TECHNICAL REPORT

Growing Valley Oak

by Tracy Hobbs and Truman P. Young

Acorn characteristics and container size affect germination and initial root and shoot growth of this important California species.

The propagation and establishment of woody seedlings are important aspects of many forest ecosystem restoration efforts. Two factors that play important roles in successfully growing woody plants are the size and overall quality of the seed and whether or not the seedlings are grown in containers. In this paper, we examine how container size, acorn size and shell integrity, and weevil infestation affect the germination, survivorship, and growth of valley oak (*Quercus lobata*) seedlings.

The issues we raise here are serious concerns for anyone restoring upland habitats in the western United States. Prior to disturbance, many of these ecosystems were populated by several tap-rooted oak species, including valley oak. These species often have not replaced themselves naturally and are difficult to restore by planting, either as seeds or container-grown seedlings (Muick and Bartolome, 1987; Adams and others, 1992; Swiecki and others, 1997). Knowing whether to be concerned about the effects of containers on tap-rooted oak seedlings and the effects of acorn size and weevil infestations of acorns on germination are, therefore, important pieces of information for restorationists working in these locales.

Previous Studies

Numerous studies have addressed how containers affect the development of seedlings in terms of both root and shoot growth (Halter and others, 1993; Gilman and Beeson, 1996; Mughal, 1996; McCreary and Lippitt, 1997; Van Iersel, 1997; Maejima and others, 1997; Marshall and Gilman, 1997; Ray and Sinclair, 1998; Wu and others, 1998, McCreary and Lippett, 2000). Most researchers have found that when plants remain in the containers too long, their roots can circle and become deformed. More importantly for restoration on dry sites, there is growing evidence that tap-rooting species grown in containers lose their tap roots permanently (Moore, 1985). This may account for their poor growth and survival on such sites (Halter and others, 1993; McCreary, 1995 and 1996; Welch, 1997). However, we lack species-specific information about how quickly tap roots reach the bottoms of containers and begin to die or become malformed. Seedling growth also depends on container size. Non-taprooting plants grown in large containers are taller than plants grown in small containers (Wu and others, 1998, Van Iersel, 1997). However, we still do not know how container size affects tap-rooted species after planting out.

Seeds are another factor. Growers wild-collect acorns of native California oaks for direct seeding and container stock. Even within a single seed crop, this seed is highly variable. It differs in size (weight), in severity of infestation by seed predators, and in degree of cracking—all factors that might influence the effectiveness and cost of a woodland restoration project.

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Many researchers have investigated how seed size affects germination, survivorship and shoot and root growth in various species (Baker, 1972; Winn, 1988; Hendrix and Sun, 1989; Tripathi and Khan, 1990; Hendrix and others, 1991; Leishman and Westoby, 1994; Aizen and Woodcock, 1996; Long and Jones, 1996; Murali, 1997; Negi and Todaria, 1997; Vera, 1997; Chacon and others, 1998; Kormanik and others, 1998; Bonfil, 1998; Ke and Werger, 1999). In most cases, large seeds had a higher probability of germination, germinated earlier, and produced seedlings with greater root and shoot weights than did small seeds. Seedlings grown from larger seeds may also have post-germination advantages. Seedlings produced from heavier acorns grew faster and had higher rates of survival in both tropical (Tripathi and Khan, 1990) and temperate (Bonfil, 1998) oak species. Rice and his colleagues (1993) found that in Douglas oak (*Q. douglasii*) seedling emergence increased significantly with seed size on dry sites, but not on mesic sites.

Studies on the effects on acorns of infestation by weevil larvae have produced contradictory results. Kaushal and his colleagues (1993) found that injury by weevil larvae reduced both germination and seedling growth, whereas Steele and his colleagues (1993) showed that partially consumed acorns had equal or greater germination percentage than undamaged acorns. The holes made by the weevils facilitate imbibition, but this may be offset by damage to the embryo or by the reduction in stored resources by the larvae.

