

Variability in growth, carbon isotope composition, leaf gas exchange and hydraulic traits in the eastern Mediterranean cedars *Cedrus libani* and *C. brevifolia*

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Summary Four Turkish provenances and five Lebanese provenances of *Cedrus libani* A. Rich. and one Cypriot provenance of *C. brevifolia* Henry were compared during the third year of growth in a controlled-climate greenhouse after exposure to a well-watered or moderate-drought treatment. Effects of treatment on CO₂ assimilation (*A*), stomatal conductance (*g_s*), ¹³C isotope composition (δ¹³C), growth and biomass were assessed. Hydraulic conductivity and shoot vulnerability to cavitation were measured in well-watered plants only. The Lebanese provenances of *C. libani* had the highest growth rates, but were the most sensitive to drought. The Turkish provenances of *C. libani* showed moderate growth rates and moderate drought sensitivity. *Cedrus brevifolia* had the lowest growth rate and was least sensitive to drought. For each provenance, mean biomass values were positively correlated with δ¹³C and intrinsic water-use efficiency (*A/g_s*), and negatively correlated with *g_s*. Drought reduced growth and favored carbon storage in roots, increasing the ratio of root biomass to aboveground biomass. The drought treatment increased δ¹³C and *A/g_s*. Specific hydraulic conductivity (*K_s*) was similar for the provenance groups, whereas leaf-specific conductivity (*K_l*) was lower in the Lebanese provenances than in the other provenances. Within each provenance group, provenances with the highest *K_l* were most susceptible to xylem cavitation, but were also the most productive. Growth and drought adaptation were linked with precipitation in each provenance's native range.

Keywords: biomass, ecotype variation, hydraulic conductivity, net CO₂ assimilation, stomatal conductance, water-use efficiency.

Introduction

In Lebanon, *Cedrus libani* A. Rich. covers only 2000 ha between elevations of 1500 and 1700 m. In Syria, it is widely scattered over 20,000 ha (Seigue 1985). Turkey has the largest area of *C. libani* with 99,000 ha, of which 31,000 ha are degraded stands. Other than a few small stands in the Pontus

Mountains and in Anatolia, cedar in Turkey extends from the Amanos Mountains along the eastern edge of the Mediterranean basin and west to the southern foothills of Anatolia, in the Taurus Mountain range. The purest stands are in the western Taurus Mountains between elevations of 1500 and 2400 m, but some are at lower elevations, between 500 and 650 m (Boydak 1996, 2003, Alptekin et al. 1997). *Cedrus brevifolia* Henry is restricted to slightly more than 700 ha in the Paphos forest in the south-western part of the island of Cyprus, at elevations between 800 and 1100 m (Quézel 1979). The habitats of *C. libani* and *C. brevifolia* include a wide range of bioclimatic conditions: annual precipitation varies from 450 to 1300 mm with up to 6 months of summer drought, and mean annual temperature ranges from 7.5 to 15 °C with extremes of –25 and +40 °C (Aussenac 1984). Based on the range of bioclimatic conditions experienced by cedars, large phenotypic diversity and adaptation might be expected among populations. Given the distinction between the Lebanese and Turkish *C. libani* provenances, expressed in adaptive traits such as survival and growth, and the geographic proximity of *C. brevifolia* and *C. libani*, we searched for possible functional differences among phylogenetic groups. Because of their Mediterranean origin, we focused on ecophysiological characteristics related to drought adaptation.

Trees adapted to drought are able to grow when water availability is limited, because they have a high photosynthetic water-use efficiency (WUE). Water-use efficiency is often measured directly as the ratio between net assimilation and stomatal conductance (intrinsic WUE: $WUE_i = A/g_s$), but its time-integrated value can be assessed indirectly by determining foliage stable carbon isotopic composition (δ¹³C) (Farquhar et al. 1982, Farquhar and Richards 1984). Populations of the same species may have markedly different δ¹³C values (Grossnickle et al. 2005). In some cases, differences among genotypes within a species in WUE or δ¹³C have been linked to differences in vigor, growth or yield (Flanagan and Johnsen 1995, Zhang et al. 1997, Rouspard et al. 1998, Leidi et al. 1999, Pennington et al. 1999). Several studies of the adapta-

tion of a species to an ecological gradient have shown that WUE varies across linear precipitational (Pennington et al. 1999, Li et al. 2000), latitudinal or elevational (Zhang and Marshall 1995) gradients, or across more complex gradients (Osório and Pereira 1994, Moore et al. 1999). Carbon isotope composition therefore appears to be an excellent tool to study drought adaptation at the species, provenance and individual-tree levels. We attempted to use WUE to determine variation in drought adaptation among cedars.

Xylem hydraulic conductivity and vulnerability to cavitation are important determinants of drought adaptation. In trees with an optimal water supply, vigor and growth rates are usually positively related to hydraulic conductivity (Vander Willigen and Pammenter 1998). Studies at the crown level have shown that photosynthesis depends on the water supply to the branches (Brodribb and Feild 2000, Hubbard et al. 1999, 2001) and that *A* and *g*_s increase with increasing hydraulic conductivity of stem and branches (Rust and Roloff 2002). During drought, sap flow is maintained if the xylem can withstand high negative pressures (Tyree and Sperry 1989, Tyree and Ewers 1991, Martínez-Vilalta et al. 2002, 2004, Maherali et al. 2004). Low vulnerability to cavitation has frequently been observed in species growing in regions with long dry seasons (Brodribb and Hill 1999, Pockman and Sperry 2000), as occur around the Mediterranean basin. Mediterranean cedars have a relatively low vulnerability to cavitation, and stomatal closure occurs before water potentials are sufficiently low to cause xylem embolism (Ladjal et al. 2005). Similar large margins of safety against embolism formation have been observed in species that experience severe drought in their native habitat (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002).

We focused on intraspecific variation in *Cedrus libani* by comparing provenances from Lebanon and Turkey and a *C. brevifolia* provenance from Cyprus. We measured growth, leaf gas exchange, WUE and $\delta^{13}\text{C}$ in young cedar trees grown in a greenhouse under well-watered conditions or with a restricted water supply to simulate moderate drought. Hydraulic traits of the well-watered, but not the drought-treated, plants were also measured. We assessed variation among provenances in response to the drought treatment and determined if

traits like growth, gas exchange and xylem safety and efficiency covaried. We examined whether phylogenetic patterns of variation related to geographic origin. We checked for links between ecophysiological variation among provenances and the ecological conditions characteristic of their native range.

Materials and methods

Plant material and watering treatments

We studied four Turkish and five Lebanese provenances of *C. libani* and one Cypriot provenance of *C. brevifolia* (Table 1). Two of the Turkish provenances, Avlan Elmali (T01) and Dirmil (T02), are from the inland areas of Fethiye and Finike, near Elmali in the westernmost part of the Western Taurus Mountains (Figure 1). The third provenance, Armut Alani (T03), is found slightly farther north in the Isparta region. The fourth provenance, Arslanköy (T04), is from the central Taurus to the northwest of Mersin. The five Lebanese provenances are found from north to south along the coastal mountain range: Khammouah (L09) and Hadeth el Jebbe (L10) in the northernmost part; Aïn Zhalta (L08), Barouk (L07) and Maasser-Chouff (L11) in the southern part of the mountain range southeast of Beirut. The *C. brevifolia* provenance Stavros (C12) is from the mountain forests in southwestern Cyprus.

