# CHAPTER 7

# A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean

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***submitted***

> Q: ***To begin with, could you describe this work?***
> A: ***Yes, of course. What I've done is change a glass of water into a full-grown oak tree without altering the accidents of the glass of water.***
>
> [...] Q: ***Haven't you simply called this glass of water an oak tree?***
> A: ***Absolutely not. It is not a glass of water anymore. I have changed its actual substance. It would no longer be accurate to call it a glass of water. One could call it anything one wished but that would not alter the fact that it is an oak tree.***
>
> [...] Q: ***Was it difficult to effect the change?***
> A: ***No effort at all. But it took me years of work before I realised I could do it.***
>
> (Michael Craig-Martin, from the interview
> accompanying the work ***An Oak Tree*** (1973))

## Resum

Hi ha un creixent interès en l'estudi dels efectes del canvi climàtic sobre la vegetació. A la regió mediterrània, l'efecte dominant del canvi climàtic serà probablement a través de la modificació del balanç hídric. En el present treball presentem un model orientat a predir la mortalitat induïda per sequera en plantes llenyoses sotmeses a diferents règims climàtics. El model té una base fisiològica i simula el transport d'aigua a través de plantes individuals, les quals poden estar isolades o competir per un recurs hídric comú. Suposem que la mortalitat que es pot produir durant un episodi de sequera aguda es deu a la incapacitat de les plantes de transportar aigua fins les fulles. En el cas particular que estudiem aquí, es comparen dues espècies perennifòlies, ***Quercus ilex*** i ***Phillyrea latifolia***, que van resultar diferentment afectades per l'eixut extrem que va tenir lloc a l'est d'Espanya l'estiu de 1994. Mentre en algunes poblacions de ***Q. ilex*** es van arribar a assecar completament el 80% dels individus, ***P. latifolia*** no va mostrar danys aparents. Aquestes dues espècies conviuen en un alzinar que va ser estudiat durant els anys 1999 i 2000. Les mesures de flux de saba obtingudes en aquest alzinar es van utilitzar per calibrar el model mitjançant una aproximació de tipus GLUE. L'única diferència entre espècies que es va introduir ***a priori*** va ser la major vulnerabilitat de ***Q. ilex*** a l'embolisme al xilema, basada en mesures realitzades a la mateixa zona d'estudi. Durant la calibració, la informació proporcionada per les mesures de flux de saba es va utilitzar per retenir els conjunts de paràmetres més versemblants per cada espècie, els quals van ser utilitzats en les simulacions subsegüents. El model va ser capaç de simular amb una exactitud raonable tant la transpiració com la mortalitat mesurada per ambdues espècies a l'àrea d'estudi. En les simulacions de canvi climàtic es van explorar dos factors: l'augment en la temperatura mitjana (+1.5, +3, +4.5ºC) a través del seu efecte en $E_T$, i la durada de l'eixut estival. Sota qualsevol dels escenaris les mortalitats van ser majors per ***Q. ilex***: mentre que els resultats van indicar que aquesta espècie era capaç de resistir amb mortalitats de menys del 5% sequeres de fins a 84-94 dies, la mortalitat de ***P. latifolia*** assolia el 5% entre els dies 133 i 150. Per eixuts de més de tres mesos, durada aproximada dels estius secs que es produeixen actualment a la zona d'estudi, la mortalitat de ***Q. ilex*** augmentava ràpidament. Aquests resultats són discutits en relació als possibles impactes a llarg termini que el canvi climàtic pot tenir sobre els alzinars.

## Abstract

The potential effects of climate change on vegetation are of increasing concern. In the Mediterranean region, the dominant effect of climate change is expected to be the modification of water balance. In this paper we present a model developed to predict drought-induced mortality of woody plants under different climatic scenarios. The model is physiologically-based and simulates water transport within individual woody plants, which can be isolated or competing for a common water pool. The key assumption of the model is that, within a drought event, plant mortality is caused by the inability of plants to transport water to the leaves. In the particular application that we report in this study, we compare two evergreen species, ***Quercus ilex*** and ***Phillyrea latifolia***, which were very differently affected by the acute drought that occurred in E Spain in summer 1994. While in some ***Q. ilex*** populations the amount of individuals that dried completely was up to 80%, ***P. latifolia*** showed no apparent damage. This two species grow together in a Holm-oak forest in NE Spain that was monitored during the years 1999 and 2000. A Generalised Likelihood Uncertainty Estimation (GLUE) approach was used to calibrate the model against sap-flow measurements. The only difference between species that was introduced ***a priori*** was that ***Q. ilex*** was more vulnerable to xylem embolism than ***P. latifolia*** (based on our own measurements in the study area). During the calibration the information provided by the measured sap flows was used to retain the more likely parameter sets for each species. These parameter sets were used in all the following simulations. The model was able to accurately simulate both transpiration dynamics and measured mortalities for the two species in the study area. In the simulations under climate change two factors were explored: the increase in mean temperature (+1.5, +3 and +4.5ºC) through its effect on $E_T$, and the duration of summer drought. Under any of the scenarios, mortalities were much higher for ***Q. ilex***: while this species was predicted to survive with less than 5% mortality droughts of up to 84-94 days, the mortality of ***P. latifolia*** reached 5% between the day 133 and the 150. For droughts longer than three months, which is approximately the current drought duration in the study area for dry years, the mortality of ***Q. ilex*** increased sharply. These results are discussed in relation to the possible long-term impacts of climate change on ***Q. ilex***-dominated forests.

## Introduction

Human activities are expected to cause a rapid increase in global temperature and evaporation rate during the XXI century (IPCC 2001). For the western Mediterranean basin, most climatic models predict that mean temperature will rise 2-4ºC (Palutikof & Wigley 1996, Rambal & Hoff 1998), with a corresponding increase in potential evapotranspiration (Palutikof ***et al.*** 1994). An increase both in the frequency and the intensity of acute droughts in middle latitudes is also expected as a consequence of climate change (IPCC 2001). Some of these changes are already occurring in NE Spain: Piñol ***et al.*** (1998), for example, found that between 1910 and 1994 there was a significant increase in mean temperature and daily thermal oscillation, whereas minimum relative humidity decreased and rainfall showed no significant trend. In some areas, the effects of these climatic changes on the physiology, phenology and distribution of individual species have already been reported (Hugues 2000).

In water-limited areas, such as the Mediterranean basin, the main effects of climatic changes are likely to be through their effect on the water balance (Shaver ***et al.*** 2000). Recent drought events (in particular the one that occurred in the summer of 1994 in NE Spain) have shown that some woody species that are currently very important in the Mediterranean landscape (***e.g.,*** ***Quercus ilex***, ***Pinus sylvestris***) are close to their limit to cope with water stress (Lloret & Siscart 1995, Peñuelas ***et al.*** 2000, Martínez-Vilalta & Piñol 2001). If the climate gets drier, the observed drought-induced dieback will result in vegetation shifts, particularly at the arid edges of the distribution areas of these species, as documented in other regions (***e.g.,*** Allen & Breshears 1998, Fensham & Holman 1999). Population changes in a particular area will depend on the interaction among several processes: ***in situ*** adaptation or acclimation, the balance between mortality and the establishment of new individuals, and the arrival of new species. However, for long-lived trees, for whom the anticipated warming will occur during the lifetime of many of today's individuals, adult mortality is likely to be the most critical factor.

There is increasing evidence supporting hydraulic constraints within the soil-plant-atmosphere continuum as a limit for different plant species to cope with water stress (***e.g.,*** Pockman & Sperry 2000). According to the cohesion theory plants absorb water from the soil because a water potential gradient develops between the rhizosphere and the evaporation sites in leaves. As a result, in a transpiring plant, water potential has to decrease in the direction of leaves. If we neglect any capacitance effect:

$$E = -K_h \frac{d\Psi}{dx} \qquad \text{(eq. 1)}$$

where E is the transpiration rate, $d\Psi/dx$ is the water potential gradient, and $K_h$ is the hydraulic conductivity. The whole mechanism depends on the existence of an hydraulic continuum between soil and leaves; if it breaks the plant can no longer acquire atmospheric $CO_2$ without desiccating to death. During a typical drought episode soil water potential decreases to very negative values (easily less than -2 MPa). Under these conditions several processes make it difficult to maintain an hydraulic continuum within the plant. Probably the most important of these processes are: (1) the exponential increase in soil and soil to root resistance to water as the soil dries, and (2) the vulnerability to cavitation of water inside the xylem as water potential becomes increasingly negative (Sperry ***et al.*** 1998). Although several models have studied the limitation to water uptake imposed by these processes (***e.g.,*** Newman (1969) for the first, and Tyree & Sperry (1988) for the second), few models have attempted to integrate them and study how they interact (but see Sperry ***et al.*** 1998), and how, under conditions of extreme drought, they might affect plant survival.

A number of simulation studies have dealt with the effects of climate change on woody plants (see for example the references cited by Loehle (2000) for the particular case of forests). In general these studies have relied on some sort of “climate envelope” approach which, besides the predictive difficulties that poses (Davis ***et al.*** 1998), does not add any information on the mechanisms that explain the responses of the different species. We think that a more mechanistic approach, capable of identifying the critical mechanisms, is also needed.

The model presented here attempts to compare the ability of competing species to cope with extreme drought events and predict how it might change if the climate gets drier. In the particular application that we report in this study, we compare two evergreen species, ***Quercus ilex*** and ***Phillyrea latifolia***, that were very differently affected by the 1994 drought (Lloret & Siscart 1995, Peñuelas ***et al.*** 2000). To do that we calibrated all the parameters of the model using sap flow measurements and the Generalised Likelihood Uncertainty Estimation (GLUE) approach (Beven ***et al.*** 2000). The only difference between the two species that is assumed ***a priori*** was that ***Q. ilex*** was more vulnerable to xylem embolism than ***P. latifolia*** (based on experimental data). Mortality data from the 1994 drought was used to validate the predictions of the model regarding survival of the two species under extremely dry conditions. The aims of the study are: (1) to identify which processes are more critical in determining the vulnerability to drought-induced mortality in both species, and (2) to predict the mortalities of the two species in the study area under different climate change scenarios.

