

# How Oaks Respond to Water Limitation<sup>1</sup>

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## Abstract

Oaks are extremely resilient trees. They have persisted since the mid-Cretaceous, with life forms ranging from shrubs to large trees, from evergreen to deciduous. They have two distinct, but critical, adaptations to drought that make this “mesic” taxon adaptable to dry hot environments. First, they form both arbuscular and ectotrophic mycorrhizae, with a high diversity of fungi that independently evolved many times. This means that a single tree forms mycorrhizal symbioses with partners adapting to different conditions and accessing many different resources. Oaks also have deep roots. This allows access to water resources deep in the groundwater, and with hyphae that extend into the granite matrix. Thus, water can be accessed even during drought periods when surface soils are extremely dry. Fine roots and mycorrhizal hyphae persist utilizing hydraulically-lifted water, and can even take up nutrients during these extremely dry conditions. These mycorrhizal hyphae remain viable during drought periods allowing them to rapidly utilize surface precipitation from summer monsoonal events. Together, these adaptations should allow oaks to persist and even thrive under the projected climate change, unless conditions become too harsh. That remains a critical task of future research and monitoring.

*Key words:* anthropocene, drought, mycorrhiza, nitrogen, nutrient, oak, root

## Introduction

Oaks represent one of the most adaptable and resilient trees present on earth. They occupy multiple continents and environments ranging from tropical cloud forests to desert woodlands. They have persisted since sometime in the mid-Cretaceous. Their life forms range from shrubs to majestic trees, from drought-tolerant “live oak” evergreens, to cold-tolerant deciduous trees. All of these lifeforms thrive in California, and create the well-known image of the classical California ecoregion.

California is largely arid, and even where mesic, subject to seasonal and extended drought. To survive, oaks have undergone many evolutionary adaptations to deal with drought and to persist. Among the 18 species and 30-some varieties of oaks in California, taxa range from lowland coastal and inland valleys, up hillsides and foothills, to higher elevation mountain plant communities. Although there is a plethora of adaptations to drought stress, in this treatise, I focus on belowground characteristics that allow oaks to access water deep into the profile, and nutrients and water in the surface soils even during drought. I will also focus on the work from my laboratory and colleagues in southern California. Although there is excellent work throughout the state, the mechanisms responsible for oak survival in southern California are reflective of those that work throughout the state and across oaks in general.

I focus on two mechanisms in particular that give oaks a distinct advantage in the Mediterranean-type climate that characterizes California. First, oaks form mycorrhizae, a mutualistic symbiosis with fungi, with a large diversity of fungi.

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These include arbuscular mycorrhizae (AM) with Glomeromycota, an ancient monophyletic group of fungi, and ectomycorrhizae (EM) with a high diversity of Ascomycetous and Basidiomycetous fungi. Oaks are able to switch between these two mycorrhizal types both developmentally and environmentally (for example, Egerton-Warburton and Allen 2001). This provides oaks with the ability to form a symbiosis with a large diversity of fungi that have independently evolved multiple times, with many different structural and physiological characteristics. Second, oaks have very deep roots. Oak roots emerging in Texas caves have been found as deep as 25 m (Jackson and others 1999). This allows oaks to tap groundwater resources or water pockets deep in the regolith, characteristic of California geomorphology.

In our studies, we have developed an understanding of both deciduous and evergreen oaks from three sites. These are stands of evergreen coast live oak (*Quercus agrifolia*) in riparian woodlands extending up the hillside at the Shipley Reserve (Querejeta and others 2009) and in the Santa Margarita Ecological Reserve (Borynasz others 2005), and a mixed stand of coast live oak and deciduous California black oak (*Q. kelloggii*) located within a mixed evergreen forest at the James Reserve NRS (Kitajima and others 2013).

## Belowground architecture of California's oaks

Oaks form both surface and deep roots. This variation allows them to tap both the surface moisture from individual storms, and deeper water that is either stored in the regolith or is flowing in groundwater. Without the ability of oaks to tap stored or flowing deep water, it is unlikely that oak stands would survive extended, dry summers (for example, Kitajima and others 2013).