Seeds of all provenances were planted in a nursery (Les Milles, Aix en Provence, France; 43°30' N, 5°24' E, 130 m a.s.l.) in spring of 1996 in 400-cm³ containers filled with equal parts of peat and chipped, composted pine bark. In spring 1997, seedlings were transplanted to 3-l pots containing a 1:1:1 (v/v) mix of organic soil:peat:pine bark and raised under standard nursery conditions. In spring 1998, the containers were placed under controlled conditions in a greenhouse in southern France near Avignon (43°55' N, 4°53' E, 25 m a.s.l.). Half the plants were watered to field capacity 2–3 times a week throughout the growing season (well-watered treatment, predawn water potentials between –0.5 and –0.7 MPa). The remaining plants received half the water supplied to the well-watered plants from April 1 to June 24, 1998 (first drought

Table 1. Geographic locations and ecological traits of the 10 provenances of *Cedrus libani* and *C. brevifolia*.

Provenance	Country	Latitude (N)	Longitude (E)	Elevation (m)	Exposure	Rainfall (mm year ⁻¹)
<i>Cedrus libani</i>						
T01, Avlan Elmali	Turkey	36°31'	29°44'	1600	N-E	540
T02, Dirmil	Turkey	37°08'	29°32'	1650	N	630
T03, Armut Alani	Turkey	37°50'	31°18'	1550	N	450
T04, Arslanköy	Turkey	37°00'	34°14'	1800	S-W	800
L07, Barouk	Lebanon	33°36'	35°41'	1500–1700	W/S-W	1300
L08, Aïn Zhalta	Lebanon	33°39'	35°43'	1300	W	1300
L09, J-Kammouah	Lebanon	34°30'	36°13'	1250–1800	W	1300–1500
L10, Hadeth el Jebbe	Lebanon	34°14'	35°55'	1560	N	1400–1500
L11, Maasser-Chouff	Lebanon	33°34'	35°41'	1600	S-W	1300
<i>Cedrus brevifolia</i>						
C12, Stavros	Cyprus	34°50'	33°06'	800–1100		815

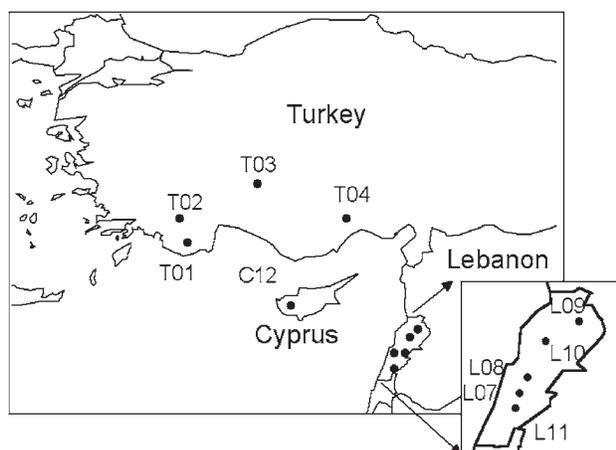


Figure 1. Geographic distribution of cedar (*Cedrus*) provenances in Turkey (T01 = Avlan Elmali; T02 = Dirmil; T03 = Armut Alani; and T04 = Arslanköy), Lebanon (L07 = Barouk; L08 = Aïn Zhalta; L09 = Kammouah; L10 = Hadeth el Jebbe; and L11 = Masser-Chouff) and Cyprus (C12 = Stavros).

treatment), and were then well watered until August 20 before being subjected to a second drought treatment until September 22 (predawn water potentials between -0.7 and -1.2 MPa). Once a week, all seedlings received a balanced liquid fertilizer (N,P,K: 7.5,7.5,7.5 + 0.4 MgO + oligoelements) diluted to 5% in their water supply.

Growth and biomass measurements

Height growth and diameter increment were measured at the end of each year, providing data for about 150 one-, two- and three-year-old plants of each provenance. Biomass of a sample of plants was measured each year. Relative height growth was calculated as the difference in height between 1997 and 1998 relative to the height in 1997. Needles, stems, fine roots (diameter less than 1 mm) and large roots were separated and dried at 65 °C to constant mass. Samples consisted of 15 plants per provenance at the end of the first year (1996), nine plants per provenance at the end of the second year (1997), and eight plants per provenance and per watering regime at the end of the third year (1998).

Leaf gas exchange

Leaf gas exchange was measured during the third year at the end of the last drought cycle in a subset of eight plants per provenance per watering regime. The plants were transferred to a climate-controlled chamber at the end of the second drought treatment (September 22, 1998). Micro-climatic conditions in the chamber were: day/night air temperature = $25/19$ °C; relative humidity = 80%; CO_2 concentration = 360/400 ppm; and photosynthetic photon flux = $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a 12-h photoperiod. The plants were watered to the point of substrate saturation for 48 h before measurements to ensure that leaf water potential was identical in both treatments and that only the effect of drought was taken into account.

Values of g_s and A were measured with a portable closed-

circuit photosynthesis meter (LI-6200, Li-Cor). We calculated A ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and g_s ($\text{mol m}^{-2} \text{s}^{-1}$) on a projected needle area basis. Projected needle area was measured with a DIAS2 system (Delta-T Devices). Intercellular CO_2 concentration (C_i) was calculated in relation to the CO_2 concentration of air (C_a) as:

$$C_i = C_a - 1.6A/g_s \quad (1)$$

Intrinsic WUE was calculated as:

$$\text{WUE}_i = A/g_s = \frac{C_a}{1.6} \left(1 - \frac{C_i}{C_a} \right) \quad (2)$$

Carbon isotope composition

To determine needle $\delta^{13}\text{C}$, needles were dried to constant mass at 65 °C then finely ground (0.2-mm mesh). One mg of needle powder was burned in helium with 3% oxygen at 1050 °C and the combustion gases analyzed by mass spectrometry (Finnigan Delta S mass spectrometer, Finnigan-Mat). For the 3-year-old seedlings, we analyzed all needles used for the gas exchange measurements as representative of the current-year needles.

