Forest Ecology and Management 302 (2013) 34–42

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Relationships between stomatal regulation, water-use, and water-use efficiency of two coexisting key Mediterranean tree species

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ARTICLE INFO

Article history:
Received 11 January 2013
Received in revised form 25 March 2013
Accepted 26 March 2013

Keywords:
Transpiration
Isohydric/anisohydric
Gas exchange
Tree-ring
Water yield

ABSTRACT

This study aims to test the hypothesis that as leaf water potential decreases, stomatal conductance (g_s) and total water use decrease faster in trees tending toward isohydric behavior than in coexisting anisohydric trees.

We measured leaf gas exchange rates in two key Mediterranean species: *Pinus halepensis* (isohydric) and *Quercus calliprinos* (anisohydric) growing together in two different sites during seven field campaigns over 14 months. Intrinsic water-use efficiency (WUE_i) was calculated from gas exchange ratios, and independently from carbon isotopic composition, $\delta^{13}C$, of annual tree-ring sub-sections in four representative growth years.

As expected, g_s was greatly restricted already at VPD < 3 kPa in pine trees whereas in oak trees g_s was dynamically adjusted even at VPD > 5 kPa. Consequently, mean transpiration rates were 0.2–2.2 and 0.5–3.9 mmol $m^2\ s^{-1}$ in coexisting pines and oaks, respectively. Mean $\delta^{13}C$ values were 1.5‰ higher in tree-rings of the pine compared to the oak trees, consistent with the differences in WUE_i between 75 and 64 μmol CO_2 mol^{-1} H_2O in pines and oaks, respectively, based on the short-term gas exchange measurements.

A preliminary attempt to upscale the results to typical forest stands of the two species, on annual timescales, demonstrated that the differences in stomatal regulation and water-use could imply ~30% higher water-use (or ~70% lower water yield) in oak stand compared to pine stand, related to its tendency toward anisohydric behavior. This sets the limit for typical 300 trees ha^{-1} oak and pine stands at the 460 and 360 mm iso-precipitation lines, respectively, consistent with their current distribution along the precipitation gradient in our region. The results can help predict or manage changes in species composition in the face of increasing water limitations in Mediterranean regions.

1. Introduction

Stomatal regulation is vital for plant function, especially when water supply is limited. Tardieu and Simonneau (1998) distinguished between isohydric species, where stomatal regulation maintains fairly constant leaf water potential (Ψ_l) during the day, and anisohydric species, where Ψ_l markedly decreases with changes in evaporative demand. The effect of stomatal regulation (isohydric/anisohydric) on the ability of trees to survive adverse conditions has been addressed in numerous studies (e.g. West et al., 2007a; McDowell et al., 2008; Klein et al., 2011). Yet little attention was given to the effect of stomatal regulation on leaf gas exchange rates and tree water-use, arguably an equally important effect. Leaf gas exchange is fundamental to ecosystem- and global-level fluxes of water and CO_2, in turn affecting soil water availability and atmospheric CO_2 concentration. Enhanced gas exchange between vegetation and the atmosphere may increase carbon sequestration rates (e.g. Grunzweig et al., 2007; Baldocchi et al., 2010) but simultaneously decrease water yield (Jackson et al., 2005; Farely et al., 2005). Drought-tolerant tree species, which are usually characterized by anisohydric stomatal regulation, maintain leaf transpiration at very low Ψ_l, and are therefore expected to use more water than coexisting isohydric species under drought (Schultz, 2003; Mereu et al., 2009). When applied to whole canopies, such leaf-scale differences may be translated into major forest-scale changes in hydrological fluxes (van der Molen et al., 2011).

Two major forest types in the Mediterranean are the dry coniferous forest and the mixed maquis, dominated by pine species (e.g. *Pinus halepensis*, *Pinus pinea*, *Pinus maritima*) and sclerophyllous oak species (*Quercus ilex*, *Quercus calliprinos*, *Quercus coccifera*, *Quercus suber*) respectively. *P. halepensis* is a needle-leaf coniferous tree with maximum height of 10–20 m (depending on precipitation

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http://dx.doi.org/10.1016/j.foreco.2013.03.044

amounts, *P*), and a relatively shallow root system usually reaching not deeper than 5 m (Klein et al., 2012b). It populates large forest areas across the Mediterranean, usually as monoculture but also accompanied by other *Pinus* or *Cupressus* species (Quezel, 2000; Maestre and Cortina, 2004). During summer, *P. halepensis* avoids drought by reducing stomatal conductance to a minimum at $\Psi_l < -2.8$ MPa, characterizing it as an isohydric species (Klein et al., 2011). *Q. calliprinos* is a sclerophyllous broad-leaf tree with maximum height of ~5 m and up to 10 m deep root system. It is a dominant species in the Eastern Mediterranean maquis, usually accompanied by *Pistacia spp*. and a well-developed understory (Schiller et al., 2003; Sever and Neeman, 2008). *Q. calliprinos* is productive year-round, tolerating drought by maintaining stomatal conductance at $\Psi_l < -4.0$ MPa, an anisohydric behavior common to related species, e.g. -5.0 MPa in *Q. coccifera* (Damesin et al., 1998; Noltsakis and Tsiouvaras, 1990) and *Q. ilex* (Lansac et al., 1994). Stomatal conductance and water-use efficiency of oaks and pines were compared in previous studies (Guehl et al., 1995; Kolb and Stone, 2000; Ferrio et al., 2003). However, the relationships between these water-use parameters and the mode of stomatal regulation have not yet been tested.

Stomatal regulation should also affect carbon uptake rates, with direct impact on plant metabolism and growth. Moreover, under prolonged drought, isohydric plants might risk depletion of internal carbon reserves (McDowell et al., 2008; Sala et al., 2010). The ability to maximize photosynthesis under conditions inducing tight stomatal control, associated with increase in intrinsic water-use efficiency ($WUE_i = A/g_s$, the ratio of the rate of photosynthetic assimilation to stomatal conductance), is hence a key for growth and survival (Maseyk et al., 2008; Klein et al., 2011). Intrinsic WUE, i.e. the ratio between photosynthesis and stomatal conductance, is readily calculated from leaf gas exchange data. Yet in field conditions, large fluctuations in these fluxes mean that point measurements can only provide transient values. On the other hand, tree-ring stable carbon isotope composition, $\delta^{13}C$, provides a time-integrated indicator of WUE_i, reflecting the ratio of intercellular to atmospheric CO_2 concentrations during the period in which the carbon was fixed. This methodology capitalizes on the understanding of ^{13}C fractionation during leaf carbon uptake (Farquhar et al., 1982), further improved by Seibt et al. (2008). Numerous studies have therefore used tree-ring $\delta^{13}C$ in this context (e.g. Leavitt and Long, 1989; Saurer and Siegenthaler, 1989; Robertson et al., 1997; Ferrio et al., 2003; Maseyk et al., 2011; Klein et al., 2012a), including the verification of the association to leaf gas exchange (Klein et al., 2005).