Mycorrhizae are mutualistic symbioses formed between plant roots and fungi. The fungi radiate out from roots into the soil accessing nutrients in forms and in spatial locations inaccessible to the plant roots. In tapping those nutrient resources, the fungal hyphae also provide a continuous network whereby water can flow from areas of higher to lower moisture. By including mycorrhizae in the soil-plant-atmosphere continuum, I have previously advocated the concept of the SMPAC (soil-mycorrhiza-plant-atmosphere continuum) that provides both nutrients and water to the plant (Allen 2007). Hyphae can either form a dense network around individual roots or can be more diffuse but extend several meters outward. These fungi also release enzymes and organic acids into soil that mineralizes both organic and inorganic forms of nutrients making N and P, and even Fe and Ca available for uptake (for example, Allen and others 2003). Mycorrhizae also alter carbon balance. The plant provides carbon to the fungus in exchange for nutrients, wherein the fungus forms compounds resistant to decomposition. Mycorrhizal fungi form compounds that are relatively resistant to degradation (Treseder and others 2005), including glomalin, a glycoprotein (Rillig and others 1999) that binds soil aggregates, and chitin, a long-chain polymer of N-acetylglucosamine (Treseder and Allen 2000) that can bind with CaCO<sub>3</sub> forming hard rhizomorphs and even large mats (Allen and others 1996). Thus, mycorrhizal fungi are important in sequestering carbon directly. Our estimates of carbon allocation to mycorrhizal fungi in California mixed forests range from 20 to 35 percent of the net primary production based upon hyphal production and turnover, and N isotopic fractionation (Allen and Kitajima 2014, Allen and others 2014).

Oaks are among a select group of trees that form both arbuscular mycorrhizae (AM) and ectomycorrhizae (EM) (Egerton-Warburton and Allen 2001). Members of the Fagaceae are among the most ancient of plants that formed EM, between 100 and

200 million years ago. But oaks also retained their ability to form the original, primitive AM that evolved with the invasion of the land, somewhere between the Ordovician and Silurian Periods (Redecker and others 2000). This means that oaks are able to take advantage of a wide range of mycorrhizal fungi that have a multitude of different strategies for dealing with environmental variability. Oaks form AM during drought years and up hillsides, in largely inorganic soils, and when their roots extend into grasslands where AM predominate (Querejeta and others 2007). In stands where large amounts of organic matter accumulate and N is largely immobilized, oaks will form EM with a high diversity of fungi, including many with the ability to break down organic N and transfer it to the plant (Bledsoe and others 2014). Oaks will switch between AM and EM mycorrhizae depending upon the location, season and yearly precipitation (for example, Querejeta and others 2009).

Finally, as oak roots grow through fractures in the bedrock, their mycorrhizae grow with them. The roots remain within the fractures, but if the bedrock is weathered, the mycelial network actually grows into the granite matrix (Bornyasz and others 2005).

## **Temporal and spatial variation in water availability for oaks**

In California, precipitation varies in extremes by amount and form. Annual rainfall for oak stands can vary from a few centimeters to a meter or more, depending upon the location and the year. During wet years, precipitation can come as snowfall from northern fronts or from the “pineapple express” bringing heavy tropical rains. Monsoonal events, even occasional hurricanes, can bring moderate to heavy local rains during the summer drought. These different storm types have different signals that can be identified using  $\delta^{18:16}\text{O}$  and  $\delta\text{H:D}$ . Groundwater isotopic signatures can reflect those different storms and the plants that tap these water sources can be identified by analyzing xylem water as a marker.

As precipitation falls on the soil surface, it penetrates the soil in nearly random “wetting fronts”. Water from an individual storm may penetrate only a few millimeters, or may saturate the soil down to groundwater, depending upon the form (snow melt or rain), duration, amount, and intensity. Importantly, water penetration follows channels downward, including along roots or rock fractures. Although precipitation varies greatly, that variation may not be reflected in the soil moisture. During years of high precipitation, or following heavy snowfall, the soil becomes saturated, and the groundwater is recharged. But during moderate, and even low precipitation years, the surface soils generally still saturate (Kitajima and others 2013). During these years groundwater recharge is reduced.

## **Adaptations to drought by southern California oaks**

Seedling establishment is dependent upon microsites with sufficient moisture for germination. If seedlings emerge in the grassland or hillside away from mature trees, they become AM (Lindahl 2002). AM fungal hyphae provide nutrients and water by increasing access to soil resources. However, a seedling that emerges within a stand of mature trees taps a network largely of EM fungi (Bledsoe and others 2014). Once the seedling receives full sunlight (either in an open canopy, or with a gap formation in a previously closed canopy), the taproot extends vertically through the shallow soils and into the regolith and the secondary roots extend horizontally through the

soil. In the surface soils, these secondary roots utilize most of the soil that can flow into roots and root hairs. However, the mycorrhizal hyphae can cross soil gaps and tap soil water found either in small soil pores (Allen 2007) or across air gaps (fig. 1). These hyphae, from both EM and AM fungi, allow the plant to access both moisture in the saturated soils, but also importantly, soil moisture provided by monsoonal events during the summer droughts when there are air gaps in soil pores.