## Material and Methods

### *Study area*

The study area is located in the Prades Mountains, NE Spain (41º 13’ N, 0º 55’ E), at approximately 990 m asl. The climate is Mediterranean, with moderate rainfall (annual mean of 537 mm for the 1981-1995 period) and moderately warm temperatures (10.0ºC mean at Prades, 1000 m asl). The substrate consists of fractured schist, and soils are xerochrepts with clay loam texture. Additional information about the study area can be found in Hereter & Sánchez (1999).

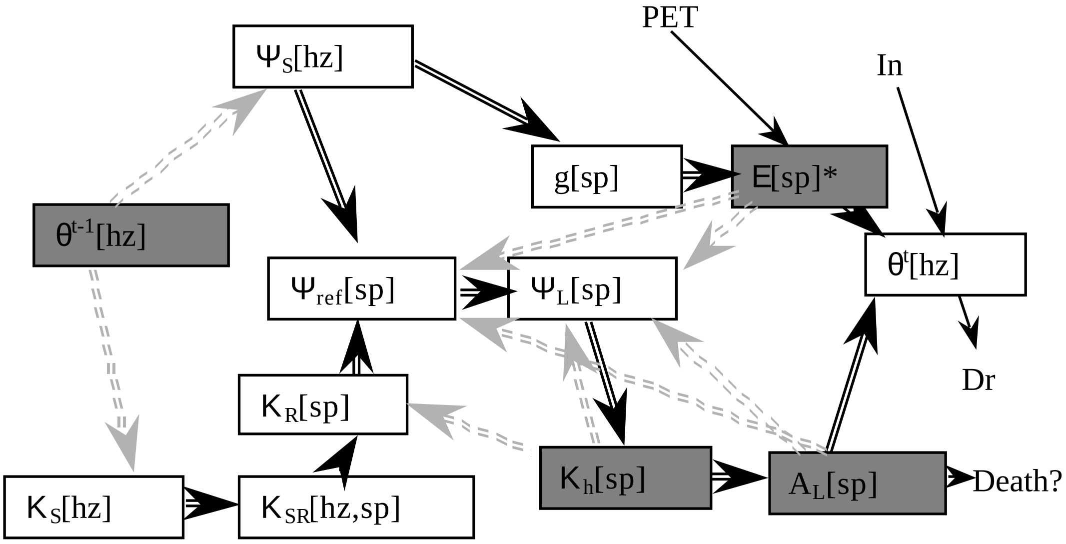


**Figure 1.** Diagram showing the relationships between the different variables in the model (see table 1 for the meaning of the symbols). Solid lines indicate the direction in which the model runs in each time step. Shaded compartments and dotted lines show influences of the previous time step (t-1) on the present one (t).

**Table 1.** Abbreviations used to refer to the model variables and the internal parameters that appear in the text.

| | |
|---|---|
| **Model variables** | |
| ***Plants*** | |
| $A_L$ | Leaf area (m$^2$). |
| E | Transpiration rate (mm$^3$ m$^{-2}$ s$^{-1}$). |
| g | Leaf conductance in relation to the maximum (per unit). |
| $\Psi_{ref}$ | Water potential at the bottom of the trunk (MPa). |
| $\Psi_L$ | Leaf water potential (MPa). |
| $K_R$ | Total conductivity of the root system (mm$^4$ MPa$^{-1}$ s$^{-1}$). |
| $K_h$ | Stem hydraulic conductivity (mm$^4$ MPa$^{-1}$ s$^{-1}$). |
| ***Soil horizons*** | |
| In | Water entering each horizon (mm). |
| Dr | Water flowing out of each horizon to the horizon below (mm). |
| θ | Soil water content (m$^3$ m$^{-3}$). |
| $\Psi_S$ | Soil water potential (MPa). |
| $K_S$ | Bulk soil hydraulic conductivity (mm$^2$ MPa$^{-1}$ s$^{-1}$). |
| ***General*** | |
| R | (Net) rainfall (l m$^{-2}$). |
| $E_T$ | Potential evapotranspiration (l m$^{-2}$). |
| $K_{SR}$ | Soil to root hydraulic conductivity for each horizon and plant (mm$^4$ MPa$^{-1}$ s$^{-1}$). |
| **Internal parameters** | |
| $N_{sp}$ | Number of species (or soil horizons) in the simulation. |
| sp | Species. |
| $D_R$ | _ of the mean distance between adjacent fine roots (mm). Calculated from root density. |
| PLC | Percent loss of hydraulic conductivity (%). |
| hz/hz’ | Horizon. When used as super index denotes that the variable refers only to a particular horizon. |

| | |
|---|---|
| $L_S$ | Soil depth (mm). |
| $R_S$ | Soil radius available to plants (mm). |
| $R_S^o$ | Soil radius available to plants at the soil surface (mm). |
| $A_S$ | Soil area available to plants at the soil surface (mm$^2$). |

## The model

The model simulates water transport within individual woody plants, which can be isolated or competing for a common water pool. An aggregated (big leaf) Soil Plant Atmosphere Continuum (SPAC) approach is used, with Equation 1 driving the flux. Time resolution is one hour, except for leaf area that changes on a daily basis. An outline of the structure of the model is presented in Figure 1 (see also Table 1). The amount of water lost by the plants is assumed to depend (within a time step) on atmospheric demand (potential evapotranspiration, $E_T$) and soil water potential (via stomatal regulation). Water potential in absorbing roots is determined on the one hand by the structure and the water content of the soil and, on the other, by the morphology of the root system. An integrated water potential at the base of the trunk ($\Psi_{ref}$) is then calculated at each time step taking into account the hydraulic status of all the soil horizons within the rooting depth of the plant. Leaf water potential is obtained by subtracting to $\Psi_{ref}$ the fall of water potential due to transpiration flow. Steady-state conditions are therefore assumed, which seems to be reasonable for non-conifer species and the required time resolution (but see Holbrook 1995). A percent loss of hydraulic conductivity (PLC) for the entire xylem is determined by leaf water potential (Sperry 2000). Whenever the PLC is higher than a critical value ($PLC_{AL}$) there is a percent loss in leaf area. Mortality occurs when a plant passes a critical time with less than 5% of the original leaf area (***i.e.,*** ceases to acquire carbon). It is assumed that low leaf water potentials cause no direct damage to the physiological machinery of the leaf (at least over the range down to the values causing a 100 PLC) (Jones & Sutherland 1991).

Climatic data (rainfall and $E_T$) is introduced via data files with measured (or calculated) hourly data. The model can be run with one or more plants in the same soil volume. Competition can be simulated in the sense that when several plants are added, they take water from the same reservoir. The soil is partitioned in different horizons in a way that each plant can absorb water only from the soil volume that is above its maximum rooting depth.

### Soil and soil to roots compartments

The volume of each horizon is calculated assuming that soil radius available to plants decreases exponentially with depth ($R_S = R_S^{o} \times \beta^{L_S}$), to simulate the decline in root density. Rainfall is the only water input to the first horizon. As the main point of the model is to compare different plants in the same place, and rainfall is quantitatively small during dry periods, we neglected interception and assumed that net rainfall equals above canopy rainfall. For each horizon, drainage to the horizon below starts when water content surpasses a critical value ($\theta^*$), and the amount is proportional to the water input. In horizons deeper than a fixed value ($L_S^*$) there is another water input that consists of deep water flow from outside the system. The amount of deep flow is proportional to the volume of a reservoir, which is filled with rainfall and decreases exponentially with time. In all the simulations the reservoir was initialised with 10 mm of water. The values that we assigned to all these parameters in the simulations are best guesses based on our previous knowledge of the system (see Rodà ***et al.*** 1999), but their relevance during dry periods is very low, as showed by previous simulations changing the values even an order of magnitude (data not shown). If we wanted to use the model during wet periods a more thoughtful analysis would be required.

Both soil water potential and soil hydraulic conductivity of each horizon depend on the volumetric water content in the following way (Campbell 1974):

$$\Psi_S = \Psi_c \ (\theta / \theta_{sat})^{-B}$$

(eq. 2)

$$K_S = K_{sat} \ (\theta / \theta_{sat})^{2B+3}$$

(eq. 3)

where the parameter B can be related to soil texture data (Saxton ***et al.*** 1986).

The hydraulic conductivity of the soil is used together with root characteristics to calculate the conductivity of the soil to root pathway (Newman 1969):

$$K_{SR} = \frac{4 \ \pi \ K_S \ d_A \ A_S \ D_R}{Ln(D_R^{\,2} / R_R^{\,2})}$$

(eq. 4)

### *Plant xylem*

First of all a total conductivity for the root system is calculated adding the hydraulic conductivity of the xylem corresponding to the root pathway to the conductivity of the soil to root interface. An integrated water potential at the base of the trunk ($\Psi_{ref}$) is then calculated for each plant. We assume that a plant absorbs water from a horizon proportionally to its soil to root hydraulic conductivity, so $\Psi_{ref}$ is close to the water potential of the wettest horizon available (but always more negative). The following formula is used:

$$\Psi_{ref} = \frac{\sum^{N_{sp}} \left( \prod_{hz' \neq hz}^{N_{sp}} L_S^{hz'} \ \Psi_S^{hz} \ K_R^{hz} \right) - E \ A_L \ \prod^{N_{sp}} L_S^{hz}}{\sum^{N_{sp}} \left( \prod_{hz' \neq hz}^{N_{sp}} L_S^{hz'} \ K_R^{hz} \right)}$$

(eq. 5)

Water potential in leaves is calculated from that reference water potential in the following way:

$$\Psi_L = \Psi_{ref} - \frac{E \ A_L \ L}{K_h}$$

(eq. 6)

Leaf water potential is used to calculate a percent loss of hydraulic conductivity due to xylem embolism in a way analogous to Pammenter & Vander Willigen (1998):

$$PLC = \frac{1}{1 + e^{a \, (\Psi_L - b)}}$$

(eq. 7)

The preceding equation applies when the plant is losing conductivity. When the plant is recuperating it (refilling of previously embolized vessels) an hysteresis effect is supposed (b is divided by 2), so hydraulic conductivity is recovered at a lower rate than it is lost. Although it was previously thought that embolisms were irreversible in trees, several recent studies have pointed out that embolism formation and removal is a dynamic process that may be concurrent with transpiration (Holbrook & Zwieniecki 1999).

Whenever the PLC at the end of the day falls below a critical level ($PLC_{AL}$) that depends on the species, the plant drops a fraction (s) of its leaf area and, hence, its total transpiration rate is equally reduced. Leaf area can not be recuperated within a simulation.

