MADROÑO, Vol. 54, No. 4, pp. 269–274, 2007

LONG-TERM GROWTH AND PERSISTENCE OF BLUE OAK (*QUERCUS DOUGLASII*) SEEDLINGS IN A CALIFORNIA OAK SAVANNA

WALTER D. KOENIG
Hastings Reservation and Museum of Vertebrate Zoology, University of California Berkeley, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924
koenigwd@berkeley.edu

JOHANNES M. H. KNOPS
School of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, NE 68588

ABSTRACT

We report on growth and survivorship of two cohorts of blue oaks *Quercus douglasii* Hook. & Arn. (Fagaceae) monitored at Hastings Reservation in Monterey County, California, the first growing in an unprotected old field and measured as seedlings in 1965 and the second planted as acorns in 1985 in several sites differing in their degree of protection from grazing. Growth of all individuals was extremely slow: among those surviving in the first cohort, mean (± SD) height in 2006 was only 76.7 ± 45.0 cm for an average growth rate of 1.8 cm yr^{-1}, and only one of the original 73 oaks had grown taller than 1.5 m while one was still a seedling 28 cm in height 41 yr after being first marked. Of the second cohort, mean height 21 yr after planting was 54.3 ± 31.4 cm. None of these latter individuals had grown out of the sapling stage while 25% were still seedlings < 30 cm in height. Growth of this second cohort was significantly greater when protected from grazing and when growing in the open rather than in the shade. Although growth was slow, survivorship of oaks first measured in 1965 was high, indicting that individuals can live for decades despite significant grazing pressure. Our results confirm the difficulties of inferring age from size of blue oaks, since individuals just achieving the height at which they are typically cored may be 50 or more years old. They also indicate that regeneration, although very slow, can occur in open oak savannas in California despite significant grazing pressure. Whether the observed amount of regeneration is sufficient for long-term sustainability will require continued monitoring and modeling of oak demography.

Key Words: blue oak, *Quercus douglasii*, regeneration, seedling growth, survivorship.

The health and status of California's vast oak woodlands is one of the more vexing questions currently facing the state's ecologists and rangeland managers. Are they declining, and if so, is it due to grazing, competition from exotic grasses, fire suppression, climate change, or some combination of factors (Griffin 1981; Muick and Bartolome 1987; Gordon and Rice 2000; Kueppers et al. 2005; Tyler et al. 2006)? In the case of the blue oak *Quercus douglasii* Hook. & Arn. (Fagaceae), a species dominating nearly 2×10^6 ha in the state (Standiford 2002), the evidence is mixed, as demographic surveys almost uniformly reveal limited recruitment but long-term studies have generally shown no decline in tree density (Tyler et al. 2006).

Resolving this problem lies in obtaining more extensive data on the demography of the species in question. Unfortunately this has not proved to be easy, since individuals can live hundreds of years and are logistically difficult to age, making it virtually impossible to estimate when prior regeneration events occurred, much less the extent to which such events are episodic and dependent on particular ecological circumstances.

Here we report on the persistence and growth of blue oaks planted as acorns or first marked as natural seedling recruits as part of studies going back to 1965. Our results indicate that the relationship between size and age in this species may be even more problematical than previously suspected. They also confirm the remarkable degree to which blue oak saplings can cling to what appears to be a precarious existence over many years until such time that they are able to achieve sufficient height to escape browsing.

METHODS

The study was conducted at Hastings Reservation, Monterey County, California, established in 1937. Thus, although cattle grazing, clearing, and various agricultural activities occurred historically, no such disturbances took place during the time period covered by this study. Hastings is located approximately 50 km from the coast and averages 53.3 cm of rain $year^{-1}$ (mean of 67 yr between 1 July 1939–30 June 1940 and 1 July 2005–30 June 2006; records from Reserve headquarters). Individual oaks followed were either planted or monitored in two areas of the Reserve. The first, North Field, was an old field cleared around 1900 and used until 1937 for hay and grapes. North Field was left open the entire time and was thus regularly grazed by mule deer (*Odocoileus hemionus*) as well as smaller mammals including gophers and mice. The second area (Arnold Road Flat) was within a large exclosure built in 1983 for a separate study and thus was not grazed by large herbivores during the study, but was open to smaller mammals.

