SEROTINY IN CALIFORNIA OAKS

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Abstract

Although prolonged seed retention, or serotiny, is believed to be an adaptation to highly variable environments such as the Mediterranean regions of California, no prior study has systematically investigated the prevalence of seed retention among California oaks (family Fagaceae), the dominant woody taxon in California foothill woodlands. We quantified the extent to which acorns were retained into and through the winter and spring within the canopy of five species of California oaks at Hastings Reservation, Monterey County. Significant serotiny was found in coast live oak (*Quercus agrifolia*) and, to a lesser extent, valley oak (*Q. lobata*), but was absent in blue oak (*Q. douglasii*), canyon live oak (*Q. chrysolepis*), and California black oak (*Q. kelloggii*). In both species where serotiny was observed, seed retention was primarily predicted by the size of the focal tree's acorn crop. In addition, serotiny in coast live oaks was more prevalent in dry years and when the overall acorn crop of coast live oaks was large. We found no evidence that acorn fall in these species is triggered by a specific environmental event. Prolonged seed retention in California oaks renders acorns available in the canopy to wildlife throughout the winter in some years with potentially significant effects extending beyond those of acorn abundance per se.

Key Words: Acorns, acorn retention, oaks, serotiny.

Serotiny is an adaptation of plants to retain their seeds for an extended period of time, in some cases for years or decades, often, although not necessarily, releasing them in response to some specific environmental trigger (Lamont 1991). A common and widespread trigger is fire, and there has been extensive study of species that release their seeds in response to fire or intense heat (Lamont et al. 1991; Bond and Van Wilgen 1996). The factors known to facilitate seed release in serotinous species are varied, however, and include plant or branch death, solar radiation, and dryness (Cowling and Lamont 1985; Lamont et al. 1991; Nathan et al. 1999). Serotiny has been suggested to be particularly common in environments subject to high spatial and temporal variation in water availability (Evanari et al. 1982; Nathan et al. 1999).

Mediterranean climates are notable for their high temporal variability in rainfall, frequency and intensity of extreme events, and potential sensitivity to climate change (Sánchez et al. 2004; Xoplaki et al. 2004). Thus, to the extent that serotiny is important in environments that are highly variable in water availability, it would be surprising if oaks (genus *Quercus* L.) — the dominant tree taxon in California woodland-savanna (Griffin and Critchfield 1972; Allen-Diaz et al. 2007) covering some 5×10^6 ha of hardwood rangeland in the state (Standiford 2002) — failed to exhibit some degree of serotiny, with potentially important consequences to the diverse community of wildlife depending on acorns for food (Pavlik et al. 1991).

As part of a more comprehensive investigation of acorn production in California oaks, we quantified acorn retention over a 10-year period by five species of oaks at Hastings Natural History Reservation, Monterey County, central coastal California. Here we report on the degree of serotiny observed in these populations and explore correlations between seed retention and environmental factors with the goal of understanding the extent and potential significance of this phenomenon to California oak woodlands.

TABLE 1. TAXA AND SAMPLE SIZES SAMPLED FOR SEED RETENTION AT HASTINGS RESERVATION, 2002–2011 SEASONS.

Common name	Scientific name	Comments	Elevational range (m)	N trees, 2002–2005	N trees, 2006–2011
Valley oak	*Q. lobata*	White oak (sect. *Quercus*), deciduous, matures acorns in one year	476–875	16	20
Blue oak	*Q. douglasii*	White oak (sect. *Quercus*), deciduous, matures acorns in one year	538–847	15	24
Coast live oak	*Q. agrifolia*	Red oak (sect. *Lobatae*), evergreen, matures acorns in one year	484–875	17	17
California black oak	*Q. kelloggii*	Red oak (sect. *Lobatae*), deciduous, matures acorns in two years	800–850	—	7
Canyon live oak	*Q. chrysolepis*	Intermediate oak (sect. *Protobalanus*), evergreen, matures acorns in two years	800–875	—	8

METHODS

We quantified acorn production and retention on marked individuals of five species of oaks at Hastings Reservation at monthly intervals when they were present on trees between September 2002 and April 2012. Acorns of all five species generally mature in late September or October and typically fall off the trees in October and November. Acorns were counted using the visual survey method of Koenig et al. (1994a) and involved a subset of the trees whose patterns of acorn production are described and analyzed elsewhere (Koenig et al. 1994b; Koenig et al. 1996). Trees were individually marked and included valley (*Quercus lobata* Née), blue (*Q. douglasii* Hook. & Arn.), and coast live (*Q. agrifolia* Née) oaks between the 2002–2003 and 2005–2006 seasons. Starting in autumn 2006 the survey was expanded to include additional valley and blue oaks as well as a small number of canyon live (*Q. chrysolepis* Liebm.) and California black (*Q. kelloggii* Newb.) oaks (Table 1).

