

## **DROUGHT AND FOREST DECLINE IN THE IBERIAN PENINSULA: A SIMPLE EXPLANATION FOR A COMPLEX PHENOMENOM?**

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### **ABSTRACT.**

Different episodes of forest decline have been reported in several areas of the Northern Hemisphere during the 20th century. The explanation of this process included anthropogenic (air pollution), biotic (pathogens) and climatic factors. Among the climatic factors, the effect of acute or chronic droughts have been the most common explanation for the massive dieback observed. In the Iberian Peninsula, besides the pathogenic explanation which gives a paramount relevance to the fungus *Phytophthora cinnamomi* in many situations, the role of an increment in aridity (chronic) or the consequences of severe droughts (acute) have been empirically supported. The evident synchronism between forest decline and abnormally adverse climatic conditions, in addition to the reversibility of the process when precipitation intensity increased, are

two major arguments for supporting the climatic involvement in the phenomenon. Nevertheless, the two most affected species in the episodes of oak decline in the Iberian Peninsula were *Quercus ilex* and *Q. suber*, which are representatives of the so-called mediterranean woody flora and which have been considered as more drought resistant than the temperate oak species that co-occur in this territory. The climatic complexity of the Iberian Peninsula, the many mechanisms for coping with water stress that have been described within the sclerophyllous mediterranean flora and the effects of human management partially explain this paradox.

Other forest species have also been affected by massive decline. *Pinus sylvestris* and *Abies alba*, which have their southern distribution limit in the mountain ranges of the Iberian Peninsula, are two examples of this situation. Both cases, besides the immediate effects of some climatic perturbations, need the incorporation of different predisposing factors – mainly historical aspects – to obtain a complete image of the process.

## **1- INTRODUCTION.**

The Iberian Peninsula has been traditionally considered, besides other countries of southern Europe, a paradigm of mediterraneity, a classic reference for geobotanist when the effect of summer drought on plant existence has to be introduced. Woody plant species, which can not escape from the water stress by performing all the vegetative cycle outside the stress period or through the synchronous leaf shedding as a mechanism to reduce transpiration, have to withstand this stressful period situation by different functional adaptation. However, the severity and frequency of several extreme droughts during the last decades starts to be concerning. In fact, it is assumed by climatologists that it is expected an increment of aridity due to a chronic and progressive temperature increasing joined with a reduction in precipitation. How long the present mediterranean

landscape will be able to stand this climatic changes is more than a pointless discussion. The future of many plant and animal species and the future of many traditional human practices associated to the different mediterranean landscape can be jeopardized.

One effect that can be expected is a reduction in net carbon gain and tree growth, as long as the primary productivity is reduced by water stress whereas respiration rises as a response to temperature increase. However, the progressive change in the climatic scenario will have more significant and evident effect in the landscape through a progressive change in the species composition of the forest communities. Some species will be substituted by others, which are better adapted to this higher aridity. This fact implies the disappearance of those species worse adapted to this new level of aridity in areas where they are now present. The massive forests decline that is reported throughout the Northern Hemisphere since the 1950s may be interpreted as the result of this phenomenon.

In fact, processes of massive forest decline, affecting different forest species, are progressively more common in this territory. Although the process is considered to be dependent of many factors, some evidences would suggest the intensity and frequency of droughts as the main causes for this decline. Three processes have been studied in depth by the authors: the mediterranean oak species decline, the progressive death of many specimens of silver fir (*Abies alba* Mill) in different areas of the southern distribution limit of this species in the Pyrenees and some sporadic but very intense processes of massive death on Scots pine (*Pinus sylvestris* L.) in the higher mediterranean mountains of the Iberian System.

The study of these three examples of forest decline has revealed two different dynamics in the influence of the climatic changes: a chronic trend, which is responsible of a rising in the mediterranean influence in mountain areas and some acute situations, when some

severe droughts – as those of the last decade of 20th century - induced the massive dieback of whole trees or the partial loss of the standing crop in many coppice stands.

However, in spite of the many evidences supporting the climatic influence on the episodes of forest decline in the Iberian Peninsula, the complete portrait of the situation is not fully concluded. We would like to put into evidence some circumstances that can be modulating the influence of drought on forest trees survival. The so-called “holm oak decline paradox” by us in this chapter is an example of the high complexity of this process of massive dieback registered in one of the most characteristic species – *Quercus ilex* - of the mediterranean flora in southern Europe. Attempting to explain this paradox, we will try to give a more detailed explanation of i/ the climatic heterogeneity in the Iberian Peninsula, ii/ the different plant strategies that have been described for withstand drought and iii/ the combined effects of summer aridity and low winter temperatures on the growth and survival of the mediterranean woody flora.

Moreover, the history of the Iberian Peninsula, both that subjected to geological events (such as glaciations) or to human influence, has created a complex mosaic of forest stands occupying ecological situation which are close to the functional limit of the species. The predisposing factors associated to this situation on the tree survival is also discussed, both when attempting to explain the holm oak and Scots pine decline as the consequence of soil degradation or increased plant vulnerability to water stress associated to overageing in abandoned coppice stands. Of course, the policy of reforestation, which has induced the presence of several conifer species out of the optimum ecological range, must be also taken into consideration.

## **2. FOREST DECLINE**

## **2.1. A historical overview.**

Several processes of massive tree death were reported during the 1970s and 1980s in Central Europe and Northwestern America, which had a great incidence in several forest areas dominated, among others, by species of *Quercus* L., *Pinus* L., *Abies* Mill. or *Populus* L. The symptoms were quite regular and inespecific in their appearance, where the whole tree death was only the end of a large series of functional or morphological changes. Namely, crown defoliation and decoloration, morphological and architectural changes in the branches, profuse epicormic or adventitious shoot formation, root death, reduced growth rate, or premature senescence were observed (Hertel 1988, Brasier et al., 1993; Brasier 1996; Sánchez et al. 2000b).

Such an “unprecedented” and “unusual” phenomenon, as it was considered during the first bouts, soon achieved a great resonance, under the concept of “forest decline” or under the German term *Waldsterben*. Among the several processes of forest decline which were observed and documented, that affecting different species of genus *Quercus*, -“oak decline” - had a very big social impact. This was partly due to the extreme importance of the different oak species in the culture, history or even economy of the affected countries. Thus, similar episodes of oak decline were reported in different areas of the northern Hemisphere (Donabauer & Ciesla 1992, Starkey et al. 1995, Rizzo & Garbelotto 2003), and a great deal of evidence supported the idea that this process was quite a regular phenomenon throughout the 20th century, both in Europe (Eisenhauer 1991, Tomiczek 1993, Luisi et al. 1993, Scortichini et al 1993, Przybyl 1994, Sicoli et al 1998) and in North America (Lewis 1978, Lewis & Oliveira 1979, Kessler 1989, Biocca et al 1993, Dwyer et al 1995, Oak et al 1996).

## **2.2. Social reactions and the scientific quest for an explanation.**

Both foresters and scientists were concerned about the forest-decline, and the quest to find an explanation still goes on, as long as oaks and other tree species continue dying back in many areas at present. The public concern in those countries where the forest constitutes a part of their traditions and culture was extreme, due to the global significance of the process. Thus, as an example, the fir-decline process – which is mainly known as *tannensterben* – not only implied the progressive extinction of the “keystone species” (*Abies alba*) but also the loss of many other animal and plant species, which are absolutely dependent on the silver-fir habitat. The process has also implied the loss of some well-preserved forests, which are of paramount importance as biomass reservoirs, in the form of trunk and branches of living trees or as accumulated dead biomass, mainly as a part of the soil litter. Taking into account that in terms of carbon storage, the conservation of ancient forests is a more efficient strategy than reforestation with young trees, the implications of forest decline in a global context of carbon cycling and the Kyoto Protocol seem quite obvious (Schulze et al. 2000). The loss of mature silver fir forest and beech forest, and their subsequent substitution by young forests is a process occurring in many areas of the Spanish Pyrenees nowadays. This substitution would imply a net carbon loss, a net atmospheric carbon gain and a positive feed back in the global warming due to the greenhouse effect.

The abundance of scientific meetings which have been held within a relatively narrow time interval was a clear symptom of the concern aroused. During 1990, two monographic meetings took place, namely the Joint Annual Meeting of the American Phytopathological Society and the Canadian Phytopathological Society, in Grand Rapids (USA), under the title “Global climate change as a general mechanism of forest dieback”, and the International Congress on Oak Decline in Kornik (Poland) under the title “Oak Decline in Europe”. The concern about the reasons for this process still

remained still so great that another meeting took place in Brindisi two years later (1992), entitled “Recent Advances in Studies on Oak Decline”. In this congress, experts from many countries all around the northern hemisphere gathered together to explain what was considered a global phenomenon.

The need for an urgent explanation, caused by the social impact, hastened the search for a common and single agent responsible for this whole situation, although the forest decline was located in different geographical areas, ecological situations and the process was affecting many different woody species, occurring in wet or dry habitats (Donabauer & Ciesla 1992).

### **2.3. Anthropogenic and biotic factors.**

In effect, in the very early studies on forest decline, most of the forest experts suggested the existence of a common “syndrome”, as discussed in Camarero et al (2004). Concretely, acid rain (Schütt & Cowling 1985) or ozone effects (Schmieden & Wild 1995) were proposed as the agents which related air pollution to forest decline. The fact that the first decline episodes had been reported in densely populated areas with an intense industrial activity supported this idea. More recently, some other evidence relating air pollution and oak decline episodes has been contributed (Bussoti et al 1995, Bussoti & Ferretti 1998, Güllü et al 2002). In spite of this fact, nowadays it is widely accepted that air pollution, as a single factor, cannot be considered the reason for explaining forest decline except in a very scant number of situations (Thomas et al 2002).

Many other research works have suggested that forest decline may be the immediate consequence of a pathogen attack. Some classic examples for these can be found in the epidemic North American “oak wilt” disease, mainly affecting live oak (*Quercus*

*virginiana* Mill) (Appel 1995), the “tracheomycosis” caused by the fungus of Genus *Ceratocystis* Ellis & Halstead as the cause for *Q. petraea* (Matt.) Liebl. dieback in Slovakia and Hungary (Führer 1998), or the *seca* (from the spanish verb *secar*, to wilt or to dieback) in Spain. This last phenomenon was first explained as being the immediate effect of *Phytophthora cinnamomi*. Rands. In fact, and to the extent of the present knowledge, this fungus is one of the most destructive plant pathogens, which causes the whole death of the absorbent roots and , as an immediate consequence, severely reduces the tree’s ability to capture water and nutrients (Jönsson 2004), inducing very similar wilting symptoms, to those observed in a woody plant under severe water stress (Brasier 1992, 1996, Brasier et al 1993, Tusset et al 1996, Sánchez et al., 2000a; 2000b; 2002). In all the situations where the problem can be explained through a single mechanism (e.g. the relationship between host and pathogen), a method for mitigating the damage has been proposed, such as the use of intravascular injections with different substances as a way to control the pest (Appel & Kurdyla 1992, Escobar et al 1999). Many other pathogens, besides the above mentioned, have been proposed as being the reason for the massive forest dieback, especially when oak species have been affected (Luque & Girbal 1989, Przybyl 1994, Luque et al 2000), and often associated with inadequate management practices. However, the evidence of many forest decline processes where no pathogen attacks have been reported (Fernández-Cancio et al. 2004) questions the consideration of tree dieback as the result of a single factor, standing in contradiction with the categorical conclusions of many previous studies.

