

What limits evaporation from Mediterranean oak woodlands – The supply of moisture in the soil, physiological control by plants or the demand by the atmosphere?

Dennis D. Baldocchi ^{*}, Liukang Xu ¹

Ecosystem Sciences Division, Department of Environmental Science, Policy and Management, 137 Mulford Hall, University of California, Berkeley, Berkeley, CA 94720, United States

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Abstract

The prediction of evaporation from Mediterranean woodland ecosystems is complicated by an array of climate, soil and plant factors. To provide a mechanistic and process-oriented understanding, we evaluate theoretical and experimental information on water loss of Mediterranean oaks at three scales, the leaf, tree and woodland. We use this knowledge to address: what limits evaporation from Mediterranean oak woodlands – the supply of moisture in the soil, physiological control by plants or the demand by the atmosphere?

The Mediterranean climate is highly seasonal with wet winters and hot, dry summers. Consequently, available sunlight is in surplus, causing potential evaporation to far exceed available rainfall on an annual basis. Because the amount of precipitation to support woody plants is marginal, Mediterranean oaks must meet their limited water supply by a variety of means. They do so by: (1) constraining the leaf area index of the landscape by establishing a canopy with widely spaced trees; (2) reducing the size of individual leaves; (3) by adopting physiological characteristics that meter the use of water (e.g. regulating stomatal, leaf nitrogen/photosynthetic capacity and/or hydraulic conductance); (4), by tapping deep supplies of water in the soil; (5) and/or by adopting a deciduous life form, which reduces the time interval that the vegetation transpires.

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1. Introduction

The emerging field of ecohydrology is concerned with understanding and quantifying how the competing roles between supply and demand for water influence evaporation from vegetated landscapes [1,2]. From a biophysical standpoint, an ecosystem cannot use more water (through transpiration and evaporation from the soil and wetted surfaces) than is available (through precipitation minus runoff and infiltration). To balance its water supply individual plants and assemblages of plants can exploit a variety of plausible mechanisms. On short, time scales (hours to sea-

son), physiological adjustments, such as down-regulation by stomata closure [3] or by changes in hydraulic conductance [4,5] can be invoked to reduce transpiration. On longer, (years to millennia) morphological and ecological adaptations or modifications can lead to reduced transpiration. For instance, a plant can: (1) develop smaller leaves that convect heat more efficiently [6]; (2) produce more reflective leaves that reduce its solar heat load [7]; (3) adopt drought-deciduous behavior so it can drop leaves when soil moisture deficits are severe [8]; (4) produce deep roots that tap alternate sources of water [9] or (5) utilize the alternate photosynthetic pathways (e.g. C₄ or CAM) that are associated with a higher water use efficiency [10]. At the landscape scale, groups of plants must obey a natural law that requires them to acquire more carbon, through assimilation, than they lose by respiration, or they die. Because

^{*} Corresponding author. Tel.: +1 510 6422874; fax: +1 510 6435098.

E-mail address: baldocchi@nature.berkeley.edu (D.D. Baldocchi).

¹ Licor Bioscience, Lincoln, NE, United States.

photosynthesis is tied to transpiration [11], the leaf area index it establishes scales with the amount of water that is available [12–14].

This preamble sets the stage for assessing the competing factors that control evaporative water use by Mediterranean oak woodlands. Oak woodlands, growing in the Mediterranean regions of Spain ('dehesa'), Portugal ('montado') and California, experience wet and cool winters and hot, dry and sunny summers [15,16]. This asynchrony between the supply and demand for water causes annual potential evaporation to exceed annual precipitation [1,15,17,18]. Through evolution and natural selection oak trees in Mediterranean woodlands have developed structural and physiological attributes that enable them to survive on a limited annual water supply and through seasonal extremes in temperature and soil dryness. In sum, Mediterranean oaks meet their water balance by: (1) constraining the leaf area index of the landscape by establishing a canopy with widely spaced trees [1,19]; (2) reducing the size of individual leaves [6]; (3) by adopting physiological characters that meter the use of water (e.g. regulating stomatal or hydraulic conductance) [20,21]; (4), by tapping shallow and deep supplies of water in the soil [21,22]; (5) and/or by adopting a deciduous life form, which reduces the time interval that the vegetation transpires [23].

The impending change in climate, as CO₂ continues to rise, is expected to cause significant warming and changes in the timing and amount of precipitation received in Mediterranean regions of the world [24]. The structure and composition of these ecosystems are vulnerable to long term changes in precipitation because they exist in rainfall transition zones which receive just-enough rain to support either grassland, shrublands and open woodlands [25,26]. Consequently, a thorough understanding of the climatic and edaphic conditions that supply and reserve moisture and the biotic and abiotic factors that control evaporation from Mediterranean oak woodlands is needed to assess how changes in climate will affect their supply (through winter rainfall) and demand (temperature and humidity deficits) of water.

In this article, we investigate what limits evaporation from Mediterranean oak woodlands – the supply of moisture in the soil, physiological control by plants or the demand by the atmosphere? This synthesis is based on original and published data and mechanistic and process-oriented models. It conducted by examining information at three scales, the leaf, tree and woodland.

