Photo by Douglas D McCreary

Initial mortality and root and shoot growth of

VALLEY OAK SEEDLINGS

outplanted as seeds and as container stock under different irrigation regimes

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ABSTRACT

Direct seeding of valley oak *(Quercus lobata* Nee [Fagaceae]), commonly used in restoration in the Central Valley of California, may be preferable to using container stock, at least in nonirrigated sites and where acorn predation can be controlled. In a stratified random experiment we tested initial growth and survival of oaks either: 1) outplanted as acorns; 2) outplanted as 3-mo-old container seedlings; 3) outplanted as 3-mo-old container seedlings that had been transplanted into larger containers 6 wk before outplanting; and 4) outplanted as 1-y-old container seedlings (commercial stock). We subjected each of these to 3 different irrigation regimes: 1) none; 2) drip; or 3) overhead. Half of the irrigated oaks were watered for 1 y, and half for 2 y. In nonirrigated plots, oaks grown from acorns that survived initial seed predation survived significantly better than oaks planted from containers. Across stock type (acorns, plants of different ages, and different sizes of containers), initial differences in plant height remained after 18 mo of growth, but growth rates were similar. Oaks grown in containers usually had more branched and more distorted root systems but all stock types successfully produced deep roots. Irrigated plants grew faster than nonirrigated plants. Plants weaned from irrigation during their second year grew as well thereafter as those that were never irrigated.

The successful propagation and establishment of seedlings is an important component of many restoration efforts. Many of the woody plants planted for restoration in upland habitats in the western US are xeric taprooted species, including several oak species. There have been particular problems establishing native California oaks (Adams and others 1992). Recruitment failure seriously hinders restoration efforts, which often attempt to establish oak seedlings through either direct seeding or outplanting of seedlings initially established in containers.

Both outplanting of container stock and direct seeding are standard practices in restoration. For example, we surveyed 6 restoration projects in Yolo County, California, where valley oaks (*Quercus lobata* Nee [Fagaceae]) were being outplanted, and noted that 4 projects used container stock and 4 used direct seeding (2 of the sites made use of both techniques). Propagation in containers may restrict taproot growth (Moore 1985), and this can hinder the growth and survival of taprooted species including valley oaks (see below). The development of a deep taproot may be vital to the long-term success of oaks in nonirrigated landscapes and on restoration sites.

Many studies examined how containers affect seedling development in terms of root and shoot growth (Halter and others 1993; Gilman and Beeson 1996; Maejima and others 1997; Marshall and Gilman 1997; Mughal 1996; McCreary and Lippitt 1997; Van Iersel 1997; Ray and Sinclair 1998; Wu and others 1998). If plants remain in containers, the roots can circle and become deformed. More importantly for xeric restoration, evidence is growing that taprooted species grown in containers lose their taproots permanently (Moore 1985), and this may account for their poor growth and survival after outplanting on xeric sites (Halter and others 1993; McCreary 1995, 1996; Welch 1997; see review in Young and Evans 2001). None of these studies, however, compared the performance of container stock and direct seeding in restoration contexts or with different irrigation treatments, container sizes, or ages of container stock. Container size also affects oak seedling growth (Hanson and others 1987; Cogliastro and others 1995).

Irrigation is an expensive but common amendment used in restoration settings. Although it can increase initial survival of outplanted species, its use is not without problems. Irrigation layouts can cost several times the value of the land itself. Irrigation can favor undesirable species, or one outplanted species over others (Padgett and others 2000). In addition, some species that thrive under irrigation in restoration sites die shortly after irrigation ceases (Hershey 1999). It is difficult to determine whether this is due to unsuitable plantings or to the inability of the plant to adjust to xeric sites after initially being irrigated. This paper examines the effect of propagation techniques on establishment of valley oaks in a simulated restoration setting.

