Original article

Stomatal response of *Quercus pyrenaica* Willd to environmental factors in two sites differing in their annual rainfall (Sierra de Gata, Spain)

M Rico, HA Gallego, G Moreno, I Santa Regina

Instituto de Recursos Naturales y Agrobiologia, CSIC, Apdo 257, 37071 Salamanca, Spain

Summary — *Quercus pyrenaica* natural forests located in the Sierra de Gata (Salamanca Province, Spain) were studied. Two permanent sampling sites were selected at the two extremes of a rainfall gradient in this area. Diurnal courses of transpiration rate, stomatal conductance and leaf water potential were determined approximately every 2–3 weeks in 1991 and 1992 during the active leaf period at different levels in the tree canopy. Current variations in photosynthetically active radiation (PAR) incident to the leaf surface, air and leaf temperature, vapour pressure deficit (VPD) and soil moisture were also measured. Boundary-line response curves between leaf conductance and four variables were studied to determine the general stomatal response patterns. Leaf conductance increased rapidly at first, with small increases in PAR. Above 50 µmol m^{-2} s^{-1}, no additional increases in conductance were observed. The optimum temperature ranged between 18 and 22 °C. Conductance remained constant at low and moderate VPD values and strongly decreased after a given threshold value (2.4 KPa). The response was sharper at the humid site. Beyond a threshold leaf water potential level (–2 MPa), stomatal conductance decreased rapidly as water potential continued to decline.

Quercus pyrenaica / stomatal conductance / leaf water potential / deciduous oak

Résumé — **Réponse stomatique de *Quercus pyrenaica* Willd aux facteurs de l'environnement dans deux forêts différant par la pluviosité annuelle (Sierra de Gata, Espagne).** *Cette étude a été menée dans des forêts naturelles de* Quercus pyrenaica *Willd situées dans la Sierra de Gata (province de Salamanque, Espagne). Deux parcelles permanentes correspondant aux deux extrêmes d'un gradient pluviométrique ont été sélectionnées dans cette région. Durant les années 1991 et 1992, l'évolution journalière de la transpiration foliaire, de la conductance stomatique et du potentiel hydrique foliaire a été déterminée à différents niveaux de l'arbre lors de la phénophase feuillée ; les variations de rayonnement photosynthétiquement actif (PAR) incident sur la surface de la feuille, de la température de l'air et de la feuille, du déficit de pression de vapeur (VPD) et l'humidité du sol à différentes profondeurs ont été mesurées. Afin de déterminer le modèle global de réponse stomatique, on a analysé les réponses individuelles de la conductance stomatique par rapport à quatre variables. La conductance stomatique croît rapidement avec le PAR aux faibles valeurs d'éclairement. À partir de 50 µmol m^{-2} s^{-1}

on n'observe plus d'augmentation de cette conductance stomatique. La température optimale varie entre 18 et 22 °C. La conductance stomatique reste constante avec des valeurs faibles et modérées de VPD et décroît brusquement à partir d'une valeur seuil (2,4 KPa). La réponse est plus prononcée dans la parcelle la plus humide. En ce qui concerne le potentiel hydrique, il se produit une rapide diminution de la conductance à partir d'une valeur seuil (–2 MPa). À partir des fonctions partielles extraites des réponses individuelles à chaque facteur, on a élaboré un modèle empirique du fonctionnement stomatique suivant la formulation décrite dans la bibliographie. Pour la validation du modèle, une corrélation linéaire a été établie entre conductances mesurées et calculées à l'aide du modèle. Cependant, une analyse plus en détail montre que le modèle ne restitue pas tout à fait correctement les variations de conductance stomatique mesurées.

Quercus pyrenaica */ conductance stomatique / potentiel hydrique / chênes caducifoliés*

INTRODUCTION

Among the environmental factors affecting stomatal opening, solar radiation, soil water availability, atmospheric vapour pressure deficit and temperature are known to be important (Schulze, 1986; Winkel and Rambal, 1990; Turner, 1991).

Whereas only a few studies have been made of certain intrinsic factors (such as leaf age [Field, 1987], position in the canopy and hydraulic architecture [Tyree and Ewers, 1991], internal CO_2 concentration [Jarvis, 1986], hormonal equilibrium, previous growing conditions and nutrient availability [Chapin, 1991; Kleiner et al, 1992]), several models have been proposed that relate stomatal aperture to simultaneous variations in environmental factors and plant water potential at leaf level (Jarvis, 1976; Avissar et al, 1985; Lloyd, 1991; Jones, 1992) and at canopy and regional scale (Jarvis, 1980; Jarvis and McNaughton, 1986; McNaughton and Jarvis, 1991).

One approach used to determine the stomatal response to environmental factors is the boundary-line analysis, which may approximate the response when no other factors are limiting. The argument for the existence of a boundary line is biological rather than mathematical (Webb, 1972). This approach is difficult to quantify statistically since the upper points that define the

boundary line are measured with some degree of error (Jones, 1992). Perhaps the best method for analysing stomatal conductance is to use a multiplicative model (Jarvis, 1976) with appropriate nonlinear components where the individual functions are obtained from environmental studies.

