

***Quercus lobata* Seedlings and Conspecific Neighbors: Competitors or Allies?¹**

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Abstract

In conducting oak restoration, it is common to plant at least two acorns per location to increase the probability that at least one will germinate and produce a seedling. If both seedlings successfully establish, one is generally removed to reduce possible competition. To test the assumption that the near neighbors are competing, we examined several cohorts of valley oak (*Quercus lobata*) seedlings established from acorns planted at the University of California Sedgwick Reserve in Santa Barbara County. We assessed correlations between presence/absence of neighbors and individual performance, hypothesizing that seedlings that emerged without a near neighbor (only one of the two acorns produced a seedling) would have better survival and growth than those with both acorns producing seedlings within one planting location. However, over a 7 to 10 year period, we found that survival rates and mean height of *Q. lobata* with neighbors did not differ significantly from those that emerged and grew without a near neighbor. We also conducted removal experiments in which pairs of established near neighbor seedlings were randomly assigned to one of two treatments: control (both seedlings remain intact) and removal (one seedling in the pair is removed and the target remains). Growth (height, stem diameter at base, absolute and relative growth rates) was not significantly different between control and removals for any year (2011–2014). We also measured access to water via pre-dawn xylem pressure potentials (PDXPPs) in early fall. Contrary to predictions, PDXPPs were not significantly different between the treatments for any year (2011–2014). Both our observational and experimental findings indicate that near neighbors do not have negative impacts on performance for early life stages in *Q. lobata*. We also suggest that there may be advantages to allowing near neighbors to coexist in restoration plantings, where survival of the target individual is still uncertain.

Key words: competition, neighbor, predawn xylem pressure potential, seedling growth, seedling survival, water availability

Introduction

Ecological theory predicts that when resources are limited, intraspecific competition may be particularly strong since members of the same species are likely to be using the same resources in the same way (Connell 1983). Thus, it is reasonable to assume that an oak seedling with a “near neighbor”—a seedling emerging from an acorn deposited in the same microsite—will face competition and have reduced access to resources resulting in reduced growth and/or survival.

Oak seedlings may establish with near neighbors under natural or artificial circumstances. Acorn “planters” such as jays, magpies, or ground squirrels may cache or scatter-hoard multiple acorns per location (Carmen 1988) and some of those acorns may survive to germinate. Humans conducting oak restoration also disperse acorns in clusters, generally planting at least two acorns per location to increase the probability that at least one will germinate and produce a seedling (Bernhardt and Swiecki 1991). If both seedlings successfully establish, one is generally removed to

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reduce competition (McCreary 2001); that is, we assume that near neighbors in such close proximity are competing. In Mediterranean climates such as southern California, water availability is low during the summer drought and can limit growth of young oaks (Mahall and others 2009). However the interactions of oak seedlings as near neighbors and their effects have not been previously investigated.

To test the hypothesis that there is competition between near neighbors, we examined several cohorts of valley oak (*Quercus lobata*) seedlings established from acorns planted at UC Sedgwick Reserve, employing both observational and experimental approaches. *Q. lobata* is a California endemic species that has been severely impacted by human activities (reviewed in Tyler and others 2006) and even in remnant stands is generally in decline, with continued future declines likely (Davis and others 2011). These trends have contributed to interest in public and private conservation and restoration planting of this species (Alagona 2008, Giusti and others 2004). Thus, understanding the interactions of restored seedlings may be useful in guiding this effort.

Methods

Research was conducted at the University of California Santa Barbara's Sedgwick Reserve, located in central Santa Barbara County, California. The climate is Mediterranean, with hot dry summers and cool wet winters. Mean annual rainfall (calculated for the period 1950-2014) is 404 mm.

As part of large-scale field experiments related to oak restoration, acorns of coast live oak (*Q. agrifolia*) and valley oak have been planted at the reserve across a range of savanna and open woodland sites, starting in 1997 (Tyler and others 2002). For the present study we examined a subset of those plantings, specifically several different cohorts of valley oak seedlings established from acorns. In all cases, two acorns per planting location were sown in planting holes that were approximately 15 cm wide. Thus, acorns were placed within 5 cm from each other. Plantings were carried out in January-February of the given year. Here we only include seedlings that had been caged to exclude herbivores and seed predators, in order to examine interactions of seedlings in the absence of other potentially confounding factors. Protection from vertebrate animals was achieved with 1 cm mesh hardware cloth cylinders (diameter 10 cm, height 1.2 m). No supplemental water was provided to seedlings at any stage. Detailed methods described in Tyler and others (2002).

