

UNIVERSITÀ DEGLI STUDI DI SASSARI



SCUOLA DI DOTTORATO DI RICERCA Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari

Indirizzo: Agrometeorologia ed ecofisiologia dei sistemi agrari e forestali

Ciclo XXIV

Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maquis species

dr. Matteo Cabras

Direttore della Scuola Referente di Indirizzo Docenti Guida prof. Alba Pusino prof. Donatella Spano

prof. Donatella Spano - dr. Simone Mereu

Index

Abstract	4
Riassunto	5
1. INTRODUCTION	6
1.1. The vegetation maquis	6
1.2. Adaptive response of woody plants to environmental stresses	18
1.3. Study of woody growths	24
1.4. Wood anatomical traits	27
2. OBJECTIVES	29
2.1. Presentation and aim of work	29
3. MATERIALS AND METHODS	31
3.1. Study area	31
3.2. Study site description	33
3.2.1. Piscinas	33
3.2.2. Alà dei Sardi	35
3.2.3. Capocaccia	36
3.2.4. Sette Fratelli – Corongiu station	37
3.3. Description of the species	38
3.3.1. Cistus Monspeliensis L	38
3.3.2. Quercus ilex L.	40
3.3.3. Pistacia lentiscus L.	42
3.3.4. Phyllirea angustifolia L.	44
3.3.5. Arbutus unedo L.	46
3.4 Experimental design	48
3.5. Preparation of samples	48
3.6. Anatomical analysis and microscope measure	49
3.7. Chronology building	50
3.8. Climatic variables and correlations with the growth	53 2

Dr. Matteo Cabras – Titolo: Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maquis species.

Tesi di dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari.

3.9 Wood anatomical description of studied species	55
4. RESULTS	57
4.1 Dendrochronologies	57
4.2. Chronological statistics	57
4.2.1. Alà dei Sardi	61
4.2.2. Piscinas	63
4.2.3. Sette Fratelli	65
4.2.4. Capocaccia	67
4.3. Raw dendrochronologies series	69
4.4. Stem diameter	71
4.5. Leaf Area/Sapwood Area (LA/SA)	73
4.6 Specific leaf area (SLA)	76
4.7. Wood anatomy	78
5. DISCUSSION	83
5.1. Dendrochronology	83
5.2. Wood anatomy	86
6. CONCLUSION	87
7. REFERENCE	89
8. APPENDIX	99

Abstract

Wood anatomical and structural features are key elements in the water relations of plants.

To verify if the plants grown in four sites characterized by different climatic gradients

modify the distribution of biomass were recorded biometric and wood features in five

shrub species (3 individual for species) as Quercus ilex, Arbutus unedo, Phyllirea latifolia,

Pistacia lentiscus, Cistus monspeliensis typical of Mediterranean ecosystems in the

Sardinia region.

The characterization of the species has required the measurement of the following

parameters: leaf area (A_{leaf}), leaf dry weight (PS), specific leaf area (SLA), amplitude of

the growth rings and mean diameter of the xylem vessels of the basal portion of the stem.

The research has also provided the integration of dendrochronological analysis of ring

woody with climate data (precipitation and temperature) of the study sites examined and

the analysis of the anatomical features of the wood at the ultrastructural level. Through the

observation of digitized photos of microsections transverse, have been measured wood

vessels diameter. Our results suggested that aridity, rather than winter temperature,

controls stem xylem response in the studied shrub species.

The study aims to provide information on the ecological role of plant species under study

and the functions of the conduction is the key to survival in conditions of stress caused

summer aridity.

Riassunto

Le caratteristiche anatomiche e strutturali dello xilema sono elementi chiave per le relazioni idriche delle piante. Per verificare se le piante cresciute in quattro siti nella Regione Sardegna, caratterizzati da differenti condizioni climatiche in termini di precipitazioni e temperature, possono modificare le caratteristiche ultrastrutturali dello xilema sono stati studiati caratteri morfoanatomici del legno e fogliari in cinque specie arbustive della macchia mediterranea (3 individui per specie) come Quercus ilex, Arbutus unedo, Phillyrea latifolia, Pistacia lenticus, Cistus monspeliensis. Lo studio delle 5 specie ha richiesto la misurazione dei seguenti parametri: area fogliare (A_{leaf}), peso secco fogliare (PS), area fogliare specifica (SLA), ampiezza degli anelli di crescita e del diametro medio dei vasi dello xilema della porzione basale del tronco. La ricerca ha previsto, inoltre, l'integrazione di analisi dendrocronologiche di rotelle legnose prelevate alla base delle piante campione con i dati climatici (precipitazioni e temperatura) dei siti di studio presi in esame e l'analisi delle caratteristiche anatomiche del legno a livello ultrastrutturale. Attraverso l'osservazione di foto digitalizzate di microsezioni trasversali del legno, è stato misurato il diametro medio dei vasi dello xilema. I nostri risultati suggeriscono che l'aridità, piuttosto che la temperatura invernale controlli l'attività dello xilema nelle specie arbustive studiate. Il lavoro si propone di fornire informazioni sul ruolo ecologico delle specie vegetali oggetto di studio e sulla funzionalità dell'apparato di conduzione che rappresenta il fattore chiave di sopravvivenza in condizioni di stress provocate dall'aridità estiva.

1. Introduction

1.1 The maquis vegetation

Mediterranean ecosystems are characterized by a climate conditioned by seas and oceans, with a regimen of transition between moderate and tropical-dry climates (Di Castri and Mooney, 1973). These climatic conditions are found mainly in the western areas of the continents, in correspondence with a belt of 15° (approximately) around the 35° parallel, in both the boreal and austral hemisphere, with excursion to the 45° parallel north and 30° parallel south. Within this area a Mediterranean type vegetation is found in an area more or less extensive in southern Europe and the Near East and in an area with still uncertain boundaries between Afghanistan and Pakistan. The other regions are California, central Chile, the Cape region of South Africa and Western Australia. All these regions are included roughly between 30° and 45° latitude in both hemispheres. The total area is less than 5% of the earth's surface, nevertheless Mediterranean climate ecosystems are home to around 50,000 species of vascular plants, 20% of total existing on earth (Cowling et al., 1996). Its species richness is second only to tropical forest ecosystems. The Mediterranean climate is interpreted as a transition between temperate and tropical-arid climates that evolved during the Tertiary from hot humid conditions (Di Castri and Money, 1973). It is characterized by rainfalls concentrated in winter, a distinct period of variable length of summer drought, with high variability in annual rainfall, hot summers and cold winters with mists in the absence of temperature typical of continental climates. Frosts and snowfalls are rare and generally sell out within days. In these regions the vegetation is very heterogeneous, consisting mainly of evergreen forests and is characterized by the presence

of massive formations of evergreen shrubs, leaf leathery (sclerophyllous). These formations take various names: *garrigue* and *maquis* in the Mediterranean Basin, *chaparral* in California, *mattoral* in Spain and Chile, *mallee* in Australia, *fynbos* in South Africa (Di Castri and Mooney 1973, Di Castri et al, 1981).

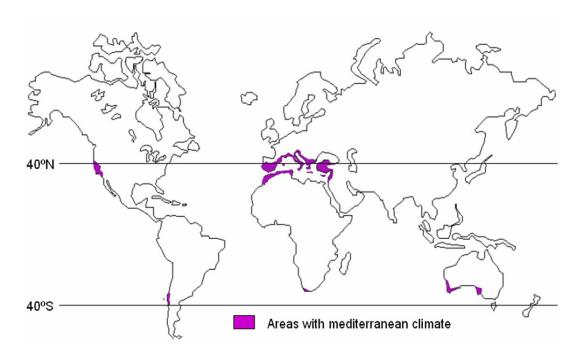


Figure 1. Geografical exstension of the Mediterranean maquis (Tommaselli, 1977).

Italy is a Mediterranean country of particular interest because, in the Mediterranean and southern European species, is a meeting point between the Iberian and North African flora and Asian and Balkan flora.

Giving a single definition covering all the heterogeneus formations embraced by the denomination of "Mediterranean-type shrublands" is almost impossible, and it becomes even more hazardous considering how many diverse approaches are followed and how distinct terminology is adopted by different authors (Di Castri et al, 1981). In general terms, Mediterranean shrublands are scrub formations, found primarily within the xerothermic range of Mediterranean climates, characterized by the dominance of woody shrubby plants with evergreen, broad and small, stiff and thick (sclerophyll) leaves, an

overstory of small trees sometimes being present, and with or without an understory of

annuals and herbaceous perennials. It is a fire-prone vegetation and may represent different

successional stages according to climate, slope aspect and other topographical features, and

human impact.

According to Camarda (2004) Mediterranean maguis has a complex structure and a

variable floristic composition. Depending on height of the individuals and on the degree of

soil cover it was proposed to subdivide on structural differences of the physiognomy: scrub

forest (> 4 meters), high scrub (2-3 meters), low scrub (<2 meters). In Sardinia, the maquis

is mainly characterized by evergreen shrub species including Pistacia lentiscus L., Arbutus

unedo L., Phillyrea angustifolia L., Quercus ilex L. and Cistus monspeliensis L.

In degraded areas or in bedrocks the floristic composition and physiognomy change and is

characterized by suffruticose species, spiny species, and aromatic xerophillous species.

Bernetti (1998) identifies the Mediterranean forest with the Holm oak forest trees, or with

mixed holm and cork oak, while by maguis the Author means a type of vegetation that

includes a broad category of shrubs or trees of lower size. In conditions of extreme soil

degradation and adverse effect of the local climate, maquis cannot grow beyond a certain

height and is composed of species frugal or resistant (primary maquis).

The maquis can be an aspect (silvofacies) degraded of the *Quercus ilex* forest (Viburnum-

Quercetumilicis) and, in this case, we can distinguish a typology based on the prevailing

species (e.g., with Erica arborea and Quercus sp). In hot and arid environments, the spot

represents a formation climax or para climax of the Ceratonion-Olea association. In Italy,

we can distinguish the following forms:

- Riparian formations with oleander, in rivers and temporary torrents where the period of

dryness is very long;

- Kermes oak maquis, found especially in Puglia and Sicily;

- Juniper scrub, coastal dunes consolidated especially in Sicily and Sardinia;

- Oleaster and Pistacia maquis, a very thermophilous formation that represents the most

common type of coastal scrub (there are variations with Euphorbia dendroides and with

Calicotome spinosa);

- Low maguis with *Erica* sp., *Cistus* sp. and *Lavandula* sp., is an extreme form of

degradation before the scrubland, and is developed on acid soils poor in nutrients and

frequently crossed by fire.

The garrigue (scrubland from the French name of Kermes oak) is one of the most degraded

forms of scrub vegetation and is characterized by low and sporadic vegetations with large

tracts of bare soil. The garrigue contains a great diversity of flora and is a typical habitat

for numerous species of orchids. Further stages leading to the degradation of native scrub

steppe, with a prevalence of grasses and grassy topsoil.

In general, the term "secondary maquis" identifies the residue of degradation of forests or

the result of the invasion of pastures or abandoned arable land.

The interpretation of the Mediterranean shrub formations is everywhere quite difficult.

This formations in fact, are the result of human intervention including different story

grease (logging, grazing, farming, fire more or less frequent). The most evolved plant

groups of maquis are characterized by the presence of *Erica* sp. and *Arbutus* and scrub oak.

The less evolved formations are composed of *Cistus* spp., which are linked to shrubland.

The consortia are not fully developed and affected by soil characteristics (pH, calcium

content) and climate (especially drought).