#### **2.4. A climatic explanation: Do acute or chronic drought underlie the forest decline?**



On the other hand, the process of forest decline has been attributed in many other studies to functional plant disorders explained by the negative influence of different abiotic factors. Climatic perturbations, both in the form of events recording unusual climatological values (e.g. **acute droughts**), or associated with a global mechanism of climatic change (e.g. **chronic aridity**), are the main axis in these interpretations. In fact, Führer (1998) suggested that oak decline could be due to an impairment of the water balance and metabolic disorders of the tree, regardless of any local variation and in spite of the consideration of the process as a complex (multifactorial) phenomenon.

Indeed,, drought is the climatic factor which has been repetitively suggested as the main, if not the only, reason for explaining forest decline throughout the northern Hemisphere, especially in temperate (mesic) species (Tainter et al 1984, Landmann et al 1993, Rösel & Reuther 1995, Bréda 2000, Corcuera et al 2004a). Empirical evidence of the direct effect of drought on forest decline has been presented throughout the 20th century. Tainter et al (1983) reported an unusually high incidence of red oak decline and death in the Nantahala National Forest, North Carolina, (USA) in the 1970's, proposing that this was probably the result of an unusual series of extremely dry summers starting in 1968 and worsening in 1973-78. In the same direction, Tainter et al (1990) considered that a series of severe regional droughts in the early 1950's severely affected red oak growth in southeastern United States, with a clear expression in the trees' basal area increment. This acute phenomenon induced a chronic effect on tree growth in some populations, which are defined as "declining" by these authors. After a moderately severe drought in the early 1980's , the declining populations showed a marked crown deterioration or even crown death. Auclair et al. (1992) explained some occurrences of oak decline in central Europe as a combination of acute drought periods and extreme winter temperature fluctuation, which is known to induce xylem embolism in woody

plants (Cochard & Tyree 1990, Pockman & Sperry 1997, Davis et al 1999). Drought-induced xylem dysfunction in *Populus deltoides* Bartr. Ex Marsch., *P. balsamifera* L. and *P. angustifolia* James was considered the main physiological reason for explaining riparian ecosystem decline in Alberta (Canada) by Tyree et al (1994), which can be interpreted as the result of a chronic alteration in the water table in dammed rivers. Siwkcki & Ufnalski (1998) compared annual growth rings in *Quercus robur* L. stands in Poland and Walter's climatic diagrams. The authors concluded that declines in oak-forest ecosystems were associated with an increase in the frequency of dry years, especially when drought occurs at the beginning of the growing season, e.g. in May-June. However, to what extent these drought episodes are an acute climatic phenomenon or the consequence of a chronic climatic change is a matter that remains unsolved.

### **3. CLIMATE AND FOREST DECLINE IN THE IBERIAN PENINSULA: SUPPORTING EVIDENCES.**

Several episodes of forest decline have been reported in the Iberian Peninsula, which mainly affected holm oak (*Quercus ilex* L.) and cork oak (*Q. suber* L.) populations during the 1950's. These bouts of oak decline were disguised among others that affected tree species of genus *Castanea* Mill. and *Ulmus* L., which were considered as being the result of the severe attack of some very aggressive pathogens (*Endothia parasitica* (Murr.) Anderson, *Phytophthora cinnamomi* Rands and *P. Cambivora* (Petri) Buiss., *Ceratocystis ulmi* (Buis) Moreau). The phenomenon of oak decline was very intense from 1989 to 1999, especially in 1993 and 1994, unleashing massive tree deaths in the Mediterranean area of the Iberian Peninsula. A strong reactivation of the process started in 1998, with a remarkable massive dieback of a large number of forest species

belonging to different genera in the western and southwestern area of the Iberian Peninsula. This trend has continued up to the present moment.

The early detection of *Phytophthora cinnamomi* in the roots of the declining trees, as explained above, reinforced the conception of oak decline in Spain and Portugal as being a disease, with a clear biotic origin (Tuset 1996). However, and according to Shigo (1993, 1994), a few pathogens are able to kill a tree not previously weakened by other causes, tree decline being the irreversible loss of its vitality, once the threshold of its maximum stress resistance is exceeded. Among the factors that can weaken the genetically programmed plant resistance and place it in a critical situation are, without any doubt, those of a climatic nature. The importance of holm oak and cork oak in the landscape and even in the economy of many areas of the Iberian Peninsula has triggered the accumulation of many studies about the causes of this massive dieback process. The empirical evidence provided has forced the consideration of climate, besides pathogens, as a reason for oak decline in this area (Peñuelas *et al.* 2001, Corcuera *et al.*, 2004a, 2004b).

Fernandez-Cancio *et al.* (2004) also support the idea that the origin of most of the forest decline processes in Spain lies in climatic factors, concretely in an increase in aridity due to the decrease in rainfall since 1980 and, especially, to a marked temperature increase. **Acute** droughts caused by rainfall decrease seem to be temporary, whereas droughts due to an increase in temperature could turn into being **chronic** and they would not need any previous aridity conditions.

These authors provided a chronology of decline phenomena, combining them with several very hard climatic periods during the last decades. This synchronization between decline and unfavourable climatic events is the main evidence of any climatic explanation of forest decline.

Thus, considering a broad temporal context - the last ten centuries - droughts recorded in the 1980's (1980-1985) and 1990's (1990-1994) can be included within an extremely variable period, from a climatic point of view, that approximately coincides with the second half of the 20th century (Manrique & Fernández-Cancio 2000). The great variability in the climate data recorded seems to be one of the main factor affecting tree growth in the context of the global climate change (Tardif et al. 2003). The areas under a Mediterranean climate in the Iberian Peninsula have become drier and hotter throughout the 20th century. However, this change has not been progressive, and many scattered drought periods have been recorded, alternating with wetter ones. For instance,, the summer of 1994 was extremely dry, as it was the culmination of a five-year period with a severe water deficit. This fact is of paramount importance from a global perspective of the phenomenon and has direct implications for the design of forest management practices or in governmental conservation policies. Indeed, the pulsed appearance of some **acute** drought episodes has veiled the effect and consequences for the vegetation of a **chronic** climate change. The consideration of the dieback processes as a response to abnormal climate conditions implies that a few practices, if any, could be designed in order to ameliorate the effects of drought. In fact, the subsequent recovery of many affected areas, as will be explained below, has encouraged the adoption of a passive attitude by the foresters in most cases. However, if we assume that all these episodes of atypical climate records are the consequence of a chronic process the need for a global forest policy arises.

The existence of a monitoring network, designed for recording forest damage since 1987, permitted the monitoring of the effects of the 1994 drought (Montoya 1995, Montoya & López Arias 1997). These surveys indicated that 80% of the 190 plots studied showed damage in the arboreal stratum, which could be attributable to drought.

Moreover, Martínez-Vilalta & Piñol (2002) surveyed the massive Scots pine (*Pinus sylvestris*) mortality in *Sierra de Prades* (Tarragona, Spain) after the 1994 and 1998 droughts, reporting percentages of dead trees ranging from 8% to 20%. Corcuera et al. (2004a, 2004b) studied the effects of the 1993-94 drought on coppice stands of *Q. ilex* subsp. *ballota* (Desf.) Samp. and *Q. faginea* Lam. in the Iberian System (Zaragoza, Spain). In this area, the effect of an especially severe drought period on tree functions was confirmed: two consecutive dry winters (1992-1993 and 1993-1994) were followed by the very dry 1994.

This quite evident synchronism between forest decline and abnormally adverse climate conditions inherently implies a clear fact. Tree growth and vigor should revert to the previous values after the adverse episode, provided that the rainfall reaches higher records. We can consider this fact as being the reversibility of the process, which, in fact, can be considered as a “negative” image of the synchronism. The recovery of the vegetation status after a drought period when annual precipitation intensity increases has been found at both an individual and population level (Fernandez-Cancio 1997, Camarero et al 2004, Gil et al 2004). This reversibility of the process is one of the major support factors for the climatic explanation of forest decline:

Is there any empirical evidence supporting the reversibility of the forest decline in the Iberian Peninsula? In fact, the recovery of the vegetation status in many severe attacks of oak decline observed in coppice stands of holm oak (*Quercus ilex*) in the northeastern Iberian Peninsula is a clear demonstration of this reversibility. After suffering the effect of the 1992-1994 extremely dry period, many of these coppice stands lost most of their standing crops. The favourable climate period that followed this drought, with quite high rainfall records, caused the nearly complete recovery of the crown in the wilted specimens as a consequence of profuse resprouting. This process was assessed and

documented by using LandSat-TM5 image processing (Aït-Bachir 1998, Aït-Bachir et al. 2000).

Evident recoveries of the healthy status of many forest stands have also been observed when other tree species were involved. The recovery is sometimes greater in the most affected populations, i.e. those which had formerly shown a higher degree of decline. In this sense, the benefit of a lower competition, in terms of resource acquisition, could explain this fact (Martínez-Vilalta & Piñol 2002). However, at the individual level, those plants showing a better recovery were less affected by the previous stress period. This process also depends on the plant size, the larger plants being those which made a better recovery, probably as the result of a better resource acquisition efficiency (Camarero et al 2004).

#### **4. THE PARADOX OF THE IBERIAN *SECA*: WHY DO THE MORE XERIC OAK SPECIES SUFFER A GREATER DECLINE?**

Oak decline in Spain and Portugal has been considered to be within the global processes of oak decline in the northern hemisphere. The majority of the studies relating drought and forest decline have addressed situations where temperate, mesic species, with a lower degree of drought tolerance than other congeneric xeric species (Cavender-Bares & Holbrook 2001) are affected. A climate episode that could lead to massive decline in tree species with a poor ability to withstand drought is not hard to assume.

However, the two species most affected by the phenomenon of forest dieback in the Iberian Península throughout the last decades have been those formerly mentioned – *Quercus ilex* and *Q. suber* – following Fernandez-Cancio et al (2004) - both genuine representatives of the Mediterranean woody flora (Corcuera et al 2002). Many physiological features indicate a high degree of drought tolerance in these two species,

including quite a high resistance to water stress-induced xylem embolism, as reported by Tyree & Cochard (1996) and Corcuera et al (2002). However, and surprisingly, other much more drought-sensitive oak species— *Q. petraea* and *Q. robur* — have not suffered such a severe decline process.