Changes in vegetation cover have significant implications on local and regional water balance (Brown et al., 2005 and references therein). Catchment studies have been widely used to quantify such effects, considering the impact of processes such as afforestation, deforestation, and thinning, with or without regrowth (Sahin and Hall, 1995; Stednick, 1996; Zhang et al., 2001; Brown et al., 2005). In cases where forest is dominated by a few tree species, such as many Mediterranean and temperate forests, water relations at the tree level can be more easily scaled up to the stand level, indicating its effect on the local water balance, and in particular on the local water yield (WY; the difference between precipitation and evapotranspiration). While stand density effects on the forest WY were tested in numerous studies, more data is needed to quantify the effect of tree species composition on WY.

The aim of this study was to examine the relationship between the stomatal regulation, leaf gas exchange, and tree water use in two coexisting key Mediterranean tree species with contrasting stomatal regulation strategies. Specifically, we tested the hypothesis that as leaf water potential decreases (e.g. during drought periods), stomatal conductance (g_s) and total water use decrease faster in isohydric trees than in coexisting anisohydric ones. A secondary hypothesis was that WUE_i must be higher in the isohydric pine species than in the anisohydric oak to explain their comparable growth rate.

2. Materials and methods

2.1. Plant material and site description

In May 2010 three *P. halepensis* trees and three *Q. calliprinos* trees were selected in the 1-ha experimental plot (EP) of ARO Volcani Center in Beit Dagan, Israel (31°59′N 34°48′E, elevation 20 m). The plot is located in the coastal plains, 20 km south-east of Tel-Aviv, 10 km east of the Mediterranean Sea shore, and its soil is deep sandy to sandy-loam. Mean annual temperature and precipitation are 20 °C and 570 mm respectively. Trees were planted in 1991 in parallel rows with 2 × 4 m spacing and were not thinned since. Diameter at breast height (DBH) of *P. halepensis* trees ranged between 13.7 cm and 19.9 cm; diameter of the main coppice at 0.5 m (DMC) of *Q. calliprinos* trees was 11.5–18.5 cm. In December 2010 three other *P. halepensis* trees and three *Q. calliprinos* trees were selected in an afforestation plot (AP) at Harel forest, Israel (31°43′N 34°57′E, elevation 320 m). The plot is located on a hilltop 4 km south-west of Beit Shemesh, and its soil is shallow light rendzina overlying white chalk and flint bed. Mean annual temperature and precipitation are 20 °C and 490 mm respectively. Selected trees are young (10–15 years) second generation trees which grew naturally from seeds of the first generation of trees which were planted in the 1930s. DBH of *P. halepensis* trees was 8.7–20.7 cm; DMC of *Q. calliprinos* trees was 6.4–9.6 cm. Both plots were rain-fed (no irrigation) with the annual water input restricted to October–May, with timing and amounts typical to the study area (Klein et al., 2012a).

2.2. Leaf gas exchange and water potential

In each of the twelve selected trees, two leaves/ needle cohorts (twelve 1-year needles) per tree were marked for repeated gas exchange measurements in seven field days between May 2010 and July 2011 (see summary of main meteorological conditions in Table 1). Leaf stomatal conductance (g_s, in mol H_2O m^{-2} s^{-1}), net carbon assimilation (A, in μmol CO_2 m^{-2} s^{-1}) and transpiration (*T*, in mmol H_2O m^{-2} s^{-1}), were measured on three trees per species in Harel and Beit Dagan plots. Leaf chamber conditions were adjusted as close as possible to ambient conditions (e.g. light intensity, temperature and relative humidity) and all gas exchange fluxes, including rates of CO_2 assimilation and water vapor loss, were expressed on a projected leaf area basis. Measurements of g_s assumed stomatal ratio of 1 and 10 for *P. halepensis* and *Q. calliprinos*, respectively. Three to four cycles of measurements were made from 8:30 to 14:00 using a Li-6400 Photosynthesis System (Licor Inc., Lincoln, NE, USA), also simultaneously measuring air temperature, photosynthetically active radiation (PAR, in μmol m^{-2} s^{-1}) and vapor pressure deficit (VPD, in kPa). These measurements were used in the calculation of intrinsic water-use efficiency (WUE_i, in mmol CO_2 mol^{-1} H_2O) according to:

$$WUE_i = A/g_s \quad (1)$$

Paired values of *A*, g_s, and WUE_i for each field day were compared by student's *T*-test with significance level of 0.05. During the April 2011 field day, gas exchange measurements were accompanied by measurements of leaf water potential (Ψ_l) using the pressure chamber technique (Scholander et al., 1965; Holbrook et al., 1995). Small (5–7 cm long) shoots were cut from the same trees used for the gas exchange measurements and put in pressure chamber (Model 600; PMS instrument Co., Albany, OR, USA) fed by nitrogen gas cylinder and equipped with a lamp-carrying magnifying glass. Gas pressure

Table 1
Diurnal temperature extremes (T_{max}, T_{min}) and average relative humidity (RH) for the seven field days at the Beit Dagan experimental plot (EP) and at the Harel afforestation plot (AP).

Date (Site) parameter	12 May 10 (EP)	16 August 10 (EP)	2 November 10 (EP)	7 December 10 (AP)	20 January 11 (AP)	24 April 11 (EP)	4 July 11 (AP)
T_{max} (°C)	25.8	33.1	26.8	21.3	19.5	24.1	32.2
T_{min} (°C)	15.7	25.9	7.4	13.6	10.0	11.2	19.9
RH (%)	72	71	56	75	54	64	59

within the chamber was gradually increased (~1 MPa min^{-1}) until water emerged from the protruding twig surface, and the pressure value was recorded as leaf water potential (Ψ_l).