Two sets of oaks were examined. The first, called the "White" cohort, consisted of 73 naturally-recruiting blue oak seedlings in North Field that were tagged and measured (height only) in April 1965 by K. L. White. Three of the seedlings were new in spring 1965. All others were pre-1965 seedlings when tagged. Their ages were not known, but all were short (mean ± SD = 6.5 ± 3.2 cm, range 2–18 cm) and were presumably thought to have been from acorns produced in fall of 1963 that sprouted in spring 1964. It was not possible to identify the original 1965 vs. pre-1965 seedlings, and thus all individuals in the White cohort are assumed to have been at least 42 yr old in 2006.

Subsequent to marking, seedlings and saplings were monitored and measured by J. R. Griffin on 10 occasions (June 1969, January 1976, September 1979, January 1984, June 1986, June 1987, August 1988, June 1989, June 1990, and February 1991). With some exceptions, at each sampling period the height of tallest sprout from each remaining seedling was measured, while starting in 1988, the greatest width of each seedling was measured. Finally, on 5 October 2006, we examined all individuals whose identity we could be confident of and measured their height, width, and the basal diameter of stems > 0.5 cm at 5 cm above the ground. When multiple stems were present, they were combined to yield a single value for the overall diameter that matched the total basal area of all stems. Size and growth rates are based on the 14 individuals we identified and measured in 2006.

The second set of oaks used in the study, called the "Menke" cohort, consisted of individuals from a study of water relations of California oaks by J. W. Menke initiated in 1985. Blue oak acorns were planted in several 5 × 5 blocks varying in their degree of protection from grazing and openness. Block 1 (not protected; shaded) was planted adjacent to several blue oak trees near North Field, but otherwise not protected from grazing in any way. Block 2 (protected; open), also near North Field, consisted of acorns planted in the open, but protected by wire mesh baskets up to 40 cm in height that were opened up in 1992 to allow free growth of saplings that had in some cases had grown out of or up to the top of the baskets. Two additional sets of acorns were planted within a deer exclosure on Arnold Road Flat. Block 3 (protected; open) was planted in an open area within the plot, while block 4 (protected; shaded) was planted under partial cover of a mature blue oak within the plot; seedlings in both these blocks were also protected by wire mesh baskets 40 cm in height. For analysis, we divided individuals into those that were not protected (block 1) vs. protected (blocks 2–4)(variable "protection"), and those that were growing in the open (blocks 2 and 3) vs. those that were shaded (blocks 1 and 4)(variable "shade").

We measured the maximum height, maximum width, and basal diameter at 5 cm above ground on 5 October 2006 of all individuals we could unambiguously identify as having been from the original set of acorns based on remaining wooden stakes and their location within the original grid on which acorns were originally planted (Fig. 1). All individuals were thus known to be 21 yr old at the time they were measured. No data from prior years was available. We used the two categories of "protection" and "shade" to quantify the effects of these variables on growth of the saplings using general linear models. Survivorship could not be measured in these oaks, as we could not be certain how many had been planted initially.

Following Phillips et al. (1997), we classify individuals as "seedlings" (<30 cm in height), "saplings" (30–150 cm in height), "poles" (150–300 cm in height), and "adults" (taller than 3 m). Significant browsing by deer, where present, is expected up until individuals reach the pole size class (McCreary 2001). Values presented are means ± SD.

Results

White Cohort

Of the original 73 seedlings marked in 1965, J. R. Griffin found 64 (88%) in June 1969 and 18 (24.7%) in February 1991, while we successfully located 14 (19.2%) in 2006 (Fig. 2). These values represent minimum survivorship of the original seedlings, since other seedlings and saplings were present in the plot and it is possible that some lost their tags during the course of the study and could no longer be identified.

Growth of the seedlings varied considerably, with individuals at the end of the study an average of 76.7 ± 45.0 cm (range 28 to 200 cm) in height (Fig. 3), 90.6 ± 43.8 cm (range 13 to 174 cm) in width, and 4.3 ± 2.0 cm (range 0.7 to 7.7 cm) in basal diameter. The rate of growth was < 1 cm yr^{-1} in height during the first three decades (Fig. 4), and in one case (7% of surviving individuals) the oak was still in the seedling category (28 cm in height) in 2006, 41 yr after being initially marked. Of the remaining 13 oaks, 12 (86%) graduated to the sapling size class by 2006 and one (7%) achieved pole status, thereby being the only one of the original 73 seedlings to

FIG. 1. One of the Menke plots in December 2006. The wire mesh exclosures are approximately 40 cm in height. Note the wooden stakes and grid spacing of the seedlings used to identify them in 2006.

have completely escaped likely grazing by deer after (at least) 42 yr. Overall, the mean increase in height over the 42 yr was 1.83 cm yr^{-1} (range 0.67–4.76 cm yr^{-1}) and the mean increase in basal diameter of the 14 oaks (conservatively assuming that their original diameter was 0) was 0.10 cm yr^{-1} (range 0.05–0.18 cm yr^{-1}).

