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On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective

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Abstract. We assessed the differential advantages of deciduousness and evergreenness by examining 26 site-years of carbon dioxide, water vapor, and energy flux measurements from five comparable oak woodlands in France, Italy, Portugal, and California (USA). On average, the evergreen and deciduous oak woodlands assimilated and respired similar amounts of carbon while using similar amounts of water. These results suggest that evergreen and deciduous woodlands have specific, and similar, ecological costs in mediterranean climates, and that both leaf habits are able to meet these costs.

What are the mechanisms behind these findings? Deciduous oaks compensated for having a shorter growing season by attaining a greater capacity to assimilate carbon for a given amount of intercepted solar radiation during the well-watered spring period; at saturating light levels, deciduous oaks gained carbon at six times the rate of evergreen oaks. Otherwise, the two leaf habits experienced similar efficiencies in carbon use (the change in carbon respired per change in carbon assimilated), water use (the change in carbon assimilation per change in water evaporated), and rainfall use (the change in evaporation per change in rainfall).

Overall, leaf area index, rather than leaf habit, was the significant factor in determining the absolute magnitude of carbon gained and water lost by each evergreen and deciduous oak woodland over an annual interval; the closed canopies assimilated and respired more carbon and transpired more water than the open canopies.

Both deciduous and evergreen mediterranean oaks survive in their seasonally hot/dry, wet/cool native range by ensuring that actual evaporation is less than the supply of water. This feat is accomplished by adjusting the leaf area index to reduce total water loss at the landscape scale, by down-regulating photosynthesis, respiration, and stomatal conductance with progressive seasonal soil water deficits, and by extending their root systems to tap groundwater.

Key words: carbon dioxide exchange; deciduousness vs. evergreenness; ecosystem ecology; eddy covariance; FLUXNET; mediterranean oak woodlands; Quercus *spp.*

Introduction

Why are trees evergreen or deciduous? This question remains one of the more fundamental questions that have been asked by many botanists and ecologists over the past 40 years (Monk 1966, Mooney and Dunn 1970, Chabot and Hicks 1982, Aerts 1995, Givnish 2002). The main explanations are derived from the fields of biogeography and ecophysiology and they tend to employ ecological "economics," cost/benefit reasoning, and climate-based rules.

The advantages of adopting an evergreen leaf habit are many. Foremost is the fact that evergreen leaves photosynthesize longer than deciduous ones. Consequently, the amortized costs of construction and acquiring nutrients are lower for evergreen trees than for deciduous trees (Aerts 1995, Givnish 2002). In addition, evergreen trees are known to have lower hydraulic conductances than deciduous trees, an architectural feature that promotes water savings and enhances tolerance during dry periods (Tyree and Cochard 1996, Eamus and Prior 2001). On the other hand, evergreen trees experience metabolic and ecological expenses and stresses not faced by deciduous trees. Long-lived leaves must withstand herbivory over longer periods and produce volatile organic compounds that serve as defenses to herbivory (Penuelas and Llusia 2004). In addition, evergreen leaves must endure an assortment of stresses, due to freezing, drought, high light and temperature, or a combination of factors. Evergreen trees generally accommodate for these unfa-

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vorable conditions by producing leaves that possess lower nitrogen contents, lower photosynthetic capacities (Reich et al. 1997, Wright et al. 2005), and lower nitrogen loss rates at senescence (Aerts 1995, Silla and Escudero 2003, Kobe et al. 2005). Hence, evergreen trees are favored on nutrient-poor soils because the concomitant effect of lower photosynthetic capacity can be compensated by assimilating carbon over a longer growing season (Monk 1966, Hollinger 1992, Aerts 1995, Givnish 2002).

Deciduous trees generally compensate for a shorter growing season by producing leaves that have higher photosynthetic rates per unit mass than do evergreen trees; shorter-lived leaves require less investment in structure and chemical defense compounds (Mooney and Dunn 1970, Wright et al. 2004). Furthermore, winter deciduousness is widely recognized as a way to avoid or and circumvent freezing and to reduce respiratory losses when the potential for carbon gain is low.

These ecophysiological and biogeographical viewpoints contain a variety of pros and cons. The strength of ecophysiology-based explanations is their ability to characterize interactions between physiology, competition, and natural selection in a mechanistic manner. Limitations of the ecophysiological viewpoint are associated with one or a combination of the following factors: (1) the approach tends to be nonquantitative, e.g., rule-based (Mooney and Dunn 1970, Blumler 1991); (2) it tends to be restricted to certain ecological ranges (Mooney and Dunn 1970, Damesin et al. 1998); and (3) it tends to ignore belowground components and whole-plant integration (Givnish 2002). Furthermore, leaf traits, associated with a single-age cohort, may not represent canopy traits; canopies consist of the integrative and differential responses of a multiage cohort (Aerts 1995, Silla and Escudero 2003) and exhibit emergent-scale properties. The biogeographical models tend to be descriptive and are based on rules, empirical functions, and empirical climate thresholds (Holdridge 1947, Woodward 1987, Prentice et al. 1992). Biogeographical explanations capture spatial patterns of evergreenness and deciduousness well, but they fail to provide a mechanistic explanation for the spatial distribution of these leaf habits (Givnish 2002). Consequently, biogeographical models may be limited in their ability to predict how ranges of evergreen and deciduous forests may expand or contract with global warming. Overall, a universal explanation for deciduousness and evergreenness remains lacking because few explanations consider the coupled plant–soil–atmosphere at the ecosystem scale (Hollinger 1992, Givnish 2002).

Although a body of work exists on the attributes of deciduous and evergreen leaves, no one has attempted to address this topic by synthesizing information on carbon gains and losses and water use at the ecosystem scale. Here, we present a comparative analysis on the carbon, water, and energy flux attributes of ecosystems with broad-leaved evergreen and deciduous trees that exist in a similar climate and ecological space and are predominated by a common genus. This condition is met in mediterranean-type climate zones of Europe and California. The mediterranean-type climate provides an ideal laboratory for testing theories on ecological factors that confer advantages to evergreenness or deciduousness because it possesses a rich array of oak (*Quercus* spp.) tree life-forms, different degrees of canopy coverage, and a wide range in soil moisture availability and temperature over the course of a year. For, example, oak (*Quercus* spp.) trees may be deciduous, evergreen, or mixed, and their canopies can range from open and sparse to closed (Griffin 1988, Barbour and Minnich 2000, Quezel and Medail 2003, Joffre et al. 2007). Selective pressures affecting the presence or absence of mediterranean-type deciduous and evergreen oak woodlands include climate, soils, vegetation history, fire frequency, grazing, and human selection for acorn production, cork, or coppice potential (Barbero et al. 1992).

In this paper we use carbon, water, and energy flux measurements and climate information that was acquired over multiple years from deciduous and evergreen oak woodlands in France, Italy, Portugal, and California to ask, and answer, several questions regarding the ecosystem ecology of deciduousness and evergreenness. (1) What factors and processes (e.g., leaf area index, leaf nitrogen, gross photosynthesis, ecosystem respiration, evaporation) favor or discriminate against deciduousness or evergreenness at the stand scale? (2) Is deciduousness, or evergreenness, at a competitive advantage in mediterranean oak woodland ecosystems, or are they two ways of accomplishing the same task, e.g., acquiring enough resources (carbon, water, energy, nitrogen) to sustain themselves?

MATERIALS AND METHODS

This analysis is based on carbon, water, and energy flux measurements that were made at five field sites in mediterranean-type climate zones, 2001–2006. Three sites, located in France, Italy, and Portugal, are inhabited by evergreen oak woodlands; two sites, in Italy and California, are dominated by deciduous oak woodlands. Together, these five sites represent a range of canopy closure for each leaf habit; the French and Italian sites form closed canopies and the Portuguese and Californian sites are open woodlands (see Plate 1). These sites are the only ones in the FLUXNET database (which contains data from more than 200 sites worldwide), that are suitable for this analysis (database *available online*).[7]

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[7] ⟨http://www.fluxdata.org⟩

Biogeographical and climate ranges

Evergreen holm oak (*Quercus ilex*) spans a domain (65 000 km^2 in area) that crosses North Africa, eastern Portugal, Spain, southern France, Corsica, and the western Italy, and extends toward Greece (Barbero et al. 1992). Q*uercus ilex* has two morphologically different subspecies, which also have distinct geographical distribution areas. *Q. ilex* ssp. *ilex* can be found in coastal areas from Greece to eastern Spain, and *Q. ilex* ssp. *rotundifolia* is dominant in continental and western Iberian Peninsula and North Africa. Deciduous turkey oak (*Quercus cerris*) spans the Italian peninsula (south of the Alps) to the western cost of Turkey. Deciduous blue oaks (*Quercus douglasii*) are endemic to California; their habitat, on the coastal and mountain foothills that ring the Great Central Valley (Griffin 1988, Barbour and Minnich 2000), covers an area of ~76 000 km^2 (Thompson et al. 1999).