Observational study

In two cohorts (planted in 1998 and 2003) we assessed correlations between presence/absence of neighbors and individual performance, comparing survival and growth of seedlings that emerged without a near neighbor (only one of the two acorns produced a seedling) to those with both acorns producing seedlings within one planting location. Measurements of survival (presence or absence) and growth (stem height, diameter at base and absolute and relative growth rates) were made annually in late spring to early summer.

Experimental study

We established removal experiments in 2010 using seedling pairs that had been planted as acorns in 2003, and remained with both neighbors surviving to 2010. As above, all seedlings had established within cages to exclude herbivores. These

plantings were distributed across two different sites at the reserve (Lisque and Figueroa). Within each site, seedling pairs were stratified by size and then randomly assigned to either the control treatment (both seedlings left intact) or removal treatment, in which the smaller of the two seedlings was removed. Growth was measured annually (2010-2014). At one site (Figueroa) we also measured access to water via pre-dawn xylem pressure potentials (PDXPPs) in early fall, 2010-2014.

Results

Observational study

Germination and establishment rates were high in all locations in both cohorts. A large proportion of planting locations in both 1998 and 2003 cohorts established with two seedlings (both acorns germinated and emerged). Of the 144 locations planted in 1998, more than half (53 percent) had both acorns germinate and thus two seedlings establish, and 32 percent had one acorn germinate with a seedling established. In 2003, 59 percent of the 100 planting locations had two seedlings establish, and 24 percent had one seedling establish.

In each of these two planting cohorts, we compared survival of seedlings that emerged without a near neighbor (only one of the two acorns produced a seedling) to those with both acorns producing seedlings within one planting location (fig. 1). In neither cohort was survivorship higher for the seedlings growing alone, that is, without a neighbor. For the 1998 cohort, overall survivorship for the 10-year period from 1998 to 2008 was 51 percent for seedlings that started with two per location (with a near neighbor) compared to 45 percent for seedlings that started with one per location. Similarly, for the 2003 cohort, overall survivorship from 2003 to 2010 was 80 percent for seedlings starting with a neighbor, and 71 percent for those starting without a neighbor.

We compared the growth of seedlings that began with two per location and retained a neighbor for the whole study interval, to those that began with one per location (fig. 2). In both cohorts we found that seedling height (fig. 2), growth, and relative growth rates were not significantly different with vs. without a neighbor in any year (independent samples t-tests for each year and parameter, $P > 0.05$).

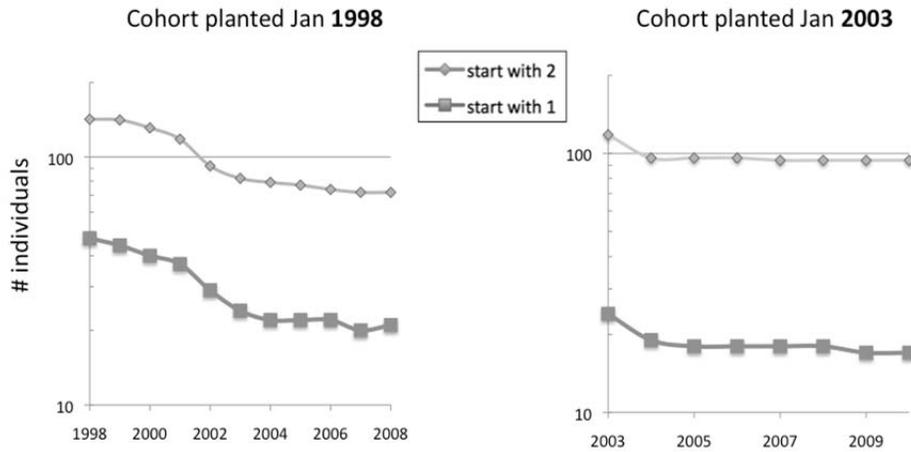


Figure 1—Number of individuals surviving over time. Plotted separately are the seedlings that started with two individuals per planting location (with a near neighbor) and those that started with only one per location. Data are for two different planting cohorts (1998 and 2003), and are plotted on a log-scale to facilitate comparison of survival rates since starting numbers vary.

