

Indications of hydraulic lift by *Pinus halepensis* and its effects on the water relations of neighbour shrubs

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Abstract

We measured the stable deuterium isotopic composition of xylem sap, the shoot predawn and midday water potentials, and the leaf $\delta^{13}\text{C}$ of Mediterranean shrubs *Pistacia lentiscus*, *Globularia alypum* and *Rosmarinus officinalis* in a south-oriented transect from a large (12 m tall) Aleppo pine tree, *Pinus halepensis*. We aimed to study the possibility of hydraulic lift from the deep roots of this pine tree to the shallow soil layers and its influence on these neighbour shrubs. These same traits were also studied in several individuals of the shrub *Pistacia lentiscus* growing with different types of neighbours: just shrubs, a small (3 - 4 m) pine tree, and the above mentioned large pine tree. The greater the distance from *P. halepensis* the plants grew, the higher xylem water δD , the lower the soil water content, and, the lower the predawn and midday water potentials were found. These results suggest the existence of an hydraulic lift from deep roots to shallow soil in this big tree. Further indication of this existence is provided by the improved water status of *P. lentiscus* (higher water potentials and δD , and lower $\delta^{13}\text{C}$ and, therefore, lower water use efficiencies) when growing close to the big pine in comparison with the same shrub species growing close to small pines or just surrounded by other shrubs. Moreover, all these trends occurred in the dry summer season, but disappeared in the wet spring season.

Additional key words: Aleppo pine, *Globularia alypum*, δD , $\delta^{13}\text{C}$, Mediterranean shrubs, *Pistacia lentiscus*, *Rosmarinus officinalis*, water potential.

Introduction

Water availability is the most important factor limiting plant growth in Mediterranean ecosystems (Mitrakos 1980, Mooney 1982, Peñuelas 2001). In these ecosystems, where precipitation is scarce, vegetation, although adapted to summer drought, is often living in a threshold situation (Peñuelas *et al.* 2001) and, therefore, must make a conservative use of available water and use all possible water sources (Peñuelas 2001, Terradas 2001).

Hydraulic lift is the process of transferring water acquired by roots from deep and moister soil layers to upper and dryer soil layers (Richards and Caldwell 1987). Thus, hydraulic lift provides a mechanism for the temporary storage each night of water external to the plant in the upper soil layers, and a way for the plant to obtain additional moisture. Hydraulic lift has been proposed as a mechanism that can buffer plants against

water stress during water deficits (Caldwell and Richards 1989, Dawson 1993). This water is also very important to the performance of the neighbourig plants. Some studies (Caldwell and Richards 1989, Dawson 1993, Horton and Hart 1998) have indicated that the hydraulically-lifted water was also used by the neighbour plants, and that this additional water can effectively ameliorate the performance and growth of the tree and the neighbouring vegetation in case of drought. Moreover, the existence of hydraulic lift in a community has indirect consequences on nutrient acquisition, biogeochemical nutrient cycling processes and root growth and persistence.

Since Mooney *et al.* (1980) attributed to the "hydraulic lift" the transfer of water from mesquite roots to soil in the Atacama desert, several works have presented evidences of this process in different species growing in arid, semiarid and even mesic environments

Received 1 August 2002, accepted 1 November 2002.

Abbreviations: ANOVA - analysis of variance, SEM - standard error of the mean.

Acknowledgements: We thank financial support by CICYT REN 2000-0278/CLI and REN 2001-0003/GLO (Spanish Government).

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(Caldwell *et al.* 1998). It has been suggested that hydraulic lift may be a general root system phenomenon, although it has only been reported in some species (Caldwell *et al.* 1998). Although hydraulic lift has been demonstrated in some species from Mediterranean climates (Jackson *et al.* 2000), this process has been scarcely described in the Mediterranean basin.