The maquis can be in general viewed as the result of several degenerative processes, often anthropogenic, which can lead from the climax to simpler associations plant (Fig. 2): bush >garrigue> wilderness > bare soil.

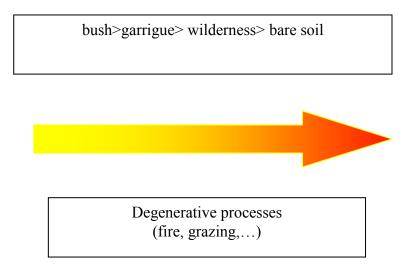


Figure 2. Degenerative process of the Mediterranean maquis ecosystem.

Although extremely simplified, this involution represents the history of Mediterranean evergreen forests subjected to unsustainable management by man. As the regressive series progresses, the protective effect of vegetation decreases exponentially up to the irreversibility of the process (Lopez et al., 1990). Additionally, the fragility of these ecosystems accentuates the weight of the factors that can lead to degradation (Naveh, 1995).

Anthropogenic disturbances such as deforestation, grazing, agricultural development, and fire management are factors that influence plant community structure and diversity for a very long period of time (Aschmann 1973a; b; Naveh and Dan, 1973).

The problems of landscape disturbance and associated desertification in the Mediterranean Basin are major ecological issues, which can be associated with three sets of linked processes: physical, biological, and socioeconomic (Fantechi and Margaris,1986; Perez-Trejo, 1992). Physical processes that promote desertification include a degradation in soil

structure, reduced infiltration capacity and salinization, all of which work in concert to

promote secondary effects of increased severity of erosion and changes in hydrologic

processes related to ground water recharge and surface flow. These hydrologic factors, in

turn, may promote salinization.

Biological disturbance processes are those related to decreasing plant cover, and the

obvious feedbacks that this has on animal population structure and physical processes as

greater amounts of soil are exposed to wind, stronger temperature excursions, and runoff.

High disturbance regimes in the semiarid Mediterranean basin are generally associated

with significant reductions in the diversity of vegetation structure and plant species

(Rundel, 1998).

Socio economic events which strongly affect processes of desertification can be seen in the

dramatic intensification of land use in the Mediterranean Basin, over the past few decades.

Mechanization of agriculture, urbanization, and a rapidly developing tourist industry,

which have impacted all the Mediterranean coasts, have caused rapid changes in landscape

utilization in more arid regions (Naveh et al., 1973). These changing patterns of land use,

and associated effects on fragmentation of natural plant communities, rate of soil erosion,

fire frequencies and intensities, and water resource availability have all promoted

desertification with dramatic reduction in natural biodiversity, and in general a decrease of

ecosystem services. (Meeus et al., 1990; Perez-Trejo, 1992)

The stability of Mediterranean ecosystems is strongly linked to the nature of grazing, fire

regimes, and other socioeconomic activities. As plant communities have developed with

moderate grazing pressure as a natural selective regime, plant species have evolved

reproductive strategies linked to this disturbance. There also has been adaptation, over

11

evolutionary time, to fire as a natural environmental factor, and reproduction strategy in

many species is strongly related to fire frequency and intensity (Trabaud at al., 1993).

In fact, Mediterranean communities area characterized by a high resilience to fire since

regeneration of the preexisting community is quite rapid. Plant abundance and cover

change only briefly with time since fire, and under most fire regimes, species composition

does not change significantly from one fire cycle to the next (Clemente et al., 1996). Hanes

(1971) describes this process as "autosuccession". Community regeneration is

accomplished by a massive seedling recruitment from a dormant seed bank- obligate

seeders- or by sprouting from belowground vegetative buds – obligate resprouters, some

species resprouting after fire can also establish seedlings – facultative affect regeneration

after fire.

The frequency and magnitude of fires in the Mediterranean basin has doubled in the past

two decades, causing decreased forest vigor and sharp alterations on forest structure and

soil stability (Kuzucuoglu, 1989; Naveh, 1990).

Water stress is considered one of the most important factors limiting plant performance

and yield worldwide (Boyer, 1982). Mediterranean summer drought is also considered the

primary constraint to the productivity and distribution of the Mediterranean vegetation

(Larcher, 2000). Indeed, many studies have described reductions in photochemical

efficiency and low photosynthetic rates during summer drought (e.g.: Harley et al., 1987,

Tenhunen et al., 1990, Damesin and Rambal, 1995, Valladares and Pearcy, 1997, Gratani

et al., 2000, Llorens et al., 2003b). In addition, temperature during the Mediterranean

summer may reach potentially damaging thresholds for physiological processes (Epron,

1997), especially when drought-induced stomatal closure limits the ability of plants to

avoid heat stress by transpirational cooling (Ladjal et al., 2000).

Moreover, the climate in the western Mediterranean basin tends to become warmer and

drier (Pinol et al., 1998), as a result of global change (IPCC, 2001). For example climate

models predict that, for the western Mediterraean basin, temperature will rise 3-4 °C

during the next century (Rambal and Hoff, 1998). These simulation also predict, for the

same period a decrease in annual rainfall of 43-110 mm, 20-56% of this reduction

occurring in the summer. This trend has been already observed, for example, on NE for the

XX century by direct analysis of climatic series (Pinol et al., 1998). On the whole, an

increase in the frequency and intensity of extreme droughts is expected (Houghton et al.,

1996). Also IPPC (2001) predicts drier and warmer conditions for the Mediterranean basin

in the future.

The limitation to plant growth imposed by low water availability is mainly due to

reductions of plant carbon balance, which is dependent on the balance between

photosynthesis and respiration (Lambers et al., 1992). The regulation of photosynthesis by

drought has been extensively studied and debated (Hsiao, 1973).

Respiration rates are often an order of magnitude lower than photosynthesis rates.

However, photosynthesis is limited temporally (e.g. to daytime hours) and spatially (e.g. to

green biomass), while respiration occurs continuously in every plant organ. Respiration is

thus an equally important factor that controls plant productivity, particularly when

photosynthesis in largely depressed, such as in drought conditions.

The array of adaptations to drought that Mediterranean vegetation has developed, results in

a high diversity of growth forms. Plants have developed a range of physiological

mechanisms to cope with drought, including morphological adaptations, tight stomata

control, osmotic adjustment and photoprotective mechanisms for energy dissipation. Also

the cessation of shoot growth (Pereira and Chaves, 1995) is another response to water

deficit, often followed by prompt recovery of growth when available water is restored in

the soil profile.

Plants experiencing drought conditions also tend to decrease transpiration. Some species,

like Euphorbia dendroides L. and Calicotome villosa L., reduce transpiration by leaf

abscission in the summer, whereas others (e.g. Cistus spp) are facultative summer

deciduous since they roll and shed their leaves only under extreme stress. However, most

Mediterranean sclerophyllous plants regulate their transpiration rate by stomatal control

(Hinkley et al., 1980; Acherar e al., 1992; Gucci at al., 1997; Rambal, 1993).

Drought resistance mechanism adopted by Mediterranean also differ in time scale (Rambal

1993, Sperry 2000).

Stomatal closure is the fastest process to limit transpiration and avoid irreversible damage

to the plant hydraulic system (Jones and Sutherland 1991, Sperry 2000). On a longer time

scale, stomatal conductance is controlled by the hydraulic conductance of the soil to leaf

pathway (Hubbard et al., 2001), which decreases under drought either by soil drying or by

the occurrence of xylem embolism (Sperry and Tyree, 1988). Xylem embolism occurs

when the xylem tension becomes sufficiently negative to force air seeding through conduit

wall pores, thus disrupting the continuous column of water and reducing the hydraulic

conductance (Sperry and Tyree 1988). High levels of xylem embolism under severe

drought can be avoided by reducing the transpiring leaf area (Rambal, 1993; Maseda and

Fernandez, 2006).

Besides stomatal regulation, other mechanisms have been developed by species adapted to

long period of drought. For instance, differences in drought resistance strategies have been

shown for Ceratonia siliqua L., Olea oleaster L. and Laurus nobilis L. (Lo Gullo and

Salleo, 1998). Seasonal changes in plant water relations have been reported for both woody

14

perennials and perennial grasses growing under Mediterranean climate conditions. These

changes have been related to species-specific differences in rooting patterns, stem

hydraulic resistance, leaf orientation, canopy architecture, elastic properties of the leaf

cells, osmotic adjustments, and synthesis of compatible solutes.

We can say that the strategies that the Mediterranean species have developed to survive

summer dryness can be classified into two broad categories: strategies for 'resistance' and

strategies of 'tolerance'. The first consists in the set of mechanisms that enable the plant to

prevent the onset of stress, the strategies of tolerance, however, allow the plant to perform

its vital functions normally even in situations of water scarcity. Strategies of resistance (or

avoidance, according to the old terminology) are leaf abscission, reducing the vegetative

apparatus, the reduction of transpiration through stomatal closure. Among the tolerance

strategies, various mechanisms of opposition to dehydration through the activation of

protoplasmic properties, must be accounted, however these mechanism are not yet

completely clear. One of the most interesting, and long-studied adaptations to the

Mediterranean climate is the Sclerophyllous, e.g. the thickening of the leaves, usually

small, that are leathery. It is generally accepted that the adaptive response to sclerophyllous

is a summer water deficit typical of Mediterranean climates, but it should be noted that the

sclerophyllous species are not exclusive to these environments, and are widespread in hot,

humid regions such as Macaronesia (Canary Islands).

It has been therefore suggested that the sclerophyllous habitus of the Mediterranean species

is derived from anatomical structures of type "laurophyllic" in species developed in

wetlands and only later naturalized in arid climates (De Lillis 1991). The Sclerophyllous is

also considered as an adaptive secondary phenomenon, linked to low fertility of the soil on

15

which this vegetation has evolved, especially in relation to the deficiencies of phosphorus

and nitrogen.

The leaf structure of sclerophyllous Mediterranean is characterized by thick cuticles and a

very dense mesophyll, consisting of several layers of fabric fence. In this way, the

intercellular spaces are scarce, and this implies a constraint on gas diffusion. This protects

the leaf from excessive transpiration, but at the same time, it reduces the photosynthetic

efficiency and, ultimately, the capacity for growth. In addition, the leaves are often

impregnated with substances that have a protective function, but have a very high

metabolic cost and thus partially subtracting energy from growth.

A remarkable contribution to typical leaf anatomy in sclerophyllous was given by Choong

et al. (1992). They found that specific leaf area (dry weight/area, SLA) did not correlate

with total leaf thickness nor with any cell layer, such as palisade, in contrast with Grubb

(1986) who concluded that upper epidermal walls, cuticle and palisade are significantly

thicker in sclerophyllous. Recently, Reich et al. (1997, 1999) put forward the idea that

plant species from different biomes evolutively converge towards common leaf structural

and functional traits including specific leaf area (SLA), leaf nutrient content, conductance

to water vapour and net photosynthesis. Their extensive ecological studies showed that

species with low SLA (high sclerophylly) have a longer lifespan, and lower nitrogen

content, net photosynthesis and transpiration rates than malacophylls.

Similarly to specific leaf area for leaves, wood traits are associated with a variety of

morphological and physiological stem traits that are closely related to the function of trees.

Adaptations to different environments are the causes of trade-offs between different

functions. Such trade-offs, however, might be compensated by the size, number and

structure of the elements of the wood. For example, hydraulic conductance depends not

16

only on the stem cross-sectional area occupied by vessels but also on the size and number

of these vessels.

