Short Communication

Acorn Dispersal of California Black Oak after a Stand-Replacing Fire

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ABSTRACT

We investigated California black oak (*Quercus kelloggii* Newberry) acorn dispersal by rodents and birds in the months after a stand-replacing fire in a mixed conifer forest in the San Bernardino Mountains of southern California, USA. The objective of this study was to compare scatter-hoarding in a high-severity burn to that in an unburned forest. In the fall of 2007, we placed 600 magnet-bearing acorns under trees in the unburned area. Of the 600, we recovered 77 (13 %). Dispersers moved acorns an average distance of 5 m and buried them to an average depth of 30 mm. By spring of 2008, 90 % of the cached acorns were missing. In the high-severity burn, we recovered 59 (9.8 %) of the 600 acorns placed under top-killed oaks; these had been scatter-hoarded an average of 5.27 m from the source plots and buried an average of 22 mm. By spring of 2008, 55 % these acorns were missing, and many of those that we relocated had been re-cached in new locations. Our results suggest that scatter-hoarding of acorns may be a common phenomenon after fire, and likely plays an important role in seedling recruitment.

Keywords: acorn dispersal, California black oak, magnet-bearing acorns, *Quercus kelloggii*, San Bernardino Mountains, southern California, stand-replacing fire

Citation: Borchert, M.I., and C.M. Tyler. 2010. Acorn dispersal of California black oak after a stand-replacing fire. Fire Ecology 6(3): 136-141. doi: 10.4996/fireecology.0603136

INTRODUCTION

Rodents and birds are indispensable to seedling recruitment of oaks (*Quercus* L.) worldwide, both as dispersers and planters (Steele and Smallwood 2002, Pons and Pausas 2007). Members of the Corvidae (*Garrulus*, *Aphelocoma*, *Cyanocitta*) move hundreds, or even thousands, of acorns both short (meters and tens of meters) and long (hundreds of meters to kilometers) distances from fruiting trees (Gómez 2004, Pons and Pausas 2007, Purves *et al*. 2007). Rodents in the genera *Sciurus*, *Eutamias*, *Tamias*, *Peromyscus,* and *Apodemus* also scatter-hoard substantial numbers of acorns, but generally carry them shorter distances (<25 m) than birds (Iida 2006, Jones *et al*. 2006, Takahashi *et al*. 2006, Moore *et al*. 2007).

Despite the prevalence of fire in oak communities throughout the world, no experimental studies have investigated whether rodents and corvids scatter-hoard acorns after fire. So far, nearly all acorn dispersal studies have been carried out in unburned forests (Gomez 2004, Moore *et al*. 2007, Gomez *et al*. 2008, Zhang *et al*. 2008), although several have documented dispersal from undisturbed to disturbed habitats (e.g., cut over stands: Takahashi *et al*. 2006) or from undisturbed forests to those undergoing succession (Crow and Adiksson 1994).

In mid-September 2007, a 5600 ha wildfire burned Jeffrey pine (*Pinus jeffreyi* Balf.)-white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.)-black oak (*Quercus kelloggii* Newberry) forests in the San Bernardino Mountains of southern California, USA. In the high-severity portion of the burn, thousands of acorns covered the ground beneath black oaks and continued to fall in the weeks thereafter. Steller's jays (*Cyanocitta stelleri* Gmelin) and acorn woodpeckers (*Melanerpes formicivorus* Swainson) immediately began to harvest acorns from the leafless canopies and, in the case of Steller's jays, from the ground as well. Merriam's chipmunks (*Tamias merriami* Allen) retreated to the larger rock outcrops, as did California ground squirrels (*Otospermophilus beecheyi* Richardson). Both species exploited acorns under oaks growing in and around outcrops. Western gray squirrels (*Sciurus griseus* Ord) collected acorns from the burned canopies as well as from the ground, but unlike chipmunks and ground squirrels, they often foraged well away from the cover of outcrops. All of these vertebrates consume acorns and, except for acorn woodpeckers, they scatter-hoard them as well (Best and Granai 1994, Carraway and Verts 1994).

In the weeks after the fire, we initiated acorn dispersal experiments to assess the prevalence of post-fire scatter-hoarding. Specifically, we wanted to know if vertebrates scatter-hoard acorns in either the unburned area or in the high-severity burn and, if so, we wanted to know how many acorns were hoarded and at what distances from the source trees. Although we expected that scatter-hoarding was taking place in unburned forests, we expected little or no scatter-hoarding in the high-severity burn mainly because foraging cover and caching microsites (coarse woody debris, shrub cover, and litter) had been all but eliminated there.

METHODS

Study Area

California black oak is a tall (50 m), winter-deciduous tree that is distributed from central Oregon to southern California, primarily in inland mountainous areas between elevations of 600 m and 2300 m. Fruit maturation requires 18 to 20 months after pollination and mature acorns begin to drop in early to late September, having fallen by early to mid-November.