Stable isotope analysis can serve to study plant performance over extended periods. The origin of the water used by a plant can be determined from the stable isotopic composition of xylem water (White 1988, Ehleringer and Dawson 1992, Jackson *et al.* 1995, Farrington *et al.* 1996, Schulze *et al.* 1996, Filella and Peñuelas 2003). The different deuterium isotope composition, δD , of the different water sources provides a means of determining the relative use of these water sources by individuals in a community as there is no isotope fractionation during the transfer of water from the soil to the plant (White *et al.* 1985, Dawson and Ehleringer 1991). The origin of the water used can thus be determined by comparing water δD composition in plants and in all potential water sources. On the other hand, leaf carbon isotope composition provides information on relative water-use efficiency integrated

over extended periods (Farquhar *et al.* 1989, Peñuelas *et al.* 2000).

We measured the deuterium isotope composition of xylem sap, the water potentials and the leaf $\delta^{13}C$ of *Pistacia lentiscus*, *Globularia alypum* and *Rosmarinus officinalis* Mediterranean shrubs in a south-oriented transect from a large (12 m tall) *Pinus halepensis* tree in order to study the possibility of hydraulic lift from its deep roots to the shallow soil layers and its influence on the functioning of these neighbour shrubs. These same traits were also studied in several individuals of the shrub *Pistacia lentiscus* growing with different types of neighbours: just shrubs, a small (3 - 4 m) pine tree, and the above mentioned large pine tree, in order to study the effect of these different neighbours on the functioning of this species through possible hydraulic lift processes. Our aims were *a)* to find indications of hydraulic lift by *P. halepensis* trees, *b)* to find out whether there are seasonal differences between the wet spring and the dry summer, *c)* to elucidate the effect of the distance from the tree on the water relations of the neighbour plants, and, *d)* to test the effect of the size of the tree on the hydraulic lift and on the functioning of the neighbour plants.

Materials and methods

Experimental sites and design: The study was conducted during the summer drought (and also in the wet spring season as reference) in an experimental site located at the Natural Park of Garraf in Catalonia (NE Spain) (41°18' N, 1°49' E). The Garraf hills are a calcareous formation 35 km South of Barcelona. Their latitude and their location near the seashore determine a typical Mediterranean climate with mild temperatures (mean annual temperatures of 15 °C) and few but torrential rains during spring and autumn (mean annual precipitation 450 mm). The winters are tempered and the summers hot and dry. The high permeability of these carstic zones implies great losses of water that is no longer available for plants. The soils in Garraf are very thin and discontinuous. The plant community is a short Mediterranean macchia dominated by shrubs.

In the study site, a plain with a "big" *Pinus halepensis* tree (ca. 12 m high) that was growing surrounded by shrubs, we studied the *P. halepensis* tree, and several shrub species in a south-oriented transect: *Pistacia lentiscus* (1.5 m from the pine), *Globularia alypum* (3.2 m from the pine) and *Rosmarinus officinalis* (5 m from the pine). For each one of these plants: *a)* we collected stem samples for determination of xylem hydrogen isotope composition, *b)* we measured predawn and midday shoot water potential, and *c)* we collected leaf samples for carbon isotope and N analyses in the morning. Finally, we also measured soil water content in

the transect.

For one of the studied species, *P. lentiscus*, we also measured three plants in each one of two other nearby (50 m and 500 m away) areas, growing in different situations, near a small pine the former and surrounded by shrubs the latter.

Shoot water potential and soil water content: Water potentials of small apical shoots were measured at predawn and at noon using a Scholander-type pressure bomb (PMS Instruments Co., Corvallis, USA). Soil moisture was measured using time domain reflectometry (TDR). Volumetric water content was estimated using a cable tester (1502B, Tektronix, Beaverton, USA).