This apparent paradox – the higher the resistance to drought the higher the level of decline – needs a complex explanation, which lies in the three peculiarities of the oak decline process in the Iberian Peninsula: i/ the climatic complexity of this territory, ii/ the lack of any single functional response in the so-called sclerophyll Mediterranean flora, with special attention to the physiological differences found within holm oak populations and iii/ the sign of the historical landscape management in the quality of the soil where most of the Mediterranean oak populations occur at present.

#### **4.1. The climatic complexity in the Iberian Peninsula.**

The Iberian Peninsula is mainly situated in the so-called Mediterranean area, which comprises all the territories under the influence of the Mediterranean type climate. In fact, this climate has been considered as a transitional climate, between the humid-temperate climate— with regular precipitations due to the influence of the depressions associated with the Polar Front— and the arid climate of the high-pressure areas in the subtropical belt (Balairón 1997). According to Köppen's climate classification, Mediterranean climate extends from 30° to 45° north and south and is characterized by humid winters and dry summers, which partially reflect the features of the arid subtropical climate from lower latitudes and the humid climate from higher ones.

Walter (1985) proposed the zonobiome IV as the “zonobiome of sclerophyllic woodlands”, which includes the areas of the earth under the influence of a Mediterranean type climate (Breckle 2002). This zonobiome comprises the

Mediterranean sclerophyllic forest and *macchia* in Eurasia (Giovannini et al. 1992), the Californian *chaparral* and *encinal* in North America (Hanes 1971, Peinado et al. 1997), the Chilean *matorral* and *espinal* in South America (Montenegro et al. 2004), the *fynbos* in South Africa (Campbell & Berger 1988, Cowling & Campbell 1980), and the *mallee* (Robinson et al. 2006) and *kwongan* in Australia (Yates et al. 2007, Wisheu et al. 2000). In spite of this clear predominance of the Mediterranean-type climate conditions (see Figure 1), the northern areas of the Iberian Peninsula are under the influence of a **humid-temperate** climate, with a floristic composition belonging to the EurosIberian region (Rubio et al 2002). According to Walter's classification (Walter 1985), this area should be included within the zonobiome VI, or zonobiome of deciduous forests and temperate nemoral climate. The climate of zonobiome VI, with a warm vegetational season of 4-6 months with adequate rainfall and a mild winter lasting 3-4 months, is very suitable for the deciduous tree species of the temperate climate zone. Such trees avoid the extreme maritime as well as the extreme continental regions and favour what is termed the nemoral zone. In the Iberian Peninsula, a **sub-mediterranean** zone is intercalated between the Mediterranean and nemoral zones. Although there are still winter rains, the summer drought is no longer pronounced and frost occurs regularly in all the winter.

At this point, it should be highlighted that the orography, as a secondary causing factor of rainfall distribution, affects the climate, turning the Iberian Peninsula into a mini-continent with a wide range of phytoclimates. The orography has a direct effect on the distribution of humid fronts, as long as the mountain ranges block the incoming of humid air, increasing the continental nature towards the interior of the Iberian Peninsula. Thus, the orography prevents the eastern areas of the Iberian Peninsula from receiving oceanic rainfalls, which are responsible for the temperate nature of the



northern and northwestern areas (Eurosiberian region, temperate areas or zonobiome VI).

This orographic effect on the arrival of humid fronts to the eastern areas of this territory is the reason for the existence of very arid phytoclimates – of a semidesertic nature – in this part of southern Europe. Under these conditions, the only contribution to mitigating the extreme aridity is the arrival of humid air directly from the Mediterranean Sea, inducing the autumn rains only in the coastal areas.

In the northern areas, the Pyrenees, which is the highest mountain range in the whole Iberian Peninsula, keep out the summer rains common in Central Europe. Therefore, these summer rains are only present in the northern areas without the influence of this mountain range.

Orographic complexity also influences the local climate conditions in the Iberian Peninsula in spite of the main latitudinal trends, by incorporating some modulating factor. One of these, which can produce a marked difference in the meteorological records in a short distance - inducing very strong physical gradients - is air adiabatic cooling as the altitude increases. The temperature decrease, in combination with the orographic or relief rains, allows the genesis of altitudinal vegetation belts in the main mountain ranges in the Iberian Peninsula. Therefore, the existence of local climates which are cooler and wetter than expected, is the explanation for the presence of many isolated populations of some tree species, which are common in northern latitudes. These populations, in the form of small “temperate islands” in Mediterranean surroundings, can be very vulnerable to abnormal climate episodes. The populations of *Fagus sylvatica* L. in the Spanish Central System mountain range or the pedunculate oak (*Quercus petraea*) forests in the Iberian System mountain range are examples of the situation mentioned above. According to Breckle (2002), these situations must be

considered as **orobiomes** with local features, although they are of great significance in the vegetation of the zone.. Finally, it should be noted that the Iberian Peninsula shows strong variations in its vegetation as a consequence of the marine influence on the thermal regime, which can be considered as being an additional factor in the climatic diversity of this territory.

This climatic diversity can be expressed in the form of different types and sub-types of phytoclimates or zonobiomes throughout the territory (Walter 1985, Allué-Andrade 1990, Breckle 2002). Thus, the zonobiome VI, according to Walter (Breckle 2002), defined as the “zonobiome of deciduous forests” or “zonobiome of temperate nemoral climate”, predominates in the northern and northwestern areas of the Iberian peninsula. The European beech (*Fagus sylvatica*) and some mesic oak species (*Q. robur* and *Q. petraea*) could be selected as genuine representatives of this climate type, which is considered as humid-perhumid with a mean value of minimum temperature equal to or lower than 4 ° C. These climate conditions are sometimes associated with the presence of large mountain ranges ( such as the Pyrenees and Picos de Europa) to induce altitudinal belts, with a direct correspondence with the so-called “alpine” and “sub-alpine” belts (Breckle 2002).

This phytoclimate can become drier, cooler or both drier and cooler. (Figure 1 and 2). This trend in the evolution of climate conditions makes it necessary to distinguish some transitional sub-types, already described in the early geobotanical synthesis (cf. Breckle 2002). The transitional climate types, as long as they are distinguishable from the genuine main types, have their own tree species, with some special features. Among them, several oak species can be mentioned, which are not strictly mesic in their physiological performance but share many functional attributes with the genuine temperate species (Corcuera et al 2002). The winter deciduousness, sometimes under a

special form named “marcescence” (Abadía et al 1996), and the ring-porous xylem are examples of these resemblances (Corcuera et al. 2006). These transitional oaks could have been the dominating tree species in the forest occurring in most areas of the Iberian Peninsula, many times associated with the existence of local conditions due to orographic influences on climate, before any human effect on the landscape. This last factor, the anthropogenic influence, has caused the irremediable substitution of these transitional species by evergreen and sclerophyllous Mediterranean species of genus *Quercus*, like *Q. ilex* (Corcuera et al 2004a). These oak species, especially *Q. faginea*, is able to withstand the winter frost in some continental subtypes within the genuine zonobiome VI, which is ecologically close to the treeless cold steppes (subtype VI(VII)).

Under climate conditions of a greater summer aridity than that common in the temperate areas some of these transitional species can survive, when soils guarantee a large enough water reserve to allow their survival throughout the moderate arid summer. In some cases, it is hard to find a clear ecological reason for the presence of these transitional oak species instead of the more temperate representatives of the genus. In fact, *Q. pyrenaica* Willd, which is more water demanding than *Q. faginea* (cf. Corcuera et al 2006, Estesó et al. 2006), co-occurs with *Q. petraea* and *Q. robur* in many areas under a direct oceanic influence. Low air humidity values in the clear and sunny days of the Iberian mountain ranges and the need for withstanding the very high water potential gradients in the soil atmosphere continuum should be taken into consideration in order to explain the ecological role of this species. In fact, the very low hydraulic resistance in the deeply lobed leaves of this species, as compared to the values recorded by leaves of *Q. robur* and *Q. petraea*, could be a functional advantage for stress avoidance through a water spending strategy (Sisó et al. 2001).

All these considerations on the climatic diversity of the Iberian Peninsula clash with the simple image given by some early geobotanical classic works, that consider this territory as being under the influence of a single, predominant climate. The existence of a drought period during summer and a humid period during winter leads to the predominance of evergreen and sclerophyllous tree species. Holm oak would be the main tree dominating the landscape, according to this early idea. All these features are common and typical of the so-called zonobiome IV (Breckle 2002). However, and in spite of most of the land being under the influence of a Mediterranean type climate, which fits the former features, a great floristic variation and forms of vegetation can be found in the Iberian Peninsula, associated with the many different local conditions found.. Even within the more or less genuine Mediterranean climate, the distance from the sea signifies a variation axis in terms of continentality (Fernandez Cancio et al. 2004). Thus, the potentiality of the landscape in this zonobiome in the Iberian Peninsula induces the formation of sub-tropical forests in the northeastern coast, with the presence of *Q. ilex* subsp. *ilex* L. and *Q. suber* as dominant species, or shrublands occupied by *Q. coccifera* L., *Rhamnus lyciodes* L. and *Pistacia lentiscus* L., where the ecological limits for the survival of the holm oak are exceeded (cf. Corcuera et al 2004b). In fact, the vegetation and climate in some areas of the southeastern Iberian Peninsula are closer to that common in the zonobiome III (zonobiome of hot deserts or zonobiome of subtropical arid climates) than those of a genuine Mediterranean zonobiome.

As can be concluded from the previous explanation of the climatic diversity in the Iberian Peninsula, the effect of both acute or chronic changes in the typical meteorological records do not affect the ecological limitations for tree growth or survival under the different climate subtypes in the same way. Evergreen oaks, and especially *Quercus ilex* , occur in many limiting situation throughout this climatic or

environmental mosaic. However, the mesic oak species, throughout the long history of landscape use in southern Europe, have taken refuge from drought in the more humid situation of northern and northwestern Iberian Peninsula on the mountain slopes, with both situations far from suffering drought, even under the most severe episodes recorded in the 20th century. However, evergreen oaks have to withstand drought in situations in which a slight increase in aridity would cause an incompatible climate scenario with tree survival. In fact, these treeless areas for climatic reasons, are, as explained above, quite common in the most arid areas of the Iberian Peninsula.

#### **4.2 Different strategies for withstanding water stress during the summer drought.**

As explained above, and in spite of the rather simplified concepts in the literature when a global view of the Earth is presented, the plant-climate interactions in Mediterranean areas respond to more complex mechanisms. In this sense, summer drought has been widely proposed as being the main stress period in those regions under the influence of a Mediterranean-type climate. However, this assumption is far from being a general principle. This simple ecological model for plant life in Mediterranean areas should be complemented with the incorporation of some other ecological factors.