MATERIALS AND METHODS

Study Species and Site

Valley oak is an endemic tree species in California that grows up to 30 m (100 ft) tall. It occurs sporadically statewide except in deserts at elevations below 1700 m (5600 ft), and on the Channel Islands (Hickman 1993). It can be locally abundant along rivers, but it is also found on mesic slopes, valleys, and savannas. It is perhaps the most commonly planted tree species in riparian restoration projects in the Central Valley of California (personal observations).

We carried out this research in a tilled research field of the University of California at Davis from 1998 to 2000. The area has a Mediterranean climate with mean annual rainfall of 400 mm (15.7 in) that primarily falls from November–May (Major 1988).

Experimental Design

We established a field experiment to evaluate the effects of plant stock type and watering regime on the establishment success of valley oak seedlings. Nine 3 x 30 m (10 x 98 ft) areas were grouped into 3 blocks. Within each block, a strip was assigned to each of 3 watering treatments. Within each strip, there were 6 plots, each with an array of 9 plants in a 3 x 3 grid, 2 m (6.5 ft) apart. Two of these plots were assigned either seeds, 3-mo-old container seedlings, or 1-y-old container seedlings in a random stratified design. Therefore, we had 6 replicate plots (54 plants) for each of the 9 combinations of plant stock type and irrigation regime (486 plants total).

One-y-old valley oak seedlings that had been grown in potting soil in pots at a commercial native plant nursery were outplanted into their assigned grids in January 1998 (n = 162). Hares caused initial damage to some shoots, but only 2 plants were killed. Thereafter, we put up a protective fence around the entire field and browsing by hares declined dramatically.

We obtained approximately 500 valley oak acorns from a commercial source (Mistletoe Seeds) that were collected near Los Robles, California, in October 1998. The acorns were placed in cold storage until January 1999 when radicles began to emerge. A random selection of 162 acorns were outplanted into their assigned grid locations in the field experiment and covered with a thin layer of soil (approximately 1 cm [0.4 in]).

In a lath house, 272 acorns were placed onto the surface of potting soil in pots, placed on benches, and watered regularly. On 25 February (week 5) half of the lathhouse seedlings were randomly selected and transplanted into larger pots. In late March, 162 of these 3-mo-old seedlings (randomly selecting 81 from each of the 2 container sizes) were outplanted into the experimental plots as outlined above. The seedlings from small and large containers were alternated within each plot. By this time, the plants from larger pots were nearly 3X as tall as plants from smaller pots (see also Hobbs and Young 2001).

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After outplanting, plants received only natural precipitation from winter rains until May 1999. At that time, we began to irrigate some plots. Each individual oak in the 3 strips designated "Drip" received water weekly through a drip system with 7.3 l/h emitters. The volume applied, 4 l (1.1 gal) per plant per week, was sufficient to replace reference evapotranspiration for a 1000 cm^2 (155 in^2) area around each plant, based on the Davis station for the California Irrigation Management Information System (CIMIS). The 3 strips designated "Overhead" received water applied over the entire strip through spray sprinklers. We adjusted the overhead sprinkler irrigation so that the entire plot received the same amount of water per unit area as in the area around each drip-irrigated plant (and therefore more total per plot). The remaining 3 strips received no irrigation. In the second year, we ceased irrigation on half of the irrigated plots within each irrigated strip. We chose not to keep the plots entirely free from weeds to better simulate a restoration setting. We did, however, weed within 40 cm (16 in) of each oak and did general weed control when the weeds got thick.

All plants were surveyed for growth and mortality over the next 2 y. When no seedling appeared aboveground for a planted acorn, the site was excavated to see if the acorn was still present. Height to the highest stem tip was measured for each oak twice each year.

