Atmospheric *vs* soil water deficit as leaf conductance regulator in Mediterranean trees: a correlational approach

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Abstract

Both soil and atmospheric water deficits have been considered as the main variable determining stomatal closure in native Mediterranean species in the field, depending on the species and places studied. In this study, field data on leaf conductance of *Arbutus unedo*, a shallow-rooted tree, correlates higher with the predawn leaf water potential than leaf conductance of *Quercus ilex*, a deeprooted tree. Leaf conductance of mature individuals of both species correlates higher with vapour pressure deficit than leaf conductance of resprouts, which have lower leaf area. Data presented suggest that the relationship between root depth and leaf area in each individual could determine the relative importance of soil water deficit and vapour pressure deficit on controlling leaf conductance.

Key words: *Arbutus unedo, Quercus ilex,* root: shoot ratio, leaf conductance, water balance.

Resum. *Importància relativa del dèficit hídric del sol i de l'atmosfera sobre la regulació estomàtica en arbres mediterranis: una aproximació correlacional*

Segons les espècies i els indrets considerats, tant el dèficit hídric atmosfèric com el dèficit hídric del sòl han estat considerats com la variable principal que determina el tancament estomàtic en espècies mediterrànies en condicions de camp. En aquest estudi, la conductància foliar obtinguda al camp en *Arbutus unedo,* una espècie d'arrels superficials, està més correlacionada amb el potencial hídric a l'alba que la conductància foliar de *Quercus ilex*, que presenta un sistema radicular més profund. D'altra banda, la conductància foliar dels individus adults de les dues espècies està més correlacionada amb el dèficit de pressió de vapor que la conductància foliar dels rebrots de les mateixes espècies, que tenen una menor àrea foliar. Les dades presentades suggereixen que la relació entre la profunditat de les arrels i l'àrea foliar en cada individu podria determinar la importància relativa del dèficit hídric del sòl i del dèficit de pressió de vapor sobre el control de la conductància foliar.

Paraules clau: *Arbutus unedo, Quercus ilex,* proporció parts aèries/parts subterrànies, conductància foliar, balanç hídric.

Introduction

Although stomatal responses to environmental changes are quite well understood for plants growing in growth-chambers and greenhouses experiments, there is less certainty about the factors controlling stomatal conductance in natural vegetation growing in field conditions. Three mechanisms of stomatal response to atmospheric or soil water deficit have been described (Ludlow, 1980; Farquhar and Sharkey, 1982; Schulze and Hall, 1982; Schulze, 1986): direct response of stomata to air humidity, response through changes in mesophyll water status as a hydraulic signal, and response to soil water deficit through a chemical root signal. The mechanisms and the relative contribution of each process to controlling stomatal conductance are still uncertain (Kramer, 1988; Schulze et al., 1988). In native Mediterranean species, evidence has been presented to support the dominance of one or other of these mechanisms, depending on species and places. Tenhunen et al. (1987) showed that stomatal conductance was more clearly related to soil rather than leaf water potential in several Mediterranean trees and shrubs; data presented by Crombie et al. (1987) in *Eucalyptus marginata,* Morrow and Mooney (1974) in *Heteromeles arbutifolia* and *Arbutus menziesii,* and Gollan et al. (1985) in *Nerium oleander,* support this dependency of stomata on soil water content. On the other hand, leaf water status was described by Roberts et al. (1981) as the main inducer of stomatal closure in some species of the chaparral. Greater importance of soil water potential in relation to vapour pressure deficit was indicated in *Eucalyptus globulus* by Pereira et al. (1987). However, Turner et al., (1984) in *Arbutus unedo* and *Nerium oleander,* and Beadle et al. (1985) in *Pinus sylvestris,* showed the dominant effect of vapour pressure deficit on conductance, both directly on the leaf epidermis and through leaf water potential.