In effect, the combination of high temperatures and low rainfall during summer leads to the consideration that one single stress period modulates the potential vegetative period for plant growth. On the contrary, it could also be suggested that a prolonged and continuous period, quite favourable for plant growth, extends throughout the non-arid months from autumn to spring. Such a long vegetative period and the low productivity shown on average by Mediterranean forests – as compared to temperate ones – stand in contradiction, suggesting that other circumstances influence plant metabolism and growth at other moments than this summer stress period. It is not hard to accept that,

besides the physiological limitations to plant growth caused by drought throughout the summer, the low winter temperatures negatively affect plant metabolism in the coldest areas under the influence of the more continental subtypes of the Mediterranean climate. In fact, cold or very cold winters are relatively common in the central part of the Iberian Peninsula, due to its high average altitude and distance from the temperate marine influence.

In this sense, as already stated by Mitrakos (1980), we should consider two potential stress periods when explaining the ecological functioning of Mediterranean vegetation: dry summers and cold winters. The different combinations in the intensity of drought and low temperatures are the key to any attempt to model the ecological potentiality, in terms of the landscape, of any of the different areas of the Iberian Peninsula (Di Castri 1981, Corcuera et al 2005).

The extremes of these possible combinations are i/ areas under the influence of prolonged, dry and very hot summers followed by mild and humid winters and ii/ areas with a relatively humid summer and extremely cold winters, climatic circumstances, which are, in fact, quite similar to those common and characteristic of the temperate climate (zonobiome VI, sensu Walter). The low temperatures during the winter in these quasi-temperate subtypes of the mediterranean climate are partly compensated for by the lower intensity of the summer drought, which allows the concentration of the vegetative effort throughout a single and continuous period (Nahal 1981, Allué Andrade 1990).

Between these two extremes can be distributed, as a continuum, the rest of the environmental situation, following the assumptions of this two-dimensional model defined by summer aridity and winter cold. Contrasting with the continuous nature of

the climate variations, Mediterranean sclerophyll plants have a rather narrow, genetically programmed, phenotypic plasticity (Valladares et al 2002).

Under high summer aridity conditions, inducing heavy decreases in photosynthetic activity (Vilagrosa et al 2003), water availability is the main factor affecting the productivity of the Mediterranean ecosystems (Di Castri 1981, Blondel & Aronson 1999). The combination of high temperatures and low rainfall severely reduces soil water availability due to the high evapotranspiration rates resulting from this combination of factors (Mediavilla & Escudero 2003, Corcuera et al. 2005). The low water availability causes water stress in plants, which promotes two types of biological responses, namely i/ mechanisms for **avoiding** or preventing the stress and ii/ mechanism for **tolerating** or resisting the stress. The different mechanisms indicating how plants withstand stress have been called **strategies**, which are, in fact, species-dependent (Larcher 1995, Valladares et al. 2004).

Different strategies have been distinguished with the aim of classifying plant response to drought (Vilagrosa 2002). Thus, in the hypothetical situation of a single and extremely severe stress period during summer in a Mediterranean context, it might be possible to obviate it by carrying out the whole vegetative cycle outside the stress period. In such a case, plants avoid (Kozłowski et al. 1991, Jones 1992), evade (Larcher 1995) or escape from the water stress (Levitt 1980, Turner 1986). In some small woody plants, closely linked to the most severe and arid Mediterranean type climates, an important, or even complete, foliar loss can be observed, as a mechanism for reducing the transpiring area during the most stressful moments. This strategy, which can be considered as a way for temporarily escaping from the stress, is known as summer deciduousness, and it has been described in many chamaephytes and small

phanerophytes (Armesto & Martinez 1978, Nilsen & Muller 1981, Comstock, & Ehleringer 1986, Lev-Yadun & Ne'eman 2004).

Nevertheless, most of the woody plants within the Mediterranean flora with a larger size (shrubs and trees) are typically evergreen, which implies that summer drought has to be withstood without reducing the leaf area. These species have to develop mechanisms that allow them to bear these periods of higher stress maintaining all their photosynthesis machinery, in order to recover the optimal metabolic activity under more appropriate conditions (Corcuera et al 2005). Some different mechanisms or strategies have been proposed in order to classify the specific response found by these plants.

The ability to avoid cell deshydration in spite of environmental aridity has been defined as a stress-avoidance strategy (Levitt 1980, Jones 1992), stress tolerance with high water potential (Turner 1986) or dehydration postponement strategy (Kozłowski et al. 1991). Larcher (1995) denominated the species able to avoid dehydration as desiccation avoidant – arido active species. The plant species which can avoid water stress do not let their living cells reach low osmotic values, by minimizing tissue dehydration, as long as they are very sensitive to it (RWC letal > 50%). The species able to use this strategy can be characterized by their ability to keep up a high leaf water potential through two different mechanisms. Both mechanisms are seemingly equal in their effectiveness but quite opposed in their functional basis, as far as some empirical studies have shown (cf Vilagrosa et al 2003a):

- The dehydration avoidance of their leaf tissues by an excellent ability to compensate their transpirational losses with an efficient water flow through the xylem. Thus, this strategy relies on high water “spending”, which has proven to be an efficient mechanism providing that the soil water reserve has not been completely depleted. A high hydraulic conductivity through the liquid pathways



of water flowing from roots to leaves is of paramount importance in this strategy (cf. Tyree 1999).

- The dehydration avoidance of the leaf tissues by mechanisms that make a good water economy possible. Several physiological features allow the plant to develop this saving strategy. In this sense, an ability for the generation of very high water potential gradients in spite of low water losses due to the inelastic nature of the cell walls, which present a high bulk modulus of elasticity (Corcuera et al 2002), is a common characteristic of a “water saver” plant. A relatively low value of maximum stomatal conductance, even under optimal water availability conditions and the rapid stomatal response to low water losses are also very effective mechanisms for maintaining the tissue water content sufficiently high. Under extreme conditions, these plants can partially or totally lose their leaf area, as an ultimate way to save water.

Finally, plants can tolerate cell dehydration, thus being considered as a species that develops a tolerance strategy (Levitt 1980, Jones 1992), a tolerance with a low water potential strategy (Turner 1986,) or a dehydration tolerance strategy (Kozlowski et al. 1991). Larcher proposed the designation of “desiccation tolerant-arido tolerant species” for all the plants capable of developing this strategy (Larcher 1995). These species can tolerate a low water potential, both in leaves and xylem, and keep the stomata open even after their tissues reach a low relative water content. In fact, , cells of this plant species show a high resistance to low or very low osmotic potential and hydration level without suffering any permanent injury (lethal RWC < 25%). Efficient osmotic adjustment, a highly elastic cell wall and very stable cell membrana are common features in these plant species. From a metabolic point of view, these plants are able to accumulate osmoprotective substances (proline, betaine), to develop antioxidative systems, and to

preserve the composition and long-term functional stability of the photosystem II (Vilagrosa 2002).

There can be no doubt that this “functional strategies” model cannot be considered, in spite of its theoretical strength, as a way to establish an absolute rank in the whole flora of a complex territory. It would be better used as a procedure for a comparison of the ecological performance between similar species or even between co-occurring ones (Salleo & LoGullo 1989, Vilagrosa et al 2003a, Vilagrosa et al 2003b). The comparison between very different ecological or functional species by using this classification system usually leads to uncertain results or to irrelevant conclusions. On the other hand, some plant species have shown that they are able to develop different strategies, according to the circumstances and conditions. Thus, *Pistacia lentiscus* performs as a “water spender” during the early summer, when the soil water availability is still high, showing quite elevated transpiration and growth rates (cf Vilagrosa et al 2003a). However, the same species develops a very efficient mechanism for “water saving” when the soil water availability drops in the late summer. Under an extreme water stress, the leaf tissues of *Pistacia lentiscus* has shown a good “stress resistance” (Vilagrosa et al 2002). This fact can illustrate how the attempt to classify plants into rigid stereotypes is not always successful.

In fact, and this should be considered as one of the bases of our contribution, a valid model has not yet been found that can explain, as a whole, the diversity of functional responses that can be found in sclerophyllous Mediterranean flora. The lack of a single response to the different stresses is at present hindering the development of a predictive model to be used in the forecasting of vegetation changes caused by the global climate change.

#### **4.3. Mediterranean sclerophyllous plants: A common physiognomy but different functional strategies.**

Mediterranean climate and evergreen sclerophyllous vegetation with small, narrow leaves (Traisier et al. 2004) have been historically linked by geobotanists (Di Castri 1981, Walter 1985). The “microsclerophyll” leaf type, a designation that aims to distinguish it from the larger “megascleophyll” leaves common in tropical rain forests (Medina et al. 1990), has been considered as an adaptation to warm, dry summers, which can be considered the main characteristic of the Mediterranean climate or the “zonobiome of the Arido-Humid Winter Rain Region”, in Walter’s classification (Breckle 2002). The morphological convergence existing in Mediterranean vegetation has been associated with a physiological convergence (Kummerov 1973). In this sense, Walter (1985) considered the ecological significance of sclerophyll due to its ability to greatly decrease transpiration by means of stomatal closure, when water supply from the soil is severely restricted. This mechanism allows plant survival until the end of the drought period with no changes either in plasmic water content or in leaf area reduction. Therefore, these plants could be considered, according to this author, as “water saver”, in the sense described above of this term. In this way, several authors have established correlations between leaf and morphological features by means of interspecific comparisons. For example, Tenhunen et al. (1981) found that, under water stress conditions, a midday decrease in transpiration rates and net photosynthesis in leaves of *Arbutus unedo* and *Quercus ilex*, two typical species of e Mediterranean sclerophyllous vegetation. In the same way, Corcuera et al. (2002) compared parameters derived from the analysis of pressure-volume curves in seventeen *Quercus* species from contrasting phytoclimates: six Mediterranean evergreen species (*Q. agrifolia* Née, *Q. chrysolepis* Liebm., *Q. coccifera*, *Q. ilex* subsp. *ballota*, *Q. ilex* subsp. *ilex* and *Q. suber*), seven

nemoral deciduous species (*Q. alba* L., *Q. laurifolia* Michx., *Q. nigra* L., *Q. petraea*, *Q. robur*, *Q. rubra* L. and *Q. velutina* Lam.) and four nemoro-Mediterranean deciduous species (*Q. cerris* L., *Q. faginea*, *Q. frainetto* Ten. and *Q. pyrenaica*). These authors found a certain degree of functional convergence within the three phytoclimatic groups studied, which was characterized by a differential physiological response to the water stress. On one hand, the genuine Mediterranean oak species developed mechanisms to avoid an excess of cell water loss, when water potential decreased, through a high bulk modulus of elasticity. On the other hand, nemoral oak species tended to maintain turgor pressure by means of large cell water losses. Finally, nemoro-mediterranean oak species showed an intermediate performance between Mediterranean and nemoral oak species. Furthermore, Corcuera et al. (2002) found a high relationship between leaf mass area and bulk modulus of elasticity, although the linking mechanism between both parameters has not yet been found..