Hydraulic conductivity and xylem vulnerability to embolism

Stem hydraulic conductivity (K_h ; $\text{mmol m MPa}^{-1} \text{s}^{-1}$) was measured at the end of the growing season on a sample of eight plants per provenance from the well-watered treatment, as described by Sperry and Tyree (1988). Because leaf water potential remained above the cavitation threshold, we assumed that there was no xylem embolism (Ladjal et al. 2005). An aqueous solution of HCl (pH 2) was degassed and filtered at $0.1 \mu\text{m}$, then injected under pressure (6.5 kPa) into the stem segments. Four hydraulic traits were determined for each stem segment: (1) specific hydraulic conductivity ($\text{mol m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$); $K_s = K_h/S_a$, where S_a is the stem segment cross-sectional area (m^2); (2) leaf-specific conductivity ($\text{mmol m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$); $K_l = K_h/L_a$, where L_a is the leaf surface area (m^2) at the distal end of the segment; and (4) the Huber value ($\text{m}^2 \text{m}^{-2}$) $\text{HV} = S_a/L_a$. Vulnerability to cavitation was investigated in eight well-watered plants randomly chosen from each provenance. Under water, each plant was severed at the collar and a stem sample was excised. All steps described hereafter were carried out under water. The bark on a 10-cm-long stem segment was split and removed. Hydraulic conductivity was measured for each segment as described by Ladjal et al. (2005) to obtain maximum conductivity ($K_{h,\text{max}}$). The segments were then subjected to 5-min periods of increasingly high pressure separated by 30-min rest intervals; hydraulic conductivity ($K_{h,i}$) was measured at the end of each rest phase. Pressures applied ranged from 3 to 9 MPa. The percentage of conductivity loss (PLC_i) was calculated for each pressure applied (i) as:

$$\text{PLC}_i = 100 \left(1 - \frac{K_{h,i}}{K_{h,\text{max}}} \right) \quad (3)$$

To calculate the air pressure inducing 50% loss of conductivity (Ψ_{PLC50}), vulnerability curves were fitted for paired datasets (i , PLC_i) with a model described by Pammenter and Vander Willigen (1998) and nonlinear regression.

Statistical analysis

Significances of watering treatment, phylogenetic group corresponding to the country of origin, watering treatment \times phylogenetic group interaction and provenance within phylogenetic group (nested effect) were determined by analysis of variance. Two linear models were used: (1) $Y_{ijk} = \mu + \text{Phylogenetic group}_i + \text{Provenance}_j(\text{Phylogenetic group}_i) + e_{ijk}$; and (2) $Y_{ijkl} = \mu + \text{Treatment}_i + \text{Phylogenetic group}_j + (\text{Treatment} \times \text{Phylogenetic group})_{ij} + \text{Provenance}_k(\text{Phylogenetic group}_j) + e_{ijkl}$, where Y is the dependent variable, μ is the mean of Y over the entire population and e is the residual error. Model 1 was applied when data from each watering treatment were analyzed separately, and Model 2 was applied when watering treatment was included in the analysis.

The individual tree was the experimental unit and the experimental design was completely random. There were 8–15 trees per watering regime and provenance. Differences among means were tested with the Duncan test when the main effect was significant ($P < 0.05$). Linear regressions were performed on pairs of variables (2 by 2) based on mean values for each provenance and, if necessary, for each watering regime. We then carried out a global principal component analysis, using mean values for each provenance, of all the variables: plant height, diameter and biomass, $\delta^{13}\text{C}$ in needles of 3-year-old seedlings, gas exchange parameters (A , g_s , WUE_i and C_i/C_a) and hydraulic traits (K_s , K_i and Ψ_{PLC50}).

Results

Growth and biomass production

Table 2 shows mean values for plant size and biomass at the end of each year for all provenances combined. The drought treatment reduced height growth by 64%, diameter growth by 44%, needle biomass by 67% and total plant biomass production by 62%.

There was a large phylogenetic group effect on the biomass variables studied (Table 3). However, variation among prove-

nances was high, and the effect of provenance within a phylogenetic group was significant for most traits in both the well-watered and drought treatments. In both treatments, mean plant height and diameter were greater for the Lebanese provenances than for the Turkish provenances; the Cypriot provenance had the smallest height and diameter. Relative height growth differed between plants in the well-watered and drought treatments in 1998. In the well-watered plants, relative height growth did not differ significantly between the Lebanese and Turkish provenances; whereas in plants in the drought treatment, the relative height growth of Turkish provenances was higher than that of Lebanese provenances. There were large differences in relative height and diameter growth among provenances (Figure 2). In all cases, total plant biomass varied in the same way as stem diameter (Table 3). The relative proportions of aboveground and root biomass varied, mostly as a function of watering regime. In the well-watered plants, both the ratio between root biomass and aboveground biomass (R/S) and the ratio between fine root biomass and needle biomass (F/N) were higher for the Cypriot and Turkish provenances than for the Lebanese provenances. In drought-treated plants, the Turkish provenances had higher R/S and F/N ratios than those of the Lebanese and Cypriot provenances.

Well-watered plants were larger, grew more quickly and produced more biomass than plants in the drought treatment. For all provenances, drought-treated plants invested relatively more in the root system than in aboveground biomass. The parallel trends for R/S and F/N as functions of plant biomass are evident (Figure 3). The least productive provenances under well-watered conditions had a relatively high investment in the root system.

Carbon isotope composition and leaf gas exchange

Mean $\delta^{13}\text{C}$ was -29.12‰ for well-watered plants (-30.29 to -27.89‰ depending on provenance) and -27.13‰ for drought-treated plants (-27.83 to -26.14‰ depending on provenance), and the treatment difference was significant (Table 4). Within both watering regimes, the Cypriot provenance had the most negative $\delta^{13}\text{C}$ values, whereas the Lebanese and Turkish provenances had less negative mean $\delta^{13}\text{C}$ values; however, the difference between groups was not significant (Table 4). Water-

Table 2. Overall mean values and annual increments for metric traits, all provenances together, at the end of the first two years and for each treatment at the end of the third year. Abbreviations: W, well-watered treatment; D, drought treatment; R/S , root to aboveground biomass ratio; and Sensitivity (%), percent decrease in increment between W and D. Values followed by different letters differed significantly between treatments ($P < 0.05$, Duncan's Multiple Range Test).

Year	n	Height (cm)		Diameter (mm)		Needle biomass (g)		Total plant biomass (g)		R/S
		Mean	Increment	Mean	Increment	Mean	Increment	Mean	Increment	
1	165	18.3		4.2		2.1		5.3		0.548
2	98	27.3	9.0	8.3	4.1	6.8	4.7	25.7	20.4	0.741
3, W	88	59.1 a	31.9	14.0 a	5.7	31.8	25.0	107.4 a	81.7	0.509
3, D	88	38.8 b	11.5	11.5 b	3.2	15.0	8.3	57.2 b	31.5	0.712
Sensitivity (%)			63.9		43.5		66.9		61.5	

Table 3. Significance of effects of treatment (Tr), phylogenetic group (PhG), Tr × PhG interaction and provenance within PhG (Prov(PhG)) on height, diameter and their annual increments and on biomass variables determined by analysis of variance (ANOVA). Abbreviations: W, well-watered treatment; D, drought treatment; Biomass, total plant biomass; *R/S*, ratio of root biomass to total aboveground biomass; *F/N*, ratio of fine root biomass to needle biomass. All biomass measurements were made at the end of 1998; *n* = 80 for height and diameter, and *n* = 8 for biomass variables. Rank of PhG mean values are indicated (C = Cyprus; L = Lebanon; and T = Turkey), and PhG linked with the same line are not significantly different according to Duncan's multiple range test. Asterisks indicate significance: *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001; ****, *P* < 0.0001; and ns, not significant.