2.3. Tree-ring $\delta^{13}C$

Trunk cores were sampled from five *P. halepensis* trees and three *Q. calliprinos* trees growing in Beit Dagan and used in the gas exchange measurements. Cores were collected using a 200 mm increment borer (core diameter 5.15 mm) equipped with starter (Haglof, Sweden), at breast height at 0° (N). To test the long-term differences in tree-ring $\delta^{13}C$ between the two species, a sequence of four well-identified annual tree-rings was selected. Tree-rings of the growth years 1997–2000 were identified, cut into 4–12 equal intra-annual sub-sections and their $\delta^{13}C$ values analyzed as described in Klein et al. (2005). The tree-ring of the 1999 drought year was identified only in one of the three cores sampled from *Q. calliprinos*, and hence no repetitions were available for that tree-ring. To minimize analysis time and resources, isotopic analysis was performed on whole wood samples rather than cellulose, which is generally coherent (McCarroll and Loader, 2004 and references therein). The $\delta^{13}C$ results were used to calculate the discrimination of the tree against ^{13}C (Δ) expressed in delta notation as parts per thousand (‰) deviations from the international carbon isotope standard (Coplen, 1994):

$$\Delta = (\delta^{13}C_a - \delta^{13}C_t)/(1 + \delta^{13}C_t) \tag{2}$$

where $\delta^{13}C = (\delta^{13}C/\delta^{12}C)_{sample}/(\delta^{13}C/\delta^{12}C)_{reference} - 1$ and the reference is PDB carbonate, and subscripts *a* and *t* stand for atmospheric air and the tree-ring material, respectively. Δ values were further used in the derivation of the tree's intrinsic water-use efficiency (WUE_i^*) using the following equation (adapted from Farquhar et al. (1982); Seibt et al. (2008)):

$$WUE_i^* = C_a/r\{[b - \Delta - f(\Gamma^*/C_a)]/[b - a + (b - a_m) * (g_s/g_i r)]\} \tag{3}$$

where C_a is the atmospheric CO_2 concentration in ppm (an annual global average; Robertson et al., 1997); *r* is the ratio of the diffusivities of CO_2 and water in air (1.6); *a*, a_m, *b* and *f* are the leaf-level discriminations against ^{13}C in the diffusion through the stomata (4.4‰), during dissolution and liquid phase diffusion (1.8‰), during biochemical CO_2 fixation (29‰), and in photo-respiratory CO_2 release (8‰), respectively; Γ^* is the temperature-dependent CO_2 compensation point of *ca.* 30–45 ppm for both species (Maseyk et al., 2008); g_s/g_i is the ratio between stomatal and internal conductances to CO_2 respectively (0.5, according to Maseyk et al. (2011)).

2.4. Upscaling from leaf to forest stand

Measurements of leaf transpiration (*T*) were used for the estimation of diurnal tree-scale transpiration amounts for each species and field day, using our simple algorithm:

$$T_d = T_m \times LA \times LC \times t_T \times 3600 \times 18/1000 \times 10^{-6} \tag{4}$$

where T_d is the diurnal transpiration (mm $tree^{-1}$ d^{-1}), T_m is the estimated average transpiration rate during the day, based on of 3–4 measurements in the morning and afternoon (mmol H_2O m^{-2} s^{-1}), *LA* is the mean total leaf area of a mature, 15-cm DBH/DMC tree (40.0 and 37.7 m^2 for *Q. calliprinos* and *P. halepensis*, respectively) calculated with our local allometric equations (Schiller et al., 2003 for *Q.* calliprinos; Grunzweig et al., 2007 for *P. halepensis*), LC is the time-averaged portion of leaf cover (100% for *P. halepensis*, 87.5% for *Q. calliprinos*, due to ~50% defoliation 3 months a year), t_T is the number of hours allocated for transpiration (8–11 h per 24 h, depending on the season), and the numerical ratios required for upscaling from s to h and from mmol H_2O to mm. A similar upscaling procedure was confirmed by testing against whole-tree sap-flow measurements in *P. halepensis* growing in a forest site 45 km from the afforestation plot. An annual total tree-scale water use amount, T_t (mm $tree^{-1}$ $year^{-1}$), was calculated for each species by integration of the T_d values of the seven field days across a theoretical annual cycle, assuming constant seasonal variation. To that matter we used the data from both sites, based on their common climate and tree age and size (Section 2.1). Such upscaling is sensitive to weather conditions on the specific field days and we therefore checked for representativeness of our data by comparing (Student *t*-test) T_{max}, T_{min}, and RH during our measurement days (Table 1) to long-term monthly averages provided by the Israel Meteorological Service. Differences between observed values and the long-term averages of the three parameters were not significant at $\alpha = 0.05$. Regression between observed and multiannual average T_{max} yielded slope of 1.04 and r^2 of 0.92.

The difference between precipitation (*P*) and evapotranspiration (ET) for a particular area is defined as water yield (WY = *P* – ET). To assess the influence of the species-specific tree water-use on WY, T_t was identified as one of four components of stand-scale ET:

$$ET = sd^* T_t + T_u + I + E_s \tag{5}$$

where *sd* is stand density, T_u is transpiration from understory vegetation; *I* is evaporation of water intercepted by plant foliage; and E_s, evaporation from soil. The magnitude of each of the three fluxes largely depends on the local annual *P* and stand density at each forest site (*sd*; trees ha^{-1}). T_t itself also changes with *sd*, because of density effects on tree-scale transpiration. At low *sd* of 100 trees ha^{-1}, tree-scale transpiration is 22% higher than at higher *sd* (unpublished data from a thinning experiment in Yatir forest). For a first approximation of the stand-scale ET flux, quantification of the three, generally smaller, non-tree fluxes (T_u, *I*, and E_s) was adopted from Raz-Yaseef et al. (2010a,b), confirmed in subsequent studies (Raz-Yaseef et al., 2012; Klein et al., 2012b) and assuming that little difference in leaf area should result with similar values for pine and oak.

3. Results

3.1. Stomatal regulation in P. halepensis and Q. calliprinos

Mean (*n* = 13) leaf water potential (Ψ_l) and stomatal conductance (g_s) at mid-day during April 2011 showed large differences between the two species, in agreement with their contrasting mode of stomatal regulation (Fig. 1). The oak leaves had significantly lower Ψ_l than the pine leaves (–2.8 ± 0.38 vs.