A common climatic attribute of all five sites, in their native range, is the fact that they experience cool, wet winters, hot, dry summers, and large interannual variation in rainfall. *Q. ilex* spans a climate range where mean annual rainfall is ~500–900 mm/yr. *Q. cerris* spans a climate space where rainfall ranges between 600 and 1000 mm/yr (Perini et al. 2007). The climate space of *Q. douglasii* overlaps that for *Q. ilex* and *Q. cerris*, but is shifted toward drier conditions by about 100 mm per year; annual precipitation ranges between 400 and 800 mm/yr (Griffin 1988, Major 1988).

Site information

We summarize geographic, climate, vegetation, and edaphic information for the specific sites in Table 1, and give brief accounts of the key site attributes.

France.—The French study site is located 35 km northwest of Montpellier (southern France) in the Puéchabon State Forest (43°44′ N, 3°36′ E; elevation: 270 m a.s.l.), and is situated on a flat plateau. The stand is representative of woodlands in the *garrigue*. Vegetation is dominated by a dense overstory of the evergreen oak *Quercus ilex* ssp. *ilex*. The understory is composed of a sparse (<25%) shrubby layer less than 2 m in height. The soil is extremely rocky, from hard Jurassic limestone parent material; on average, the volumetric fractional content of stones and rocks is 75% for the top 0–50 cm and 0.90 below. The stone-free fraction of the soil is a homogeneous silty clay loam (USDA texture triangle) in the 0–50 cm layer (38.8% clay, 35.2% silt, and 26% sand). The soil fills up the space between the stones and rocks, and this provides a source of water throughout the long, dry summers for the deep-rooted *Q. ilex*. About 90% of the root mass (perennial roots and burls) can be found in the first 50 cm, but some roots have been found up to 4.5 m deep. With regard to site history, the stand was managed as a coppice for centuries and was last cut in 1942. Additional site information is reported in papers by Allard et al. (2008) and Rambal et al. (2003, 2004).

Portugal.—The Portuguese field site is located near Évora, which is ~150 km southeast of Lisbon (38°32′ N, 8°00′ W; elevation 243 m a.s.l.). The trees consist of a mix of broad-leaved evergreen oaks (*Quercus ilex* ssp. *rotundifolia* and some *Q. suber*). These trees are scattered across the landscape, forming a savanna-like, open woodland (*montado*). The understory consists of a mixture of annual herbaceous C_3 plants and shrubs, dominated by rock rose *Cistus* spp., and it is grazed by cattle. Site topography is slightly undulating. The soil is a very shallow (30 cm deep) sandy Cambisol overlying fractured gneiss rock. Soil water retention capacity is rather low. Maximum available water storage in the upper 0.3 m of soil profile is 24 mm. Additional information on the site and instrumentation is provided by Pereira et al. (2007).

Italy.—One Italian site (Roccarespampani) is near the village of Tuscania (42°23′ N, 11°55′ E). The site is flat to slightly sloping and its elevation is 234 m a.s.l. The predominant oak trees, *Quercus cerris*, are deciduous and form a closed canopy; other species at the site (5–10% of the total) are *Q. pubescens*, *Acer* spp., and *Fraxinus ornus*. A few evergreen oaks (*Q. suber*) are found at the site, too. The site has been coppiced on a 15–20 year rotation over the past 200 years, and the current trees are about 20 years old. The soil is a sandy clay (Luvisoil) ~70 cm deep, and the underlying rock is of volcanic origin. Additional information on the site can be found in Tedeschi et al. (2006) and Rey et al. (2002).

The second Italian site is near the town of Castelporziano (41°45′ N, 12°22′ E), 25 km west of Rome, and is within 2 km of the Mediterranean Sea. The site is on the estate of the President of Italy and is being maintained as a natural reserve. The vegetation is dominated by evergreen oak (*Quercus ilex*). The trees are over 50 years old and are 10–15 m tall. They grow on a sandy soil at a density of 1500 stems/ha, forming a closed canopy with a leaf area index near 3.5 (Manes et al. 1997, Tirone et al. 2003). Soil water deficits at this site during the dry summer are moderated by the presence of a shallow water table, which is tapped by the tree roots (Manes et al. 1997).

California.—The Californian site is located on the foothill range of the Sierra Nevada, near Ione, California, USA (38°26′ N, 120°58′ E). The site is nearly flat and its elevation is 177 m a.s.l. Deciduous blue oaks (*Quercus douglasii*) dominate the savanna site, but cover only ~40% of the landscape; scattered gray pines (*Pinus sabineana*) are found across the site. The savanna understory and open grassland are dominated by cool-season C_3 annual species and are grazed during the winter and spring. The soil of the oak–grass savanna is an Auburn, very rocky silt loam (Lithic haploxerepts). The soil profile is ~0.75 m deep and overlays fractured rock. More detail on the site has been reported in papers by Baldocchi et al. (2004) and Ma et al. (2007).

TABLE 1. List of site characteristics with regard to location, climate, canopy structure and function, soil properties, and mean ecosystem fluxes of five mediterranean oak woodlands.

Variable	Units	Puechabon, France	Evora, Portugal	Roccarespampani, Italy	Castelporziano, Italy	Ione, California, USA
Data years		2001–2006	2003–2005	2002–2006	2001–2006	2002–2006
Site						
Species		*Q. ilex,* ssp. *ilex*	*Q. ilex,* ssp. *rotundifolia*	*Q. cerris*	*Q. ilex*	*Q. douglasii*
Leaf area index, LAI		2.8	0.5	3.75	3.6	0.71 ± 0.41
Height	m	5	7.3	16.5	12.5	9.41 ± 4.33
Stem density	no./ha	6885	35–45	2450		144
Fraction of vegetation	%	100	39	100		40
Latitude		43.74	38.48	42.39	41.75	38.43
Longitude		3.59	−8.02	11.92	12.37	−120.96
dbh	m	0.07	0.34	0.165	0.16	0.22
Climate						
Annual precipitation	mm/yr	907 ± 272	665 ± 182	876	821	562 ± 200
Mean annual air temperature	°C	13.4	15	15.5	15	16.5
Total solar radiation	$GJ \cdot m^{-2} \cdot yr^{-1}$	5.36	6.24	5.42	5.43	6.6
Potential evaporation	mm/yr	829	1111	964	1112	1027
Leaf characteristics						
C	%	45	46.11 ± 2.83	48		44.8 ± 0.76
N	%	1.26	1.38 ± 0.23	2.0–2.5	1.5	1.84 ± 0.297
Stable C isotope, ^{13}C	‰	−27.46	−28.07 ± 0.71	n/a		−27.89
Leaf mass per area	g/m^2	224	229	108		132.3
C:N		35.7	34.08 ± 4.32	21		25.2
Maximum photosynthetic capacity	$\mu mol \cdot m^{-2} \cdot s^{-1}$	70	47.9	n/a	n/a	127
Soil						
Water-holding capacity	mm	205	240	n/a		180
Depth to rocks	m	n/a	0.3	0.9	0.6	0.60–0.80
Water table depth in winter	m	n/a	1–2	n/a		7
Water table depth in summer	m	n/a	≥5	n/a		12
Soil C	%	7.4 ± 1.46	1.6 under crown; 1.0 in open	0.698	0.65	3.88
Soil N	%	0.48 ± 0.06	0.12 under crown; 0.08 in open	0.217	0.0065	0.31
Ecosystem						
Gross primary productivity	$g\ C \cdot m^{-2} \cdot yr^{-1}$	1296	796	1403	1527	1069
Ecosystem respiration	$g\ C \cdot m^{-2} \cdot yr^{-1}$	1065	709	1115	976	971
Evaporation	mm/yr	377	155	439	431	227

Note: Variation around the mean is reported as ±SE; n/a indicates not applicable.