According to the Hagen–Poiseuille law, the hydraulic conductance scales with the fourth

power of the vessel radius. Wider vessels therefore contribute to a larger hydraulic

conductance (Sperry et al., 2006) which, in turn, facilitates higher stomatal conductance

and more photosynthetic carbon gain (Santiago et al., 2004). By contrast, smaller vessels

imbedded in a matrix of dense tissue lead to a higher hydraulic safety because of less risk

of vessel implosion (Hacke et al., 2001) and cavitation, as small vessels have lower risk of

air-seeding because they have a smaller pit membrane area (Hacke et al., 2006).

The nature of wood traits may vary from community to community (Jacobsen et al., 2008).

Although the adaptive value is often inferred, it is not clear how these wood traits relate to

whole-plant performance in the field or to the life history strategies of tree species.

Interspecific comparisons are often made by comparing different species measured in

different sites (Maherali et al., 2004), thus potentially confounding interspecific and

environmental effects.

The Mediterranean species, from the phenomorphologic point of view, may use a broad

spectrum of possibilities to complete the life cycle. This allows optimization of

environmental resources and a minimal competition between species that coexist in the

same habitat.

1.2 Adaptive response of woody plants to environmental stresses

Plant responses to water scarcity are complex, involving adaptive changes and/or

deleterious effects. Under field conditions these responses can be synergistically or

antagonistically modified by the superimposition of other stresses. Plant strategies also

vary with genotype (Chaves et al., 2002). This complexity is well espressed in

Mediterranean-type ecosystems where plants with predominant drought-avoidance

strategies (e.g. deep-rooted perennials or winter/spring annuals) which die when they run

out of water, coexist with drought-tolerant sclerophylls.

The sclerophyllous adaptations, developed under the morphological appearance or

physiological, have the purpose of limiting the impact of moisture deficit, slowing water

loss by evaporation from tissues, or to activate physiological mechanisms that allow the

survival in critical conditions for a long period.

The adaptation to drought is not necessarily accompanied by an adaptation to high

temperature: the drought of an environment may be due to poor rainfall and poor water

supply even in cold environments. However, the high temperature is one of the main

factors that enhance evapotranspiration, therefore sclerophyllous adaptations are often

accompanied by adaptations to high temperatures.

In this case the plants are also called termoxerophyte or termoxerophytic. This category

includes plants typical of arid or desert regions of the tropical and warm temperate areas.

The morphological adaptations are intended to increase the resistance to the passage of

water vapor in the atmosphere with the maintenance of a gradient of humidity between

phyllosphere and atmosphere, increasing the efficiency of the roots in the transport of

water, constitute reserves of water within the tissues to respond to evaporation losses.

Additionally, these adaptations generally accompany a particular habitus of the plant, but

on the other hand not all adaptations are necessarily present in the same species, therefore

the sclerophyllous habitus may present different expressions.

Sclerophyllous habitus is in general an approach to reduce the interception of direct light

and, consequently, the transpirition. Expressions of an adaptation of this type are the

following:

Reduced growth in height;

• Shortening of the internodes;

• Shrub instead of arboreal.

The reduced development in height is a property determined both as an adaptation and as a

result of adaptation. The lower photosynthetic efficiency, caused by long periods of

cessation of photosynthesis, determines a lower energy input during the life of the plant,

so the vegetative growth is subject to reproduction: the species allocates resources for

reproduction, rather than to the increase in size of individual species. On the other hand the

reduced development creates the conditions for a lower exposure to the action of wind and

insolation, thus attenuating the complex factors that enhance transpiration.

An example of this concept can be derived by examining the development in height of the

plant associations in relation to rainfall in biomes. Forests reach the greater heights and

greater coverage where rainfall is higher (40-60 meters in the tropical rainforest, temperate

rainforest in 80-100 meters). At the same latitude, the reduction in rainfall leads, with

varying degrees of progression, to a transition from forest to bush, the bush to grassland,

until the total disappearance of the vegetation.

The shortening of the internodes is a condition which favors the formation, inside the

canopy, of a microenvironment which slows down the dispersion of the water vapor in the

19

atmosphere, creating a gradient of humidity between phyllosphere and atmosphere: a

compact foliage, determined by the dense branching and shortening of the internodes,

obstructs the ventilation inside ensuring that it creates, in proximity of the leaves a zone of

air less dry compared to the open space. Compact foliage also determines a greater shading

within the canopy, reducing the weight of the factors favoring evapotranspiration.

Shrub shape is an adaptation which in general is accompanied to the previous ones and

leads to the formation of a canopy more compact and less exposed, on the whole, to the

action of wind and insolation. Different types of wood Mediterranean assume different

behaviors in relation to rainfall environment in which they settled, one of the most

representative species is the holm oak: wettest stations has a bearing trees and woodlands

tends to be 20-25 meters high (Mediterranean forest evergreen), while in the drier sites it

reduces the development up to take on a shrub-like plant 2-3 meters to 4-6 meters in height

(Mediterranean maquis).

These adjustments are taken to the extreme in plants with spherical form, with the

characteristic shape of a pulvinus typical of many species that live in arid scrubland of the

Mediterranean coast: the sphere is in fact the geometry that opposes the lower surface at

constant volume and allows to best achieve the objective of reducing the transpiring

surface with equal development. Shrubs with spherical form grow with a densely branched

canopy, often thorny, and with a compact and almost impenetrable exposed surface. This

adaptation is also a defense to grazing, in order to minimize the losses of biomass caused

by herbivores.

If the general architecture is genetically determined, biomass partitioning among organs

displays some plasticity depending on the environmental growth conditions. To adapt to

different climates, plants may modify the leaf area/sapwood area ratio (LA/SA), which is

influenced by water availability, site fertility and plant competition. In terms of biomass

partitioning, a general pattern can be observed where trees in arid regions have less leaf

area per unit branch cross-sectional area at the branch base than trees in wetter sites. Plant

responses to water deficits in the soil and humidity deficits in the atmosphere vary

temporally and spatially (Kozlowski 1983, Kramer 1983). Over short time scales, leaves

can acclimate through osmotic regulation, by changing stomatal behavior or by increasing

water use efficiency. Over longer time scales, structural modifications can be of major

importance and growth patterns can change as a consequence of plant water stress. For

example, leaf surface and productivity are reduced, whereas the depth of the absorbing root

system and the root/stem ratio are increased.

Also adjustments of stomatal conductance and carbon allocation are both considered an

important response mechanisms to drought. The reduction of transpiration by stomatal

closure should be considered as an "elastic" plant response, while the reduction of

transpiration triggered by a change in allocation patterns (less carbon to the transpiring

surfaces, more carbon to the conducting tissues) may lead to a "plastic" acclimation

response.

Plasticity is defined as the ability of an organism to adjust its performance by altering its

morphology and/or physiology in response to varying environmental conditions (Sultan,

1995; Navas and Garnier, 2002). Since strategies to cope with full sunlight significantly

differ from those to cope with shade, plant species must either specialize to one end of this

environmental gradient or enhance their capacity to accommodate their phenotypes to the

light currently available at each particular site (Valladares, 1999). Sun leaves compared to

shade ones are generally smaller and thicker and contain less chlorophyll per unit leaf

mass. Adaptation to irradiance also involves changes in leaf biochemistry: since a

significant fraction of leaf nitrogen is invested in form of photosynthetic proteins, a strong positive correlation between leaf nitrogen content and irradiance has been found (Meletiou-Christou et al., 1994; Reich et al., 2003; Niinemets and Valladares, 2004; Takashima et al., 2004). Moreover, leaves grown in high light conditions have a higher light-saturated photosynthetic capacity per unit leaf area and a greater carbon gain than leaves grown in low light conditions. Most studies of plant response to light have been aimed at underlining morphological and physiological mechanisms, and ecological implications of the tolerance to the extreme (i.e. tolerance to either sun or shade), but noticeably less effort has been invested in the exploration of trends in the plastic response to light (Valladares, 2000; Valladares et al., 2000b). Mediterranean evergreen species exhibit remarkable leaf-level morphological and physiological adaptations to cope with high light intensity (Larcher, 2000; Martinez-Ferri et al., 2000; Gratani and Varone, 2004). The heterogeneous light environment within a plant crown leads to different stresses for leaves in different position, and morphological and physiological responsiveness to light of individual leaves within the crown determines the overall plant productivity (Caldwell et al., 1986; Valladares et al., 2000a). The existence of two kinds of leaves in the same plant can be considered as a special case of adaptation (Rhizopoulou et al., 1991). Thus, leaf plasticity is crucial for their tolerance of excessive light (Valladares and Pearcy, 1999). Moreover, very little is known about seasonal variations of leaf functioning at the different canopy levels (Rhizopoulou et al., 1991).

An important trait used as a predictor of plant response is the Specific Leaf Area (SLA, leaf area per unit dry mass) (Westoby, 1998). The prevailing view is that SLA reflects the expected return on previously captured resources, and that high – SLA leaves are productive (Poorter et al., 1988; Van der Werf et al., 1998) but are necessarily also short –

lived and vulnerable to herbivores (Coley et al., 1985; Grime et al., 1996). They therefore

work best in resource-rich environments. In contrast, low-SLA leaves work better in

resource-poor environments where retention of captured resources is a higher priority

(Wilson et al., 1999).

Environmental factors also, do affect some aspects of xylem structure, as shown for soil

fertility and wood density (Muller-Landau, 2004), soil water and vessel diameter

(Stevenson and Mauseth, 2004), climate and growth rings (Wang et al., 2005), and

temperature and vessel diameter (Thomas et al., 2007). In particularly the following traits,

xylem vessel diameters, vessel length, and leaf size, have been clearly associated with

drought resistance.

Xylem water transport linked with xylem vessel anatomy in plants is the subject of

intensive research because of its ecological implications. In other words factors affecting

water transport parameters are important determinants of drought tolerance and relative

habitat adaptations of native species (Sperry at al., 1990) and predictors of biological traits

in growth models (WBE model). Water availability exerts a strong influence over wood

anatomical structure and clear patterns of differentiation in the conduit structure have long

been recognized between dry and wet climates (Carlquist, 1977). Furthermore, global

examination of hydraulic traits as a function of climate have demonstrated a significant

correlation between resistance to cavitation and mean annual precipitation in evergreen

angiosperms (Maherali et al., 2004).

1.3 Study of annual wood growth rings

Extensive research by several authors (Fahn, 1962; Liphchitz et al., 1986) have improved

the knowledge on the geographical origin and the degree of adaptation to environments in

temperate Mediterranean climate of many forest species that produce annual wood growth

rings, arguing that the activity exchange may be related to climatic factors. According to

Ephrat (1971) the cambial activity would be strongly controlled by winter temperatures

and summer drought.

In particular, cambial activity of trees and shrubs in temperate climate, stops during the

cold season, and annual tree rings, which can be used to reconstruct the climatic

characteristics of the growing season, are formed (Schweingruber, 1988; 1996; Cherubini

et al., 2003).

Dendroclimatology is a subdiscipline of dendroecology, which is focused on the study of

climate trends in relation to the performance histories of rings obtained by sampling trees.

The researches carried out in this field are based on two fundamental principles:

• trees of the same species living in the same geographical area produce the same

amount of annual time series: the thickness of these rings, in fact, varies each year

depending on weather conditions;

• it is possible to compare the annual sequences of trees living in the same

geographic area and in the same period.

Thanks to Dendroclimatology it is possible to obtain information on past and present

climatic conditions and trace the foundations for future projections. Using the time series

obtained from trees of different ages and species, on different sampling areas, it is possible,

in fact, to extend meteorological series to the past. In addition, the analysis of long series

ring can provide valuable assistance in understanding the causes of long-term climatic fluctuations (Schweingruber, 1988).