Although water relations in sclerophytic oak species have been well documented (Rambal and Leterme, 1987; Salleo and Lo Gullo, 1990; Oliveira et al, 1992; Rambal, 1992; Sala, 1992; Sala and Tenhunen, 1994), there have been fewer studies on deciduous oak species (Chambers et al, 1985; Kubiske and Abrams, 1992; Epron and Dreyer, 1993). However, the functional characteristics of these species are of interest for understanding different adaptive mechanisms.

The aim of this work was to study the effects of weather variables and leaf water potential on the stomatal response of *Quercus pyrenaica* Willd grown in the field under Mediterranean climatic conditions.

Q pyrenaica, whose chorology corresponds to the southwestern region of Europe, is a yet poorly studied deciduous Mediterranean oak species with a short growing season, which might govern its distribution. The water relations of *Q pyrenaica* differ from that reported for other deciduous oaks (Acherar and Rambal, 1992); this could be related more to environmental con-

ditions than to the actual physiology of the tree (Gallego et al, 1994).

In order to interpret plant responses to fluctuations in several major environmental factors, a boundary-line analysis was applied. A semi-empirical model of stomatal conductance was used to improve understanding of the sensitivity to water deficit in deciduous oak species, in contrast to that of the evergreen species described by other authors.

MATERIALS AND METHODS

The study was carried out in *Quercus pyrenaica* natural forests, classified as *Quercion robori-pyrenaicae* communities, located in the Sierra de Gata (Salamanca Province, Spain).

Two permanent sampling sites (Fuenteguinaldo [FG]: 40°2'40"N, 3°0'50"W, 870 m asl and Navasfrías [NV]: 40°17'N, 3°10'27"W, 1 000 m asl) were selected at the two extremes of a rainfall gradient in this area (annual mean precipitation ranging from 720 mm at FG, with characteristics of greater continentality according to the hygrocontinentality index of Gams, to 1 580 mm at NV, with more oceanic characteristics). The climate is humid Mediterranean with most rainfall in the cold part of the year and no rainfall during the warm season. The soils are humic cambisols.

Differences in the rock substrate (calcoalkaline granite at FG and schists and graywackes at NV), vegetation structure, tree-cover density (730 trees/ha at FG and 820 trees/ha at NV), tree biomass (98 Tm/ha at FG and 64 Tm/ha at NV), leaf area index (LAI) (FG: 2.57 in 1991 and 1.85 in 1992; NV: 1.75 in 1991 and 1.30 in 1992), mean tree height ($\approx$12 m at FG and $\approx$13 m at NV) and soil water availability (usable water at 110 cm depth is 146 mm at NV and 131 mm at FG) were considered.

Rainfall, global shortwave radiation, air temperature, relative humidity and wind velocity were recorded as hourly means at different canopy levels (meteorological station at 13 m in FG and 15 m in NV, approximately 1 m over the canopy top), with a Starlog 7000B (UNIDATA).

Soil water content was measured with a neutron moisture gauge (TROXLER 3321A 100mc

of Americium/Berylium) in 12 access tubes both stands. Soil water was measured every 20 cm from 0 to 100 cm depth, and approximately every month for 3 years (1990–1992). Calibration curves for each layer at each site were determined from gravimetric samples and dry bulk density according to Haverkamp et al (1984).

Two towers, 13 m high up to the canopy top, were also installed at the permanent sampling sites, to afford access to the different canopy levels.

During each sampling time, four trees at each site were sampled at four canopy levels. Two leaves from each tree were measured at each level. The sampling was sometimes reduced in certain daily measurements (predawn or sunset) in order to obtain a more efficient sampling for comparative effects among levels, and also at the end of the growing season due to leaf senescence. All records were made on the same leaves except for the leaf water potential.

The diurnal courses (measurements made every 2 h from predawn) of photosynthetically active radiation (PAR) incident to the leaf surface, abaxial leaf surface temperature (T_l), air temperature near the leaf (T_a), transpiration rate (E), stomatal conductance (g_s) and leaf water potential (ψ) were measured along the growing season (June–October) in 1991 (18 June, 9 July, 30 July, 13 August, 4 September, 3 October and 26 October in FG and 19 June, 8 July, 29 July, 12 August, 3 September, 1 October and 30 October in NV) and 1992 (1 July, 23 July, 23 September and 7 October in FG and 2 July, 22 July, 18 August, 22 September and 8 October in NV). These measurements were operated with a Li-Cor LI-1600 steady-state porometer (Li-Cor Inc, Lincoln, NE, USA, with a 1600-01 Narrowleaf aperture cap with a total exposure area of 1 cm^2) and a Scholander pressure chamber. It should be noted that while the T_l, g_s and E measurements made here are useful in a comparative sense, the data obtained do not represent actual in situ rates, since the leaves sampled were subject to boundary-layer disturbance and possible modifications in T_l during measuring (Tyree and Wilmot, 1990). Variations in vapour pressure deficit (VPD) were calculated from the wet and dry bulb air temperatures, measured with a psychrometer at the top of the canopy.

The semi-empirical model of stomatal conductance used has been described by Jarvis (1976), Winkel and Rambal (1990) and Jones (1992). This model is based on known relation-

M Rico et al

ships between stomatal conductance (g_s, mmol
m^{-2} s^{-1}) and PAR (µmol m^{-2} s^{-1}), VPD (KPa),
T_a (°C) and leaf water potential (ψ MPa). Its gen-
eral form is:

$$g_s = g_{sm}.g(PAR).g(T_a).g(VPD).g(\psi) \qquad [1]$$

where g_{sm} is the maximum conductance of a
given species and each g is the partial function for
the indicated independent variable ($0 \le g \le 1$).