In March 2001, we excavated the root systems of 28 trees, using a backhoe and a pneumatic blower. Trees were chosen visually to sample representative individuals from each combination of stock type and irrigation treatment. We sampled only 1 tree of a stock type in each plot to maintain statistical independence. We followed all roots as far as possible, usually until they were less than 2 mm (0.1 in) in diameter. After excavation, we measured the length of the deepest root (standardized to the depth at which the roots tapered to less than 2 mm (0.1 in). We counted the number of roots > 5 mm (0.2 in) in diameter at a depth of 20 cm (8 in), and the number > 2 mm (0.1 in) at a depth of 40 cm (16 in). We also recorded the presence and depths of branch points (where the taproot branched to become two or more essentially equal roots) and "kinks" (where the root departed from vertical at sharp angles $\geq 60°$; see Figure 4). We measured the fresh and dry biomass of the roots and the shoots of each excavated plant, and calculated dry root-to-shoot ratios (including leaves).

On 13 August 2001, we measured the field water potentials of the remaining trees in early afternoon (see Shackel and others 2000). None had been irrigated since the previous year. We used a standard pressure bomb (Soil Moisture Equipment Corp, Goleta, California) on a single leaf from each of 4 or 5 plants from each combination of irrigation type and stock source (42 plants total).

Statistical Analysis

Mortality rates were calculated for each combination of stock type and watering regime in each of the 3 blocks. Height data were square-root transformed to achieve normality for analysis, but the results presented in the figures are from untransformed data. The effects of block, watering regime, and plant stock type on growth, mortality, and root data were analyzed using analyses of variance (ANOVA). *A posteriori* tests were used to distinguish which aspects of watering regime or plant age contributed to significant effects. We tested the effects of pot size on 3-mo-old plantings with a separate one-way analysis of variance.

Mortality

Approximately 40% of the acorns disappeared in the first 2 mo after outplanting, probably taken by ground squirrels or other seed predators. Of the remainder, 90% successfully germinated (see also Hobbs and Young 2001). The mortality reported below is for those oaks that both survived this predation and successfully germinated.

Watering regime had a significant effect on plant mortality across all stock types (F = 36.5, *P* < 0.001). This was due to the higher mortality of the nonirrigated plants (Figure 1). Mortality rates were similar for plants given drip and overhead watering regimes.
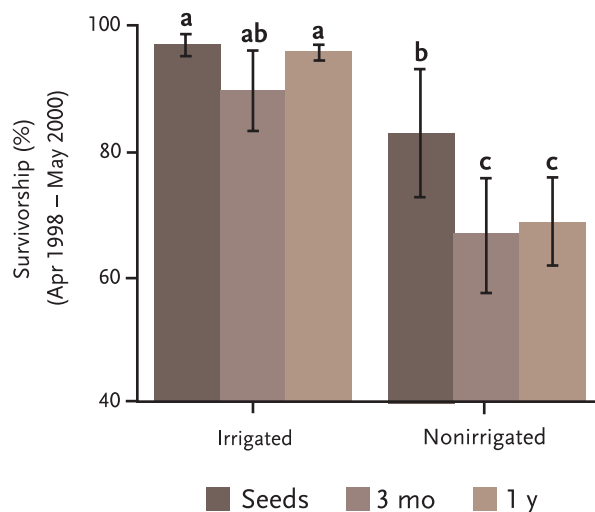

Figure 1. Survival rates of different kinds of oak plantings in irrigated and nonirrigated plots. Bars represent standard errors, which are large because of block effects, that were controlled for in the ANOVA and because these data are not log-transformed. Bars sharing a letter are not significantly different based on separate *a posteriori* analyses of irrigated and nonirrigated plants (N = 3 blocks).

Mortality varied significantly among plants outplanted at different ages (F = 3.51, *P* = 0.05). Oaks derived from outplanted acorns had half as many deaths as oaks grown in containers for 3 or 12 mo, and this was almost entirely due to differences in the nonirrigated plots (Figure 1). Among 3-mo-old oaks grown in containers, those transplanted into larger pots 6 wk before outplanting had half the mortality as those grown the entire 3 mo in the same container (18/81 versus 10/81), but this difference was not quite statistically significant (X^2 = 2.15, *P* < 0.15).

Mortality among oaks from different treatments in the second year of the experiment was similar. Plants that were irrigated the first year, but not the second, had similar mortality to those that had not been irrigated in either year.