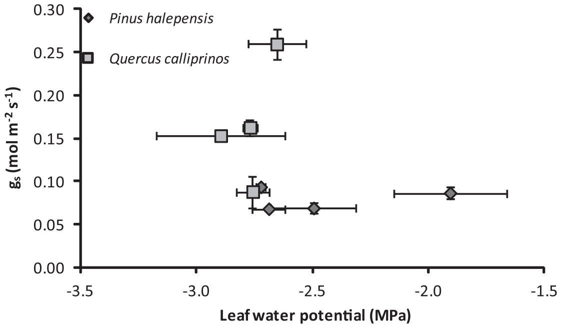

Fig. 1. Stomatal conductance (g_s) vs. leaf water potential for *P. halepensis* and *Q. calliprinos* during a wet season day at Beit Dagan. Each data-point is mean ± SE (n = 3–4) of measurements taken in 9:00, 10:00, 11:00, and 12:30.

-2.4 ± 0.43 MPa respectively, $P < 0.01$) and higher g_s (0.17 ± 0.060 vs. 0.08 ± 0.015 mol H_2O m^{-2} s^{-1} respectively, $P < 0.001$). In general, for any given Ψ_l, g_s of *Q. calliprinos* was ~2-fold that of *P. halepensis*.

3.2. Stomatal adjustments and transpiration

The response of g_s to increasing levels of vapor pressure deficit (VPD) was measured in the two species. Under moderate VPD (from 1 to 4 kPa) both species reduced g_s in response to VPD increase (Fig. 2a, right panel). The oak leaves had higher g_s than the pine leaves (0.15 ± 0.102 vs. 0.07 ± 0.035 mol H_2O m^{-2} s^{-1} respectively, $P < 0.01$) although the decrease rate was rather similar (-0.017 vs. -0.012 mol H_2O m^{-2} s^{-1} kPa^{-1} respectively). A continued reduction in g_s at increasingly higher VPD (from 3 to 8 kPa) was observed in *Q. calliprinos*. However in *P. halepensis* g_s was reduced to levels below 0.005 mol H_2O m^{-2} s^{-1} (Fig. 2a, left panel). Very low g_s levels were maintained in *P. halepensis* throughout the morning and afternoon hours of a summer day (Fig. 2b, left panel), in contrast with relatively large stomatal adjustments in *Q. calliprinos*. The ability of *Q. calliprinos* to open stomata in the morning (at VPD < 4 kPa), unlike *P. halepensis*, was also shown in a spring day (Fig. 2b, right panel). The rate of transpiration (T) was measured and was shown to reflect the relationship $T = g_s \times \text{VPD}$, demonstrating large differences in T between the two species in spring (2.1 ± 1.09 vs. 2.9 ± 1.65 mmol H_2O m^{-2} s^{-1}, respectively, $P < 0.01$), and further in summer (0.2 ± 0.06 vs. 0.8 ± 0.26 mmol H_2O m^{-2} s^{-1} respectively, $P < 0.001$; Fig. 2c).

3.3. Seasonal gas exchange patterns

Periodic measurements of transpiration (T) and net assimilation (A) during seven field days (four in Beit Dagan and three in Harel forest) showed seasonal gas exchange patterns of the two species. In both species mean T and A rates were higher in winter and spring (1–4 mmol H_2O m^{-2} s^{-1} and 3–12 μmol CO_2 m^{-2} s^{-1}, respectively) and lower in summer and fall (0.2–1.0 mmol H_2O m^{-2} s^{-1} and 1–3 μmol CO_2 m^{-2} s^{-1}, respectively), as expected for trees growing in a Mediterranean ecosystem characterized by a single, short rainy season. In five out of seven field days, mean T from the oak leaves was ~2-fold higher than from the pine

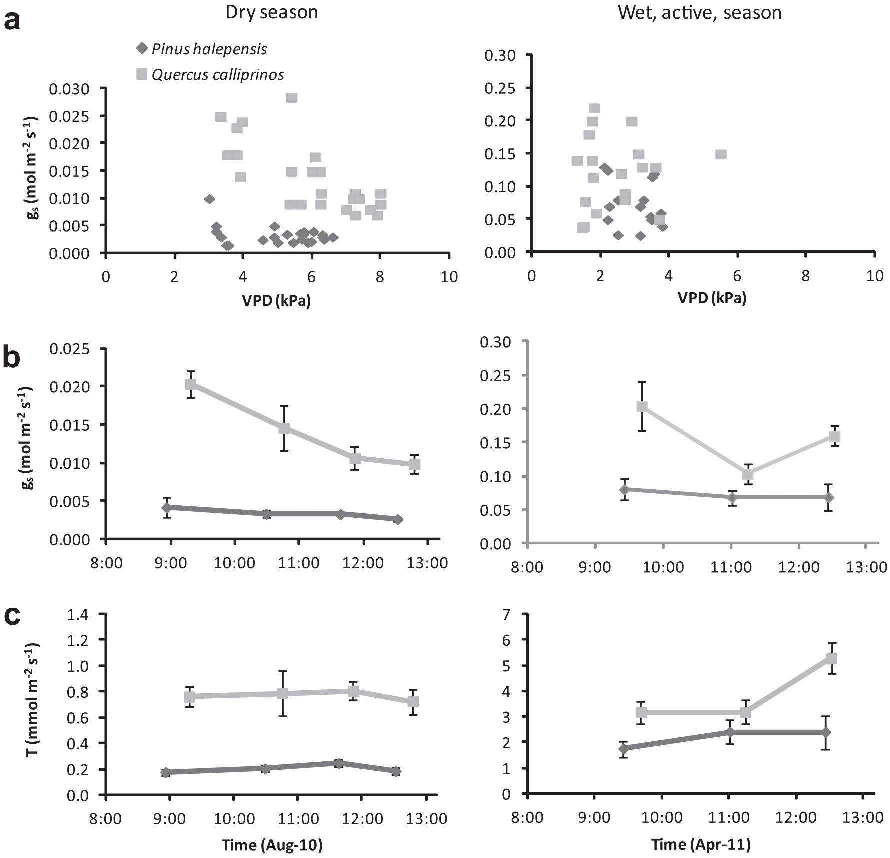

Fig. 2. Relationships between stomatal conductance (g_s) and vapor pressure deficit (VPD; a) in *P. halepensis* and *Q. calliprinos* along the morning and afternoon hours of a summer day (left column) and a spring day (right column) at Beit Dagan. Changes in g_s (b) and transpiration (T; c) for the two species on the respective days at Beit Dagan. All data are from *in vivo* leaf chamber measurements. *Error bars* represent the standard error of the mean (n = 6). The two species responded to increase in VPD by reduction of g_s, except for *P. halepensis* in the summer, when g_s was close to zero. g_s and T were up to 4-fold higher in *Q. calliprinos*.