During initial surveys each September, two observers using binoculars counted as many acorns that they could during 15-second counts. Counts were added (N30) and *ln*-transformed (ln(N30 + 1) = LN30) to reduce the correlation between the mean and the variance. Subsequent surveys were conducted similarly, except that only intact acorns still remaining on the trees were counted (i.e., empty caps still attached to a branch were ignored). Although values were *ln*-transformed for analysis, we graph the untransformed data.

In order to quantify the length of time acorns were retained on the trees, we determined, for each tree, the month in which its LN30 value first dropped below two (that is, < seven acorns were counted during the 30-second sampling period), an arbitrary cut-off corresponding to a significant number of acorns still remaining on the trees. Thus, trees for which < seven acorns were counted during the initial survey were excluded from analyses of the factors influencing serotiny, since acorn retention in such trees could not be meaningfully measured. Concordance across years among individuals was calculated using Kendall's coefficient of concordance (Sokal and Rohlf 1981).

We tested a total of eight variables (nine for valley oak) for their potential effects on the degree of serotiny using linear mixed models. On an annual basis, we looked at the initial size of the focal tree's acorn crop (*ln*-transformed) (LN30), the mean *ln*-transformed acorn crop size of all trees of the target species surveyed, mean average daily temperature, and total rainfall, the last two variables measured from 1 November to 31 March, the main period during which acorns were retained by trees in years when serotiny occurred. On an individual tree basis, we tested for the effects of tree size, water availability, soil nitrogen availability, soil phosphorus availability, and spring leaf phenology during the prior spring. Spring leaf phenology was available for valley oaks only as part of a study of the relationship between this character and acorn production in this species.

Weather was measured at Hastings Reservation headquarters, within 3.5 km of all trees. Tree size was measured by the diameter at breast height (dbh). Water availability was estimated by predawn xylem water potential using a pressure bomb during September 1991 and 1994–1998 (Knops and Koenig 1994). Differences in xylem water potential among trees have been shown to be concordant among years (Knops and Koenig 2000); that is, despite annual variation in overall water availability, trees that are relatively wet because they have good access to ground water are relatively wet in both wet and dry years. Thus, we used xylem water potential values from 1991, when all trees were measured. Nitrogen (N) and phosphorus (P) availability was estimated using four ion-exchange resin bags placed under

each tree (at a depth of 5–10 cm) between October 1992 and April 1993 (Knops and Koenig 1997). Bags were then analyzed for NO_3, NH_4, and PO_4 to estimate available nitrogen and phosphorus levels (soil nitrogen and soil phosphorus). Spring leaf phenology of valley oaks was quantified by means of weekly surveys for budburst and flowering activity conducted between 2003 and 2011 (Koenig et al. 2012). For the analyses conducted here, we used the date on which budburst occurred (defined as >5% of the tree having leafed out and turned green).

Analyses were conducted using the 'lme' function in the R library 'nlme' (Pinheiro et al. 2013) in which the number of months at least seven acorns were counted on the tree during surveys (than is, for which LN30 > 2) was the dependent variable and 'tree' was included as a random factor. We compared a set of 11 (10 for coast live oak) candidate models as listed in Table 2. Most of these included the focal tree's initial acorn crop along with one or two of the other variables; also included were the null model (intercept only), the full model, and a model with only the overall mean acorn crop of all conspecific trees counted each year ($N = 85$ [valley oak]; $N = 62$ [coast live oak]).

Models were ranked within species using the Akaike information criterion corrected for sample size (AIC_c) with the 'AICctab' function in the R package 'bbmle' (Bolker 2012). We then model-averaged coefficients (mean ± standard error) from analyses of models with competing support (i.e., $DAIC_c < 10$). All statistical analyses were conducted in R2.15.1 (R Development Core Team 2012).

