

Growth, resource storage, and adaptation to drought in California and eastern Mediterranean oak seedlings

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Abstract: Low recruitment of new plants as currently observed in several California oak species might partly result from insufficient storage of vital resources (reduced ability to regrow after disturbance) or from low adaptation to environmental stress, such as drought. We conducted two studies under divergent environmental conditions to compare seedlings of California oaks with ecologically equivalent species from the eastern Mediterranean region, where recruitment has been substantial over the past 25–30 years. Resource concentrations (nonstructural carbohydrates and nitrogen) in taproots and the ratio of root resource content to shoot biomass did not provide evidence that Californian oak seedlings have smaller reserves for resprouting than eastern Mediterranean species in these studies. However, we observed lower seedling survival among California species, when compared with Mediterranean species, under conditions of higher drought stress. In the California deciduous *Quercus douglasii* Hook. & Arn., water-use efficiency as measured by leaf gas exchange and leaf $\delta^{13}\text{C}$ was lower compared with its Mediterranean equivalent *Quercus ithaburensis* Decne. In addition, stomatal conductance in the California evergreen *Quercus agrifolia* Née appeared to be less sensitive to vapor pressure deficit than in its Mediterranean equivalent *Quercus calliprinos* Webb. Our results suggest lower adaptation to drought in the California species tested here as compared with Mediterranean species, which will negatively impact recruitment of oaks from California under the currently drier soil conditions.

Résumé : Le faible recrutement de nouveaux plants observé actuellement dans le cas de plusieurs espèces californiennes de chênes pourrait en partie être le résultat du stockage insuffisant de ressources vitales (capacité réduite de se remettre à croître après une perturbation) ou d'un manque d'adaptation à un stress environnemental tel que la sécheresse. Nous avons réalisé deux études dans des conditions environnementales divergentes pour comparer les semis des chênes de la Californie avec des espèces écologiquement équivalentes provenant de la région est de la Méditerranée où le recrutement a été important au cours des 25–30 dernières années. La concentration des ressources (hydrates de carbone non structuraux et azote) dans la racine pivotante et le rapport entre le contenu en ressources des racines et la biomasse de la tige n'a pas permis de démontrer que les semis des chênes californiens avaient moins de réserves pour produire des rejets que les espèces de l'est de la Méditerranée que nous avons étudiées. Cependant, nous avons observé un taux de survie plus faible chez les espèces californiennes comparativement aux espèces méditerranéennes dans des conditions de stress hydrique plus intense. Chez *Quercus douglasii* Hook. & Arn., une espèce californienne décidue, l'efficacité de l'utilisation de l'eau, mesurée par les échanges gazeux foliaires et la valeur de $\delta^{13}\text{C}$ dans les feuilles, était plus faible comparativement à l'espèce méditerranéenne équivalente *Quercus ithaburensis* Decne. De plus, la conductance stomatale de *Quercus agrifolia* Née, une espèce californienne sempervirente, a semblé être moins sensible à un déficit de pression de vapeur que l'espèce méditerranéenne équivalente *Quercus calliprinos* Webb. Nos résultats indiquent que les espèces californiennes testées ici sont moins bien adaptées que les espèces méditerranéennes, ce qui aura un impact négatif sur le recrutement des chênes de la Californie dans les conditions actuelles caractérisées par un sol plus sec.

[Traduit par la Rédaction]

Introduction

Oak woodlands, chaparrals, and maquis are important and diverse components of the landscape in Mediterranean-type

regions (Barbour and Major 1977). In California, many of the oak woodlands are now characterized by low regeneration rates among several major oak species (White 1966; Bolsinger 1988; Swiecki et al. 1997; McCreary 2004; Tyler

Received 25 January 2007. Accepted 8 August 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 8 February 2008.

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et al. 2006). Poor regeneration has been observed at plot to landscape scales and, partly, may be related to low recruitment rates of new seedlings and low transition rates from seedlings to saplings (Standiford et al. 1997; Bartolome et al. 2002). In contrast to California, oak regeneration in the Mediterranean region, partly by seedling recruitment, has been substantial after cessation of disturbance (see Carmel and Flather 2004). Because many of the environmental factors posited to explain poor recruitment in California have been present in the Mediterranean Basin for several millennia at least, differences in recruitment rate may be based on genetic differences in key functions among the oak species of the two regions.

Recruitment of oak seedlings in the Mediterranean environment is affected by numerous factors, among them the ability to resprout from surviving plant parts after disturbance, such as fire and grazing (Phillips et al. 1996; Pons and Pausas 2006), and the grade of seedling adaptation to environmental stress, such as drought (Griffin 1971). Many oak species develop a large root system that allows for remobilization of stored compounds to ensure survival in case of catastrophic tissue loss (Larsen and Johnson 1998; Abrams 2003). Remobilization of carbohydrates and nitrogen (N) has been shown to critically influence regrowth success and the number, biomass, and leaf area of resprouts in seedlings and saplings of oaks and other species (Sakai et al. 1997; McPherson and Williams 1998; Sakai and Sakai 1998; Landhäusser and Lieffers 2002; El Omari et al. 2003; Hoffmann et al. 2003).

Adaptation to environmental conditions under a Mediterranean-type climate implies that plants must use water in an efficient way. In oaks and other species, low water-use efficiency (WUE) has been related to a decline in performance of seedlings and saplings after drought events (Ponton et al. 2002; Lloret et al. 2004). Oak species in California might have evolved under slightly wetter conditions than their ecologically equivalent species in the eastern Mediterranean basin. Recent changes in soil water availability in California may be the result of invasion of exotic annual grasses and replacement of native perennial grasses. The change in vegetation, potentially enhanced by changes in land use and climate (Corbin and D'Antonio 2004), may cause surface soil water to be tied up earlier in the season (Welker and Menke 1990; Gordon and Rice 1993). As a consequence of the change in grass type and density (Momen et al. 1994) and possibly of soil compaction by livestock (Tyler et al. 2006), emerging oak seedlings have been left with less moisture in the top soil layers during the dry summer season (Holmes and Rice 1996). Similar anthropogenic vegetation-mediated increase in drought stress has been reported for drylands in other regions, such as South Africa (Le Maitre et al. 2007). This human-induced vegetation change has probably occurred in the eastern Mediterranean thousand of years earlier, allowing oak species to evolve under drier conditions.