Environmental, carbon, and water flux measurements

Flux measurements of carbon dioxide and water vapor were made at each site using the eddy covariance method (Baldocchi 2003). The French, Italian, and Portuguese teams used the Carbo-Europe suite of instruments, including closed- (IRGA, model LI-6262, LI-COR, Lincoln, Nebraska, USA) or open-path infrared spectrometers to measure water vapor and carbon dioxide and three-dimensional sonic anemometer (model 1210R3, Gill Instruments, Lymington, UK) to measure wind and turbulence in three orthogonal directions (Aubinet et al. 2000). The California site used an open-path infrared spectrometer (LI7500, LICOR, Lincoln, Nebraska, USA) and a three-dimensional sonic anemometer (Gill Windmaster Pro, Lymington, UK) to measure absolute and fluctuating components of water vapor, carbon dioxide, temperature, and wind, respectively.

Eddy flux systems were installed above and below the Californian oak woodland. This dual-system approach enables us to measure fluxes associated with the tree canopy by difference; this dual system approach has been used with success at this site (Ma et al. 2007) and at other closed oak forests in the past (Baldocchi et al. 1987).

At all sites, weather and soil conditions were measured. Refer to the primary citations for each of these sites for additional information on instrumentation.

Data analysis

The eddy flux data were quality checked, filtered for periods of insufficient turbulent mixing and instrument malfunction, and gap-filled using standard software developed by the FLUXNET community (Reichstein et al. 2005, Papale et al. 2006). In this instance, gap-filling of missing flux data was based on techniques that binned carbon and water vapor flux data according to light and temperature conditions. Missing data were replaced via a look-up table using corresponding meteorological conditions. In recent years, this look-up table approach has been refined with the "marginal distribution sampling" method that produces a "moving" look-up table based on conditions for a fixed window about the data gaps. To provide a mechanistic understanding of stand-level anabolism and catabolism, net fluxes of CO_2 between vegetation and the atmosphere were partitioned into photosynthetic and respiratory components, e.g., gross primary productivity (GPP) and ecosystem respiration (R_{eco}). Net carbon fluxes were partitioned using day and night data. Daytime respiration is evaluated with a temperature- and moisture-dependent model that is derived from nocturnal periods with sufficient turbulent mixing (Reichstein et al. 2005).

Uncertainties associated with hourly and annual fluxes of carbon, water, and energy depend upon a number of measurement and sampling errors; these include instrument response, sampling frequency, calibration stability, the occurrence of advection and nonsteady conditions, spike detection and removal, and gap-filling procedures (Hollinger and Richardson 2005, Loescher et al. 2006). Errors associated with the flux instrumentation systems and data processing software tend to be small; tests performed with an independent roving flux system, supported by the AmeriFlux network, typically shows no significant differences in heat, water vapor, and CO_2 fluxes measured between side-by-side flux systems (Baldocchi et al. 2001, Hollinger and Richardson 2005). Sampling errors over an hour are on the order of ±10–20% and many random errors become much smaller over the course of a year (Moncrieff et al. 1996). Unfortunately, most flux sites suffer from some degree of systematic bias errors due to low nocturnal turbulence and advection. These systematic bias errors produce uncertainties in annual carbon fluxes that typically range between 30 and 100 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Loescher et al. 2006).

Because the canopies differ in leaf area index, we evaluated canopy photosynthesis in terms of intercepted global solar radiation (I), rather than incident global solar radiation (R_g). We estimated intercepted global solar radiation, I, by multiplying R_g by one minus the probability of beam penetration through the canopy, P_0. In this case, we estimated P_0 on a daily basis, using Beer's Law: $P_0 = \exp(-kL)$; the extinction coefficient, k, was assumed to equal 0.5 and L represents leaf area index (DeWit 1965).

We used the multivariate analysis of variance (MANOVA) technique to evaluate statistical differences between groups (deciduous vs. evergreen), and other independent class variables such as leaf area index, on a set of dependent variables, e.g., GPP, R_{eco}, and ET. We tested differences in slopes of environmental response functions, e.g., carbon use efficiency, water use efficiency, and rain use efficiency, using one-way analysis of covariance (ANCOVA). Statistical calculations were performed by using the standard statistical software package SAS (Version 9.1, SAS Institute, Cary, North Carolina, USA).

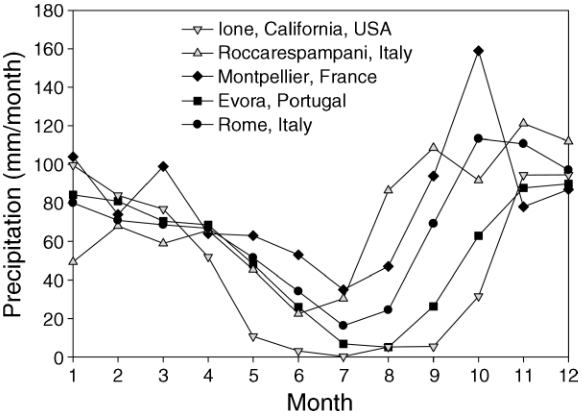

FIG. 1. Seasonal variation in rainfall based on 30-year climate records at the field site (or nearest city). Annual rainfall for the sites are: Puechabon (Montpellier), France, 957 mm/yr; Evora, Portugal, 657 mm/yr; Roccarespampani, Italy, 860 mm/yr; Ione, California, USA, 558 mm/yr; Castelporziano (Rome), Italy, 821 mm/yr. Month 1 is January.

RESULTS

Climate

The first question we must ask is whether there is a ranking or segregation of deciduous and evergreen oak woodlands by climate. The seasonality of mean monthly rainfall for the five sites is shown in Fig. 1. We find evergreen and deciduous oak woodlands at both the wetter (Italy and France) and drier locations (Portugal and California) (Table 1). In general, annual rainfall contributes to the presence of closed canopies (with high leaf area index) on the wetter sites, and open canopies (with low leaf area index) on the drier sites; this behavior is consistent with ecohydrology equilibrium theory as it pertains to native vegetation (Specht 1972, Baldocchi and Meyers 1998, Eamus and Prior 2001).

When studying the plant–climate interactions of seasonal mediterranean ecosystems, it is critical to recognize that annual sums of precipitation may tell us little about the availability of rainfall during the period when physiological function is most active and the demand for water is greatest. Generally, ample rainfall occurs during the winter after the soil moisture profile has become replenished, so a portion of this rain either runs off or drains below the rooting zone. Consequently, this excess moisture is not available to the trees during the ensuing hot, dry summer (Rambal 1984, Baldocchi et al. 2004, Joffre et al. 2007). Consequently, net annual carbon fluxes of mediterranean oak woodlands scale better with springtime cumulative rainfall than with annual cumulative rainfall (Ma et al. 2007, Pereira et al. 2007, Allard et al. 2008). In addition, we find that that one set of deciduous and evergreen sites (France and

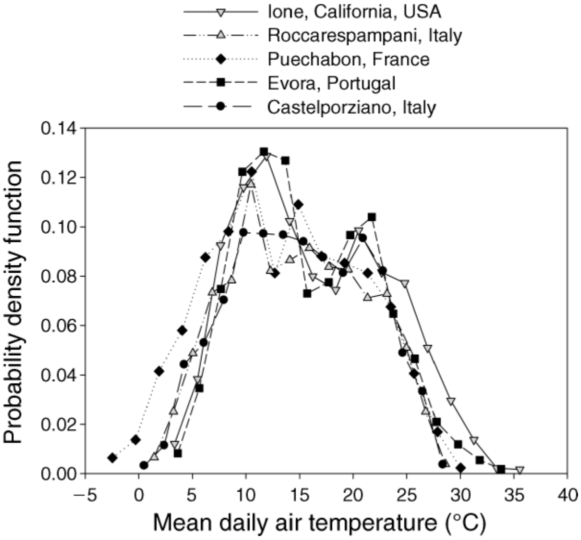

FIG. 2. Probability distribution of mean daily air temperature for five mediterranean oak ecosystems.