Plant Height

There were significant effects on plant height of planting age and irrigation regime (Table 1). Irrigated plants were significantly taller than nonirrigated plants, and those watered with overhead sprinklers were taller than those on drip irrigation (Table 2).

Plants grown from acorns were 23% smaller than oaks outplanted as 3-mo-old container stock, which were 28% smaller than oaks outplanted from 1-y-old container stock. Within the 3-mo-old container stock, oaks outplanted from smaller containers were 20% smaller than those transplanted into larger containers before outplanting and were the same size as plants grown from acorns directly seeded in the ground (Table 2). No significant interaction between irrigation regimes and planting age (Table 1) was found.

Height growth by November 2000 was essentially the same for all planting stocks (F = 0.42, *P* = 0.65) and pot sizes (F = 0.04, *P* = 0.84). The differences in height in May 2000 were mainly due to differences in the sizes of the plants at the time of outplanting (Figure 2). The height advantage of having been initially grown in a larger pot gradually decreased over the first 18 mo of the experiment and was relatively small by November 2000 (Figure 3).

Root Excavations and Water Potentials

Roots on all excavated trees had penetrated deeply after only 2 y of growth. Roots at least 2 mm (0.1 in) in diameter were found at a 2 m (6.5 ft) depth for every excavated tree. Rooting depth and dry root-to-shoot ratios among different stock types or among different irrigation regimes were similar. Seedlings outplanted from pots, however, were significantly more likely to have branched root systems than direct-seeded plants. Oaks started in containers often had branches at depths corresponding to container depths and often were grossly contorted ("kinked") at these depths (Table 3, Figure 4). Watering regime and stock type had no significant effect on root-to-shoot ratios or on 2001 field water potentials.

TABLE 1

Results of analysis of variance of May 2000 height (on ln transformed data). All surviving plants included. "Stock" types were seeds, 3-mo container plants, and 1-y container plants.

Source	df	Sum of squares	Mean square	F	P
Block	2	41.5	20.8	9.35	0.001
Irrigation regime	2	15.6	7.8	3.51	0.031
Stock	2	171.3	85.6	38.55	< 0.001
Stock x Irrigation	4	4.4	2.2	0.50	0.74
Error	353	784.2	2.2		

TABLE 2

Height (cm in May 2000) of oaks from different planting stock and irrigation regimes (one standard error). Numbers in parentheses are sample sizes. Includes both browsed and nonbrowsed plants.

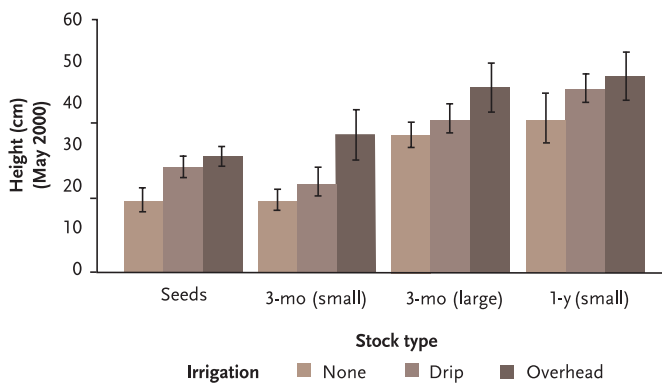|	IRRIGATION REGIME			
Stock	**None**	**Drip**	**Overhead**	**Mean**
Seed	17.4 ± 2.4 (25)	25.1 ± 2.6 (40)	27.5 ± 2.7 (33)	23.9 ± 1.6 (98)
3-mo (small)	17.5 ± 2.3 (17)	21.5 ± 3.2 (22)	32.9 ± 5.1 (24)	24.8 ± 2.4 (63)
3-mo (large)	33.1 ± 2.9 (19)	36.0 ± 3.4 (25)	41.5 ± 4.7 (24)	37.2 ± 2.2 (68)
3-mo (all)	25.8 + 2.3 (36)	29.3 ± 2.6 (47)	37.2 ± 3.5 (48)	31.2 ± 1.7 (131)
12-mo (browsed)	31.1 ± 2.9 (23)	45.9 ± 3.7 (32)	49.1 ± 3.2 (40)	43.7 + 2.1 (95)
12-mo (nonbrowsed)	36.6 ± 5.8 (8)	43.8 ± 3.4 (20)	47.2 ± 5.3 (12)	43.4 ± 2.6 (40)
12-mo (all)	32.5 ± 2.6 (31)	45.1 ± 2.6 (52)	48.7 ± 2.8 (52)	43.6 + 1.7 (135)
Mean	25.8 ± 1.5 (92)	34.0 ± 1.7 (139)	40.6 ± 2.0 (125)	33.8 + 1.06 (364)