Sampling of xylem and leaves and isotope analyses: Xylem samples were collected by cutting a stem section away from transpiring leaf surfaces. Bark was removed and stem segments were immediately inserted in a glass tube with a rubber stopper, stored at 4 °C and taken to the laboratory where the stem segments were frozen at -30 °C until water was extracted. Water was extracted by cryogenic vacuum distillation (Dawson and Ehleringer 1991). The extracts were stored in vials at -30 °C until analysis. Several sun-oriented leaves of the studied plants were sampled for carbon isotope and N determination. They were dried up to constant mass, finely ground and stored until analysis.

Stable hydrogen isotope composition was determined on a mass spectrometer (*Delta S, Finnigan MAT*, Bremen, Germany). δD was determined after equilibration of water samples with H_2 in the presence of a platinum catalyst. δD was expressed as:

$$\delta D (\text{‰}) = [(R_{\text{SAMPLE}}/R_{\text{VSMOW}}) - 1] \times 1000$$

where R_{SAMPLE} and R_{VSMOW} are the $^2H/^1H$ ratio of the sample and Vienna Standard Mean Ocean Water (VSMOW), respectively.

The foliar $\delta^{13}C$ was measured on a *SIRA Series II* isotope ratio mass spectrometer (*VG Isotech*, Middlewich, UK) operated in direct inlet continuous flow mode after combustion of the samples in an elemental analyzer (*NA1500, Series 1, Carlo Erba Instrumentazione*, Milan, Italy). The reference CO_2 , calibrated against standard *Pee Dee belemnite* (PDB) was obtained from *Oztech* (Dallas, USA). A system check of analysis was achieved with interspersed working standards of cellulose, atropine and urea (*Sigma*, St. Louis, USA). The accuracy of the measurement was $\pm 0.1 \text{ ‰}$ for $\delta^{13}C$. The isotopic composition of a sample ($\delta^{13}C_p$) was calculated as the ratio (‰):

$$\delta^{13}C_p = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$$

where R_{sample} and R_{standard} are the $^{13}C:^{12}C$ ratios of the sample and the Pee Dee Belemnite (PDB) standard respectively.

Carbon (C) and nitrogen (N) leaf concentrations were analysed with an elemental analyser (*Model NA 1500, Carlo Erba*, Milano, Italy), using the standard configuration for those determination.

Statistical analyses: For the study of *P. lentiscus* two-way analyses of variance (ANOVA) with season and neighbourhood as the main effects were conducted for all the studied variables after testing for normality and homogeneity of variance. Statistical analyses were conducted using Statistical program packages *Statview 5.0.1* (*Abacus Concepts Inc.*, Berkeley, USA) and *SYSTAT 5.2* (*SYSTAT Inc.*, Evanston, USA).

Results and discussion

The δD of xylem water, the predawn and midday water potentials and the values of soil moisture showed a marked gradient from the pine tree in summer contrasting with the absence of any gradient in spring (Fig. 1). In summer, the xylem water δD shifted to more enriched values the greater the distance from *P. halepensis* the plants grew (Fig. 1A). More negative δD values correspond to deeper water since during the seasonal drought the isotopic fractionation due to evaporation in the upper soil layers results in variation of the isotopic composition of soil water with depth (Jackson *et al.*