The objective of this study was to test the relative importance of soil and atmospheric water deficit on the regulation of leaf conductance in contrasting situations, using a correlational approach. Results were obtained for nature plants and resprouts of *Arbutus unedo* and *Quercus ilex,* two woody Mediterranean trees. Resprouts have a lower leaf area than mature plants, and *Q. ilex* individuals have deeper roots than *A. unedo.* Thus, we may assess the stomatal response among plants with very dissimilar relationship between leaf area and root depth. Although the correlational approach can not be used to provide evidence for mechanisms involved in the regulation of stomata, the results may help to understand the response of stomata to the environmental conditions and their ecological implications.

Materials and methods

The study site is located at an elevation of 350 m, on a Southern slope (15-20°) of the Collserola Natural Park in Northeast Spain, very close to Barcelona (41° 25' 25" N, 2° 6' 30" E). The vegetation burned in the summer of 1973. The plant canopy during the study period was near closure, dominated by *Arbutus unedo* L., *Quercus ilex* L. and *Pinus halepensis* Mill. During the sampling year (June 1990 - May 1991), total rainfall was 940 mm (mean 725 mm). The dry period occurred in July and August, when there were only 29 mm of rainfall (Figure 1).

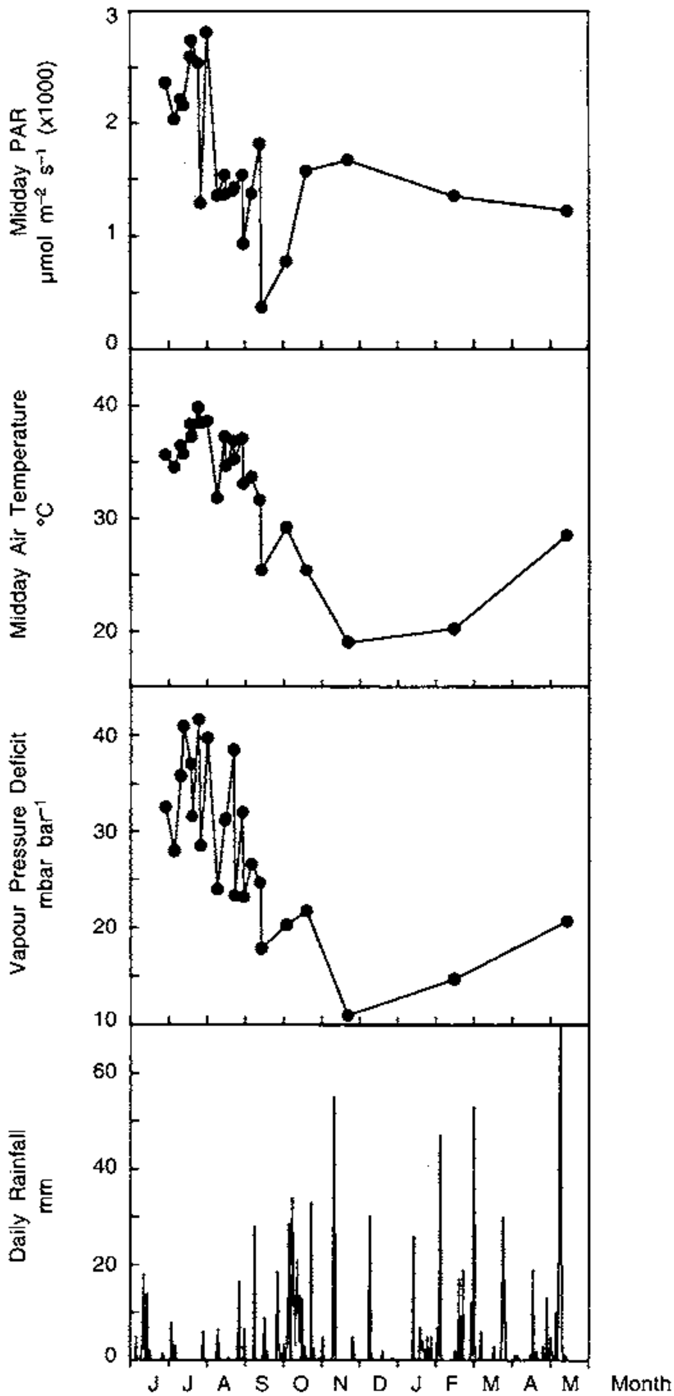

Figure 1. Environmental conditions from June 1990 to May 1991. Shown from top to bottom in the figure are average midday photosynthetically active radiation, air temperature and vapour pressure deficit estimated from the porometer measurements, and daily rainfall measured at the study site.

Mean annual temperature was 13.6 °C. The soil is a very shallow (19 + 1 cm, n = 18), loamy clay developed on Palaeozoic schists with a very low water storage capacity *(lithic xerorthent).*

The species considered were *A. unedo*, a laurophyllous shallow-rooted tree and *Q. ilex*, a schlerophyllous deeprooted tree. Plants of *Arbutus unedo* selected for study were on the average 3 meters in height and 5 meters in diameter, with three to five main stems. Excavated root systems of *A. unedo* individuals at the study site were restricted to the 20 cm thick soil layer and never penetrated the bed-rock. Plants of *Quercus ilex* were on the average 4 meters in height and 4 meters in diameter, with three to five main stems per individual. Tap roots of *Q. ilex* penetrated the bed-rock and still had a diameter of greater than 4 cm at the maximum depth we were able to observe (approx. 