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Different ability of three Mediterranean oak species to tolerate progressive water stress

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Abstract

Inter-comparisons in the gas exchange patterns and root characteristics under both well-watered and drought conditions were done in three-years-old seedlings of three oak species (*Quercus cerris* L., *Q. frainetto* Ten., and *Q. ilex* L.) growing in controlled environment. Well-watered *Q. cerris* had greater physiological performances than other oaks, but under drought it was not able to face the water stress showing also structural modifications such as reduction of root length and average diameter. On the other hand, *Q. ilex* maintained root growth both in drought or well-watered soils. Moreover, it was able to keep open stomata also under water stress, although stomatal conductance (g_s) was low. *Q. frainetto* had an intermediate position in regard to its physiological and root structural characteristics between *Q. cerris* and *Q. ilex* under drought stress. For all oaks the relationship between g_s and the ratio of sub-stomatal and ambient CO_2 concentration (C_i/C_a) highlighted the dynamic adaptation of g_s to the increase of hydraulic resistances of leaf, stem, and roots portions, more evident during the air humidity change and progressive soil dehydration. This suggests a well-triggered above- and under-ground mechanism to endure the drought stress.

Additional key words: gas exchange; *Quercus*; net photosynthetic rate; root morphology; seedlings; species differences; stomatal conductance to water vapour; transpiration; xylem.

Introduction

The resistance of plants to stress is the consequence of two possible strategies that Levitt (1980) and Martìnez-Ferri *et al.* (2000) attribute to the ability to exclude or tolerate the stress. Species that employ a drought-avoidance mechanism prevent damage by early stomatal closure before any change in leaf water status occurs, whereas drought-tolerant species exhibit simultaneous decreases in stomatal conductance and water potential (Guehl *et al.* 1991, Picon *et al.* 1996). In drought-tolerant *Quercus* species, drought-induced stomatal closure does not markedly limit carbon assimilation (Epron and Dreyer 1993, Damesin and Rambal 1995). In the Mediterranean environment a deep, wide-spreading, much branched root system is the most effective safeguard against drought injury, both in native vegetation and in crop plants (Kramer 1983). Nevertheless, shrubs of the California chaparral show that the root systems are less important than leaf adaptations in drought tolerance (Kummerow *et al.* 1978). As consequence, it is necessary to link leaf and canopy gas exchange rates to root characteristics, and to physical and chemical soil characteristics (Sharp and Davies 1979, Mooney and Winner 1988) to fully understand the responses of plants to water deficit (Turner 1986, Nardini *et al.* 1999). The aim of this paper is to characterise the functional response to the increasing soil dehydration stress of three *Quercus* species (two deciduous species – *Quercus cerris* and *Q. frainetto,* and one evergreen – *Q. ilex*) through measurements of the gas exchange rates, water balance, and structural characteristics of the root apparatus.

Materials and methods

Plants and experimental conditions: *Quercus cerris* L. (Turkey oak) is a deciduous, mesophyllous species, best suited for deep, well-drained but moist soils. *Q. frainetto* Ten. (Hungarian oak) is a deciduous, somewhat smaller

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Abbreviations: C_a – ambient CO_2 concentration; C_i – sub-stomatal CO_2 concentration; E – leaf transpiration rate; g_s – stomatal conductance to water vapour; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; RH – relative humidity; VPD – vapour pressure difference; Ψ – leaf water potential.

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oak species of south-eastern Europe, and *Q. ilex* L. (holm oak) is an evergreen xerophillous Mediterranean species. Three-years-old *Q. cerris*, *Q. frainetto*, and *Q. ilex* seedlings of uniform size were taken from natural woods of the Castel Porziano Estate located at 20 km from Rome (Manes *et al.* 1997a), and grown in pots with garden soil. After watering to field capacity, twenty-four seedlings of each species were placed in controlled chambers (model *CT15*, *LABCO,* Rome, Italy). The growing conditions were: 25/18 °C day/night temperature, 300 μmol m^{-2} s^{-1} PPFD, 12-h photoperiod. Relative humidity (RH) was maintained at 45 % during the first two weeks of the experiment, and at 35 % for the remaining four weeks. This reduction was imposed to increase the vapour pressure difference (VPD) values adding thus also the air water vapour deficit stress to the soil dehydration, just as occurs in the field. For each oak species, three experimental treatments of eight plants each were established: Set *A* received 25 cm^3 of tap water per day which were sufficient to keep potted soil at full field capacity, Set *B* received 12 cm^3 of tap water, and set *C* no water. Treatments were interrupted when 50 % of each treated set of plants appeared fully wilted. No recovery assessment has been carried out on wilted plants due to the reaching of critical physiological conditions.

