The Response of Native Oaks From California and Israel to Drought[1]

Douglas McCreary,[2] José M. Grünzweig,[3] Yohay Carmel,[4] and Curtis H. Flather[5]

Abstract

California and Israel are both characterized by Mediterranean climates, and the native oaks growing in these two locales occupy similar ecological niches. However, in California certain oak species are having difficulty regenerating adequately, while in Israel this is not a problem. From 2004 to 2006, a series of greenhouse studies were conducted in both Israel and California to sort out the role of evolutionary history in influencing species regeneration rates and strategies. These studies have evaluated survival and growth, as well as the response of the species to disturbance including simulated browsing and fire. In 2006, an out-planting study was initiated at the University of California Sierra Foothill Research and Extension Center in Yuba County to determine how the species respond under normal field conditions. Three California oak species, including *Quercus agrifiolia*, *Q. douglasii* and *Q. berberidifolia*, as well as two Israeli oak species (*Q. ithaburensis* and *Q. calliprinos*) were planted in a common garden. This latter study was designed to evaluate phenology, growth rates, and how seedlings respond to summer drought in terms of pre-dawn plant moisture stress (PMS). Unfortunately, high field mortality prevented assessing plant moisture stress or field growth rates so the results reported here include only initial size, bud burst date and survival. Results indicate that the deciduous species from both locations (*Q. douglasii* and *Q. ithaburensis*) break bud far earlier than their evergreen counterparts. Growth in containers varied greatly by species, with *Q. agrifolia* from California and *Q. ithaburensis* from Israel growing far more rapidly that the other species. Finally, a comparison of the survival of evergreen and deciduous species from Israel with those from California suggests that California species tended to die earlier. These results are consistent with results from the greenhouse studies that found that the California species were generally less water-use efficient and might be less adapted to drought stress than Israeli species.

Keywords: Bud burst, Mediterranean climate, oak regeneration, oak survival.

Introduction

Both evergreen and deciduous oaks grow in Israel and California and are able to survive in the often-harsh Mediterranean climates that characterize both regions. While the absolute rainfall amounts vary greatly both within and between regions, both areas have a lengthy dry period from late spring until early fall. Plants adapted to these Mediterranean climates must be able to withstand drought and have evolved

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[2] Natural Resources Specialist, University of California at Berkeley, 8279 Scott Forbes Road, Browns Valley, CA 95918. email: mccreary@nature.Berkeley.edu.

[3] Faculty of Agricultural, Food and Environmental Quality Sciences, The Hebrew University of Jerusalem, Rehovot, Israel. e-mail: jose@agri.huji.ac.il.

[4] Faculty of Civil and Environmental Engineering, Technion – Israel Institute of Technology, Haifa, Israel. e-mail: yohay@techunix.technion.ac.il.

[5] Research Wildlife Biologist, USDA, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, United States. e-mail: cflather@fs.fed.us.

various mechanisms to do so. However, regeneration in California is problematic as three California deciduous species (*Q. douglasii* – blue oak; *Q. lobata* – valley oak; and *Q. engelmannii* – Engelmann oak) appear to have insufficient natural regeneration in portions of their ranges to replace mortality (Muick and Bartolome 1986, Bolsinger 1988).

It is also not clear exactly what adaptive mechanisms the different species use to withstand drought and whether deciduous or evergreen species have an advantage. It may be that evergreen oaks are better suited to withstand periodic droughts in such environments since, unlike their deciduous counterparts, they can continue to photosynthesize in winter, thus avoiding activity during the extended period of drought. On the other hand, deciduous oaks have the ability to go dormant and shed their leaves under extremely dry conditions, thus preventing moisture loss and avoiding lethal desiccation.

This study is part of a larger project titled "The Role of Evolutionary History in Determining Vegetation Dynamics: A Comparative Study of Mediterranean Ecosystems in California and in Israel," underway since 2002. The larger project was designed to compare evergreen and deciduous species from both Israel and California and to evaluate the growth and performance in a greenhouse setting, including their response to disturbance. Initial results were reported in 2004 (Carmel and Flather 2004). The study described in this report was an opportunistic tangent that allowed us to compare our greenhouse findings of seedling response (Grünzweig and others, in press) with those of seedlings outplanted to natural field conditions using extra seedlings from that larger project.

Methods

Five species were evaluated in this study. They included Palestine oak (*Q. calliprinos*), an evergreen oak from Israel; taber oak (*Q. ithaburensis*), a deciduous species from Israel; coast live oak (*Q. agrifolia*), an evergreen oak native to coastal regions of California; blue oak, a widely distributed deciduous oak endemic to California; and scrub oak, *Q. berberdifolia*, a widely distributed shrubby evergreen species native to California.

