly, the positive effects of weeding on calcium and magnesium are not easily explainable. Both elements tend to be more strongly adsorbed to soil particles, however, and may have been more available to the oaks without competing vegetation. The positive effect of ash on boron levels may have been a fertilizing effect of the ash, but the negative influence of heating is not clear, as boron would not have been volatilized by the mild soil heating. In general, the seedling nutrient results were not helpful in interpreting the growth responses.

Our field acorn studies confirmed through indirect evidence that wildlife utilize acorns, a well-established fact across the range of all oaks (Fuchs et al. 2000, McShea and Healy 2002). Our first year study showed that all acorns can be removed in a short period of time (Figure 3) if not buried. This illustrates the importance of acorns to wildlife, and the importance of burial for successful establishment of oak seedlings (Fuchs et al. 2000). We could not track whether the removed acorns were consumed or simply translocated and cached. Our 2000 field study showed that even with protection from some wildlife (smaller mesh and burial of acorns), acorns were still removed.

In the Puget lowlands, oak woodlands are commonly invaded by Scot's broom (Figure 5). Low intensity fires can be prescribed to underburn the oaks and kill much of the Scot's broom. The oak overstory can be maintained without significant foliar scorch, so that basal sprouts would not be encouraged. Although bole damage is not strongly related to sprouting, it should be avoided where overstory thinning is not an objective, as it encourages stem decay and bole consumption by subsequent fires. A second prescribed fire within 3 yr, or successive fires, will be needed to kill regenerating Scot's broom, and this second fire should result in a depleted seed bank for Scot's broom. One problem associated with the second fire is that if the Scot's broom seedlings are dense, their foliar moisture may be sufficiently high, even in summer, to retard fire spread, so that the most dense broom patches may not burn in low-intensity fires. Adding flammable mulch, or seeding sterile annual grass, might provide enough fuel to carry a second fire, but neither of these methods has been operationally tested. If the literature on cutting of Scot's broom is a guide (Bossard

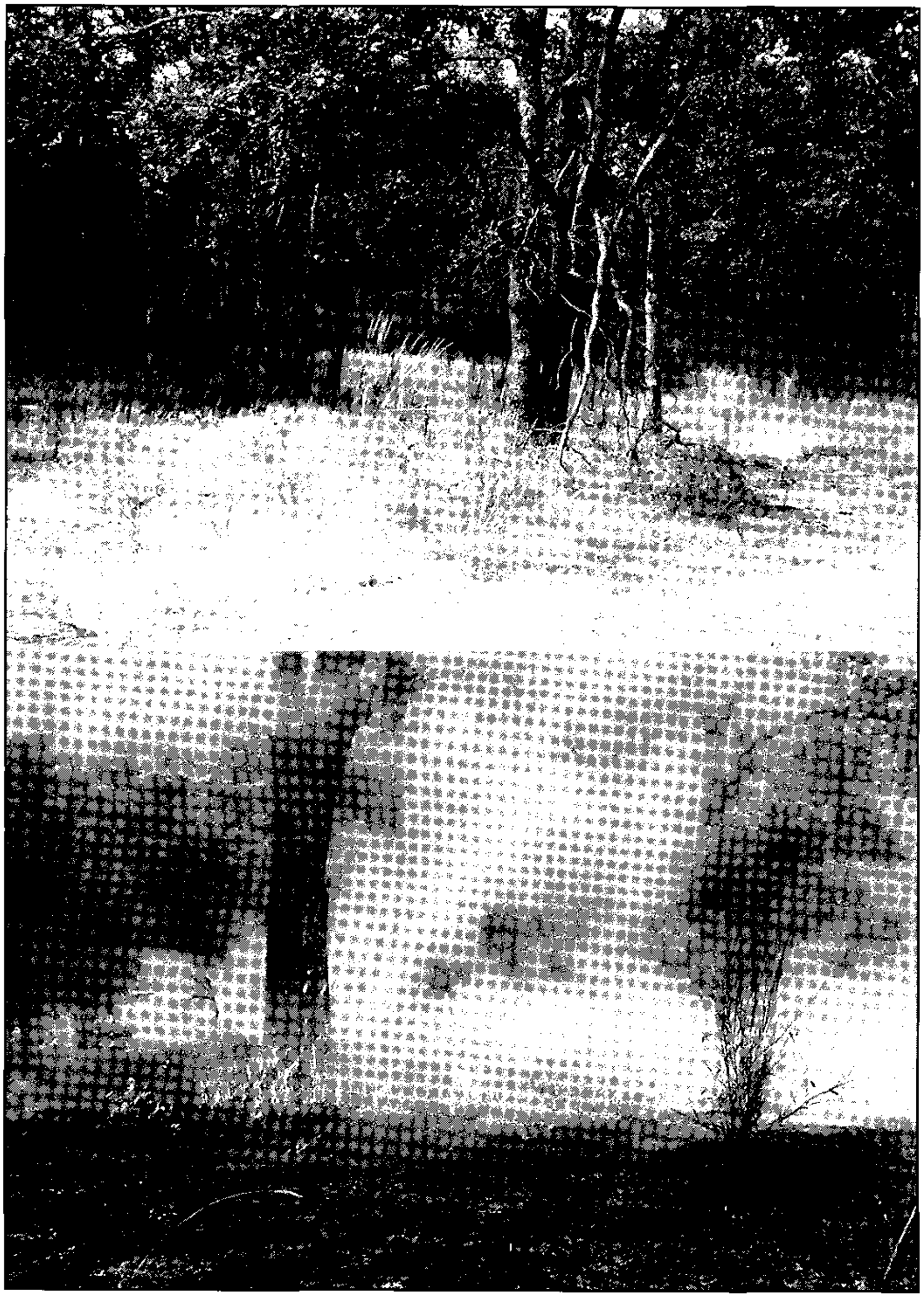

Figure 5. A. (Upper) Example of a typical fringe oak stand with Scot's broom in the understory. B. (Lower) A typical prescribed fire that might be applied in the summer, resulting in herb and shrub topkill but little oak scorch.

and Rejmarek 1994, Ussery and Krannitz 1998), burning should be most successful in summer rather than late winter to early spring. Fires spread better in summer, and may be more effective in killing mature broom, compared to early season burning.

Even if the initial fires are considered successful, longer-term effects of repeated fires need to be evaluated. Tveten and Fonda (1999) suggested that fire return intervals at Fort Lewis of 3-5 yr appeared more likely to favor native understory species than either annual burning or fire exclusion. Peterson and Reich (2001) evaluated effects of fire return intervals on oak woodlands in Minnesota. They suggested two fires in quick succession followed by fires at >2 yr intervals appeared optimum for maintaining savanna-like structure. Repeat burns within a 5 yr period in our study area decreased Oregon white oak density much more than single fires (Figure 1) but the reduction was primarily due to large numbers of small stems. We conclude that this mortality is acceptable for these stands, but monitoring of the third, fourth, and subsequent fires will provide stronger evidence for the most appropriate fire return interval. Varying the fire return intervals around the mean is desirable to provide local biodiversity associated with short and long fire return intervals (Agee 1996b).

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