

Water Shortage: Conservation Mechanisms in Oak Seedlings

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Seasonal drought is a major problem for vegetation in California. As a result of high temperatures and variable amounts of precipitation, the availability of water itself is a form of stress. Finding sources of water is absolutely critical for survival and growth, and it often determines whether or not a plant will survive until the next growing season. In the case of newly established oak seedlings, this is especially true.

Within California's Mediterranean regions, conditions have placed a great deal of stress on two species of oak. *Quercus lobata* (valley oak) and *Quercus agrifolia* (coastal live oak) are in jeopardy because new seedlings are not surviving beyond the first or second year after germination. This in turn suggests that few seedlings reach adulthood and that a younger generation of oaks has not yet replenished older oaks in the population. The most common oaks visible along California's coasts and valleys are those that are more than one hundred years old. Without the further establishment of seedlings and the development of a younger generation of oaks, there is a clear natural regeneration problem.

Of course, many variables have to be considered when determining potential factors that affect natural oak regeneration. Herbivory by small and large native animals, ranching, aquifer use, and summer drought are all possible stress factors that prevent the establishment of seedlings. The specific factor addressed in this study, however, is the lack of available groundwater in conjunction with California's predominantly Mediterranean climate. In particular, the study was designed to analyze the various mechanisms *Q. lobata* and *Q. agrifolia* used to cope with drought.

Water Stress: Drought

Drought is a factor that many oaks face in the wilderness. For example, in the event that water is scarce, oaks respond to the lack of water in a variety of ways. It is known that some oaks close their stomata to prevent further water loss (water savers), while others leave theirs open and utilize

all available water resources to compensate for excessive transpiration rates (water spenders).¹ An oak experiencing water stress might also use a mechanism like the xanthophyll cycle to down-regulate its photosystems and dissipate excess amounts of absorbed radiation.^{2,3} Whether or not oak seedlings can respond to drought effectively is still not clear. What is clear, however, is the high seedling mortality rate in California and the possibility that lack of water is the cause.

The number of valley oak communities has rapidly decreased over the past century. In 1910, it was reported that 400 square miles of valley oak woodland covered the eastern San Joaquin Valley. Current values show that only 18.75 square miles of riparian valley oak woodland (12,000 acres) are left intact. In total, valley oaks currently occupy about 275,000 acres scattered throughout California, and even this value is still highly debated. Of this remaining acreage, approximately 10 percent is located on reserves. The remaining 90 percent is found on privately owned property. Even worse, it is estimated that there is one sapling for every 10 mature trees.⁴ As a result, the long-term reproductive success of the valley oak is at risk.

Coastal live oak communities, in contrast, have a one-to-three sapling-mature tree ratio and cover much more acreage.⁵ However, even though the coastal live oak is less at risk when compared to the valley oak, the reproductive success of this species has also been very low.

Additional Stress Factors

Underground water levels tend to vary significantly throughout California. This variance is due largely in part to differences in annual amounts of precipitation, rain that actually penetrates deeper layers of soil, surrounding environmental conditions, and the amount of water used by both plants and animals in the region. Due to California's Mediterranean climate, coastal areas receive on average between 20 and 80 inches of annual precipitation in the form of rain and fog. Inland areas receive between 6 and 30 inches.⁴

Human intervention also adversely affects water supplies in given regions. The act of build-

ing roads and cities on drainage basins decreases the recharge area for the local aquifer, thereby preventing desperately needed precipitation from seeping into the ground. Humans also use the aquifer for their own special purposes. Activities such as irrigation, gardening, farming, and ranching inevitably lead to the lowering of the water table and decreases in the total amount of underground water. Ranching and farming, in particular, lead to greater compaction of the soil, thereby changing the soil characteristics of a particular region and decreasing the likelihood of water penetration. In dry conditions, such human activities provide additional stress factors for saplings to overcome.