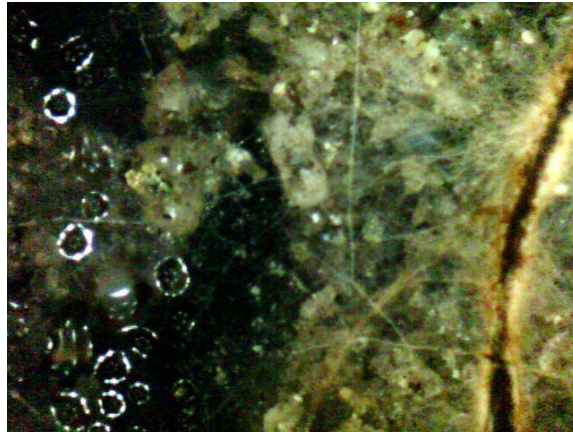


Figure 1—Arbuscular mycorrhizal fungal hyphae crossing air gaps. The water droplets have been absorbed by root hairs and fine roots (right), but AM fungal hyphae extend across air gaps accessing water droplets on the other side of the gaps. Those droplets adjacent to the hyphae were gone by the next day. Images were collected in situ using the Soil Observatory System (Allen and Kitajima 2013).

During drought, the mycelial network can provide access to water, drawn from deep in the profile and transported to hyphae via hydraulic lift (for example, Allen 2007, Egerton-Warburton and others 2007, Querejeta and others 2003). At night, a negative gradient in water potential develops from plant to the surface soils. As stomata close, water moves back through roots, fine roots, and into the mycorrhizal fungal hyphae (Querejeta and others 2003). Mycorrhizal fungal hyphae are sustained well into the dry season when it should be too dry for the hyphae to survive (Kitajima and others 2013). Further, even nutrients such as N, can be tapped by this hydraulic lift during the dry season. The hyphae near the roots are hydrophobic, so water remains within the hyphae. The hyphal tips, however, are hydrophilic, and permeable to water. Droplets emerge from the hyphal tips, absorb N (experimentally added in the form of  $^{15}\text{N}$ ). When the stomata re-open the next morning, the SMPAC gradient is re-established, and the  $^{15}\text{N}$  dissolved in the drop is transported to the plant (Egerton-Warburton and others 2008).

Mature trees tap deep water, and this water is especially critical during the dry season (Kitajima and others 2013). During the winter and early spring, when temperatures are cool and often before leaf out by deciduous oaks, soil water is recharged and water enters the deeper layers, and can even flow laterally through the groundwater (Kitajima and others 2013). During the summer drought, there is a greater use of water than can be provided by soils, so that deeper water is tapped by mature oak roots. During the driest part of the year, the deep roots transport deep water to the tree. At night, some of that water is transported to the mycorrhizal fungi via hydraulic lift (Querejeta and others 2003) and, once in the network, on to adjacent seedlings that have tapped the mycorrhizal mycelial network (Egerton-Warburton

and others 2007). This process is especially notable in the valley riparian stands where deep water is available during the summer dry season (Querejeta and others 2009).

As the taproot extends vertically, it may find fractures in the granite matrix, often created by earthquakes (Bornyasz and others 2005). If the granite has weathered sufficiently, hyphae from mycorrhizal fungi extend into the matrix providing a large water source to the deeper-rooted plants (Bornyasz and others 2005). Isotopic analyses show that both uptake of water from the granite matrix and hydraulic redistribution contribute to a seedling’s water balance (Allen 2006, Kitajima and others 2013).

## **Projections of future impacts: intersections of perturbations**

Evolutionarily, oaks are physiologically adapted to mesic conditions with summer precipitation (Mensing 2005). That they have been able to persist, even thrive during the drier periods in California’s paleo-past, provides important clues to their current capability to adapt to the expected stressors of the future. As we peer into the 21<sup>st</sup> century, we can envision a suite of interacting perturbations affecting oak woodlands, presenting challenges to managing this critical element of California’s landscape (table 1).

**Table 1—Anthropogenic impacts affecting California oaks, and the likely response of the oak woodland ecosystem**

<b>Impacts</b>	<b>Parameter changing</b>	<b>Response</b>
Direct	Elevated CO <sub>2</sub>	Increased water-use efficiency Increased C sequestration due to greater allocation to roots and mycorrhizae
	N deposition	Decreased water-use efficiency Decreased C sequestration due to reduced allocation to fine roots and mycorrhizae
	Invasive grasses	Increased fire frequency
Indirect	Rising temperatures	Greater water stress
	Increased drought stress	Greater seedling mortality
	Decreased groundwater	Reduced deep water sustaining plants during drought Reduced hydraulic lift, reducing fungal persistence during summer drought and reduced water allocation from deep-rooted mature trees to seedlings within the fungal network