50 cm). In both species, three individuals were cut down on 7 May 1990 to produce resprouts, and three more individuals were left as mature plants. In addition, six more *A.unedo* plants, three resprouted and three mature, were watered during the summer drought (July and August). In all plants, leaf conductance was measured at midday with a porometer (ADC Ltd., model LCA-2, Hoddesdon, UK); predawn leaf water potential (PWP), as an indicator of soil water deficit, was measured with a pressure chamber (Soil Moisture Inc., model 3005, Santa Barbara, CA, USA); additionally, we calculated the midday vapour pressure deficit (VPD) in order to use it as a atmospheric water deficit indicator. Samples were taken weekly during the summer, and approximately every month during the rest of the year, from June 1990 to May 1991.

For each group of plants, regressions were performed between midday leaf conductance over the whole year as the dependent variable, and daily values of PWP and VPD as the independent variables. The regression used was the one showing the highest coefficient of determination: power regression for PWP-conductance, and linear regression for VPD-conductance. Regressions were characterized by their standardized regression coefficient (Beta coefficient, Norusis, 1985). Beta coefficient permit us to compare the effect of different independent variables removing the effect of unities; higher values of Beta indicate greater response of leaf conductance to changes in the independent variable.

Results and discussion

Decreases in leaf water potential and leaf conductance in resprouts and mature plants of both species occurred rapidly after the onset of summer drought and recovered after heavy rains of late-Summer (Figure 2), as typically observed previously at other sites (Tenhunen et al., 1985). These data are largely discussed in two previous papers (Castell and Terradas, 1994; Castell et al.,1994).

Beta coefficients obtained for the regressions in each group of individuals are graphically represented in the figures 3 and 4. *A. unedo* and *Q. ilex* individuals show similar values of Beta for VPD-conductance regression, but Beta values for PWP-conductance regression are much higher in *A. unedo* (Figure 3). On the one hand, similar leaf area in individuals of both species may be the reason to explain the similar response of conductance to atmospheric water deficit; on the other hand, the deeper root system of *Q. ilex* individuals probably leads to a weaker con-