The objective of the current research was to investigate whether some of the oak species presently characterized by low seedlings recruitment in several locations in California had lower resource storage potential and lower adaptation to drought than ecologically equivalent species from the eastern Mediterranean basin. We compared three Californian (CAL) with two eastern Mediterranean (MED) oak species

in two shadehouse studies involving evergreen tree, evergreen shrub, and deciduous tree growth forms. To test whether results were consistent under different environmental conditions, the two studies were set at different locations (California versus Israel) under divergent growing conditions (concerning water supply, nutrient supply, and substrate). Measurements included seedling growth and survival, carbohydrate and N contents, leaf gas exchange, stable carbon (C) isotopes, and specific leaf area (SLA).

Materials and methods

Species selection

We used five oak species in these studies: three of CAL and two of MED origin. The dominant evergreen oak in the MED region, *Quercus calliprinos* Webb (Palestine oak) (Toumi and Lumaret 2001), develops either as a tall tree or a shrub with several stems (Zohary 1973) and, thus, was compared to both a CAL evergreen tree and a CAL evergreen shrub. The CAL evergreen tree was *Quercus agrifolia* Née (coast live oak), an abundant oak in central California (Tyler et al. 2006). The CAL evergreen shrub was *Quercus berberidifolia* Liebm. (formerly referred to as *Quercus dumosa* Nutt.; Nixon 2002), the most common scrub oak of the Coastal Ranges of central California, which often occupies an ecological niche similar to *Q. calliprinos* (Naveh 1967; Zohary 1973). Finally, *Quercus douglasii* Hook. & Arn. (blue oak), a widespread CAL deciduous tree species of warm and dry climates (Tyler et al. 2006), was compared with *Quercus ithaburensis* Decne. (Tabor oak), its ecological equivalent and a dominant deciduous oak in the MED region (Dufour-Dror and Ertas 2004). Determination of ecological similarity between specific species in both regions is based on a comparison of the species' habitats in California (Barbour and Major 1977) and in Israel (Zohary 1973). Our assignment of equivalence agrees with an earlier comparison conducted by Naveh (1967).

Study sites and growing conditions

Oaks were grown at two sites to create different conditions for the two studies, which would enable more general conclusions about the comparisons among oak species. Study I was performed in the nursery of Rana Creek Habitat Restoration, Carmel Valley, California, USA (36°26'08"N, 121°37'03"W). Mean annual temperature at the nearby Hastings Natural History Reservation (~10 km away) was 13.8 °C, daily mean temperatures in July and January were 20.1 and 8.6 °C, respectively, and mean annual precipitation was 534 mm, with minimal or no rain between June and September (64 year means; www.hastingsreserve.org). Study II was set at the Golani Nursery of the Jewish National Fund in the Lower Galilee, Israel (32°46'12"N, 35°24'36"E). Mean annual temperature at the nearby Tabor meteorological station (~9 km away) was 20.0 °C, daily mean temperatures in July and January were 27.1 and 11.4 °C, respectively, and mean annual precipitation was 497 mm, with no rain between May and September (15 year means; Bitan and Rubin 1991).

Acorns were harvested from many oak trees at two or three different locations in Carmel Valley, central California, or the Lower Galilee and Mount Carmel, northern Israel,

between late October and mid-November 2002. All trees were subjected to typical Mediterranean-type conditions. For each species, acorns from all trees and locations were combined to ensure a wider genetic diversity and to minimize any maternal effects. All acorns collected in both California and Israel were sent to Frances Crim Memorial Inspection Station, Linden, New Jersey, for fumigation (schedule T203-e; USDA 2002) and phytosanitary certification. One-half of the acorns of each species were used for study I, and the other half for study II. Acorns of CAL species that were sent to Israel for study II were taken to quarantine by the Plant Protection and Inspection Services, Ministry of Agriculture of Israel.

For study I, acorns were sown in early December 2002 into trays consisting of 420 cm³ compartments containing a substrate that included redwood, sand, and quarried filter clay. Groups of four to eight trays consisting of the same species were randomly arranged within a shadehouse. During 2003, seedlings received moderate growing conditions according to the following local practice of cultivating native plants: low irrigation frequency (watering once a week to drainage; a one-time missing irrigation event occurred in July 2003, which resulted in severe drought) and no nutrient addition on top of a slow-release fertilizer applied within the potting mixture. Germination rates varied between 60% and 100%.

In study II, acorns were sown in early January 2003 into trays consisting of 340 cm³ compartments containing a substrate that included peat, tufa (porous stone of volcanic origin), and polystyrene foam. Groups of two to five trays consisting of the same species were randomly arranged within a shadehouse. According to local nursery practice of providing good growing conditions, seedlings were irrigated at high frequency (once a day; 20 L·m⁻² ground area·day⁻¹) and received liquid nutrient addition (6:3:6 (N:P:K) + microelements) once or twice a week on top of slow-release fertilizer in the potting mixture. Germination rates of the CAL species ranged 20% to 50%. Because of unknown reasons, germination rates of the MED species were very low in study II, with only a few individuals germinating. Therefore, we had to use a different set of plants as a replacement and chose seedlings that were grown for afforestation purposes in the same nursery. Seed sources of replacement plants were equivalent to sources of the original seeds, and growing conditions were identical to those of the rest of the species in study II. Comparisons between replacement seedlings and the few viable original *Q. calliprinos* and *Q. ithaburensis* plants showed very similar seedling development and leaf gas exchange (data not shown). For a second growing season, each seedling was transplanted in mid March 2004 to a 15 L bag containing the same substrate as in 2003. Five to 10 groups of seedlings per species were randomly placed in the shadehouse. Seedlings were irrigated each day to drainage by sprinklers until May 2004 and by dripping irrigation thereafter. No fertilizer was added on top of the slow-release fertilizer during 2004.

Seedlings in both studies were grown in potting mixtures rather than being outplanted in native soil, because marked differences in soil conditions (pH and fertility) between locations could have negatively influenced the foreign species (MED species in study I, CAL species in study II). Irrigation

was stopped during the rainy winter season in both studies. Seedlings were grown under 50% shade (reduction of photosynthetic photon flux density by 50%) in both studies to create light conditions intermediate to the range of conditions under which oak seedlings from both regions naturally germinate and grow (Griffin 1971; Alon and Kadmon 1996). Fifty percent shade versus full light reduced photosynthetic capacity but did not significantly affect seedling biomass and root/shoot ratio of *Q. agrifolia* and *Q. douglasii* (Callaway 1992).

Acorn dry matter (65 °C) was determined for sets of 50 individual CAL acorns and from 21 (*Q. calliprinos*) and 11 (*Q. ithaburensis*) groups of 10 individual MED acorns. All acorns were collected in October–November 2004 from the same sites and by similar methodology as the original sampling in 2002. Acorn dry masses were 2.51 ± 0.06, 1.31 ± 0.05, 3.59 ± 0.10, 3.09 ± 0.17, and 8.13 ± 0.19 g (mean ± SE) for *Q. agrifolia*, *Q. berberidifolia*, *Q. calliprinos*, *Q. douglasii*, and *Q. ithaburensis*, respectively.