### Transpiration

Stomatal conductance is assumed to depend on soil water potential (in a way similar to Tardieu & Davies (1993)). Although leaf water potential and other environmental variables can have an important role in stomatal activity in the short term (reviewed in Jones (1998)), long-term stomatal dynamics are probably regulated mainly by soil water availability (it should be noted, for example, that leaf and soil water potentials are highly correlated). All the control of transpiration at the leaf level is assumed to be through stomatal activity. The stomatal conductance relative to the maximum is calculated from the following equation:

$$g = \frac{g_{\min} + e^{f\ \Psi_S^{mean}}}{g_{\min} + 1} \qquad \text{(eq. 8)}$$

Transpiration rate (E, in a leaf area basis) is calculated as the product of g and potential evapotranspiration ($E_T$, in a soil area basis):

$$E = \frac{g\ E_T}{LAI} \qquad \text{(eq. 9)}$$

### *Model calibration*

A strict calibration of the model would have required mortality data under known meteorological conditions and with high temporal resolution. As this is extremely difficult to obtain, we used simulated transpiration flows to first calibrate the model. Total sap flow (Granier method; Granier 1987, Smith & Allen 1996) was measured in an hourly basis in 4 ***Quercus ilex*** and 4 ***Phillyrea latifolia*** individuals in the study area during the years 1999 and 2000 (see Chapter 6) for details). In two cases the measurements were very fragmentary during the summer (less than one month of measurements from June to September) and were not used in the calibration or validation of the model. From the 6 remaining combinations of individual and year per species, 4 were used in the calibration of the model (from 4 different individuals, two from each year) and the other two in the validation. A micrometeorological station was operating in the study area during the years 1999 and 2000, in which temperature, relative humidity, PAR, rainfall and wind speed were measured every 30 min. Hourly $E_T$ was calculated using the Penman-Monteith equation (Monteith & Unsworth 1990), assuming a constant $r_c$ of 70 s $m^{-1}$. Soil water content was also monitored during the study period using the TDR methodology (see Chapter 6). The volumetric water content of the first 25 cm of soil measured by 42 sensors was averaged for the beginning of the simulated period and was used to initialise the soil water content in the simulations (0.27 in 1999 and 0.29 in 2000).

We used the GLUE methodology (Generalized Likelihood Uncertainty Estimation; Beven & Binley 1992) to calibrate the model against the sap flow measurements. The GLUE procedure has certain characteristics that make it particularly suitable to cope with predictive uncertainty: (1) it rejects the idea that there is an optimum parameter set in favour of the idea that many parameter sets can give acceptable simulations (equifinality), and (2) it recognizes that calibrated parameter values may be valid only inside the particular model structure used. The procedure is based upon making a large number of runs of the model with different sets of parameter values, chosen randomly from specified parameter distributions (Monte Carlo sampling). Each parameter set is given a likelihood depending on how well it is able to simulate the measured data. Model runs that do not achieve a certain likelihood threshold are rejected as “non-behavioural”, and the remaining ones (“behavioural”) are used in the validation and predictive stages of the model. It should be noted that, as the parameters are always treated as sets, some information on the covariation amongst parameters will naturally appear in the behavioural simulations. This methodology has been successfully applied to models in different fields (Freer ***et al.*** 1996, Franks & Beven 1997, Piñol ***et al.*** 1997, Hankin & Beven 1998, Schultz ***et al.*** 1999).

In the present study, the GLUE methodology was applied to 8 plant parameters, two from each of 4 potentially critical processes controlling plant water transport (modified from Rambal 1993): root absorption, xylem transport, stomatal activity, and leaf area control (Table 2). The ranges of the studied parameters and the values of the other, “constant” parameters (mainly from the soil compartment), were selected according to the literature and our previous knowledge of the system (Table 2). All the ranges of the studied parameters were identical between species except for the parameter of centrality (b) of the vulnerability curve. This parameter was measured in branches and roots of both species in the study area (see Chapter 3), and the selected ranges were based on the results obtained for branches. For each individual tree and simulation period 20,000 random sets were generated from uniform distributions across the specified ranges and the model was run for each of these sets. Uniform distributions were used because there was no reason to use strong assumptions about parameter interactions. Within the GLUE approach, the evaluation of the different parameter sets in terms of how well they reproduce the observations will result in any interactions being reflected in the posterior distribution of behavioural parameter sets. The time span of each run comprised, for each year, the end of the spring rains, the whole dry period of the summer, and the first autumn rains (from June to September in 1999 (174.2 mm of rainfall, 65% of it in the last two weeks) and from July to September in 2000 (25.2 mm)). Within each run the transpiration predicted by the model (for each time step or for each day) was compared to the measured sap flow. As plant transpiration in the model was expressed per unit of leaf area whereas sap flow data was per unit of sapwood, an additional parameter was needed to compare them. We preferred to adjust this parameter (scaling factor) within the model, instead of using our data on the relation of leaf to sapwood area ($A_L$:$A_{SW}$) of the species studied, to take into account the existing uncertainty on the scaling to whole trees of the sap flow measurements with the Granier method (Goulden & Field 1994, Granier ***et al.*** 1996).

**Table 2.** Input parameters of the model. The studied parameters are marked by shaded rows.

| Name | Description | Values | Source |
|---|---|---|---|
| ***Plants*** | | | |
| $A_W$ | Stem diameter ($dm^2$). | - | Measured for each individual |
| $A_L$:$A_{SW}$ | Leaf to sapwood area (ad.) | 2000 (Qi)<br>2400 (Pl) | Measured in terminal branches in the study area |
| L | Aboveground height (m). | 6 | Measured in the study area |
| $L_R$ | Rooting depth (mm). | 500-9,000 | - |
| $d_A$ | Root density (mm $mm^{-2}$). | 0.5-10 | - |
| $R_R$ | Mean fine root radius (mm). | 0.5 | Estimated (Canadell ***et al.*** 1999) |
| $g_{min}$ | Approximately equal to the minimum leaf conductance (per unit). | 0.01-0.3 | - |
| f | Sensitivity of leaf conductance to soil water potential ($MPa^{-1}$) | 0.05-5 | - |
| $K_h^o$ | Maximum xylem hydraulic conductivity ($mm^4$ $MPa^{-1}$ $s^{-1}$). | 5e6-1.5e8 | - |
| a | Slope of the vulnerability curve ($MPa^{-1}$). | -1.5 | Averaged from measurements |
| b | Parameter of the vulnerability curve ($\Psi_L$ (in MPa) causing 50 PLC). | -2-(-4) Qi<br>-4-(-8) Pl | - |
| $PLC_{AL}$ | % embolism beyond which leaf shedding begins (=100-shedding K). | 50-95 | - |
| s | Leaf area fraction that is shed each time step if PLC > $PLC_{AL}$. | 0.03-0.3 | - |
| $t_{death}$ | Time (days) plants are able to survive with < 5% of the initial leaf area. | 20 or 30 | Estimated range |
| ***Soil horizons*** | | | |
| $\theta^o$ | Initial soil water content ($m^3$ $m^{-3}$). | - | Measured/estimated |
| $\theta^*$ | Water content ($m^3$ $m^{-3}$) above which drainage starts. | 0.3 | Estimated |
| $\theta_{sat}$ | Maximum soil water content (porosity, $m^3$ $m^{-3}$). | 0.4 | Measured in the study area |
| Q | Proportion of input water that is drained when $\theta>\theta^*$ (ad.). | 0.5 | Estimated |
| $\Psi_c$ | Air entry water potential (MPa). | -0.03 | Estimated from soil texture |
| $K_{sat}$ | Saturated hydraulic conductivity of the soil ($m^2$ $MPa^{-1}$ $s^{-1}$). | 200 | Estimated from soil texture |
| B | Exponent that relates $\psi_S$ and $K_S$ to $\theta$ (ad.). | 4 | Estimated from soil texture |
| ***General*** | | | |
| C' | Characterizes the exponential decline of the deep water reservoir ($h^{-1}$). | 0.002 | Estimated |
| C | Relates deep flow to the water reservoir (ad.) | 0.0005 | Estimated |
| $\beta$ | Determines the decrease in the soil radius available to plants (ad.) | 0.9995 | Estimated |
| $L_S^*$ | Critical soil depth (mm). Any horizon deeper than $L_S^*$ has a deep flow water | 2,500 | Estimated |

| | | | |
|---|---|---|---|
| | input. | | |
| LAI | Leaf area index ($m^2$ $m^{-2}$) | 4.5 | Measured in the study area (Sala ***et al.*** 1994) |

Previous to the calibration simulations we carried out 1,000 runs for each individual tree in which the scaling factor varied randomly an order of magnitude around the mean $A_L$:$A_{SW}$ measured for the species. The value of the scaling factor that produced the best fit (higher likelihood) for each tree was selected, and allowed to vary by 10% in the following calibration simulations.

We preferred to use daily instead of hourly likelihoods to illustrate the performance of the model because we are more interested in the long-term response, and the circadian dynamics of transpiration are largely dominated by $E_T$, which is an input of the model. The likelihood measure used in this study is based on the sum of squares of the residuals (Beven & Binley 1992):

$$\ell = (\sigma_e^2)^{-N} \quad \text{(eq. 10)}$$

where $\ell$ is the likelihood, $\sigma_e^2$ is the variance of the residuals, and $N$ is a shaping parameter. In our case an $N$ of 1 was selected.

### *Validation of the model*

The output of the 20,000 calibration runs for each individual tree consisted of a set of 9 parameters (the 8 studied ones plus the scaling factor) with its associated likelihood. We selected the best (highest daily likelihood) 5% of parameter sets for each tree and constructed a new file with these parameter sets. The ranking of the simulations was very similar regardless of the likelihood (hourly or daily) that was used. In the case of ***P. latifolia***, all the parameter sets from one of the calibration individuals (Pl-6; Table 3) were rejected because they fitted very badly to the measured sap flows. The measured period was also much shorter for this tree than for any other calibration individual. Thus, in total, we had 4,000 selected parameter sets for ***Q. ilex*** and 3,000 for ***P. latifolia*** (1,000 parameter sets per individual). These parameter sets were used in all the following simulations. For each of the 4 validation trees, the model was run for each of the parameter sets of the corresponding species (without the scaling factor). The only parameters that varied among individuals of the same species were the diameter of the stem (measured at 1.5 m) and the scaling factor (we used the values obtained for the corresponding tree in the calibration process, or the species mean if the tree had not been calibrated). To determine the uncertainty bounds at each time step, the predicted transpirations were ranked to form a cumulative distribution and the 5%, 50%, and 95% quantiles were used to compare with the measured sap flows.