The parameters that describe stomatal open-
ing in response to the four independent variables
were estimated from field measurements by least
squares regression. Boundary-line response
curves were used to analyse these single vari-
able responses of g.

RESULTS

A schematic representation of the seasonal
trend of rainfall, Penman-PET, soil water
content and predawn leaf water potential is
shown in figure 1. The four parameters fol-
low a similar pattern at both plots; during
the summer months there was low rainfall
and high PET, without significant differences
between plots; in contrast, spring and
autumn rainfall was clearly larger in the wet
site, with significant differences ($P < 0.01$).
In addition, both soil water amounts and soil
water consumption are significantly higher at
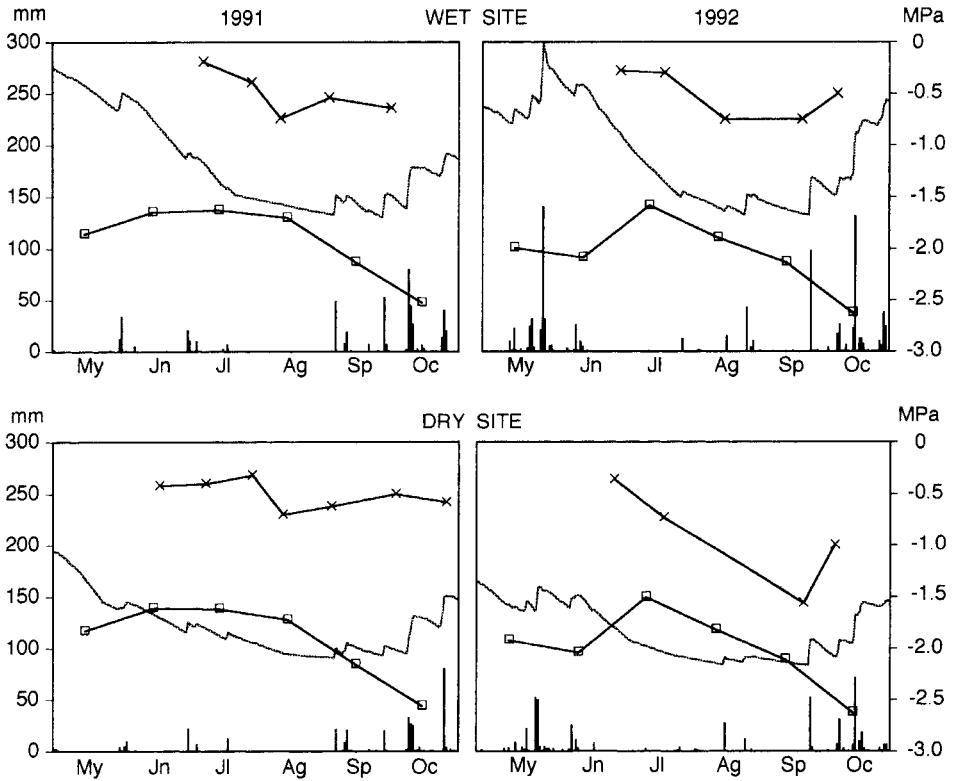the wet site ($P < 0.01$).

Fig 1. Representation of the seasonal trend of soil water content (dotted line), daily rainfall (bars, mul-
tiplied by 2 for a better visualization), monthly PET (lines with squares) and predawn leaf water poten-
tial (lines with Xes), as measured on two *Quercus pyrenaica* stands in the Sierra de Gata (Spain).

At both plots, the available soil water was practically exhausted halfway through the summer, a situation of water deficit arising; this occured earlier and lasted longer at the dry site. Nevertheless, predawn leaf water potentials were not very low, and differences between plots were only found at the end of the summer of 1992, with a lower value at the dry site. The soil water storage declined bud burst to the end of the summer by 119 mm in the wet site and 78 mm in the dry site in 1991; in 1992, by 161 and 75 mm, respectively.

Detailed descriptions of these results have been published previously (Gallego et al, 1994; Moreno et al, 1996). In short, it can be stated that was soil water deficit slightly more pronounced and longer at the dry site.

Boundary-line analysis of stomatal conductance

Boundary-line response curves between leaf conductance and four variables – PAR, air temperature (these two were measured with the porometer), VPD (measured with the psychrometer at the top of canopy) and leaf water potential (measured with the Scholander chamber) – were studied to determine the general response patterns. The results for the two sites with all the mean values for canopy level (450 values averaged out from four trees and two leaves per tree, were taken into account) are shown in figures 2 to 5.

Leaf conductance increased rapidly at first, with small increases in PAR (fig 2). Above 50 µmol m^{-2} s^{-1}, no additional increase in conductance was observed as the stomata presumably became light saturated. The drier site (FG) appeared to display light saturation values lower than those reported for the more humid site (NV).

The high conductance values (above 180 mmol m^{-2} s^{-1}) sometimes reached at the drier site (FG) for a PAR below 10 µmol m^{-2} s^{-1} suggests that the stomata sometimes remained partially open in the dark (Foster, 1992). This was probably an artefact due to the presence of dew on the leaves during early morning.