Plant analyses

Survival rates were presented as means across all germinated seedlings per species (data for replicates not available). Five seedlings from each species were harvested in September 2003 (studies I and II) and in July 2004 (study II), were separated into plant parts in the field, and were transported on ice to the laboratory. After 1 h at 90 °C to stop enzymatic activity, all plant material was dried at 65 °C until no mass loss was recorded. Analysis of soluble sugars and starch was conducted on ground plant material according to Tinus et al. (2000). Stable C isotope ratio and N concentration were determined in a ratio mass spectrometer (Optima; Micromass, Manchester, UK) after quantitative combustion in an elemental analyzer (EA 1108; Carlo-Erba, Milan, Italy). Carbon isotope ratio was expressed as $\delta^{13}\text{C}$ (‰) = $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$; the standard was Vienna Peedee belemnite. Precision of the ¹³C analysis was ±0.1‰. Assuming identical ¹³C composition of atmospheric CO₂ among sites (e.g., www.cmdl.noaa.gov/ccgg/index.html), plant $\delta^{13}\text{C}$ is an index of long-term WUE (Farquhar et al. 1989; Dawson et al. 2002) that was previously used in California and Mediterranean oaks (e.g., Rice et al. 1993; Damesin et al. 1997; Matzner et al. 2001; Lloret et al. 2004).

Leaf gas exchange

Leaf gas exchange was measured in study II on recent fully developed leaves of 5–12 seedlings of four species with a portable photosynthesis system (LI-6400; LI-COR Inc., Lincoln, Nebraska). *Quercus berberidifolia* was not measured because of small leaf size and difficulties in locking leaves within the measuring chamber. In 2003, data for leaf gas exchange were presented for early afternoon hours (12:00–14:30 Israel Standard Time, GMT+02:00), which constituted more stressful conditions in terms of leaf–air vapor pressure difference (VPD) than morning hours (data not shown). In the 2004 growing season, measurements were conducted every 6–7 weeks during a longer time period (midmorning and midafternoon, 10:00–14:30) to allow for more replications than in 2003. In most cases in 2004, there was no significant trend of gas-exchange variables with time

of day (data not shown). Measurements were carried out at ambient conditions, except for a constant photon flux density of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which was imposed with an artificial red–blue light source (LI-6400-02B; LI-COR Inc.). Stomatal sensitivity to atmospheric evaporative demand was plotted as the natural logarithm of stomatal conductance over VPD (Eamus and Cole 1997; Mediavilla and Escudero 2003).

Statistical analyses

Biomass variables, specific leaf area, $\delta^{13}\text{C}$, and carbohydrate and N variables were analyzed using model I one-way ANOVA, with a priori planned comparisons between pairs of CAL and MED ecologically equivalent species performed by contrast analysis (JMP IN 5.1; SAS Institute Inc., Cary, North Carolina). Leaf gas exchange was analyzed by model I two-way ANOVA between species and date; contrast analyses were performed between ecologically equivalent species. Regression slopes were compared using Student's *t* test. Where necessary, values were transformed prior to the analyses to meet the assumptions of ANOVA. Statistically marginally significant differences were defined as $0.05 < P \leq 0.1$.

Results

Seedling growth and survival

Growth and biomass production differed considerably among equivalent oak species in both studies. In study I, mean biomasses of plant parts were 55%–110% larger in the CAL evergreen tree, *Q. agrifolia*, than in the MED counterpart, *Q. calliprinos* (Table 1). In study II, the two species did not differ, except for 34% lower lateral root biomass and 50% higher stem + branch biomass in *Q. agrifolia* in second-year seedlings. Height increase was similar among the two species in first-year seedlings, but *Q. agrifolia* grew considerably higher than *Q. calliprinos* in the second year (Fig. 1), presumably because *Q. agrifolia* invested less in branching (total stem and branch length) than its MED counterpart (Table 1). The evergreen shrubs did not differ considerably in study I, whereas the CAL shrub was significantly smaller than its MED equivalent in study II, with biomass of *Q. berberidifolia* being less than 20% of *Q. calliprinos* biomass in second-year seedlings. The CAL deciduous tree, *Q. douglasii*, had 30%–90% smaller biomass components than the MED deciduous tree, *Q. ithaburensis*, in both studies. Notably, *Q. douglasii* invested relatively more in the taproot than *Q. ithaburensis*, which resulted in a wider taproot/shoot ratio in the former species in both studies. Evergreen species had a smaller taproot and a narrower taproot/shoot ratio than deciduous species ($P \leq 0.001$ for both variables in both studies).

One year after sowing, seedling survival in study I, with moderate water and nutrient application and a severe drought event (see Study sites and growing conditions in the Materials and methods), was considerably lower in CAL than in MED oaks for each of the three comparisons of ecologically equivalent species. Survival was 54% in *Q. agrifolia* and 31% in *Q. berberidifolia* as compared with 68% in their common MED equivalent, *Q. calliprinos*. Among the deciduous tree seedlings, survival was 68% in *Q. douglasii* and 91% in *Q. ithaburensis*. In study II with good growing

conditions, survival ranged 88%–96%, with no trend among species (data not shown).

Specific leaf area and stable isotope composition

Mean SLA was 35% greater in the CAL than in the MED evergreen tree seedlings in both studies and 24% greater in the CAL than in the MED evergreen shrub seedlings in study I (Table 1). In contrast, SLA in deciduous species was 14% smaller in *Q. douglasii* compared with *Q. ithaburensis* in study II.

Leaf $\delta^{13}\text{C}$ was similar among most species comparisons in study I, except for the lower (more negative) value in *Q. douglasii* compared with *Q. ithaburensis* (marginally significant; Table 2). In study II, leaf $\delta^{13}\text{C}$ was significantly lower in *Q. berberidifolia* and *Q. douglasii* than in their respective equivalent MED species. Values of $\delta^{13}\text{C}$ were higher in study I than in study II in all species and both plant parts ($P = 0.001$ – 0.008) with the exception of *Q. agrifolia*, which had similar $\delta^{13}\text{C}$ values in both studies ($P = 0.339$). The $\delta^{13}\text{C}$ values were higher in taproots than in leaves, possibly because of the high starch content in the taproot (Gleixner et al. 1993; Göttlicher et al. 2006).