Although overall growth was slow, growth rate increased considerably near the end of the study (Fig. 4), presumably as height or width finally became sufficiently large to provide some protection against grazing. Overall, height was relatively well predicted by models including age as either a squared or exponential term (quadratic model: height $= -0.866 * \text{age} + 0.054 * \text{age}^2 + 15.1$, $F_{2,160} = 81.7$, $R^2 = 0.50$, $P < 0.0001$; exponential model: height $= 9.27 * e^{0.0399*\text{age}}$, $F_{1,161} = 140.8$, $R^2 = 0.46$, $P < 0.0001$).

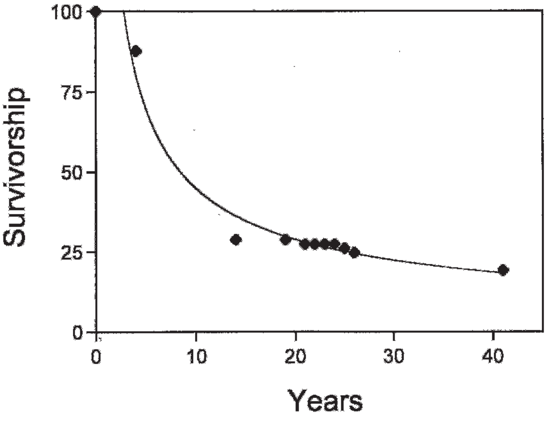

FIG. 2. Survivorship curve for the 73 White cohort first marked in 1965 as seedlings. The overall annual survivorship between 1965 and 2006 based on this sample is 96.1% $year^{-1}$. Line drawn is fit by a power curve: percent survivorship $= 193.3 \times (\text{years})^{-0.634}$.

Menke Cohort

We identified and measured a total of 32 oaks in the four Menke plots (Fig. 4). Overall, the mean height of the individuals in 2006 was 54.3 ± 31.4 cm (range 6–112 cm), while the mean diameter was 1.6 ± 0.5 cm (range 0.6–2.8) cm. After 21 yr, 8 of 32 (25%) were still seedlings < 30 cm in height, while the majority were saplings < 150 cm in height. Mean increase in height was 2.59 cm yr^{-1} (range 0.29–5.33 cm yr^{-1}) and mean increase in diameter was 0.074 cm yr^{-1} (range 0.029–0.133 cm yr^{-1}). Both protection (positively) and shade (negatively) affected height of the oaks, while only shade (negatively) influenced diameter (Table 1). At 21 yr of age, the height of these individuals was generally within the range expected from the White cohort, given that none of the latter had been protected from grazing in any way (Fig. 4).

DISCUSSION

Because of low survivorship, there have been few prior studies of growth by blue oaks seedlings and none that have covered as long a time period as that reported on here. Previous work by Phillips et al. (1997, 2007a, b) is the most extensive, demonstrating that up to 18% of blue