With every passing year, humanity's influence on water supplies grows stronger. In recent decades, California's population growth has been unprecedented. In the past 10 years alone there has been an increase of 13.8 percent in California's population (around 4,100,000 people). California's current population estimates cite almost 34 million inhabitants and rising.⁶ It is not surprising that the extent of urbanization and agricultural development goes hand in hand with population growth. Residential, industrial, commercial, and agricultural development projects have necessarily picked up the pace to appease the demands of a growing population. Most regions being developed, however, are some of the most ecologically diverse areas in the state. The effect of such population growth on California's fragile ecosystem has been of great concern.

Also, the herbivory of oak saplings is a very important factor preventing greater rates of seedling establishment. Small animals such as gophers and squirrels living near valley oak and coastal live oak communities have hindered the establishment of seedlings by consuming them at an early age. Studies conducted in the Santa Barbara region have shown greater survival rates among *Q. lobata* and *Q. agrifolia* seedlings when protected from rodents.⁷

The Study

To test how well seedlings cope in the event of

a drought, seedlings of *Q. lobata* and *Q. agrifolia*, deciduous and evergreen species, respectively, were grown at the University of California at Santa Barbara (UCSB) from acorns gathered at Sedgwick Ranch located in the Santa Ynez Valley, California. To limit genetic variation within both test populations, acorns from each species were gathered from a single parent tree.

Seeds were first germinated in plastic tubes (height 21cm, diameter 4cm) to let roots grow lengthwise. Two weeks later, seedlings were transferred from the tubes to 3-gallon-deep pots. Pots were rectangular in shape and had thin pieces of fabric mesh placed on their bases to allow drainage but prevent oak roots from growing out. Regular UC soil (1 vermiculite; 1 perlite; 1 sand; 1 peat moss; 1 oak leaf mold; 1 common soil) was used and was pounded uniformly in the pot with a wooden block so that each layer of soil would be dense and compact, simulating soil characteristics at Sedgwick Ranch. After soil compaction, every pot was watered to field capacity (about 640 ml of water per kilogram of soil). And lastly, each pot had 250 ml of pebbles (diameter 4 mm) spread over the surface of the soil to prevent excessive evaporation. Such precautions were taken so that the majority of measured water loss would be a result of stomatal opening and closure.

A total of 60 seedlings were used for the study at UCSB. Since it was decided that a representative sample would be used from each species, 30 of the 60 were *Q. lobata* and 30 *Q. agrifolia*. Each group of 30 was subdivided into two groups of 15 for water stressed and control (well-watered)

treatments. Control plants received a 500 ml refill of water every two days, while water-stressed plants received none.

The additional reason for using a representative sample of both *Q. agrifolia* and *Q. lobata* in the study was to observe the response of deciduous oaks to drought as compared to evergreen responses. In addition, it allowed for an investigation into the importance of sclerophylly, defined as the characteristic of having more leaf mass per unit area.

The role of sclerophylly as a water-conserving adaptation is still unclear. It was once thought that sclerophylly increased a plant's resistance to drought. Armed with thicker cuticles and a greater leaf thickness, it was believed that a plant with sclerophyllous leaves would fare better under water-deprived conditions and would prevent the loss of vital amounts of water through its leaves.¹ The experimental design of the study facilitates a comparison between sclerophyllous and nonsclerophyllous oaks.

To assess overall plant health and productivity, several measurements were taken over the course of the study. Measurements of overall photosynthetic rate were extrapolated from carbon dioxide uptake values. Stomatal conductance, the rates at which leaf stomata open and close during the day, was extrapolated from the amount of water transpired. Both measurements were taken with the aid of an Infrared Gas Analyzer (Li-Corr 6400, Li-Corr Corporation, Nebraska). In addition, predawn leaf water potentials were taken on the morning of each test day using a pressure bomb (PMS Instruments