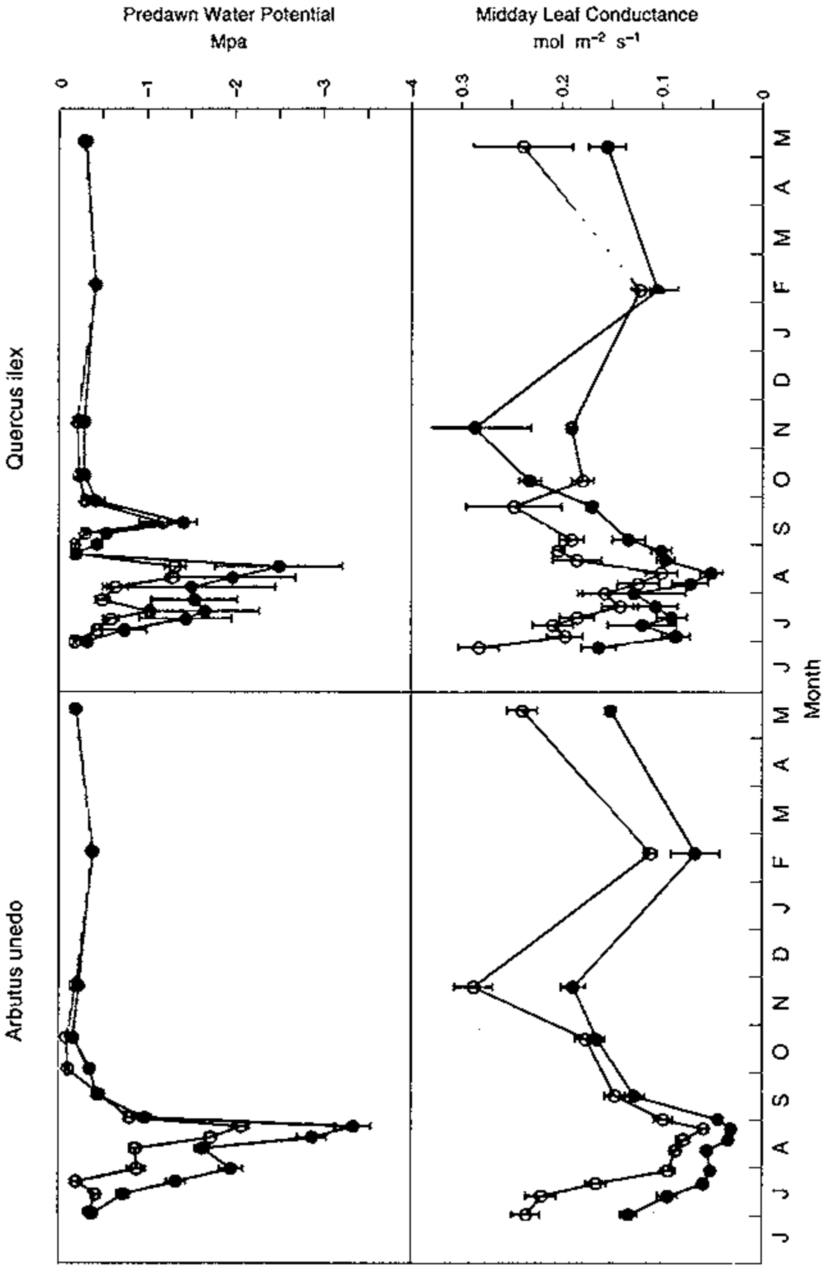

Figure 2. Seasonal course of the predawn leaf water potential (top) and midday leaf conductance (bottom) of mature plant and resprout leaves of *A. unedo* (left panel) and *Q. ilex* (right panel) in the field from June 1990 to May 1991. Mature —●—; Resprouts —○— .

ductance correlation with soil water deficit than in the more shallow-rooted *A. unedo* individuals. In the case of resprouts vs. mature plants, resprouts show lower values of Beta for VPD-conductance regression in both species, and also a lower value for PWP-conductance regression in *Q. ilex*. The weaker conductance correlation with atmospheric water deficit in resprouts is probably related to their lower leaf area.