Figure 2. Height of oaks outplanted at different ages across irrigation regimes. Does not include oaks that were browsed by hares between September 1999 and May 2000. Error bars are one standard error (N = 3 blocks).
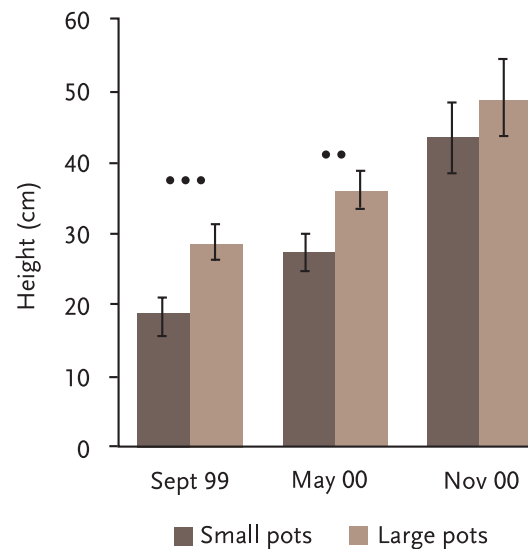

Figure 3. Height through time of oaks outplanted at 3 mo from either large or small pots, averaged across irrigation regimes. Error bars are one standard error (N = 3 blocks). *** = P < 0.001; ** = P < 0.01.

DISCUSSION

The greater initial mortality of container-grown oaks than field-planted acorns (after accounting for acorn predation) may seem surprising, but several other studies have shown similar patterns (Young and Evans 2001). Saplings of lodgepole pine (*Pinus contorta* Loudon) grown from seeds fared better than did container stock even after 11 y (Halter and others 1993). Young blue oaks (*Quercus douglasii* Hook & Arn.) had higher survival and growth rates than did container stock (McCreary 1995). Just 2 y after sowing, plants of big sagebrush (*Artemisia tridentata* Nutt.) grown from seeds were larger and had higher survival and reproduction than that of container stock (Welch 1997).

These patterns may be due to root problems in containers. Root circling and taproot loss are both symptoms of plant production in containers (McCreary 2001). In our study, even plants grown in large containers for as little as 3 mo had greater mortality than plants that were seeded directly. The fact that this effect was most pronounced in the nonirrigated plots suggests a root problem. Restoration ecologists may find in these results further justification for direct seeding, at least for large-seeded taprooting species. The fact that these difficulties appear only in nonirrigated plots may explain why they have received little attention in traditional horticulture, where most landscape plantings receive supplemental water. Leaf potentials in our study were only taken after 2 y of growth, when these negative effects were no longer evident.

Although the larger oak seedlings were still taller after a year and a half of growth, their growth rates were similar and it appears that this initial height advantage is not associated with a growth advantage (Figure 2). Not only do older stock and stock in larger containers cost more to produce but also they require more time to plant than individual acorns. It appears that the greater time and energy needed to produce and plant older and larger valley oak stock may not be justified, given their relatively poor field performance on this study site, especially if acorn predation is not a problem or can be controlled.