Carbohydrate and N analyses

The taproot was the main storage organ for nonstructural carbohydrates (NSC) in oak seedlings. Concentration of NSC in the taproot of *Q. agrifolia* did not differ significantly from concentrations in *Q. calliprinos* in study I ($P = 0.364$) but was 30% ($P = 0.007$) lower in *Q. agrifolia* in study II (Fig. 2). In contrast, taproot NSC concentrations were 31% ($P = 0.005$) and 44% ($P < 0.001$) higher in *Q. berberidifolia* than in *Q. calliprinos* in studies I and II, respectively. The respective concentrations of NSC were 44% ($P < 0.001$) and 36% ($P < 0.001$) higher in *Q. douglasii* than in *Q. ithaburensis*. In those species comparisons, concentration of both starch and soluble sugars were considerably higher in the CAL than in the MED species. Trends in NSC concentrations of stems and leaves were less significant than those in taproots (Fig. 2).

Leaf N concentration was 42% ($P = 0.015$) higher in *Q. agrifolia* than in *Q. calliprinos* in study I (Fig. 3). In the same study, stem + branch N concentrations were 39% ($P = 0.013$) and 50% ($P < 0.001$) higher in the CAL evergreen shrub and deciduous tree species, respectively, than in their equivalent MED species. No differences between pairs of species were observed for the taproot in both studies. When leaf N concentration was expressed per unit leaf area instead of leaf dry mass, differences were significant for *Q. agrifolia* versus *Q. calliprinos* (–25%; $P < 0.001$) and for *Q. douglasii* versus *Q. ithaburensis* (+19%, $P = 0.018$) in study II (Fig. 3). Nitrogen concentration was lower in study I than in study II, and evergreen species had lower N concentrations than deciduous ones in each plant organ of each study (mean 30%; $P < 0.001$). Regression analyses showed that differences among species in carbohydrate and N concentrations were not a function of plant size (data not shown).

The ratio of total taproot NSC content to total shoot dry mass (taproot NSC content per shoot biomass) was 108% ($P = 0.025$) and 207% ($P < 0.001$) higher in *Q. berberidifolia* than in *Q. calliprinos* in studies I and II, respectively (Fig. 2, bottom panels). *Quercus douglasii* had 182% ($P <$

Table 1. Biomass, taproot/shoot ratio, total stem + branch length, and specific leaf area in first-year seedlings of study I and in first- and second-year seedlings of study II.

Life form and species ^a	Species origin	Seedling age	Lateral root biomass (g)	Taproot biomass (g)	Stem + branch biomass (g)	Leaf biomass (g)	Total plant biomass (g)	Taproot/shoot ratio	Specific leaf area (cm ² ·g ⁻¹)	Total stem + branch length (cm)
Study I										
Evergreen tree										
<i>Q. agrifolia</i>	CAL	First year		1.57 (0.15)	0.71 (0.09)*	1.11 (0.13)**		0.90 (0.12)	73.4 (2.6)**	
<i>Q. calliprinos</i>	MED	First year		1.01 (0.14)	0.39 (0.06)	0.53 (0.08)		1.14 (0.12)	54.6 (1.7)	
Evergreen shrub										
<i>Q. berberidifolia</i>	CAL	First year		1.11 (0.12)	0.23 (0.06)	0.45 (0.07)		1.75 (0.25)	67.9 (2.3)*	
<i>Q. calliprinos</i>	MED	First year		1.01 (0.14)	0.39 (0.06)*	0.53 (0.08)		1.14 (0.12)	54.6 (1.7)	
Deciduous tree										
<i>Q. douglasii</i>	CAL	First year		1.96 (0.31)	0.21 (0.06)	0.40 (0.05)		3.34 (0.55)**	85.6 (9.5)	
<i>Q. ithaburensis</i>	MED	First year		4.08 (0.74)**	1.30 (0.22)***	1.02 (0.18)***		1.77 (0.26)	74.8 (6.6)	
<i>P</i>				<0.001	<0.001	<0.001		<0.001	0.005	
Study II										
Evergreen tree										
<i>Q. agrifolia</i>	CAL	First year		1.63 (0.21)	3.55 (0.83)	2.26 (0.44)		0.31 (0.05)	81.3 (1.7)***	
<i>Q. calliprinos</i>	MED	First year		1.73 (0.29)	2.15 (0.41)	2.66 (0.38)		0.37 (0.04)	60.3 (3.2)	
<i>Q. agrifolia</i>	CAL	Second year	3.45 (0.27)	3.13 (0.53)	14.59 (1.48)*	11.79 (0.89)	32.96 (2.64)	0.12 (0.01)		196 (8)
<i>Q. calliprinos</i>	MED	Second year	5.19 (0.49)*	3.27 (0.21)	9.72 (0.90)	11.69 (1.20)	29.88 (2.34)	0.16 (0.01)		223 (23)
Evergreen shrub										
<i>Q. berberidifolia</i>	CAL	First year		1.56 (0.63)	1.13 (0.60)	1.00 (0.26)		0.71 (0.06)**	65.1 (3.2)	
<i>Q. calliprinos</i>	MED	First year		1.73 (0.29)	2.15 (0.41)	2.66 (0.38)**		0.37 (0.04)	60.3 (3.2)	
<i>Q. berberidifolia</i>	CAL	Second year	0.82 (0.16)	1.06 (0.19)	1.95 (0.37)	1.74 (0.19)	5.57 (0.69)	0.29 (0.05)		79 (14)
<i>Q. calliprinos</i>	MED	Second year	5.19 (0.49)***	3.27 (0.21)***	9.72 (0.90)***	11.69 (1.20)***	29.88 (2.34)***	0.16 (0.01)		223 (23)***
Deciduous tree										
<i>Q. douglasii</i>	CAL	First year		3.74 (0.29)	1.58 (0.24)	1.39 (0.15)		1.30 (0.10)***	71.6 (1.6)	
<i>Q. ithaburensis</i>	MED	First year		5.25 (0.45)**	4.75 (0.96)**	2.17 (0.34)		0.83 (0.10)	83.0 (5.8)*	
<i>Q. douglasii</i>	CAL	Second year	2.81 (0.58)	8.17 (1.35)	5.53 (1.20)	4.78 (1.08)	21.28 (3.25)	0.93 (0.27)***		68 (5)
<i>Q. ithaburensis</i>	MED	Second year	7.06 (1.19)***	10.37 (1.27)	18.27 (2.90)***	13.93 (2.26)***	49.63 (6.33)***	0.37 (0.05)		258 (17)***
<i>P</i>		First year		<0.001	0.010	0.029		<0.001	<0.001	
		Second year	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		<0.001

Note: Comparisons were conducted for three pairs of ecologically equivalent Californian (CAL) and eastern Mediterranean (MED) oak species in September 2003 (first-year seedlings) and July 2004 (second-year seedlings). Values are means with SEs given in parentheses ($n = 3-10$ individuals or groups of plants). *P* values for one-way ANOVA across all species per study and seedling age are given. Contrast analysis between ecologically equivalent species within the same study and year were performed for significant ANOVAs: * $P \leq 0.05$, ** $P \leq 0.01$, and *** $P \leq 0.001$.