There are both direct and indirect anthropogenic impacts on vegetation. Both can affect the water uptake and allocation in oaks that will impact their growth, reproduction and survival. The direct human impacts that will alter water uptake and utilization by oaks include elevated atmospheric CO<sub>2</sub> due to fossil fuel consumption. Elevated CO<sub>2</sub> would not, in itself, be detrimental to plants. Increased atmospheric CO<sub>2</sub> increases water use efficiency because the higher partial pressure means a higher CO<sub>2</sub>:H<sub>2</sub>O exchange rate. It also means that nutrients become more limiting, thereby resulting in increased mycorrhizal activity (see Allen and others 2003). But along

with elevated CO<sub>2</sub>, the use of fossil fuel results in greater N deposition. The NO<sub>x</sub> deposition results in a net fertilization of a site. This deposition reduces the root:leaf ratio and the relative amount of EM activity in some obligately EM plants (Allen and others 2010). Interestingly, AM plants may adjust to the added CO<sub>2</sub> and N by increasing root and mycorrhizal activity to match aboveground productivity (Allen and others 2003, 2010). Since oaks are switchers, they may readily adapt to both elevated CO<sub>2</sub> and NO<sub>x</sub> deposition (fig. 2). They have previously lived through periods of both higher CO<sub>2</sub> (creating conditions of N limitations), and low CO<sub>2</sub> (creating conditions where N becomes more available).



Figure 2—Cork oak (*Quercus suber*) under high N deposition from Portugal. High ammonia emanated from the feedlot operation, extending nearly a km into the cork oak-brome grass pasture. Data from Cristina Cruz, Universidade de Lisboa (Shvaleva and others 2014). (photograph from Michael Allen)

Invasive grasses have a mixed impact on oaks. The presence of the grasses themselves reduces EM activity (Allen and Karen, unpublished data) and the oak roots that extend beyond the canopy into a grassland or seedlings that establish in the adjacent grasslands tend to be AM, not EM. While oaks form AM, this mycorrhizal association is not as effective for oak seedling growth as EM associations (Egerton-Warburton and Allen 2001). In addition, grasses carry fire more extensively and frequently than do widely-spaced shrubs. But, the fire is not as hot as in dense shrub stands, potentially resulting in lesser injury to mature oak trees. In the past, California Indian tribes burned the understory of oak stands, in part to sustain the harvest of mushrooms. Most of the mushrooms produced under these conditions are EM fungal sporocarps (Anderson and Lake 2013).

The major indirect concern to oaks is global-to-regional climate change resulting from elevated CO<sub>2</sub>. That atmospheric CO<sub>2</sub> increases global temperatures has been known for over a century. But how it plays out at regional scales and the implications for greater water loss with increasing atmospheric temperatures, and groundwater extraction by both native plants and human needs becomes a critical topic for further research. If the increased water demand, due to greater temperatures, is coupled to less groundwater (Famiglietta 2014), a longer summer drought could become limiting to oak survival.

Alternatively, oaks have tended to become more dominant during the warmer, drier periods since the Pleistocene (Mensing 2005). Fagaceae likely arose and began forming EM during the late Jurassic, when atmospheric CO<sub>2</sub> levels were far higher than today (Allen 1996). Higher atmospheric CO<sub>2</sub> drives not only global

temperatures, but also results in higher carbon:nutrient ratios (Allen 1996). This forcing factor could well be a driver to develop ectomycorrhizal associations in which the fungi mineralize and transport organic N to the host. In fact, using isotopic fractionation between sporocarps, soil, and leaves, we estimate that oaks receive between 50 and 90 percent of their N via this mechanism (Allen and Cario, unpublished data). Oaks appear to have arisen during the Miocene (Mensing 2005), an interesting geological period with low CO<sub>2</sub> but high temperatures (Knorr and others 2011). AM systems are more tolerant of a broader temperature and moisture range than EM systems (for example, Vargas and others 2010). One could hypothesize that oaks kept their AM affinities even while other Fagaceae from mesic climates became almost exclusively EM. This allowed oaks, generally mesic taxa, to utilize both EM and AM to survive especially well in relatively mesic patches during arid periods in California's geological record.

These evolutionary adaptations could prove especially valuable as we move into the Anthropocene. Climate projections show warming conditions between 3 and 5 °C across the next century. Precipitation projections are inconclusive, but in any case, warming temperatures will increase evaporative demands on plants, inducing drought stress. Further, greater variability is likely, again resulting in increasing drought periods. But oaks have an incredible ability to form deep roots and switch mycorrhizae as dictated by conditions. Based on past climate history (Mensing, The paleohistory of California oaks, these proceedings), we should expect an increase in oak stands, unless the extremes are too large. That is a question for future monitoring and research.

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