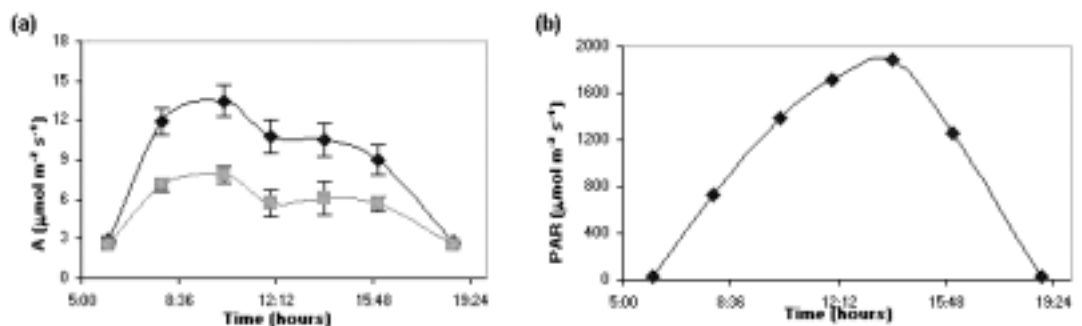


Figure 1. Photosynthetic rates (A) and corresponding light intensities (PAR). (a) photosynthetic rates (A) of *Q. lobata* (diamonds) and *Q. agrifolia* (squares) under 100% field capacity

(n=15 for both *Q. lobata* and *Q. agrifolia*). (b) light intensities present for photosynthetic rates graphed in (a).

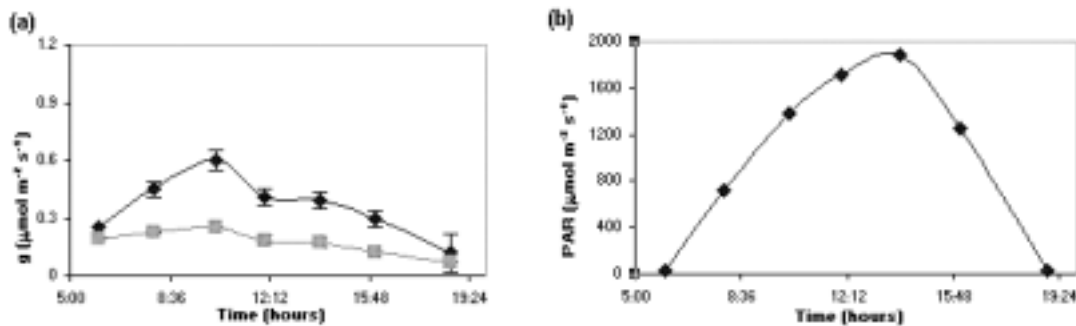


Figure 2. Stomatal conductance (g) and corresponding light intensities (PAR). (a) stomatal conductance of *Q. lobata* (diamonds) and *Q. agrifolia* (squares) under 100% field capacity (n=15

for both *Q. lobata* and *Q. agrifolia*). (b) light intensities present for conductance rates graphed in (a).

Company, Corvallis, Oregon) and fluorescence measurements were taken using a Hansatech Fluorometer (Hansatech Instruments Ltd., Norfolk, England) to assess plant photosystem health.

Daylight temperatures near the university greenhouses ranged between 21°C and 27°C, while solar radiation intensities usually reached around 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ by midday.

Results and Implications

The plants grown at UCSB did not exhibit signs of water stress because of the large amounts of water still present inside the pots. The last measurements showed that soil was at 70 percent of field capacity for both species and that soil moisture was still very high. Signs of water stress in oaks generally appear when soils exhibit water levels between 20 percent and 30 percent of field capacity.⁸ Unfortunately that was not the case at this point in the experiment. Oaks are generally more water stressed during the months of August and September. Therefore, it was too early to make a full analysis of how oaks respond to water stress.

Photosynthetic Rate Patterns

Under nonwater-stressed conditions, both species of oak experienced photosynthetic rates characterized by morning peaks, midday depressions, constant photosynthetic levels for about one hour thereafter, and small photosynthetic bursts in late afternoon (Figure 1a). The rise in photosynthetic rate during early morning hours is a result of the presence of optimal photosyn-

thetic conditions. Seedlings took advantage of the moderate morning temperatures and light intensities. As midday approached, rapid increases in both temperature and light intensities resulted in decreased photosynthetic rates (Figure 1b). Late afternoon bursts of photosynthesis are a result of optimal photosynthetic conditions, as during the early morning hours of the day.