Valley Oak

Valley oak is a deciduous white oak endemic to California that grows up to 90 feet tall. It occurs sporadically throughout the state at elevations below 5,600 feet (though not in deserts) and on the Channel Islands. It can be locally abundant on slopes, valleys, savannas, and along rivers. It is a common species in riparian restoration projects in California. The acorn is typically 1.2-2.0 inches long and 0.5-0.8 inches wide (Hickman, 1993)

Like most oaks, valley oak has tremendous year-to-year variation in acorn production (Koenig and others, 1994; Healy and others, 1999). Although research has focused on explaining the occasional years of high acorn production in various oak species (Sork and others, 1993), occasional years of exceedingly low production have received less attention. It is these years of reproductive failure that are a serious concern for those involved in restoration, especially since oaks (including valley oak) do not exhibit seed dormancy. Even in years of moderately low acorn production, sufficient seeds and seedling stock are usually available. However, major acorn crop failures disrupt restoration projects that depend on the availability of seeds in a particular year. Past patterns suggest that acorn production in other North American oak species was exceedingly low in previous El Niño years (1983-84 and 1991-92, see Figure 1 in Sork and others, 1993), and this is confirmed by the nearly total failure of valley oaks to set seed in the El Niño year of 1998. (The 1998 pattern is based on conversations with commercial providers of oak seeds and seedlings, and our own observations).

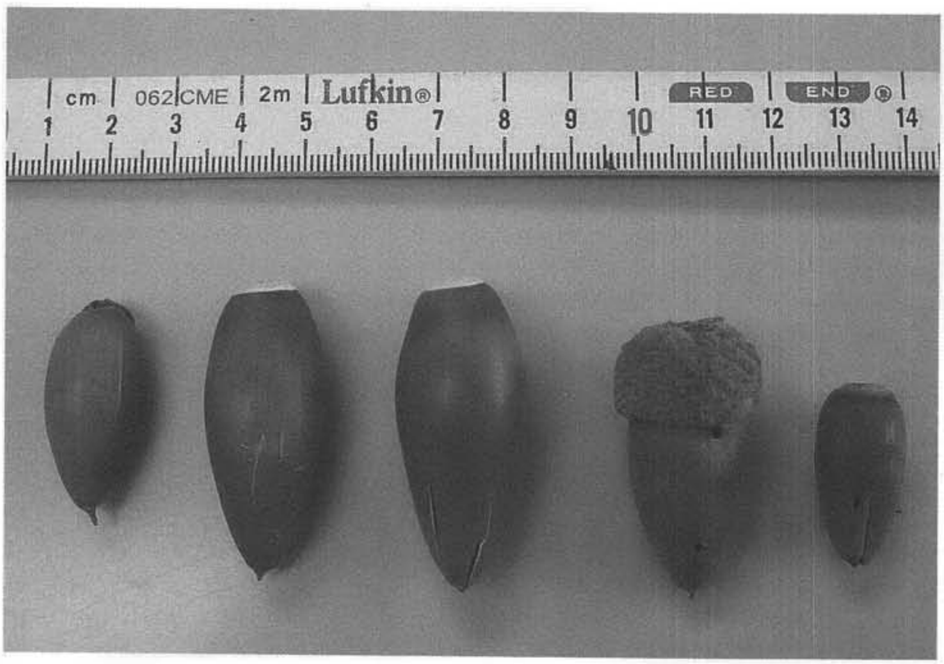


Figure 1. Valley oak acorns (left to right): small intact acorn; large intact acorn, acorn with cracks; acorn with two bruchid exit holes; acorn with both cracks and an exit hole. *Photo by Truman Young*

The Study

In the fall of 1998, we checked more than 100 valley oak trees in the vicinity of Davis and Winters, California without finding a single acorn other than a few aborted ones less than 0.2 inches in diameter. Commercial native-plant nurseries and seed suppliers were experiencing similar problems. We were fortunate to obtain about 500 valley oak seeds from a commercial source (Mistletoe Seeds) collected near Los Robles, California in October 1998.

We put the acorns in (-34°F) wet storage (conditions recommended by McCreary and Koukoura, 1990) until January 1999, when radicles began to emerge. On January 21 we weighed each acorn to the nearest milligram and scored it for the presence of cracks and the number of weevil exit holes (see Figure 1). In cracked acorns, cracks usually appeared as several splits at the distal ends. We divided the acorns randomly into two groups. We planted the first 162 acorns in a field experiment, spaced 2 meters apart and covered with about a centimeter of soil. We monitored these seeds only for predation and germination. We planted the second group of 272 acorns in a lath house, placing them on the surface of standard potting soil in 6x6x25-cm pots, which we then placed on benches and watered regularly.

From February 4 to March 11, we checked the lath house seeds weekly for germination, survivorship and additional exit holes. As the seedlings grew, we checked the bases of the pots regularly to determine whether the roots had exited the holes at the base of the pots. We also checked the field plantings at regular intervals for germination.