2. Setting the stage: water budgets in the mediterranean climate

2.1. The supply of water

On an annual basis, oak woodlands, in the Mediterranean climates of California, Spain and Portugal receive between 400 and 1000 mm of precipitation per year

Table 1

Mean annual precipitation oaks habitats in the Mediterranean climate of California and Europe

Oak woodland types	Mean annual precipitation, mm
California	
<i>Quercus agrifolia</i>	425
<i>Quercus douglasii</i>	480
<i>Quercus kelloggii</i>	940
<i>Quercus lobata</i>	420
<i>Quercus wislizeni</i>	610
Mediterranean Basin	
<i>Quercus ilex</i>	804 ± 260
<i>Quercus suber</i>	807 ± 287

Data are derived from Thompson et al. [17] and Joffre and Rambal [1].

[1,15,17] (Table 1). Superimposed on this mean level of precipitation is considerable inter-annual variation in rainfall. *El Nino* and *La Nina* weather regimes contribute to the inter-annual variability because they modulate winter storm tracks that bring rainfall to Mediterranean oak woodlands. It is noteworthy that Mediterranean vegetation endures many years with meager rainfall during their long life span [1,18]. The upper limit of the range of rainfall seems ample, but it must be qualified. A substantial portion of this quantity may not be available to the trees. The many storms occur during the winter period after the soil becomes saturated, so rainfall either runs off or infiltrates past the root system [1,18]. Another portion of the winter rainfall (20–40%) is used by the grass understory [27]. And many oak woodlands are on sloping terrain, so an appreciable amount of precipitation will run-off the site [18].

2.2. Demand for water

Potential evaporation is the rate of evaporation from a well-watered, vegetated surface. The Priestley–Taylor equation is a popular equation used by meteorologists to compute potential evaporation rate (E_p) [28] It is defined as 1.26 times equilibrium evaporation (E_{eq}). Equilibrium evaporation is defined as:

$$E_{eq} = \frac{s}{\lambda(s + \gamma)} (R_n - S) \quad (1)$$

where R_n is net radiation flux density, S is the soil heat flux density, s is the slope of the saturation vapor pressure-temperature curve, γ is the psychrometric constant (0.665) and λ is the latent heat of evaporation.

In sunny Mediterranean climates, annual sums of potential evaporation generally exceed annual precipitation (Table 2). Exceptions to this rule occur at sites near the coast, where humidity deficits are lower (e.g. Castelporziano, Italy), or where coastal fog reduces evaporative demand, as in the coastal foothills of northern California.

Another climate index, relevant to evaluating the supply and demand of water in Mediterranean climates, is the Budyko aridity index. It is defined in terms of the ratio

Table 2

Estimates of the Budyko Aridity Index for FLUXNET sites with oak woodlands associated with the FLUXNET (<http://www.daac.ornl.gov/FLUXNET/>) and MEDEFLEX (melody.cfe.cnrs-mop.fr/medflux/medflux.htm) projects, [21,30,31] or a long term watershed study [18]

	Precipitation (mm)	E_p (mm)	ppt/ E_p
Puechabon, France	812	950 (a)	0.854
Castelporziano, Italy	795	780 (a)	1.01
Ione, CA	558	1089 (a)	0.512
Browns Ferry, CA	708	1916 (b)	0.369
Evora, Portugal	665	1760 (b)	0.377
Evora, Portugal	665	1087 (a)	0.611

E_p is annual potential evaporation computed either with the Priestly–Taylor model (a) or measured from pan evaporation (b). ppt is precipitation.

between annual precipitation and potential evaporation [29]. Referring back to Table 2, it is evident that the majority of Mediterranean sites, evaluated here, possess aridity indices that are less than one.

Direct measurements of annual evaporation from oak woodlands, in Mediterranean climates, are scarce. In Table 3, we present a compilation of available data. These data are derived from measurements of evaporation with the eddy covariance and water balance methods and measurements of transpiration with the sap flow technique. In general, annual evaporation from Mediterranean oak woodlands ranges between 350 and 600 mm per year. Only when there are instances of severe drought do transpiration sums fall below 200 mm per year and evaporation sums fall below 300 mm per year [1,18,32]. Another key fact, deduced by comparing Tables 2 and 3, is that actual evaporation is much less than potential evaporation for Mediterranean oak woodlands, as is deemed necessary to remain viable.

The open nature of Mediterranean oak woodlands provides a niche for an herbaceous understory. Herbs and grasses are able to thrive in the understory and compete with the trees for precious water. Their mode of function

Table 3

Survey of annual evaporation from oak woodlands in Mediterranean climates

Annual evaporation (mm)	Species	Location	Reference
380 (1); 2002	<i>Q. douglasii</i>	Ione, CA	[27]
427 (1); 2003	<i>Q. douglasii</i>	Ione, CA	This study
295 (1); 2004	<i>Q. douglasii</i>	Ione, CA	This study
443 (2)	<i>Q. agrifolia</i>	Stanford, CA	[33]
570 (2)	<i>Q. durata</i>	Stanford, CA	[33]
368 ± 89 (3)	<i>Q. douglasii</i>	Browns Valley, CA	[18]
517 ± 126 (3)	<i>Q. ilex</i>	Castilblanco, Spain	[1]
484 ± 79 (3)	<i>Q. ilex</i>	El Pedroso, Spain	[1]
557 ± 167 (3)	<i>Q. suber</i>	Cazilla, Spain	[1]
169–205 (2)	<i>Q. ilex</i>	Seville, Spain	[32]
411–453 (1)	<i>Q. ilex</i>	Castelporziano, Italy	[30]
414 (2)	<i>Q. rotundifolia</i>	Evora, Portugal	[21]