Analyses: Gas exchange parameters, *i.e.* net photosynthetic rate, P_N [μmol(CO_2) m^{-2} s^{-1}]; leaf transpiration, *E* [mmol(H_2O) m^{-2} s^{-1}]; stomatal conductance, g_s [mmol(H_2O) m^{-2} s^{-1}], and sub-stomatal CO_2 concentration, C_i [μmol mol^{-1}], were measured with a portable instrument (*CIRAS I*, *PP Systems*, Hitchin, Herts., UK). Moreover, ratio of C_i and ambient CO_2 concentration, C_a [μmol mol^{-1}] was calculated. All physiological measurements were carried out at growth chamber temperature. Leaf water potential, Ψ_L [MPa] was measured weekly by using a pressure chamber (*PMS Instruments*, Oregon, USA). All measurements were carried out from 14:00 to 15:00 h at the half of photoperiod.

At the end of the experimental period, three randomly selected plants for each species were extracted from their pots. Root systems were cleaned gently, spread on paper, and photocopied. Diameters at collar and shoot height were also measured. The digitised images of roots were analysed with *DT-SCAN* software (*Delta-T Devices*, Cambridge, UK). Parameters reported were: shoot volume, D^2H [cm^3], where D was the shoot diameter [cm] at ground level and H shoot height [cm] (Ruehle *et al.* 1984), root volume [cm^3], total root length [cm], relative length of fine roots [%], relative area of fine roots [%], mean root diameter [mm], and mean root volume ratio [dimensionless]. The diameter of xylem vessels was also measured in control plants, on shoot sections taken 10 cm from the shoot tip, by using a compound microscope (40×) (*Zeiss*, Oberkochen, Germany) equipped with a micrometric scale.

Data analyses: *STATISTICA 6.0* (*StatSoft*, Tulsa, OK, USA) was used to perform the descriptive statistics, regression, and correlation analyses of physiological data regarding all oak species. Analysis of variance (ANOVA) and the Student-Neumann-Keuls' test, at a significance level of 0.05, were performed on morphological and physiological data. All data were reported as mean ± SD, or as otherwise specified.

Results

Gas exchange: The control set (*A*) did not show any significant variations of the average P_N during the experimental period (5.10±0.98, 4.20±1.35, and 3.73±1.35 μmol m^{-2} s^{-1} in *Quercus cerris*, *Q. frainetto*, and *Q. ilex,* respectively; Fig. 1*A–C*). The P_N of set *B* plants showed a slower reduction rate than set *C* for all species. In the set *C* plants, P_N reached very low values after 21 d of stress for *Q. cerris*, 25 d for *Q. frainetto*, and 35 d for *Q. ilex* (Fig. 1*A–C*). The g_s values highlighted a strong control on the gas exchanges. Different *Quercus* species of set *A* showed different average values of g_s ranging from 112.12±44.29 mmol m^{-2} s^{-1} in *Q. cerris* to 51.55±22.50 mmol m^{-2} s^{-1} in *Q. ilex* (Fig. 1*D–F*). In the set *C*, higher average values of g_s were measured in *Q. ilex* than in *Q. frainetto* and *Q. cerris*. *Q. cerris* was the most sensitive species to the variation of relative humidity showing an increase of g_s values (+26 %) in well-watered plants (on average 176 mmol m^{-2} s^{-1}), whereas an immediate strong reduction of g_s was instead observed in the set *C* plants at RH of 35 %. Although the same response of g_s to the change of RH was observed in the other two *Quercus* species, it was not so rapid as in *Q. cerris* plants. Well-watered plants of *Q. ilex* did not show any great sensitivity to the change of RH, and the water stressed plants (set *C*) kept their stomata open in the following three weeks after the change of RH, even though g_s values were low (23.89±16.44 mmol m^{-2} s^{-1}). *Q. frainetto* showed an intermediate sensitivity of g_s response to the variation of RH.