According to Jones (1992), the relationship between conductance and PAR can be described by the equation:

$$g(PAR) = 1 - \exp(-PAR/K1) \qquad [2]$$

The $K1$ parameter value is 16.6904 µmol m^{-2} s^{-1}. Once the fit has been obtained for 95% relative stomatal conductance, a PAR of 50 µmol m^{-2} s^{-1} is reached.

The boundary-line response between conductance and temperature (fig 3) suggests an increase in conductance from low to moderate temperature followed by a decrease in conductance as temperature increases above an optimum level. This optimum temperature ranges between approximately 18 and 22 °C, the highest conductance values for this range being found at the more humid site (NV).

The response curve may be written (Jones, 1992):

$$g(T_a) = 1 - K2(T_a - T_o)^2 \qquad [3]$$

where T_a is air temperature and T_o is the optimum temperature for stomatal opening ($g(T_o)=1$). Values of $T_o = 20.55$ °C and of $K2 = 0.00381$ °C^{-2} were obtained with our data.

In different species, the increase in VPD leads to a response that is reflected in stomatal closure (Schulze, 1986; Turner, 1991). Stomatal behaviour with respect to humidity may be linear or nonlinear (Jarvis, 1976; Winkel and Rambal, 1990) depending on the type of control mechanism. The boundary-line response (fig 4) shows that conductance initially remains constant at low
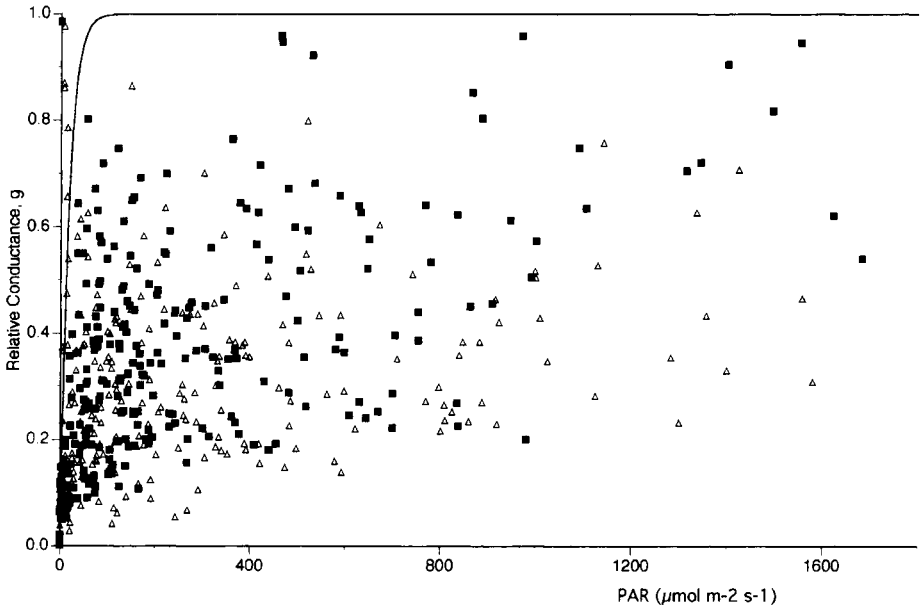
Fig 2. Scatter diagram of stomatal conductance (g) against photosynthetically active radiation (PAR) measured on the two *Quercus pyrenaica* sites. Partial function derived from the boundary-line response curve. $\triangle$: dry site; $\blacksquare$: wet site; $---$ boundary line: $g(\text{PAR}) = 1 - e^{-\text{PAR}/16\,6904}$.
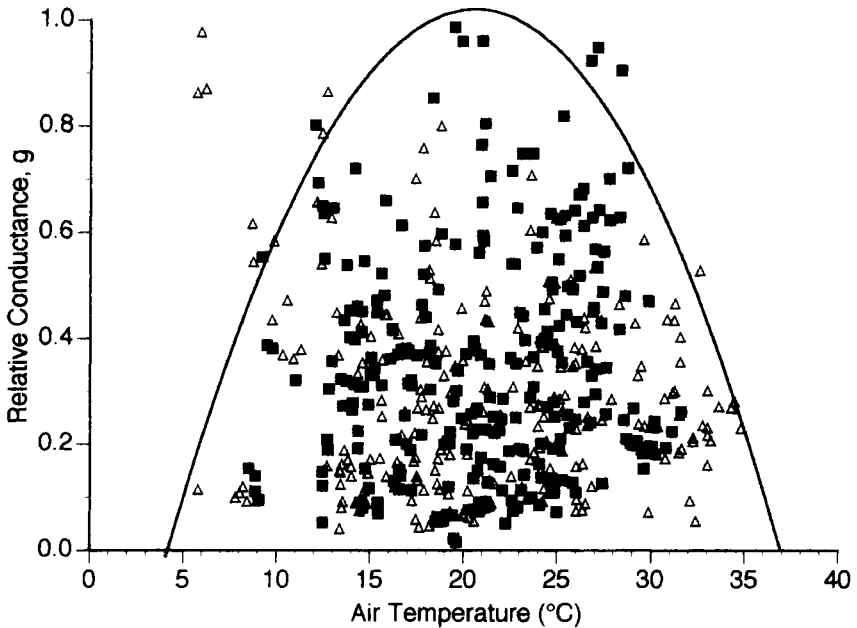