### *Simulations of the summer of 1994*

An additional qualitative validation of the model was carried out using data from the extreme drought that occurred in southern and eastern Spain in the summer of 1994. The documented mortalities were used to test the ability of the model to predict the mortalities of the studied populations. In response to that drought event several species were severely affected (Peñuelas ***et al.*** 2001). In NE Spain the amount of dry individuals reached the 80% in some ***Quercus ilex*** populations, whereas ***Phillyrea latifolia*** showed almost no damage (at least in respect to crown status) (Lloret & Siscart 1995, Peñuelas ***et al.*** 2000). In the most affected populations of the study area, up to the 48% of ***Q. ilex*** and to the 10% of ***P. latifolia*** individuals dried completely during the summer of 1994 (A. Bernabé & A. Escarré, unpublished results). The parameter sets retained after the calibration process for each species were used to run the model under the climatic conditions of the summer of 1994 (from June to September; 83.3 mm of rainfall, mostly in September). The underlying assumption was that the retained parameter sets were an adequate representation of the variability present in the studied populations of the two species. Although we only used 3-4 individuals to calibrate the model, the fact that they gave a very consistent between-species pattern (see the "Results and Discussion" section) suggests that we were able to capture enough variability to characterise the studied populations.

**Table 3.** Calibration and validation results. Correlation coefficients and slopes are between simulated (the median in the case of validations) and measured daily sap flows (independent variable)[a].

| **Species** | **Individual (year)** | **Correl. coef.** | **Slope** | **Scaling factor** | **N (days)** |
|---|---|---|---|---|---|
| Calibration[b] | | | | | |
| ***Q. ilex*** | 4 (2000) | 0.96 (0.97) | 0.86 (0.95) | 1295.9 | 90 |
| ***Q. ilex*** | 8 (1999) | 0.94 (0.95) | 0.76 (0.90) | 2290.3 | 112 |
| ***Q. ilex*** | 9 (2000) | 0.87 (0.88) | 0.77 (0.84) | 1156.1 | 85 |
| ***Q. ilex*** | 19 (1999) | 0.89 (0.91) | 0.77 (0.85) | 1846.5 | 114 |
| ***P. latifolia*** | 5 (2000) | 0.93 (0.93) | 0.97 (0.98) | 1322.7 | 90 |
| ***P. latifolia***[c] | 6 (1999) | 0.61 (0.62) | 0.45 (0.47) | 579.0 | 31 |
| ***P. latifolia*** | 7 (2000) | 0.87 (0.87) | 0.99 (0.94) | 1112.2 | 90 |
| ***P. latifolia*** | 18 (1999) | 0.81 (0.81) | 0.92 (0.89) | 1798.1 | 84 |
| Validation | | | | | |
| ***Q. ilex*** | 8 (2000) | 0.89 | 0.56 | 2300.0 | 54 |
| ***Q. ilex*** | 19 (2000) | 0.91 | 0.62 | 1850.0 | 84 |
| ***P. latifolia*** | 7 (1999) | 0.80 | 0.63 | 1100.0 | 118 |
| ***P. latifolia*** | 20 (1999) | 0.88 | 0.91 | 1400.0 | 57 |

[a] Each value is the average for the corresponding plant.

[b] The correlation coefficients and slopes of the best simulation (in terms of daily likelihood) are in brackets.

[c] This individual was not used in the calibration (see text).

As climatic data from the study site was not available that year, we used data from the nearby Constantí Meteorological Station (23

Km from the study area). The values of rainfall and potential evapotranspiration measured the summer of 2000 in this station were regressed against the values measured in the study site, and the resulting regression coefficients were used to correct the 1994 measurements. We assumed that the initial water content of the soil was 0.2. Three different sets of simulations were carried out, depending on the way competition was treated and on the value assigned to the critical time a plant was able to survive without leaves: (1) without explicit competition and $t_{death}$=30 days. Each tree was supposed to be isolated, as had been done in the calibration and validation stages, and the only competition effect was introduced via the parameter values: as long as the studied trees were not growing isolated and the sap flow measurements that we used to calibrate the parameters contained some sort of "competition effect", this information was included in the retained parameter values. (2) With the explicit introduction of competition and $t_{death}$=30 days. In this set of simulations the model was run with two plants, one of each species, absorbing water from the same soil volume (maintaining the Leaf Area Index). In each run the parameter sets from each species were sampled randomly until all the parameter sets per species had been used. (3) With the explicit introduction of competition and $t_{death}$=20 days.

### *Predictions under climate change*

The same parameter sets resulting from the calibration process were used to simulate the behaviour of the two studied populations under different climatic scenarios. Two climatic components were explored: temperature (through its effect on $E_T$), and the duration of summer drought as affected by rainfall distribution. In relation to temperature four scenarios were considered: (1) current (mean of 1999 and 2000 values); (2) an increase in mean temperature of 1.5ºC, distributed uniformly across the summer months, causing a 8% rise in total $E_T$; (3) a 3ºC increase in mean temperature (17% increment in $E_T$); and (4) an increase of 4.5ºC in mean temperature (25% increment in $E_T$). Regarding the duration of summer drought, all simulations were run for a period of 5 months without rainfall (from May to September), which was considered a reasonable maximum in the context of the predicted increase in climatic variability. In this way we could compare the percent survival of the two populations under each of the temperature scenarios and for any duration of the summer drought. In all the simulations $t_{death}$ was 20 days and competition was explicitly introduced as explained in the previous section. The initial water content of the soil was 0.2.

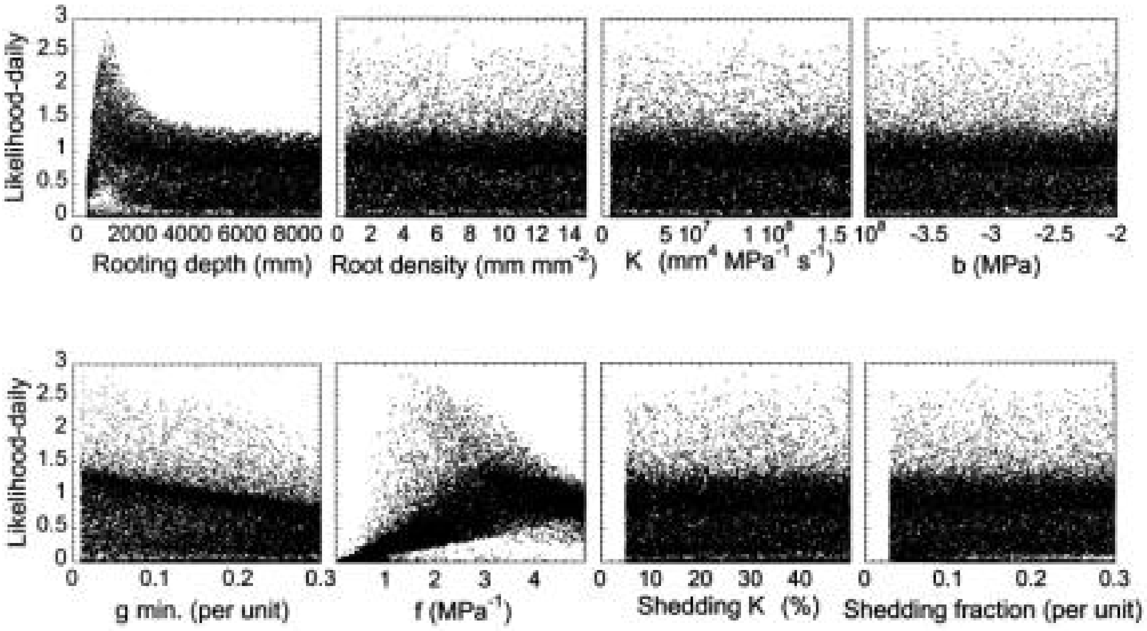
## Results and Discussion

### *Calibration of the model*

The mean correlation coefficient between the simulated daily transpirations (of the behavioural runs) and the measured daily sap flows was 0.92 for ***Q. ilex*** and 0.87 for ***P. latifolia***. The mean slope of the regression of measured sap flows against simulated transpirations was 0.79 for ***Q. ilex*** and 0.96 for ***P. latifolia*** (Table 3). It is interesting to note that the difference in performance between the “best” (***i.e.,*** most likely) simulation and the mean of the behavioural ones, or even the worst of them, was always very small (Table 3). This result is in agreement with the concept of equifinality behind the GLUE methodology. The mean value of the scaling factor predicted by the model was $1.65 \cdot 10^3$ for ***Q. ilex*** and $1.41 \cdot 10^3$ for ***P. latifolia*** (Table 3), reasonably similar to the values of $A_L$:$A_{SW}$ measured in terminal branches (Table 2) and to the values estimated for whole trees of the two species in the study area (Chapter 6).