Italy) receives some summer rain (>20 mm/month) and the other set of evergreen and deciduous oak forests (Portugal and California) receives little or no summer rain (<10 mm/month). Thus the presence or absence of summer rain does not determine whether or not deciduousness or evergreenness is favored.

The thermal climate of all five sites is very comparable, as deduced by the similarity of the probability distributions of their mean daily air temperature (Fig. 2) and their mean annual air temperatures (Table 1); the latter are confined between 13.5° and 16.5°C. In general, the probability distributions for mean daily air temperature are bounded between 0° and 35°C and they tend to be bimodal, reflecting cool and warm season peaks.

Only the French site experiences a number of days when average daily air temperature is below freezing. Because the evergreen oak *Quercus ilex* encounters many freeze events over its multiyear life span, it must achieve some freezing tolerance. This function is achieved by its ability to construct narrow xylem vessels (Cavender-Bares et al. 2005), which lowers its hydraulic conductivity and makes the xylem less vulnerable to xylem embolism. In general, the occurrence or absence of prolonged winter freezing did not act as a discriminating factor in leaf longevity in the mediterranean climate zone.

Fluxes of energy, carbon, and water: who wins, who loses, how, and why?

Conceptually, trees, whether they are deciduous or evergreen, must assimilate more carbon than they lose via respiration and they must evaporate less water than they gain by rainfall, on an annual time integrals, if their presence is to be sustained. In this section, we investigate the roles of leaf habit and canopy closure on annual fluxes of carbon assimilation, respiration, and water evaporation. Next, we examine a set of functional relationships, e.g., the efficiencies of light use (change in carbon gained per change in intercepted solar energy), carbon use (change in carbon lost by respiration per change in carbon gained via assimilation), water use (change in carbon gained per change in evaporation), and rain use (change in water lost by evaporation per change in rainfall). We also discuss the seasonal patterns in canopy photosynthesis, ecosystem respiration, and evaporation to evaluate whether evergreen and deciduous woodlands took different dynamic routes to meet these constraints and if any differences in carbon gain and water use are conditional with time.

We first conducted a statistical analysis and compared measurements of mean annual sums in gross primary productivity (GPP), ecosystem respiration (R_{eco}), and evapotranspiration (ET) between the evergreen and deciduous oak woodlands (Table 2). On average, the deciduous oak woodlands assimilated 1251 ± 68 g $C \cdot m^{-2} \cdot yr^{-1}$, while respiring 1050 ± 56 g $C \cdot m^{-2} \cdot yr^{-1}$ and evaporating 343 ± 37 mm of water; these statistics are derived from 11 site-years of data; all values are means ± SE. In contrast, the evergreen oaks assimilated 1288 ± 83 g $C \cdot m^{-2} \cdot yr^{-1}$, while respiring 958 ± 49 g $C \cdot m^{-2} \cdot yr^{-1}$ and evaporating 368 ± 29 mm of water; these statistics are derived from 15 site-years of data. According to Duncan's statistical grouping test, none of the paired fluxes, by leaf habit, were statistically different from one another at the 5% level of significance ($\alpha < 0.05$).

The deciduous and evergreen woodlands in our study have established both open and closed canopies, so it is incumbent upon us to examine whether these results are an artifact of canopy closure. To address this question, we subjected these data to a multivariate analysis of variance (MANOVA) that examined two leaf habits (evergreen vs. deciduous) and leaf area index with a general linear model (Table 3). Based on 26 years of data (25 degrees of freedom with 2 associated with the model (leaf habit and leaf area index) and 23 degrees of freedom associated with the error), we find that there were no significant differences (at $\alpha < 0.05$) in the specific ecosystem-scale carbon and water vapor fluxes that were compared between the deciduous and evergreen oak woodlands. On the other hand, we find that

TABLE 2. Analysis of deciduous vs. evergreen leaves (mean ± SE) for annual total gross primary productivity (GPP), ecosystem respiration (R_{eco}), and evapotranspiration (ET).

Variable	Units	Deciduous	Evergreen	LSD
GPP	$g\ C \cdot m^{-2} \cdot yr^{-1}$	1251 ± 69	1288 ± 83	152
R_{eco}	$g\ C \cdot m^{-2} \cdot yr^{-1}$	1050 ± 56	958 ± 49	137
ET	mm/yr	343 ± 37	368 ± 29	46

Notes: The database consists of 11 site-years for deciduous oaks and 15 site-years for evergreen oaks. For all variables and both leaf types, each flux pair was found to be identical according to Duncan's test. LSD is least significant difference at $\alpha = 0.05$.

TABLE 3. General linear model between dependent variables (GPP, R_{eco}, ET) vs. leaf habit (deciduous vs. evergreen) and leaf area index.

Dependent variable	Mean	R^2	CV	RMSE	Leaf habit			LAI		
					Type I SS	*F*	*P*	Type I SS	*F*	*P*
GPP	1273 g $C \cdot m^{-2} \cdot yr^{-1}$	0.60	14.5	185	8542	0.25	0.6229	1 198 378	34.86	<0.0001
R_{eco}	997 g $C \cdot m^{-2} \cdot yr^{-1}$	0.283	16.4	16.85	53 248	1.90	0.182	201 659	7.18	0.0134
ET	357 mm/yr	0.77	15.4	55.1	4094	1.35	0.258	232 255	76.4	<0.0001

Notes: The model contains 26 degrees of freedom (2 for the model and 24 for the error). For leaf habit and LAI, df = 1 for all relationships. Abbreviations: CV, coefficient of variation; RMSE, root mean square error; SS, sum of squares.

degree of tree cover, as quantified by leaf area index, played a statistically significant role in the ranking of GPP, R_{eco}, and ET among the sites. Variations in leaf area index explained 60% of the variance in GPP, 28% of the variance in R_{eco}, and 77% of the variance in ET.

Although the annual fluxes of these treatments are similar, how did they arrive at these values? At a first approximation, canopy assimilation scales with intercepted solar radiation when soil moisture is available and ample (Monteith 1977, Ruimy et al. 1995). Across the mediterranean climate zone, deciduous and evergreen oak woodlands occupy niches that receive a relatively narrow range of solar radiation (Table 1), so this factor does not discriminate against one leaf habit or another in this climate region; the deciduous Californian and evergreen Portuguese sites, with low and comparable leaf area indices, received between 6.2 and 6.6 GJ/m^2 of solar energy per year and the deciduous and evergreen Italian and the evergreen French sites, with higher and comparable leaf area indices, received between 5.36 and 5.42 GJ/m^2 of solar energy per year.

"Light-response" curves allow us to explore and quantify the differential advantages of evergreen and deciduous leaf habits in harvesting sunlight. Fig. 3 shows that the deciduous oak woodlands assimilated more carbon over a day for comparable values of intercepted solar radiation, I, than did the evergreen oaks when intercepted sunlight was high (>15 $MJ \cdot m^{-2} \cdot d^{-1}$) during well-watered periods in the spring. On the other hand, the open deciduous and evergreen oak canopies assimilated similar amounts of carbon, given similar amounts of intercepted sunlight (~5 $MJ \cdot m^{-2} \cdot d^{-1}$).

Fitting daily-integrated gross primary productivity on intercepted sunlight data (I) with a nonlinear hyperbola, which mimics the Michaelis-Menten function ($GPP = aI/(b + I)$), we derived information on canopy photosynthetic capacity (a) and the initial slope (a/b) of the light response function, a measure of light use efficiency. The deciduous oak woodlands achieved photosynthetic capacities that were six times greater than those of the evergreen oak woodlands ($a_{decid} = 33.6 \pm 4.19$ g C vs. $a_{ever} = 5.55 \pm 0.27$ g C). The evergreen oak woodlands, on the other hand, were able to achieve lower Michaelis-Menten rate constants ($b_{ever} = 2.38 \pm 0.649$ MJ; $b_{decid} = 39.4 \pm 7.00$ MJ), which yielded greater light use efficiencies for the evergreen woodlands (2.33 g C/MJ) than the deciduous oaks 0.853 g C/MJ.