Watering treatment basically involves a decrease of Beta values for PWP-conductance regression, both in *A. unedo* resprouts and mature plants (Figure 4). Thus, an increase in soil water availability causes conductance correlation with soil water status to decrease.

In summary, leaf conductance of each group of individuals seems to show higher correlation with soil or atmospheric water deficit, depending on which is the more limiting. In addition to soil water status and VPD existing at a given time and place, on an individual level, the relationship between root depth and leaf area could also determine the relative importance of soil and atmospheric water deficit. So, *A. unedo* resprouts, with low soil water availability and low transpiring area, are more limited by soil water availability than by vapour pressure deficit. On the contrary, mature individuals of *Q. ilex,* with a deep root system but also with a high leaf area, are more limited by atmospheric water deficit and less limited by soil water deficit than *A. unedo* resprouts.

In conclusion, water balance in the plant depends on input. I by root absorption, and output water flow by leaf transpiration. Data presented here suggest that the abiotic factor controlling each flow, soil and atmospheric water deficit, may be the main variable determining leaf conductance, depending on which is the most limiting in the water balance of each individual.

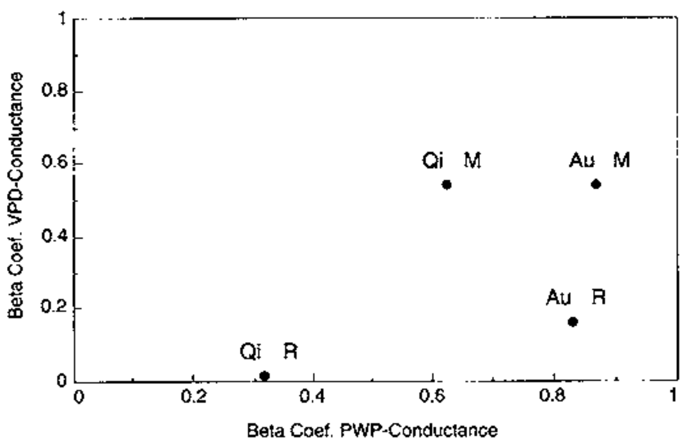

Figure 3. Beta values corresponding to the regressions between predawn water potential and leaf conductance (x axis), and vapour pressure deficit and leaf conductance (y axis), in the different groups of individuals (Qi M = Mature plants of *Q. ilex;* Qi R = Resprouts of *Q. ilex;* Au M = Mature plants of *A. unedo;* Au R = Resprouts of *A. unedo*).

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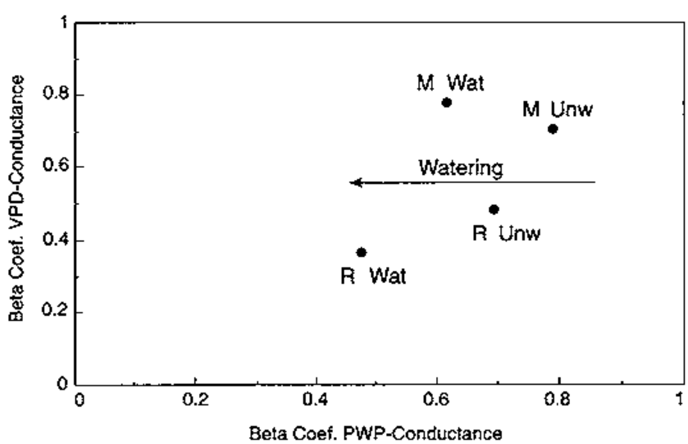

Figure 4. Effect of watering on the Beta values corresponding to the regressions between predawn water potential and leaf conductance (*x* axis), and vapour pressure deficit and leaf conductance (*y* axis), in resprouts and mature individuals of *A. unedo* (M Wat = Watered mature plants; R Wat = Watered resprouts; M Unw = Unwatered mature plants; R Unw = Unwatered resprouts).

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