On February 25 (week five), we selected half of the lath house seedlings at random and transplanted them into larger pots (15x15x40 centimeters). In the week of March 11 (week seven) we measured all of the seedlings for shoot height to the nearest centimeter. We measured the shoot heights again on March 21 (week 13).

We used regression analysis to determine the effects of seed size and number of exit holes on germination, survival and growth. To control for the earlier emergence of larger seeds, we also regressed the residuals of the regression between date of emergence and seedling size (growth) against seed size. We analyzed the effects of cracking and container size using one-way analyses of variance.

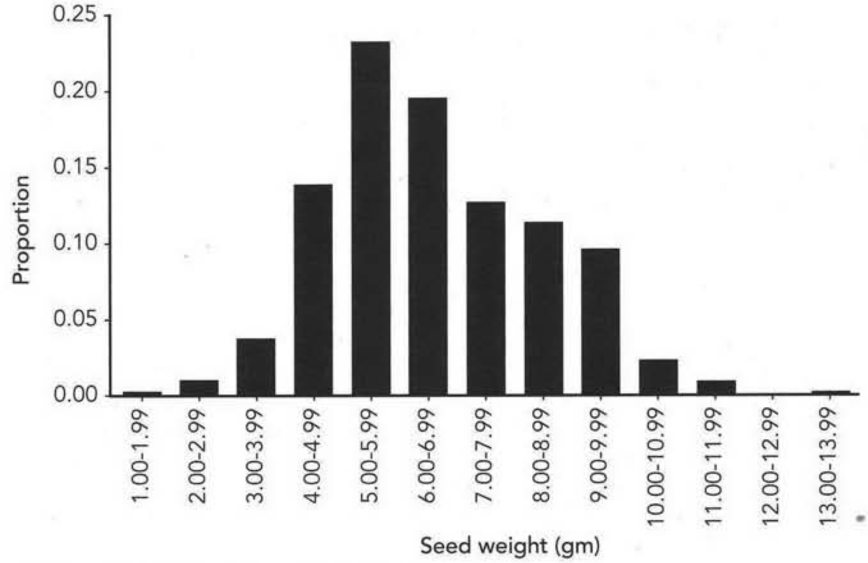


Figure 2. Size distribution of acorns, based on live weight.

Results

Germination

Approximately 40 percent of the field-planted acorns disappeared during the first two months after planting, presumably removed by seed predators, such as hares, ground squirrels, jays, and crows. Of the remaining acorns, 92 percent germinated. This was very similar to the germination percentage in the lath house (90 percent). Most of the acorns that germinated did so in the first four weeks after planting. Four percent of the acorns planted in the field and 13 percent of the acorns planted in the lathhouse produced a radicle but no above-ground shoot ("faulty germination") and died.

Root growth

Of the 167 acorns that both germinated and sprouted in the greenhouse, half had their tap roots reach the bottoms of the 10-inch deep pots within four weeks; 72 percent of the tap roots had reached the bottoms of the smaller pots by six weeks. Transplantation into 40-inch deep pots postponed root emergence by only two to three weeks.

Seed weight

Seed weight of the entire sample (n = 412) was highly variable, averaging 6.62 grams (standard deviation [S.D.] 1.90; range 1.26-13.65 grams), with more than 90 percent of the acorns weighing between 4.0 and 10.0 gm (Figure 2). Although 90 percent of all planted seeds germinated, larger seeds were more likely to germinate ($X^2 = 22.72$, $p < .0001$), and most germinated earlier ($F=21.61$, $r^2 = 0.08$, $p < .0001$) than smaller seeds. Larger seeds also had significantly earlier root emergence from the bottom of the pots ($F = 16.65$, $r^2 = 0.11$, $p < 0.0001$). Seeds with roots emerging in week four weighed 8.09 grams on average, whereas seeds with roots emerging in weeks six and seven weighed only 7.25 grams and 5.96 grams on average, respectively. Larger seeds also had greater shoot growth at week seven (Figure 3a, $F = 27.32$, $r^2 = 0.10$, $p < 0.0001$) than smaller seeds. However, seed weight accounted for only 8 percent of the variation in date of germination and 10 percent of the variation in plant height. The greater shoot growth and root growth of seedlings from larger acorns were still significant after controlling for earlier germination ($F = 9.24$, $r^2 = 0.04$, $p = 0.003$), although the effects of weight now accounted for only 3 percent of the variation in plant height.

