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Initial mortality and root and shoot growth of oak seedlings planted as seeds and as container stock under different irrigation regimes

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ABSTRACT

Valley Oak (*Quercus lobata*) is a tree commonly used in restoration in the Central Valley of California. We tested initial growth and survivorship of oaks either a) planted as acorns, b) planted out after growing in small containers for three months, c) same as b) but transplanted into larger containers for the last six weeks before planting out, and d) planted out after growing in small containers for one year (commercial stock). We subjected each of these to three different watering regimes, in a stratified random experiment. The oaks were either a) not irrigated, b) drip irrigated or c) overhead irrigated. Water to half of the irrigated oaks was stopped after the first year. Oaks grown from seeds had significantly greater survivorship than oaks planted from containers in non-irrigated plots. Across stock type (acorns, plants of different ages) initial differences in plant height remained after 18 months of growth, but growth rates were similar. Plants grown from pots usually had more branched and more distorted roots systems, but all stock types successfully produced deep roots. It appears that direct seeding may be preferable to using container stock, at least in non-irrigated sites. These oak saplings showed a strong ability to survive sometimes severe initial browsing by hares, which preferentially attacked larger plants. Irrigated plants grew faster than non-irrigated plants, but those weaned from irrigation did no worse in their second year than those that were never irrigated.

INTRODUCTION

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 United States are xeric tap-rooted species, including several oak species. There have been problems with the establishment of native oaks, both naturally and at restoration sites (Adams *et al.* 1992). Lack of natural recruitment seriously hinders restoration efforts, which often attempt to establish oak seedlings through either direct seeding or planting of seedlings initially established in containers.

The planting of container stock in preference to direct seeding appears to be a standard practice in restoration. In a survey of six restoration projects in Yolo County, CA where Valley oaks are being planted, four have been planting container stock and four direct seeded (two sites did both; TPY, unpublished data). Propagation in pots may restrict taproot growth (Moore 1985), and this can hinder the growth and survivorship of tap-rooted species including Valley oaks (see below). The growth of a deep taproot may be vital to the long-term success of oaks in non-irrigated landscapes and restoration sites.

There have been numerous studies on how containers affect the development of seedlings, in terms of both root and shoot growth (Halter *et al.* 1993; Gilman & Beeson 1996; Mughal 1996; McCreary & Lippitt 1997; Van Iersel 1997; Maejima *et al.* 1997; Marshall & Gilman 1997; Ray & Sinclair 1998; Wu *et al.* 1998). If plants remain in the containers for too long, all types of roots can circle and become deformed. More importantly for xeric restoration, there is growing evidence that tap-rooting species grown in containers lose their taproots permanently (Moore 1985), and this may account for their poor growth and survival when planted into xeric sites (Halter *et al.* 1993; McCreary 1995, 1996; Welch 1997; see review in Young & Evans 2001).

Container size also affects seedling growth. Non-tap-rooting plants grown in larger containers are taller than plants grown in smaller containers (Wu *et al.* 1998), because they grow faster (Van Iersel 1997). However, we still do not know how container size affects the establishment of tap-rooted species.

Irrigation is an expensive and common amendment in restoration settings. Although it can increase initial survival of planted 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 planted species over others (Padgett *et al.* 2000). In addition, some species that thrive under irrigation in restoration sites die shortly after the irrigation is removed (Hershey 1999). It is not usually known whether this is due to unsuitable plantings in the first place, or to the plant's inability to adapt to xeric sites while being irrigated.

The research reported here examines how propagation techniques affect the establishment of Valley Oaks (*Quercus lobata*) in a simulated restoration setting. Our data indicate that in non-irrigated situations, seedlings grown from acorns have similar growth rates and significantly higher survival rates than oaks planted as container stock. Irrigated plants grew faster than non-irrigated plants, but those weaned from irrigation did no worse in their second year than those that were never irrigated.

STUDY SPECIES AND SITE

Valley Oak (*Ouercus lobata*) is a California endemic that grows up to 30m tall. It occurs sporadically throughout the state at elevations below 1700m (though not in deserts), and on the Channel Islands. It can be locally abundant along rivers, but it also found on mesic slopes, Valleys, and savannas. The acorn is usually 30-50mm long and 12-20mm wide (Hickman 1993). It is perhaps the most commonly planted tree species in riparian restoration projects in the Central Valley of California.