All acorns for this study were collected in their native ranges between late October and early November 2002. In California, the acorns were all collected in Carmel Valley, approximately 30 km inland from the Pacific Ocean and between 300 and 400 m in elevation. For each of the five oak species, acorns from two to three sites were collected and combined to ensure wider genetic diversity. They were sown in January 2003 at the nursery of Rana Creek Restoration in Carmel Valley, California. This area has a Mediterranean climate with long-term average annual precipitation of 534 mm with little or no rain between June and September. Acorns were initially planted in trays consisting of 34 cm^2 compartments. Seedlings were irrigated once a day and the potting soil contained a slow-release fertilizer. Seedlings also received a liquid fertilizer once or twice a week. In late February 2004, seedlings were transplanted to 15 L bags made of woven plastic synthetic fabric. The substrate used for transplanting contained medium and coarse redwood, tufa (porous stone of volcanic origin), Perlite, and slow-release fertilizer. Seedlings of each species were randomly divided into 5 or 10 groups consisting of 25 to 33 seedlings, which were then randomly placed in a shade-house. During their stay in the shade-house, the seedlings were kept well watered by overhead irrigation. In August 2005, most of the seedlings were harvested and a variety of morphological and physiological measurements were recorded, including height and basal diameter, shoot-root ratio, ratio of small roots to the taproot, and tissue nutrient concentrations. However, a sub-sample of 20 seedlings from each species was brought to the University of California Sierra Foothill Research and Extension Center (SFREC) near Marysville, California, for out-planting and further assessment. These seedlings were "leftover," but were similar morphologically to those that were harvested.

These seedlings were initially placed under a white canvas, open-sided canopy and watered daily until they were outplanted in mid-February 2006. Seedlings were planted in a randomized block design with each block consisting of five 5-seedling rows, with each row containing seedlings from one of the species. Within each block, species were randomly assigned to rows. Rows were 1.5 m apart, as were seedlings within each row. Prior to planting, a hole was excavated at each planting spot to an approximate depth of 0.5 m using a 0.3-m diameter tractor-mounted auger.

All seedlings were planted in a single day and were watered-in to ensure adequate initial soil moisture, good root-soil contact, and to eliminate any air pockets. Before planting, the entire plot was treated with glyphosate to eliminate weed competition, since the density of the weeds was highly uneven within the plot and we wanted to make sure that soil moisture conditions remained as uniform as possible.

Eight days after planting, the height and basal diameter of each planted seedling were measured and recorded. Starting in March, the plants began breaking bud and leafing out. At this time, we began assessing each seedling for bud burst approximately every 10 days using the rating system below:

0 - Buds firm, no swelling,

1 - Some bud swelling, but no buds partially or fully open,

2 - Most advanced buds open and expanding, but no stem elongation,

3 - Buds fully open, some stem elongation, but leaves not yet fully expanded and formed,

4 - New leaves fully formed.

For each species and on each evaluation date, the bud-burst ratings were calculated to generate an average bud-break rating. In early June, we noticed that the leaves on some of the deciduous species were turning brown and falling off. This was noted, but we felt that is was probably the result of some dry soil conditions near those particular seedlings and these seedlings were shedding foliage to maintain a more favorable moisture status. Such drought-deciduousness has been previously observed for blue oaks during extremely dry years (McCreary 1990). At the end of June, some leaf drop was still occurring but most seedlings were still green. In early July, some seedling mortality was noted but it was still within an acceptable range. July, however, was one of the hottest months on record, and for 13 straight days the maximum daily temperature exceeded 36^{o} C, reaching a high of 42.6^{o} C on July 22 (CIMIS data). By early August, almost 90 percent of the seedlings appeared dead, precluding measurements of field growth and plant moisture stress. We expected the mortality to increase further and that few of the seedlings would either leaf out normally next spring or sprout from their base because, as noted above, the plants appeared dead. However we will assess the plot next year to determine if all of the seedlings that appear dead really are dead. While we are extremely disappointed in this turn of events, we do believe some useful information can still be gleaned from this experiment as we outline below.

Statistical Analyses

We compared seedling height, basal diameter, bud burst, and survival among species using ANOVA and Fisher's Protected Least Significant Difference (LSD) tests. The data for these analyses were the averages for the 5-seedling species rows in each replication. Unless there were significant differences ($P < 0.05$) among means in the analysis of variance, species were not considered significantly different. If there were significant differences, however, an LSD test was conducted to determine which species were significantly different ($P < 0.05$) from one another.