On the contrary, Acherar & Rambal (1992), when comparing water relations and drought stress response in two evergreen (*Q. ilex* and *Q. suber*) and two deciduous (*Q. afares* Pomel. and *Q. faginea*) Mediterranean species, found that midday stomatal closure, in response to drought stress, was higher in deciduous than in evergreen species. This fact indicated that the evergreen species was much more sensitive to edaphic drought than the deciduous one. In terms of drought resistance, deciduous species avoided water stress by means of a rapid stomatal closure, at the expense of a considerable reduction in net CO<sub>2</sub> assimilation. However, evergreen species were able to maintain high photosynthesis rates at low water potentials. Therefore, according to these authors, Mediterranean oak species have several common biological features that allow them to maintain positive values of carbon balance with relatively high transpiration rates during drought stress periods. Paradoxically, according to the

classification suggested above, these features are not exactly compatible with the strategy of a water saver but with the functional mechanisms which are common in water spender or water tolerant species (Levitt 1980).

From our point of view, the consideration of Mediterranean vegetation as a functional unit, based on a water saving strategy, is a matter of opinion. Thus, Lo Gullo & Salleo (1988) found different drought-resistance strategies in three Mediterranean sclerophyllous species (*Olea oleaster* L., *Ceratonia siliqua* L. and *Laurus nobilis* L.) growing under the same environmental conditions. On one hand, *O. oleaster* was considered as a drought-tolerant species. On the other, two other species were considered as drought-avoiding species, *C. siliqua* by means of a water-spender strategy and *L. nobilis* by means of a water-saver strategy. Martinez-Vilalta et al. (2003) also found different strategies in water use in three sclerophyllous evergreen species that co-occur in a holm oak forest in north-eastern Spain. Whereas *Quercus ilex* and *Arbutus unedo* L. showed a great stomatal control over water loss, *Phillyrea latifolia* L. maintained high rates of sap flow at lower water potentials than the other species, by means of mechanisms that allow it to bear a high xylem tension without suffering irreparable damages. According to this result, *Q. ilex* and *A. unedo* seem to avoid water stress, whereas *P. latifolia* seems to risk using a strategy based on a greater ability to resist water stress. At this point, the question is, if the sclerophyllous woody vegetation typical of the Mediterranean climate can be included in a common functional syndrome. In fact, contrary to what some authors had suggested, (Poole and Miller 1975, Turner 1994), Salleo & Nardini (2000) showed that sclerophylly, one of the morphological features associated with Mediterranean vegetation, cannot be considered as being a mechanism for avoiding water stress, but as a mere epiphenomenon due to the excess of incident solar radiation existing in the Mediterranean region (Ogaya & Peñuelas 2006).

Moreover, although sclerophyll is related to some anatomical features which could be associated with the development of barriers against excessive water losses, such as thick outer epidermal cell walls and cuticles, it is also related to other features not so clearly linked to dry habitats, such as leaf thickness or to the abundance of sclerenchyma (Medina et al. 1990). In this sense, Verdú et al. (2003) postulated that sclerophylly originated in the context of tropical vegetation during the Tertiary, before the Mediterranean climate appeared during the Quaternary (Valladares et al. 2004).

At this point, the question to be raised concerns the role of sclerophylly as a common leaf trait of the Mediterranean vegetation. In this direction, Medina et al. (1990) found that nutrient content, specific leaf area and leaf thickness of some species from upper Rio Negro rain forests were comparable to those of sclerophylls from Mediterranean climates, to the extent that they could be classified morphologically as sclerophylls. However, the authors concluded that the leaves of the species studied were relatively drought intolerant and, therefore, the sclerophyllous structure was probably selected in environments poor in nutrients in spite of its drought adaptation. In this way, Campbell & Berger (1988), after studying the Cape vegetation in the mountains of South Africa, found that many features of the plant species of this vegetation type (known as *fynbos*), such as scleromorphy, could be interpreted as a consequence of the nutrient-poor soil in which *fynbos* occurs, rather than in terms of xeric-mesic trends. Recently, Gonçalves-Alvim et al. (2006) found that the lower concentrations of essential macronutrients were concluded to be the main factor influencing the sclerophyll in leaves of *Qualea parviflora* Mart., a deciduous tree of the Brazilian savannas.

In the light of this evidence, we have to consider that the sclerophyll, as a common trait of the Mediterranean vegetation, only allows us to establish a mere physiognomic classification, without any implications in the consideration of this vegetation type as a

homogeneous physiological group. Otherwise, we can assume that Mediterranean woody vegetation does not respond to drought by means of developing a single strategy. Therefore, the strategy to cope with drought does not allow the grouping of the sclerophyllous woody vegetation, typical of zonobiome IV, into a single physiological cluster.

#### **4.4. Xylem vulnerability to drought induced embolism: A more accurate parameter for a functional understanding of the holm oak decline in the Iberian Peninsula.**

In spite of the many evidences indicating the lack of a single way to cope with the summer drought in the Mediterranean woody flora, it may be possible that another common feature related to the ability for withstanding long and/or severe drought stress periods could be found in this vegetation type. The vulnerability of xylem to drought-induced embolism (Tyree & Ewers 1991) could be a promising parameter, because embolism limits gas exchange and drought resistance (Cochard & Tyree 1990, Hacke & Sperry 2001, Sperry et al. 2002), unleashing irreversible damage and subsequent tree death (Davis et al. 2002, Martínez-Vilalta & Piñol 2002, Esteso et al 2006). The air-seeding hypothesis is the mechanism for drought-induced xylem cavitation with most experimental support (Sperry & Tyree 1988, Tyree & Sperry 1989, Matzner et al 2001). Basically, following the former hypothesis, cavitation occurs when an air bubble is suctioned or pulled into a water-filled conduit under tension from an adjacent air-filled conduit through the pores in the pit membranes of the conduit walls. The analysis of the parameters derived from the regression curves which relate water potential and percentage of xylem embolism allow to draw conclusions about the strategy of plant performance (Hacke et al 2006). However, contradictory conclusions are reached when

the xylem vulnerability to drought-induced embolism of Mediterranean species is compared to that found in woody plants from other habitats. Maherali et al (2004) found that median  $\Psi_{50}$  of species occurring in the most arid vegetation types (e.g. deserts and Mediterranean zones) were 6-7 times more negative than those occurring in the wettest types (e.g. tropical rain forest). On the other hand, Tyree & Cochard (1996) concluded that arid zone oak species of southern Europe (*Quercus ilex* and *Q. suber*) are less vulnerable to drought-induced cavitation than mesic zone species (*Q. robur* and *Q. petraea*). In this way, *Q. coccifera*, an oak species occurring in the most arid areas of southern Europe, shows an extremely high resistance to drought-induced xylem cavitation (Vilagrosa et al 2003a). Would this parameter be the common feature that could group together the sclerophyllous typical woody vegetation of zonobiome IV?

With regard to the subject under discussion, new evidence has demonstrated that the reality is quite different. Maherali et al. (2004) showed the existence of a great variation in cavitation resistance of Mediterranean vegetation, from -2 MPa to -10 MPa for  $\Psi_{50}$ . Tyree & Cochard (1996) also found a great variability in this parameter for Mediterranean species. Matzner et al (2001) showed that *Q. wislizenii* A.DC., an evergreen oak species that is widely distributed in California, in regions with a Mediterranean-type climate and a dry season extending from April to November, underwent a 50% loss in conductance between 1.0–1.6 MPa, although conductance declined more slowly thereafter, reaching a maximum of 21-30 % at 4.0 MPa and 7–14% at 8.0 MPa. From these results, it is hard to consider *Q. wislizenii* as a tolerant species in terms of resistance to drought-induced xylem cavitation.

*Quercus ilex* shows, in this context, a special situation that should be highlighted. This species has suffered the most severe decline episodes in the Iberian Peninsula, in spite of its consideration as one of the genuine species of the sclerophyllous forest in the



Mediterranean area (*Quercetum ilicis*, see Breckle 2002). Several studies support the *Q. ilex* paradox as one of the most surprising disagreements between physiognomic and physiological traits. On one hand, Lo Gullo & Salleo (1993) reported low values of drought-induced cavitation for this species. Martinez-Vilalta *et al.* (2002, 2003) suggested that *Q. ilex* shows a relatively high vulnerability to drought-induced xylem embolism when compared to other Mediterranean species. On the other hand, Tyree & Cochard (1996) showed two very different vulnerability curves for this species: one of them was a typical curve for a plant with a high resistance to drought-induced embolism, whereas the other was characteristic of a plant with a low level of resistance to water stress. In the same way, Corcuera *et al.* (2004b) showed two very different vulnerability curves, depending on the provenance of *Q. ilex*. Plants from the most humid habitats within the ecological range of this species showed PLC<sub>50</sub> values about -3 MPa and 100% of loss of conductivity at -6 MPa. On the contrary, plants from drier and more continental areas showed PLC<sub>50</sub> values of about -5.5 MPa, maintaining 40% of hydraulic conductivity at -6 MPa.

These two different performances partly justified the paradox mentioned above. The massive dieback of holm oak stands in the Iberian Peninsula cannot be explained as being the effect of an environmental stress on the physiology of a species with a unimodal response. The holm oak complex, as we suggest,, seems to be the sum of two or more ecological types, with some obvious functional differences between them. Whereas some specimens are extremely resistant to a prolonged drought period, others are quite vulnerable to water stress. How can this evidence be explained?

According to botanical and phytogeographical studies, *Q. ilex* included two subspecies (Amaral-Franco 1990) or, even, two different species (Govaerts & Frodin 1998), clearly divided in their distribution area (Sáenz de Rivas 1967, Lumaret *et al.* 2002). On

one hand, *Q. ilex* L. subsp. *ilex* occurs in coastal areas in the northern Mediterranean (from Greece to the northeast of Spain and Mediterranean islands), mainly over calcareous substrates and under humid climatic conditions without either any winter frosts or severe droughts. On the other hand, *Q. ilex* subsp. *ballota* occurs in areas of a higher continental nature in most of the Iberian Peninsula and the north of Africa (Tutin *et al.* 1993, Blanco *et al.* 1997). According to Lumaret *et al.* (2002), the origin of this differentiation could lie in the isolation of ancient populations existing in Europe during the glaciations. Post-glacial colonization of this species probably began from three refuges located in the Iberian, Italic and Balkan Peninsula, respectively. The early genetic differentiation between the two sub-species could have been caused by the existence of contrasting climate conditions along their distribution area (Lumaret *et al.* 2002). This fact points to a xylem adaptation in *Q. ilex* subsp. *ballota* in response to the typical climate conditions for its distribution area. However, *Q. ilex* subsp. *ilex* has developed a xylem which is less resistant to drought-induced cavitation because water restriction during summer in its distribution area is lower.

The great functional differences found between these two taxa, with otherwise such strong genetic links and morphological similarities, can serve as an example of the physiological heterogeneity within Mediterranean sclerophyllous flora. However, apart from this theoretical conclusion, the bimodal response of the holm oak allows us to partly explain the paradox of its massive dieback in the Iberian Peninsula. The “ex novo” colonization of the territory after the last Glaciation would have allowed the further co-occurrence of both taxa. In fact, Corcuera *et al.* (2004b) suggested that the more/most? mesic population could correspond to the *Q.ilex ilex*, whereas the more/most? xeric population could be *Q.ilex* subsp. *ballota*. The circumstantial incidence of the acute drought recorded in 1994 in the Iberian Peninsula (Lloret &

Siscart 1995, Peñuelas et al 2000) could have mainly affected the specimens of the mesic form of this species, which would partly explain the massive dieback.