This research was carried out in a tilled research field of the University of California at Davis. The area experiences a Mediterranean climate with mean annual rainfall of 400 mm, most of which falls November-June.

METHODS

In an experimental field, we set up a random stratified experiment on the effects of plant provenance and watering regime on the success of Valley Oak seedlings. Nine strips of land 3m x 30m were grouped into three blocks. Within each block, one strip was assigned to each of three watering treatments. Within each strip, there were six plots, each an array of nine plants in a 3 x 3 grid, 2m apart. Two of these plots were assigned either seeds, 3-month-old seedlings from containers, or one-year-old seedlings from containers. There were therefore six replicate plots (54 plants) for each of the nine combinations of plant provenance and irrigation regime (486 plants total). We purchased one-year-old Valley Oak seedlings that had been grown in standard potting soil in 6x6x25 cm pots at a local native plant nursery. These were planted into their assigned grids in January 1998 (n = 162). There was initial damage to some shoots through hare herbivory (see below), but only two plants died of this. Thereafter, we put up a protective fence around the entire field, and browsing by hares dropped dramatically.

We obtained approximately 500 *Ouercus lobata* seeds from a commercial source (Mistletoe Seeds) collected near Los Robles, California in October 1998. The acorns were placed into cool storage until January 1999, when radicals began to emerge. Selected randomly, 162 acorns were planted into their assigned grid locations in the field experiment, and covered with a thin layer of soil (-1cm).

In a lath house, 272 acorns were placed onto the surface of standard potting soil in 6x6x25 cm pots, placed on benches, and watered regularly. On 25 February (week 5) half of the lath house seedlings were randomly selected and transplanted into larger pots (15x15x40 cm). In late March, 162 of these 3-month old seedlings (randomly selecting 81 from each of the two container sizes) were planted into the experiment outlined above. The seedlings from small and large containers were alternated within each plot. The plants from larger pots were by this time nearly three times taller than plants from smaller pots (see also Hobbs & Young 2000).

These plants received only natural precipitation throughout the winter rains. In May 1999, we began to irrigate some of the plots. The three strips designated “Drip” received weekly water through a drip system with 2 gph emitters. The volume applied (4L per plant per week) was sufficient to replace reference evapotranspiration for a 1000 cm^2 area around each plant. The three strips designated “Overhead” got water applied over the entire strip through spray sprinklers in quantities similar to that provided by drip irrigation. 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. The last three strips received no irrigation. In the second year, we ceased irrigation on half of the irrigated plots within each irrigated strip to test weaning responses. We chose not to keep all weeds out of the plots to better simulate a restoration setting. However, we did weed within 40 cm of each oak, and did general weed control when the weeds got thick.

All plants were surveyed regularly for growth and mortality over the next two years. When no seedling appeared above ground for planted acorns, the site was excavated to see if the acorn was still there. For the other oaks, the height of the highest stem tip (not leaf blade) was measured to the nearest cm. Conditions of dead and apparently dying oaks were recorded.

In March 2001, we excavated the root systems of 28 trees, using a backhoe and a power-blower. Trees were chosen to sample representative individuals from all stock and irrigation treatment combinations. We followed all roots as far as possible, usually until they where less than 2mm in diameter. After excavation, we measured the length of the deepest root (standardized to the depth at which the roots tapered to less than 2mm). We counted the number of roots that were greater than 5mm in diameter at 20cm depth, and the number greater than 2mm at 40cm depth. The presence and depths of branch points and contortions ("kinks") of the roots were also recorded. We measured the wet and dry biomass of the roots and the shoots of each excavated plant, and calculated root/shoot ratios.

On 13 August 2001, we measured the field water potentials of the remaining trees. None had been irrigated since the previous year. We used a standard pressure bomb (Soil Moisture Equipment Corp., Goleta, CA) on one leaf from each of four or five plants from each combination of irrigation type and stock source (42 plants total).

Statistical analysis

Mortality rates were calculated for each combination of plant age and watering regime in each of the three 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 provenance on growth, mortality and root data were analyzed using ANOVAs**.** A posteriori tests were used to distinguish which aspects of watering regime or plant age contributed to significant effects. We separately tested the effects of early hare browsing on one-year-old stock and the effects of pot size on three-month-old plantings with separate one-way analyses of variance. We examined the effects of plant height on the probability of later hare browsing with logistic regression, and the effects of early browsing on late browsing with a chi- square analysis.