needles, and was equal only during winter (Fig. 3a). Differences in A were usually small and insignificant (Fig. 3b), showing that leaf-scale carbon uptake amounts were similar in the two species. Integrating the changes in *T* and g_s resulted with higher intrinsic water-use efficiency (WUE_i) for *P. halepensis* during most of the time (Fig. 3c).

3.4. Tree-ring $\delta^{13}C$

The fractionation of the stable carbon isotope composition, $\delta^{13}C$, was measured in tree rings of *P. halepensis* and *Q. calliprinos* and used as a marker for stomatal regulation during photosynthesis. To test the long-term differences in tree-ring $\delta^{13}C$ between the two species, we selected a sequence of four annual tree-rings formed between 1997 and 2000, yielding 34–36 sub-annual slices (Fig. 4). The mean ± SE values of $\delta^{13}C$ of *P. halepensis* and *Q. calliprinos* were $-24.9 \pm 0.2‰$ and $-26.4 \pm 0.1‰$, respectively, and the 1.5‰ difference was highly significant ($P < 0.001$). The ranges of $\delta^{13}C$ values of *P. halepensis* and *Q. calliprinos* were −22.6‰ to −26.7‰ and −24.9‰ to −27.4‰, yielding ranges of 4.1‰ and 2.6‰, respectively. Intrinsic water-use efficiency (WUE_i^* from Eq. (2); Fig. 4) showed the expected annual trends, with maximum WUE_i^* values at the start or end of each tree-ring, and minimum WUE_i^* values at the middle of the ring. The deposition of carbon into structural tree-rings is expected to be confined to the growing season, which is governed, in our thermo-Mediterranean site, by precipitation (*P*). Therefore, the $\delta^{13}C$ record reproduced the discrimination against ^{13}C between about October and April, and not throughout the entire year. Both the total amount and the distribution of precipitation can help explain the large inter-annual differences in the WUE_i^* trends of both species: (1) Higher WUE_i^* values were measured in the 1999 growing season (81.9 and 64.9 μmol CO_2 mol^{-1} H_2O vs. the overall mean 74.6 and 63.6 μmol CO_2 mol^{-1} H_2O in *P. halepensis* and *Q. calliprinos*, respectively) which was a drought year ($P = 289$ mm) and also produced very narrow tree-rings; (2) Lower WUE_i^* values were measured in 1998 ($P = 504$ mm) and 2000 ($P = 485$ mm, also characterized by two major rain events of $P > 50$ mm each); and (3) Fluctuations in WUE_i^* values during 1997 ($P = 480$ mm) are related to two large (>1 month) pauses between consecutive rain events during the growing season. Evidently, the difference in WUE_i^* between the two species was not constant throughout the 4-years period, and vanished altogether in the course of 2000.

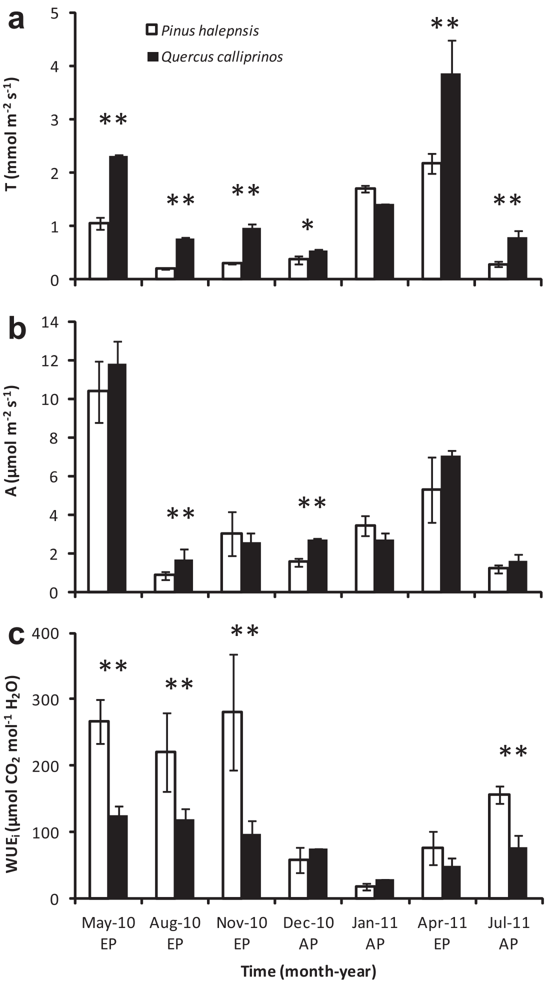

Fig. 3. Mean ± SE ($n = 12$–24) values of transpiration (*T*; a), photosynthesis (*A*; b) and intrinsic water-use efficiency (WUE_i, A/g_s; c) for *P. halepensis* and *Q. calliprinos* during the seven field measurement days at the Beit Dagan experimental plot (EP) and at the Harel afforestation plot (AP). All data are from *in situ* leaf chamber measurements. Star symbols indicate differences between paired measurements are significant at $\alpha < 0.05$ (*) or $\alpha < 0.005$ (**). Significantly higher *T* rates in *Q. calliprinos* throughout the year (a, except in winter) and similar *A* rates in the two species (b) meant that *P. halepensis* had higher WUE_i during most of the time (c).