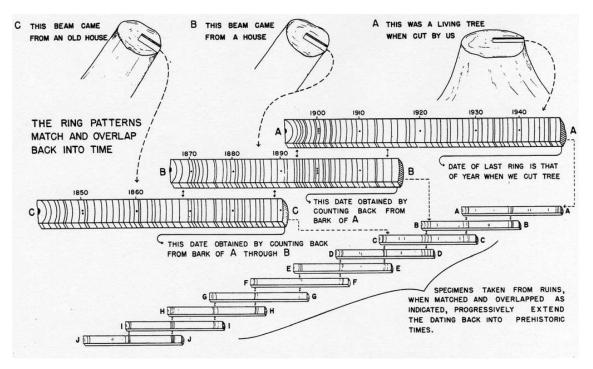


Figure 3. Reconstruction of a long chronology through the use of numerous samples taken in different areas (Fritts, 1976).

While the tree responds to climatic variations, it is also true that records in its rings show variations of other origin, due to the evolution of potential biological shaft (age) and to external factors with respect to climatic parameters (changes of soil, human interventions). To be able to extrapolate from the plant and to analyze the most relevant information on climate it is therefore necessary to isolate the signal that the latter produce. Once this is established, one can think of a time series as an aggregation of different signals, each of which, according to the purpose of research, can become the signal to isolate and analyze (Cooke et al., 1990).

A dendrochronological curve, i.e. a time series of ring width, theoretically it can be decomposed into a trend of long-term biological, to highlight common signals, due to the action of climate and exogenous disturbances, and the individual signals, related to

Dr. Matteo Cabras – Titolo: Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maquis species.

localized disturbances and the randomness. Dendroecologic approach propose to isolate in a dendrochronological series the information to study the effect of environmental factors on the dimensions of the rings woody.

1.4 Wood anatomical traits

The growth of the leaves and the stem, in terms of area and length, is determined primarily by cellular distension, according to which the cells expand due to an absorption of water inside them. The hydraulic conductance of the xylem vessels is defined as the potential capacity of a system to conduct water and the plants that grow quickly require a large xylem vessels to allow for high conductances and the rapid formation of the stem to maximize the supply of water to the leaves (Castro-Diez et al., 1998). If it is true that genetic factors determine the basic structure of wood anatomy (Fritts, 2001), however, environmental factors can affect the anatomical characteristic of wood cells, such as the size of tracheids in conifers and vessels in deciduous trees (Fonti et al., 2009).

Hydraulic features of xylem are key elements in the water relations of plants and therefore in their final performance (Tyree and Ewers, 1991). Xylem vulnerability and water flow resistance are dependent on xylem anatomy. For example, large vessels can transport a higher amount of water, but are also more prone to dysfunctions induced by embolisms than smaller conduits (Sperry et al., 1994; Tyree et al., 1994). The higher the number of vessels per unit of xylem area the lesser percentage of conductance is lostwhen the same proportion of vessels cavitates (Tyree et al., 1994). When the high xylem structural diversity existing among woody plants (Fahn et al., 1986; Baas and Schweingruber, 1987) is correlated with environmental variables several regularities appear (for instance, see Baas et al., 1983; Fahn et al., 1986), suggesting that environmental factors have acted as important selective forces in molding xylem structure (Wheeler and Baas, 1993; Woodcock and Ignas, 1994). Plant features can vary within a species under different growing conditions (Woodward 1983; Castro-DõÂez et al., 1996), allowing species to

maintain their fitness under an ample range of environmental conditions and resource

availability. Among these plant features, wood anatomy has long attracted the attention of

scientists and there is an extensive literature dealing with their responses and their

functional meaning (Chabot and Chabot 1977; Givnish 1979; Vitkowski and Lamont

1991). However, intraspecific xylem variation has been less studied in spite of its

importance to plant performance (Shumway et al., 1993). Recent studies in natural

populations provide evidence that both aridity and low temperatures can influence xylem

structure within a species (Xinying et al., 1988; Mencuccini and Grace, 1995; Sperry et al.,

1994), although the response patterns to the same environment can differ among species

(Noshiro and Suzuki, 1995). It has also been proposed that variations in vessel diameter

and density can be related with different basipetalauxin gradients associated with the

growth and ramification degree of branches (Aloni, 1987).

Investigations in this field have quickly spread to the study of temperate tree species

among Mediterranean trees species. These studies of temperate species led to a general

interpretation of their architectural sequence of development and were then extended to the

analysis of inter and intra specific architectural variations.

2 Objective

2.1. Presentation and aim of the work

The general objective of this study is to determine structural and hydraulical differences among Mediterranean woody species and to investigate possible intra-specific differences in different site conditions in terms of temperature and precipitation. In particularly the aim of this research is to investigate morphological anatomical, adaptations in response to different gradient of temperature and water avaibility of some rappresentative evergreen sclerophyllous species (*Quercus ilex L., Arbutus unedo L., Phyllireaangustifolia L., Pistacialentiscus L., Cistusmonspeliensis L.*).

The Mediterranean region is characterized by steep climatic gradients, leading to changes in composition and structure in the plant communities over short distances As in other Mediterranean regions(Kutiel et al., 1995)., In Sardinia changes in composition and structure in the plant communities over short distances can be observed for example from the dune ecosystems to Mediterranean hills.

The vegetation along this gradient is dominated by evergreen sclerophylls and semideciduous drought tolerant species, which differ in their physiological and structural adaptations to abiotic stresses. Despite the importance of aboveground biomass for community structure and function, there are several uncertainties regarding its variation in spatial distribution and quality in different types of vegetation, and also regarding regional variations of these parameters.

In the present study several individuals of five dominant Mediterranean maquis species with different architecture and leaf phenology were studied in relation to the distribution of this species at four different locations along a rainfall gradient. Specific leaf area, Leaf area

- Sapwood area ratio, vessel number and vessel diameter were measured at the peak of the

dry season

We hypothesized that species variations in SLA, LA/SA and xylem vessel diameter are

species specific and that the variation is greater in species with a lower stomatal control.

The main objective of this study are:

1. Determine whether functional convergence in morphological features of leaf is

observed among Mediterranean shrubs species

2. Compare growth and anatomical variables (tree-ring width, vessel diameter) and

evaluate the action of climatic variables (temperature and precipitation) on growth

radial annual

This work is composed of two chapters, each regarding a specific topic of research.

In the first chapter we studied the foliar traits in five shrub species occurring along a

pedoclimatic gradient.

In the second chapter we have studied the climate-plant growth relationships to verify how

the water availability influences woody anatomical structure.

Comparative studies of plants species responses to environments could contribute to

understand interspecific differences among species (Carpenter et al., 1981). Choosing

species co-occurring in the same vegetation type could elucidate their potential capability

to persist in the distribution area, in response to increasing stress like drought conditions.

In this study the biomass distribution of Q. ilex, A. unedo, P. angustifolia, C.

monspeliensis, P. lentiscus is described. Intra and interspecific variations are analysed for

these species. Finally, the influence of environmental factors on the observed architectural

variations are discussed.

30

3. Materials and methods

3.1. Study area

The study was carried out in four sites located in Sardinia, Italy (Fig. 4) where Maquis

represent approximately 25% of the terrestrial vegetation with different precipitation

patterns (Tab. 1).

All sites are dominated by evergreen shrub species, including Arbutus unedo L, Q. ilex L,

Cistus monspeliensis L., Phyllirea angustifolia L., Pistacia lentiscus L. Piscinas site is a

sand dune ecosystem located on the west coast (55 m a.s.l.) where the climate is semiarid

Mediterranean (mean annual temperature 17.4 °C, and annual sum of precipitation, 600

mm). Sette fratelli site is located in the south east part of the inland, and at an altitude of

490 m a.s.l. (10.5 °C and 950 mm). The third site, Alà dei Sardi (621 m .a.s.l.), is located

in the north east where climate conditions are generally wetter and colder (9.5 °C and 1300

mm). The fourth site is located in the riserva di Porto Conte Capocaccia (12 °C and 700

mm, 40 m a.s.l.) where the vegetation is more open and scattered, characterized by a higher

frequency of more xeric species and shrub forms (such as Cistus monspeliensis and Cistus

salvifolius). In all sites, the vegetation is undisturbed by fire and human impacts with the

exception of grazing.

Table 1. Geografical coordinates of the sites.

Location	Latitude N	Longitude E	Altitude (m)	MAT (°C)	Precipitations
Sette Fratelli	40°37'	9°16'	490	10.5	950
Piscinas	39° 31'	8°27'	55	17.5	600
Capocaccia	39° 20'	8°16'	40	12	700
Alà dei Sardi	40°41'	9°19'	621	9.5	1300

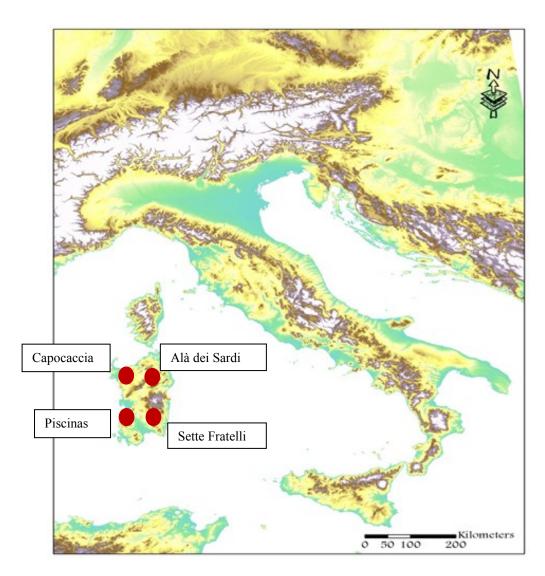


Figure 4. Distribution of experimental sites in the Sardinian region.

3.2. Study site description - Climatic aspect

3.2.1. Piscinas

The climate of this area can be defined as bi-seasonal (i.e. it is characterized by a hot-dry season alternating with a cold-wet season). A peculiar characteristic of the Sardinian climate is given by the uncertainty and variability of the meteorological spring period, both as regards the rainfall that as regards the temperature. In fact, during the spring months can occur excessive temperature elevations, with hot waves, then with a sudden return of cold weather: all this leads to inevitable damage to crops which may vary annually.

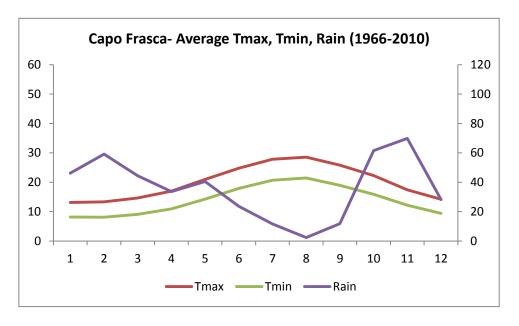


Figure 5. Rainfall and monthly temperature diagram of Capofrasca station. Every data is the mean of 44 years observations.

The rainfall variability is very evident during the autumn: the season may occur in advance (for example, in September), while in other cases it may delay its appearance until mid-November, resulting in long periods without rainfall.

The intensity of hourly rainfall in this area is highly variable, because of stormy character

of many rainfall events.

The winds much more frequent from the western side act on the vegetation determining

tipical physiognomies of the plants more exposed. The prevailing wind is the mistral,

which blows during all seasons.

From these meteorological elements, phyto-climatically you can frame this territory into

the zone of Lauretum area, hot subzone.