RESULTS

Mortality

Within two weeks of planting the one-year-old container plants, hares had nipped the stems of 114 of the 162 oaks, leaving on average 10cm of stem. Subsequently we erected a protective fence around the plots. The only two oaks nipped to less than 2 cm from the ground died. However, overall mortality rates were -10% for both browsed and unbrowsed oaks, and independent of the degree of herbivory (Table 1). Our exclosures decreased, but did not eliminate, hare browsing. We conservatively estimated plants that lost at least 2cm between September 1999 and May 2000 had been browsed by hares (16% of all plants). Overall, taller plants were significantly more likely to be browsed during this later period than were shorter plants (Logistic regression; $X^2 = 17.80$, $P < 0.001$). However, the tallest plants appeared to be escaping by height from hare browsing (Table 2). One-year-old plants browsed in January 1999 were significantly less likely to be browsed later than were plants not browsed early (16% vs. 50%, $X^2 = 15.94$ $p < 0.001$). Approximately 40% of the field-planted acorns disappeared in the first two months after planting, probably taken by ground squirrels or other seed predators. Of the remainder, 90% successfully germinated (see also Hobbs & Young 2000). The mortality reported below is for those oaks that both survived this predation and successfully germinated.

Table 1. Mortality (from February 1999 to May 2000) of one-year-old container Valley oaks planted out in January 1999 and suffering (naturally) differing amounts of hare herbivory in the next four weeks. The only mortality within three weeks of herbivory was of the two oaks with less than 2 cm of stem (in parentheses), all other mortality occurred over the next 16 months.

	Cm of stem left above ground after hare browsing			
	(0-)2-5 cm	6-10	11-17	Unbrowsed
# died	0(2)	5	5	5
Total number	10 (12)	49	48	41
% mortality	0 (17)	10.2	10.4	12.2

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

Table 2. Rates of browsing by hares between September 1999 and May 2000 on oak seedlings of differing heights in September 1999.

Height (cm)	0-9.9	10-19.9	20-29.9	30-39.9	40-49.9	50-59.9
Total	22	110	65	65	38	37
Browsed	1	8	11	19	15	8
%browsed	4.5	7.3	16.9	29.2	39.5	21.6

There were also significant differences in mortality of plants planted at different ages ($F = 3.51$, $P = 0.05$). Oaks grown from planted acorns had half as much mortality as oaks planted from 3 mo or 12 mo containers, and this was almost entirely due to differences in the non-irrigated plots (Figure 1). Among the oaks grown from 3 mo containers, those grown in smaller pots had nearly twice as much mortality as those that were transplanted into larger pots six weeks before planting (18/81 vs. 10/81), but this difference was not statistically significant ($X^2 = 2.15$, $P < 0.15$).

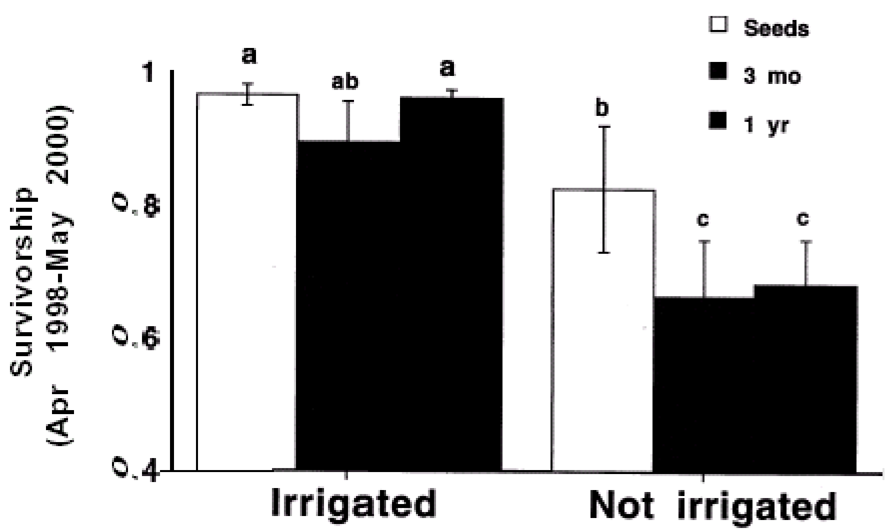

Figure 1. Survivorship rates of different kinds of Valley oak plantings in irrigated and non-irrigated plots. Bars represent standard errors, which are large because of large block effects, which were controlled for in the ANOVA and because these data are not log-transformed. Bars sharing a letter are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