Factor	Height		Diameter		Biomass	<i>R/S</i>	<i>F/N</i>
	Mean	Increment	Mean	Increment			
<i>Well-watered treatment</i>							
PhG	C < T < L ****	C < <u>L, T</u> ****	C < T < L ****	C < <u>T, L</u> ***	C < T < L ****	L < <u>T, C</u> ****	L < <u>T, C</u> ****
Prov(PhG)	****	****	****	****	****	**	ns
Model	****	****	****	****	****	****	**
<i>Drought treatment</i>							
PhG	C < T < L ****	<u>C, L</u> < T ****	C < T < L ****	<u>L, T</u> < C **	C < T < L ****	<u>C, L</u> < T ****	<u>C, L</u> < T ****
Prov(PhG)	****	****	****	ns	****	ns	*
Model	****	****	****	**	****	***	**
<i>All plants together</i>							
Treatment	D < W ****	D < W ****	D < W ****	D < W ****	D < W ****	W < D ****	W < D ****
PhG	C < T < L ****	C < L < T ****	C < T < L ****	C < <u>L, T</u> ns	C < T < L ****	<u>L, C</u> < T ****	<u>L, C</u> < T ****
Tr × PhG	****	****	****	****	****	**	*
Prov(PhG)	****	****	****	****	****	ns	**
Model	****	****	****	****	****	****	****

ing regime had no significant effect on WUE_i . Intrinsic WUE was lowest in the Cypriot provenance, in the mid-range in the Turkish provenances, and highest in the Lebanese prove-

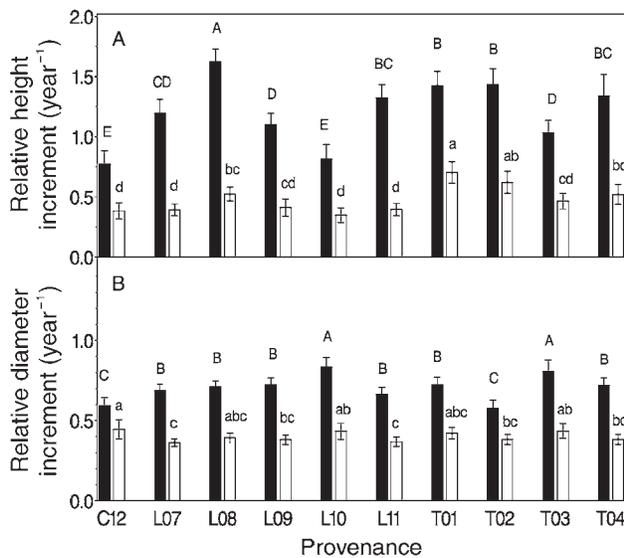


Figure 2. Mean (\pm SE) relative (A) height and (B) diameter increments (from 1997 to 1998) in the well-watered (filled bars) and drought-treated (open bars) cedar (*Cedrus*) provenances (C = Cypriot; L = Lebanese; and T = Turkish). Different letters denote significant differences between provenances for a given parameter and treatment (*n* = 80, *P* = 0.05, Duncan's multiple range test).

nances, but differences among the three origins were not always significant. The C_i/C_a ratio, which represents the link between WUE and $\delta^{13}C$, varied inversely to A/g_s ; however, when A and g_s were analyzed separately, the results revealed no clear geographic structure. The C_i/C_a ratio was higher for well-watered seedlings than for drought-treated seedlings. Watering regime had no effect on A or g_s .

Based on provenance, $\delta^{13}C$ was negatively correlated with g_s and with the C_i/C_a ratio, and positively correlated with WUE_i (Figure 4). These correlations were similar for both watering regimes and were significant. No correlation was found between A and $\delta^{13}C$.

Leaf gas exchange, WUE, $\delta^{13}C$ and biomass production

Water vapor and CO_2 gas exchange, WUE_i and $\delta^{13}C$ against total plant biomass production were analyzed by regression (Figure 4). The provenances with the highest growth in both treatments had the highest (least negative) $\delta^{13}C$ values and therefore discriminated less against ^{13}C ; these provenances had the highest A/g_s ratios. Higher WUE was associated with a decrease in g_s rather than with an increase in A , especially in drought-treated plants. Correlation coefficients among variables were higher for well-watered plants than for plants in the drought treatment, mainly because of the wider range of biomass values in well-watered plants (49.7–171.2 g plant⁻¹ depending on provenance) than in plants in the drought treatment (35.0–78.4 g plant⁻¹). For the same biomass, well-watered seedlings from the Lebanese provenances had a higher $\delta^{13}C$

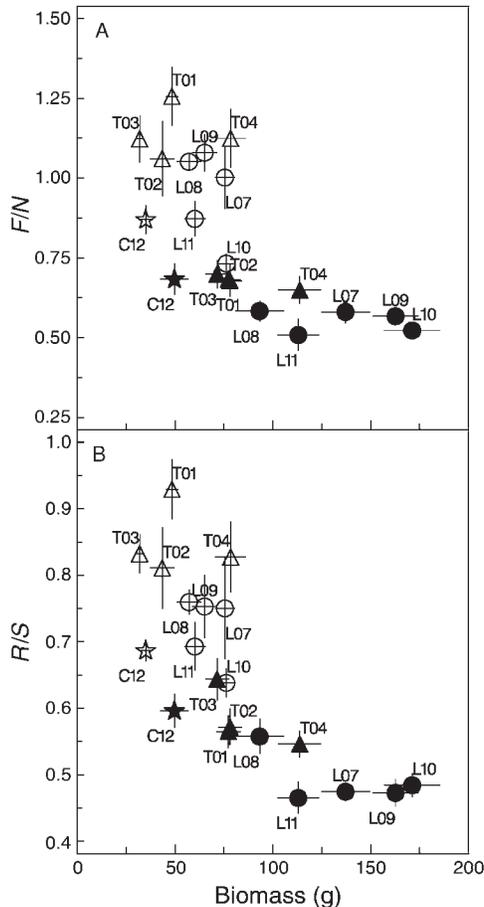


Figure 3. (A) Fine root to needle biomass ratio (F/N) and (B) root to aboveground biomass ratio (R/S) as functions of total plant biomass for the 10 cedar (*Cedrus*) provenances (\star, \blackstar = Cypriot; \circ, \bullet = Lebanese; and $\triangle, \blacktriangle$ = Turkish) from the well-watered (filled symbols) and drought (open symbols) treatments. Values are means \pm SE ($n = 8$).

than well-watered seedlings from the Turkish provenances (Figure 4).

Shoot hydraulic traits and water-use efficiency

We found wide variation in K_s among provenances (17.88–28.77 mol m⁻¹ MPa⁻¹ s⁻¹), but it did not correspond with geographic distribution (Table 5). In contrast, K_1 and HV were lower in the Lebanese provenances than in the Turkish and Cypriot provenances. Values of Ψ_{PLC50} varied from -8.52 to -6.57 MPa; however, the provenance effect was not significant. For the Turkish and Lebanese provenances, Ψ_{PLC50} varied linearly with K_1 (Figure 5). The relationship for the Cypriot provenance was similar to that for the Turkish provenances.