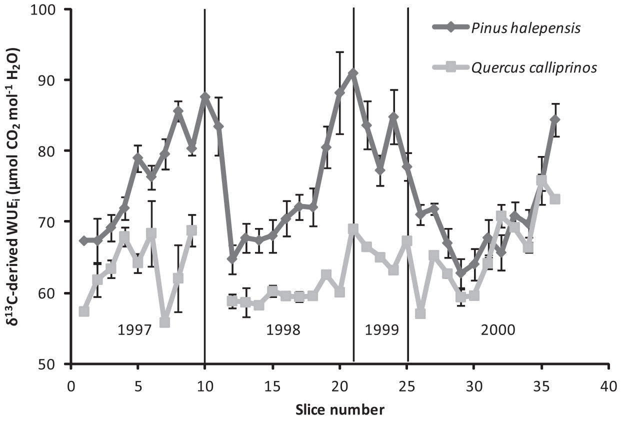

Fig. 4. Mean ± SE WUE_i values derived from $\delta^{13}C$ of the 1997–2000 tree-rings of *P. halepensis* and *Q. calliprinos* trees ($n = 1$–5) growing at the Beit Dagan experimental plot. Annual precipitation amounts were 480, 504, 289, and 485 mm for 1997, 1998, 1999, and 2000, respectively. The tree-ring of the 1999 drought year was identified only in one of three cores sampled from *Q. calliprinos*, and hence no replicates were available for that tree-ring.

3.5. Stand-scale water-use of P. halepensis and Q. calliprinos

Annual total tree-scale water use amount, T_t, was calculated to be 6.6 and 10.0 mm $tree^{-1}$ $year^{-1}$ for *P. halepensis* and *Q. calliprinos*, respectively. This is based on upscaling of leaf-scale transpiration measurements (Fig. 3a) into diurnal tree-scale water-use for *P. halepensis* and *Q. calliprinos* during the seven field days (Eq. (4)). Water-use of pine ranged between 2.9 mm $tree^{-1}$ d^{-1} in April and 0.3 mm $tree^{-1}$ d^{-1} in August; the oaks transpired 6.5 and 0.8 mm $tree^{-1}$ d^{-1} in April and late autumn (December), respectively (data not shown). The 50% higher tree-scale water-use of the oak vs. the pine reflects the combined effects of higher leaf area-based transpiration rate in the oak leaves, and comparable total leaf area (37.7 and 40.0 m^2 for 15-cm DBH *P. halepensis* and 15-cm DMC *Q. calliprinos*, respectively), and the partial defoliation during three months a year in the oak (see Section 2). Stand-scale water use was estimated using Eqs. (4) and (5) and summarized for the two stands and a range of stand densities (*sd*) and average *P* in Fig. 5. In going from *sd* of 100 to 500 trees ha^{-1}, stand water use ranged between 254 and 475 mm for pine and between 295 and

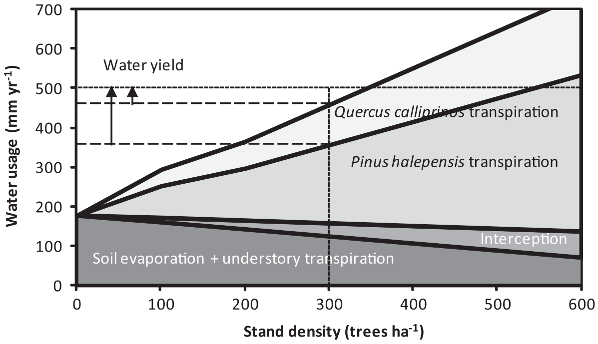

Fig. 5. Expected changes in the partitioning between hydrological flux components in response to stand density changes for a *Pinus halepensis* forest and a *Quercus calliprinos* maquis, based on upscaling of leaf-scale transpiration measurements using Eqs. (4) and (5) (see Section 2). The increasingly higher stand-level transpiration amount in an oak vs. pine stand comes on expense of the water yield. At typical stand density of 300 trees ha^{-1} and annual precipitation of 500 mm (vertical and horizontal dotted lines, respectively), the water use of *P. halepensis* and a *Q. calliprinos* stands are expected to be 357 and 459 mm (long dash lines), leaving 143 and 41 mm as water yield, respectively (arrows). Such analysis also indicates the carrying capacity for the different stands (e.g., ~350 and ~550 trees ha^{-1} for oak and pine at the 500 mm iso-precipitation region).

645 mm for oak. The partitioning between hydrological flux components also changed in response to stand density changes. Stand-scale T_t and foliage interception (I) increases with sd, although not linearly because of density effects on tree scale transpiration. Soil evaporation (E_s) and understory transpiration (T_u) decrease, as a result of reduced free surface area, increasing the effect of shading, and of inter-species competition. At a typical sd of 300 trees ha^{-1}, $E_s + T_u$ was estimated at 126 mm and I at 33 mm, while $sd * T_t$ was 198 and 300 mm for pine and oak, respectively.

4. Discussion

4.1. Relationship between stomatal regulation and leaf gas exchange

Figs. 2 and 3 confirm our first hypothesis that water use of the anisohydric *Q. calliprinos* is larger than that of the isohydric *P. halepensis*. Moreover, this was not limited to the summer drought but rather persisted during spring and fall. A typical drought avoidance strategy was demonstrated by the pine trees, restricting g_s already at VPD < 3 kPa (Fig. 2). In contrast, the oak trees dynamically adjusted g_s even at VPD > 5 kPa. The consistently higher T rates of *Q. calliprinos* are related to at least two physiological differences between the species under study: (1) higher rooting depth of *Q. calliprinos* (Oppenheimer, 1957) should increase its access to soil water resources, and (2) lower Ψ_l of *Q. calliprinos*. This means that *Q. calliprinos* has higher soil water availability than *P. halepensis* at any given soil water potential (Ψ_s). For example, while *P. halepensis* is unable to extract soil water at $\Psi_s < -2.0$ MPa, *Q. calliprinos* may extract water even at $\Psi_s < -3.5$ MPa (Schiller et al., 2003).

In both sites, trees were relatively young (15–20-year) and hence the extent to which our results are applicable to mature stands is uncertain. *Q. calliprinos* has potentially higher longevity than *P. halepensis*, but in many field sites interspecies competition and grazing (Osem et al., 2009; Reisman et al., 2010) maintain both species at similar, usually high, activity levels. Another possible interaction could be associated with trees growing in mixed plots. While this ensures similar local climatic conditions, it is unknown whether water relations of one species would be affected by the presence of the other. Despite the different rooting depths of *Q. calliprinos* and *P. halepensis*, water-use of the pines could potentially be either reduced (due to higher competition) or facilitated (by hydraulic lift) by the oaks. Upscaling to the forest scale (Section 4.3 below) showed, however, that our results from the mixed plots generally consistent with those from mono-specific stands.