3.2.2. Alà dei Sardi

The climate is semi-continental, with wet winter high water surplus. Cold period (Fig. 6) over 4 months, mean minimum temperature of the coldest month less than 3 °C; average of the minimum annual around 4-5 °C; summer dryness under 3 months with moderate water deficit, average of the warmest month less than 24 °C; so the part of the territory taken into consideration falls in Lauretum area, subarea cold, with regard to the classification of Pavari phytoclimatic classification. Snowfall, infrequent, cover with plenty especially in the higher altitudes, but remain in the ground a few days. The rainfall is very high in the winter months and sometimes it is very intense.

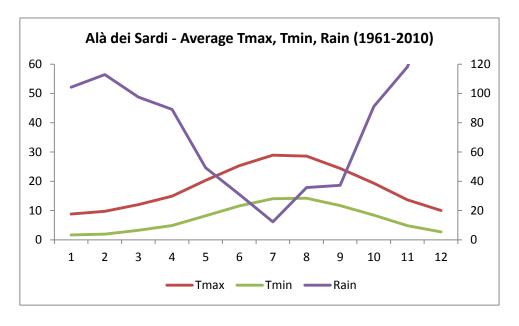


Figure 6. Rainfall and monthly temperature diagram of Alà dei Sardi station. Every data is the mean of 49 year observations.

3.2.3. Capocaccia

For the areas of Capo Caccia (Fig. 7), thermometric data and rainfall recorded in different stations throughout the territory, defining a climate characterized by mean annual temperatures ranging between 16-17 °C, precipitation of about 600 mm and a summer with strong water deficit.

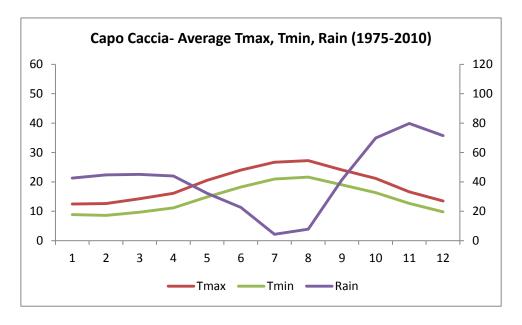


Figure 7. Rainfall and monthly temperature diagram of Capocaccia station. Every data is the mean of 35 years observations.

Regarding to the phytoclimatic characteristics, the territory is mainly on the Mediterranean horizon, characterized by low rainfall with hot-arid summer. The tipical vegetation is represented by sclerophyllous species. According to the phytogeographical setting proposed by Arrigoni (1983), the whole area falls within the North East District of the coastal and hilly sector Sardo Domain Sardinian-Corsican, it follows the analysis of the floristic component that includes, in addition to numerous species of Mediterranean-thermophile, a significant number of Sardinian-Corsican endemisms.

3.2.4. Sette Fratelli – Corongiu station

The climatic characteristics of the area, which has no surveys capable of providing a complete picture, are deducted from the examination of vegetation and some observations made from the termopluviometric station of Corongiu (Fig. 8).

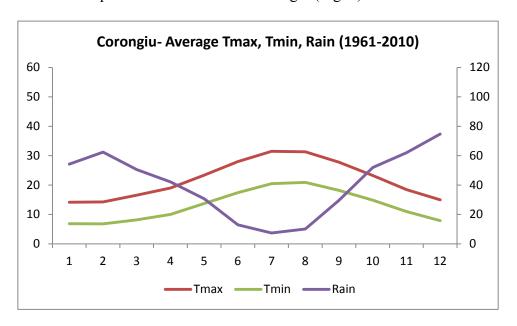


Figure 8. Rainfall and monthly temperature diagram of Corongiu station (Sette Fratelli).

Every data is the mean of 49 years observations.

Winter is rather mild: the average minimum temperature of the coldest month, with values around 3-4 °C.

The cold season continues for about two months, rarely exceeding them. Annual precipitation exceptionally snowy, referring to the data station Corongiu dam at 170 m a.s.l., are significant in the autumn and winter and decreased in spring to become very scarce in summer, reflecting the typical character of the hot summer. The climate can be described as semi-arid type, with little surplus winter water deficit and high in summer.

3.3. Description of the species

3.3.1. Cistus monspeliensis L.

Cistus monspeliensis L. (Fig. 9) is a shrub belonging to the family of Cistaceae. In the Mediterranean cistus appears in the late Pliocene, can therefore be considered a native species (Correia & Catarino, 1994). The leaves of all species of cistus are covered by glands that secrete oil and a resin composed of terpenes (Demetzos 1990). This family owned about 16 species (Demetzos 1990). In the Mediterranean basin grow only a few of these species such as *Cistus incanus* L., *Cistus salvifolius* L.



Figure 9. Inflorescence of Cistus monspeliensis.

Cistus monspeliensis L. is one of the species most widely represented in the Mediterranean (Gratani and Bombelli, 1999). This species has adapted to the Mediterranean environment through a leaf dimorphism, which can be summed up in the presence of summer leaves

Dr. Matteo Cabras – Titolo: Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maquis species.

developed on branches with shortened internodes (brachiblast) and winter developed

leaves on branches with long internodes (longhiblast). In summer leaves xeromorphic

characters are very developed, while in the winter are less evident (Aronne and De Micco,

2001).

It was shown that the seasonal dimorphism of the leaves of C. monspeliensis produces

small summer leaves from May that persist for the dry summer and fall in the autumn with

a half-life of about four months; winter larger leaves are produced by September and

persist throughout the winter and fall in the spring with an average life of about 8 months

(Gratani and Bombelli, 1999). The fall of the leaves can be due whether to a loss of

xeromorfism strategies of the structure or because of water stress. Other factors capable of

inducing the fall of the leaves are the inefficiency of water transport and the abscission to

avoid photoinhibition (Chiarello et al., 1987; Werner et al., 1999). The comparison

between a section of a winter and summer leaf of C. monspeliensis shows considerable

anatomical differences: winter leaves are flat with cells of the upper epidermis bigger and

palisade parenchyma more dense; summer leaves have a rippled sheet with many crypts

and trichomes, mesophyll cells smaller, intercellular spaces reduced with a more compact

structure (Aronne and De Micco, 2001).

3.3.2. Quercus ilex L.

Quercus ilex L. (Fig 10) is a sclerophyllous evergreen belonging to the family of Fagaceae. It is a native species that is found throughout the Mediterranean basin, because of its widespread characterizes the landscape (Blondel & Aronson, 1999).



Figure 10. Fructification of *Quercus ilex*.

The altitudinal distribution of scrub oak in Italy varies greatly due to the ecological plasticity of the oak itself. The oak can take on arboreal heights that reach up to 15-20 m. In the Mediterranean it has a bushy appearance and give shrub formations. This species has a greyish bark and very leathery leaves with dark green upper side and grey lower side. Oak bloom occurs between April and June, with male catkins 4-6 cm long and produce acorns with elongated tip.

The fall of the leaves is found throughout the year, with a maximum in October, after the

birth of the new leaves that can live up to 2-3 years. The fall of the leaves may increase

during the summer as a defense mechanism by drought. To defend themselves from the

drought, the holm oak has developed a very efficient stomatal control by opening the

stomata in the early hours of the day and closing them at dusk and almost completely

during the hottest hours of the day. In this way remains positive water balance to avoid

dehydration.

In addition to the phenological processes regarding the aerial part, oak is also developing

long roots that allow them to draw water directly from the aquifer and this is an advantage

especially in the months of summer drought characteristic of the Mediterranean climate.

The oak has a high leaf thickness due to very dense tissue and the production of tannins.

Sclerofilly allows the leaf to maintain the status of inland water unchanged. However,

despite these defense systems by drought, this species has a lower capacity for survival

than Pistacia lentiscus L. and Phillyrea angustifolia L. This allows to hypothesize that may

experience a change in the dominance of the oak by species more adapted to drought

following the rise in temperature intended for Mediterranean ecosystems in the near future

(Filella et al., 1998).

3.3.3. Pistacia lentiscus L.

Pistacia lentiscus L., mastic tree (Fig.11) is an evergreen shrub belonging the family Anacardiaceae.

The plant has a bushy, rarely tree, generally up to 3-4 meters high. The foliage is generally dense to dense branching, globular in shape. The whole plant gives off a strong resinous odor. The bark is of gray ash-wood pink color.



Figure 11. Fructification of Pistacia Lentiscus.

The leaves are alternat, paripennate, composed of 6-10 leaflets ovate-elliptic with entire margin and apex obtuse. The petiole is flattened and winged. The whole leaf is hairless.

P. lentiscus is a dioecious species with separate male and female flowers on different plants. In both sexes, the flowers are small, red, collected in inflorescence panicle cylindrical brought axil of the leaves of the branches of the previous year.

The fruit is a small drupe spherical or ovoid, 4-5 mm in diameter, red, tending to black

during ripening.

The bloom is in spring, from April to May. Red fruits are visible in summer and autumn

and mature in Winter- (Mulas et al., 1998).

It is one of the most common shrubs and representative of the Oleo-Ceratonion

community, often in association with the O. europea var. sylvestris and M. communis,

more sporadic its presence in the Mediterranean maquis and garrigue.

Thanks to its frugality and a good fire resistance is also quite common in pastures and

bushy areas most degraded residual stain.

At the mastic are recognized pedogenetic properties and is considered a species restorative

of the ground. The soil present in the bushes of this species is considered a good substrate

for gardening. For these reasons the species is important, from the ecological point, for the

recovery and the evolution of degraded areas (Mulas et al., 1998).

3.3.4. Phyllirea angustifolia L.

Phillyrea angustifolia L. (Fig. 12) belongs to the family Oleaceae and appears in the Mediterranean basin and in the arid zones of Africa (Quezel, 1985). This species can reach a height of 15 m but usually not greater than 5 m. We can find up to an altitude of 800 m, and is in that spot in the oak woods. He has gray branches characterized by opposite leaves, evergreen, leathery leaf with enlarged and polished surface. It has white flowers that sprout between March and May The fruits that follow the flowers are black drupes when they reach maturity.



Figure 12. Inflorescence of *Phyllirea angustifolia*.

To overcome periods of drought and cold, *P. angustifolia* L. has developed efficient protective mechanisms.

To avoid strong light radiation during the summer, the leaves have developed the ability to

change their inclination (Gratani & Bombelli, 1999). These inclinations are extremely

effective to prevent photoinibition phenomena and leaf overheating, as well as to reduce

transpiration during periods of limited water availability. Even the thick and glossy leaf

cuticle is an adaptive strategies to shielding the light and prevent the achievement of high

temperatures on the plate.

In the warmer months and cold, respectively in July and February in our latitudes, there

was a decrease in photosynthetic activity, which takes over in October and March, with the

development of new sprouts and the restoration of conditions not limiting (Arena et al.,

2006). Histological examination of a section of leaves of P. angustifolia L. highlights a

cuticle particularly thick, much thicker than C. monspeliensis L., with three layers of

palisade parenchyma and a very dense mesophyll, like *Q. ilex* L. leaves.

3.3.5. Arbutus unedo L.

Arbutus unedo L, strawberry tree (Fig 13) is an evergreen shrub or small tree in the family Ericaceae, native to the Mediterranean region and western Europe north to western France and Ireland. *Arbutus unedo* grows to 5–10 m tall, rarely up to 15 m, with a trunk diameter of up to 80 cm. The leaves are dark green and glossy, 5–10 cm long and 2–3 cm broad, with a serrated margin.



Figure 13. Fructification of Arbutus unedo.

The hermaphrodite flowers are white, bell-shaped, 4–6 mm diameter, produced panicles of 10–30 together in autumn. They are pollinated by bees.

The fruit is a red berry, 1–2 cm diameter, with a rough surface, maturing 12 months at the same time as the next flowering.