Patterns of g_s *vs.* C_i/C_a in all oak species undergoing three hydration treatments and the variation of RH are shown in Fig. 2. In the control sets, the mono-phase and increasing trends of g_s and C_i/C_a ratio were observed for all oak species, with significant correlation coefficients in *Q. cerris* (r = 0.48, $p<0.01$ at 45 % RH to r = 0.54, $p<0.01$ at 35 % RH), whereas in *Q. ilex* this correspondence was less evident. In the set *B* at 45 % RH, the relationship between g_s and C_i/C_a was still increasing but it was less closely correlated than in control sets. The reduction of RH to 35 % caused a loss of correlation between two variables, with a clear two-phase behaviour, which was more evident in *Q. cerris* and *Q. frainetto* than in *Q. ilex*. In set *C*, the 45 % RH maintained a positive correlation between g_s and C_i/C_a ratio, whereas the reduction of RH caused a break down of the trend.

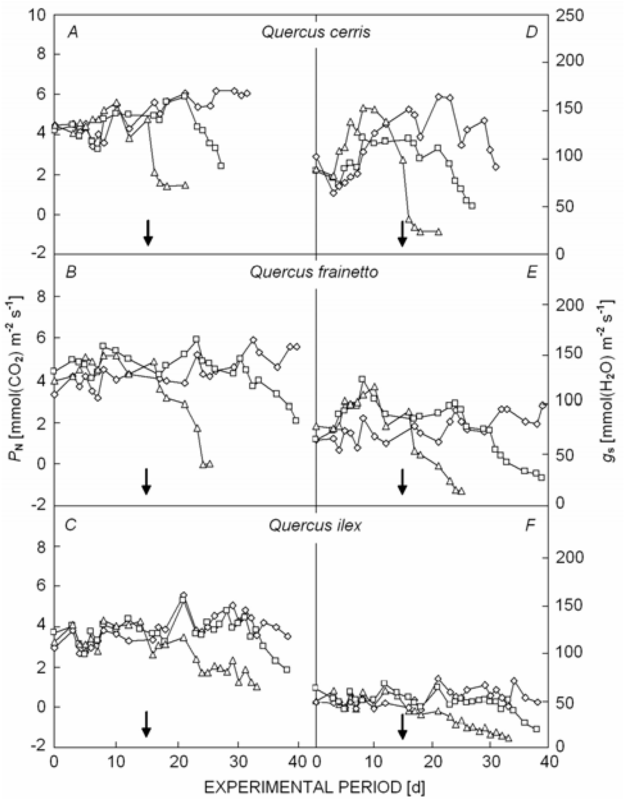

Fig. 1. Net photosynthetic rate (P_N) and stomatal conductance (g_s) measured in *Q. cerris*, *Q. frainetto*, and *Q. ilex* plants during the experimental period. *Arrows* indicate the change of relative humidity from 45 to 35 %. ◊ – set *A*; □ – set *B*; Δ – set *C*.

Leaf water potential: Well-watered plants showed almost constant values of Ψ_L during the experiment (Fig. 3*A*), although *Q. cerris* exhibited more negative values than the other two oaks. Different trends of the Ψ_L were evident in sets *B* and *C* (Fig. 3*B,C*): at the end of the experimental period *Q. cerris* showed lower values than *Q. ilex* and *Q. frainetto*, peaking to –4.87±1.34 MPa compared with –3.06±1.54 MPa of *Q. frainetto* and –1.03±0.34 MPa of *Q. ilex*. Correlation analyses carried out on Ψ_L and g_s data showed a positive correlation only in *Q. cerris* plants of set *A* (r = 0.681, $p<0.05$), whereas for the other two oaks no significant correlation was observed. A significant relationship between g_s and Ψ_L was instead observed in treated sets (r = 0.860, 0.843, and 0.99 at $p<0.05$ for *Q. ilex*, *Q. cerris*, and *Q. frainetto*, respectively, in set *B*). This highlighted soil dehydration and RH change, most evident for plants of set *C* (r = 0.941, 0.915, and 0.907 at $p<0.05$ for *Q. ilex*, *Q. cerris*, and *Q. frainetto*, respectively).