It is not surprising that irrigated plants had higher growth and survival rates than nonirrigated plants. In addition, faster growth rates may serve to help plants "escape by height" from herbivory, which can be a limiting factor in oak establishment (Hall and others 1992; McPherson 1993). Although the greater individual growth and survival rates associated with irrigation may help to fulfill contractual obligations or values, it has been suggested that there may be a "weaning" cost of irrigation, where previously irrigated plants suffer from the removal of the irrigation. Our data do not support such a view, at least for valley oaks. Irrigated oaks had roots that grew at least as deeply as nonirrigated oaks and suffered no greater mortality when eventually deprived of irrigation.

TABLE 3

Effects of stock type on root characteristics (mean and standard error), measured 2 y after outplanting. P values are for comparison between oaks from direct-seeded acorns and oaks initially grown in pots (3-mo and 1-y combined). ANOVA tests were used for quantitative traits, and Chi-square tests for categorical traits. In all cases with a significant overall difference, a post hoc analysis (Tukey's HSD) reveal that the plants from seeds were significantly different from both container types, which did not differ significantly from each other.

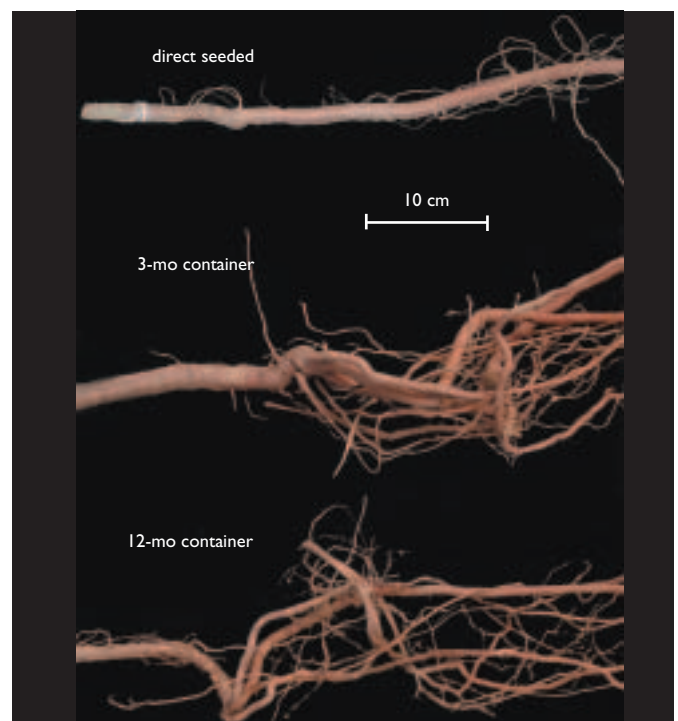|	Seed	3-mo pots	1-y pots	P
Rooting depth (cm) (2 mm diameter)	272 + 36	218 + 21	288 + 19	0.51
Root-to-shoot ratio (dry wt)	4.2 + 1.0	4.3 + 0.6	6.5 + 1.9	0.48
Number of 5 mm roots at 20 cm depth	1.1 + 0.3	2.0 + 0.5	2.2 + 0.4	0.066
Number of 2 mm roots at 40 cm depth	1.8 + 0.40	3.2 + 0.7	4.2 + 0.8	0.035
Roots kinked?	0 out of 9	11 out of 11	5 out of 8	0.001
Roots branched?	3 out of 9	10 out of 11	8 out of 8	0.002

Figure 4. Representative roots of oaks outplanted from acorns *(top)* or from 3-mo *(middle)* or 1-y old *(bottom)* container stock. Note branching and kinks in the roots from the container stock at the depth of the containers (20 cm [7.9 in]). Photos by Richard Y Evans

Herbivory on seeds and seedlings is often a limiting factor for oak species, both in natural and restoration settings (Hall and others 1992; McPherson 1993; Bonfil 1998). Acorns outplanted into the field suffered nearly 40% loss before germination, most likely from ground squirrels or other rodents. Outplanted oak seedlings were able to recover from herbivory by hares. Cages around outplanted oaks and acorns would likely prevent both forms of mortality.

ACKNOWLEDGMENTS

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