RESULTS

Interspecific and Inter-year Variability

Seed retention differed considerably among the five species (Fig. 1). In general, acorns, which mature in October and November, had largely fallen or been removed by seed predators by December, one to two months later. The most notable exception to this was among coast live oaks, which frequently retained acorns two additional months until February and in some cases into (and occasionally beyond) March and April. Similar seed retention was also observed more rarely among valley oaks. During the 10 years of the study, we documented nine individuals (seven coast live oaks [11% of the individuals surveyed] in two different years and two valley oaks [2% of the individuals surveyed] in three different years) that achieved counts of seven acorns or more (LN30 > 2) in April, five to six months following normal acorn maturation. Two of these individuals (one of each species) retained acorns in their canopies into April in two

different years (Table 3). Although systematic surveys were not conducted after April, in two cases coast live oaks surveyed in July yielded counts of at least seven acorns; both these were during the unusually large crop year of 2011–2012. Trees that retained acorns were typically trees that produced very large acorn crops initially, but this was not always the case (Table 3).

Overall, annual variation in the degree to which trees retained acorns was modest for valley oaks (Fig. 2a) and considerable for coast live oaks (Fig. 2b). There was significant concordance in seed retention across trees for both species (Kendall coefficient of concordance, valley oak: $\chi^2_{15} = 47.2$, P < 0.001; coast live oak: $\chi^2_{15} = 43.2$, P < 0.001). Virtually all acorns of the other three species had disappeared from trees by December of all years (Fig. 1).

Because significant serotiny was absent in three of the species, we only performed mixed-effects models for valley oak and coast live oak. For valley oaks, four models had non-trivial support involving four variables: the initial size of the focal tree's acorn crop, overall mean acorn crop size, mean winter temperature, and xylem water potential. Only the initial size of the focal tree's acorn crop, however, had a model-averaged estimate whose 95% confidence interval did not overlap zero (Table 2). For coast live oak, two models involving three variables garnered non-trivial support, including the size of the focal tree's acorn crop, the overall mean acorn crop size, and winter rainfall. Although the estimates of all three model-averaged variables had 95% confidence intervals that did not overlap zero, the standardized effect sizes indicated that the size of the focal tree's acorn crop was by far the most important predictor of serotiny (Table 2).

Thus, serotiny in both species was most strongly associated with the initial acorn crop size of the focal tree (Fig. 3). In addition, coast live oaks were more serotinous when the overall mean acorn crop of conspecifics was large and during dry winters.

DISCUSSION

Acorns are a major food resource for California wildlife, which at our study site include a range of species spanning birds such as band-tailed pigeons (*Patagioenas fasciata* [Say, 1823]) (Fry and Vaughn 1977), western scrub-jays (*Aphelocoma californica* [Vigors, 1839]) (Carmen 2004; Koenig et al. 2009) and acorn woodpeckers (*Melanerpes formicivorus* [Swainson, 1827]) (Koenig and Mumme 1987; Koenig et al. 2008) to mammals including mice *(Peromyscus* spp. [Gloger, 1841]) (Merritt 1974), wood rats (*Neotoma fuscipes* [Baird, 1858]), ground squirrels (*Spermophilus beecheyi* [Richardson, 1829]), mule deer

TABLE 2. RESULTS OF MIXED-EFFECTS MODELS OF SEROTINY. Variables included in each model are designated by an "X". Model averages include only models for which the model weight > 0.01 (models 1–4 for valley oak; 1–2 for coast live oak). Values are standardized estimates ± standard errors. Spring phenology was only included in the valley oak models.