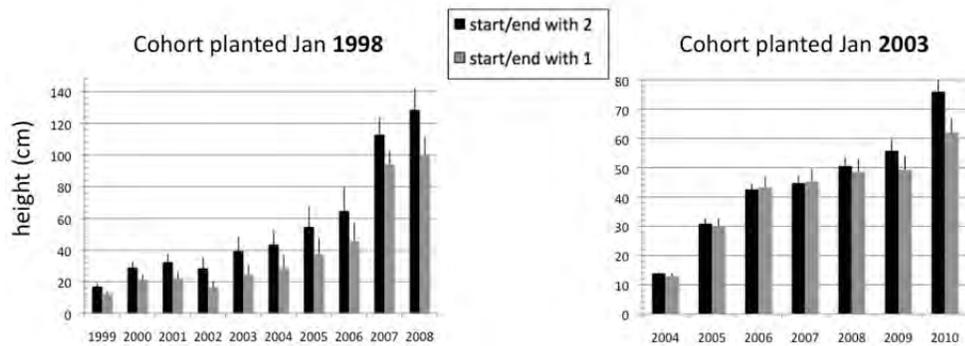


Figure 2—Mean seedling height (and one s.e.) over time. Plotted separately are the seedlings that started and ended with two individuals per planting location (with a near neighbor for the entire period) and those that started with only one per location. Data are for two different planting cohorts (1998 and 2003).

Experimental study

We compared seedlings heights of target (largest) individuals in controls (neighbor intact) to removals (neighbor removed) (fig. 3). Seedling heights did not differ in 2010 before the removal treatment was initiated (independent samples t-tests, both sites 2010, $P > 0.05$). In every subsequent year at both sites, we found no significant difference in mean target seedling height between the treatments (independent samples t-tests, both sites each year, $P > 0.05$). We found the same pattern (no statistical difference between treatments) when we examined other measures of growth (diameter at base, annual growth or relative growth rate).

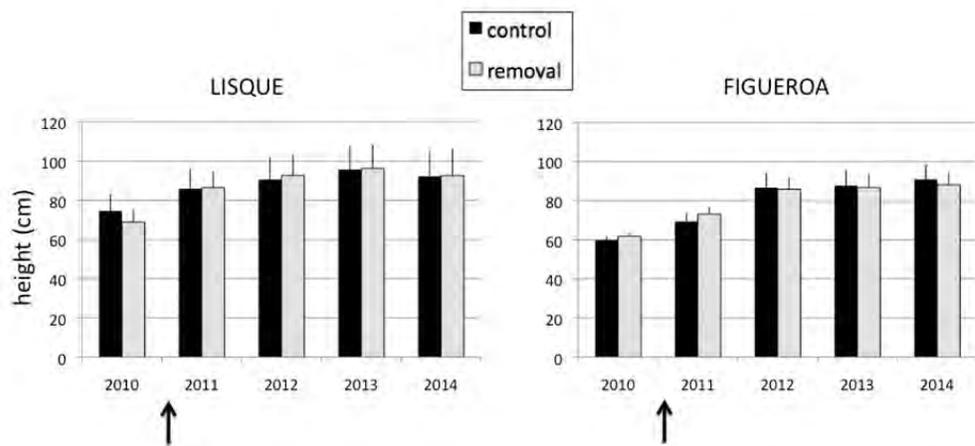


Figure 3—Effect of neighbor removal on seedling growth. Mean seedling height (and one s.e.) of target seedlings in two treatments: control (neighbor intact) and removal (neighbor removed). Data are for two different sites (Lisque and Figueroa). Arrows indicate the initiation of the experiment.

Assessment of predawn xylem pressure potentials of target seedlings in early fall from 2011 to 2014 have revealed no significant differences in water availability between seedlings grown with (controls) vs. those without a neighbor (removals) (independent samples t-tests, each year $P > 0.05$). (table 1).

Table 1—Mean predawn xylem pressure potentials, bars (1 s.e.). n = 13 for each treatment

Year	Control	Removal
2011 (Sept 23)	-18.5 (1.8)	-16.1 (2.1)
2012 (Oct 2)	-22.3 (1.4)	-21.8 (1.6)
2013 (Sept 14)	-18.3 (1.1)	-17.5 (1.1)
2014 (Aug 24)	-17.6 (1.1)	-18.5 (1.6)

Discussion

Oak seedlings that have emerged from the same microsite and are growing within a few centimeters of each other seem likely to interact in some way. Though light may not be limiting in savanna habitats, water may be (Baldocchi and others 2004, Mahall and others 2009). Valley oak is a winter-deciduous species and grows in spring as well as during the summer drought; therefore it is not unreasonable to suspect that near neighbors might be competing for water. Previous studies on valley oak seedling physiology have found that while valley oak are drought-tolerant, photosynthesis and

growth rates may be correlated positively with access to water in dry years (Mahall and others 2009).