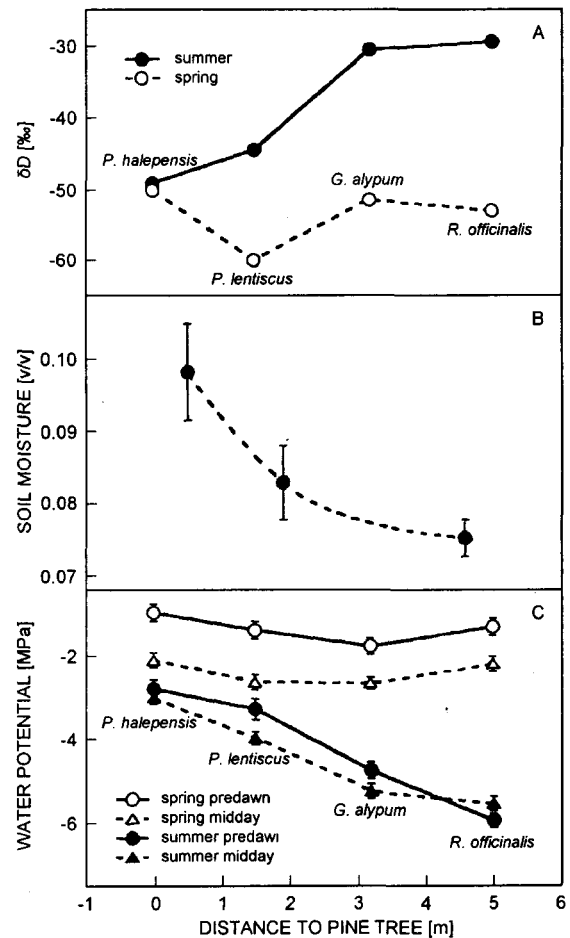


Fig. 1. A - δD of xylem water in the species growing in a south-oriented transect from a big pine tree (12 m tall) in summer and spring. B - Summer superficial soil (20 cm) water content in the transect from the pine tree. C - Shoot predawn and midday water potentials in the species (*Pinus halepensis*, *Pistacia lentiscus*, *Globularia alypum* and *Rosmarinus officinalis*) growing in the studied transect in summer and spring. Error bars indicate SEM ($n = 3$).

1999). Thus, shrubs closer to *P. halepensis* seemed to use deeper water. This deeper water is likely provided by an hydraulic lift conducted by *P. halepensis* tree, whose deeper roots have access to deeper water layers, whereas the most distant shrub of *R. officinalis* seemed to lack this access and to use more superficial water. In consonance with this trend, there was also a gradient in soil surface moisture. The soil water content was decreasing as moving away from the pine tree (Fig. 1B). Following the marked gradient in xylem water δD and soil moisture, there was also a gradient in predawn shoot water

potentials. Predawn and midday water potentials decreased when moving away from the pine tree (Fig. 1C), reinforcing the indication of lower water availability the further the shrubs were to the pine tree. The results show that there was an influence of the growing distance to the pine tree on the water source and availability of these plants. Although the alternative explanation of simply a deep root system in *P. lentiscus* (Filella and Peñuelas 2002) could also explain the δD results, the gradient found in soil surface moisture, supports the hypothesis of hydraulic lift.

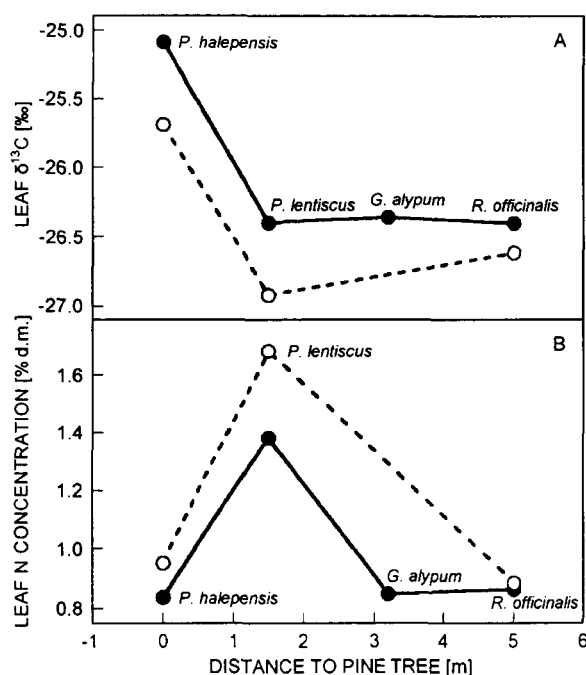


Fig. 2. Summer and spring leaf $\delta^{13}C$ (A), and leaf N concentration (B) in the species (*Pistacia lentiscus*, *Globularia alypum* and *Rosmarinus officinalis*) growing in the south-oriented transect from the pine tree.