Fig 3. Scatter diagram of stomatal conductance (g) against air temperature (T_a) measured on the two *Quercus pyrenaica* sites. Partial function derived from the boundary-line response curve. $\triangle$: dry site; $\blacksquare$ wet site; $---$: boundary line: $g(T_a) = 1 - 0.00381\,(T_a - 20.55)^2$.

and moderate VPD values and strongly decreases after a VPD threshold (2.4 KPa). In view of the distribution of points in the figure, this decrease is more attenuated but begins earlier at the drier site (FG), and shows a more linear tendency typical of species adapted to situations of greater aridity, with a more conservative adaptive strategy. The response is stronger at the more humid site (NV), apparently indicating a weaker functional adaptation and a less conservative adaptive strategy. This leads to high conductances being maintained until a threshold is reached, after which a sharp decline occurs, possibly indicating a greater sensitivity to drought of the trees at this site.

According to Jones (1992) and the boundary-line analysis, the relationship applied is:

$$g(VPD) = 1, \text{ if } VPD < 2.4 \text{ KPa}$$
(threshold value)

$$g(VPD) = K3 \exp(-K4\ VPD),$$
$$\text{if } VPD > 2.4 \text{ KPa} \qquad [4]$$

where $K3$ (8.36) and $K4$ (87 KPa^{-1} x 10^{-2}) are parameters estimated from the data set.

The boundary-line plot of conductance against leaf water potential (fig 5) revealed a range of leaf water potential values over which conductance showed little response but remained at the maximum level. At a threshold potential level, a rapid decrease in conductance occurred as potential continued to decline. This threshold value is approximately −2 MPa. Different types of behaviour were detected at each site, although less acute than for VPD. In FG, a better response to the increase in leaf drying was observed, together with a decrease in conductance that began with high Ψ values and showed a less pronounced trend than NV, with a lower threshold value. This again highlights
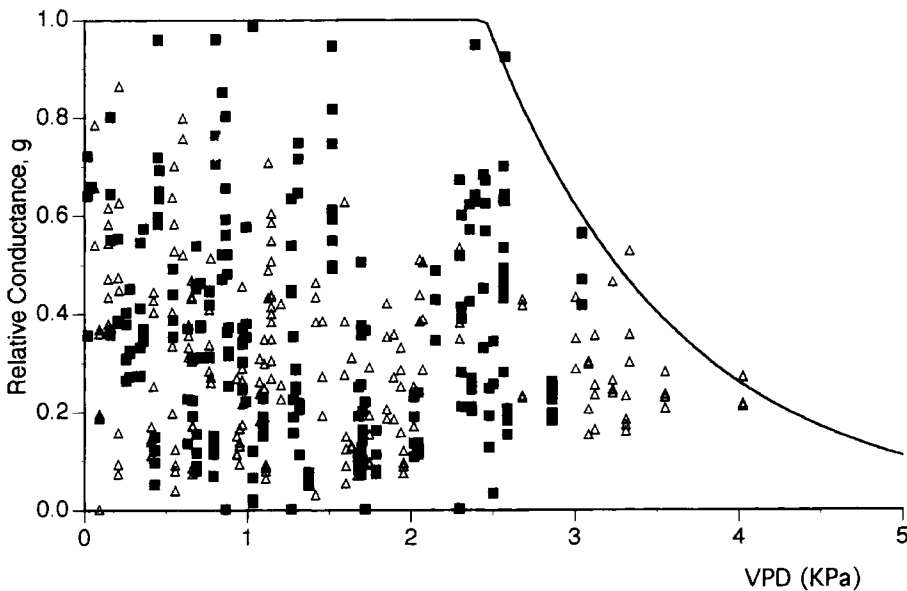

Fig 4. Scatter diagram of stomatal conductance (*g*) against water vapour pressure deficit (VPD) measured on the two *Quercus pyrenaica* sites. Partial function derived from the boundary line response curve. △: dry site; ■: wet site; − − −: boundary-line: VPD < 2.4 KPa, *g* (VPD) = 1; VPD > 2.4 KPa, *g* (VPD) = 8.3568 e$^{-0.86601\ VPD}$.
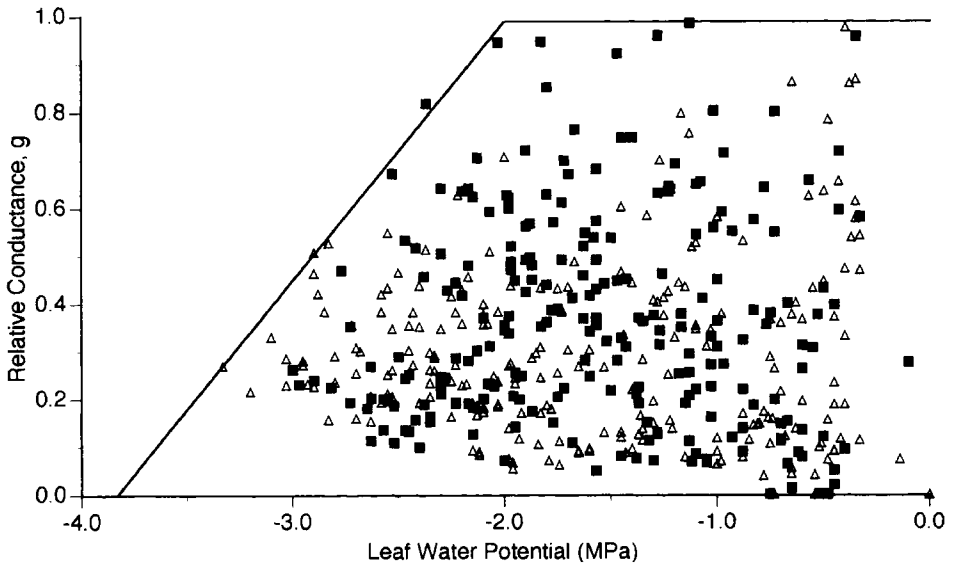
Fig 5. Scatter diagram of stomatal conductance (g) against leaf water potential (ψ) measured on the two *Quercus pyrenaica* sites. Partial function derived from the boundary-line response curve. $\triangle$: dry site; $\blacksquare$: wet site; $---$ boundary line: $0 > \Psi > -2$, $g(\Psi) = 1$; $-2 > \Psi > -3.8$, $g(\Psi) = 0.55187 \Psi + 2.10456$.