Among plants transplanted into larger containers at seven weeks, seed size continued to account for a moderate amount (12 percent) of the variation in plant height at 13 weeks (Figure 3b; $F = 12.21$, $p = 0.007$, $r^2 = 0.12$). However, among plants that remained in the smaller containers, the effects of seed size on plant size after 13 weeks (Figure 3b; $F = 3.79$, $p = 0.054$, $r^2 = 0.03$) was considerably less (3 percent of variation). This was not due to a bias in transplantation; seeds whose seedlings were randomly selected for transplanting were similar in size to seeds whose seedlings were not transplanted (7.42 ± 0.14 standard error [S.E.]. vs. 7.53 ± 0.17; $F = 0.26$, $p = 0.61$).

Exit holes

Approximately 25 percent of the acorns planted in the lathhouse had beetle exit holes, and nine percent had multiple exit holes (Table 1). Seeds with exit holes were 13 percent smaller on average than seeds without exit holes ($F = 8.16$, $r^2 = 0.03$, $p < 0.005$). Interestingly, the presence of exit holes did not significantly affect either the probability of germination ($X^2 = 1.03$, $p = 0.31$), the time of germination ($F = 1.11$,

Table 1. Frequency, weight, and fates of planted acorns with different numbers of exit holes. Faulty germination equals the production of a radicle but not a shoot.

Number of exit holes	Number (and %) of acorns	Mean seed mass (g) ± standard error (S.E).	Number (and %) germinating	Number (and %) of faulty germination	Seedling height at seven weeks (cm) ± S.E. (number in sample)
0	204 (75%)	7.52 + 0.11	188 (92%)	21 (11%)	6.03 + 0.27 (167)
1	44 (16%)	6.70 + 0.33	36 (82%)	5 (14%)	3.89 + 0.50 (31)
2	10 (4%)	6.07 + 0.57	8 (80%)	1 (12%)	3.34 + 0.78 (7)
3	7 (3%)	6.79 + 0.63	6 (86%)	2 (33%)	3.62 + 1.22 (4)
4	5 (2%)	6.93 + 0.48	4 (80%)	0 (0%)	2.92 + 0.81 (4)
5	2 (1%)	6.40 + 0.97	2 (100%)	2 (100%)	—

r^2 = 0.005, p=0.29) or the time to root emergence from the bottoms of the pots (F = 1.55, r^2 = 0.01, p = 0.22). However, acorns with exit holes that germinated were nearly twice as likely to produce a radicle without producing a shoot ("faulty germination") than were acorns with no exit holes (18 percent vs. 11 percent), although this difference was not statistically significant. Although seeds with more exit holes had 40 percent less shoot growth by week seven (F = 7.42, r^2 = 0.03, p = 0.007) than seeds with fewer or none, this accounted for only three percent of the overall variation in shoot growth.

Cracked seeds

Approximately 11 percent of the seeds had multiple longitudinal cracks at their distal (narrow) ends. There was no relationship between seed size and seed cracking. Germination probability was 9 percent less in seeds with cracks than in seeds without cracks, but this difference was not statistically significant (X^2 = 2.56, p = 0.11). Seeds with cracks germinated later than seeds without cracks (F = 8.02, r^2 = 0.03, p = 0.005) and produced roots that emerged from the bottoms of the pots significantly later (F = 6.26, r^2 = 0.05, p = 0.01). Shoot growth after seven weeks was 35 percent less in cracked seeds than in seeds without cracks, but this difference was not statistically significant (F = 2.58, r^2 = 0.009, p = 0.11).

Shoot growth, germination time and container size

Seeds that germinated earlier had roots that emerged earlier from the bottoms of the pots (F = 51.09, r^2 = 0.28, p < 0.0001) and had greater shoot growth between week 7 and week 13 (F = 11.04, r^2 = 0.04, p < 0.001). Shoot growth between week 7 and week 13 was four times greater in seedlings transplanted into larger pots than in those that remained in smaller pots (Figure 3b; F = 106.22, r^2 = 0.44, p < 0.0001).

Discussion

Root emergence

Because tap-rooting species can lose their tap roots in containers (Moore, 1985), and because this reduces their survival and growth when they are planted on xeric sites (McCreary, 1996; Welch, 1997), it is important to know how quickly tap roots of particular species reach the bottoms of containers. Our data show that even in relatively deep pots (16 inches), this happens very quickly (less than eight weeks) in valley oaks. It is likely that, even when using the deepest available pots (up to 40-inches deep), it would not be advisable to keep valley oaks in containers for more than a few weeks before planting them out. We do not know how long the tap roots of valley oaks survive after reaching the bottoms of pots. We are currently doing field trials to examine the long-term significance of container growth on valley oaks in restoration settings.