1, eddy covariance; 2, sapflow; 3, water balance; measurement year.

is to be physiologically active during the winter rainy season (this enables them to use less water than temperate grasslands) and transmit their genetic information across the hot dry summer in the form of seed. They can enhance the vulnerability of the trees to summer drought by reducing the amount of moisture that is available to the trees during the dry and hot summer period. Typically, understory evaporation from open forest canopies is on the order of 20–30% of total evaporation [34,35]. On an annual basis, an oak woodland in California lost 25% (139 mm) of its water from the grass covered understory [27].

3. Scale-dependent water use: concepts and processes

In this section, we evaluate the processes that regulate evaporation of Mediterranean oaks at the scales of leaves, trees and the canopy.

3.1. Leaves: transpiration

The rate of transpiration (E) from a leaf can be expressed mathematically in terms of a network of resistors (or its inverse, conductors) in a manner analogous to Ohm's Law for electrical circuits:

$$E \sim \frac{g_s g_b}{g_s + g_b} (e_s(T_1) - e_a) \quad (2)$$

In Eq. (2), g_s is stomatal conductance, g_b is the boundary layer conductance, e_s is the saturation vapor pressure at the leaf temperature, T_1 , and e_a is the vapor pressure of the atmosphere. The boundary layer conductance is a function of leaf size and wind speed. It is typically computed with engineering theory for plates [7,36]. Current theory computes stomatal conductance as a function of leaf photosynthesis (A), relative humidity, (rh) and CO₂ concentration [37]:

$$g_s \sim m \frac{A \cdot \text{rh}}{C_s} + g_0 \quad (3)$$

In Eq. (3), m is a proportionality constant and the intercept, g_0 , represents the cuticular conductance. For blue oak (*Quercus douglasii*) in California, m remains constant across a wide range of environmental conditions, including pre-dawn water potentials below −4.0 MPa [20]. In contrast, the stomatal conductance coefficient, m , of oaks growing in Portugal (*Q. ilex*) and France (*Q. pubescens*) decreases as predawn water potential declines during summer drought [16,38].

Mediterranean oaks typically experience extremely warm air temperatures (30–40 °C), large vapor pressure deficits (they typically exceed 4 kPa) and extremely low leaf water potentials (between −3.0 and −7.0 MPa) during the summer in California [15,20] and in Europe [32,39]. Through examination of Eqs. (1) and (2), we explore the physical and biological adaptations and processes that govern the transpiration of Mediterranean oak leaves.

In general, Mediterranean oaks have leaves that are much smaller than oaks in more mesic and temperate climate zones [40]. Leaf size also varies among microclimates in the Mediterranean region. Blue oak (*Q. douglasii*) leaves, for example, are smaller on trees growing on sunnier and drier south facing microclimates than on northern slopes [6]. Effective leaf size of oaks can also vary over the course of the growing the season. We recently observed consider leaf-roll on *Q. agrifolia* trees growing on xeric slopes during the late summer (Theresa Krebs, personnel communication).

A reduction in leaf size has ecological and evolutionary advantages in semi-arid climates. A small leaf has a thinner leaf boundary layer, which enables sensible heat to be convected away from it more effectively. In marginal environments, this adaptation can help leaves avoid lethal temperature [7,41,42].

To illustrate and quantify the effect of leaf size on surface temperature (a consequence of its rate of water use), we compare computations of leaf temperature differences between a large (0.1 m) temperate oak leaf (*Q. alba*) and a smaller (0.04 m) Mediterranean oak leaf (*Q. douglasii*) (Fig. 1). A leaf energy balance model that couples stomatal conductance to photosynthesis was used to perform the computations [43]; see Appendix A for details. Theoretically, smaller oak leaves remain up to 2 °C cooler than larger oak leaves under high light conditions, for the range of humidity deficits examined. This occurs because negative feedbacks between stomatal conductance, leaf temperature and vapor pressure deficits inhibit evaporative cooling of big leaves more. Only at low light conditions and across