Figs. 3c and 4 confirm our second hypothesis that the pines have higher WUE_i than the oaks under most circumstances. The pinyon/juniper forest of SW USA is the most studied isohydric/anisohydric forest tree system (Lajtha and Barnes, 1991; West et al., 2007a; McDowell et al., 2008). In agreement with our findings, Lajtha and Barnes (1991) showed that the isohydric tree species (pinyon, *pinus edulis*) had usually higher WUE than the anisohydric species (juniper, *Juniperus osteosperma*). However a clear implication on water-use has not been shown: while juniper trees had slightly higher sap flow rates than pinyon trees without summer precipitation, a reversed trend was observed following rain events (West et al., 2007a,b). It is possible that the observed difference in water-use between pines and oaks in our study is conditioned by the sharp precipitation seasonality of the Mediterranean. Stomatal conductance and water-use efficiency of oaks and pines were compared in previous studies (Guehl et al., 1995; Kolb and Stone, 2000; Ferrio et al., 2003; see summary in Table 2). Our results are consistent with the findings of these studies, except for the comparison of *Pinus pinaster* and *Quercus robur* (Guehl et al., 1995), where both species can be regarded as isohydric. This may indicate that the differences in g_s and WUE_i were not related to general differences (e.g. morphological, physiological) between oak and pine species, but rather to the specific differences between isohydric and anisohydric species, as in the case of the juniper and pinyon (Table 2).

4.2. Relationship between tree-ring $\delta^{13}C$ and leaf gas exchange

The multiannual trends of δ^{13}C-derived WUE_i^* (Fig. 4) confirm the observed differences between the anisohydric *Q. calliprinos* and the isohydric *P. halepensis* in g_s and WUE_i. The 1.5‰ higher δ^{13}C of the pine is expected from its tight control of g_s, compared to the oak species. Ferrio et al. (2003) found 1.5‰ higher δ^{13}C in *P. halepensis* relative to *Q. ilex*, also a Mediterranean oak species. The 1.5‰ higher δ^{13}C range of *P. halepensis* is also expected, considering its large seasonal changes in WUE_i, between 20 and 280 μmol CO_2 mol^{-1} H_2O vs. 30–125 μmol CO_2 mol^{-1} H_2O in *Q. calliprinos* (Fig. 3c). δ^{13}C-derived WUE_i^* can be partly compared to WUE_i calculated from gas-exchange, noting that tree-rings provide an integrative measure, while leaf gas-exchange observations provide an instantaneous measure. Such comparison is confined by the timing of carbon deposition into tree-rings, which is between October and April in our case. Averaging the WUE_i values corresponding to observations taken during this timeframe (November to April; Fig. 3c) yields 108.5 ± 58.6 and 62.8 ± 15.1 μmol CO_2 mol^{-1} H_2O in *P. halepensis* and *Q. calliprinos*, respectively. The δ^{13}C-derived WUE_i^* means are 74.6 ± 1.2 and 63.6 ± 0.8 μmol CO_2 mol^{-1} H_2O in *P. halepensis* and *Q. calliprinos*, respectively. The divergence of the pine values may be related to post photosynthetic fractionation (Badeck et al., 2005) and uncertainties in estimating mesophyll conductance. We speculate that the divergent in the pine values is most likely associated with matching the short-term, transient, leaf-scale gas exchange measurements (showing the potential for high values) with the integrated tree-ring based values (where high values are averaged out; note also the relatively large SE in the pine leaf-scale data, Fig. 3c). The inter-species differences in leaf gas exchange were smaller at the height of the wet season (Fig. 3) and did not carry over to the isotopic signal. However, under the very wet conditions that followed the two large rain events of the year 2000 ($P > 100$ mm each) WUE_i^* values of *P. halepensis* decreased to 62.8 μmol CO_2 mol^{-1} H_2O, similar to the *Q. calliprinos* values. This observation confirms that, conditions permitting, g_s of the pine can be as high as that of the oak, as shown in Figs. 2 and 3.

Table 2
Relationships between stomatal conductance (g_s), intrinsic water-use efficiency (WUE$_i$), and wood Δ^{13}C of *Pinus* spp. (*P.*) vs. *Quercus* (*Q.*) spp. and of isohydric (*i*) vs. anisohydric (an) tree species in this study and in four previous studies.

Species studied	g_s	WUE$_i$	Δ^{13}C	Reference
P. pinaster^{i} vs. *Q. robur*^{i}	i < an	i < an	i > an	Guehl et al. (1995)
P. ponderosa^{i} vs. *Q. gambelii*^{an}	i < an	i > an	–	Kolb and Stone (2000)
P. halepensis^{i} vs. *Q. ilex*^{an}	–	–	i < an	Ferrio et al. (2003)
P. edulis^{i} vs. *Juniperus osteosperma*^{an}	i < an	i > an	i < an	West et al. (2007b)
P. halepensis^{i} vs. *Q. caliprinos*^{an}	i < an	i > an	i < an	This study

4.3. Water-use of *P. halepensis* and *Q. calliprinos* and the forest water balance

Large differences in T_t could have significant implications for stand and larger scales hydrological budgets, with further implications for local water yield, forest sustainability, and land use management. To demonstrate this we attempted a first approximation of stand level hydrological balance using Eqs. (4) and (5) and as summarized in Fig. 5. For any given *sd*, water-use of the oak maquis is moderately higher than that of the pine forest. For a typical 300 trees ha^{-1} stand, oak water use is about 1.3 that of the pine, compared with 1.5 and ~2 for water use ratios on tree and leaf base. Large physiological differences are therefore moderated at the ecosystem level, due to phenological differences (e.g. lower time-integrated leaf cover in oak vs. pine) and the contribution of other hydrological components to the evapotranspiration (ET) flux. The pine foliage cover also fluctuated between maximum in November and minimum in March (Raz-Yaseef et al., 2010a,b) due to current year needle growth phenology (Klein et al., 2005; Maseyk et al., 2008). Yet *P. halepensis* foliage contains 3–5 needle age classes and hence such changes are marginal.