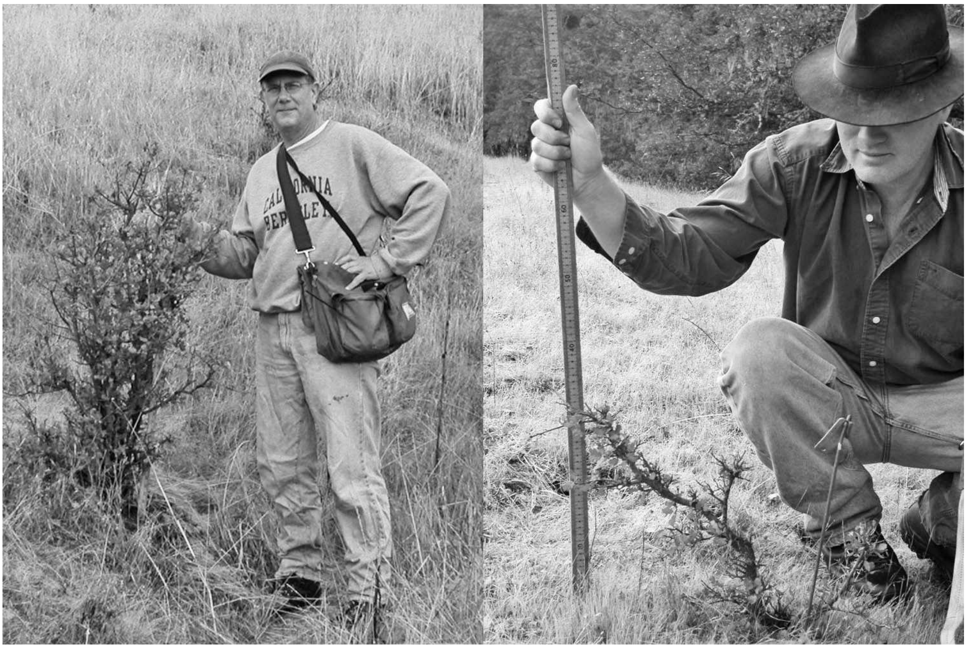

FIG. 3. The authors at two of the White individuals in October 2006. Left: tree 767, 7 cm in height in 1965, 112 cm (6.7 cm diam.) in 2006, by which time it was third-tallest tree of the 14 found. Right: tree 772, also 7 cm in height in 1965, 34 cm (1.9 cm diam.) in 2006, at which time it was the second-shortest tree still extant.

oak seedlings are 26 or more years old, that surviving seedlings grow very slowly and remain for a long time in the seedling size class, and that fencing significantly increases seedling growth. Our results confirm and extend these conclusions. Of 14 oaks known to have survived 41 yr after being marked, one (7%) was still a seedling 28 cm in height and only one successfully outgrew the sapling stage (>150 cm) during the course of the study.

Comparably slow growth was observed in a second set of oaks planted as acorns in 1985, one-fourth of which were still seedlings < 30 cm in height when 21 yr old. Growth in this second set was significantly greater among those that were protected from grazing by wire mesh baskets and (in some cases) deer fencing and among acorns that were planted in the open rather than in the shade. The latter of these findings matches the reduced photosynthetic capacity and root elongation rates among blue oak seedlings grown in the shade by Callaway (1992a, b), although Callaway's studies also found blue oak seedlings to be relatively shade tolerant and to survive better when cover was present.

In contrast, the first of these findings, that growth of seedlings was greater among those protected from grazing, is not surprising, as grazing by deer and rodents is well known to inhibit seedling growth (White 1966; Griffin 1981; Muick and Bartolome 1987; Tyler et al. 2002; Phillips et al. 2007a). However, growth rates were still low, even among individuals protected from grazing by large herbivores and, at least to some extent, by rodents as well. Of nine oaks growing within deer exclosures and protected by 40 cm wire mesh baskets, mean height after 21 yr was still only 65.6 cm (range 32–112 cm) and mean increase in height only 3.12 cm yr^{-1} (range 1.48–5.33 cm yr^{-1}).

Thus, under natural conditions, blue oaks at Hastings Reservation grow very slowly and may require several decades or more to outgrow the sapling stage even when protected from most sources of grazing pressure. Only after decades, once both the above-ground size of saplings is sufficient to provide some protection against uninhibited grazing by deer and other large herbivores and (perhaps in some cases) the below-ground roots are deep enough to access a more reliable water source, does the growth rate increase (Fig. 4).

Although growth was slow, even among protected seedlings, survivorship of seedlings was relatively high even when unprotected. Of 73 unprotected seedlings originally marked in 1965, 64 (88%) were alive four years later (Griffin 1981), for an annual survivorship of 96.8%, far higher than reported in other studies (Davis et al. 1991; Allen-Diaz and Bartolome 1992; Phillips et al. 2007b). Survivorship subsequently declined, but at least 18 (24.7%) were still alive 26 yr after marking in 1991 and 14 (19.2%) were alive in