^aNote that *Q. calliprinos* was compared with both *Q. agrifolia* and *Q. berberidifolia* (see Materials and methods).

Fig. 1. Patterns of plant height in oak seedlings in study II during 2003 and 2004. The inset figure shows the diameter during the 2004 growing season. Californian (CAL) species are shown with open symbols and broken lines, and eastern Mediterranean (MED) species are shown with solid symbols and solid lines. a, *Q. agrifolia* (CAL evergreen tree); b, *Q. berberidifolia* (CAL evergreen shrub); d, *Q. douglasii* (CAL deciduous tree); c, *Q. calliprinus* (MED evergreen tree and shrub); i, *Q. ithaburensis* (MED deciduous tree). Data points are means of 15–350 individuals.

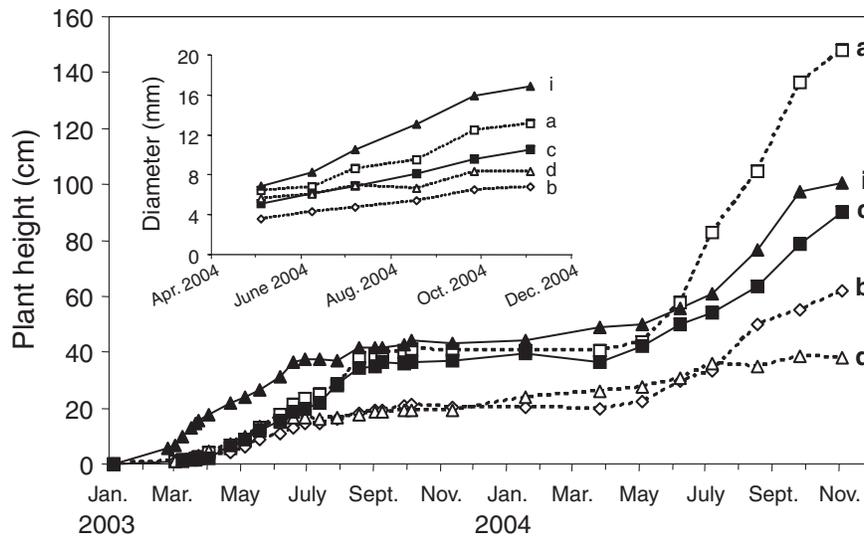


Table 2. Leaf and taproot $\delta^{13}\text{C}$ (‰) values for first-year oak seedlings in studies I and II in September 2003.

Life form and species	Species origin	Study I		Study II	
		Leaves	Taproot	Leaves	Taproot
Evergreen tree					
<i>Q. agrifolia</i>	CAL	-27.2 (0.3)	-25.7 (0.2)	-27.2 (0.2)	-26.1 (0.3)
<i>Q. calliprinus</i>	MED	-27.2 (0.2)	-24.2 (0.3)**	-27.7 (0.3)	-26.0 (0.5)
Evergreen shrub					
<i>Q. berberidifolia</i>	CAL	-27.5 (0.2)	-24.5 (0.2)	-28.7 (0.4)	-25.2 (0.5)
<i>Q. calliprinus</i>	MED	-27.2 (0.2)	-24.2 (0.3)	-27.7 (0.3)*	-26.0 (0.5)
Deciduous tree					
<i>Q. douglasii</i>	CAL	-27.4 (0.3)	-24.8 (0.4)	-28.6 (0.2)	-26.1 (0.3)
<i>Q. ithaburensis</i>	MED	-26.7 (0.4) [†]	-24.6 (0.3)	-27.8 (0.2)*	-26.1 (0.4)

Note: Values are means with SEs given in parentheses ($n = 5$ individuals; 3 individuals of *Q. berberidifolia* in study II). Two-way ANOVAs showed a significant interaction between species and plant part (marginally significant for study I; $0.05 < P \leq 0.1$ was defined as marginally significant). Contrast analysis between ecologically equivalent species within the same study and year were performed for significant one-way ANOVAs: [†] $P \leq 0.1$, * $P \leq 0.05$, and ** $P \leq 0.01$.

0.001) and 114% ($P < 0.001$) higher taproot NSC content per unit shoot biomass than *Q. ithaburensis* in the respective studies. Taproot NSC content per unit shoot biomass was considerably larger in study I than in study II, mainly reflecting differences in the ratios between taproot biomass and shoot biomass. Differences in the ratio of total taproot N content to shoot biomass between equivalent species tended to be similar, although less pronounced than differences in taproot NSC content per shoot biomass (Fig. 3, bottom panels).