| Model	Focal tree acorn crop	Overall mean acorn crop	Mean winter temperature	Winter rainfall	Tree dbh	Xylem water potential	Soil N availability	Soil P availability	Spring phenology	$DAIC_c$	Model weight
Valley oak											
1	X									0.0	0.409
2	X		X							0.7	0.292
3	X	X				X				1.3	0.065
4	X	X								3.7	0.022
5	X								X	5.9	0.002
6	X				X					11.2	<0.001
7	X			X						13.7	<0.001
8	X						X	X		20.9	<0.001
9	X	X								23.1	<0.001
10 (null)										27.3	<0.001
11	X	X	X	X	X	X	X	X	X	52.7	<0.001
Model average	0.55 ± 0.09	0.03 ± 0.10	0.12 ± 0.09	—	—	0.05 ± 0.10	—	—	—	—	—
Coast live oak											
1	X	X							—	0.0	0.972
2	X			X					—	7.9	0.019
3	X								—	10.7	0.005
4	X					X			—	11.5	0.003
5	X		X						—	13.8	0.001
6	X				X				—	20.2	<0.001
7	X						X	X	—	24.9	<0.001
8	X	X	X	X	X	X	X	X	—	37.3	<0.001
9	X	X							—	47.1	<0.001
10 (null)									—	109.6	<0.001
Model average	0.61 ± 0.08***	0.27 ± 0.07		-0.27 ± 0.06					—	—	—
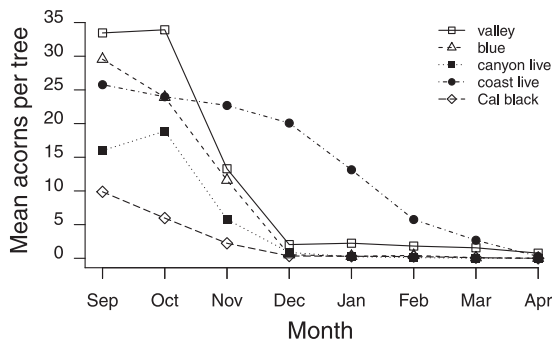
FIG. 1. Mean number of acorns counted during surveys of trees of the five species of oaks by month averaged across all years.
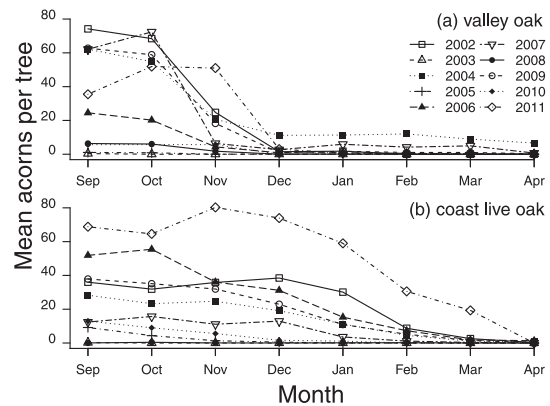

FIG. 2. Mean number of acorns counted during surveys of trees by year for (a) valley oak and (b) coast live oak. Although valley oak generally lost their acorns by December, this was not the case in 2004. Coast live oak was the most variable, retaining a large fraction of its crop into the next spring in 2011–2012 but otherwise generally dropping acorns by February.

(*Odocoileus hemionus* [Rafinesque, 1817]), and feral pigs (*Sus scrofa* [Linnaeus, 1758]) (Pavlik et al. 1991). Although most of the mammals typically forage on acorns that have fallen from trees, many of the birds frequently, and in some cases primarily, forage on acorns present in the canopy. Such species would potentially benefit by having access to trees that hold onto their acorns through the winter and into the next spring, even if such serotiny was relatively rare.

We report here on the finding that acorns of two species of California oaks are weakly serotinous, being retained in the canopy for six and rarely up to nine months post-maturity. Serotiny has not been previously recognized or quantified in California oaks, with the exception of data on two individuals of each of four species (including coast live oak, which were found to retain their acorns significantly longer than the other species) measured during a single year by Carmen (2004).

Given that wildlife in our study typically begin eating immature acorns as early as August, this means that in some years acorns are present in the canopy of a small number of trees for virtually the entire year. Although the proportion of trees with substantial number of acorns retained through the winter is small, such trees may potentially attract and benefit wildlife from a relatively wide area around individual trees. Thus acorns, although usually considered an ephemeral 'pulsed' resource (Ostfeld and Keesing 2000), are in some cases available to canopy-foraging California birds throughout the year, both through storage of mature acorns by some species but also through the retention of acorns on some trees.

Serotiny was most prevalent among coast live oaks, but was found occasionally in valley oaks as well. The latter is particularly surprising given that valley oaks are deciduous. Indeed, tree 161, which exhibited an unprecedented degree of serotiny in 2005–2006 (Table 2), retained its acorns, but not its leaves, throughout this particular winter (W. Koenig personal observa-

TABLE 3. CASES OF TREES RETAINING A SUBSTANTIAL NUMBER OF ACORNS (LN30 > 2) INTO APRIL, SIX MONTHS AFTER NORMAL ACORN MATURATION.