For well-watered plants, mean hydraulic traits of provenances were regressed against g_s and $\delta^{13}C$ (Figure 6). There were distinct linear relationships within both the Lebanese and Turkish provenance groups: relationships between g_s and K_1 were negative, whereas those between $\delta^{13}C$ and K_1 were positive. Figure 6 shows the negative relationships between g_s and Ψ_{PLC50} and between g_s and K_s for all provenances combined. Conversely, positive relationships were observed between $\delta^{13}C$

and Ψ_{PLC50} and between $\delta^{13}C$ and K_s . In all cases, there were no significant differences between the Lebanese and Turkish provenances.

Hydraulic traits depended on mean total plant biomass (Figure 7). Positive relationships were observed for K_s , K_1 and Ψ_{PLC50} with plant biomass when the Turkish and Lebanese provenances were analyzed separately, but not when all provenances were combined. Relationships for *C. brevifolia* were closer to those of the Turkish provenances than to the Lebanese provenances. The Lebanese provenances had lower K_1 than the Turkish provenances, even though they had higher total plant biomass under well-watered conditions.

General analysis of physiological data

We analyzed the principal components for all variables taken together to identify functional similarities and differences among the 10 cedar provenances. A first analysis included 38 variables: 15 to describe how the provenances acted under well-watered conditions, 11 to describe their physiological functions under moderate-drought (the hydraulic variables were not collected), and 11 to describe provenance sensitivity to drought. This analysis did not identify subgroups or pertinent distinctions among provenances (results not shown). A second analysis included only the 15 variables defined for the well-watered plants (Figure 8A). The first two axes of the principal component analysis accounted for 66 and 25%, respectively, of the total variation. Axis 1, which expressed provenance vigor (growth), was positively correlated with $\delta^{13}C$, biomass and gas exchange but was negatively correlated with g_s and C_i/C_a (C_i/C_a always varies inversely to $\delta^{13}C$). Axis 1 was also negatively correlated with the R/S ratio and with HV. Axis 2 was positively correlated with the three hydraulic variables. This axis expressed the facility with which water moves through the tree within the soil–tree–atmosphere continuum. On the resulting scatter plot (Figure 8B), the Lebanese provenances are clearly separated from the Turkish and Cypriot provenances, which are in close proximity.

Mean annual precipitation in the native range of each provenance was compared with mean values by provenance of all traits studied. We found significant (5% threshold) Pearson's correlation coefficients between precipitation and biomass (Figure 9) and most growth variables for both well-watered and drought-treated plants. Significant negative correlations were found between precipitation and K_1 and R/S ; however, no correlation was found between precipitation and gas exchange, A/g_s or $\delta^{13}C$.

Discussion

Biomass and carbon allocation

We found great disparities in total height, diameter and biomass production among provenances of *Cedrus libani*, indicating strong within-species genetic variation. In addition, the Lebanese provenances showed greater mean height growth in 1998 than the Turkish provenances. These results contradict the general observation that Turkish provenances display

Table 4. Significance of effects of treatment (Tr), phylogenetic group (PhG), Tr \times PhG interaction and provenance within PhG (Prov(PhG)) on leaf gas exchange variables and water-use efficiency ($n = 8$) determined by analysis of variance (ANOVA). Abbreviations: $\delta^{13}\text{C}$, needle carbon isotope composition; A , net CO_2 assimilation; g_s , leaf conductance; C_i/C_a , intercellular to air CO_2 concentration ratio; and $\text{WUE}_i (= A/g_s)$, intrinsic water-use efficiency. Rank of PhG mean values are indicated (C = Cyprus; L = Lebanon; and T = Turkey), and PhG linked with the same line are not significantly different according to Duncan's multiple range test. Asterisks indicate significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$; and ns, not significant.

Factor	$\delta^{13}\text{C}$	A	g_s	C_i/C_a	WUE_i
<i>Well-watered treatment</i>					
PhG	C < <u>T, L</u> **	<u>C, T, T, L</u> *	– ns	L < <u>T, C</u> ****	<u>C, T</u> < L ***
Prov(PhG)	**	ns	ns	ns	ns
Model	***	ns	ns	**	**
<i>Drought treatment</i>					
PhG	C < <u>L, T</u> ns	– ns	<u>L, T, T, C</u> **	L < T < C ****	C < <u>T, L</u> ***
Prov(PhG)	**	**	**	*	ns
Model	**	*	***	****	**
<i>All plants together</i>					
Treatment	W < D ****	– ns	– ns	D < W *	W < D **
PhG	C < <u>T, L</u> ***	<u>C, T, T, L</u> ns	<u>L, T, T, C</u> *	L < T < C ****	C < T < L ****
Tr \times PhG	ns	ns	ns	ns	ns
Prov(PhG)	****	ns	ns	**	**
Model	****	ns	ns	****	****

greater height growth than Lebanese provenances in plantations exposed to frequent summer droughts in France (Barieteau et al. 2000) and Greece (Panetsos and Avranopoulos 2000). Our results demonstrate that, although relative height increments in 1998 were similar for the Lebanese and Turkish provenances under well-watered conditions, the Turkish provenances had greater relative height growth when subjected to drought. We can therefore assume that, when growing with an optimal water supply, Lebanese provenances have a high growth potential but are more sensitive to drought than Turkish provenances. However, under field conditions, frequent summer droughts may result in more rapid height growth in the Turkish provenances than in the Lebanese provenances.

The drought treatment decreased biomass production in all the cedars. *Cedrus brevifolia*, the least productive species, was also found to be the least drought sensitive: the drought treatment reduced biomass production by only 29.6%. The Turkish provenances of *C. libani* showed intermediate biomass production rates and a 40.6% sensitivity to drought. The Lebanese provenances were the most productive, but also the most drought sensitive (50.7%). Thus, the most drought-tolerant genotypes have limited growth potential under well-watered conditions. A similar pattern was observed by Guarnaschelli et al. (2003) for provenances of *Eucalyptus globulus* Labill. A balance between growth and drought tolerance has also been observed among *Populus* clones, with the most productive genotypes displaying a large reduction in biomass production in response to moderate drought (Monclus et al. 2006).

The R/S ratio also differed between the Turkish and Lebanese provenances, and was higher for the Turkish provenances

under both well-watered and drought conditions. Drought reduced growth of the whole plant but reduced shoot growth more than root growth, thus increasing the R/S ratio, as has been shown previously (e.g., Arnott et al. (1993) for *Chamaecyparis nootkatensis* (D. Don) Spach and Otieno et al. (2001) for *Acacia tortilis* (Forsk.) Hayne and *A. xanthophloea* Benth.). However, under well-watered conditions, the R/S ratio was inversely proportional to provenance vigor. This effect reflects a pattern often found in forest tree species where the initial growth investment in roots is high, but aboveground biomass then accumulates more rapidly, the rate being dependent on water supply. Similar results have been found for such different species as pines (Cregg 1994, Jose et al. 2003), eucalypts (Costa e Silva et al. 2004) and poplars (Ibrahim et al. 1997). Furthermore, within these species, the most drought tolerant genotypes had the highest R/S ratios.