There were no differences in mortality among oaks from different sources in the second year of the experiment. Plants that were irrigated the first year, but not the second, had no greater mortality than the plants that had not been irrigated in either year. Smaller plants were more likely to die in the second year than larger plants.

Plant height

There were significant effects on plant height of block, planting age, and irrigation regime, based on a three-way ANOVA (Table 3). Watered plants were significantly taller than non-irrigated plants, and those watered with overhead sprinklers were taller than those on drip irrigation (Table 4**).**

Table 3. Results of analysis of variance of May 2000 height (on ln transformed data). All surviving plants included.

Source	d.f.	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 * Irrigation	4	4.4	2.2	0.50	0.74
Error	353	784.2	2.22		

Plants grown from seed were 23% smaller than oaks planted as three-month-old container stock, which were 28% smaller than oaks planted from one year-old container stock. Within the three-month container stock, oaks planted from smaller containers were 20% smaller than those planted from larger containers, and were virtually the same size as plants grown from seed (Table 4). There was no significant interaction between irrigation regimes and planting age (Table 3).

Table 4. Height (in May 2000) of oaks from different planting stock and irrigation regimes (+/- one standard error. Numbers in parentheses are sample sizes. Included both browsed and unbrowsed 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 (unbrowsed)	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)

The average size in May 2000 of plants browsed by hares in early 1999 was similar to plants that were not browsed, even though the browsed plants lost on average half their initial height (Table 4). However, this effect was mostly due to the inclusion of plants that were also browsed between September 1999 and May 2000 (change in height <-2cm). When these plants were excluded, height growth was similar for plants browsed in early 1999 and those not browsed. After excluding the plants browsed between September 1999 and May 2000 (change in height <-2cm), height growth was essentially the same for all planting stocks (F = 0.42, p = 0.65; Figure 2) and pot sizes (F = 0.04, p = 0.84). The height advantage of having been initially grown in a larger pot gradually decreased over the first 18 months of the experiment, and was relatively small by November 2000 (Figure 3).

Root excavations and water potentials

Roots on all excavated trees went very deep after only two years of growth. Roots at least 2mm in diameter were always found at 2m depth. There were no significant differences in rooting depth or root/shoot ratios among different provenances or among different irrigation regimes. However, plants transplanted from pots were significantly more likely to have branched root systems than direct-seeded plants. Plants grown from transplants often had branches at the depths of their corresponding pots, and were often grossly contorted ("kinked") at these depths (Table 5, Figure 4). There were no significant effects of watering regime or stock type on root/shoot ratios. There were no significant differences in leaf water potentials in 2001, based on either irrigation history or stock type.

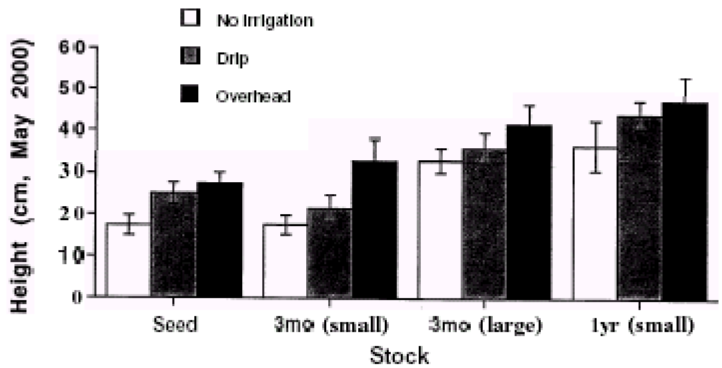

Figure 2. Height growth of Valley oaks planted at different ages, averaged across irrigation regimes. Does not include oaks that were browsed September 1999 and May 2000 (see text). Error bars are one standard error (N = 3 blocks).