Shoot and root parameters: Shoot volume was evaluated as D^2H [cm^3]. As expected, no effect was observed due to water treatment in the three *Quercus* species (F = 0.96, p=0.34) because of the limited duration of the experiment. *Q. frainetto* had a significantly lower shoot biomass (F = 6.71, p=0.008) than the other two species (3.16±1.77 *vs*. 7.38±1.27 and 7.34±0.91 for *Q. cerris* and *Q. ilex* of set *A*, respectively).

In the set *A*, *Q. cerris* had a significantly larger root system, in terms of volume and length (Table 1) than the other two oaks. The distribution of root length in diameter size classes in *Q. cerris* showed the highest percentage of root length under 0.6 mm diameter, accordingly with the lower root mean diameter than in the other two oaks (Table 1). The three *Quercus* species differed also in diameter of xylem vessels: *Q. cerris* had the highest percentage of large vessels with two peaks at 12.5 and at 22.5 µm diameter, while *Q. frainetto* showed the highest vessel diameter class at 17.5 µm, similarly to *Q. ilex*. Biomass allocated to roots, evaluated as root volume ratio, was significantly lower in *Q. ilex* well-watered plants, as compared with the other two species. Therefore the root system of *Q. cerris* may be described as an extensive root system, compared to those of *Q. frainetto* and *Q. ilex*, the latter being smaller and shorter than the other two. In the set *C*, root length of *Q. cerris* was significantly reduced in water stressed plants (Table 1), probably due to the shedding of the thinnest roots. The relative proportion of fine roots was also slightly reduced. In *Q. frainetto* water shortage reduced both volume and length of roots, whereas the mean root diameter and the thinnest fraction seemed to be not affected. Also in *Q. ilex*, the root volume was significantly reduced, although the total root length was not significantly less, and a slight increase in the thinnest fraction with a reduction in the mean root diameter could even be noted (Table 1). Total root length was significantly reduced by dehydration treatment only in the deciduous species (54.2 % in *Q. cerris* and 63.5 % in *Q. frainetto*), whereas a non-significant reduction (39.5 %) was observed also in *Q. ilex*. Mean root diameter was significantly increased in *Q. cerris* by drought treatment, whereas in *Q. ilex* a non-significant reduction was observed. Root volume as proportion of the total biomass was affected by water treatment, however, it was significant only in *Q. frainetto* (Table 1).

Discussion

In this study we have considered three oak species, two deciduous and one evergreen and sclerophyllous; these species showed similar patterns of leaf gas exchange response to soil dehydration, although at different species-specific rates. The ability to maintain the stomata open also under water stress differed among the oaks considered. In *Q. ilex* low gas exchange rates highlighted a high resistance to the change of environmental growth conditions, implying thus a typical conservative water use in dehydrated soils (Epron and Dreyer 1990). As a consequence, *Q. ilex* had low g_s values both in the control and in treated sets, whereas Ψ_L remained relatively high throughout the experimental period, proving that *Q. ilex* copes with water deficit to avoid its desiccation. *Q. cerris* seedlings maintained stomata open even at elevated soil dehydration. In fact, g_s and E did not reach zero, even after four weeks of partial dehydration. This demonstrated a good vessel resistance to cavitation or embolism (Lo Gullo *et al.* 1995), in spite of a wide cross-sectional area of vessels, which increases the risk of cavitation (Tyree and Sperry 1989, Tognetti *et al.* 1996, Sperry 2000). The importance of the hydraulic vascular system in limiting gas exchange is well documented (Hubbard *et al.* 2001, Brodribb and Feild 2000). The accepted principles of xylem-limited water relations assume that under normal conditions leaf water loss is regulated and thus hydrostatic water potential in the xylem approaches but does not transgress its cavitation limit (Sperry *et al.* 1993). This means that plants appear to avoid cavitation by closing stomata at water potentials equivalent to that responsible for incipient cavitation (Nardini *et al.* 2001, Cochard *et al.* 2002).

In *Q. cerris*, the stomatal closure of the set *C* plants was sensitive to the change of RH. However, under water stress stomatal closure could be due to the reduction of the stem/root hydraulic conductance and to the variation of soil water potential as reported by Cochard *et al.* (1996, 2000), Nardini *et al.* (1999), and Bréda *et al.* (1993) for oaks. We deem that as the soil water dehydration becomes progressively more intense, the low value of RH becomes just as important as the state of dehydration of the soil which directly affects the root hydraulic conductance.