Given a certain unit gain in carbon assimilation, what is its cost, in terms of ecosystem respiration, and does this cost, defined as carbon use efficiency, differ with evergreen vs. deciduous leaf traits? To answer this question, we evaluated carbon use efficiency, $\partial R_{eco}/\partial GPP$, based on the slopes of linear regressions fitted through GPP on R_{eco} (Fig. 4). Here, the deciduous oaks ecosystem respiration increased 0.55 ± 0.16 g $C \cdot m^{-2} \cdot yr^{-1}$ for each gram of carbon gained by ecosystem assimilation. In comparison, the evergreen oaks respired 0.467 ± 0.099 g $C \cdot m^{-2} \cdot yr^{-1}$ for each gram of carbon gained by assimilation. Although these slopes are numerically different, statistical tests, using one-way ANCOVA, indicate that there was no difference between the two regression slopes at the $\alpha < 0.05$ level of significance. Nor were there any significant difference in the regression intercepts at the 0.05 level of significance. Also noteworthy is the observation that carbon use efficiencies for mediterranean oak woodland ecosystems are much lower than the global value based on the entire FLUXNET database: $\partial R_{eco}/\partial GPP \approx 0.77$ (Baldocchi 2008).

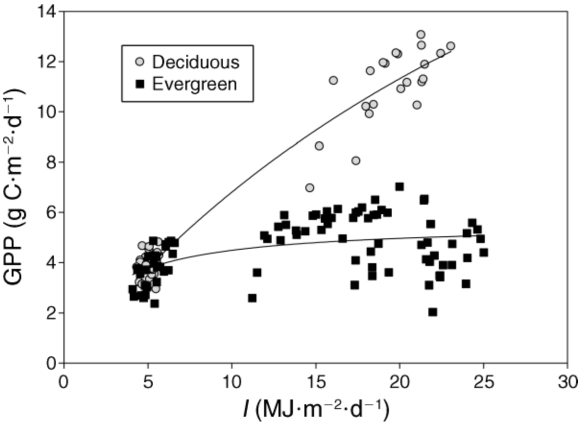

FIG. 3. The relationship between daily-integrated gross primary productivity (GPP) and daily-integrated intercepted global solar radiation (I). Deciduous flux data were pooled from California and Italy; evergreen flux data were pooled from France, Portugal, and Italy. These data are not annual sums, but daily integrals for periods when the canopies were well-watered and the deciduous canopies had achieved full leaf area (i.e., when soil moisture was not limiting).

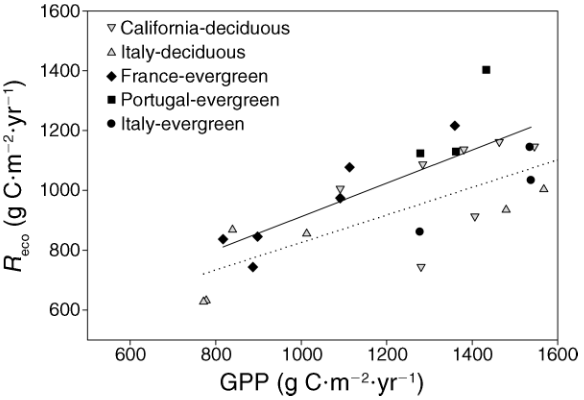

FIG. 4. Relationship between ecosystem respiration (R_{eco}) and gross primary productivity (GPP) at annual time scales. The mean slope of the linear regression is 0.458 ± 0.099 ($r^2 = 0.621$) for the evergreen oaks (solid line) and 0.555 ± 0.160 ($r^2 = 0.547$) for the deciduous oaks (dotted line).

Seasonal variation in mean daily values of GPP and R_{eco} provides an alternative perspective toward understanding the metabolic behavior of the two functional groupings (Fig. 5). The deciduous oak woodlands attain peak values of GPP during the spring. Afterward, assimilation rates decline with time as the weather becomes drier and warmer during the summer (Fig. 5A). Tree photosynthesis starts slightly earlier in California (around day 80) than in Italy (around day 90), but proceeds longer in Italy (to about day 340) than in California (around day 300). The critical eye will also notice that photosynthesis occurs before day 80 and after day 300 at the California site (Fig. 5A). However, this feature is an artifact of the green grass growing under the understory flux system.

Carbon assimilation occurs year-round at the three evergreen woodlands (Fig. 5B). The seasonal course, however, exhibits a bimodal pattern, which includes a strong down-regulation in photosynthesis during the hot, dry summer at the French and Portuguese sites. In contrast, the Italian evergreen site is able to achieve relatively high rates of carbon assimilation during the late summer because these trees are able to tap into a shallow water table (Manes et al. 1997). An ecological advantage is conferred on the evergreen oaks in the autumn when rains resume, because the leaves on deciduous trees have senesced and are unable to utilize the replenishment of the water resource.

Both the evergreen and deciduous oak woodlands experience a bimodal seasonal pattern in ecosystem respiration (Fig. 6). A key observation is a marked reduction in ecosystem respiration during the hot, dry summer at all sites. This reduction in ecosystem respiration follows the down-regulation in photosynthesis with soil water deficits (Rambal et al. 2003, Ma et al. 2007, Allard et al. 2008). The physiologically induced reduction in respiration helps these ecosystems to retain carbon when other environmental drivers, such as warm summer temperatures, tend to promote respiration (Reichstein et al. 2003, Granier et al. 2007). Fig. 6 also shows the stimulation in soil respiration when the soil is rewetted in the autumn, after the long dry season. This stimulation of soil respiration is most evident at the Portugal and California sites. It occurs because the first autumnal rains correspond with a large pool of digestible carbon that is readily consumed by the rehydrated microbial community (Xu et al. 2004, Curiel-Yuste et al. 2007, Jarvis et al. 2007).

The act of canopy photosynthesis comes with an additional expense to respiration: transpiration. In principle, this expense must be constrained in mediterranean climates because potential evaporation (800–1150 mm/yr; Table 1) far exceeds annual precipitation (562–907 mm/yr; Table 1). To accommodate this potential mismatch in the water balance, these oak woodlands down-regulate actual transpiration to evaporate less water, over a year, than the amount of rainfall, and they invest in deep root systems to exploit stored groundwater.

Fig. 7 shows that the upper limit of actual evaporation (500 mm/yr) is far less than potential evaporation and

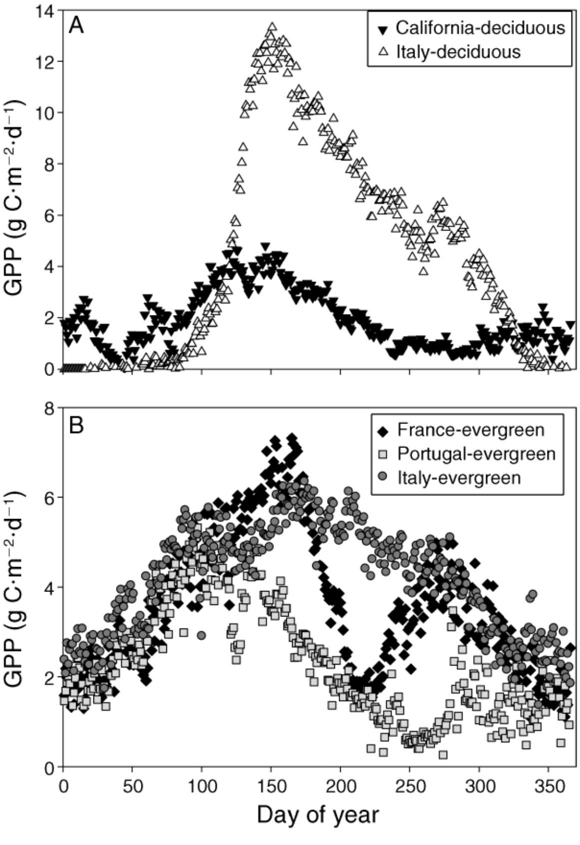

FIG. 5. Seasonal variation in daily-integrated gross primary productivity as a function of day of year averaged over the period 2001–2006 for (A) the Californian-deciduous and Italian-deciduous woodlands and (B) the French-evergreen, Portuguese-evergreen, and Italian-evergreen sites.