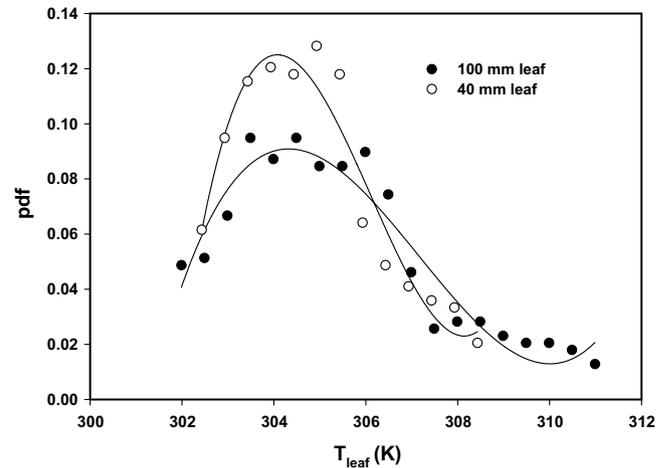


Fig. 2. The probability distribution of leaf temperature for a big and small oak leaf. The computations are based on stepping through a range of solar radiation ($400\text{--}1000\text{ W m}^{-2}$) and humidity deficits ($0\text{--}6\text{ kPa}$). Air temperature was assumed to be 303 K and wind speed was 1.0 m s^{-1} .

a range of moderate humidity deficits are larger leaves cooler. Under this set of conditions greater evaporative cooling is promoted by positive feedbacks between evaporation and vapor pressure deficits.

Because Mediterranean climates are warm, sunny and dry, temperatures of leaves on oaks in Mediterranean climates typically exceed air temperature (Fig. 2). Reducing leaf size, consequently, has many biophysical benefits. For example, smaller leaves are better able to stay within a viable range of temperatures ($273\text{--}313\text{ K}$) than bigger leaves for a typical range of environmental conditions experienced in California – 313 K is considered to be near the upper end of viable temperatures because enzymatic activity is inhibited at greater temperatures [44].

A deciduous, as opposed to an evergreen, life form is another mechanism for surviving in a climate with a limited amount of annual rainfall. However, it is inconclusive if either life strategy confers any particular advantage in Mediterranean bioclimatic zone because both life forms exist in this climate space [45–47]. Obviously, each life form has a specific set of physiological benefits and costs. Evergreen oaks transpire and photosynthesize year round, while transpiration and photosynthesis of the deciduous oaks is confined to the wet spring and a portion of the hot dry summer. Because the growing season is short for deciduous oaks, they often compensate physiologically by developing leaves that have greater photosynthetic capacities than leaves of evergreen species [23,45]. Because maximum stomatal conductance scales with photosynthesis [48], one could deduce that the maximum stomatal conductance of deciduous oaks will be greater than those of evergreen oaks, as has been observed by Hollinger [45]. However, exceptions to these ‘rules’ occur – Damesin et al. [46] found little difference in the photosynthetic capacity and maximum stomatal conductance of two co-occurring deciduous (*Q. pubescens*) and evergreen (*Q. ilex*) Mediterranean oaks.

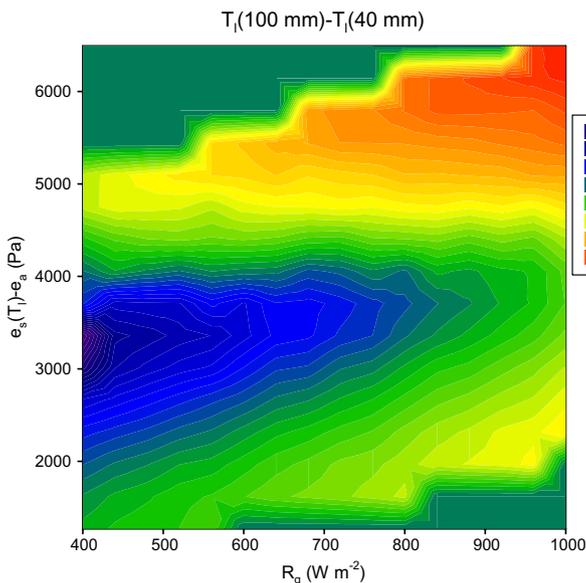


Fig. 1. Impact of leaf size on leaf temperature. Contour plots compare the differences in leaf temperature between a large (100 mm) and a small (40 mm) leaf (°C). Computations were derived from a coupled leaf energy balance-photosynthesis model. Computations assumed air temperature was 30 C and wind speed was 1 m s^{-1} . Atmospheric humidity and solar radiation were varied.

Stomatal conductance of deciduous oak trees cannot remain maximal the entire summer when evaporative demand is high. To do so would cause the plant to deplete its soil moisture reserve before the commencement of next autumn’s rain [20,49,50]. Oaks regulate water flowing through their stomata by turgor and osmotic adjustment [49,51], by altering their hydraulic conductance [21] or by the reallocation of leaf nitrogen, which reduces photosynthetic capacity and maximum stomatal conductance [20]. And in turn, the drought induced reduction in stomatal conductance reduces the internal CO₂ concentration and leaf photosynthesis [3].

The functional relationship between maximum stomatal conductance and predawn water potential, a measure of the integrated soil moisture in the root zone quantify how stomatal conductance responds to soil moisture deficits (Fig. 3). Blue oaks, *Q. douglasii*, are able to achieve significant levels stomatal conductances at much lower predawn water potentials than do *Q. ilex* or *Q. pubescens*. With ample soil moisture the stomatal conductance for *Q. douglasii* falls between the two European oaks and exceeds that for an evergreen California oak (*Q. agrifolia*). And at extremely low predawn water potentials (below -3 MPa) the stomata of blue oak remain open while the stomata of other Mediterranean oaks have shut.