Flowers are grouped in pendulous panicles that contain between 15 and 20. Corolla is

white or yellowish-pink, with 5 small teeth folded outwards 5-8 mm wide and 6-10 mm

long. The anthers are dark red with two yellow horns. Flowering takes place in October-

November. The fruit is a spherical berry about 2 cm, fleshy and red when ripe, covered

with pretty hard and a few millimeters thick tubercles.

The fruits ripen in the following year compared to the flowering giving rise, in the fall The

plant contains flowers and ripe fruit, which makes it particularly ornamental tree for the

presence of three vibrant colors: red fruits, white flowers and green leaves.

3.4. Experimental design

All shrubs used for the study of woody growths come from natural populations and without

anthropogenic alteration (grazing and fire).

The sampling sites have own micro-stational characteristics (soil, edaphic humidity,

exposure etc.) and to ensure independence between the values of the time series the trees

have been chosen so that their canopies were sufficiently spaced.

Four sampling plots were established on Sardinian island (Italy). Sites showed

characteristic micro-conditions in terms of soil moisture, soil depth and exposition. The

vegetation cover (c. 95%) was dominated by evergreen, sclerophyllous shrubs ca 1.5 m

high, and emerging Quercus ilex L. Phylllrea angustifolia L. and Arbutus unedo L. up to 2

m high. The climate was Mediterranean, with a remarkable dry period in summer.

3.5. Preparation of samples

Analysis were carried out on washers taken from three individuals per species. The trees

were chosen subjectively among those showing the average characteristics of population

and among small and medium diameter classes ($d \le 20$ cm). From each tree were taken one

washer at the base (about 30 cm from the ground) for a total of 15 washers per site.

The samples were transported in plastic bags tightly closed and stored in a dry and

ventilated place. The dendrochronological study was carried out at WSL Swiss Federal

Research Birmensdorf (CH).

48

Dr. Matteo Cabras – Titolo: Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maguis species.

3.6. Anatomical analysis and microscopic measure

The preparation of microsection has followed the following protocol:

• collection from the washers (one per individual) of a slice of wood with a thickness of

about 1 cm with cuts in the transverse direction.

• fragmentation of slice-sized pieces suitable for cutting the microtome.

• immersion of wood in water for 12 hours to 80 °C.

• cut with a thickness of 15 to 20 microns.

• staining of microsection with Safranin and Astra Blue, dyes that differentiate lignified

cell walls (in red) from the pecto-cellulose ones (blue).

• Accommodation of microsection on glass slide, application of Canada balsam and

establishing the coverslip.

• pressing and dried in an oven for 12 hours at 60 °C.

The next step was the construction of chronologies (Chronology Building). The

measurements of the growth rings were performed using instrumentation LINTAB

equipped with the software TSAP-Win (Rinnetch, Heiedelberg, Germany).

The measurement was made starting from the side of the cortex toward the center of the

section with an accuracy of 1/100 mm. For each section two dendrochronological curves

were obtained, and from these the average curve of each plant by cross-dating TSAP. We

thus obtained three curves for five species considered (15 curves).

from which it was obtained a representative curve for average species of each site. This

was then used on subsequent correlations with the meteorological parameters.

3.7. Chronology building

The definitive chronologies were obtained through the use of the program ARSTAN, developed by Cook in 1983 (Cook et al, 1999). Starting from the measurements of the rings, Arstan produces three different types of chronologies performing an analysis of the time interval common to the series. The series produced are designed to cover the most common signal and the minimal effect of disturbances. The series of the amplitudes of the rings are the expression of a combination of several factors. This report, of the linear type, can be represented by the following model (Cooket et al, 1990):

$$F_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t$$

The wood anatomical features measured in a tree-ring (F) formed in the year t is a function of an aggregate of factors:

- 1. the age-related growth trend (A) due to normal physiological aging processes,
- 2. the climate (C) that occurred during that year,
- 3. the occurrence of disturbance factors within (D1) the forest stand like a blow down of trees.
- 4. the occurrence of disturbance factors from outside (D2) the forest stand such as air pollution leading to changed growth or an insect outbreak that defoliates the trees, and
- 5. random (error) processes (E) not accounted for by the other processes.

The Greek letter δ in front of D1 and D2 indicates either a "0" for absence or "1" for presence of disturbance signal.

Each of these agents contributes to the increase in woody annual variability. Some act in the short term, others in large time scale. To find the actual plant response to climatic stimuli it is necessary to exclude the contribution to growth of non-climate factors. Through the standardization of the series you can eliminate the growth (Cook et al. 1990) due to non-climatic causes.

$$G_t = f (A_t + \delta D1_t + \delta D2_t)$$

Which produces its effects on increasing woody in the long term (low frequency variability). Generally the operation consists in dividing the measured values (Rt) for a harmonizing function (smoothing) standardized, defined by growth trend Gt. It is obtained in this way a series of indices amplitude of the rings (ring-tree index) value of

$$I_t = R_t / G_t$$

with defined media (generally equal to 1.0) and variance tends to a constant.

Ultimately, this allows you to:

- to remove the effects of the growth trend due to non-climatic factors related to age.
- to achieve an average of the series adapted to different growth trends and the different age of the tree.

The standard version of the mean is obtained by detrending (standardization) of the series, carried out by developing a function (curve) which passes through the average values of the amplitudes annular: in this way is removed much of the variance (low frequency) due to non-climatic factors (Cook and Holmes, 1999).

The detrending method used involved the creation of a negative exponential curve that best represents the decreasing trend of annual growth of a plant. This time series contains the most common signal to the series and eliminates the effect of persistence (Cook and Holmes, 1999). Through the elimination of persistence, however, it can be eliminated in same cases low-frequency part of the variance due to the climate and the physiology of the tree (Kairiukstis and Cook, 1990). ARSTAN chronology has been designed to overcome this problem and it is generated by reintroducing history residual persistence of the series

eliminated by the autoregressive model. This history contains the strongest signal possible

climate (Cook and Holmes, 1999).

Another option to choose the program is because it provides for the stabilization of the

variance of the series. Strong fluctuations of the variance may depend on individual

characteristics of the site, the species or individual tree. The increase of this parameter is

also linked to variability in the size of the samples that is independent of changes of the

variance due to environmental influence (Cook and Kairiukstis, 1990). The stabilization

occurs through the application of a harmonizing function (smoothing spline function) to the

absolute value of the average of the standardized indexes.

3.8. Climatic variables and correlation with the growths

In order to characterize climate area of the study areas were considered the data reported

an Annals of the Hydrographic Service of the Autonomous Region of Sardinia and those

provided by the Air Force of Sardinia.

The limited availability of climatic stations is a limitation in the dendroclimatic research.

However, this problem can be easily overcome by using climatic series of stations placed

also at a certain distance from the sampling site, obtaining satisfactory results. In fact, not

always the data of the stations closest to the point of observation are necessarily related to

data growth, especially in the Mediterranean environment, characterized by a marked

environmental variability.

In the specific area of the Seven Brothers were considered termopluviometric data of the

Corongiu station (Sinnai) (Lat. 39.18, Lon. 9:19, Height 126 m as.l.) in relation to an

observation period of 49 years (1961-2010), for the area of Ala dei Sardi were considered

termopluviometrici data available regarding the rain gauge Monti (Lat. 40.39, Lon. 9.19

Height 663 m a.s.l.), for an observation period of 49 years (1961-2010) for the area of

Capocaccia were considered data termopluviometrici the station site itself (Lat. 40.56, Lon.

8:16, Height 200 m a.s.l.) and finally to the area of Piscinas were considered data

termopluviometrici of Capofrasca (Lat. 39.44, Lon. 8.27, Height. 92 m a.s.l.).

Have been calculated by the following climatic parameters:

- annual precipitation (total);

- cumulated precipitations during selected periods: from January to April (PGA), from

May to August (PMA), from September to December (PSD);

- The average monthly temperature (Jan, Feb, Mar, ..., Nov., Dec.);

- Average temperatures during selected periods: from January to April (TGA), from May

to August (TMA), from September to December (TSD).

For the calculation of the cumulated precipitations (POTMAR) were considered some

periods between October of the previous year to September of the year and contemporary

to the formation of the ring. This period, which coincides with the biological year, is

classically adopted in the analysis of the relations climate / growth for the forests of the

Mediterranean region (Garfi 2000).

3.9. Wood anatomical description of studied species

Arbutus unedo L.

Heartwood distinct. Diffuse- to semi- ring porous. Pores angular to round, solitary or in

short radial files or groups. Pores infrequent to numerous. Growth ring boundary distinct.

False growth rings frequent. Parenchyma sparse, apotracheal, diffuse and scanty

paratracheal.

Quercus ilex L.

Wood diffuse-porous. Porous solitary in more or less long radial files. Libriform fibres in

more or less tangential bands. Many tangential bands of apotracheal parenchyma.

Multiseriate rays extremely broad. The ray-vessel pits are often large and vertical, a few

pits fill an intersection.

Pistacia lentiscus L.

Mostly ring-porous. Earlywood pore ring is loosely packed and is seldom more than

uniseriate. In some growth rings the large earlywood pores are absent. The size of the

earlywood pores is highy variable. In normal growth rings, the latewood pores are

arranged in radial files and clusters, sometimes also in a dendritic pattern. Cospicuous

tyloses in the earlywood vessels in the heartwood. Parenchyma sparse, mainly

paratracheal.

Cistus monspeliensis L.

Sometimes with distinct heartwood. Diffuse-porous. Pores small, rather frequent, mostly

solitary, often containing gummy inclusions. Fibre-tracheids thick-walled. Apotracheal

55

Dr. Matteo Cabras – Titolo: Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maquis species.

parenchyma sparse and diffuse. Growth ring boundary more or less distinct, false rings

frequent.

Phyllirea angustifolia L.

Heartwood indistinct. Diffuse-porous. Vessels typically small (less than 100 µm mean

tangential diameter) and sometimes extremely small (less 25 µm) with vessels grouped in

broad oblique masses (dendritic) and encircled by vasicentric paratracheal parenchyma.

Parenchyma also in uni- to 3seriate marginal bands. Fibre groups and pore groups are

distinctly separate.

4. Results

4.1. Dendrochronologies

The series reported were obtained from the raw chronologies for each species for each site. It was observed low ring width values and low annual variability of the same values. Three chronologies representative of *C. monspeliensis* (Fig. 14) are quite short. Specifically, common responses are evident in the years 2008 and 2005 (down peaks) and in the years 2007 and 2004 (upright peaks). For the site of the Alà dei Sardi ring width measured are lower than those for other sites, and in fact have an average in the neighborhood of 59 mm against 73 mm of the other three sites. Chronologies concerning *A. unedo* show, as well as those of *C. monspeliensis*, internal changes rather low and long-term stability, i.e. there are no particular trends in increasing or decreasing of mean tree ring width. Also in this species common records have been observed in the year 2005.

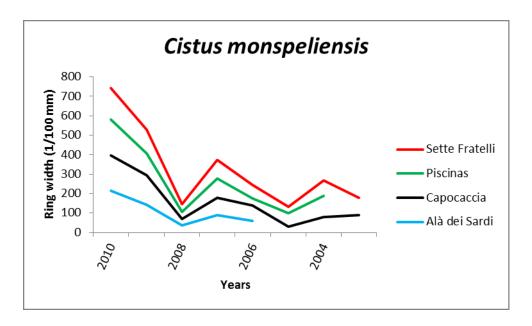


Figure 14. Average ring width chronology for *C. monspeliensis* using raw data.