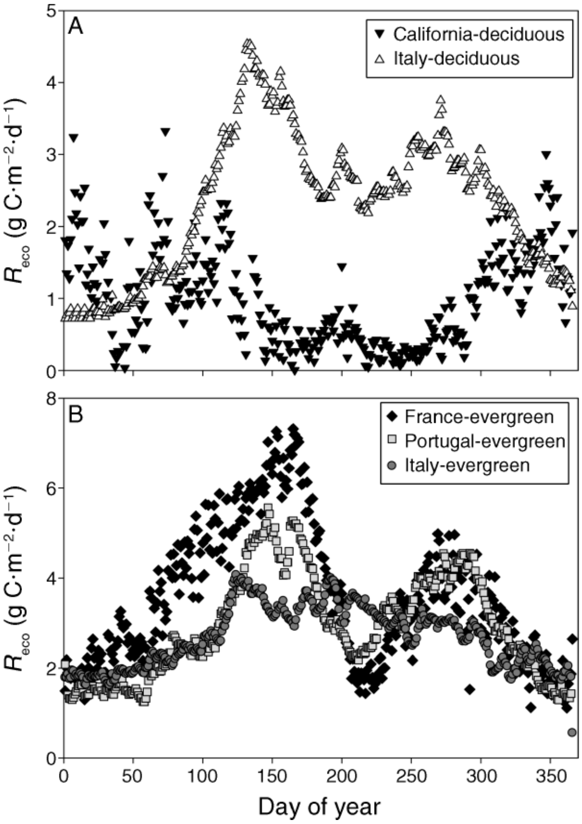

FIG. 6. Seasonal variation in daily-integrated ecosystem respiration, averaged by day of year over the period between 2001 and 2006 for (A) the Californian-deciduous and the Italian-deciduous woodlands and (B) the French-evergreen, Portuguese-evergreen, and Italian-evergreen sites.

available rainfall. The general response of evaporation to rainfall, across these five sites, supports the finding from a multiyear watershed study in the oak woodlands of California (Lewis et al. 2000) that annual evaporation equaled 279 mm/yr + 0.12(annual rainfall). The observation that actual evaporation from mediterranean ecosystems reaches a ceiling is consistent with independent evaluations, using a water balance method, for *Q. ilex* watersheds in Spain (Pinol et al. 1991).

Rain use efficiency was evaluated in terms of the slope between evaporation (ET) and precipitation (ppt), ∂ET/∂ppt. On average, the evergreen oak woodlands evaporated 25.2 ± 9 mm of water for each 100 mm of rainfall ($r^2 = 0.45$) and the deciduous oak woodlands evaporated 6.8 ± 10 mm of water for 100 mm of rainfall ($r^2 = 0.05$). However, the coefficients of determination (r^2) were very low. Consequently, the slope of the linear regression through the population of evaporation and rainfall data was not significantly different from zero at the 5% level of significance ($P > |t| = 0.0623$). Furthermore, there was no significant difference in rain use efficiency among the evergreen and deciduous oak woodlands at the 5% level of significance, based on a one-way ANCOVA ($P > |t| = 0.822$).

Inspection of the mean seasonal patterns of daily evaporation indicates that the evergreen oak woodlands are more conservative in their water use for specific rainfall regimes, compared to their deciduous counterpart, regardless of differences in leaf area index and annual sum of available solar radiation (Fig. 8). For instance, peak evaporation rates for the open, deciduous oak woodland in California are nearly double the evaporation rates from the open, evergreen oak sites in Portugal (Fig. 8A). Similarly, peak evaporation rates for the closed, deciduous oak woodland in Italy are nearly double those corresponding with the closed, evergreen oak sites in France and Italy (Fig. 8B). This finding is consistent with Tognetti et al. (2007) and Damesin et al. (1998), who reported that evergreen oaks (*Q. ilex*) are more conservative water users than the codominant deciduous oaks, such as *Q. cerris* and *Q. pubesens*. This finding counters a potential hypothesis that evergreen oaks may use more water than deciduous oaks because evergreen oaks can transpire during the fall, winter, and early spring when deciduous trees are leafless and dormant.

If we evaluate water use efficiency in terms of the change in carbon gained over a year for the change in water used, ∂GPP/∂ET, as defined by the slope of the linear regression between GPP and ET, we find that carbon is as expensive for deciduous oaks as for the evergreen oaks (Fig. 9). On average, the deciduous and evergreen oak woodlands assimilate 2.19 g C per incremental millimeter of water evaporated, and there is no significant difference between water use efficiencies of the evergreen and deciduous oaks at the 5% level of significance ($P > |t| = 0.162$).

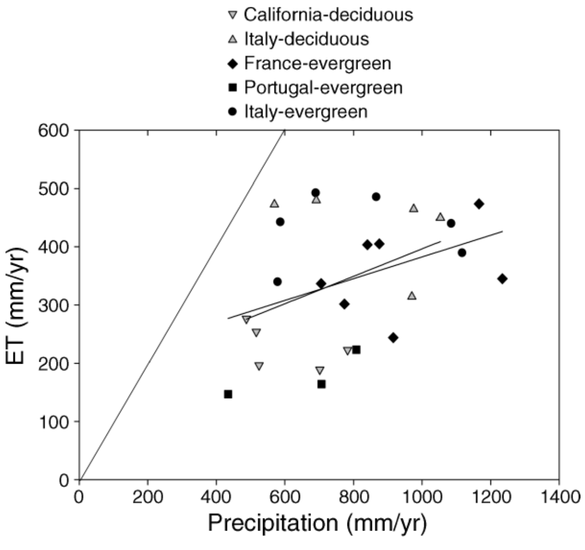

FIG. 7. Relationship between annual evaporation (ET) and annual precipitation. The mean slope for the linear regression is 0.236 ± 0.186 ($r^2 = 0.167$) for evergreen oaks and 0.187 ± 0.113 ($r^2 = 0.146$) for the deciduous oaks. The line to the left is 1:1.

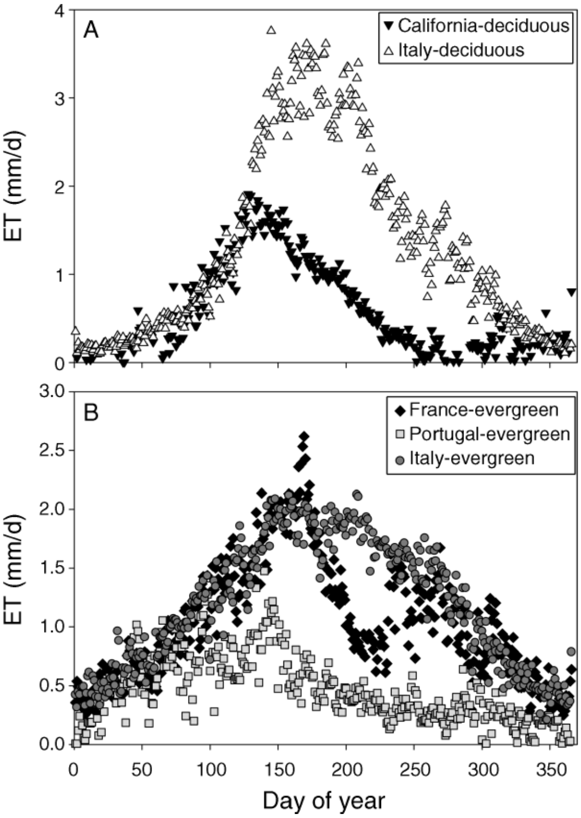

FIG. 8. Seasonal variation in evaporation (ET), averaged by day, over the period 2001–2006, for (A) the Californian-deciduous and Italian-deciduous woodlands and (B) the French-evergreen, Portuguese-evergreen, and Italian-evergreen sites.

DISCUSSION

There are numerous leaf, plant, and ecosystem attributes that explain, in tandem, the absence, presence, or coexistence of deciduous and evergreen oaks in mediterranean climates. We will now examine and discuss the roles of leaf nitrogen and photosynthetic capacity and the abilities to withstand drought, to tap deep water sources, and to withstand extreme climate conditions.