There is some controversy how g_s is modeled when the plant experiences soil moisture deficits. Sala and Tenhunen (1996) hypothesize that the m coefficient, in Eq. (3), decreases as soil dries. Modelers using the Simple Biosphere model, SiB, assume that m is constant, and instead argue that the carboxylation velocity of photosynthesis, V_{cmax} , decreases with drought (Coello et al., 1998).

To understand the connection between g_s and V_{cmax} , we must examine photosynthesis theory [52]. The rate of photosynthesis (A) is a function of the carbon dioxide assimilated by carboxylation (V_c) minus carbon dioxide lost by

oxygenation (V_o) (photorespiration) and dark respiration (R_d):

$$A = V_c - 0.5 V_o - R_d \tag{4}$$

If sunlight is ample, V_c is a function of the available substrate (CO₂) and is limited by the maximum rate of carboxylation V_{cmax} :

$$V_c = \frac{V_{c,max} C}{C + K_c(1 + O/K_o)} \tag{5}$$

The other terms in Eq. (5) refer to oxygen concentration (O) and Michaelis–Menten constants for carboxylase and oxygenase, K_c and K_o , respectively.

We have previously reported that V_{cmax} varies seasonally over blue oak as it experiences seasonal drought and there is a coordinated reduction in leaf nitrogen [20]. A re-examination of these data, shown in Fig. 4, reveal that the seasonal changes in V_{cmax} are strongly correlated ($r^2 = 0.74$) with the seasonal change in pre-dawn water potential. This result confirms the hypothesis of Coello et al. (1998), who among its members were co-developers of Eq. (3), that g_s is a function of V_{cmax} rather than a function of m , as posited by Sala and Tenhunen (1996). Incorporating the linear relation between V_{cmax} and soil water potential in biophysical models like CANOAK will assist the model in completing the feedback loop between soil moisture deficits, stomatal conductance and transpiration. It should improve how they compute energy and carbon fluxes with progressive drought [53].

Vapor pressure deficits (D) establish the atmospheric potential for leaf transpiration of small and well-coupled leaves [54]. Feedbacks between E , g_s and D , however, cause the relation between E and D to be very complex and non-linear (Fig. 5). From a physiological standpoint, an increase in D will enhance transpiration, by producing a

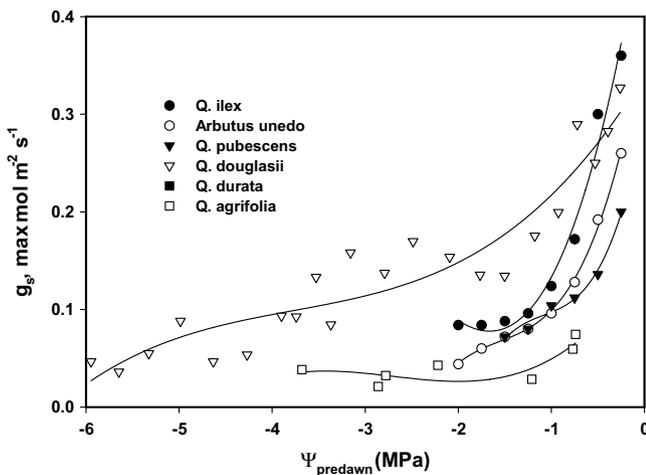


Fig. 3. Relationship between maximum stomatal conductance and predawn leaf water potential for Mediterranean oak species. Data of Goulden [33], Teixeira Filho et al. [51] and Xu and Baldocchi [20].

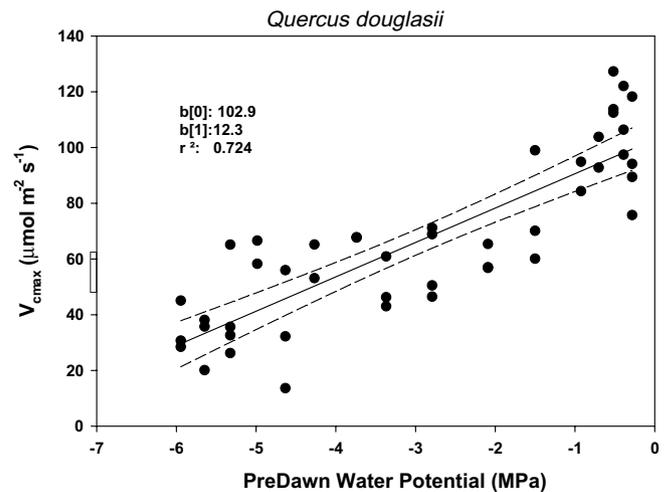


Fig. 4. The correlation between pre-dawn water potential and maximum carboxylation velocity. The data were measured on a blue oak tree growing near Ione, CA during the summers of 2001 and 2002.