Carbon isotope composition and gas exchange

We found a positive linear relationship between $\text{WUE}_i (A/g_s)$ and $\delta^{13}\text{C}$ in current-year needles of well-watered plants. Our results for mean values per provenance are therefore consistent with the theoretical relationship between A/g_s and $\delta^{13}\text{C}$, which has been verified in many studies (e.g., Guehl et al. (1995) for *Pinus pinaster* Ait., Osório et al. (1998) for *Eucalyptus globulus* and Cregg et al. (2000) for *Pinus ponderosa* Dougl. ex P. Laws.).

Leaf conductance and hydraulic traits

The Turkish and Lebanese provenances differed in K_1 because,

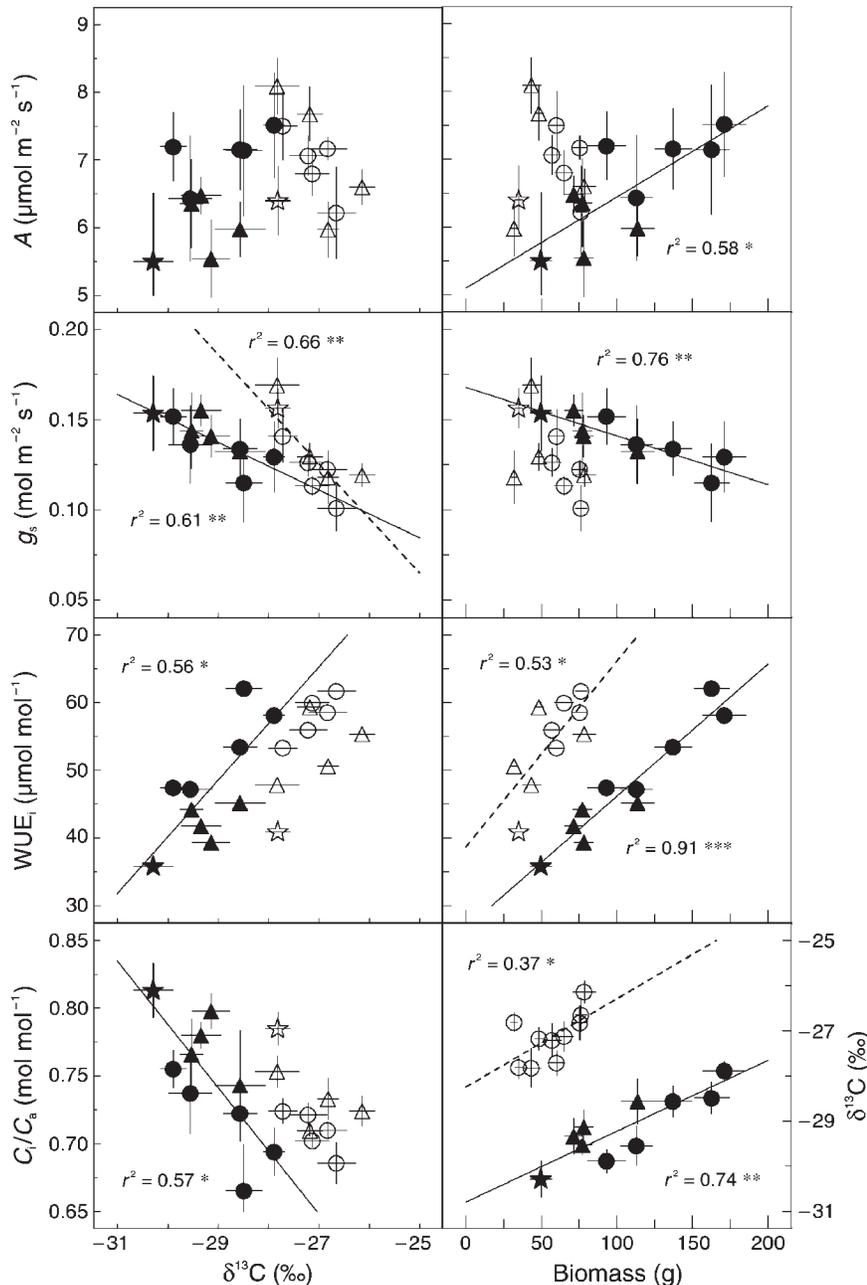


Figure 4. Needle net CO_2 assimilation rate (A), leaf conductance (g_s), intrinsic water-use efficiency ($\text{WUE}_i = A/g_s$) and intercellular to air CO_2 concentration ratio (C_i/C_a) as functions of (left) carbon isotope composition ($\delta^{13}\text{C}$) and (right) total plant biomass of the Cypriot (\star, \star), Lebanese (\bullet, \circ) and Turkish ($\blacktriangle, \triangle$) provenances of cedar (*Cedrus*). Values are means \pm SE ($n = 8$). Linear regressions are shown for the well-watered (closed symbols) and moderate-drought (open symbols) treatments with significances indicated by asterisks: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

although similar in K_s , they differed in HV. For identical-sized stem cross sections, branches from the Lebanese provenances had a higher needle surface area and thus a lower K_1 than the Turkish provenances. This likely results from different morphological and architectural characteristics inherited from the original ancestors of the Turkish and Lebanese *C. libani* provenances. Similar variations have been shown by Sabatier et al. (2003), and even though they did not assess leaf number or morphology, their results support our hypothesis. Increased K_1 values have been noted in species adapted to a dry habitat compared with species of the same genus from a mesic habitat (Preston and Ackerly 2003). We also found variation in sensitivity to cavitation among provenances of *C. libani*, but no geographical pattern was apparent, even though the range of

variation was greater for the Lebanese provenances than for the Turkish provenances. Values of Ψ_{PLC50} ranged from -8.5 to -6.6 MPa, confirming that *C. libani* and *C. brevifolia* ought to be classified as drought-tolerant species (cf. Ladjal et al. 2005).

The relationship between Ψ_{PLC50} and K_1 showed two distinct regression lines; furthermore, within phylogenetic groups of origin, high conductivity was associated with high vulnerability. This relationship suggests a trade-off between maximum plant hydraulic capacity and plant resistance to drought stress and has been observed for several species groups (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002, 2004). Based on provenance means, increases in K_s and K_1 , and the accompanying increase in xylem vessel vulnerability, were linked to de-

Table 5. Significance of effects of phylogenetic group (PhG) and provenance within PhG (Prov(PhG)) on hydraulic variables in well-watered plants ($n = 8$) determined by analysis of variance (ANOVA). Abbreviations: K_s , specific hydraulic conductivity; K_l , leaf-specific conductivity; HV, Huber value; and Ψ_{PLC50} , water potential causing 50% conductivity loss. Rank of PhG mean values are indicated (C = Cyprus; L = Lebanon; and T = Turkey), and PhG values linked with the same line are not significantly different according to Duncan's multiple range test. Asterisks indicate significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; and ns, not significant.