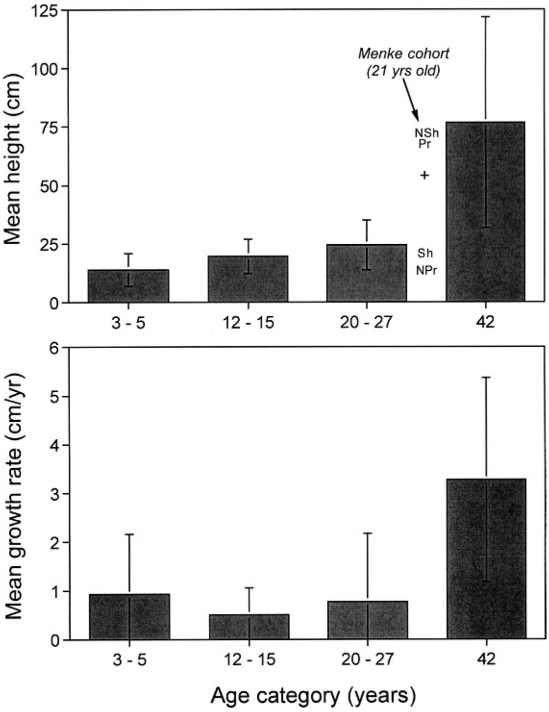

FIG. 4. Mean ± SD height (top) and mean ± SD annual increase in height (bottom) of the White cohort during the four decades of the study. Also marked in the top panel in between the last two categories are the mean heights of the 21-year-old Menke cohort, including the overall mean (+) and the means for seedlings that were not shaded (NSh), protected from grazing (Pr), shaded (Sh), and not protected from grazing (NPr).

2006, 41 yr after the start of the study. Thus, the overall survivorship of the 73 seedlings over the course of the study was at least 96.1% year^{-1}, and survivorship during the 15 yr between 1991 and 2006 was an impressive 98.3% year^{-1}. Possibly these high values are in part a result of having followed a cohort of seedlings that had already undergone considerable mortality by the time they were marked in 1965. Nonetheless, the ability of the seedlings to persist despite repeated and apparently intense browsing over decades is impressive.

Previous studies have found significant differences between the actual age structure of blue oaks stands based on tree-rings and the predicted age structure based on diameter (McClaran and Bartolome 1990; Phillips et al. 1997). Our results suggest that in at least some cases there may be even greater discord between age and size of blue oaks than previously thought because of the length of time some individuals require to achieve the height necessary to escape significant browsing damage. Of the oaks in the White cohort, only one (1.4% of the original sample) had achieved a height of over 150 cm in 41 yr, making it into the "pole" stage at which browsing by large herbivores was no longer likely to significantly inhibit further growth. Conversely, one individual remained a seedling 28 cm in height 41 yr after being first marked. In the Menke cohort, only a small proportion of individuals (3 of 32, 9.4%) had achieved 1 m in height by age 21, and none had successfully grown out of the sapling stage. Clearly by the time many of these oaks graduate into the adult population they will be well over half a century old, and in some cases possibly much older, assuming they survive. At that point, measuring their diameter at breast height (DBH) will clearly yield a gross underestimate of their age. More problematically, even coring them will not provide a good estimate of their actual age, since individuals may have been 50 or more years old by the time they reach the height at which coring is generally performed.

A recent review of recruitment in blue oaks concludes that resolving the current controversy over the sustainability of California oak woodlands will require long-term monitoring, age-structure analysis, and population modeling (Tyler et al. 2006). Our results add to previous concerns that the second of these, age-structure analysis, will have to be conducted with caution and that even with extensive coring or clearing (Mensing 1992) it may not be possible to accurately pinpoint the years or even the general time periods when regeneration has taken place in the past in established stands.

With respect to the regeneration of blue oaks, our sample is clearly too small to draw many

TABLE 1. RESULTS OF TWO-WAY ANOVAS ANALYZING THE VARIABLES "PROTECTION FROM GRAZING" (PROTECTED, NOT PROTECTED) AND "SHADE" (SHADED, NOT SHADED) ON HEIGHT AND DIAMETER OF THE MENKE COHORT IN 2006, WHEN THEY WERE 21 YRS OLD.

	Mean ± SD (N)		F-value	P-value
	Yes	No		
Height (cm)				
Protection	68.4 ± 23.1 (24)	13.0 ± 4.8 (8)	4.49	0.043
Shade	20.1 ± 13.1 (11)	72.2 ± 21.6 (21)	8.80	0.006
Diameter (cm)				
Protection	1.67 ± 0.57 (24)	1.26 ± 0.39 (8)	2.67	0.11
Shade	1.13 ± 0.40 (11)	1.80 ± 0.49 (21)	13.8	0.001

conclusions. However, it is noteworthy that survivorship of naturally recruiting seedlings was relatively high, at least subsequent to when they were first marked. Furthermore, although only one of the original 73 seedlings had successfully grown out of the sapling stage after 41 yr, other individuals in this sample may eventually join it. Thus, regeneration is occurring, albeit at a painstakingly slow rate. Whether such a slow rate of regeneration is sufficient to maintain California's blue oak woodlands over the long term remains to be determined.