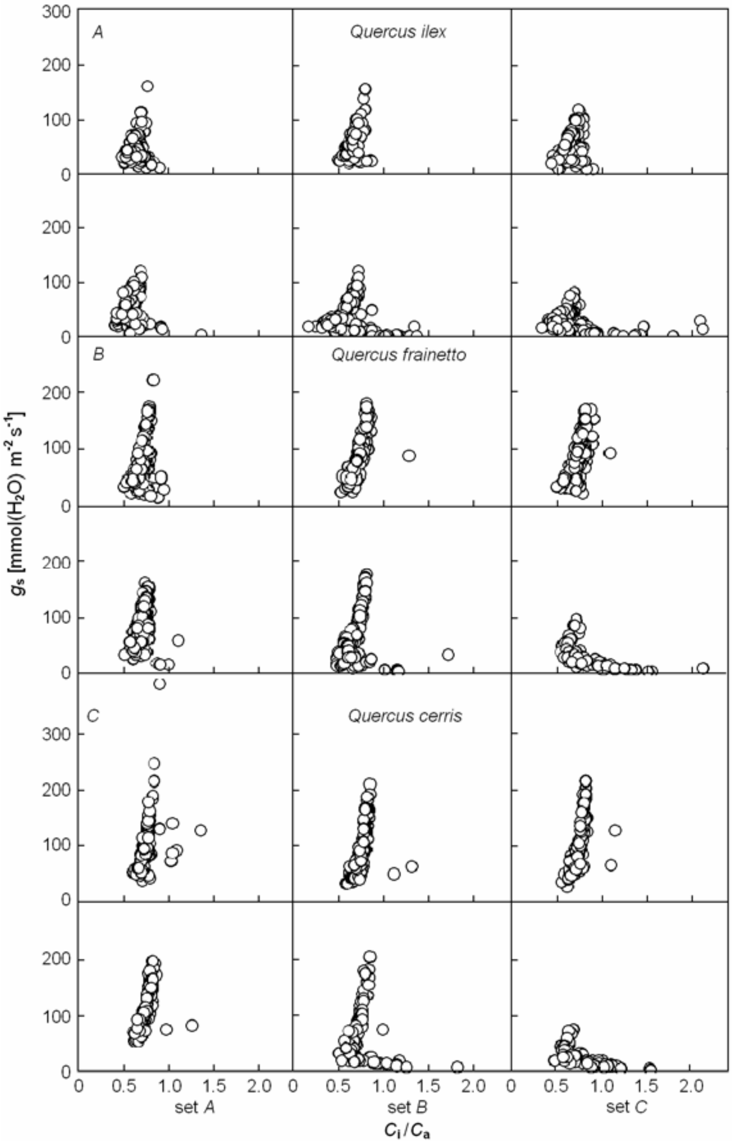

Fig. 2. Relationship between stomatal conductance (g_s) and C_i/C_a as a function of both water dehydration treatments (*A*, *B*, and *C* sets) and relative humidity (RH) values (45 % first graphs' sequence line and 35 % second graphs' sequence for each species), for the three oak species. The dynamic variation of g_s values in the time shows a two-phase trend in the water shortage sets.

Table 1. Biometric parameters measured in sets *A* and *C* of *Quercus cerris*, *Q. frainetto*, and *Q. ilex* plants at the end of experimental period. Means±SD; $n = 3$ for each species). The 2-way ANOVA tests are presented. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$, n.s. = not significant.

		Root volume [cm^3]	Root length [cm]	diameter <0.6 mm [%]	Root mean diameter [mm]	Root volume ratio
Control (set *A*)	*Q. cerris*	4.79±0.77	14249.6±1897.8	75.38±1.57	1.09±0.08	0.39±0.08
	Q. frainetto	2.05±0.54	8124.9±1936.2	67.20±2.17	1.19±0.10	0.41±0.08
	Q. ilex	1.96±0.64	5032.9±1156.0	69.90±2.40	1.23±0.09	0.21±0.03
Treated (set *C*)	*Q. cerris*	3.29±0.51	6526.9±1239.2	72.21±1.10	1.30±0.06	0.36±0.02
	Q. frainetto	0.91±0.14	2968.4±607.4	68.42±1.48	1.26±0.02	0.23±0.03
	Q. ilex	0.86±0.17	3046.9±865.1	72.52±2.79	1.11±0.10	0.13±0.01
F-ratio	Species (DF = 2)	23.44^{***}	19.37^{***}	6.44^{**}	0.44 n.s.	16.11^{***}
	Treatment (DF = 1)	12.14^{**}	32.42^{***}	0.03 n.s.	1.11 n.s.	9.65^{**}
	Interaction (DF = 2)	0.12 n.s.	3.64^{*}	1.63 n.s.	3.72^{*}	2.23 n.s.