Factor	K_s	K_l	HV	Ψ_{PLC50}
PhG	–	L < T, C	L < T, C	–
Prov(PhG)	**	ns	ns	ns
Model	**	**	*	ns

creased maximum g_s and thus, as a corollary, to increased WUE. In contrast, several studies have shown that decreased K_l is linked to decreased g_s (Sperry et al. 1993, Sperry and Pockman 1993, Hubbard et al. 2001). Rapid transpiration during drought increases water tension in the xylem and may imply a sensitive stomatal response to regulate leaf water potential and avoid xylem cavitation (Sperry et al. 1998, Oren et al. 1999, Sangsing et al. 2004, Addington et al. 2006). The observed decrease in g_s suggests that the provenances have compensated for their greater vulnerability by reducing g_s and improving the efficiency of the conductive system to limit severe tension in the xylem (Maherali et al. 1997, Maherali and DeLucia 2000). Another regulatory adaptation may be to decrease g_s . For example, root absorption capacity may be restricted by leaf surface area, thus decreasing g_s (Crombie 1997), which is what we observed; i.e., provenances with the lowest g_s also had the lowest R/S ratios, suggesting that the

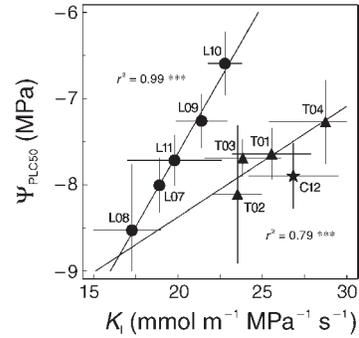


Figure 5. Water potential inducing 50% conductivity loss (Ψ_{PLC50}) versus leaf specific conductivity (K_l) in each cedar (*Cedrus*) provenance. Values are means \pm SE ($n = 8$). Linear regressions are shown for the Lebanese (●) and Turkish (▲) *Cedrus Libani* provenances. Both regressions were highly significant (***, $P < 0.001$). The Cypriot *Cedrus brevifolia* (★) data were excluded from the regressions.

range of g_s closely depends on the hydraulic conductance of the soil-to-leaf continuum (Sperry and Pockman 1993, Nardini and Salleo 2000, Meinzer 2002, Maherali et al. 2006).

Growth and physiological traits

Differences among provenances in growth and biomass production can be explained by differences in the same physiological parameters. For each provenance, biomass production was strongly positively correlated with $\delta^{13}C$ and A/g_s . Under both well-watered and drought conditions, high biomass productivity may therefore be associated with high WUE. Such a relationship has often been found in comparative studies of tree populations growing under different natural conditions, e.g., along an ecological gradient, as reported by Roupsard et al. (1998). In this case, not only do environmental conditions have a direct influence, so do the plants' adaptation to this en-

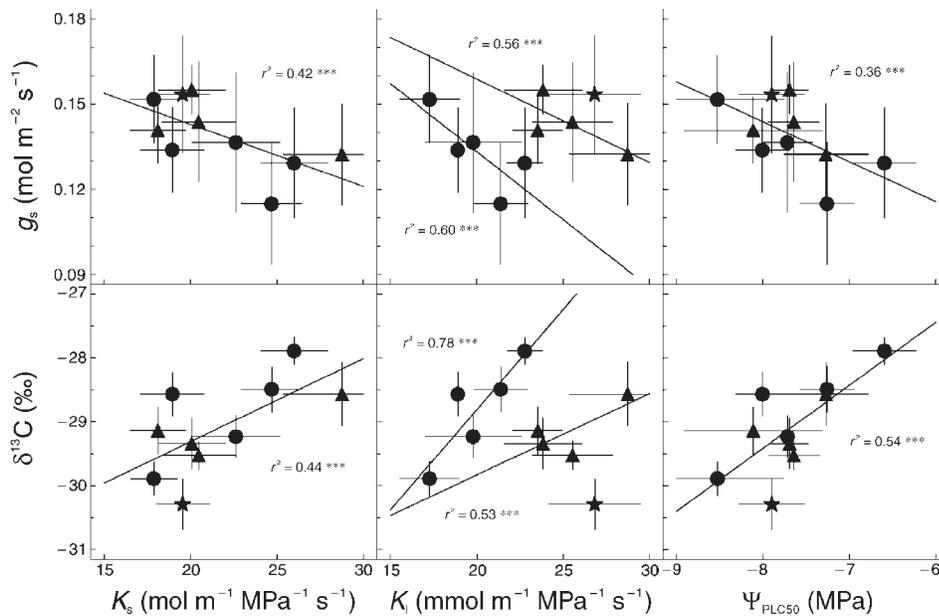


Figure 6. (Top) Leaf stomatal conductance (g_s) and (bottom) leaf carbon isotope composition ($\delta^{13}C$) expressed as functions of (left) hydraulic specific conductivity (K_s), (middle) leaf specific conductivity (K_l) and (right) water potential inducing 50% conductivity loss (Ψ_{PLC50}) for the Cypriot (★), Lebanese (●) and Turkish (▲) provenances of cedar (*Cedrus*) in the well-watered treatment. Values are means \pm SE ($n = 8$). All linear regressions were highly significant (***, $P < 0.001$).

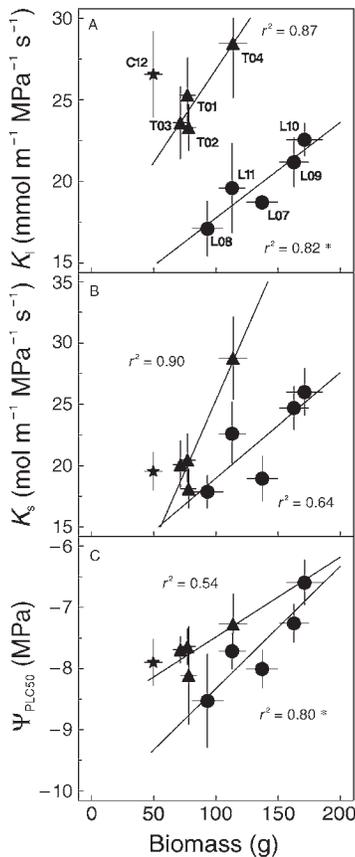


Figure 7. Relationships between total plant biomass and (A) leaf specific conductivity (K_1), (B) hydraulic specific conductivity (K_s), and (C) water potential inducing 50% conductivity loss (Ψ_{PLC50}) for the well-watered Cypriot (\star), Lebanese (\bullet) and Turkish (\blacktriangle) provenances of cedar (*Cedrus*). Values are means \pm SE ($n = 8$). Significance of linear regressions are indicated by asterisks: *, $P < 0.05$.

vironment.

Biomass production was positively correlated with A for the different provenances only in well-watered plants. Re-watering of drought-treated plants might have partially reduced the direct effects of the drought treatment on A and g_s . However, g_s was negatively correlated with biomass production; the most productive provenances had the lowest g_s . For each phylogenetic group, the most productive provenances had the highest K_s and K_1 but were also the most vulnerable to cavitation because of the trade-off between vulnerability of the vascular system and high sap flow efficiency.