The GLUE approach allowed us to identify the parameters to which the model was more sensitive for the particular conditions of the calibration. The scatter plots relating the values of the parameters to the resulting likelihood (Figure 2) showed that, for 5 of the 8 studied parameters ($d_A$, $K_h^o$, b, $PLC_{AL}$ and s), simulations with almost any likelihood were possible throughout the chosen parameter ranges. The three sensitive parameters were: root depth, minimum stomatal conductivity, and the parameter (f) that relates stomatal conductivity to soil water potential. This

a



b

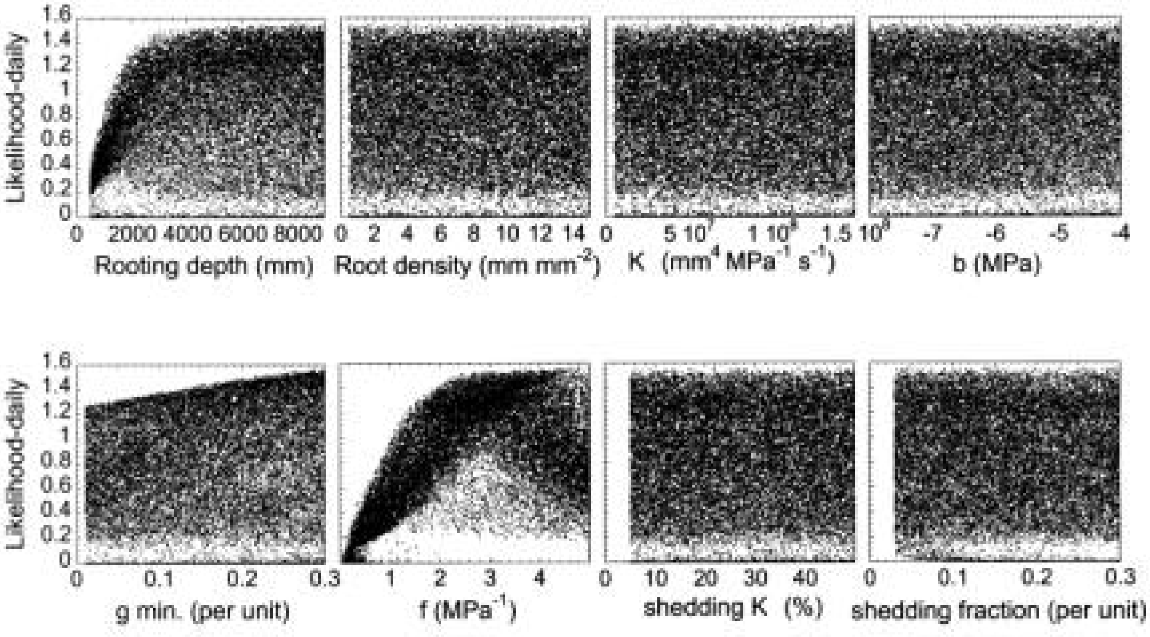


**Figure 2.** Sensitivity of the model to the studied parameters during the calibration process. Two representative cases are shown, one for each species (a: ***Q. ilex***-4, b: ***P. latifolia***-7).

pattern was exactly the same for the 8 studied individuals, although the maximum likelihoods were attained under different combinations of parameter values depending on the species (see Figures 2 and 3 and below). The fact that the model was able to produce good simulations throughout the range of 5 of the 8 parameters clearly shows that the model is over parameterised ***in relation to the data used to calibrate it***. The last remark is relevant in our study for two related reasons, that explain why we decided to retain the variability of all the parameters: (1) although it is important for the model to be able to reproduce the dynamics of transpiration, we are not primarily interested in the prediction of this variable. It is not at all clear that some of the parameters that now appear "unimportant" may not be critical in the prediction of mortality. (2) It is perfectly possible that parameters that are unimportant under "normal" conditions, like those used in the calibration, may be critical under the extreme conditions in which we want to use the model. This is one of the foundations of the GLUE methodology and in this particular case we have good reasons to think that this may be the case (see below).

### ***Model validation***

The mean correlation coefficient between the median of the simulated daily transpirations and the measured daily sap flows was 0.87. The mean regression coefficient was 0.68 (Table 3). The model captured most of the variability of the sap flow measurements both at the short and the long-term (Figures 4 and 5), although, on average, it tended to underestimate them.

As the original ranges of 7 of the 8 studied parameters were identical, the parameter sets containing only the behavioural simulations allowed us to explore the differences between the two species predicted by the model. Substantial differences appeared only for the same three parameters to which the model showed sensitivity during the calibration process: root depth ($L_R$) , minimum stomatal conductivity (g min), and the parameter (f) that relates stomatal conductivity to soil water potential (Figure 3). The model predicted higher minimum stomatal conductivities, and parameters f in ***P. latifolia***. Thus, although the stomata of ***P. latifolia*** were more sensitive to soil moisture content, they retained a higher conductivity (in relation to the maximum) under extremely dry conditions. This prediction of the model is in agreement with the literature (Tretiach 1993), with the results in Chapter 6, and with the instantaneous measurements of transpiration rates carried out in the study area (R. Ogaya ***et al.***, unpublished results). Regarding the third prediction, that of higher rooting depths also in ***P. latifolia***, there is no conclusive data from the study area.

### *Simulations for the summer of 1994*

The average mortalities predicted by the model without introducing explicit competition were 18% for ***Q. ilex*** and 0% for ***P. latifolia***. With competition, the predicted mortalities increased slightly: 22-28% for ***Q. ilex***, depending on $t_{death}$, and 1% for ***P. latifolia*** (Table 4). These values are in agreement with the higher mortalities detected in ***Q. ilex*** after the 1994 drought in NE Spain (Peñuelas ***et al.*** 2000), and with the data from the study area.

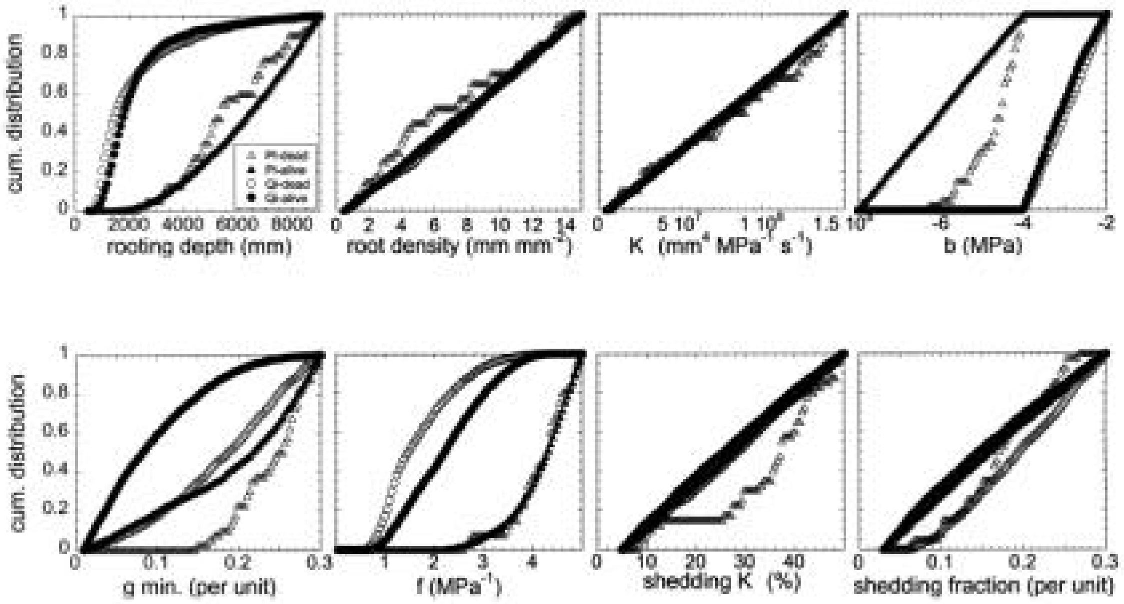


**Figure 3.** Cumulative distributions of the studied parameters (behavioural simulations). The distributions are separated for the two species (Qi: ***Q. ilex***, Pl: ***P. latifolia***) and, within a species, for individuals that were predicted to survive and to die in the simulations of the summer of 1994.

Total transpiration during the simulated period tended to be higher in ***Q. ilex***. In this species, total transpiration tended to be lower among the surviving individuals (Table 4).

The comparison of the values of the parameters for the individuals that died and for the ones that survived allowed us to identify the parameters that were more critical for plant survival for each species. Most of them were the same for the two species (Figure 3). Surviving plants tended to have slightly deeper roots, lower vulnerabilities to xylem embolism, and lower minimum stomatal conductivities; tended to start leaf shedding at slightly lower remaining hydraulic conductivities (higher PLC), and shed a smaller fraction of leaf area (s) when the hydraulic conductivity was lower than the critical value. High root density seemed to be associated with survival only in ***P. latifolia***, and the parameter f only in the case of ***Q. ilex***. Survival was unrelated to hydraulic conductivity.

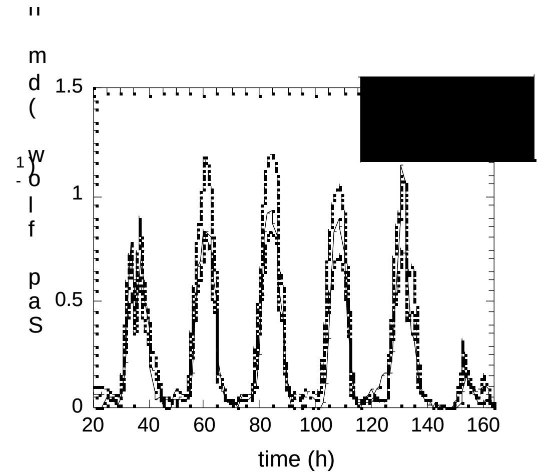


**Figure 4.** Example of validation results (Pl-20). The measured hourly sap flows are represented together with the 5 and 95% quantiles of the simulated distribution.

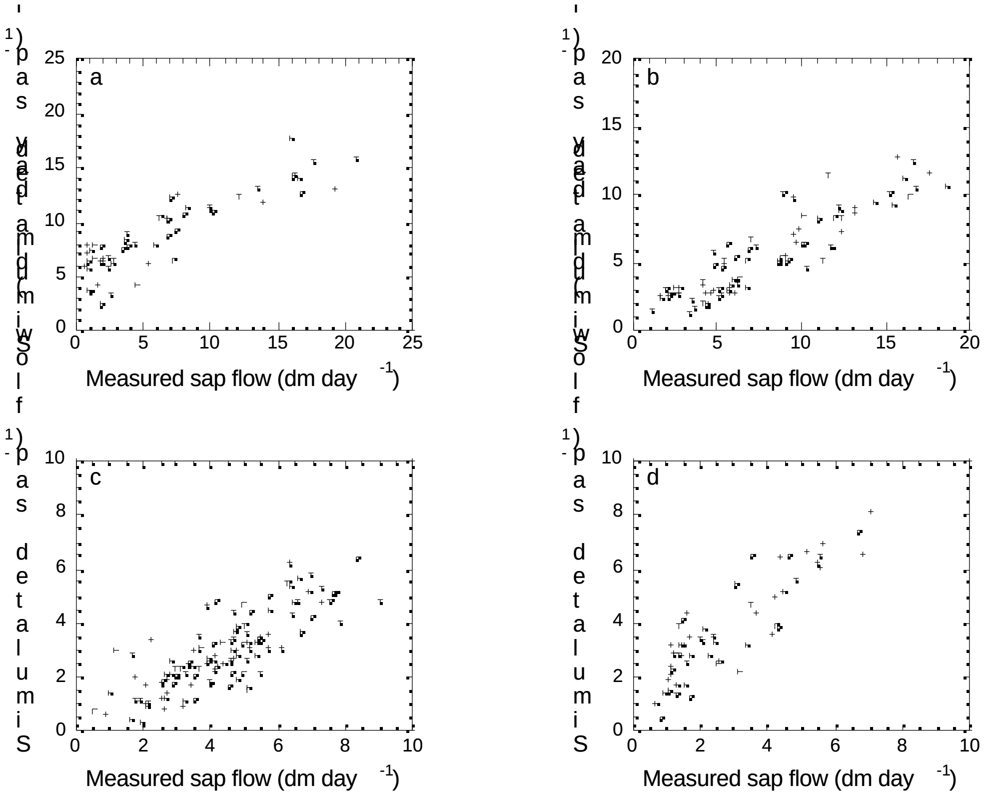


**Figure 5.** Measured ***versus*** predicted daily sap flows for the 4 trees that were used for validation (a: ***Q. ilex***-8, b: ***Q. ilex***-19, c: ***P. latifolia***-7, d: ***P. latifolia***-20).