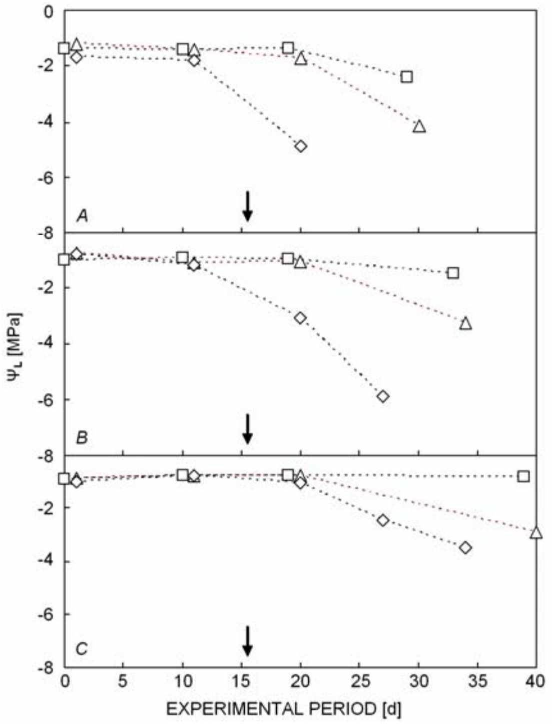

Fig. 3. Leaf water potential, Ψ_L during the experimental period in (*A*) *Quercus cerris*, (*B*) *Q. frainetto*, and (*C*) *Q. ilex*. *Arrows* indicate the change of relative humidity from 45 to 35 %. ◊ – set *A*; □ – set *B*; Δ – set *C*.

The parallel reduction of stomatal conductance and leaf water potential is a characteristic response of Mediterranean species to diurnal and seasonal water deficit which indicates the conservative water use (Archer and Rambal 1992, Castell *et al.* 1994, Manes and Blasi 1995). A close relationship between g_s and Ψ_L was, in fact, observed in both *Q. cerris* and *Q. frainetto*, whereas in *Q. ilex* this relation was evident only under extreme soil dehydration. Since *Q. cerris* showed the highest g_s and the lowest Ψ_L among oaks examined, it copes with water stress through a mechanism of dehydration tolerance by adopting a drought tolerant strategy, if the water stress is not too prolonged (Guehl *et al.* 1991).

Let us now consider the different behaviour of the relationship between g_s and C_i/C_a in regard to the sensitivity of oak seedlings to drought treatment. The two-phase trend observed in *B* and *C* sets at 35 % RH in all oaks pointed out a dynamic adaptation of physiological response to the advancing soil dehydration. In this context, the reduction of gas exchange rates could be due to non-stomatal limitation (Brodribb 1996) such as an enhancement of the photorespiration rate which was able to sustain the photochemical flux at low g_s (Schwanz *et al.* 1996).

The root analyses in *Q. ilex* highlighted the maintenance of root growth either in drought soils or in well-watered soils. The reduction of mean root diameter and distribution of both root length and surface area in the smaller diameter fractions might imply a tendency towards a thinning of roots in water-deficient *Q. ilex* samplings. Root thinning may be obtained through root elongation, thus implying an increase in surface/volume ratio and a better exploitation of the soil for availability of water. Since the total root length was actually reduced, the reduction in the average diameter and the increase of fine root portion was probably achieved through shrinking. The reduction in root length observed in the two deciduous species may be attributed to the shedding of the thinner portions, increasing thus the mean diameter. Such results, especially for *Q. cerris*, indicated a sensitivity of the root system to soil-water dehydration to an extent that may compromise the viability and the functioning of thinner roots. Species with higher *E* showed larger root systems such as *Q. cerris*, whereas *Q. ilex* was at the other extreme of transpiration (Manes *et al.* 1997b) and root extension, while *Q. frainetto* was in an intermediate position for both parameters.