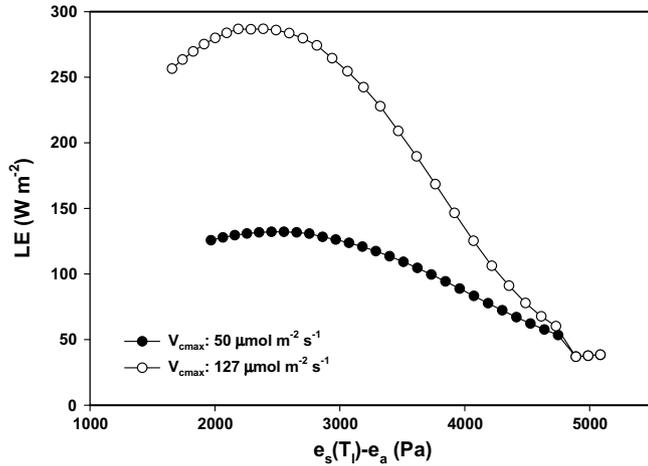


Fig. 5. Theoretical calculations of latent heat exchange of a blue oak leaf. The leaf has a length of 0.04 m, the solar radiation was 1000 W m^{-2} , wind speed was 3 m s^{-1} and air temperature was $30 \text{ }^\circ\text{C}$. Two cases were simulated. One for the spring period when soil moisture was ample and V_{cmax} was high ($127 \mu\text{mol m}^{-2} \text{ s}^{-1}$). The second case was for the summer when soil moisture was limiting and V_{cmax} had become diminished ($50 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

stronger humidity gradient between the leaf and the atmosphere. But a further increase in D will initiate a negative feedback on stomatal conductance, which will lead to a reduction in transpiration (Fig. 5).

Early in the growing season – when water is ample – V_{cmax} values of blue oak are extremely high ($\sim 127 \mu\text{mol m}^{-2} \text{ s}^{-1}$). This cited value approaches and exceeds V_{cmax} values associated with fertilized crops [55]. Photosynthetic capacity of deciduous oaks must be very high, on the short term, in order to assimilate enough carbon to sustain the tree over the dry summer and dormant winter periods, when photosynthesis is low or non-attainable. But of course this short-term high capacity comes at the expense of losing water at higher rates then. Theoretical calculations, shown in Figs. 5 and 6, provide theoretical support for the observation that a seasonal reduction in leaf nitrogen, and consequently photosynthetic capacity V_{cmax} , enables an oak leaf to reduce its water loss by reducing maximum stomatal conductance [20].

3.2. Tree transpiration

In the ‘dehesa’ on Spain, tree density increases from 10 to 50 trees per hectare as precipitation increases from 500 to 800 mm per year [56]. Though one may expect transpiration of an oak woodland to increase with tree density, the answer is not simple because of interactions between transpiration and tree size (cross-sectional area) and between tree density and tree size. With regards to individual trees, transpiration of oak trees scales with sapwood cross-section [50]. Summing transpiration of trees that are dotted across the landscape, produces a different functional relationship. Enquist [57] has shown that self-thinning and

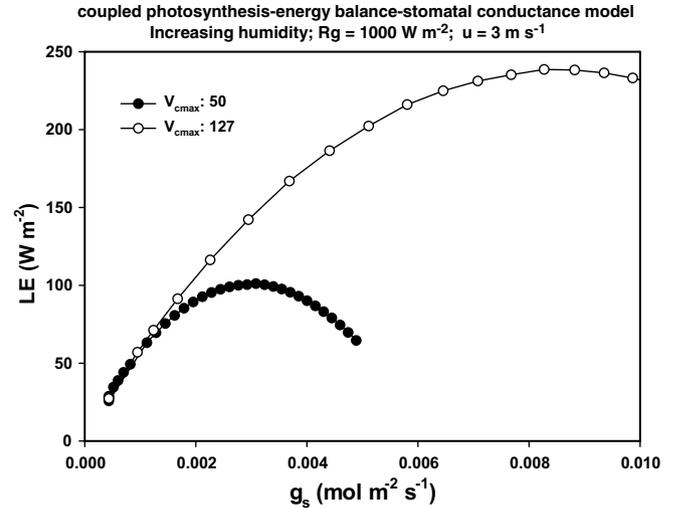


Fig. 6. The relationship between latent heat exchange of a blue oak leaf and its stomatal conductance for a series of V_{cmax} values. These are theoretical results produced by a coupled leaf energy balance-photosynthesis model.

competition for limited resources causes the maximum number of trees, N_{max} , to scale with the $-3/4$ power of plant mass, M ,

$$N_{\text{max}} \propto M^{-3/4} \quad (6)$$

and sapflow rates of individual trees, Q_{xylem} , scale with the $3/4$ power of plant mass:

$$Q_{\text{xylem}} \propto M^{3/4} \quad (7)$$

So theoretically, transpiration rates on a land surface basis, Q_{land} , is scale invariant.

$$Q_{\text{land}} \propto N_{\text{max}} \cdot Q_{\text{xylem}} \propto M^0 \quad (8)$$

While scaling theory works successfully across many orders of magnitude, there is considerable variation within specific space scales. For example, complex changes in components of the surface energy balance occur when changing tree density and leaf area index, which will feedback on latent heat change. Such factors are not included in the scaling theory of Enquist [57].