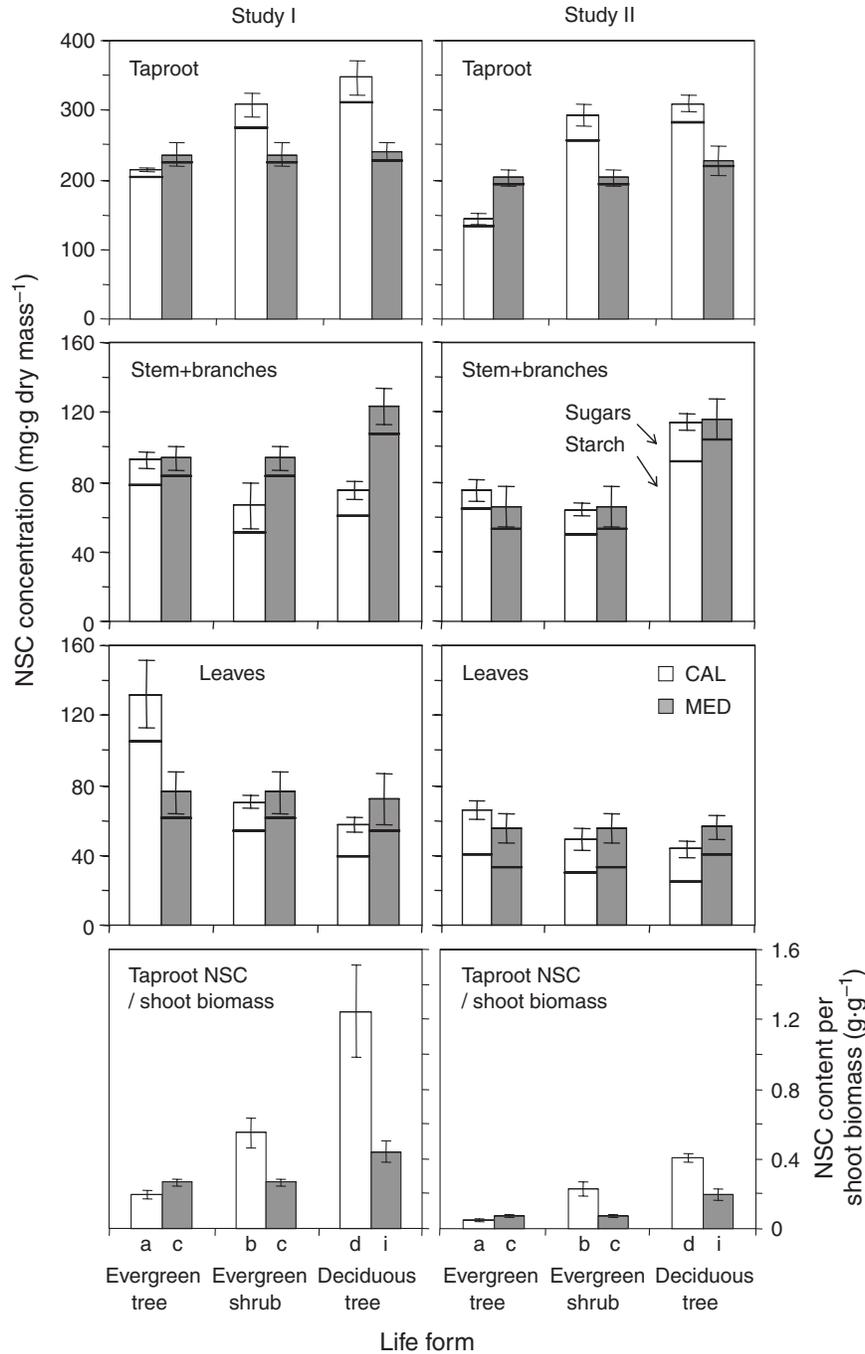
Leaf gas exchange

Net photosynthesis rate (A) was lower in first-year seedlings of *Q. agrifolia* than in those of *Q. calliprinus* (2003) but did not differ between second-year seedlings of those species (2004) (Fig. 4). Stomatal conductance (g_s) and intrinsic WUE were similar in the evergreen species during the second year, with no clear trend during the first year. Plotting $\log_e(g_s)$ versus VPD for second-year seedlings showed that stomatal

behavior was less sensitive to atmospheric evaporative demand in *Q. agrifolia* (slope of $-0.498 \text{ mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{kPa}^{-1}$ for $\log_e(g_s)$ versus VPD, $r^2 = 0.70$, $n = 42$) than in *Q. calliprinus* (slope of $-0.615 \text{ mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{kPa}^{-1}$, $r^2 = 0.74$, $n = 45$), with slopes being marginally significantly different ($P = 0.08$, Student's t test).

Seedlings of the deciduous *Q. douglasii* had lower intrinsic WUE than *Q. ithaburensis* seedlings during midseason (June – August) in both years, which was mainly related to higher g_s in 2004 (Fig. 4). In addition, leaf-internal CO_2 concentration (c_i), and the ratio of c_i to the atmospheric CO_2 concentration were significantly higher in *Q. douglasii* than in *Q. ithaburensis* (data not shown; $P < 0.001$ for both contrasts). The sensitivity of stomatal behavior to VPD was similar in the two deciduous species ($P = 0.723$), with slopes of $\log_e(g_s)$ versus VPD being -0.620 and $-0.625 \text{ mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{kPa}^{-1}$ for *Q. douglasii* and *Q. ithaburensis*, respectively.

Fig. 2. Concentrations of total nonstructural carbohydrates (NSC) and their components in first-year seedlings of three pairs of equivalent Californian (CAL) and eastern Mediterranean (MED) oak species in September 2003 (upper six panels). Bars in the upper six panels show the following NSC components: soluble sugars (upper portion of each bar) and starch (lower portion of each bar). In addition, the ratio of NSC content in the taproot to total shoot biomass is shown (bottom panels). Bars are means, and error bars are SEs (error bars in the six upper panels are SEs of NSC) ($n = 5$ individuals; 3 individuals of *Q. berberidifolia* in study II). Note the different scales on the y axes.