Results

Seedling Size

There were marked differences among species in the size of the seedlings at the time of planting, and there were significant differences among species in both height and basal diameter (*table 1*). All five species differed among each other except for *Q. calliprinos* and *Q. ithaburensis*, which did not differ in height, and *Q. berberidifolia* and *Q. douglasii*, which did not differ in diameter. There were no apparent differences related to evergreen/deciduous status or origin.

Table 1—*Average height and diameter of seedlings at time of field planting*[1].

Species	Deciduous (D) Evergreen (E)	Israel (I) Calif. (C)	Avg. Height (cm)	Avg. Diam. (mm)
Q. agrifolia	E	C	116 a	20.9 b
Q. berberidifolia	E	C	44 c	9.2 d
Q. calliprinos	E	I	62 b	11.6 c
Q. douglasii	D	C	27 d	8.5 d
Q. ithaburensis	D	I	70 b	22.8 a

[1] Different letters within the height and diameter columns indicate there is a significant difference for this variable among species, according to a Fisher's Protected Least Significant Difference (LSD) test.

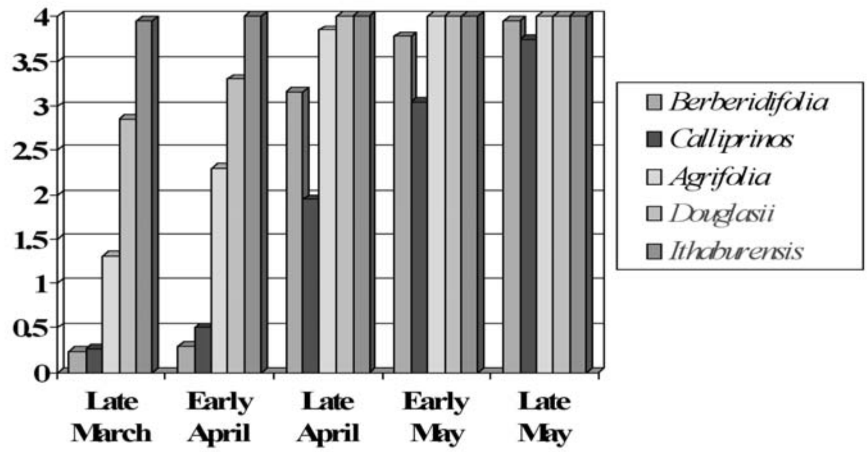

Figure 1—Bud burst averages over time for different species[1]
[1] *Quercus berberidifiolia* and *Quercus calliprinos* had significantly ($P < 0.05$) smaller bud burst ratings than the other three species on the first three evaluation dates.

Bud Burst

Species differed in bud-burst rating (*fig*. 1). As shown, the deciduous oaks from both California and Israel broke bud and began to leaf out far earlier than their evergreen counterparts. By early-April, these two species were almost fully leafed out while the evergreen species, especially *Q. berberidifolia* and *Q. calliprinos*, were just beginning to burst bud.

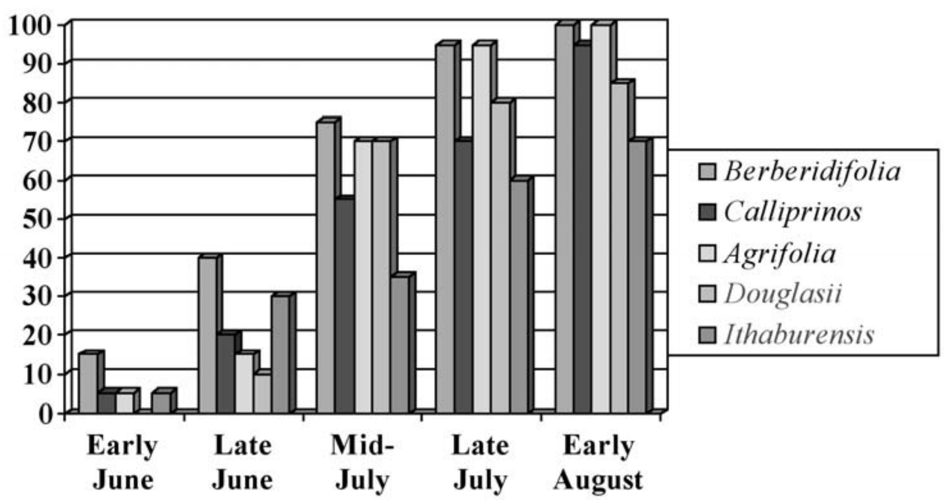

Figure 2—Average cumulative percent mortality over time for different oak species.