It is also interesting to look at the relationships between the studied parameters in the behavioural simulations (Table 5). It is known from past studies using GLUE that caution needs to be taken in interpreting parameter interactions since it is the parameter set that gives a good fit to the data and this may be the result of local interaction effects. Here, global correlations amongst the individual parameter values of the behavioural simulations were investigated. Several facts are worth noticing: (1) With only one exception, the significant correlations (0.001 level) were always compensatory: values that promote mortality in relation to one parameter were associated with values that promote survival in relation to another (***e.g.,*** high vulnerability to xylem embolism and high stomatal sensitivity to soil water). This result points out the importance of the interactions between parameters. In the calibration process we assumed that any combination of parameter values within the specified ranges was possible, but this is not necessarily true. There is considerable evidence suggesting, for example, that plants with higher hydraulic conductivity tend to be more vulnerable to xylem embolism (***e.g.,*** Pockman & Sperry 2000, Chapter 3). (2) Significant correlations between parameters were similar for the individuals that died and for the ones that survived. No single correlation was significant at the 0.001 level (see Table 5) and of different sign for surviving and dead individuals, and only three were significant for either surviving or for dead individuals. Of these, two are probably related to the fact that the number of dead ***P. latifolia*** individuals was proportionally very low (N=40) and makes it difficult to obtain significant correlations. The other one is the negative correlation between the minimum stomatal conductivity and the shedding leaf area fraction, which was only present in surviving individuals of ***Q. ilex***. The correlation was positive (although not significant) for the individuals that died. This compensatory relationship, hence, may be critical for the survival of ***Q. ilex***.

**Table 4.** Results of the simulations of the extreme drought of 1994, depending on whether competition was explicitly introduced in the model (-c: no competition; +c: with competition), and the value assigned to $t_{death}$ (in days). Mortalities and total transpirations (per unit of stem diameter, means ± standard deviations) are shown.

| | ***Q. ilex*** | | | ***P. latifolia*** | | |
|---|---|---|---|---|---|---|
| | **Mortality** | **Transp. ($dm^3$ $dm^{-2}$)** | | **Mortality** | **Transp. ($dm^3$ $dm^{-2}$)** | |
| ***Simulation*** | **(%)** | ***Alive*** | ***Dead*** | **(%)** | ***Alive*** | ***Dead*** |
| -c/$t_{death}$=30 | 18.6 | 282.8 | 335.9 | 0.0 | 233.3 | - |
| | | ±110.4 | ±106.3 | | ±67.9 | |
| +c/$t_{death}$=30 | 22.3 | 267.5 | 327.0 | 0.9 | 224.4 | 219.4 |
| | | ±106.2 | ±97.9 | | ±77.8 | ±51.3 |
| +c/$t_{death}$=20 | 28.0 | 262.3 | 311.1 | 1.0 | 224.6 | 216.5 |
| | | ±104.8 | ±95.5 | | ±77.6 | ±59.2 |

There was a significant association between the mortality of the two species (Log-linear analysis; G=8.89, P=0.003). Cases in which the two species died or the two survived were much more frequent than expected. This result suggests that a “depletion effect” (mortality tended to affect preferentially ***Q. ilex*** individuals with high transpiration rates (Table 4), that had depleted the common water resources) was more important than a “release effect” (when one of the plants died it freed resources for the other plant). The effects of competition can be seen by plotting the relationship between the values of the same parameter for the two species, depending on the output (in terms of mortality) of the simulation (Figure 6). The most clear examples are the rooting depth and the parameter f: there is mortality of ***P. latifolia*** only when ***Q. ilex*** has deep roots and when the stomatal sensitivity of ***Q. ilex*** to soil water is low (high water use). In the case of rooting depth it is also interesting to note that, for the simulations in which there is mortality of ***P. latifolia***, ***Q. ilex*** survives or not depending on the rooting depth of ***P. latifolia***.

## *Predictions under climate change*

Under any of the simulated scenarios, ***P. latifolia*** survived longer (in average) than ***Q. ilex*** (Figure 7). As expected, the survival of both species decreased as mean temperature (and $E_T$) increased, although the effect was relatively small (Figure 7). The time that both species resisted (mortality<5%) without rainfall was between 84 and 94 days for ***Q. ilex*** and 133-150 days for ***P. latifolia***. The values for ***Q. ilex*** are not far from the current conditions in the study area (5.4 mm in 77 days in the summer of 2000, that was not a particularly dry year). For longer droughts ***Q. ilex*** mortality increased quickly. For example, a 50% mortality was reached between the day 127 (+4.5ºC) and the day 145 (current temperature).

**Table 5.** Correlations between the studied parameters (behavioural parameter sets), for ***Q. ilex*** (above the diagonal) and ***P. latifolia*** (below the diagonal), and for individuals that died during the 1994 simulation (dark grey cells) and the ones that survived (light grey cells)$^{a,b}$.

| ***Q. ilex*** / ***P. latifolia*** | $L_R$ | | $d_R$ | | $K_h$ | | b | | $g_{min}$ | | f | | $\%K_{h,AL}$ | | s | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $L_R$ | ■ | ■ | (+) | | | | | | - | - | - | - | (-) | | | |
| $d_R$ | | | ■ | ■ | | | | | | | | | | | | |
| $K_h$ | | (+) | | | ■ | ■ | | | (+) | (+) | | | | | | |
| b | (-) | (+) | | | | | ■ | ■ | (-) | - | + | + | (-) | | | |
| $g_{min}$ | (+) | | | | | | | | ■ | ■ | + | + | (-) | (-) | - | |
| f | - | | | | | | | | - | | ■ | ■ | + | + | + | (+) |
| $\%K_{h,AL}$ | | | (+) | | | | | | | | | | ■ | ■ | | |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| s | | | | | | | | | | (-) | (+) | | | | |

[a] The sign indicates whether the correlation was positive or negative

[b] Signs in brackets indicate that the correlation was significant only at the 0.05 level. Signs without brackets indicate that the correlation was significant at the 0.05/N level (Bonferroni correction with N=56).

## Concluding remarks

The model was able to simulate both transpiration dynamics and measured mortalities for the two species in the study area. The only difference between species that was introduced ***a priori*** was that ***Q. ilex*** was more vulnerable to xylem embolism than ***P. latifolia*** (based on our own measurements in the study area, Chapter 3). For all the other parameters identical distributions were assumed for the two species at the beginning of the calibration process. During the calibration the information provided by the measured sap flows was used to retain the most likely parameter sets for each species, that were used in all the following simulations.

The results showed that different parameters can be important under different circumstances and for different objectives. Whereas rooting depth and the two parameters related to stomatal control were the only important ones to predict transpiration rates under “normal” conditions (Figure 2), other parameters (mostly related to the vulnerability to xylem embolism and the regulation of leaf area) took importance under extremely dry conditions because of their relation to mortality (Figure 3). It is interesting to note that the pattern was very similar for the two studied species, although they differed substantially in the actual parameter values predicted by the model (Figure 3).

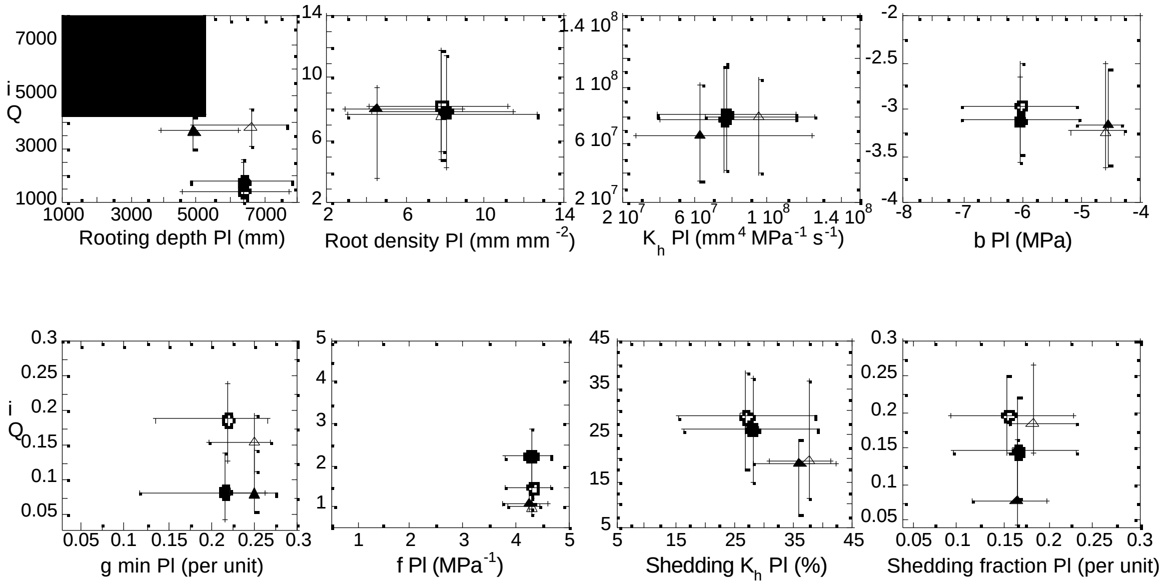


**Figure 6.** Relationships (medians ±25-75% quantiles) between the parameter values of the two species, depending on the output (in terms of mortality) of the 1994 simulation.