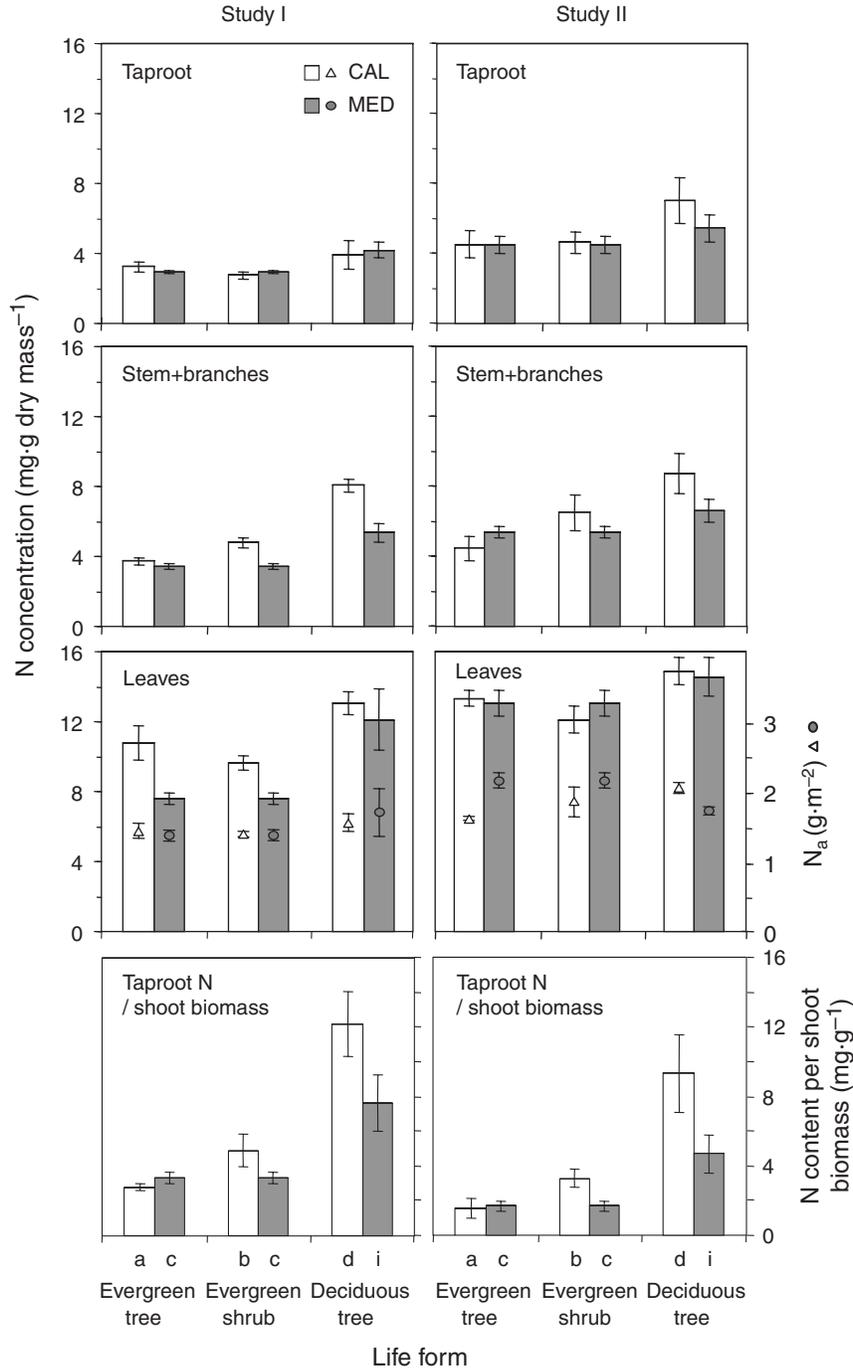
Discussion

Growth and biomass partitioning

The oak species in the current studies were grown under identical environmental conditions within each study and were not subjected to inter- or intra-specific competition.

Yet, the species obviously have different biomass-accumulation potentials and displayed different growth strategies. Species ranking in terms of biomass was similar in the two studies despite divergent environmental conditions: the CAL *Q. berberidifolia* and *Q. douglasii* being the smaller species, *Q. agrifolia* producing a larger biomass, and *Q. ithaburensis*

Fig. 3. Nitrogen concentration in first-year seedlings of three pairs of equivalent Californian (CAL) and eastern Mediterranean (MED) oak species in September 2003 (upper six panels). Leaf N was also presented as concentration per leaf area (N_a ; symbols within the bars). In addition, the ratio of N content in the taproot to total shoot biomass was shown (bottom panels). See Fig. 1 for oak species abbreviations. Bars and symbols are means, and error bars are SEs ($n = 5$ individuals; 3 individuals of *Q. berberidifolia* in study II).



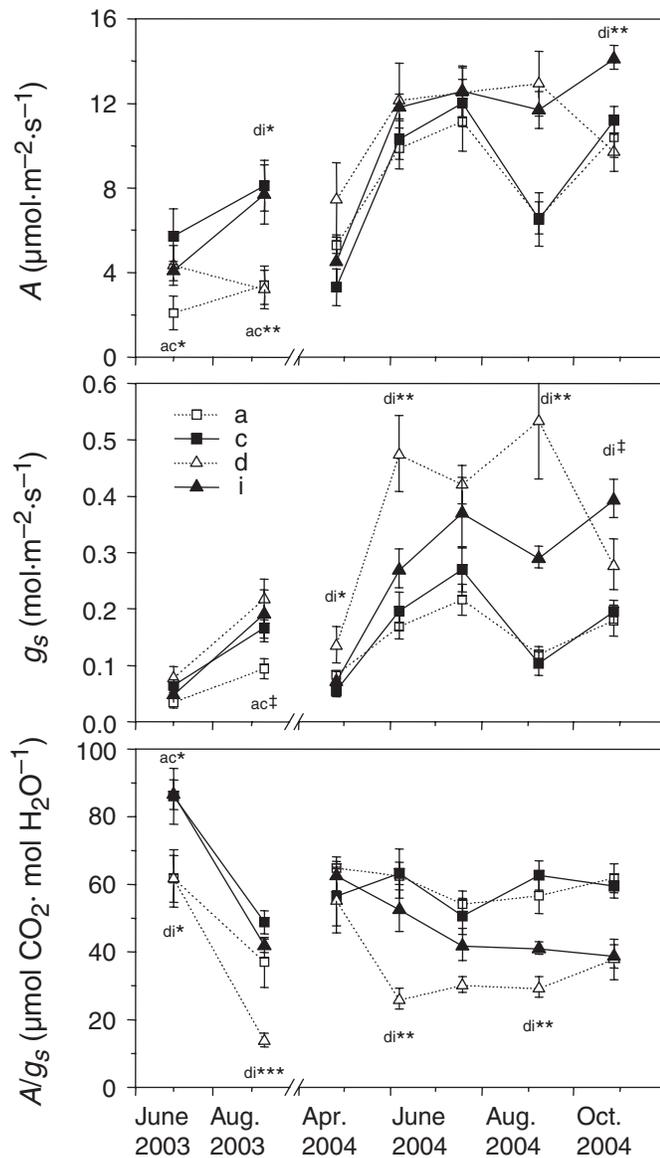
being the largest species. Only the performance of *Q. calliprinos* was somewhat more plastic, being among the smaller species in study I and among the larger species in study II. The low shoot growth in *Q. berberidifolia* and *Q. douglasii* might be caused in part by a massive investment of biomass in belowground compartments, particularly the taproot (Table 1). Partitioning of biomass to the taproot as a safe plant organ increases survival in case of catastrophic tissue loss. However,

in this way, dry matter is effectively directed away from growth because of low investment in leaf area as productive biomass (Chapin et al. 1990; Bond and Midgley 2001).

Storage of resources

Most of our observations did not support the hypothesis that the CAL oaks would store fewer resources than MED species when subjected to identical environmental condi-

Fig. 4. Net photosynthesis rate (A), stomatal conductance (g_s), and intrinsic water-use efficiency (A/g_s) in Californian (CAL; open symbols) and eastern Mediterranean species (MED; solid symbols) in first-year (2003) and second-year seedlings (2004) of study II. See Fig. 1 for oak species abbreviations. Statistically significant differences between CAL and MED evergreen (ac) and deciduous species (di) are shown: $^\dagger P \leq 0.1$, $*P \leq 0.05$, $**P \leq 0.01$, and $***P \leq 0.001$ (contrast analysis between species of two-way ANOVA). The interaction between species and date was statistically significant in two-way ANOVA for all variables. Values are means, and error bars are SEs ($n = 5$ –12 individuals).



tions. Concentrations of the main reserves of NSC and N in first-year seedlings were normally higher CAL species or similar among CAL and MED species in both studies. Tissue concentrations describe resource allocation at the organ level. The relevant whole-plant measure is the size of the stored resource stock per shoot or total biomass (Chapin et al. 1990). The high ratios of taproot NSC and N contents to shoot biomass should provide larger reserves to CAL *Q. berberidifolia* and *Q. douglasii* than to MED *Q. calliprinos*

and *Q. ithaburensis* in case of loss of a considerable fraction of the shoot (e.g., by fire or grazing). In seedlings of savanna trees from Brazil, fire tolerance (i.e., resprouting potential) was related to a high total NSC content in coarse roots relative to shoot mass (Hoffmann et al. 2004). In contrast, fire-sensitive seedlings of forest trees had a low ratio of NSC content to shoot biomass.