the adaptation of the trees to more xeric conditions, with a more conservative strategy than at NV.

The response of conductance to leaf water potential can be modelled (Jones, 1992) as follows:

$$g(\psi) = 1, \text{ if } 0 > \psi > -2 \quad\quad [5]$$
$$g(\psi) = \psi K5 + K6, \text{ if } -2 > \psi > -3.8$$

where $K5$ (55 MPa^{-1} x 10^{-2}) and $K6$ (2.10) are parameters estimated from the data set.

Predictive model based on boundary-line analyses

The predictive model (eq [1]) was derived from the equations ([2] to [5]). The model requires eight parameters: g_{sm}, $K1$, $K2$, T_o, $K3$, $K4$, $K5$ and $K6$. The field measurements of each independent variable were randomly assigned to one of two data sets, the first for the estimation of the model and the second for its validation (eg, Jarvis, 1976; Chambers et al, 1985; Winkel and Rambal, 1990; Jones, 1992; McCaughey and Iacobelli, 1993).

Of all the measurements made, those that possibly implied extreme phenological states, especially leaf senescence, were discarded, together with those involving meteorological or technical problems. Of the remaining measurements (approximately 300, considering average values by canopy level) two-thirds, including complete days, were chosen to run the model (eq [1]) and one-third for validation.

Maximum stomatal conductance was estimated from the field measurements by taking the highest value observed (eg, Jarvis, 1976; Chambers et al, 1985; Winkel

and Rambal, 1990; Jones, 1992). The g_{sm} included in the model is 380 mmol m^{-2} s^{-1} (mean of eight replicated measurements), a value similar to those given for other deciduous oaks (Reich and Hinckley, 1989) in field conditions, but lower than those reported by Acherar and Rambal (1992) under experimental conditions. The values of the other parameters, previously explained in the partial functions, are as follows:

$K1$ = 16.69 µmol m^{-2} s^{-1}
$K2$ = 38 °C^{-2} x 10^{-4}
T_o = 20.55 °C
$K3$ = 8.36
$K4$ = 87 KPa^{-1} x 10^{-2}
$K5$ = 55 MPa^{-1} x 10^{-2}
$K6$ = 2.10

The model derived from the first data set (n = 200, r = 0.83293, P = 0.0001) included the following range of environmental variables:

PAR (µmol m^{-2} s^{-1})	0–1 623
T_a (°C)	8.5–34
VPD (KPa)	0.06–4.02
ψ (MPa)	−3.3– −0.1

Validation of the model

The model was tested by comparing the observations of the second data set (n = 79) with the stomatal conductances estimated from the input variables in this set, with the parameters derived from the first set of measurements. The measured and simulated values of stomatal conductance are significantly correlated (fig 6, r = 0.87346, P = 0.0001).

Although acceptable fits were obtained when all the points were considered together, a detailed study of daily behaviour (fig 7) revealed alterations worthy of comment. By way of an example, 2 days were taken, with similar environmental characteristics but from different years. As can be seen, on comparing the 2 years, the behaviour was very similar for each site. In the case of FG, it should be noted that the data refer to the first hours of the day, and therefore their general behaviour is well defined. In all cases, the simulated values tend to approximate the observed values more closely when the conductances are low. The general scheme of stomatal functioning fits the model, particularly as regards
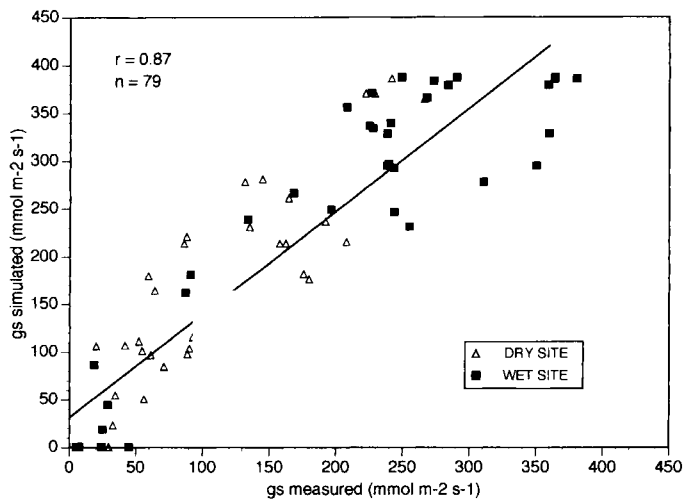