We conducted experiments in an area approximately 2 km northwest of Fawnskin, California, (34°16.51' N, 116°58.18' W) in the San Bernardino Mountains (Figure 1). The area encompassing the study sites ranges in elevation from 2125 m to 2250 m. Topography is flat to gently undulating (slopes < 5°) and is occasionally dissected by the main drainage of Grout Creek and its tributaries. Jeffrey pine-white fir-black oak woodlands and forests are the dominant overstory types. Prominent understory shrubs included mountain whitethorn (*Ceanothus cordulatus* Kellogg) and greenleaf manzanita (*Arctostaphylos patula* Greene). Hundreds of granite outcrops, ranging in size from 500 m^2 to 1.5 ha, pepper the landscape.

The climate of the study area is Mediterranean, which is characterized by cold, wet winters and warm, dry summers. Average annual precipitation recorded at the nearest weather station (Big Bear Lake) is 558 mm, most of which falls as snow from November to April. Precipitation for the year July 2007 to June 2008 was 566 mm.

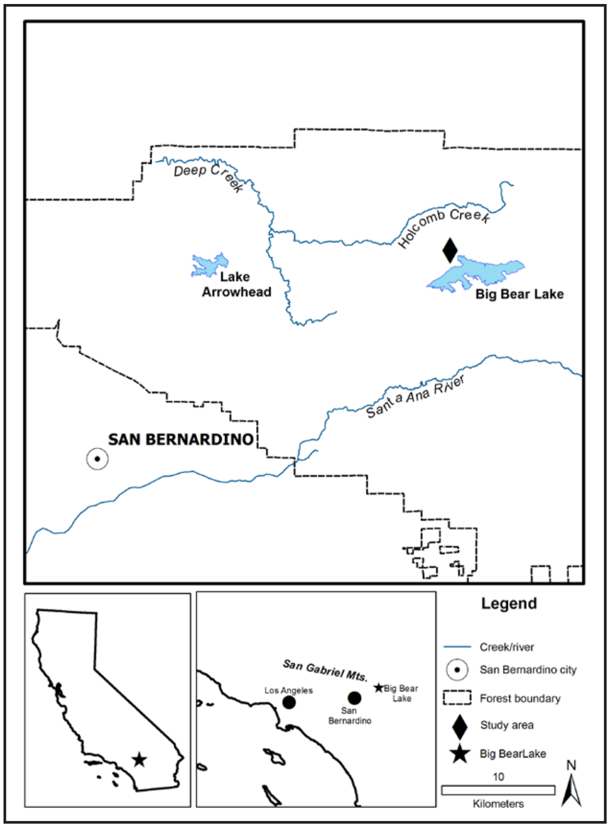

Figure 1. Study area location just north of Bear Lake on the San Bernardino National Forest east of Los Angeles, California, USA.

Acorn Dispersal Experiment

Within the burned and unburned areas, we used undamaged acorns collected in the unburned site. Into each acorn we inserted a 4 mm × 2 mm × 1 mm color-coded rare earth magnet (Indigo Instruments, Waterloo, Ontario, Canada) that allowed us to find them after they were dispersed using a magnetic locator (Schoenstedt model GA-72Cd, Kearneyville, West Virginia, USA).

In the 6 ha unburned area, we selected six oaks spaced at least 100 m apart. All oaks used in the experiment were at least 300 m from the boundary of the burn. On 12 October 2007, we deployed 100 magnet-bearing acorns under the canopy of each tree (total of 600 acorns). We placed 25 acorns in each of four 0.5 m^2 circular plots midway between the oak bole and canopy edge in the cardinal directions. Each group of 25 acorns had magnets painted with a unique color, which also was marked on the shell.

Once all the acorns had been dispersed from a tree, we searched a 1965 m^2 area (circle with a 25 m radius) around each 0.5 m^2 plot with the magnetic locator. Nylon string divided the area into eight equal-size wedges that we thoroughly searched. When we found a loose magnet, intact acorn on the soil surface, partially eaten acorn, or buried acorn, we marked its location, measured the depth to the top of the buried acorn, and determined the magnet color. After locating all acorns and loose magnets, we measured the distance and direction of each acorn (or magnet) to its source plot. We then returned all intact, uneaten surface or buried acorns to the locations where they were found (i.e., surface or buried). On 26 May 2008 of the following spring, we searched the same areas for acorns.

In the burn area, we selected six top-killed oaks also spaced at least 100 m apart. From 27 to 29 of October 2007, we placed 100 magnet-bearing acorns collected from the burn area under each tree following the same protocol used for unburned trees. We monitored acorn losses from oaks weekly until 12 December 2007. After all of the acorns had been taken from a tree, we searched for them in the same way we searched in the unburned area. We returned all intact uneaten, surface, and buried acorns to the locations where they were found. On 25 April 2008, the following spring, we searched the areas again and recorded the fate of all magnet-bearing acorns.

Statistical Analysis

To compare between-season changes in dispersal distance, dispersal direction, and burial depth, we used paired *t*-tests. Dispersal distances and burial depths were not normally distributed and had to be square-root transformed for analysis.