The analysis in Fig. 4, although preliminary, points out several important features: First, at each precipitation level, the stand-scale ET curves define the maximum *sd* for each of the two forest types. For example, with $P = 300$ mm (semi-arid climate), the maximum *sd* was 203 and 128 trees ha^{-1} for pine and oak, respectively. Note, however, that sustainability must be below the *sd* limit and must allow for drought years (Simonin et al., 2007; Ungar et al., in press). Second, the analysis indicates the minimum precipitation amount required to support each forest type at a given *sd*, information that is needed for forest management in general and for afforestation efforts in particular (Schiller and Cohen, 1998; Simonin et al., 2007; Raz-Yaseef et al., 2010a,b; Ungar et al., in press). Here too, allowance for drought years is required to ensure sustainability. Third, at a relatively low *sd* of 300 trees ha^{-1}, a *P. halepensis* forest and a *Q. calliprinos* maquis require a hydrological budget of at least 357 and 459 mm, respectively. This means, in turn, that under $P = 500$ mm conditions, such pine and oak stands would allow water yields of 143 and 41 mm, respectively, that can go to surface runoff (and possibly storage), or recharge of deeper layers (e.g. storage in the local aquifer). Likewise, reducing *sd* would increase WY accordingly.

Our preliminary estimates are consistent with sap-flow based annual tree water-use amounts reported for the two species. At 230 trees ha^{-1}, an oak stand tree water-use was 293 mm (Schiller et al., 2010) and 358 mm at 470 trees ha^{-1} in a young stand (Schiller et al., 2003). These water use values mean that the oak T_t was 12.7 mm tree^{-1} year^{-1} in the sparse maquis and 7.6 mm tree^{-1} year^{-1} in the denser, young maquis. Tree water use in a semi-arid, 400 trees ha^{-1} pine forest, was calculated at 210 mm (Schiller and Cohen, 1998), which was later reduced to 164 mm, following thinning to 300 trees ha^{-1} (Klein et al., 2012b). This means a *P. halepensis* T_t of 5.2–5.5 mm tree^{-1} year^{-1}, lower than our estimate of 6.6 mm, based on *P. halepensis* transpiration in Mediterranean sites. The observed differential distribution of the two tree species is also consistent with our results, showing a substantially higher *P* requirement for an oak maquis relative to a pine forest (Fig. 4). *P. halepensis* forests can grow at $P < 400$ mm (Maestre and Cortina, 2004; Ferrio et al., 2003) and even in semi-arid sites on the dry timberline (Rotenberg and Yakir, 2010; Klein et al., 2012a), whereas *Q. calliprinos* maquis covers large areas in the more humid Galilee region of Northern Israel ($P = 550$–1000 mm; Schiller et al., 2010). The higher water demand of the oak was reflected in a dramatic decrease of its leaf area index, from 4.0 to 1.5, following subsequent drought years in the Galilee region (Sever and Neeman, 2008).

The difference between the water yield estimates for pine and oak (Fig. 5) is substantial, especially considering the relatively small precipitation budget in our region ($P = 300$–700 mm in most sites). The effect of tree cover on WY was usually quantified in deforestation experiments (Sahin and Hall, 1995; Stednick, 1996; Zhang et al., 2001; Brown et al., 2005). In fifteen forest sites in USA where $P \leqslant 700$ mm and the area cut was 15–100%, increases in WY were 47 ± 13 mm (data adapted from Stednick (1996)), still lower than the potential WY change of ~102 mm predicted by an oak-pine conversion in our analysis. Sahin and Hall (1995), who had analyzed 145 catchment experiments around the globe, quantified 17–19 mm and 20–25 mm change in WY per 10% change in forest cover for deciduous and coniferous forest, respectively. Interestingly and in contrast to our findings, the impact on WY was larger in the coniferous forest compared to the deciduous forest. Yet WY changes in the current study are mostly attributed to species-specific stomatal behavior, rather than systematic division in the plant kingdom.

4.4. Implications for forestry under global water crisis

Recent research has focused attention on the impact of afforestation on water yield (Jackson et al., 2005; Farely et al., 2005) and the hydrological cycle (Ellison et al., 2012).

Water-use at the tree level must therefore be considered among other factors such as forest sustainability, carbon sequestration, and others. Considering the central role of *P. halepensis* and *Q. calliprinos* in many Mediterranean forest ecosystems on the one hand, and the increasing limitations on water inputs on the other hand, the issue of tree species composition can be critical for management and adaptation. In the study area in particular (Eastern Mediterranean region with transition into semi-arid biomes), *Q. calliprinos* and to a greater extent *P. halepensis* have been extensively recruited for afforestation during the last ~80 years, demonstrating the highest regeneration among all native tree species (Osem et al., 2009; Reisman et al., 2010). Major eco-physiological differences between the species include: (1) relatively high drought resistance in pines, associated with a range of drought induced ecophysiological adjustments (Schiller and Cohen, 1998; Maseyk et al., 2008; Klein et al., 2011) vs. drought-induced damage and mortality in oaks (Sever and Ne'eman 2008, Schiller et al., 2010); (2) high fire vulnerability of pines (Fernandes et al., 2008) vs. some fire resistance and fast recovery in oaks (Schiller et al., 2010); and (3) changes in biodiversity following afforestation with pines (Maestre and Cortina, 2004), making *P. halepensis* a less desirable option. Here we extend this ecophysiology balance by considering also the significantly lower water-use of this species. If forests are desired and minimizing water use is a main objective in order to allow significant water yields for other uses, "water savers" such as the isohydric *P. halepensis* are advantageous for afforestation.

Acknowledgments

The authors thank Prof. Gabriel Schiller and Eylon Kalev of ARO Volcani Center for providing access to the Beit Dagan experimental plot and for assistance with technical equipment, respectively. Scientific review by Dr. Fyodor Tatarinov of the Weizmann Institute of Science, Prof. Amram Eshel of Tel Aviv University, and two anonymous reviewers is greatly acknowledged. This work was made possible by financial support from the Israel Science Foundation (ISF), the Minerva Foundation, the JNF-KKL, France–Israel High Council for Research Scientific and Technological Cooperation, and the C. Wills and R. Lewis program in Environmental Science. Personal grants provided by the Karshon Foundation and the Rieger Foundation are acknowledged by TK.

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