Fig 6. Relationship between measured and simulated values of stomatal conductance (g_s) (r is the coefficient of correlation; n is the number of points). Δ: dry site; ■: wet site.
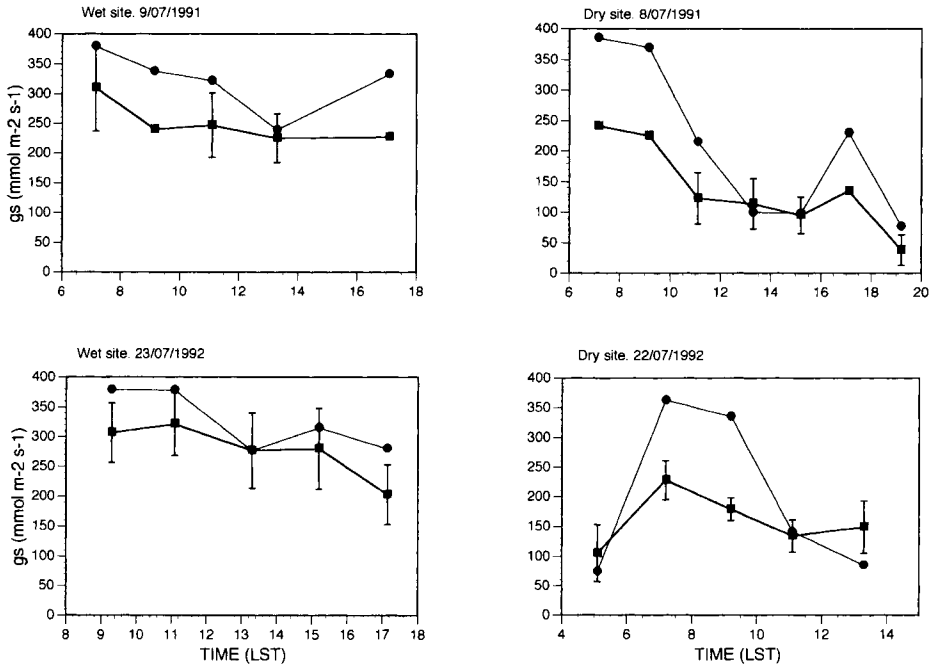
Fig 7. Diurnal variations of observed and simulated stomatal conductance (g_s). The vertical bars show the standard deviation of the observed values. —■—: observed; —●—: simulated.

stomatal closure at midday. However, the more pronounced departure at high levels of conductance suggests that maximum conductance is limited by other factors which have not been included in the model. In this sense, soil water status (Winkel and Rambal, 1993; Moreno et al, 1996), root water status (Meinzer, 1993) or the proportion of roots in dry soil (Turner, 1991) should be taken into account.

DISCUSSION

The light saturation values (above 50 μmol m^{-2} s^{-1}) are similar to those found by Chambers et al (1985) for *Quercus alba* L (50 μmol m^{-2} s^{-1}), *Q rubra* Lam (65 μmol m^{-2} s^{-1}) and *Q velutina* Lam (50 μmol m^{-2} s^{-1}), all of them deciduous oaks, and much

lower than those reported by Sala (1992) for *Q ilex* (400–600 μmol m^{-2} s^{-1} in sun exposed leaves and 100–300 μmol m^{-2} s^{-1} in shaded leaves). In an approximate way, it can be said that when conductance is 50% of the maximum the PAR is 10 μmol m^{-2} s^{-1}, a value similar to those reported by Chambers et al (1985) for different deciduous species of the genus *Quercus*.

The type of response obtained for temperature, in the form of a dome-shaped curve, is closer to those described by Jarvis (1976), Winkel and Rambal (1990), Sala (1992) and Foster (1992) than to those published by Chambers et al (1985), where they have a more pronounced maximum, with optimum temperatures from 25 to 27 °C for the three oak species studied. In our case, the optimum temperature observed was somewhat low and possibly not corre-

sponding to reality because of the interaction of temperature and VPD on conductance (Jarvis, 1976).

For VPD, the behaviour of other deciduous *Quercus* species is closer to that detected at NV (Chambers et al, 1985), with similar threshold values. The VPD value corresponding to a conductance of 50% of the maximum is 3.4 KPa, a value similar to those reported by Chambers et al (1985): 3.9 KPa for *Q rubra*, 3.4 KPa for *Q alba* and 3.5 KPa for *Q velutina*.

The threshold value for leaf water potential, approximately −2 MPa, is very close to those published by Chambers et al (1985): −1.84 MPa for *Q rubra*, −2.3 MPa for *Q alba* and −2.45 MPa for *Q velutina*. Similar responses have been reported by Jarvis (1976) and Winkel and Rambal (1990). However, Foster (1992) did not detect this type of response.