As reported for the species *C. monspeliensis*, even for *A. unedo* (Fig. 15) the years 2009 and 1988 show an increase of the amplitude ring if compare. Piscinas is the site that has a greater ring width (93 mm on average approximately) than the remaining three sites.

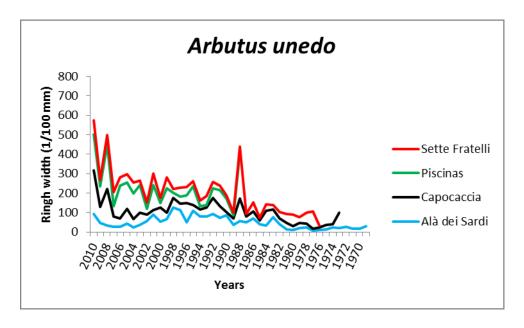


Figure 15. Average ring width chronology for *A. unedo* using raw data.

Quercus ilex (Fig 16) presents a different situation than the two previously analyzed. Chronologies show fewer down and upright peaks, and also a much more stable performance of the previous. It is also a general evident tendency of increase of the ring in time. In addition to the upright peaks yet recorded in the previous species (2009, 2004, and 2000) also the year 2007 was characterized by strong growth. There are also numerous years with a decrease in the tree ring width. Among these, the most evident ones are: 2005, 2003, and 1998.

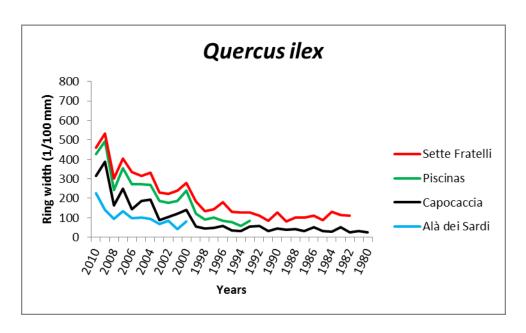


Figure 16. Average ring width chronology for *Q. ilex* using raw data.

Series relating to *Pistacia lentiscus* (Fig 17) presents, in line with the previous case, a low amount of both upright and down peaks. In addition, all chronologies have the same trend over time. Until 2002 the amplitude ring remains more or less stable in all sites and then showed a decrease in 2001.

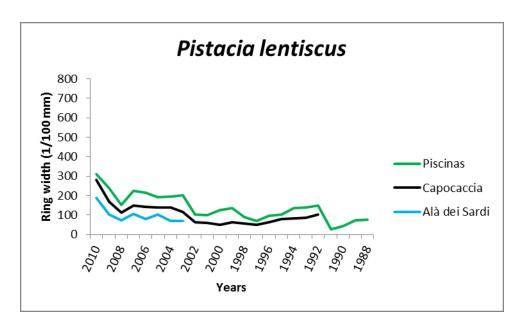


Figure 17. Average ring width chronology for *P. lentiscus* using raw data.

P. angustifolia (Fig. 18) chronologies shows internal changes rather high but long-term stability as well as in *Arbutus unedo*. There are no particular trends increasing or decreasing the amplitude of ring average over time. For this species common responses were observed during the years with reduced growth in the years 1999 and 1987.

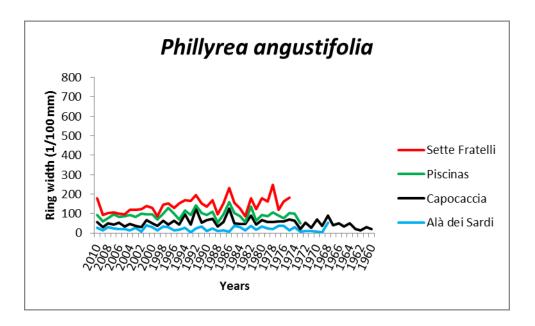


Figure 18. Average ring width chronology for *P. angustifolia* using raw data.

4.2. Chronological statistics

4.2.1. Alà dei Sardi

High temperatures in July for the *C. monspeliensis* (Fig. 19) favor the formation of large rings even if the signal is not evident in all the examined subjects. Signal is also evident in the holm oak in the month of December. Winter precipitation are relevant to the species of *Q. ilex* and *C. monspeliensis*.

C. monspeliensis seems to be affected by rain in the month of January, February, July and during the winter season (October, November and December) (Fig. 20). The oak growth is significantly correlated with the rainfall of November, December, and with the sum of annual precipitation.

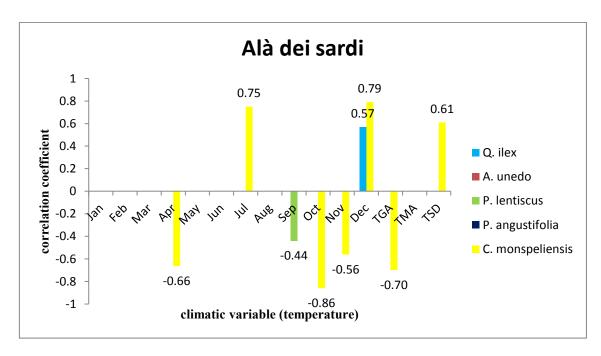


Figure 19. Significant level according to Student's t – test: P < 0.005. TGA: Janury-April; TMA: May-August; TSD: September-Dicember.

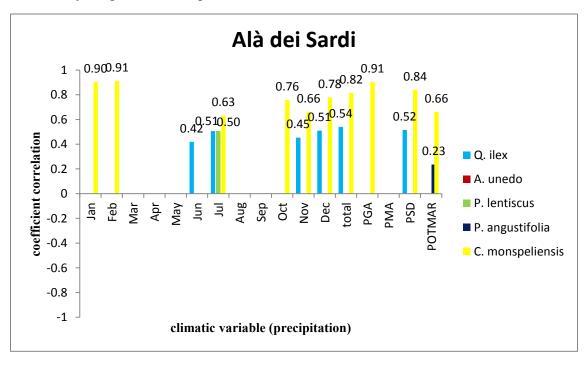


Figure 20. Significant level according to Student's t – test: P < 0.005. PGA: Janury-April; PMA: May-August; PSD: September-Dicember; POTMAR: October (previous year) – March (current year).

4.2.2. Piscinas

Temperatures of April, July and November (Fig. 21) favor the formation of large rings in *Q. ilex*. The signal is also evident in the *P. lentiscus* in May, August, and in the sum of temperatures from March to August. There is an inverse correlation for *P. angustifolia* in the month of August.

A. unedo seems to react positively to the temperatures of October.

Winter precipitation (Fig. 22) are relevant in the negative direction for *C. monspeliensis* in March, September and December. *A. unedo* reacts positively to temperatures of March and the *P. lentiscus* reacts positively to precipitation in December and negatively to precipitation in May.

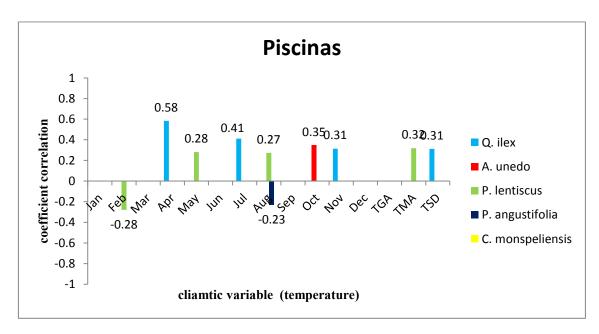


Figure 21. Significant level according to Student's t – test: P < 0.005. TGA: Janury-April; TMA: May-August; TSD: September-Dicember.

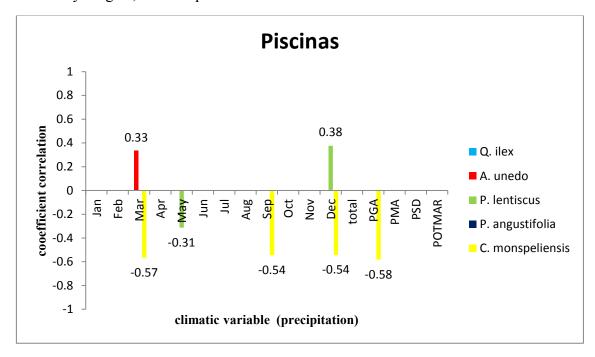


Figure 22. Significant level according to Student's t – test: P < 0.005. PGA: Janury-April; PMA: May-August; PSD: September-Dicember; POTMAR: October (previous year) – March (current year).

4.2.3. Sette Fratelli

P. angustifolia is negatively correlated with the temperatures of April, May and June (Fig. 23).

C. monspeliensis instead is positively correlated with temperature of February and negatively with temperature of October.

As for precipitation (Fig. 24), those of February March, and the total for the months of January to April positively influence the thickness of the rings of *C. monspeliensis*. *P. lentiscus* is positively correlated with precipitation in January and May.

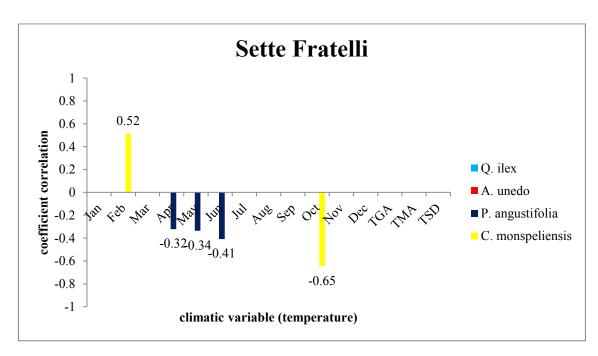


Figure 23. Significant level according to Student's t – test: P < 0.005. TGA: Janury-April; TMA: May-August; TSD: September-Dicember.

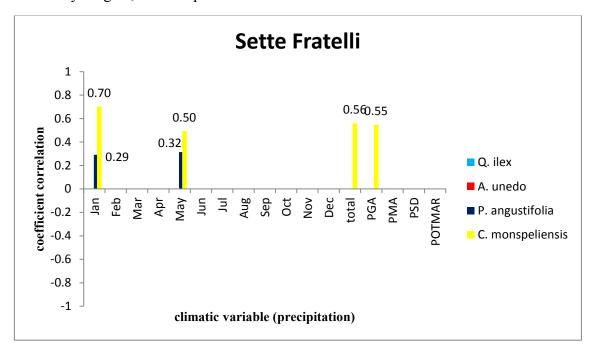


Figure 24. Significant level according to Student's t – test: P < 0.005. PGA: Janury-April; PMA: May-August; PSD: September-Dicember; POTMAR: October (previous year) – March (current year).

4.2.4. Capocaccia

In this site the signals of temperature are not evident for all subjects tested (Fig. 25). For *A. unedo* temperature in April is positively correlated. The temperature in May is positively associated with the oak growth. The *P. lentiscus* and *C. monspeliensis* are negatively correlated respectively with temperatures in June and October. Winter precipitation (Fig. 26) appear irrelevant to the oak except the amount of the precipitation of October - March (POTMAR). *A. unedo* reacts positively to precipitation of March, May, November, December, and the sum of annual precipitation. In addition, *A. unedo* reacts with the sum of precipitation from March to April, September to October and from October to March. *P. lentiscus* reacts positively to rainfall in June and July and the burden of precipitation from March to April and from October to March. *C. monspeliensis* seems to be positively affected by the rainfall in the month of June.