| Species	Tree number	Crop year	Acorns counted in September	Acorns counted in April
Valley oak	161	2004	156	93
Valley oak	161	2011	118	9
Valley oak	201	2007	108	9
Coast live oak	162	2011	59	22
Coast live oak	166	2011	64	20
Coast live oak	176	2011	62	10
Coast live oak	187	2011	42	12
Coast live oak	194	2011	24	7
Coast live oak	195	2006	85	23
Coast live oak	195	2011	83	67
Coast live oak	202	2011	132	37
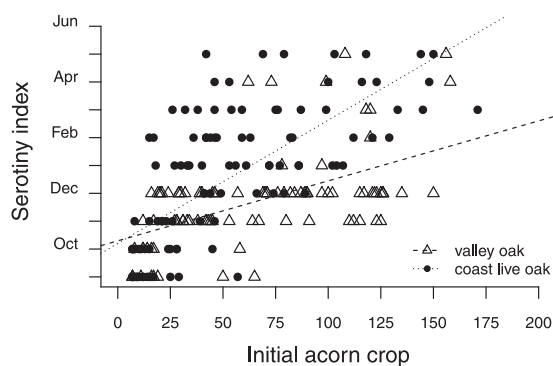
FIG. 3. The serotiny index (first month that seven or fewer acorns were counted) plotted again the initial size of the tree's acorn crop for valley and coast live oak. Only included are trees for which the initial number of acorns counted was at least seven; $N = 184$ (valley oak) and $N = 169$ (coast live oak). In both cases, the acorns of trees with larger initial crops were present in the canopy for longer than trees with smaller acorn crops.

tion). We did not observe significant serotiny in any year among blue oak, canyon live oak, or California black oak.

Among the species where serotiny was present we found that acorn retention was concordant among individuals across years; that is, trees that held onto their acorns relatively longer in one year did so in other years as well, compared to other trees in the population. To a large extent this is most likely a side effect of the strong positive relationship between seed retention and individual productivity, which varies considerably among individuals (Koenig et al. 1994b). Because of this relationship, trees that are consistently good acorn producers will inevitably exhibit greater serotiny than relatively unproductive trees.

What drives the differences in seed retention we observed? We suggest three hypotheses. First, interspecific differences correlated to some extent with differences in the water relationships of mature trees. Specifically, the two weakly serotinous species, coast live oak and valley oak, are drought-intolerant species that regularly tap into the water table, while blue oak and California black oak, which do not exhibit serotiny, are relatively drought-tolerant species whose root system often does not tap into easily available ground water (Knops and Koenig 1994). Countering this pattern is canyon live oak, another drought-intolerant species but one that did not retain acorns beyond maturity in November. Furthermore, it is unclear how or why drought tolerance of mature trees might be related to seed retention.

Second, and perhaps more likely, is that interspecific differences in serotiny are related to differences in acorn morphology, which differ

considerably among species and have important consequences for water loss and desiccation resistance of acorns (Xia et al. 2012). Snow (1991), for example, found that harvested coast live oak acorns desiccated faster than Engelmann oak acorns (Q. engelmannii), a result that he related to differences in distributions of these species at the Santa Rosa Plateau in Riverside County, California. Seed retention in coast live oaks might thus serve to reduce dehydration and extend the lifespan of acorns during dry winters, a hypothesis supported by the significant negative relationship between serotiny in this species and winter rainfall. Studies of the morphology and water relations of California acorns are needed in order to critically test this possibility.

Third, acorn retention may facilitate dispersal by scatter-hoarding birds, which would have a longer time to harvest and disperse acorns before they fall to the ground and are consumed by rodents or deer. The bird species most likely to be involved is the western scrub-jay, which is well-known to harvest and store large numbers of acorns (Grinnell 1936; Carmen 2004; Koenig et al. 2009); the other major avian acorn harvest in this habitat, the acorn woodpecker, stores acorns in granaries (Koenig and Mumme 1987) and is a relatively inefficient acorn dispersal agent.

There are no data to support the hypothesis that either of these species preferentially harvest or store either coast live oak or valley oak acorns (Koenig and Benedict 2002; Koenig et al. 2008), and thus this hypothesis cannot explain the interspecific differences in serotiny we observed. This hypothesis may, however, play an important role in selecting for serotiny in general among these species, since individuals trees could potentially gain considerable benefits by retaining acorns in the canopy beyond the time they are available from other trees, thereby enhancing the harvesting and dispersal of their seeds. Clearly the drivers of interspecific differences in seed retention in oaks deserve further study.

CONCLUSION

Intraspecifically, we found that serotiny in both coast live oak and valley oak is strongly related to a tree's initial crop size. Beyond this, we detected no significant factor predicting serotiny in valley oak while among coast live oak serotiny was more pronounced during dry winters and when the overall coast live oak acorn crop was large. Thus, there appears to be no simple driver of differences in seed retention among years or within species in California oaks beyond a relationship in coast live oak with winter rainfall. Other potentially important factors remain to be examined; for example, it is possible that differences in the frequency or strength of winter storms (which is potentially correlated with

winter rainfall) drives annual differences in serotiny. Similarly, the possibility that seed retention has coevolved with avian seed dispersers remains a strong possibility. There is much to be learned by further study of the causes and consequences of seed retention in California oaks, as well as other California taxa.

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