Surprisingly, both our observational and experimental studies found no significant differences in performance of seedlings that are growing in close proximity to a conspecific neighbor to those without a neighbor (potential competitor). In fact, though not statistically significant, our survey of seedlings over a 10 year (1998 cohort) and 7 year (2003 cohort) period revealed that survivorship was slightly higher for seedlings growing with a neighbor. This result suggests that either the planting locations where two acorns germinate and two seedlings establish might be “better” in general, or that there may even be a positive interaction between neighboring seedlings. However, if the latter were true, we would expect to see a negative effect of neighbor removal, which was not the case in our experimental studies.

Rather, our finding of no significant differences in all cases—both observational studies and removal experiments—suggests that there are neither net negative (competitive) nor net positive (facilitative) interactions of these near neighbors in early life stages. It has been stated that “neutralism” should not be considered a type of ecological interaction (Arthur and Mitchell 1989), yet it appears in the present study that “neutralism” is the most appropriate term describing the net intraspecific interaction observed in young oak seedlings.

Our results have restoration implications, in that we found no evidence to advocate removal of neighbors in the seedling or even sapling size classes. We propose that there may in fact be justification for retaining near neighbors in restoration plantings where they are present. The first reason is that even seedlings that start with a neighbor may lose that neighbor eventually to various natural causes of mortality. If those locations had been culled to one seedling artificially, there is no “understudy” to take its place if it dies. A second reason to maintain a neighbor adjacent to the desired or target individual is that a neighbor may protect against or reduce impacts from herbivores. For example, at our study site we have observed large lone saplings become heavily damaged by bark stripping or damaged due to antler rubbing by deer. We suggest that such damage may have been less severe if another (especially a shorter) neighbor had been present. Such predictions warrant further experimental investigation. Based on our studies and additional observation, we propose that a conspecific near neighbor could in fact serve as an ally or at the very least be a neutral companion in the first decade in the life of a valley oak.

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References

- Alagona, P.S. 2008. **Homes on the range: cooperative conservation and environmental change on California's privately owned hardwood rangelands.** *Environmental History* 13: 325–349.
- Arthur, W.; Mitchell, P. 1989. **A revised scheme for the classification of population interactions.** *Oikos* 56: 141–143.
- Baldocchi, D.D.; Xu, L.; Kiang, N. 2004. **How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak–grass savanna and an annual grassland.** *Agricultural and Forest Meteorology* 123:13–39.
- Bernhardt, E.A.; Swiecki, T.J. 1991. **Minimum input techniques for valley oak restocking.** In: Standiford, Richard B., tech. coord. Proceedings of the symposium on oak woodlands and hardwood rangeland management. Gen. Tech. Rep. PSW-126. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 2–8.
- Carmen, W.J. 1988. **Behavioral ecology of the California scrub jay (*Aphelocoma coerulescens* California): a non-cooperative breeder with close cooperative relatives.** Berkeley, CA: University of California, Berkeley. Ph.D. dissertation.
- Connell, J.H. 1983. **On the prevalence and relative importance of interspecific competition: evidence from field experiments.** *American Naturalist* 122: 661–696.
- Davis, F.W.; Tyler, C.M.; Mahall, B.E. 2011. **Consumer control of oak demography in a Mediterranean-climate savanna.** *Ecosphere* 2(10): art108.
- Giusti, G.A.; Standiford, R.B.; McCreary, D.D.; Merenlender, A.; Scott, T. 2004. **Oak woodland conservation in California's changing landscape.** Berkeley, CA: University of California, Berkeley Integrated Hardwood Range Management Program.
- Mahall, B.E.; Tyler, C.M.; Cole, E.S.; Mata, C. 2009. **A comparative study of oak (*Quercus*, Fagaceae) seedling physiology during summer drought in southern California.** *American Journal of Botany* 96: 751–761.
- McCreary, D.D. 2001. **Regenerating rangeland oaks in California.** Pub. 21601. Oakland, CA: University of California, Agriculture and Natural Resources.
- Tyler, C.M.; Kuhn, B.; Davis, F.W. 2006. **Demography and recruitment limitations of three oak species in California.** *Quarterly Review of Biology* 81: 127–152.
- Tyler, C.M.; Mahall, B.E.; Davis F.W.; Hall, M. 2002. **Factors limiting recruitment in valley and coast live oak.** In: Standiford R.B.; McCreary, D.; Purcell, K.L., tech. coords. Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. Gen. Tech. Rep. PSW-GTR-184. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 565–572.