Seed Size

Acorn size correlates with several aspects of the growth and survivorship of valley oak seedlings. Larger seeds germinate both earlier and at higher rates. This has been shown in a number of other studies for oaks and other species. Larger seeds may have higher germination rates due to larger resource reserves—either nutrients or moisture, or both. Valley oak seedlings from larger acorns were taller than seedlings from smaller acorns, as in other oak species (Tripathi and Khan, 1990; Rice and others, 1993; Kormanik and others, 1998). Larger seeds also produced faster growing roots. Hendrix and his colleagues (1991) found that seedlings grown from large seeds had greater root mass than seedlings grown from small seeds.

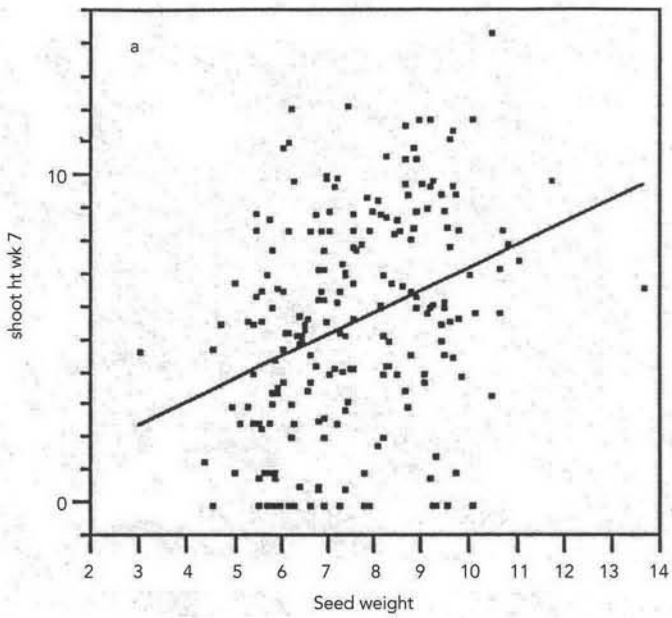
To our knowledge, however, ours is the first study to demonstrate that roots of seedlings grown from large seeds emerge from pots faster than those grown from small seeds. This greater shoot and root growth may be due to the larger resource reserves in larger seeds, in addition to their earlier germination.

However, the roots of all seeds, regardless of size, were reaching the bottom of the pots within eight weeks of planting. Valley oaks invest heavily in taproot growth. When we checked this by digging up naturally established valley oaks, we found that seedlings with shoots less than 10 inches tall often had tap roots more than a meter long.

Once the roots emerge from the base of the pot, they are air pruned—that is, they are killed by exposure to dessicating air—and do not grow any longer. This determines the length of time tap-rooted species can be left in pots before transplanting. Valley oak grows in an environment that is dry during the summer growing season, so producing a deep tap root is important to its establishment and survival. The deep tap root enables the seedling to reach moisture in deeper soil layers that are less likely to dry out during the summer months or to reach groundwater reserves that are available year-round.

Exit holes

One source of variation in seed size appears to be weevil infestation. Some of the seeds had uniform, pencil-lead sized holes, which we presume were made by acorn weevil larvae (Curculionidae) as they exited the acorn (see Figure 1). The seeds with holes were 13 percent smaller on average than seeds without holes. This