This type of photosynthetic pattern is characteristic of some Mediterranean evergreen oak species.⁸ Surprisingly *Q. lobata*, a deciduous oak, exhibited similar photosynthetic patterns.

Changes in Stomatal Conductance

The opening and closing of leaf stomata necessary for CO₂ uptake is absolutely the greatest water investment a plant makes during the day. Almost all of the water a plant loses is a result of transpiration, which in turn is a direct result of stomatal conductance. Therefore, to see how seedlings react to a lack of water, stomatal conductance observations would be of great value.

Measurements taken on experimental seedlings (oaks at 100% to 70% of field capacity) revealed that average stomatal conductance rates were characterized by rises during early morning hours, decreases during midday, fairly constant levels for about an hour, and declines during late afternoon (Figure 2a). It should be noted that conductance patterns were somewhat parallel to photosynthetic rates.

Sclerophylly

Additionally, there is no significant difference between the responses of deciduous oaks and

Recommended Reading

Griffin JR. "Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California." *American Midland Naturalist*; 95:422–435.

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2. Adams III WW, Demmig-Adams B. "Harvesting sunlight safely." *Nature* 2000; 403:371–374.
3. Martinez-Ferri E, Balaguer L, Valladares F, et al. "Energy dissipation in drought-avoiding and drought tolerant tree species at midday during the Mediterranean summer." *Tree Physiology* 2000; 20:131–138.
4. The USDA Forest Service (<http://www.fs.fed.us/database/feis/plants/tree/quelob/introductory.html>)
5. The USDA Forest Service (<http://www.fs.fed.us/database/feis/plants/tree/queagr/all.html>)
6. California Department of Finance (<http://www.dof.ca.gov/HTML/DEMOGRAP/2000Cover.htm>)
7. Mahall B, Davis FW, Tyler CM. "Santa Barbara County Oak Restoration Program: Yearly Progress Report for the Period July 1998–June 1999."
8. Mata C. "Which tree species copes better with desiccation: the evergreen *Q. suber* or the deciduous *Q. faginea*?" Thesis 1999.

evergreen oaks. The data suggested that sclerophylly made no significant contribution to *Q. agrifolia*'s resistance to drought. However, since the study did not run to completion, it is too early to draw a definite conclusion on this matter.

Interdependence

The close relationship between stomatal conductance and photosynthetic rate is no surprise. Photosynthetic productivity is largely determined by the amount of carbon dioxide present in the leaf. And in turn, levels of carbon dioxide depend almost entirely on how often leaf stomata open and close over the course of the day.

Since stomatal conductance is influenced by a lack of water, one would expect that photosynthetic rate, by default, would be adversely affected as well. Unfortunately, the experimental oaks were last measured under normal conditions (70% of field capacity). The amount of measured water loss from the soil per day for both species of oak averaged 30 ml. Such a slow rate of drying led to the failure of the experiment. Due to the onset of winter and a worsening climate, the experimental oak saplings at UCSB were not allowed to reach greater degrees of water stress, and the

experiment had to be abandoned. Further study is needed to assess the full effect that drought has on *Q. lobata* and *Q. agrifolia* saplings.

Previous Research

Studies involving the evergreen oak *Quercus suber* and the deciduous oak *Quercus faginea* addressed the same question. Of interest was whether or not the dominance of *Q. suber* over *Q. faginea* in southwestern Portugal was a result of drought. The results showed that the evergreen oak species *Q. suber* was more capable of adapting to drought over the deciduous *Q. faginea* because of certain mechanisms that allowed it to conserve vital amounts of water. For example, stomatal conductance for *Q. suber* declined during midday, even when not water-stressed, thereby preventing excess transpiration of water. Also, the amount of water *Q. suber* stored in its leaves was significantly less.⁸

Such differences were not apparent in the study conducted at UCSB, but it does provide grounds for further research.

Acknowledgments

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