Physiological adaptation

Physiological insight on the relative advantages of deciduous and evergreen leaf traits can be gleaned by focusing on studies based on co-occurring broad-leaved deciduous and evergreen trees. In the mediterranean climate zones of California, deciduous oaks (*Quercus lobata*) have higher rates of photosynthesis and more nitrogen per unit mass than co-occurring evergreen oaks (*Quercus agrifolia*), while the evergreen oaks have greater mass per unit area and higher water use and nitrogen use efficiency than deciduous oaks (Hollinger 1992). On an annual basis, the evergreen habit theoretically offsets its lower photosynthetic capacity by assimilating carbon throughout the year (Hollinger 1992). In general, these findings, based on deciduous and evergreen oak trees in California, are supported by studies of co-occurring evergreen and deciduous oaks in Spain and Japan. For example, Spanish investigators report that the deciduous oak, *Q. faginea*, has greater leaf nitrogen levels, maximum rates of leaf photosynthesis, and stomatal conductances than the local evergreen oak, *Q. rotundifolia* (Mediavilla et al. 2002, Niinemets et al. 2004). And Japanese investigators report that seasonal maximum values of the carboxylation velocity, V_{cmax}, a measure of leaf photosynthetic capacity, were greater for the deciduous oak *Q. serrata* (32.9 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) than the evergreen oak *Q. glauca* (24.0 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) (Kosugi and Matsuo 2006).

The ranking of physiological attributes, such as photosynthetic capacity, among deciduous and evergreen oaks is not universal. In the mediterranean region of France, deciduous oaks (*Quercus pubescens*) do not achieve greater rates of photosynthesis than co-occurring evergreen holm oaks (*Quercus ilex*) for a wide range of pre-dawn water potentials (Damesin et al. 1998). In this case, *Q. pubescens* has a lower area-based construction cost than *Q. ilex*, as quantified by the sum of carbohydrates, starch, cellulose, lignin, and lipids (Joffre et al. 1999); the two oak species had identical construction costs when expressed on a unit mass basis (Damesin et al. 1998). This difference in construction cost of leaves is supported by a later study in Spain (Villar et al. 2006), which found greater differences in construction costs related to phylogeny (different plant families) than between the two leaf habits (evergreen vs. deciduous) of oak and other families. In sum, differences in leaf habit may not be great enough to distinguish between co-occurring evergreen and deciduous oaks in the mediterranean region, leading Joffre et al. (2007:301) to conclude: "… despite differences in biochemical composition, size, and mass per unit area, the leaves of the two species … (evergreen, *Q. ilex* and deciduous *Q. pubesens*) … respond similarly to water-limited condi-

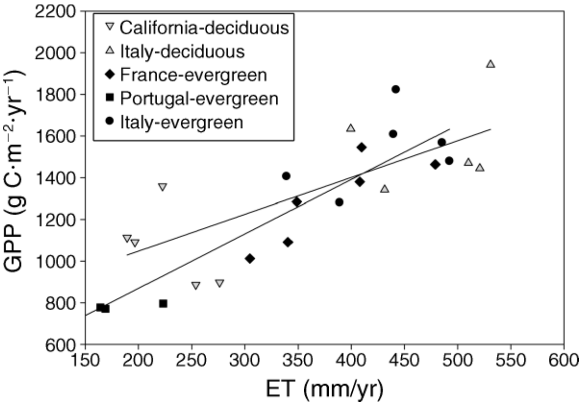

FIG. 9. The relationship between evaporation and gross primary productivity. The slope is 1.76 ± 0.55 g $\mathrm{C \cdot m^{-2} \cdot mm^{-1}}$ ($r^2 = 0.55$) for the deciduous oaks and 2.61 ± 0.31 g $\mathrm{C \cdot m^{-2} \cdot mm^{-1}}$ ($r^2 = 0.83$) for the evergreen oaks.

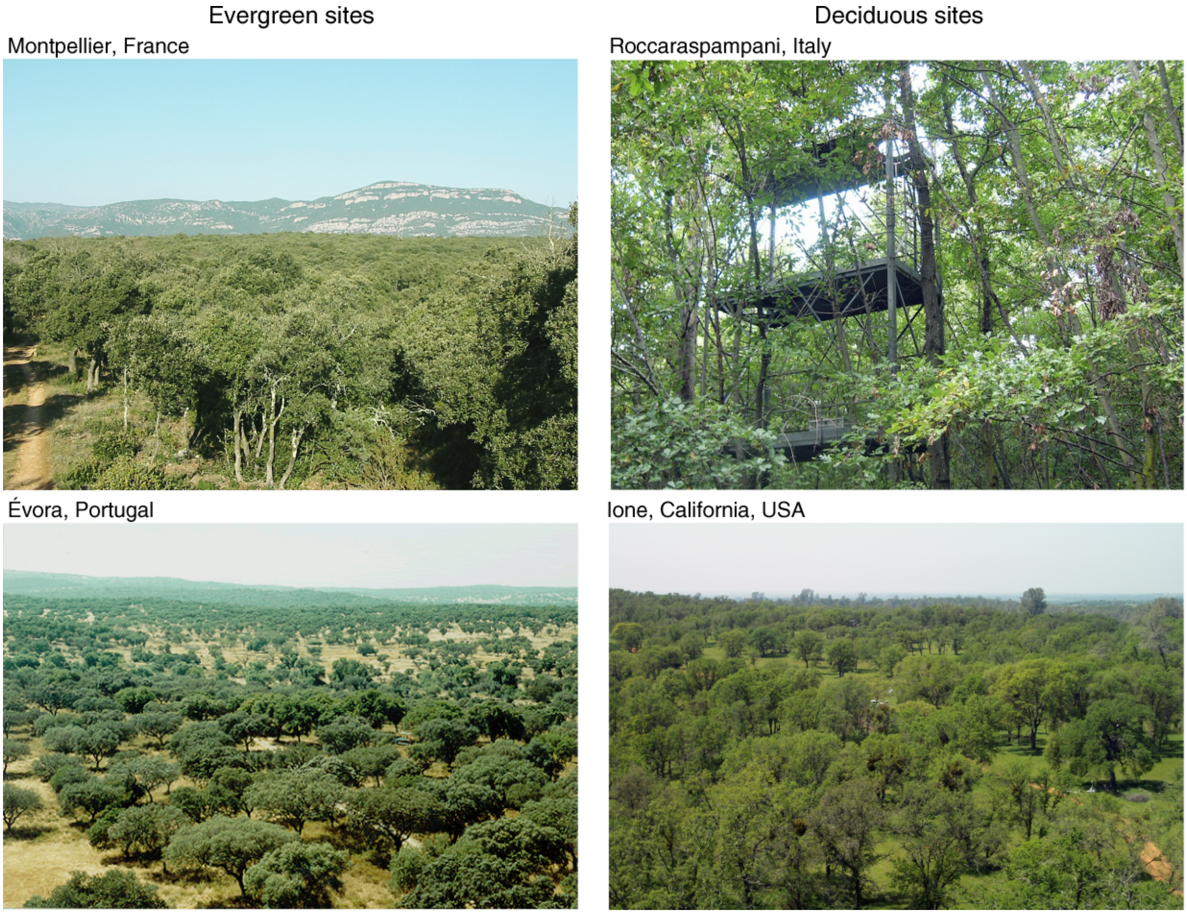

PLATE 1. Examples of evergreen and deciduous oak woodlands in France, Portugal, Italy, and California (USA). Photo credits: France, S. Rambal; Italy, Francesco Mazzenga; Portugal, J. Periera; California, D. Baldocchi.

tions and have similar intrinsic water use efficiencies (Damesin et al. 1997). These results indicate that key factors distinguishing the functioning of the deciduous species from evergreen ones are more important at the higher level of organization (individual and ecosystem) than at the leaf level."

Leaf age introduces an additional complication in interpreting differences in leaf physiological capacity of evergreen and deciduous trees. About half of the leaves on evergreen oaks, e.g., *Q. ilex* and *Q. rotundifolia*, are more than a year old (Silla and Escudero 2003, Niinemets et al. 2004). This feature is noteworthy because leaf nitrogen, photosynthetic capacity, and stomatal conductance decrease with increasing leaf age (Niinemets et al. 2004, Wright et al. 2004). Consequently, greater physiological advantage can be conferred on the deciduous oaks at the tree and canopy scales if we consider the age-weighted rates of photosynthesis, although this advantage will come at the expense of greater transpiration because stomatal conductances will also be greater.