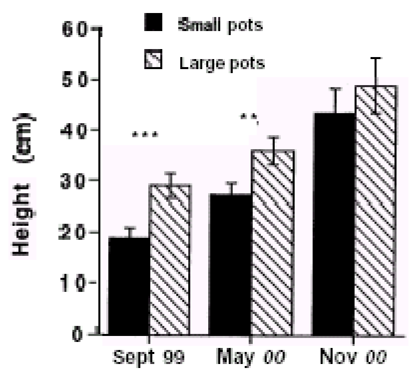

Figure 3. Height though time of Valley oaks planted at 3 months, from either large or small pots, averaged across irrigation regimes. Error bars are one standard error (N = 3 blocks).

DISCUSSION

Herbivory of seedlings is often a limiting factor for oak species, both in natural and restoration settings (Hall *et al.* 1992, McPherson 1993, Bonfil 1998). On our site, hares were initially a major source of herbivory, and likely would have limited recruitment had we not protected the plants (see also Hull & Quiroz-Nietzen 1999). Once protected, however, these oak seedlings were able to recover from severe herbivory. Acorns planted into the field suffered nearly 40% loss before germination, most likely from ground squirrels or other rodents. Cages around planting sites would likely prevent both forms of mortality.

The greater initial mortality of container-grown oaks than field planted acorns may seem surprising, but several other studies have shown similar patterns. Saplings of lodgepole pine (*Pinus contorta*) grown from seed fared better than did container stock even after 11 years (Halter *et al.* 1993). Young blue oaks (*Ouercus douglasii*) had higher survivorship and growth rates than did container stock (McCreary 1995). Just two years after planting, plants of big sagebrush (*Artemisia tridentata*) were larger and had higher survivorship and reproduction than plants planted from container stock (Welsh 1996).

These patterns have been attributed to root problems in containers. Root circling and taproot loss are both symptoms of plants kept too long in containers. In our study, even plants grown in large containers for as little as three months still fared more poorly than plants that were seeded directly. The fact that this effect was most pronounced in the non-irrigated plots suggests a root problem. It is not known if this result can be generalized to a wider array of restoration species. In any case, restoration ecologists may find in these results further justification for direct seeding, at least of large-seeded tap-rooting species. The fact that these difficulties appear only in non-irrigated plots may explain why they have received little attention in traditional horticulture, where most landscape plantings receive supplemental water.

Table 5. Effects of stock provenance on root characteristics, measured 2 years after planting out. P values are for comparison between direct seeded plants and plants initially grown in pots (3 mo and 1 yr combined). ANOVA tests for quantitative traits (mean and s.e.), Chi-square tests for categorical traits.

Provenance	Seed	3 mo pots	1 yr pots	P
Rooting depth (2mm diam)	272 ± 36	218 ± 21	288 ± 19	0.51
Root/shoot ratio	4.16 ± 1.01	4.33 ± 0.62	6.50 ± 1.94	0.48
# of 5mm roots @ 20cm depth	1.11 ± 0.26	2.00 ± 0.54	2.25 ± 0.37	0.066
# of 2mm roots @ 40cm depth	1.78 ± 0.40	3.18 ± 0.71	4.25 ± 0.75	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

Although the larger oak plantings were still larger after a year and a half of growth, their growth rates were similar and it appears that this initial height advantage does not translate into a growth advantage (Figure 2). This was true even after controlling for the fact that taller plants were more likely to be browsed than shorter plants. Not only does older stock and stock in larger containers cost more to produce or purchase, but these also require more time to plant than individual acorns. Again, it appears that the greater time and energy that goes into older and larger Valley Oak stock may not be justified by greater field performance.

Figure 4. Representative roots of Valley Oaks planted from (left to right) seed, 3-month-old or l-year-old container stock. Note branching and kinks in the roots of the container stock at the depth of the containers (20cm).

It is not surprising that irrigated plants had higher growth and survivorship rates. The higher growth rates of overhead watering compared to drip irrigation were likely due to the fact that these plots received more water overall. Faster growth rates did serve to help plants “escape by height” from hare herbivory. Although the greater individual growth and survivorship 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 plants had roots that grew at least as deeply as non-irrigated plants, and suffered no greater mortality when eventually deprived of irrigation.

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