The inability of *Q. cerris* to limit water efflux through transpiration, coupled with the decrease of water absorption by the reduced root system and the increase of hydraulic resistances, implies that the last resort to extreme drought for this species was to shed leaves, which was effective at the end of the experiment. As expected, *Q. ilex* was the best adapted to drought stress among *Quercus* species considered here. The higher drought resistance of *Q. ilex* was based on a drought-tolerant water-saving strategy (Levitt 1980). This is due to the morpho-anatomic characteristics of the sclerophyllous leaves and their longer physiological functioning in time (De Lillis 1991, Manes *et al.* 1997b), to low transpiration rates, and to the root system which is able to adapt and to resist to dehydrated soils. *Q. frainetto* showed an intermediate ability of resistance to drought.

Large root systems *per se* did not seem to be a safeguard against drought, unless coupled with morpho-functional adaptations of leaves linked to different hydraulic resistances and some degree of plasticity. Modulation of gas exchange in relation to the variation of hydraulic resistances of leaves, stem, and roots pointed out a well-triggered above- and under-ground mechanism allowing a good water balance for oak species (Bucci *et al.* 2003, Buckley *et al.* 2003, Katul *et al.* 2003, Lo Gullo *et al.* 2003).

The co-occurring observations of the morphological and physiological responses in leaves and roots to water stress have permitted a better understanding of the underlying mechanisms that govern plant water relationships. These mechanisms are of primary importance for seedlings in order to overcome the typical seasonal water stress period in the Mediterranean area, which can be exacerbated by the increase of temperature foreseen in the 21st century.

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Govindjee, Fork, D.C.: **Charles Stacy French 1907 − 1985.** – National Academy of Sciences, Washington 2006. 28 pp.

It is not usual to publish in Photosynthetica reviews on tiny booklets. Nevertheless, this one presents an interesting summary of life and work of one of the greatest photosynthesis scientists of the 20th century and I would like to pay in this way a tribute to him. Another reason is that for almost a quarter of century Dr. French served on the Editorial Board of Photosynthetica.

Both authors of the reviewed booklet worked with Stacy French, the first one for a shorter time but the second one was staff member of the Department for many years, and both studied also some topics of the main interest of Dr. French. At least three discoveries of C.S. French will never be forgotten: of excitation energy transfer from phycobilins to chlorophyll *a*, of diverse spectral forms of chlorophyll-protein complexes, their analysis, and their functions, and of photosystems in various types of algae. Certainly, algae and photosynthetic bacteria were his favourite experimental objects. Dr. French was a master at projecting and building ingenious experimental devices, which were mostly hand-made and did use mechanical principles typical of that époque. I hope that even at present every researcher of photosynthesis has ever met "French Press" and knows that this name does not mean some printers' press produced in France. The "gadgets" of French were well known among photosynthesis researchers and they were really phantastic, *e.g.* the large derivative spectrophotometer. I learned only in this memoir that French proposed the name "Hill reaction" for the well known photosynthetic effect. In connection with the recent boom of photosynthesis research in China it should be mentioned here that the first paper of C.S. French (with P.S. Tang) was published in the "Chinese Journal of Physiology". For some time French taught at universities. But for a long period (1947−1973) he was a director of the Department of Plant Biology of the Carnegie Institution of Washington in Palo Alto (California). A list of 85 scientists who ever worked in this laboratory (among them many top scientists) clearly shows also this kind of contribution of French to the development of photosynthesis. And I must stress that he was a very kind, generous, pleasant, and open-minded man, which is confirmed also by the published recollections of some of his research fellows. The Palo Alto place was in his times the most free, friendly, and stimulating research laboratory I can imagine. I shall also never forget the three sunny days I spent in his house.

Reading the text of this booklet is easy and stimulating, the explanations are clearly put, there are also some interesting basic facts of life of Dr. French. An attached selected bibliography shows where to find information on his main endeavours.

The booklet is volume No. 88 of the series "Biographical Memoirs" published by the National Academy of Sciences in Washington, D.C. and is available to anyone on internet (http://books.nap.edu/html/biomems/cfrench.pdf). I believe that the next prepared volume on W.A. Arnold will also bring interesting information to everyone interested in history of photosynthesis research.