At this point, the question is how the massive mortality of holm oak can be explained where the xeric form dominates the landscape (Ait-Bachir et al 2000). Other mechanisms must be considered before giving an explanation for this phenomenon.

#### **4.5. Winter drought can also explain oak decline under mediterranean conditions.**

As explained above, the summer drought is not the only factor limiting plant growth in the Mediterranean region. The low temperatures recorded during the winter months in the most continental areas or on the slopes of the mountain ranges also constitute a strong limitation for forest productivity. A way of escaping from this stressful situation is the winter deciduousness, as this is common in tree species living under the climate conditions of zonobiome VI. Among winter deciduous oaks which occur in the Iberian Peninsula, there are some typical representatives of the temperate forests, such as *Quercus robur* and *Q. petraea* besides others previously defined as transitional species (*Q. faginea*, *Q. pyrenaica*, *Q. canariensis* Willd.), with a similar phenological habit to the temperate oaks.

Deciduous oak species have a ring-porous xylem, characterized by the existence, within the annual ring, of two very different populations of conductive elements. In the early spring, before the bud-burst, one or several series of wide vessels are produced, typically known as **spring-vessels** or **early wood** vessels (Aloni 1991). After this moment, once the new foliage has already been constructed, the tree secondary growth leads to the production of the **latewood**, with abundant fibers and a few narrow vessels and tracheids (Corcuera et al 2006). The wide early wood vessels, which can reach 500 microns in diameter, have a great water transport efficiency (cf. Tyree 1999), but are

very prone to lose their conductivity by freeze-thawing embolism (Tyree & Sperry 1989), as long as the risk increases with the vessel dimension (Pittermann & Sperry 2003). So, the only functional annual ring in those species with this type of xylem is the current one, as long as the previously formed rings have lost their functionality due to the complete embolism of the wider vessel during the winter months. This is a wellknown phenomenon, already stated in Zimmerman & Brown (1971).

On the contrary, evergreen oaks in the Mediterranean region of southern Europe have a diffuse-porous xylem, with narrower vessel on average than deciduous oak species, and showing an unimodal diameter distribution (Corcuera et al 2004b). Holm oak can maintain the leaf functionality for quite a long period, as confirmed by the seasonal monitoring of the photosynthesis capacity of leaf cohorts through time in this species (Ogaya & Peñuelas 2003, Corcuera et al 2005). These leaves are dependent of the previous year's annual rings, as long as the leaf hydraulic conductivity of the whole crown seems to lie in the hydraulic conductivity of, at least, three of these annual growth rings (Gil et al. 2004). The smaller size of the vessels of these evergreen oaks of the Iberian Flora can be a way to improve their safety at the expense of their hydraulic efficiency (Hacke et al 2006). The question which arises is if these narrow vessels are really invulnerable to the phenomenon of freeze-thaw induced embolism under the common environmental circumstances that define the survival limit of these plants. (Cavender-Bares et al 2005).

Some authors, in fact, have proposed that the embolism associated with this process is the key to explaining the ability of *Quercus ilex* to occupy the cold areas of the territories where the species is present (LoGullo & Salleo 1993, Nardini *et al.* 2000). These two studies again clearly reveal the intraspecific variability that exists within the taxonomically so-called *Q. ilex*. In effect, there are too many examples of holm oak

populations occurring in cold or very cold areas of the Iberian Peninsula. The conclusions reached by Lo-Gullo & Salleo (1993) and by Nardini et al (2000) are not compatible with the temperature values during winter in these continental areas of the central part of the Iberian Peninsula. It is clear that some structural and functional differences from Italian populations are to be found in the Iberian holm oaks that allow them to withstand the high frequency of freeze-thaw events. In fact, the average vessel diameter in the foliated shoots of these continental populations of holm oak are below 40 microns (Corcuera et al 2004b), a critical value proposed by Davis et al (1999) as a threshold for having a “safe” xylem in terms of freezing-induced embolism.

Nevertheless, Pittermann & Sperry (2006) showed that this phenomenon of conductivity losses by freeze-thaw events was dependent on the xylem water potential reached in the shoots subjected to this process in conifer species. The winters of 1992 and 1993 were extremely dry and this circumstance in fact preceded one of the severest episodes of holm oak decline in the central areas of the Iberian Peninsula. The occurrence of this situation – two consecutive dry, cold winters – is very uncommon in these areas, as Corcuera *et al.* (2004a) reported. The dry summer of 1994 could later have induced a severe process of runaway embolism (Tyree & Sperry 1989), as long as the hydraulic conductivity had already been reduced during the previous winter months. More recently, it has been shown that cavitation caused by the freezing of the xylem water is not the only process that reduces hydraulic conductivity in woody plants with narrow xylem conduits during the winter. Indeed, Mayr et al (2006) showed that frost drought during the winter is the main reason for explaining the high degree of xylem embolism found in conifers growing at the alpine timberline. Tracheids of these conifers, due to their dimensions, are not prone to cavitating due to freeze-thaw stress but the occurrence of many of these cycles can probably amplify the drought-induced cavitation. Although

these processes may partially or totally explain the negative incidence of dry winter on evergreen populations dieback, we have not been able to empirically demonstrate this hypothesis, as long as such stressful conditions – two consecutive dry winters followed by a very dry summer – have not occurred again in these areas.

In short, these populations of holm oak found in the cold and continental areas of the inner parts of the Iberian Peninsula are in fact occupying habitats which are much more common to the winter deciduous oak species, which are able to complete a single growth period during the relatively mild summer (Corcuera et al. 2004a, Corcuera et al. 2006). Under these climate conditions, characterized by a relatively humid summer and a cold winter, an evergreen species finally adapts its functioning to the environmental rhythms. Thus, when the summer aridity is the main stressful period, the photosynthesis reaches a minimum value at that moment and a maximum one during the mild winter (Ogaya & Peñuelas 2003). However, the situation reverses radically when the low winter temperatures are so stressful that they prevent the photosynthesis activity (Corcuera et al 2005). So, it is apparently hard to explain the presence of these evergreen oaks in the habitats of the winter deciduous ones. The understanding of this apparent paradox allows us to contribute a third reason for explaining the massive holm oak decline in most inner areas of the Iberian Peninsula.

#### **4.6. Predisposing factor for oak decline in the Iberian Peninsula: soil degradation and stand overaging.**

Many holm oak forests in the Iberian Peninsula grow on very poor soils, due to the severe landscape degradation throughout the intense history of this territory. This fact has been suggested as being the ultimate causal factor for Mediterranean forest decline during the acute drought episodes recorded at the beginning of the 1990's (Lloret &

Siscart 1995). As suggested above, the justification for this soil degradation process is almost always a consequence of the recurrence of land overexploitation and land abandonment cycles. In most cases, the presence of an evergreen oak species under climate conditions typical for the development of nemoro-mediterranean oaks (García-López et al. 2002) can only be explained by the negative influence of soil degradation on the amount of water reserve available for plant functioning during the dry Mediterranean summer.

In fact, from a historical point of view, the substitution of deciduous oaks by evergreen sclerophyllous oak species – such as holm oak - in the Iberian landscape has been one of the most noteworthy processes observed in the Mediterranean Basin. The results of the application of phytoclimatic models have shown that this phenomenon could have been caused by soil erosion encouraged by human activities (González-Rebollar 1996) with the synergistic effect of the temperature increase due to the climate change (González-Rebollar et al. 1995).

Effectively, during the last centuries, mid-mountain deciduous forest have been gradually substituted by Mediterranean holm oak forests (Ibañez et al. 1997). In this way, deciduous forests of *Q. canariensis* were replaced by evergreen forests of *Q. suber*, a species more resistant to drought stress, in northern Morocco and possibly in southern Spain, (Reille & Pons 1992, Marañón et al. 1999). As a consequence of human influence, a great part of the Mediterranean forests were destroyed, in order to create crops and pastures, whereas the rest of them were transformed into coppice stands for an intensive wood production due to the great resprouting ability of oak species (e.g. *Q. pyrenaica* and *Q. faginea*).

The abusive exploitation of these woodlands, when historical circumstances made it necessary to develop pastures, followed by the land abandonment, placed these stands

under extreme conditions that can trigger a “threshold response” (Carrión et al. 2001). Valladares et al. (2004) showed that some pollen sequences revealed sudden vegetation changes that could not be explained as the immediate consequence of a previous climate event. On the contrary, the vegetation changes could only be explained by assuming the existence of a strong inertia followed by rapid responses once a certain vulnerability threshold of the system was surpassed. These responses can be associated with massive decline phenomena when the landscape surpasses this threshold. In our case, the degradation of soil properties prevents the recovery of original species in this territory, because soil water retention is below the minimum needed for these species to withstand summer drought periods. The colonization of this territory by evergreen species has been the solution, as long as mean precipitation values were higher than those typical for Mediterranean climates. However, during severe drought periods (1992, 1993 and 1994), even a very drought resistant species was not able to maintain its biomass, and, consequently, a massive dieback was induced (Thomas & Hartmann 1996, Demchik & Sharpe 2000, Peñuelas et al. 2000).

When this process of soil degradation affects territories under more arid climatic conditions, the consequence is the substitution of the tree species – mainly holm oak in the Iberian Peninsula - by nanophanerophytes and chamaephytes and the appearance of an anthropogenic shrubland (Camarero et al 2004).

On the other hand, a great number of forest decline episodes have been explained taking into account the two major components of the so-called “global change”: the climate changes (increasing temperature and frequency of droughts) and changes in biogeochemical cycles (acid rain and ozone). However, most authors have obviated a third component of the “global change” that explains to a great extent the structure and dynamic of the forest: the great changes in land use during the last century (Vitousek



1994). As mentioned above, the Mediterranean landscape has been affected by several phases of land use and abandonment, which has implied woodcutting, shrubland burning, ploughing, pasture development and, many times, the natural or artificial reforestation after decades of land management when the human activity decreases. This cycle has been repeated several times throughout the history of forest-and-man coexistence in the Iberian Peninsula (Barberó et al. 1992). A great number of genuine Mediterranean (e.g. *Q. ilex*) or nemoro-mediterranean species (e.g. *Q. faginea*, *Q. pyrenaica*) have been used as charcoal and firewood sources because of their poor wood quality (Camarero et al 2004). The great metallurgical activity in the Iberian Peninsula before Roman times (Burillo-Mozota 1999), which required a great amount of combustible provided by these stands, suggested that these changes in the forest structure were common in Ancient Age.