The above trends in first-year seedlings were observed under divergent growing conditions, which were reflected by differences in plant performance: moderate conditions with a severe drought event and lower temperatures in study I resulting in lower biomass production, higher taproot/shoot ratio, higher $\delta^{13}\text{C}$, and lower N concentrations compared with study II; these responses are in agreement with general observations (Chapin 1991). Despite divergent growing conditions between the studies, patterns of NSC and N contents were the same in both studies (Figs. 2 and 3), indicating a strong genetic control over these traits.

Water-use efficiency and adaptation to drought

Survival rates of seedlings in study I were considerably lower in CAL than in MED species (see Seedling growth and survival in the Results). Growing conditions of study I were characterized by a moderate watering intensity and a severe drought event in midsummer. Drought stress in study I was further indicated by the generally higher $\delta^{13}\text{C}$ values in plant tissues relative to the values obtained in study II with good watering conditions. Water availability is considered the major environmental factor influencing plant $\delta^{13}\text{C}$ (Dawson et al. 2002). Therefore, it was assumed that drought was the main cause of seedling mortality in that study. Alternatively, seedling survival might be related to large acorn mass, because oak species with large seeds produced a larger and potentially deeper root system (Long and Jones 1996), which might enable survival under naturally xeric conditions. However, under restricted rooting volume as in the current studies, large plants might in fact suffer more from drought than smaller ones because of increased water use by a larger canopy. However, no negative correlation between seedling size and survival was observed among the CAL and MED species. Thus, it appeared that, in line with our hypothesis, CAL oak seedlings in our studies were less adapted to drought compared with their ecologically equivalent MED species. Drought, together with browsing by animals and competition from grasses, has been proposed as the main environmental factor impeding recruitment of *Q. agrifolia*, *Q. berberidifolia* (still called *Q. dumosa* at that time), and *Q. douglasii* under field conditions in central California (Griffin 1971).

Lower adaptation to drought in some of the CAL compared with the MED species was also suggested by leaf gas exchange and stable isotopes. Stomatal sensitivity to atmospheric evaporative demand was lower in *Q. agrifolia* than in *Q. calliprinos*, suggesting less conservative water use in the CAL species (see Leaf gas exchange in the Results; marginally significant). Similarly, in small *Q. agrifolia* trees, leaf $\delta^{13}\text{C}$ did not respond to interannual variation in water availability (Goulden 1996), suggesting insensitivity of WUE to drought stress. In contrast, in oaks of the western Mediterranean Basin (e.g., in the evergreen *Quercus ilex* L.), conservative water use was observed (Mediavilla and Escudero

2003; Serrano and Peñuelas 2005), and seedlings of three out of four oak species showed higher WUE with increasing drought stress at high and intermediate irradiance levels (Quero et al. 2006).

Quercus douglasii showed lower gas exchange derived WUE (first- and second-year seedlings) and lower $\delta^{13}\text{C}$ (first-year seedlings) than its MED counterpart, *Q. ithaburensis*. Intrinsic WUE derived from leaf gas exchange is independent of immediate environmental conditions and allows for a wider interpretation despite the short-term nature of the measurements. In Australia, WUE was high in plant species adapted to dry conditions as compared with species from more moist sites (Wright et al. 2001). Low WUE in *Q. douglasii* might result from high g_s (Fig. 4), potentially resulting from high water availability mediated by a large root system relative to leaf biomass (Table 1). This allowed the photosynthetic apparatus of *Q. douglasii* to operate at higher c_i . However, leaf $\delta^{13}\text{C}$ was lower in *Q. douglasii* than in *Q. ithaburensis* in both studies, which indicates lower WUE in the CAL species under both wetter and drier conditions. Adult *Q. douglasii* trees seemed to have photosynthetic and stomatal mechanisms that perform well under dry summer conditions (Xu and Baldocchi 2003). However, seedlings appeared to be less adapted to drought, showing lower midseason g_s , lower xylem water potential and lower ^{13}C -derived WUE than adult plants (Matzner et al. 2003).

Higher SLA also suggested lower adaptation to drought in *Q. agrifolia* than in *Q. calliprinos*. SLA is often used as an indicator of resource conditions, such as water availability, in the plant environment (Cornelissen et al. 2003). In Australian perennial vegetation, SLA decreased in taxonomically related pairs of species when moving from a region with high precipitation to a region with low precipitation (Cunningham et al. 1999), indicating that species adapted to drought have lower SLA. Likewise, genotypes of *Quercus rubra* L. and other hardwood species from dry sites tended to have lower SLA than genotypes from mesic or wet sites (Abrams 1994).

Conclusions

Resource storage potential in CAL oaks was higher than or similar to that in MED oaks in most species comparisons under two different sets of environmental conditions. Therefore, recruitment of CAL oak seedlings in these studies seemed not to be limited by reserves for regrowth following disturbance. However, seedling survival rates, and to some extent leaf gas-exchange measurements and stable isotope composition, suggested that CAL species were less adapted to drought than MED species. Assuming that Californian soils are drier today because of compaction and invasion by exotic annual grasses, lower adaptation to drought will have implications for growth and survival and, thus, for recruitment of CAL oak seedlings.

Acknowledgments

We acknowledge the supervision of the studies by Hiro Yamara (Jewish National Fund) and Pat Regan (Rana Creek Habitat Restoration), the provision of the nursery and operating supplies by the Jewish National Fund in Israel, the logistical help provided by Mark Stromberg and Hastings Natural

History Reservation in California, and the N and stable C isotope analyses performed by Dan Yakir and Manuela Negeanu. We also thank Ran Lotan for supervision and monitoring of study II and Malik Kochva, Noami Agur, Inbar Baruch, Lih Avital, Amir Halperin, Jerry Tecklin, Marsha Stone, Morgan Wilkinson, Saori Zurita, Brandon McMahan, Einar Namer, Gilad Ben Meir, and Lilach Katzir for technical assistance. These studies were funded by the USDA Forest Service, Inventory and Monitoring Institute. The studies comply with the current laws of the United States and Israel.

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