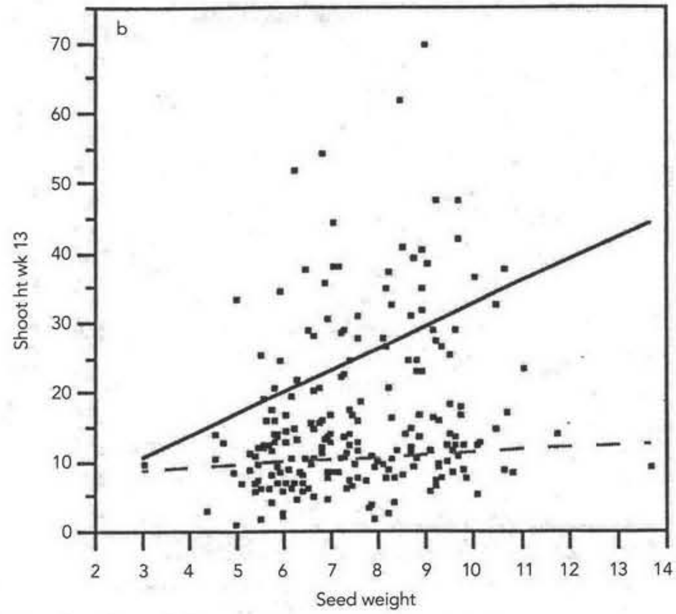


Figure 3a. The relationship between acorn size and plant height after seven weeks (all in small containers). b. The relationship between acorn size and plant height after 13 weeks for plants that remained in the smaller containers (lower, dashed line) and plants that were transplanted into larger containers (upper, dark line). (Note the different scales of the two graphs.)

may be due to the larvae using the seed as a food source as it develops. Other studies have reported such an effect. Kaushal and his colleagues (1993) showed that infestation by acorn weevils reduced germination and seedling growth. However, Steele and his colleagues (1993) found that partially consumed acorns had rates of germination equal to or greater than intact acorns. In our study, the presence of exit holes did not significantly affect the probability or the rate of germination despite the fact that smaller seeds on average had lower germination rates.

Shoot and root growth, however, were less in seedlings grown from seeds with more exit holes than in seedlings from seeds with fewer or none. Similarly, weevil infestation delayed root emergence from the base of the pots, though not significantly. These factors may be linked to seed size, and so the reduction in seed size—and, therefore, reserve size due to weevil infestation—might be expected to affect the growth and survival of oak seedlings.

Cracked seeds

We know of no other studies of how cracks in acorns affect germination or seedling growth. Cracks in the woody shell of acorns might be expected to promote imbibition, accounting for earlier germination and faster root and shoot development. Conversely, these cracks may increase dehydration of the acorn prior to planting, or provide routes for increased infection by pathogens. McCreary and Koukoura (1990) have shown that natural dessication severely reduces germination rates of blue oak acorns. In any event, cracked acorns had only slightly lower germination rates than uncracked acorns, and cracked seeds actually germinated later than non-cracked seeds.

Shoot growth

Roots of seedlings from seeds germinating earlier emerged from the base of the pots earlier, and had faster-growing shoots than seeds that germinated later. These results parallel our seed size findings. Larger seeds both germinated earlier and produced seedlings with faster shoot growth. Our analysis suggests that both emergence time and seed size itself independently contributed to this faster growth. Seedlings with faster shoot growth also had earlier root emergence.

Shoot growth was highly variable among plants. Variations in seed size, exit hole number, and seed cracking often had moderate and statistically significant effects on germination and shoot and root growth. However, these traits failed to account for more than 10 percent of the variation in germination rate and initial growth. It may not be cost effective to sort collected seed by these traits before planting. However, better control of other sources of variation in the success of seeds and seedlings—as yet not identified—may increase the predictive value of these acorn traits. In addition, small initial advantages may be amplified in competitive environments (Harper, 1977). It would be appropriate to do further studies to discover whether this is the case with the interspecific competitors that can be so detrimental to initial planting success (Hall and others, 1992; McPherson, 1993).

Container size

When seedlings were transplanted into larger pots, their shoot growth was four times greater than that of non-transplanted seedlings. Studies of herbaceous species produced similar results (see, for example, Van Iersal, 1997; Ray and Sinclair, 1998). The roots quickly reached the bottom of the larger pots. If this root emergence is associated with the death of the tap root, then for valley oaks even a few weeks growth in containers would be long enough for long-term deleterious effects like those demonstrated by Welch (1997), McCreary (1995), and Halter and colleagues (1993). We are currently undertaking a field trial to test this.

Conclusions and Implications

Our study has two main implications for restoration. First, although we have shown that the size, beetle infestation, and cracking of valley oak acorns may have significant (and sometimes large) effects on germination rate and initial growth rate, these effects were small relative to the total variation in seed and seedling success. Therefore sorting seeds by these traits may not be cost effective. On the other hand, if other sources of variation not studied here can be identified and brought under control, then the residual effects of these seed traits may indeed be considerable and worth attention.

Second, valley oak seedlings grown in pots can quickly reach large sizes, and those in larger pots can grow even faster, and their tap roots quickly reach the bottoms of the pots. It appears that even a short time in pots may prevent healthy taproot development. Therefore even short periods of container growth may have deleterious effect on the future success of seedlings planted out in restoration sites, and direct seeding may be preferable.

Acknowledgments

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