In addition to regulating transpiration at the leaf scale by closing their stomata, Mediterranean oak trees endure the extremely warm and dry conditions of summer through several avoidance and adaptation mechanisms, at the tree scale. Oaks trees avoid severe water deficits by tapping deeper sources of soil water than competing grasses [21,22,58] or they can remedy soil moisture deficits through hydraulic lift [59]. Thirdly, oaks may adapt to severe soil water deficits by decreasing their hydraulic conductivity. This is accomplished by reducing leaf area, root density and sapwood area [33,39] or by drought induced embolisms. In contrast, a case study on the sap flow of blue oak did not observe a seasonal reduction in hydraulic conductivity [50].

3.3. Canopy-scale evaporation

At the canopy scale, the Penman–Monteith equation can be used to identify and quantify the factors governing rates of evaporation to the atmosphere [54].

$$\lambda E = \frac{s(R_n - S) + \rho \cdot C_p \cdot G_H \cdot D}{s + \gamma + \gamma \frac{G_H}{G_s}} \quad (9)$$

In Eq. (9), ρ is air density, C_p is specific heat of air, and G_H and G_s are the canopy-scale conductances for boundary layer and surface. Conceptually, perturbations in canopy surface conductance of a forest canopy are due to variations in leaf area index, maximum stomatal conductance and drought [12,60,61].

Examining how rates of latent heat exchange, normalized by their equilibrium evaporation rate, $\lambda E/\lambda E_{eq}$, vary with canopy resistance provides an illustrative way to examine the interactive effects of leaf area index/canopy coverage, photosynthetic capacity and soil water deficits on the partitioning of net radiation into latent heat transfer of Mediterranean woodlands and the mechanism for achieving a wide range of evaporation rates over the course of a year. Fig. 7 shows that $\lambda E/\lambda E_{eq}$, for an oak woodland in California, decreases linearly with a logarithmic increase in canopy resistance, R_{canopy} (Fig. 7). When the canopy was dry and at full leaf and soil moisture was ample, the maximum value of $\lambda E/\lambda E_{eq}$ attained by the oak woodland was about 0.9. This value is about 30% less than the values associated with evaporation from green, well-watered, and fertilized C_3 crops, like wheat—they attain normalized evaporation rates close to the Priestley–Taylor coefficient (~ 1.26) [12,28].

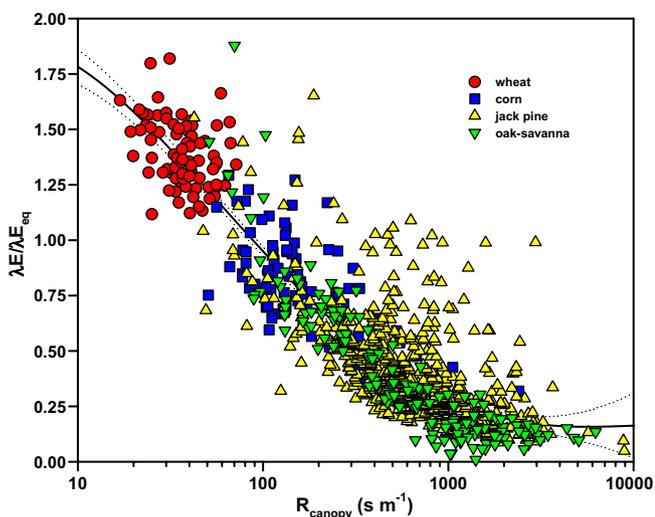


Fig. 7. The relationship between normalized latent heat exchange and canopy resistance. Latent heat exchange rates are normalized by the equilibrium evaporation rate λE_{eq} . For reference we plot data from contrasting cases, a well-watered and fertilized wheat crop, an open corn canopy and a jack pine stand. Those data are reported in Baldocchi et al. [34].

Theoretical studies indicate that $\lambda E/\lambda E_{eq}$ only approaches the Priestley–Taylor coefficient of 1.26 when surface resistance is less than 60 s m^{-1} [62]. In contrast, a combination of ecological and physiological factors prevented the minimum canopy resistance for the dry oak woodland canopy from dropping below 100 s m^{-1} , thereby explained the sub-maximal rates of evaporation when soil moisture was ample.

As the summer progressed and the soil moisture profile was depleted, R_{canopy} increased and the ratio $\lambda E/\lambda E_{eq}$ decreased in synchrony, reaching levels below 0.10. We find that these data overlapped with evaporation measurements from a sparse jack pine forest growing on dry sandy soil in the boreal region of Canada.

Alternatively the Penman–Monteith Equation can be deconstructed into its equilibrium (E_{eq}) and imposed (E_{imp}) components [54]:

$$E = \Omega E_{eq} + (1 - \Omega) E_{imp} \quad (10)$$

Omega, Ω , is the coupling coefficient. It varies between 0 and 1, depending on leaf size, stomatal conductance and leaf boundary layer resistance. Plants with small leaves and canopies that are aerodynamically rough have small omega values. This condition implies they are highly coupled to their environment so their evaporation rates are tightly coupled with D and G_s , as is the case for Mediterranean oaks [39].