The management of these forests lies in the excellent resprouting ability of these species. This fact results in the formation of coppice stands with a large number of small trunks, which are used as excellent charcoal and firewood sources. This process is carried out every 15-25 years, depending on the species and site quality. The great demand for this resource suddenly decreased in Spain at the end of the 20th century, due to the utilization of fossil fuels for industrial and home use. Nowadays, the cutting frequency has been delayed in many areas, whereas in others exploitation has even been suspended. This fact has caused drastic changes in the structure and performance of these forests, which is known as the “overaging” of coppice stands.

In overaged coppice stands of nemoro-mediterranean species, such as *Q. pyrenaica*, at least 50% of branches older than 16-years did not produce latewood (overaged zone in figure 3). In fact, the latewood also contributes to the hydraulic support of the tree, in spite of its main structural role due to its fiber richness. The very small diameter of

latewood vessels and tracheids makes its hydraulic conductivity on an area basis much lower (Tyree & Ewers 1991) than that of the earlywood (Corcuera et al. 2004a). On the other hand, Corcuera et al. (2006) showed that small diameter vessels of latewood still remained functional at water potentials low enough to induce the full cavitation of the wide earlywood vessels. This inverse relationship between safety and efficiency has been recently revised by Hacke et al (2006), supporting a possible functional explanation for this process.

The complete absence of latewood, as a safety element in the case of cavitation of earlywood vessels, makes the overaged trees more sensitive to acute droughts causing embolism than those not-overaged, which show both types of wood in the same annual ring. In fact, the absence of latewood could constitute a functional and structural definition of “overaging” in the case of ring-porous species.

From a global perspective, the decline processes reported in the holm oak forests out of their typical ecological range and in the overaged coppices are examples of the importance of predisposing factors, besides climate, in the explanation of forest dieback episodes, in the sense given to this term by Manion (1991) and Manion & Lachance (1992).

## **5. SCOTS PINE (*PINUS SYLVESTRIS* L.) DECLINE IN ITS SOUTHERN GEOGRAPHICAL LIMIT. CLIMATIC AND HISTORICAL INFLUENCES.**

Scots pine decline in Spain can be considered as an example of the key role of predisposing factors on forest decline phenomena. In effect, since the beginning of the 21st century, massive dieback of Scots pine populations has been reported in almost the whole distribution area of this species in Spain. The study of this process, or processes, has allowed us to understand the great importance of certain predisposing conditions in

the stands as an ultimate causal factor of their present state. To understand these conditions, we should clarify several basic aspects of the presence of Scots pine in this territory. According to Breckle (2002), this species is typically associated with the climate conditions of the zonobiome VIII or zonobiome of the taiga, characterized by a cold-temperate boreal climate. However, the effect of the orography on climate allows this species to occur in more southern areas, as an orophyllous species in many mountain ranges of the Eurosiberian continent (e.g. Alps, Carpathians, Pyrenees, Balkans, Iberian System), where climate conditions are similar to those typical ones of a boreal climate. This species has its southern distribution limit in the Iberian Peninsula, where it occurs at a latitude of 37° N in Sierra Nevada (Granada, Spain).

The presence of Scots pine in the landscape of Spain is very significant (Costa et al 1997), because several historical circumstances have favoured its spread, to the detriment of some other forest species of a lower economic value (Valladares et al. 2004). Moreover, Scots pine and other pine species have been widely used during the 20th century as a way for land reclamation by reforestation in many areas of Spain (Ortigosa et al 1990). In fact, Cañellas et al (2000) considered that 674.800 ha occupied by this species (more than the 50% of its total area in Spain) are a direct consequence of reforestation programs. In other cases, land management in former centuries has negatively affected its presence in the territory, as long as the need for pastures caused the indiscriminate deforestation of many areas naturally occupied by this species (Querol 1995). The alternation of regression and expansion episodes throughout history has been a more common phenomenon than expected and recorded, which makes it quite hard to understand the present existence of the Scots pine species in many parts of its distribution area in the Iberian Peninsula.

One of the most representative examples of this situation can be found in the east of

Andalusía (Spain), which has a considerable amount of reforested populations of several pine species (*Pinus halepensis* Mill., *P. pinaster* Aiton., *P. nigra* Arnold. and *P. sylvestris* L.). In some cases, these stands represent the dominant tree species in the zone. A representative case of this status is found in the “Sierra de los Filabres”, which ranges from east to west in the central zone of Almería province (Spain), one of the most xeric territories in the Iberian Peninsula (Peñas et al. 1995). It is a mountainous area with a wide altitudinal range (between 300 and 2168 m.a.s.l.) that produces a gradient in the existing climate conditions. The different environmental conditions are more affected by the effects of temperature decrease due to the adiabatic gradient than by the precipitation increase. According to the geobotanists (Rivas Martínez 1987, Valle, 2003), the zones of this mountain range below 800 m.a.s.l. are under semi-arid conditions, whereas the climate becomes sub-humid above 1650 m.a.s.l. The presence of Scots pine in this mountain range is due to the reforestation programs carried out since 1955 to 1983 (Sanz et al., 2001). A progressive decline episode of Scots pine stands has been observed since 2002, to such an extent that there is damage in 66% of the 6000 ha occupied by this species, with severe damage affecting 6% of the 6000 ha. (Navarro et al., 2007).

The initial symptoms and the spatial pattern of the decline episodes make several authors think of the existence of biotic factors or air pollution as the ultimate causal factor. Air pollution was earlier precluded when possible pollution sources and the chemical composition of soils and needles were studied (De la Hoz 2006). Moreover, no biotic agents were isolated in root studies and entomological observations.

The lack of a single explanation for Scots pine decline in these stands directed the studies towards a climatic explanation of the process. Thus, a simulation of the climatic potential of the region was made by means of the software GENPT (Manrique &

Fernández Cancio 2001), using 63 variables related to precipitation and temperature patterns of the zone, based on the phytoclimatic system developed by Allué (1990). The algorithms of this software work with lineal regression models from mid values, regressions and stabilization of the variance of variables. The mean square error is below 0.5 °C in temperature and 5-10% in precipitation if the reference meteorological stations are good-quality (Fernández Cancio et al., 2001).

As a first conclusion, it should be noted that estimated mean precipitation in Sierra de los Filabres is 387 mm (with a minimum value of 288 mm since 1962 to 1989), which is much lower than 428 mm, considered as the mean annual precipitation value recorded in the regions with a natural presence of Scots pine in Spain (Nicolás & Gandullo 1969, Gandullo & Sánchez Palomares 1994). Moreover, summer aridity in this area is longer than 3 months. This nuance is of paramount importance to understand the worldwide distribution area of Scots pine, associated with evergreen coniferous forests in the humid subtypes of the zombiome VI or, typically, in the zombiome VII (cf. Breckle, 2002). A summer aridity longer than 3 months could be incompatible with the typical climate conditions for this species. The apparent stability (up to the present decline episode) and the survival ability under critical climate conditions could be justified by the soil water reserves due to the snow cover.

In view of this evidence, we could consider the decline episode of Scots pine in the Sierra de los Filabres as an apparently unavoidable phenomenon caused by the existence of predisposing factors due to the non-natural condition of these populations. Although these stands have survived for ages, they have finally come to a distressing state of collapse.

How could Scots pine have been selected for reforestation programs in the higher altitude zones of this area? There is no doubt that some factors led to a misleading

consideration about the potential of Scots pine in this zone. In the 1960s and at the beginning of the 1970's, when Scots pine was selected for reforestation programs in this area, meteorological data since 1950 were only available. The selection of the period from 1950 to 1970, which reflected an extremely rainy period in that millenium, for the characterization of the climate conditions of the zone probably led to a mistake in the species selection for this reforestation program. The extremely humid climate conditions of that period (the mean annual precipitation was 419 mm) were close to the minimum acceptable values for Scots pine. However, mean annual precipitation from 1970 to 2002, corresponding to the period of maximum growing rate of these stands, was only 348 mm, which was 17% lower than the minimum annual precipitation value in the southern natural stands of Scots pine over its worldwide distribution range. Therefore, the selection of this species for reforestation programs in the higher altitudes of Sierra de los Filabres was correct, taking into account the meteorological data available. The availability of previous or subsequent data had shown that the real mean annual precipitation in this area precluded the establishment of Scots pine populations. The distance between real and minimum precipitation values is not the only parameter that reveals the negative evolution of Scots pine in this zone. Indeed,, the study of interannual values of climate variables indicated that in the 1970's a climatic pertubation started in the southeast of the Iberian Peninsula, which caused a precipitation decrease, a temperature and thermal oscillation increase and, therefore, an aridity increase. The present temperature increase could be a negative influence on the snow-covered periods, which was the only buffer element that guaranteed the stability of these Scots pine populations, because of the increase in evapotranspiration and early snow melting, reducing the water surplus necessary for the survival of these stands.

As mentioned above, the current presence of Scots pine in Spanish mountain ranges is sometimes due to changes in the anthropic exploitation of the territory. In the Sistema Ibérico range, located in northeastern Spain, during centuries stockbreeding was given priority due to the economic importance of wool, causing the massive expansion of pastures in areas potentially occupied by trees (Querol 1995). The subsequent abandonment of this activity, very recent from a historical point of view, has allowed the expansion of Scots pine throughout this territory, frequently over degraded soils. In this sense, it should be highlighted that these populations of Scots pine are most frequently found over superficial calcareous substrates that are only 10-30 cm in depth (Catalán-Bachiller et al. 1991). In many cases, the lack of bedrock fractures prevents the root system of Scots pine from penetrating into the soil to look for water resources. This fact, which makes these trees more sensitive to water stress, has been checked by means of prospections with a georadar system and geological excavations (Figure 4 and Figure 5).

Most of these populations have suffered periodic episodes of massive death during the last decades. The last of these episodes was observed during the winter of 2002, affecting 14000 ha of Scots pine. This process was characterized by needle yellowing and subsequent browning, followed by severe defoliation on the crown. Although the phenomenon happened in an acute and severe way, several signs reveal the existence of a chronic stress in these population, with the combination of degraded soils and unfavourable climate conditions for this species justifying this episode. On one hand, the study zone is under too xeric climate conditions for the Scots pine, because the mean annual precipitation should be twice that recorded in the nearby weather station. It should be pointed out that, in spite of the total amount of precipitation, the rainfall pattern is highly irregular, which conditions the regular water availability for the tree.

Under such conditions, the role of the soil as a buffer element for water availability can be critical, such as is described for the status of Scots pine in the Sierra de Filabres.

Some bioclimatic models (Montero de Burgos & González Rebollar 1983) add the role of soil as a buffer element for plant water availability (Pemán & Navarro 1998). Applying this model to this landscape, and taking into account the climate data available, the existence of two potential stress periods were seen for this species at high altitudes (1800 m.a.s.l.): summer drought and winter cold that shortens the vegetative period. If we consider the state at which the water retention ability of the soil is minimal, Scots pine reaches a critical state, showing very low values of production capacity. Furthermore, comparing these theoretical conditions with the reality in this areas, the degree of resemblance is very high.