Regarding the simulations under climate change, the model predicted that increased temperature (and $E_T$) will cause higher mortalities in the two studied populations. However, the most important factor is predicted to be the duration of drought events. ***Q. ilex*** seems to be very close to its limit to cope with water stress under the current climatic conditions, at least in the study area. If, as predicted by most climate change models (Osborne ***et al.*** 2000), there is an increase in the frequency and duration of extreme droughts, mortalities can increase substantially (Figure 7). As a result, some species, such as ***P. latifolia***, can be favoured and the composition of communities currently dominated by ***Q. ilex*** can change drastically in some areas. It should be noted, however, that in GCM precipitation scenarios (both in terms of mean changes and of distribution) are much more uncertain than temperature changes (Palutikof & Wigley 1996).

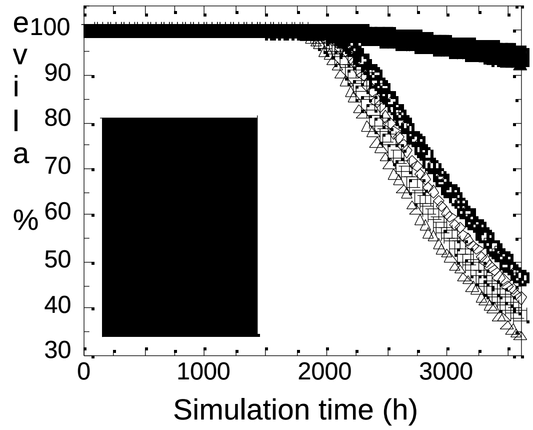


**Figure 7.** Survival curves predicted by the model for the studied populations of ***Q. ilex*** (Qi) and ***P. latifolia*** (Pl) under different climate change scenarios: current temperatures (cur), current + 1.5ºC, current + 3ºC, and current + 4.5ºC.

Some additional considerations about the predictions under climate change should be noted. In particular, the increase in the concentration of atmospheric $CO_2$ and other greenhouse gases is likely to have other effects that we have not considered and are potentially relevant for the problems discussed here. Elevated CO2 may reduce leaf-level transpiration (Drake ***et al.*** 1997, Medlyn ***et al.*** 2001) and/or increase the hydraulic conductivity of the xylem per unit of leaf area (Heath ***et al.*** 1997, Maherali & DeLucia 2000). These effects would ameliorate the consequences of water stress (Osborne ***et al.*** 2000). A decrease in leaf conductance (and leaf area), has been found in ***Q. ilex*** populations growing in $CO_2$ springs in Italy (Tognetti ***et al.*** 1998). However, the effect was small and decreased under high vapour pressure deficits (summer). It is unlikely that this acclimation would be enough to compensate for the predicted increase in aridity.

In addition, we have been treating complete drying as synonymous of plant death, but this is not an exact correspondence because the two studied species are capable of resprouting if the conditions after the drought are favourable. In fact, the long-term mortality of ***Q. ilex*** after the 1994 event in the study area was much lower than the percentage of individuals that dried completely that year. However, it is clear that a tree that dries and has to resprout every few years is in big disadvantage in relation to undamaged trees. Our point is that, although resprouting could delay the demographic effects of acute droughts, the final outcome will be that predicted by the model provided that extreme droughts are frequent enough.

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# CHAPTER 8

# Concluding remarks

***Y en el caso mejor, cuando nuestro libro nos evoca nuestra alma***
***de ayer con la viveza de algunos sueños que actualizan lo pasado,***
***echamos de ver que, entonces, llevábamos a la espalda un copioso haz***
***de flechas que no recordamos haber disparado***
***y que han debido caérsenos por el camino.***
(A. Machado, preface to ***Páginas escogidas*** (1917))

## Mechanism of freezing-induced xylem embolism

Our results showed that the effect of minimum freezing temperature on freezing-induced xylem embolism observed in previous studies (Lo Gullo & Salleo 1993, Pockman & Sperry 1997) is associated with intracellular freezing of xylem parenchyma cells (Chapter 2). These results have implications for the current debate on the mechanism of water transport in plant xylem. Substantial evidence is accumulating supporting that transpiring plants are able to repair cavitated xylem conduits (Chapter 1). This is difficult to fit into the accepted cohesion theory of sap ascent because refilling would need to occur under substantial xylem tensions. The apparent contradiction between theory and experimental results has led to the alternative compensating pressure theory (Canny 1995, 1998), which has been criticised both on theoretical (Comstock 1999) and experimental grounds (Stiller & Sperry 1999). Refilling could occur at negative pressures provided that cavitated conduits are hydraulically isolated from functional ones, and that there is a flux of water into the conduits until the gas phase is forced back into solution. It has been suggested that living parenchyma cells provide the driving force for refilling (Holbrook & Zwieniecki 1999). Additionally, recent measurements support that the properties of vessel walls allow the required compartmentalization of the repair process (Zwieniecki & Holbrook 2000).

Most of the data on refilling under negative xylem pressures come from studies of drought-induced xylem embolism. Taken together with these data, our results suggest that living parenchyma cells may have an active role in embolism repair regardless of the mechanism involved in the formation of embolisms. If this is true, the activity of parenchyma cells would have potential and unstudied implications for the acclimation of plants to freezing and drought. Clearly, additional studies on the subject are required. Although the cohesion theory remains the most parsimonious explanation of the ascent of sap in plants, it is becoming increasingly clear that some of the mechanisms involved in sap ascent are more complex than previously thought and may involve living cells.

## Xylem structure and function in roots and stems

There is increasing evidence showing that roots live closer than stems to the water potentials causing catastrophic levels of drought-induced xylem embolism (Chapter 1). Our data from two different Mediterranean communities, a Holm oak forest (Chapter 3) and a conifer plantation in coastal dunes (Chapter 4), are in agreement with this evidence. As a result of this pattern, it has been suggested that root xylem may often be the weakest link between soil and leaves during drought, thus limiting water transport and transpiration (***e.g.,*** Jackson ***et al.*** 2000). There is very little information on the role of root xylem in response to freezing. Our results showed that despite ***Larrea tridentata*** roots are also more vulnerable to freezing-induced xylem embolism than stems, they suffer lower levels of embolism, presumably because of the insulating properties of soil.

These results agree with the recent findings by Jaquish & Ewers (2001).

The different vulnerabilities to embolism in roots and stems seem to be part of a more general gradient in xylem structure and function within individual plants. Conduit size, specific hydraulic conductivity, and vulnerability to xylem embolism consistently increase from twigs to surface roots (Chapter 1). Recent data indicate that the gradient extends further underground (Wan ***et al.*** 1994, Pate ***et al.*** 1995). Xylem conduits were 1.5 ±0.2 times wider in deep roots located in caves (depth>7 m) than in surface roots from the same species (***Juniperus ashei***, ***Quercus fusiformis*** and ***Q. sinuata***) (J. Martínez-Vilalta ***et al.***, unpublished results). In the only species from the previous study in which vulnerability to drought-induced xylem embolism was measured, ***J. ashei*** deep roots resulted much more vulnerable than both stems and surface roots (WT Pockman ***et al.***, unpublished data; see also Jackson ***et al.*** 2000). The reason of this remarkable pattern, in which plants “adjust” their internal properties to the gradient in water potential through their xylem, is normally approached from an adaptive point of view (Chapters 1, 3 and 4). Although it is clear that this adjustment may be advantageous to plants, some considerations are relevant. There are developmental reasons to expect vessels to increase in size from twigs to deep roots (Aloni 1987). If there is an obligate trade-off between conducting efficiency and safety in the xylem of individual plants (Chapter 1), a gradient in vessel size would be enough to generate the whole pattern observed. To what extent natural selection and developmental constraints have interacted to shape the pattern is a question that requires further study.

Whatever the reason of the observed gradient in xylem function, it has critical implications for plant water transport (Chapter 1). In this context, the ratio between mean vessel diameter in terminal branches and surface roots may be an important component of the hydraulic architecture of plants. This ratio seems relatively constant among woody species, with most values falling in the range 1.5-2 (Ewers ***et al.*** 1997, Sperry & Ikeda 1997, Hacke ***et al.*** 2000). Substantial deviations from that range, 1.2 in ***L. tridentata*** (Chapter 2) or 3.6 ±0.1 in the two pines of Chapter 4, may reflect particular environmental conditions and require especial attention.

Unlike aboveground tissues, root systems typically span through an extraordinarily heterogeneous environment, in which critical properties can vary several orders of magnitude both spatially and temporally (***e.g.,*** Hillel 1980). In this context, plasticity is probably of primary importance. It is known that soil water content influences vessel size in root xylem (Lovisolo & Schubert 1998, Arnold & Mauseth 1999). Besides, it has been found that vulnerability to cavitation can vary within a single root system in association with soil humidity (Sperry & Ikeda 1997). In our opinion, a complete understanding of root functioning and its role in limiting gas exchange would require systematic studies of the variability of root properties within root systems, and the integration of other factors such as root demography.

## Trade-off between conducting efficiency and security in the xylem

The existence of a trade-off between hydraulic conductivity and resistance to drought-induced xylem embolism among different species has been one of the most debated issues in plant hydraulic architecture (Chapter 1). In Chapter 3 we report a power relationship with exponent ***ca***. –2 between conductivity and resistance to embolism, a result which is consistent with the existence of a trade-off, and agrees with other studies that have focused in a single community (***e.g.,*** Pockman & Sperry 2000). In the same chapter a simple model is provided that explains the observed dependence between conductivity and resistance in Angiosperms. The main assumption of the model is that there is a linear relationship between the diameter of a vessel and the size of its largest pit pore. The results in Chapter 4 also agree with the existence of an inter-specific trade-off. However, in conifers the relationship between conductivity and resistance to embolism may be different to that of Angiosperms because of the presence of bordered pits (Zimmermann 1983).

The shape of the relationship between conductivity and resistance to embolism that we have found in Chapter 3 has interesting implications. In the first place, it helps to explain why the existence of a trade-off has remained so elusive. For a study to obtain a clear correlation between both variables, the studied species/tissues need to be in the central part of the relationship or span over a broad range of values. Another, more relevant implication is that for species/tissues situated at the extremes of the relationship, any "improvement" with regard to one of the variables (higher conductivity, lower vulnerability) would be at the expense of a large "worsening" in the other. This is important because it implies that once a species/tissue has "fallen" into one of the tails of the curve it would be very difficult for it to change substantially its xylem properties. As a result, we may find species whose xylem traits evolved under environmental conditions different to those prevailing in areas they currently occupy, and have remained almost unaltered since then. ***Ilex aquifolium*** may be an example of such a species (Chapter 3).