4. Concluding remarks

By nature of their climate, Mediterranean oak woodlands forests experience temperate and wet winters and hot and dry summers. Consequently, these trees have evolved to survive on 500–1000 mm of precipitation per year and endure extended periods when potential evaporation exceeds precipitation. Survival and reproductive success on a limited water balance is accomplished by adopting a combination of particular structural and functional (physiological) attributes. The adoption of a deciduous life form and smaller leaves and the development of a sparse open canopy are examples of structural features that enable Mediterranean oak trees to transpire less, precious water. Functional attributes that enable Mediterranean trees to survive on a limited supply of water include the down-regulation of stomatal conductance, the tapping of deep sources of water or physiological adjustments that enable the leaf to function at water potentials much below the conventional permanent wilting point (-1.5 MPa). The grass understory simply avoids summer drought and is active only during the winter and spring, when soil moisture is ample.

There are several soil factors that complicate the assessment of evaporation by Mediterranean oak woodlands that were not considered in this chapter, and merit mention. Topography affects the water balance and transpiration of Mediterranean oak woodlands on hilly terrain where runoff is high. But run-off does not necessarily produce a

net loss. In the case of trees growing on topographic draws, runoff from lateral zones can provide an additional source of water and be the factor distinguishing whether the landscape is pure grassland or an oak grass mix. The water holding capacity of soils also plays an important, long-term role on the ability of Mediterranean oaks to survive and thrive. The input of organic matter to the soil, by leaf drop, produces radial gradients in soil water holding capacity, which is greater under trees.

In closing, long-term and integrated studies evaporation of oak woodlands need to continue to quantify their sensitivity to inter annual variations in climate and document their response to impending global climate change. A combination of watershed, eddy covariance and sap-flow measurement studies and a hierarchy of mechanistic soil-plant-water transfer models, coupled with weather and satellite observations should be used to up-scale information from a few specific sites across much wider areas.

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Appendix A

Original data evaluated in this paper are based on water vapor and energy exchange measurements made over an oak savanna near Ione, CA (latitude: 38.4311°N; longitude: 120.966°W; altitude: 177 m). The eddy covariance method was used to measure water, heat and CO₂ flux densities between the biosphere and atmosphere. Wind velocity and virtual temperature fluctuations were measured with a three-dimensional ultra-sonic anemometer. Carbon dioxide and water vapor fluctuations were measured with an open-path, infrared absorption gas analyzer. The set of micrometeorological instruments was supported 23 m above the ground (~10 m over the forest) on a walk-up scaffold tower. Other environmental measurements made at the oak woodland include upward and downward facing visible quanta, solar and net radiation, air temperature and relative humidity, rainfall and soil moisture. Details of the experiment are reported elsewhere [27].

Latent heat exchange (λE ; W m⁻²) and surface-air temperature differences (ΔT ; K) were computed analytically by solving quadratic equations associated with these dependent variables [63]:

$$a\lambda E^2 + b\lambda E + c = 0 \quad (\text{A1})$$

$$d\Delta T^2 + e\Delta T + f = 0 \quad (\text{A2})$$

The coefficients (*a.f.*), associated with the quadratic Eqs. (A1) and (A2), can be derived through the algebraic manipulation of a set of equations describing the surface energy balance. This derivation starts with the definition of available energy, the sum of net incoming short and long-wave energy (Q ; W m⁻²):

$$Q = R_g(1 - \alpha) + \varepsilon L \downarrow \quad (\text{A3})$$

In Eq. (A3), R_g is the flux density of incoming shortwave solar radiation (W m⁻²), α is albedo, $L \downarrow$ is the flux density of incoming longwave radiation (W m⁻²) and ε is emissivity. Next we define the flux density of net radiation as the balance between Q and the long-wave energy emitted by the surface, which is a function of its temperature (T_s) to the fourth power:

$$R_n = R_g(1 - \alpha) + \varepsilon L \downarrow - \varepsilon \sigma T_s^4 \quad (\text{A4})$$

In Eq. (A4) σ represents the Stefan–Boltzman constant. At the landscape scale, net radiation is consumed via sensible (H), latent (λE) and soil (G_{soil}) heat exchange.

$$R_n = H + \lambda E + G_{\text{soil}} \quad (\text{A5})$$

Sensible and latent heat flux density can be expressed using an Ohm's Law analog that expresses the energy flux density as a product of a network of resistances and a potential difference:

$$H = \frac{\rho_a C_p (T_s - T_a)}{R_a} \quad (\text{A6})$$

$$\lambda E = \frac{m_v / m_a \lambda \rho_a (e_s(T_s) - e_a)}{P(R_a + R_s)} \quad (\text{A7})$$

In Eqs. (A6) and (A7), ρ_a is air density, λ is the latent heat of vaporization, R_a is the aerodynamic conductance for sensible heat transfer (m s⁻¹), R_s is stomatal conductance (m s⁻¹), C_p is the specific heat of air (J kg⁻¹ K⁻¹), m_v and m_a are the molecular weights of vapor and dry air (g mol⁻¹), P is pressure (kPa), e_s is saturated vapor pressure (kPa) and e_a is the ambient vapor pressure (kPa). Further details on these calculations are presented elsewhere [64].

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