RESULTS

In the unburned area, all magnet acorns disappeared within three days. In the fall, we relocated a total of 12.8% of the acorns (77 out of 600), and of these, the majority (49) had been scatter-hoarded (Table 1). Of the 49 buried acorns, 24 were in single-acorn caches, two groups were three-acorn caches, one was a four-acorn cache, and one was a cache of 15 acorns. Scatter-hoarded acorns had been moved an average of 5 m from their original location and were buried to an average depth of 30 mm (Table 2). By the following spring, only 27 magnet-bearing acorns were relocated (4.5% of the original 600). The majority of these were partially consumed and only 5 (0.8% of the original 600) were buried (Table 2), indicating a 90% reduction in acorns cached the previous fall. Buried acorns retrieved in the spring were in three single-acorn caches and one two-acorn cache. Between fall and spring, the distance of buried acorns from their source plots increased an average of 2.6 m (Table 2). Moreover, acorns found in spring were buried an average of 9 mm deeper than those buried and found in the fall (t_{51} = −2.35, P = 0.02), suggesting that many shallow (<20 mm) caches had been removed, leaving only deeply buried acorns (Table 2).

From burned oaks, we recovered 59 of the 600 magnets (9.8%) in the fall. Scatter-hoarded acorns had been moved an average of 5.3 m from their original location and were buried to an average depth of 22 mm (Table 2). Of the 42 buried acorns, 38 were in single-acorn caches and two in a two-acorn cache. The between-season loss of cached acorns was 54.8%, as only 19 buried acorns were recovered in the spring. All of these 19 cached acorns retrieved in the spring were single-acorn caches. Distances of acorns from source plots was ~3 m greater in the spring (t_{59} = −2.12, P = 0.04) than in the previous fall, but burial depth did not differ significantly between seasons (Table 2).

DISCUSSION

This is the first study to quantify scatter-hoarding of black oak acorns, and the first study we know of to document early postfire acorn dispersal. Even though the overall percentage of magnet acorns buried was comparatively small (9.8% to 12.8%), scatter-hoarding was widespread in both the high-severity burn and the unburned areas. Moreover, despite the near absence of shrub cover, litter, and coarse woody debris in the burned area, average dispersal distances for acorns were similar to those reported in unburned forests (Takahashi *et al*. 2006, Lopez-Barrera *et al*. 2007, Moore *et al*. 2007, Gomez *et al*. 2008).

Unfortunately, we were not able to determine which vertebrates scatter-hoarded magnet acorns; however, the absence of observable jay caching suggests rodents dispersed most, if not all of them. Merriam's chipmunks and

Table 1. Fate of magnet-bearing acorns recovered from oaks in the burned and unburned areas. Given are the numbers of acorns recovered (and percentages) out of 600.

Site and season	Partially consumed	Surface intact	Buried intact	Total acorns recovered
Unburned				
Fall 2007	14 (2.3%)	14 (2.3%)	49 (8.2%)	77 (12.8%)
Spring 2008	22 (3.7%)	0	5 (0.8%)	27 (4.3%)
Burned				
Fall 2007	12 (2.0%)	5 (0.8%)	42 (7.0%)	59 (9.8%)
Spring 2008	16 (2.7%)	2 (0.3%)	19 (3.2%)	37 (6.2%)

Table 2. Dispersal distances and burial depths of buried magnet acorns recovered from oaks in the burned and unburned areas. Values are means ± 1 SE. Within each column by site category, different letters indicate a significant difference between seasons using paired *t*-tests.

Site and season	*n*	Distance (m)	Depth (mm)
Unburned			
Fall 2007	49	4.97 ± 0.71[a]	30.09 ± 3.39[a]
Spring 2008	5	7.60 ± 2.83[a]	55.88 ± 9.50[b]
Burned			
Fall 2007	42	5.27 ± 0.60[a]	22.07 ± 1.93[a]
Spring 2008	19	8.04 ± 1.47[b]	19.05 ± 3.36[a]

California ground squirrels took refuge in the scattered outcrops and may have cached some portion of the residual crop. Although uncommon, western gray squirrels roamed widely in burned and unburned forests. Gray squirrels are active acorn hoarders and may have cached many acorns in open areas well away from rock outcrops.

The results of this study suggest that acorn scatter-hoarding may play an important role in post-fire seedling recruitment. Although acorn mortality was complete after this fire (M.I. Borchert, Forest Service, unpublished data), it can be lower after moderate and low intensity fires (Cain and Shelton 1998). Acorns surviving the fire could be scatter-hoarded to microsites favorable to seedling establishment such as those with higher light conditions away from the tree canopy, or to mineral soils lacking a litter layer (Wang *et al*. 2005). Moreover, animal-buried acorns would be less prone to predation and less likely to desiccate than those on the surface. Even though the percentage of acorns scatter-hoarded in this study was relatively low (Table 2), many thousands could be dispersed in mast years, perhaps resulting in a significant contribution to seedling recruitment.

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