In the boundary-line analysis of stomatal conductance, the different responses of the sites studied become clear. With more favourable environmental conditions (water availability), NV reached higher conductance values, although stomatal functioning fell off sharply starting with a threshold value, mainly VPD and Ψ. Under drier conditions, FG showed more homogeneous conductance values, with a less pronounced but more immediate and constant response to environmental variability. This could be interpreted as a kind of functional adaptation, implying a more conservative strategy. According to the terminology used by Jones (1992), *Q pyrenaica* would show a more pessimistic water use behaviour at the dry site (FG), and a more optimistic one at the wet site (NV). *Q petraea* (Matt) Liebl and *Q robur* L, two mesophytic oak species, also display a certain degree of tolerance to drought (Epron and Dreyer, 1993): the main features of this tolerance are probably deep rooting, maintenance of high transpiration and stomatal conductance during drought, and low susceptibility to xylem embolism

(Cochard et al, 1992). Plant response to stress involves several mechanisms acting over large time scales; hydraulic resistance to water flow between roots and leaves and the root/shoot ratio (Winkel and Rambal, 1990) could provide an explanation for the differences in water relations between the two sites studied.

That this adaptation implies genotypic differences is no more than a hypothesis, which is why it seemed best to treat both sites together throughout this study (the most pronounced differences were detected in the response to VPD, and, to a lesser extent, in Ψ), while discussing the differential behaviour in a general way. Such intraspecies variability in water relations has also been reported by other authors for several Mediterranean oaks. Oliveira et al (1992), suggested that, for *Q suber*, this is related to hydraulic conductivity differences in the root-to-leaf pathway; Kubiske and Abrams (1992) found ecotypical differences in ecophysiology in *Q rubra* that are consistent with site moisture conditions.

In the application of the model, the larger differences between observed and simulated conductance in the case of FG can be explained in part by the overall formulation, although the stomatal behaviour pattern is perfectly clear.
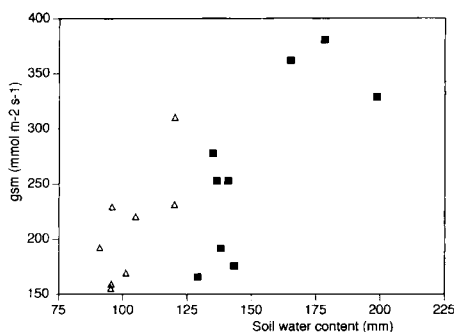

Fig 8. Relationship between soil water content (upper 110 cm) and maximum daily stomatal conductance (g_{sm}). $\triangle$: dry site; $\blacksquare$: wet site.

The model affords overestimated values possibly due to the decrease in daily maximum conductance as the soil dries up (fig 8). In this sense, the diurnal variations in g_s cannot be simply attributed to the influence of leaf water potential or VPD. Winkel and Rambal (1993) suggest that, besides physiological and weather variables, the leaf water relations are partially mediated by soil and/or whole-plant hydraulic factors. Indirect evidence suggested an influence of soil water status on the diurnal stomatal activity. According to Meinzer (1993), leaf water status does not always play a role in causing stomatal closure in droughted plants. Chemical signalling between the roots and the shoot represents a feedforward means of regulating leaf water status, that links stomatal conductance to the hydraulic capacity of the soil and roots to supply water to the leaves. This coupling of vapour phase with liquid phase conductance serves to maintain nearly constant leaf water status as the soil dries. Meinzer (1993) concluded that optimal control of xylem embolism would require that stomata respond to root water status in addition to leaf water status.

These types of limitation of the empirical model have been previously noted. According to Jarvis (1976), interpretation of the response to environmental variables in this way is useful in practical terms in the sense that the parameters can be used to make predictions, but it is not wholly satisfactory. Due to the functional relationships, these predictions are only useful at the original site. The parameters are of limited physiological meaning because the model is descriptive and not mechanistic. These aspects are clearly shown in our study, where the differential behaviour of the same species at two sites barely 15 km apart is highlighted. Regarding the limitations pointed out by Chambers et al (1985), one must add the one due to spatial variability. The generality of these models needs to be widely tested in a broader range of environmental conditions, including conditions of water deficit (Turner, 1991). Comparative studies collecting a large amount of information (Acherar and Rambal, 1992) will therefore be of great interest.

CONCLUSION

Boundary-line analysis suggests that PAR was the primary influence on conductance, with light saturation occurring above 50 μmol m^{-2} s^{-1}. There appeared to be an optimum T_a for conductance between 18 and 22 °C. In this study, Q pyrenaica showed evidence for threshold VPD (2.4 KPa) and ψ (–2 MPa) for stomatal closure.

Although no clear situations of stress were detected, Q pyrenaica can be said to be sensitive to environmental variations, a decrease in stomatal activity having been observed that can sometimes be identified with a certain degree of stomatal closure, in accordance with the daily variations in environmental factors and water status. Its rather nonconservative water-use strategy (Rambal, 1984), together with the resistance to water flow, on days of high VDP, elicits low leaf water potentials and decrease in stomatal activity.

Regarding the sites studied, the results offered here point to the existence of a certain functional adaptation at Fuenteguinaldo to drier conditions whereas at Navasfrías, at the most humid extreme of the rainfall gradient, the trees seem to show greater sensitivity to environmental fluctuations. Further studies directed at confirming this should be performed.

ACKNOWLEDGMENTS

acknowledged. The English translation was supervised by N Skinner.

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