In order to estimate the water use efficiency of these different species we measured their leaf $\delta^{13}C$. *P. halepensis* presented the highest $\delta^{13}C$ (Fig. 2A), what is surely linked to its higher crown area in relation to the other species (Sala *et al.* 1996, Peñuelas *et al.* 1999). *P. lentiscus*, *G. alypum* and *R. officinalis* presented similar leaf $\delta^{13}C$ values (Fig. 2A). They did not follow the expected gradient considering the values found on the water source and availability commented in the last paragraph from which lower $\delta^{13}C$ the nearer to the pine tree would be expected. Other species-specific responses may also affect these carbon isotopic signatures and mask the effects of drought on carbon isotope discrimination. Species differences in $\delta^{13}C$ are not only due to water use but also to differences in photosynthetic capacities between the species. Gebauer and Ehleringer (2000) attributed a correlation between $\delta^{13}C$ and leaf N concentration to responses of carbon discrimination to

photosynthetic capacity since higher N (greater photosynthetic capacity) should cause c_i/c_a to decline, and, hence, $\delta^{13}C$ to rise. In fact, *P. lentiscus* presented higher leaf N concentrations than the other species (Fig. 2B), what, following Gebauer and Ehleringer (2000), could have increased their expected lower leaf $\delta^{13}C$ values attending to their higher water availability (Fig. 1).

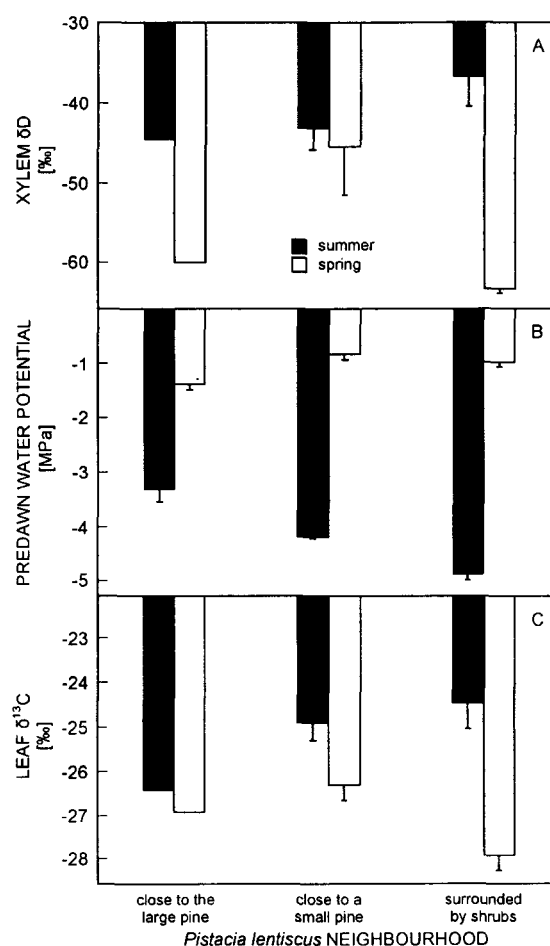


Fig. 3. Xylem water δD (A), predawn water potential (B), and leaf $\delta^{13}C$ (C) for *Pistacia lentiscus* growing in different neighbourhoods: close to the big (12 m tall) pine, close to small (3 - 4 m tall) pines, and surrounded only by shrubs. Error bars indicate SEM ($n = 3$).