It remains to be explained why when different communities are put together the relationship between hydraulic conductivity and resistance to drought-induced xylem embolism is confounded (Tyree ***et al.*** 1994, Pockman & Sperry 2000). In any case, the lack of a strong relationship at the global scale does not invalidate the existence of a strong trade-off within communities nor the hypothesis that there is a linear relationship between vessel and pore size. The incongruence between scales simply suggests that the fundamental relationships underlying the observed patterns may vary as a function of environmental variables.

The possible existence of a trade-off between hydraulic efficiency and security in the conducting system fits into a growing body of evidence supporting that a small number of functional relationships may explain a large part of the variability we observe in plant traits (Reich ***et al.*** 1997, Stratton ***et al.*** 2000, Enquist & Niklas 2001, see also Chapter 1). The clarification of these fundamental relationships has a great potential for deepening our current understanding of plant ecophysiology.

## Safety margins

Since Tyree & Sperry (1988) suggested that plants operate at water potentials close to the values causing catastrophic xylem dysfunction, considerable evidence has accumulated supporting their hypothesis (Chapter 1). A linear correlation between the vulnerability to xylem embolism of a given species and the minimum water potential it experiences is usually found, with safety margins increasing from humid to xeric habitats (Pockman & Sperry 2000, Sperry 2000). The general relationship between vulnerability and minimum water potential seems to hold also within species, although in one of the few studies comparing subspecies it was found that safety margins were slightly wider in the more humid subspecies (Kolb & Sperry 1999a).

Our data from the coastal dune community in Guardamar (E Spain) is consistent with the general picture outlined in the previous paragraph (Chapter 4). In contrast, in the Holm oak community (NE Spain) the relationship between vulnerability to embolism and minimum water potential was parabolic, with wide safety margins for species experiencing very high or very low water potentials (Chapter 3). The interpretation of this result is difficult because very few studies have compared the safety margins of more than 3-4 species from the same community. However, we suspect that the parabolic shape is just an “artefact” of the particular species being measured. For plants to operate close to the critical water potentials causing xylem dysfunction, there need to be disadvantages in having an overly resistant xylem. It is normally considered that the trade-off between conducting efficiency and security provides the main drawback. In the present case, the shape of the trade-off implies that for a species that is very resistant to xylem embolism (and thus has low conductivity) to become more conductive, it would need to decrease disproportionately its resistance to embolism. As a result, the advantage of reducing safety margins disappears (see previous section).

Although the study of safety margins has been limited to drought-induced xylem embolism, the same basic ideas can be applied to freezing-induced embolism. In that case safety margins would be the difference between the temperatures causing catastrophic levels of embolism and the minimum temperatures experienced under field conditions. Our results indicate that although the ***L. tridentata*** population from the Chihuahuan desert (NM, USA) was slightly more resistant to embolism than the Sonoran population (AZ, USA), the difference was not enough to compensate for the much colder climate. As a result, the Chihuahuan population was also more limited by freezing (Chapter 2). Additional studies are required to clarify whether safety margins in relation to freezing follow a pattern similar to those with respect to drought.

The analysis of safety margins allows us to identify the species/tissues whose xylem is more hydraulically limited. However, it has important limitations. Firstly, it is based on coarse estimations of the water potentials in the xylem the tissues being analysed. In second place, it fails to consider other potentially relevant components of the SPAC (***e.g.,*** non-xilary transport in the plant, rhizosphere) that may also limit water transport. A more holistic approach combining information from the whole SPAC with realistic models is required to fully understand the transport constraints on water use (***e.g.,*** Sperry ***et al.*** 1998, Kolb & Sperry 1999b, our Chapter 7 to a certain degree). In addition, any analysis of transport constraints has to be considered within the general strategy that the species being studied uses to cope with water shortage.

## Strategies to cope with drought

The study of the limitation that xylem embolism poses on plant water transport has improved substantially our understanding of the response of plants to drought (Chapter 1). In the particular case of the studies collected in this thesis, transport constraints provide likely causes for two of the most conspicuous effects of the extreme drought of 1994 in NE Spain: the mortality of ***Pinus sylvestris*** (Chapter 5) and ***Quercus ilex*** (Chapters 3, 6 and 7).

There are four main components that determine the response of a plant to water shortage (modified from Rambal 1993): (1) water uptake in roots, (2) regulation of water transport in the xylem, and control of water loss via (3) stomatal activity or (4) leaf area control. The interaction among these components, which operate at different but partially overlapping temporal scales, defines the strategy that a species uses to cope with drought. While species coexisting in a dry area can have almost any characteristic regarding the previous components considered individually, only certain combinations of attributes are possible. Although these combinations allow survival in a particular area, they are not necessarily equivalent, and often determine the vulnerability of a given species to extreme droughts or to long-term modifications of water availability.

Our results give some examples of the previous considerations. Pines tend to have relatively high vulnerabilities to xylem embolism and, at the same time, show little variation in vulnerability among species or populations (Chapters 4 and 5 and references therein). This fact suggests that other mechanisms play a major role in adaptation and acclimation to drought stress. It has long been known that pines normally have a strict stomatal control (Rundel & Yoder 1998). Besides, there is a large body of evidence showing that in pines: (1) leaf-to-sapwood area ratios ($A_L$:$A_{SW}$) are lower than in other conifers (Margolis ***et al.*** 1995, Piñol & Sala 2000), and (2) biomass allocation is the key factor explaining the different responses to drought of populations and species (Mencuccini & Grace 1995, DeLucia ***et al.*** 2000). Our results in Chapter 5 support the key role of $A_L$:$A_{SW}$ in determining the resistance to drought of different pine populations.

***Quercus ilex***, ***Phillyrea latifolia*** and ***Arbutus unedo*** have been the object of several comparative ecophysiological studies (Chapter 6 and references therein). Our results provide additional elements that, in our opinion, clarify the strategies that these species use to cope with water shortage. Low vulnerability to xylem embolism allowed ***P. latifolia*** to have a less strict stomatal regulation and maintain transpiration at lower water potentials than the other two species. In contrast, ***A. unedo*** and ***Q. ilex*** needed a strong stomatal control over water loss to avoid low water potentials that could cause dangerous levels of embolism. Under extremely dry conditions, stomatal control was not enough for these species to avoid high losses of hydraulic conductivity, particularly in the case of ***Q. ilex*** (Chapters 3 and 6). Although the dynamics of leaf area were not studied, the three species are evergreen and, thus, major differences in the regulation of leaf area are unlikely (see also Chapter 7). The role of water stress in limiting the distribution of ***Q. ilex*** has been recognized in previous studies (***e.g.,*** Terradas & Savé 1992). Some implications of the different strategies outlined in this paragraph will be discussed in the next section.

If, as suggested in the previous paragraph, ***Q. ilex*** growth and survival is strongly limited by water availability, what explains the fact that it is one of the most widely distributed trees in the Mediterranean basin? The xylem of ***Q. ilex*** has an exceptionally high hydraulic conductivity, both per unit of cross sectional area and per unit of supported leaf area (Chapter 3). This high conductivity allows ***Q. ilex*** to have higher maximum transpiration rates and greater $A_L$:$A_{SW}$ than ***A. unedo*** and ***P. latifolia*** (Chapter 6). As a result, maximum growth rates are probably larger in ***Q. ilex***, allowing this species to outcompete the others when water is not particularly limiting.

As it is apparent from the previous paragraphs, water uptake has been the forgotten element in our studies (and in plant water relations in general). While there are good practical reasons for this, recent results suggest that belowground processes may be the key to improve our understanding of water relations at scales from the plant to the whole biosphere (Jackson 2000, Jackson ***et al.*** 2000).

## Effects of climate change

According to the last report of the Intergovernmental Panel on Climate Change, most models predict an increase in global average temperature of 1.4-5.8ºC during the XXI century (IPCC 2001). Precipitation scenarios are more uncertain and are also subject to more regional variability. However, when the effects of temperature and moisture are combined, aridity is predicted to increase over most areas (IPCC 2001). At the same time, many extreme events, such as acute droughts, are likely to increase (IPCC 2001). All these changes will have (and are already having in some cases), an impact on biological systems (Hughes 2000).

Our results in Chapter 2, combined with those in Pockman & Sperry (1997), suggest that freezing-induced xylem embolism limits the distribution of ***Larrea tridentata*** in southern USA. The increase in temperature over this area of North America is predicted to be greater than the Earth average. As a result, the number of frost days and the absolute magnitude of extreme minimum temperatures are very likely to decrease (IPCC 2001). If we consider the relationship between minimum temperature and xylem embolism in ***L.***

***tridentata*** (Chapter 2), an increase of just a few degrees in minimum temperatures will result in much lower levels of embolism. In consequence, ***L. tridentata*** may expand its distribution northwards into the central prairies.

In the Mediterranean basin, warming is also projected to be larger than average. At the same time, it is one of the few regions of the Earth where precipitation may decrease substantially (IPCC 2001). In warm and dry regions, such as the Mediterranean, the major impacts of climate change are predicted to be through altered water availability (Shaver ***et al.*** 2000). ***Pinus sylvestris*** and ***Quercus ilex*** were severely affected by the acute drought occurred during the summer of 1994 in NE Spain (Chapters 3, 5, 6 and 7). In Catalonia (NE Spain), these species are two of the three most abundant trees, covering ***ca.*** 35% of the total forested area (CREAF 1998). Our results showed that these species, and others less important in the landscape, may be at their limit to cope with water shortage in many areas. In consequence, they may be substituted by more drought-resistant plants if extreme droughts become more frequent. The model presented in Chapter 7 predicts that global warming is likely to cause extensive dieback in ***Q. ilex***, while the co-occurring ***Phillyrea latifolia*** is predicted to suffer minor damage. In this respect, our results agree with earlier studies suggesting a possible substitution of ***Q. ilex*** by ***P. latifolia*** (***e.g.,*** Peñuelas ***et al.*** 1998). Although the effects of climate change on other, not studied stages of the life cycle are potentially relevant, the ability of adults to survive poses a clear limit on the long-term survival of a tree species in a particular area.

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