Oak trees must withstand prolonged summer droughts in mediterranean climates, so we must consider how well deciduous and evergreen leaf traits respond to drought at the leaf and tree scales. One study shows that deciduous turkey oak (*Q. cerris*) has greater photosynthetic capacity than evergreen *Q. ilex* when they are well-watered, but under drought, *Q. ilex* is better able to maintain root growth and keep its stomata open (Manes et al. 2006). This work confirms earlier studies showing that *Q. ilex* is better adapted to drought than the deciduous oak *Q. pubesens* because it maintained high photosynthetic rates to lower desiccation levels (Larcher 1969) and higher hydraulic conductivity at low water potentials (Tyree and Cochard 1996). Other comparative studies on mature oak trees (Damesin et al. 1998) and saplings (Epron and Dreyer 1990) found that photosynthesis of *Q. ilex* and *Q. pubescens* responded similarly to changes in predawn water potential, down to −4.0 MPa. We also note that there is variability among deciduous oaks in their ability to withstand drought. For example, the deciduous oak *Q. cerris* is more drought tolerant than the deciduous oak *Q. pubescens* (Tognetti et al. 2007), and the evergreen oak *Q. ilex* is more drought resistant than another co-occurring evergreen oak, *Q. suber* (Tyree and Cochard 1996, David et al. 2007).

Tree scale

At the tree scale, differences in rooting depth and xylem architecture may be important factors for discriminating between deciduous and evergreen leaf traits. With regard to maintaining a water balance, schlerophyllous, evergreen oaks tend to grow where they can tap groundwater (Griffin 1973, Blumler 1991, David et al. 2004). In southern France, this trait enabled evergreen oaks to meet 12–23% of their water demand (Rambal 1984). In Portugal, considerable tree transpiration continues during the summer in *Q. ilex* ssp. *rotundifolia* and *Q. suber* because these trees tap water from depths down to 7 m (Otieno et al. 2006); more than 70% of the water transpired during summer was taken from groundwater sources (David et al. 2007), with substantial assistance from hydraulic lift (Kurz-Besson et al. 2006).

The record is mixed with regard to whether or not deciduous oaks tap groundwater in mediterranean-type climates. One set of studies concludes that winter-deciduous oaks along the coast range of California do not tap groundwater reserves (Griffin 1973, Blumler 1991). Instead, they are thought to gain an advantage over schlerophyllous evergreens by dropping leaves during the summer drought (Mooney and Dunn 1970, Blumler 1991).

One comparative study of plant–water relations in an evergreen oak, *Q. suber*, vs. a deciduous oak, *Q. cerris*, suggested that the latter had restricted access to deep soil and thus suffered greater dehydration than *Q. suber* over the summer (Nardini et al. 1999). Another set of studies indicates that deciduous oaks in mediterranean climates keep their leaves during the growing season and are able to tap deep stores of water below a fractured rock layer at 0.6–0.75 m deep (Lewis and Burgy 1964, Baldocchi et al. 2004, Tognetti et al. 2007). Although there may be contention about how much groundwater deciduous oaks tap, we argue that the trees only need to tap enough groundwater to remain viable over the most extreme period of the dry summer. The general ability of mediterranean oaks to tap deep sources of water challenges the conventional wisdom, which presumes that evergreens will "win" when the growing season is nine months long and deciduous trees will "win" if the growing season is less than nine months because they do not need to invest in deep roots to maintain transpiration during seasonal drought (Givnish 2002).

Canopy scale

At the canopy/ecosystem scale we find that evergreen and deciduous leaf habits are different, but effective, ways of existing and being successful in mediterranean climate zones. The deciduous oak forests are able to compensate for a shorter growing season by producing leaves with higher nitrogen content that, in turn, sustain higher rates of photosynthesis than do evergreen oak leaves, when water is ample (Hollinger 1992, Xu and Baldocchi 2003, Niinemets et al. 2004, Wright et al. 2005).

Ultimately, both leaf forms succeed in the seasonally wet/cool and hot/dry mediterranean climates by adopting a variety of tolerance, resistance, and avoidance mechanisms. For example, evergreen and deciduous oaks: (1) adjust their leaf area to the climatic rainfall; (2) regulate stomatal control to ensure that evaporation remains less than precipitation, on the annual time scale; (3) establish deep roots to tap groundwater during the driest summer period to sustain their leaves (Rambal 1984, David et al. 2004, Baldocchi and Xu 2007, Joffre et al. 2007); (4) possess a distinct xylem anatomy that enables them to withstand very low water potentials or withstand freezing (Rambal 1984, Tyree and Cochard 1996); (5) down-regulate photosynthesis during the hot, dry summer, thereby protecting their photosynthetic apparatus against excess light via thermal dissipation involving the xanthophyll cycle (Methy et al. 1996, Faria et al. 1998, Xu and Baldocchi 2003); and (6) reduce their respiration rates during the hot, dry summer.

There are many aspects regarding the presence and absence of evergreen and deciduous oaks that remain unexplored in this analysis. Key factors that require additional investigation include the roles of fire, land use history, topography, soil type, and nutrient availability (N and P). For example, evergreen trees are known to store nitrogen in older leaf cohorts and translocate this nitrogen to support the growth and functioning of new leaves. Both deciduous and evergreen oaks are known to withdraw and reallocate nitrogen from their leaves to their stems before abscission (Damesin et al. 1998, Silla and Escudero 2003, Xu and Baldocchi 2003, Kobe et al. 2005). Hence, leaves with lower nutrition drop to the soil during autumn; this nutritional level may contribute to a reduction in microbial respiration rates, compared to litter with higher nitrogen levels, affecting the nutrient status of the soil for supporting future leaves.

Statistical representativeness

A common criticism of comparative ecological studies using sparse networks of eddy flux towers is pseudo-replication, defined as "... the use of inferential statistics to test for treatment effects with data from experiments where either treatments were not replicated (though samples may) or replicates are not statistically independent" (Hurlbert 1984:190). Pseudo-replication can be avoided: "... replicate samples or measurements are dispersed in space (or time) in a manner appropriate to the specific hypothesis being tested is the most critical aspect of the design of a mensuration experiment" (Hurlbert 1984:189–190). Although expanding and contracting flux footprints (Schmid 2002) enabled us to sample different and relatively large portions of the woodlands (tens of hectares) across a range of environmental conditions through 26 site-years, we concede that our analysis may be guilty of some criticisms associated with pseudo-replication. However, we counterargue that novel and fruitful insights on the comparative metabolism of whole ecosystems are still gained through the utilization of sparse flux networks. The desired alternative (a highly replicated comparison of the metabolic fluxes of deciduous and evergreen oak woodlands with a perfect statistical design) would be practically impossible to reproduce without extraordinary costs in infrastructure, personnel, logistics, and time.

Conclusions

We attempted to answer various questions relating to the pros and cons of evergreen and deciduous leaf habits by comparing carbon and water fluxes of five oak woodland canopies growing in mediterranean climates in France, Italy, Portugal, and California. These ecosystems experience similar climate conditions and differ in leaf longevity (evergreen vs. deciduous) and canopy cover (closed vs. open). In this analysis we found several scale-emergent rankings and relationships.

1) Deciduous oak forests assimilate more carbon per unit energy of solar radiation intercepted by the ecosystem than do evergreen oak forests when ample soil moisture is available.

2) Deciduous oak forests assimilate the same amount of carbon per unit lost by ecosystem respiration as do evergreen oak forests.

3) Deciduous oak forests experience a shorter growing season and compensate by producing leaves with greater nitrogen levels, enabling them to assimilate as much carbon as corresponding evergreen oak forests over a year.

4) Canopy closure affects the amount of carbon gained and water lost by a range of evergreen and deciduous oak woodlands.

5) Across mediterranean climates, oak woodlands vary their leaf area index, adjust their stomatal openings, and extend their root system to tap groundwater to ensure that evaporation is less than its water supply.

6) Evergreen and deciduous oak trees assimilate a similar mass of carbon (in grams) for each millimeter of water evaporated.

Despite many differences in structure and function, our data indicate that deciduous and evergreen leaf traits are both successful strategies in mediterranean climates. Each leaf habit is associated with a different path in acquiring carbon and energy and using water.

The scope and duration of this study allowed us to consider the whole system and belowground resources. However, it did not allow us to address the role that other ecological factors such as disturbance (fires, grazing, coppice, herbivory), regeneration, and recruitment may play in determining the presence or absence of deciduous and evergreen oaks (Koenig et al. 1994, Tyler et al. 2006), and how climate change may affect their relative distribution (Kueppers et al. 2005).

Acknowledgments

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