Some studies have formerly attributed the improved growth conditions for plants growing close to trees to factors induced by a more favourable tree-modified microclimate, such as increased soil organic matter or greater nutrient availability (Caldwell *et al.* 1991) or lower irradiance, temperature and evapotranspiration. Hydraulic lift may constitute another important factor to contribute to this improvement in growing conditions for neighbouring plants (Dawson 1993). To further test the hypothesis that *P. halepensis* conducted hydraulic lift, we compared δD , water potentials and $\delta^{13}C$ in similar size

plants of *P. lentiscus* growing near the *P. halepensis* tree, near a small *P. halepensis* tree (3 - 4 m high), or growing surrounded by other shrubs and we observed a gradual decrease in their water availability (Fig. 3). The δD values tended to gradually decrease (Fig. 3A) indicating the use of deeper water the closer the plants were to trees and the bigger these trees were. These differences in δD values reinforce the likelihood of *P. lentiscus* use of water hydraulically lifted by the pine trees. There was also a marked significant ($P < 0.05$) gradient in the predawn water potential from the *P. lentiscus* near the big pine, with higher predawn water potential values, to the *P. lentiscus* surrounded by shrubs, with lower values (Fig. 3B), showing a gradient of water availability. In consonance with these results, leaf $\delta^{13}C$ values also showed this trend, with lower values, and, thus, lower water use efficiency, and likely greater water consumption, in the *P. lentiscus* near the pine, and higher values in *P. lentiscus* growing beside other shrubs, indicating higher water use efficiency, and likely lower water consumption.

These results indicate that the presence of a tree close

to *P. lentiscus* improved the performance and water status of this species, and, that hydraulic lift likely conducted by the neighbour pine tree contributed to this effect, especially considering that we always chose shrubs close to the south oriented sides of the trees and tried to avoid shade area as much as possible. They also show that this phenomenon is significantly important in the dry summer but not in the relatively wet spring (see Fig. 1A,C), and that it also depended on the size of the tree (and the corresponding root depth). These different water status traits of *P. lentiscus* in summer depending on the different neighbours, together with the gradient found in soil surface moisture (Fig. 1), reinforce the hypothesis of hydraulic lift to explain the gradient in δD shown in the transect from the large pine tree (Fig. 1).

These results suggest: a) that *Pinus halepensis* trees conduct hydraulic lift, b) that this phenomenon is important for the neighbour plants in the dry summer but not in the wet spring, c) that the effect decreases with the distance to the pine tree, and d) that the hydraulic lift and its influence on neighbour plants are greater in larger trees (with deeper roots).