In short, the phenomenon of Scots pine decline in these populations again takes up the model of Manion, establishing climate, edaphic and historical predisposing factors, which jeopardize the long-term growth and survival of these stands, making them more sensitive to sudden changes in climate conditions, in the context of an increase in water deficit.

## **6. SILVER-FIR DECLINE IN THE SPANISH PYRENEES: CLIMATIC VARIABILITY, LOGGING AND NATURAL PROCESSES.**

The current silver-fir (*Abies alba* Mill.) decline in the western and central Spanish Pyrenees started in the mid 1980s when severe and successive droughts were observed (Camarero *et al.*, 2002). In temperate forests dominated by conifers such as fir or spruce, an increase in crown defoliation or transparency seems to be directly associated with a more severe summer drought (Solberg, 2004). Indeed, the role of climatic variability and water stress as controls of silver-fir vitality has been frequently



evidenced through retrospective approaches based on dendrochronological methods (Lévy & Becker 1987; Becker 1989; Camarero *et al.*, 2002). In the Pyrenees, the southernmost silver-fir forests from the Pre-Pyrenees ranges are experiencing an increase in water stress since the 1970s, which was more severe since 1980, due to climate warming (Macias *et al.*, 2006). The increasing water stress might be explained considering a longer summer season characterized by a negative water balance until late September. The rise in water stress might lead to growth decline and a greater mortality in these populations which are highly fragmented causing local extinction in some sites. The main role of climate as a driver of silver-fir decline is further supported indirectly by: i/ the fact that the most vulnerable trees are dominant individuals located in stands which have experienced frequent thinning; and ii/ the lack of direct relationship between forest vitality and the presence of pathogenic root fungi (Oliva & Colinas, 2007). A similar decline phenomenon associated with severe water stress was described in Scots pine forests from the north-eastern Iberian Peninsula (Martínez-Vilalta & Piñol 2002), despite this pine species is less vulnerable against xylem cavitation and summer drought than silver fir. In other tree populations located near the species southern distribution limit as in beech (*Fagus sylvatica*) there have been negative growth responses to the temperature rise which could modify the species distribution area in the future (Jump *et al.* 2006). Nevertheless, none of the cited studies have considered explicitly predisposing factors as land-use changes despite the long management history of silver-fir forests in the Pyrenees (Cabrera 2001). In addition, the sharp microclimatic changes associated with forest opening due to logging may affect negatively silver-fir performance and reduce its growth (Aussenac 2002; Peguero-Pina *et al.* 2007).

The pretended increase of decline episodes have coincided with the acceleration of the incidence of several global-change factors such as climate warming or changes in forest

management which have motivated the search of conceptual models to adequately explain these phenomena and to try to predict their incidence. So, Manion (2003) has recently re-assessed his conceptual model of forest decline (Manion & Lachance 1992). The forest-decline concept as a “problem of forest pathology” has evolved towards the consideration of the “healthy amount of disease” required to support forest dynamics. Following this argument, forest decline may be regarded as a natural and recurrent process which renovates the forest through the elimination of the most susceptible individuals, frequently the dominant trees (Mueller-Dombois 1986, Auclair 2005). Forest management is a key predisposing factor because silvicultural selection with economic objectives selects dominant trees thus generating stands formed by trees very susceptible to decline episodes in response to inciting factors as severe droughts. We require approximations based on large spatial scales and long-term retrospective studies to test if forest-decline episodes follow pseudo-cyclic patterns and to check if these disturbances are recurrent events which promote forest succession.

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## FIGURE LEGENDS

Figure 1. Distribution in Spain of the aridity, expressed as the Aridity Index (a). The index a, as explained in Allué (1990), is the number of months when the curve of monthly mean temperature lies above the monthly precipitation curve in ombro-thermal Gausse-type diagram. When a reaches a value equal or higher than 2 it is considered a mediterranean type climate.

Figure 2. Distribution of the Thermal Index, as defined by Rivas-Martínez (1987). The lower the value for this index the colder the climate. The interior areas, affected by a high continentality, show the lower values for the Thermal Index.

Figure 3. Photograph showing the wood anatomy in an overaged resprout of *Quercus pyrenaica*. The overaged zone lacks latewood. See text for a functional explanation of this fact.

Figure 4. Scarce soil development, general view (upper) and detail (lower) in areas affected by severe Scots pine decline in Spain.

Figure 5. Fissures in the bedrock are the only way for tree growth in many areas of the spanish territories prone to register forest dieback processes.



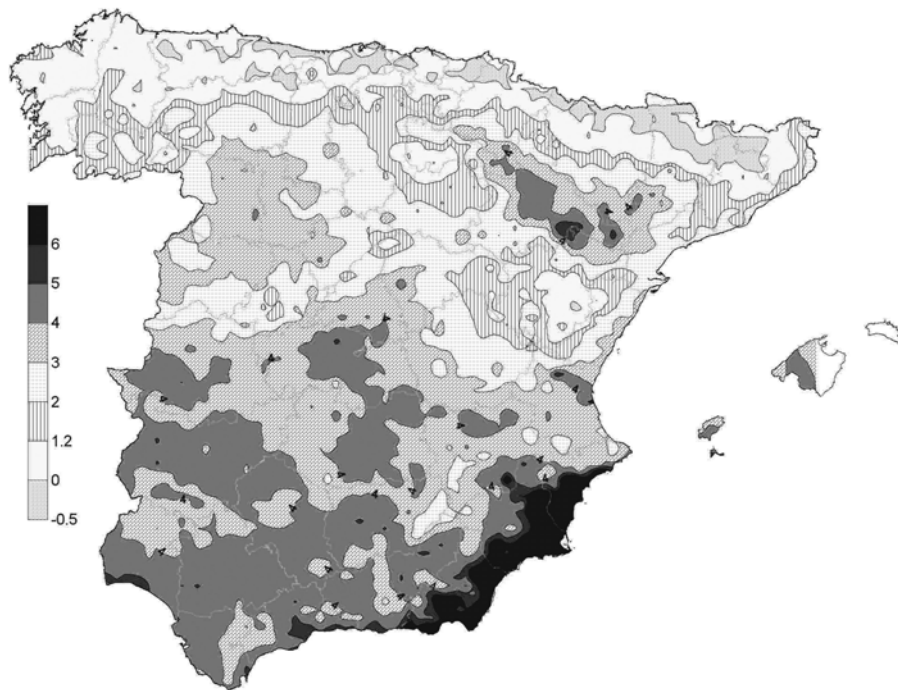


Figure 1.

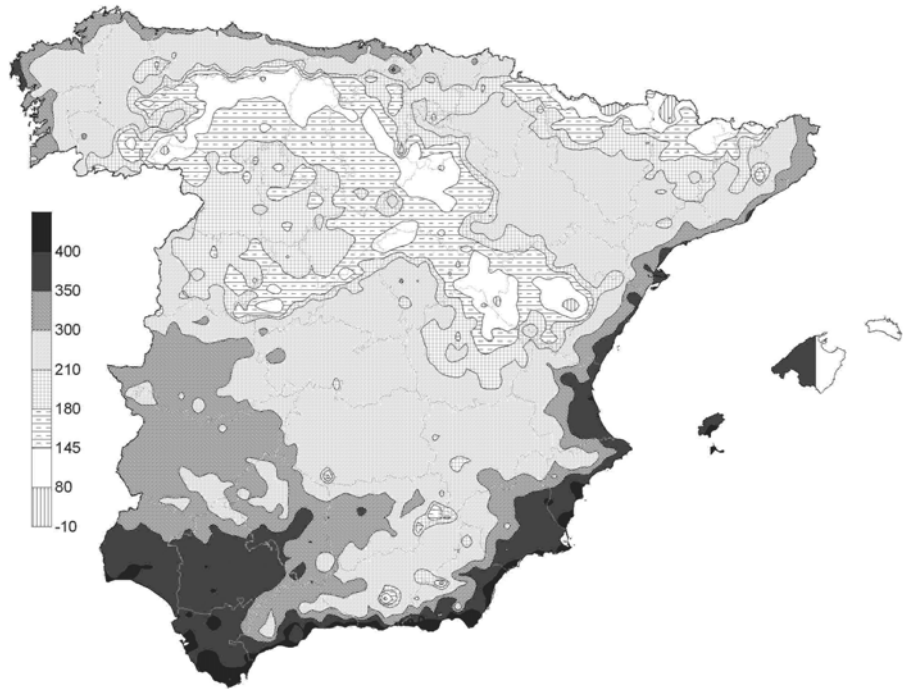


Figure 2.

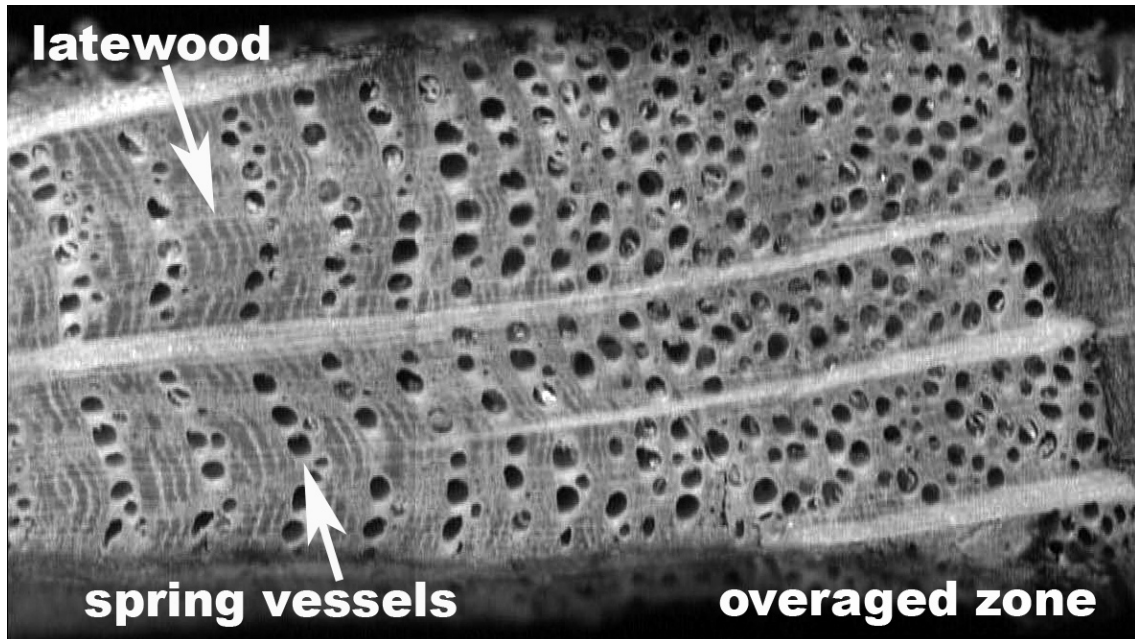


Figure 3.



Figure 4.



Figure 5.