Mortality

Most seedlings appeared alive and well until late June (*fig. 2*). By mid-July, however, mortality had increased dramatically, and by early August nearly 90 percent of all seedlings appeared dead. However, the timing of mortality varied greatly by species. The deciduous species *Q. douglasii* and *Q. ithaburensis* survived longer than the other species and by early-August, over 20 percent of these seedlings still had green leaves, in contrast to the other three species that had a total of only two seedlings (out of 60) with some green leaves. This was the only evaluation period in which there was a significant difference among species, with *Quercus ithaburensis* having significantly lower mortality than the other four species.

Discussion

As indicated above, one of the primary purposes of this study was to compare the plant moisture stress of the different species to determine if they exhibited different strategies to deal with drought. This was not possible because of the unexpected high mortality and the lack of viable seedlings to assess. However, we were able to compare size, bud break, and survival, and gain some insights into how different seedlings perform.

Seedlings varied greatly in how much they grew while still in the planting bags. The two largest species at the time of field planting, both in terms of height and basal diameter, were *Q. ithaburensis* – a deciduous oak from Israel – and *Q. agrifolia* – an evergreen oak from California. The other three species were all fairly similar in size and included a deciduous oak from California (*Q. douglasii*), an evergreen oak from Israel (*Q. calliprinos*) and an evergreen oak from California (*Q. berberidifolia*). Clearly there was no discernable relationship between growth or size and country of origin or whether or not plants were deciduous or evergreen.

As indicated above, most seedlings appeared dead by late July. The cause of mortality is uncertain and could have been the result of the unseasonable heat, or because of the accompanying drought – or perhaps because of the “pampered” conditions the seedlings were raised in. In any case, by late July large numbers of seedlings began to turn brown and die. We felt they were not simply exhibiting drought-deciduousness because the change in leaf color was accompanied by the stems becoming extremely dry and brittle.

By late August, the two deciduous species, *Q. douglasii* and *Q. ithaburensis*, had the highest average survival. Some had lost considerable foliage, but as noted above, over 20 percent of these appeared alive. It is also interesting that these two species began breaking bud and leafing out far earlier that the evergreen oaks, regardless of origin. This would indicate that these species have evolved a strategy to take advantage of favorable environmental conditions in the early spring by developing the photosynthetic apparatus to capture the sun’s energy. These two species were at opposite ends of the size rankings when they were planted. Of all of the species, *Q. douglasii* was the smallest in terms of height and basal diameter, while the Israeli *Q. ithaburensis* had the largest basal diameter and was the second tallest of the five species. It therefore does not appear that initial size of the species at time of planting is correlated either with bud burst date or survivability.

A comparison of evergreen Israeli and California species suggests that the species from Israel had higher initial survival than California evergreen species. Further, the Israeli deciduous species (*Q. ithaburensis*) had significantly higher survival on the last evaluation date than *Q, douglasii*, its deciduous counterpart. These results are consistent with results from the greenhouse studies that found that the California species were generally less water-use efficient and might be less adapted to drought stress than Israeli species (Grünzweig and others, in press).

There was also no pattern related to country of origin and growth in containers, as by far the two largest species (*Q. agrifolia* and *Q. ithaburensis*) were from different locales. However, this does not imply that location had no effect on seedling morphology or physiology, as measurements on shade-house-grown seedlings in both Israel and California indicated that California species in general had lower seedling survival, lower water-use efficiency, greater specific leaf area and greater changes in stable carbon isotopes (Grünzweig and others, in press).

Conclusions

We detected no consistent differences between Israeli and California oak species in terms of growth in containers, bud break after out-planting, or survival in the field. This is not to say that all species performed the same, as there were substantial differences among species for all of these variables. It is just that these differences did not appear to be correlated with the location in which the species naturally grow. However, evergreen and deciduous species did respond differently after out-planting, and a comparison of the survival of evergreen and deciduous oaks from Israel with those from California does suggest that California species may be less well adapted to drought. Regardless of origin, the two deciduous species in this study broke bud far earlier that their evergreen counterparts and also survived longer under the harsh out-planting conditions. The notion that California oak species do not adapt as well to drought is speculatory and based on only five oak species and a relatively small number of seedlings within each species. These results also suggest that whether or not species are evergreen or deciduous may play a larger role in their responses to harsh environmental conditions than where they come from.

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