References

- Caldwell, M.M., Dawson, T.E., Richards, J.H.: Hydraulic lift: consequences of water efflux from the roots of plants. - *Oecologia* **113**: 151-161, 1998.
- Caldwell, M.M., Richards, J.H.: Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. - *Oecologia* **79**: 1-5, 1989.
- Caldwell, M.M., Richards, J.H., Beyschlag, W.: Hydraulic lift: ecological implications of water efflux from roots. - In: Atkinson, D. (ed.): *Plant Root Growth: An Ecological Perspective*. Pp. 423-436. Blackwell, Oxford 1991.
- Dawson, T.E.: Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. - *Oecologia* **95**: 554-565, 1993.
- Dawson, T.E., Ehleringer, J.R.: Streamside trees that do not use stream water. - *Nature* **350**: 335-337, 1991.
- Ehleringer, J.R., Dawson, T.E.: Water uptake by plants: perspectives from stable isotope composition. - *Plant Cell Environ.* **15**: 1073-1082, 1992.
- Farquhar, G.D., Ehleringer, J.R., Hubick, K.T.: Carbon isotope discrimination and photosynthesis. - *Annu. Rev. Plant Physiol. Plant mol. Biol.* **40**: 503-537, 1989.
- Farrington, P., Turner, J.V., Gailitis, V.: Tracing water uptake by jarrah (*Eucalyptus marginata*) trees using natural abundances and deuterium. - *Trees* **11**: 9-15, 1996.
- Filella, I., Peñuelas, J.: Partitioning of water and nitrogen in co-occurring species of a mediterranean shrubland. - *Oecologia*, in press, 2003.
- Gebauer, R.L.E., Ehleringer, J.R.: Water and nitrogen uptake patterns following moisture pulses in a cold desert community. - *Ecology* **81**: 415-424, 2000.
- Horton, J.L., Hart, S.C.: Hydraulic lift: a potentially important ecosystem process. - *Trends Ecol. Evol.* **13**: 232-235, 1998.
- Jackson, P.C., Cavelier, J., Goldstein, G., Meinzer, F.C., Holbrook, N.M.: Partitioning of water source among plants of a lowland tropical forest. - *Oecologia* **101**: 197-203, 1995.
- Jackson, P.C., Meinzer, F.C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P.R., Caldas, L., Iglar, E., Causin, F.: Partitioning of soil water among tree species in Brazilian Cerrado ecosystems. - *Tree Physiol.* **19**: 717-724, 1999.
- Jackson, R.B., Sperry, J.S., Dawson, T.E.: Root water uptake and transport: using physiological processes in global predictions. - *Trends Plant Sci.* **11**: 482-488, 2000.
- Mitrakos, K.A.: A theory for Mediterranean plant life. - *Acta oecol.* **1**: 245-252, 1980.
- Mooney, H.A.: Habitat, plant form, and plant water relations in Mediterranean-climate regions. - *Ecol. medit.* **8**: 481-488, 1982.
- Mooney, H.A., Gulmon, S.L., Rundel, P.W., Ehleringer, J.R.: Further observations on the water relations of *Prosopis tamarugo* of the Northern Atacama desert. - *Oecologia* **44**: 177-180, 1980.
- Peñuelas, J.: [Atmospheric and climatic changes, and their effects on functioning and structure of the Mediterranean ecosystems.] - In: Pugnaire, F., Zamora, R. (ed.): *Mediterranean Ecosystems. Functional Analyses*. Pp. 423-455. CSIC, AEET Press, Granada 2001. [In Span.]
- Peñuelas, J., Filella, I., Piñol, J., Siscart, D., Lloret, F.: Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. - *Biol. Plant.* **43**: 47-53, 2000.
- Peñuelas, J., Filella, I., Terradas, J.: Variability of plant nitrogen and water use in a 100-m transect of a subdesertic depression of the Ebro valley (Spain) characterized by leaf $\delta^{13}C$ and $\delta^{15}N$. - *Acta oecol.* **20**: 119-123, 1999.
- Peñuelas, J., Lloret, F., Montoya, R.: Severe drought effects on Mediterranean woody flora in Spain. - *Forest Sci.* **47**: 214-218, 2001.
- Richards, J.H., Caldwell, M.M.: Hydraulic lift: substantial

- nocturnal water transport between layers by *Artemisia tridentata* roots. - *Oecologia* **73**: 486-489, 1987.
- Sala, A., Smith, S.D., Devitt, D.A.: Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave desert floodplain. - *Ecol. Appl.* **63**: 888-898, 1996.
- Schulze, E.-D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Ioretti, J., Oesterheld, M., Ehleringer, J.R.: Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. - *Oecologia* **108**: 503-511, 1996.
- Terradas, J.: Ecología de la Vegetación. De la Ecofisiología de las Plantas a la Dinámica de Comunidades y Paizajes. [Vegetation Ecology. From Plant Ecophysiology to Community and Landscape Dynamics.] - Omega, Barcelona 2001. [In Span.]
- White, J.W.C., Cook, E.R., Lawrence, J.R., Broecker, W.S.: The D/H ratio of sap in trees: implications for water sources and tree ring D/H ratios. - *Geochim. cosmochim. Acta* **49**: 237-246, 1985.
- White, J.W.C.: Stable hydrogen isotope ratios in plant: a review of current theory and some potential applications. - In: Rundel, P.W., Ehleringer, J.R., Nagy, K.A. (ed.): *Stable Isotopes in Ecological Research*. Pp. 142-162. Springer-Verlag, New York 1988.