Principal component analysis gave a more integrated overview of the combined effects of the physiological parameters studied, and allowed us to differentiate between the Lebanese provenances with higher biomass production and WUE and the Turkish provenances with lower biomass production and WUE. Another factor discriminating between the Turkish and Lebanese provenances was shown by the second bisector of the plane created by the first two axes of the principal component analysis. This line was linked negatively to K_1 , HV and R/S and discriminated between the Lebanese provenances

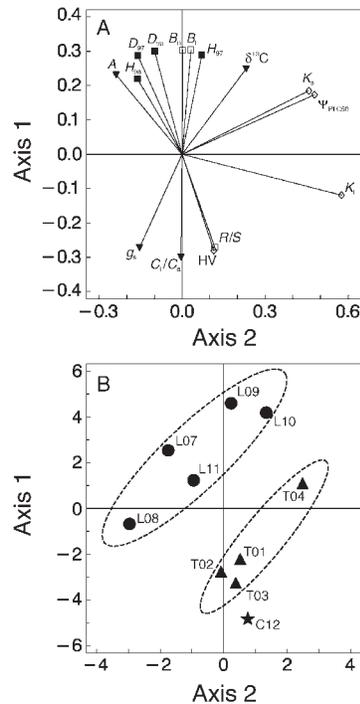


Figure 8. Principal component analysis of global variability in 15 traits of 10 cedar (*Cedrus*) provenances grown under well-watered conditions. Axis 1 (66% of total variation) represents biomass and gas exchange variables. Axis 2 (25% of total variation) represents hydraulic traits. (A) Distribution of the 15 traits on the correlation circle related to the first two principal components. (B) Distribution of the 10 provenances (\star = Cypriot; \bullet = Lebanese; and \blacktriangle = Turkish provenances) on the Axis 1–Axis 2 plan, segregating the Lebanese and Turkish origins. Abbreviations: A , net CO_2 assimilation rate; H_{97} and H_{98} , tree height in 1997 and 1998, respectively; D_{97} and D_{98} , tree diameter in 1997 and 1998, respectively; B_n , needle biomass; B_t , total plant biomass; $\delta^{13}\text{C}$, leaf carbon isotope composition; K_s , hydraulic specific conductivity; K_1 , leaf specific conductivity; Ψ_{PLC50} , water potential inducing 50% conductivity loss; R/S , root to aboveground biomass ratio; HV, Huber value; C_i/C_a , intercellular to air CO_2 concentration ratio; and g_s , leaf stomatal conductance.

with lower K_1 linked to lower HV values and lower R/S ratio, and the Turkish provenances with higher K_1 and HV values and higher R/S ratio. However, there was large variation within both groups; furthermore, within each group, the fastest-growing provenances always had higher K_s and were the most vulnerable to cavitation.

Phylogenetic interpretation

Differences between the Turkish and Lebanese provenances for most of the traits studied and the position of *C. brevifolia* in relation to the two groups are consistent with recently published results on cedar genetics. Several studies on genetic markers have shown clear speciation of *C. atlantica* (Endl.) Manetti ex Carr. and *C. deodara* (Roxb.) Loud., and have also revealed separation between the Turkish and Lebanese provenances of *C. libani* and the closeness of *C. brevifolia* to one or other of these geographical groups. Based on isozyme studies,

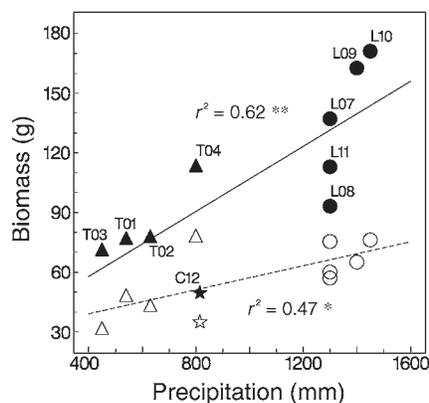


Figure 9. Relationship of total plant biomass under well-watered (closed symbols) and moderate-drought (open symbols) conditions with mean annual precipitation at the location of origin of the Cypriot (★, ☆), Lebanese (●, ○) and Turkish (▲, △) provenances of cedar (*Cedrus*). Significance of linear regressions are indicated by asterisks: *, $P < 0.05$; and **, $P < 0.01$.

Scaltsoyiannes (1999) and Fady et al. (2000) found strong similarities between *C. brevifolia* and the Turkish provenances of *C. libani*. Similar results were obtained with AFLP markers by Bou Dagher-Kharrat et al. (2007).

The differences observed in K_1 among Lebanese and Turkish provenances and Cypriot species may stem from this fragmentation of the *Cedrus libani* distribution range. These differences reflect morphological variations (branches with similar cross sections having different numbers of needles with different total surface areas or biomass) and could indicate ecological adaptation to drought, according to the genetic origin of the groups of populations. Thus, the Turkish provenances and Cypriot species have higher K_1 than the Lebanese provenances that could be related to their adaptation to drought.

At the provenance level, we found strong correlations between vigor (biomass production and growth) and several physiological parameters (gas exchange, hydraulic traits, $\delta^{13}\text{C}$), but correlations were independent of the geographic origin of the provenance, except for K_1 . However, annual rainfall in the native range explained some of the differences in performance. These factors were significantly correlated, though not closely ($r^2 = 0.62$); this limited correlation may be associated with the poor reliability of the annual rainfall data taken from documents designed to define provenance zones for Mediterranean conifers (Topak 1997) and from certificates accompanying seed shipments. Annual precipitation is difficult to quantify for countries included in our study because of a lack of recording stations, especially for the mountainous regions. Nonetheless, our rainfall data agree with the climatic maps of Turkey prepared by Akman and Daget (1971) and Atalay (1987), and with data collected by Khouzami and Nahal (1983) defining the bioclimatic zones where *C. libani* occurs.

All of the Lebanese provenances studied originate from the humid bioclimatic zone (Daget 1977) characterized by mild to cool winters, an annual precipitation of more than 1300 mm and a 5-month dry summer period. These provenances showed

regular growth during our study; however, the performance of trees growing under natural conditions in southern France on limestone soils at elevations between 250 and 500 m has been poor (Bariteau et al. 2007). We explain this poor growth on the basis of the relative drought sensitivity of these provenances; however, some authors have noticed a phenological difference between plantation trees in Lebanon and France, with trees in the French plantations showing earlier bud burst, greater spring frost damage and growth cessation earlier in the summer season than trees in the Lebanese plantations (Bariteau and Ferrandès 1992).

Among the Turkish provenances, those from the eastern Taurus Mountains (T04, Arslanköy) had the highest biomass productivity. Along with other provenances from the same region, Provenance T04 has also outperformed trees growing under natural conditions in French plantations. The Taurus Mountains region is sub-humid with an annual precipitation of about 800 mm. The three other Turkish provenances in our study, from the western Taurus Mountains, are from a semi-arid bioclimatic zone with cool to cold winters and less than 600 mm of annual rainfall. Their growth was mediocre, which can be linked to their native semiarid habitat where drought survival is favored over growth under well-watered conditions.

Although *C. brevifolia* had the lowest growth rate of the cedars studied, it had the best drought tolerance. This species grows on the island of Cyprus at elevations between 800 and 1100 m in a semiarid bioclimatic zone with mild winters. *Cedrus brevifolia* specimens found today are remnant trees, subjected to heavy human use, growing on poor compacted soils (Quézel 1979). The trees do not occur above 1100 m, even though ecological conditions should be more favorable for their growth at higher elevations.

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