ACKNOWLEDGMENTS

We thank Keith White, Jim Griffin, and John Menke for planting and following the oaks used in this study and Mark Stromberg for archiving their field notes and pointing out the existence of their plots. The manuscript was improved by the comments of Claudia Tyler and an anonymous reviewer. Support for this project came from the University of California's Integrated Hardwoods Range Management Program.

LITERATURE CITED

ALLEN-DIAZ, B. H. AND J. W. BARTOLOME. 1992. Survival of *Quercus douglasii* (Fagaceae) seedlings under the influence of fire and grazing. Madroño 39:47–53.

CALLAWAY, R. M. 1992a. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology 73:2118–2128.

———. 1992b. Morphological and physiological responses of three Calfornia oak species to shade. International Journal of Plant Sciences 153: 434–441.

DAVIS, F. W., M. I. BORCHERT, L. E. HARVEY, AND J. C. MICHAELSEN. 1991. Factors affecting seedling survivorship of blue oak (*Quercus douglasii* H. & A.) in central California. Pp. 81–86 *in* R. B. Standiford (tech. coord.), Proceedings of the symposium on oak woodlands and hardwood rangeland management. U.S. Department of Agriculture Pacific Southwest Forest Range and Experiment Station General Technical Report PSW-126.

GORDON, D. R. AND K. J. RICE. 2000. Competitive suppression of *Quercus douglasii* (Fagaceae) seedling emergence and growth. American Journal of Botany 87:986–994.

GRIFFIN, J. R. 1981. Oak regeneration in the upper Carmel Valley, California. Ecology 52:862–868.

KUEPPERS, L. M., M. A. SNYDER, L. C. SLOAN, E. S. ZAVALETA, AND B. FULFROST. 2005. Modeled regional climate change and California endemic oak ranges. Proceedings of the National Academy of Sciences (USA) 102:16281–16286.

MCCLARAN, M. P. AND J. W. BARTOLOME. 1990. Comparison of actual and predicted blue oak age structures. Journal of Range Management 43:61–63.

MCCREARY, D. D. 2001. Regenerating rangeland oaks in California. University of California Agriculture and Natural Research Publication 21601, Oakland, CA.

MENSING, S. A. 1992. The impact of European settlement on blue oak (*Quercus douglasii*) regeneration and recruitment in the Tehachapi Mountains. Madroño 39:36–46.

MUICK, P. C. AND J. W. BARTOLOME. 1987. Factors associated with oak regeneration in California. Pp. 86–91 *in* T. R. Plumb and N. H. Pillsbury (tech. coords.), Proceedings of the symposium on multiple-use management of California's hardwood resources. U.S. Department of Agriculture Pacific Southwest Forest Range and Experiment Station General Technical Report PSW-100.

PHILLIPS, R. L., N. K. MCDOUGALD, R. B. STANDIFORD, D. D. MCCREARY, AND W. E. FROST. 1997. Blue oak regeneration in southern Sierra Nevada foothills. Pp. 177–181 *in* N. H. Pillsbury, J. Verner, and W. D. Tietje (tech. coords.), Proceedings of a symposium on oak woodlands: ecology, management and urban interface issues. U.S. Department of Agriculture Pacific Southwest Research Station General Technical Report PSW-GTR-160.

———, ———, E. R. ATWILL, AND D. MCCREARY. 2007a. Exclosure size affects young blue oak seedling growth. California Agriculture 61:16–19.

———, ———, D. MCCREARY, AND E. R. ATWILL. 2007b. Blue oak seedling age influences growth and mortality. California Agriculture 61:11–15.

STANDIFORD, R. B. 2002. California's oak woodlands. Pp. 280–303 *in* W. J. McShea and W. M. Healy, Oak forest ecosystems. Johns Hopkins University Press, Baltimore, MD.

TYLER, C. M., B. E. MAHALL, F. W. DAVIS, AND M. HALL. 2002. Factors limiting recruitment in valley and coast live oak. Pp. 565–572 *in* R. B. Standiford, D. McCreary, and K. L. Purcell (tech. coords.), Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. U.S. Department of Agriculture Pacific Southwest Research Station General Technical Report PSW-GTR-184.

———, B. KUHN, AND F. W. DAVIS. 2006. Demography and recruitment limitations of three oak species in California. Quarterly Review of Biology 81:127–152.

WHITE, K. L. 1966. Structure and composition of foothill woodland in central coastal California. Ecology 47:229–237.