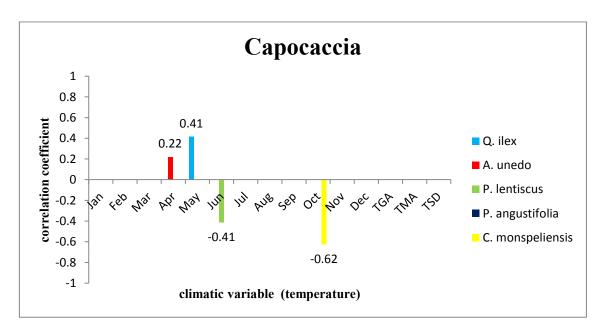


Figure 25. Significant level according to Student's t – test: P < 0.005. TGA: Janury-April; TMA: May-August; TSD: September-Dicember.

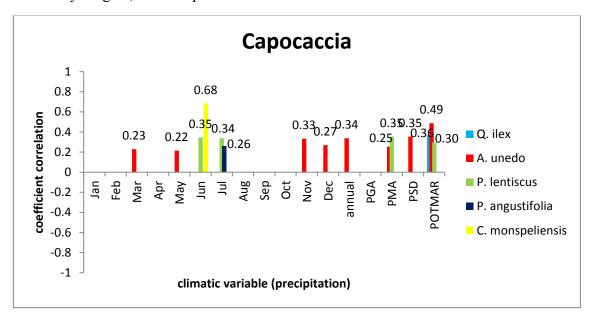


Figure 26. Significant level according to Student's t – test: P < 0.005. PGA: Janury-April; PMA: May-August; PSD: September-Dicember; POTMAR: October (previous year) – March (current year).

4.3. Raw dendrochronological series

The correlation functions provide different climate signals in all chronologies examined. In

wet sites, chronologies show a strong relationship with rainfall than arid sites. In appendix

are reported the correlation values for all the species. In general the analysis show a direct

correlation with winter precipitation, July and August of the current year. The only inverse

relationship in Sette Fratelli site exist in the month of August and for the month of March

and May at the site of Ala dei Sardi. As regards the temperatures there is a substantially

behavior in the two sites arid. In the dry sites (Piscinas and Capocaccia) species react

differently as regards the precipitation and in the same way as regards the temperatures. In

particular, Q. ilex (Tab. I) has a positive correlation in temperatures during the growing

season. A. unedo (Tab. II) presents a positive correlation similarly to Q. ilex in the months

from April to November.

The behaviour of *P. lentiscus* (Tab. III) instead is completely opposite as regards the

temperature. While in Capocaccia site during the growing season there is an anticorrelation

with temperature, in Piscinas site the exact opposite occurred. As regards the P.

angustifolia (Tab. IV) there is an anticorrelation in the site of Piscinas in the months from

March to November and a positive correlation in the Capocaccia site. Q ilex on Sette

Fratelli site and Ala dei Sardi site react in the same way with respect to temperature. In

fact, there is a negative correlation in the months from March to August and a positive

correlation in the months of January, October, November and December. Even the A.

unedo react almost the same way with a negative correlation during the growing season

from March to August.

P. lentiscus present only at the site of Ala dei Sardi has a positive behavior in the months

of February, March and April, and a negative correlation in the months of August,

September and October. With regard to the precipitation Q. ilex is positively correlated

during the months of June, July, November and December and the sum of annual

precipitation. It is also positively correlated with seasonal precipitation from September to

December. Only at the site of the oak Capocaccia is correlated with rainfall from October

to March.

A unedo is positively correlated with precipitation in March, May, November and

December in the only site of Capocaccia. It is also correlated with the amount of annual

rainfall and seasonal rainfall from March to April and September to October.

P. angustifolia is positively correlated with temperature in May at the site of the Seven

Brothers, and in July at the site of Capocaccia. On the site of Ala dei Sardi, *Phillyrea*

angustifolia is positively correlated with precipitation from October to March.

P. lentiscus presents positive correlations with precipitation in July at the site of Ala dei

Sardi and rainfall in June and July at the site of Capocaccia. It is also correlated with

seasonal rainfall in March-April and the values of precipitation from October to March. P

lentiscus is also positively correlated with precipitation in May at the site of Piscinas.

C. monspeliensis (Tab. V) is positively correlated with precipitation in July and with the

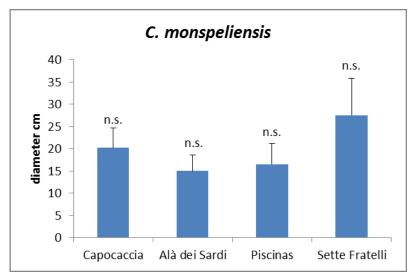
values of precipitation in the winter months, October, November and December. It is also

positively correlated with the amount of annual rainfall and the sum of the seasonal rainfall

from January to April and from September to December.

4.4. Stem diameter

In all experimental sites the diameter of the stem is not significantly affected by the different climatic conditions (Fig. 27-28).



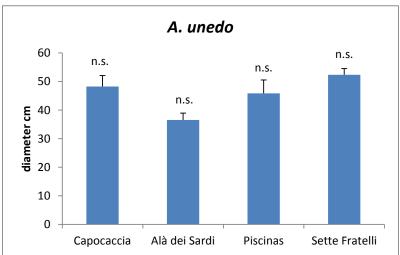
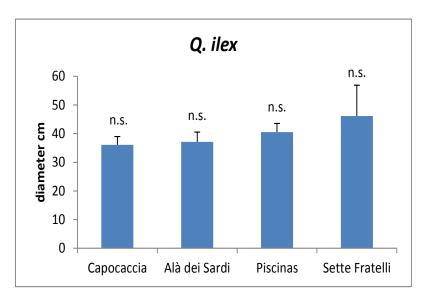
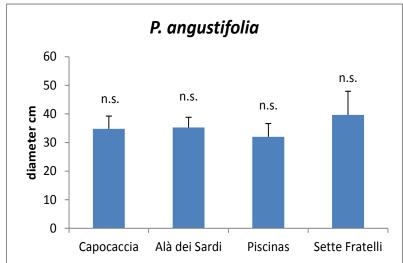


Figure 27. Stem diameter value of *C. monspeliensis* and *A. unedo* in different sites.





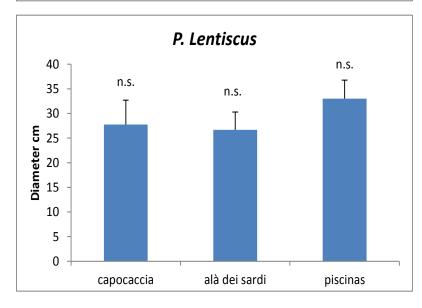


Figure. 28. Stem diameter value of Q ilex, P. angustifolia and P. lentiscus in different sites.

4.5. Leaf Area/Sapwood Area (LA/SA)

The leaf area:sapwood area ratio, based on measured values obtained from individual sample trees, did not differ significantly among crown classes in *Q. ilex* and *C. monspeliensis* (Fig 29-30).

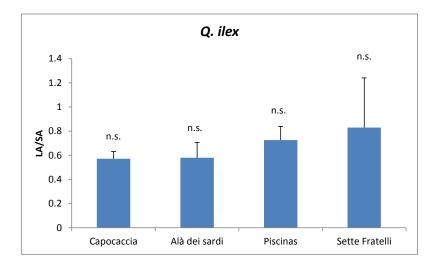


Figure 29. Different value of LA/SA for *Q. ilex* in different site.

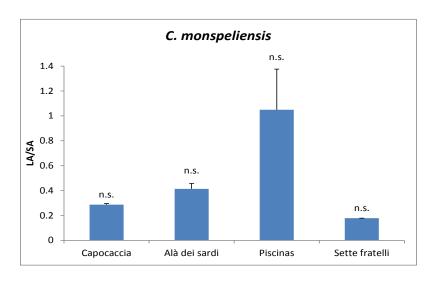


Figure 30. Different value of LA/SA for *C. monspeliensis* in different sites.

Some authors (O'Hara and Valappil, 1995) investigated the hypothesis that the conducting tissue of some tree, because of greater transpirational demands, can support a lower

amount of foliage than other tree of the same species, but found no significant effects of canopy position on the leaf area:sapwood area ratio. We observed the opposite trend in *A. unedo*, (Fig 31) and in *P. angustifolia* (Fig 32) in which upper-crown-class trees generally had higher leaf areas per unit of sapwood area than lower-crown-class trees, although these differences were not statistically significant.

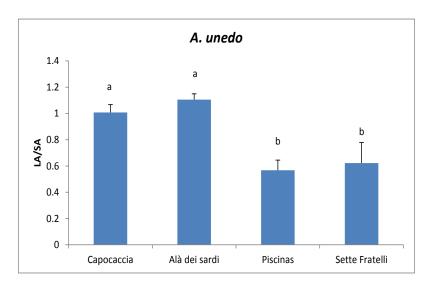


Figure. 31. Different value of LA/SA for *A. unedo* in different sites.

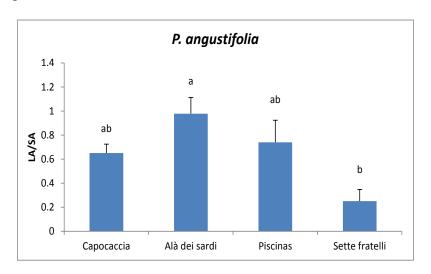


Figure 32. Different value of LA/SA for *P. angustifolia* in different sites.

No signification we have found in *P. lentiscus* also (Fig 33).

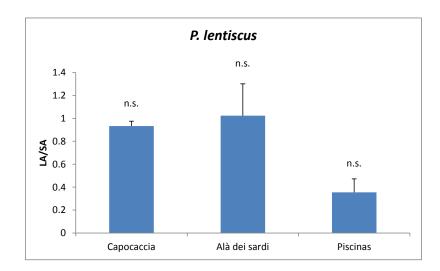


Figure 33. Different value of LA/SA for *P. lentiscus* in different sites.

Leaf area:sapwood area ratio is generally higher for mesic, shade-tolerant species than for xeric, shade-intolerant species (Kaufmann and Troendle 1981, Waring et al. 1982). The sapwood of mesic species is believed to support a greater amount of foliage than an equivalent area of sapwood in xeric, shade-intolerant species.

In our study, the leaf area:sapwood area ratio was greater in A. unedo than in Q. ilex.

This seems to indicate that *A. unedo* is either more shade tolerant or grows on more mesic sites than *P. angustifolia*.

Some characteristic other than shade tolerance or site type, such as soil moisture availability, may be responsible for differences in the leaf area:sapwood area ratio between the four species..

4.6. Specific leaf area (SLA)

Specific leaf area, or leaf area per unit weight of foliage differed significantly. The values of specific leaf area (SLA) of a species (Tab.2-3), in most cases, are positively correlated with its potential growth rate, or the rate of photosynthetic activity based on the mass (Cornelissen et al., 2003). Lower values tend to correspond to a relatively high investment in the defenses of the leaf (in particular those structural) and to a long duration of life of the leaf. Interspecific variation in the size of the leaf, however, have been associated with changes in climate, geology, altitude or latitude and stress situations that tend to select relatively small leaves and many other factors (size of plant ecological strategies related to environmental disturbance, phylogenetic factors, etc.). (Cornelissen et al., 2003).

Table 2. SLA values between species. Letters refer to the significance of one-way ANOVA: different letters correspond to significantly different values (p < 0.05).

	A. unedo	C. monspeliensis	P. angustifolia	Q. ilex	P. lentiscus
Alà dei Sardi	39.3 a	54.7 a	42.3 ns	44.7 a	83.3 a
Sette Fratelli	74.7 b	74.0 ab	60.0 ns	47.7 a	
Capocaccia	44.7 a	43.3 ab	48.7 ns	61.7 b	52.7 b
Piscinas	49.3 a	71.7 a	40.0 ns	44.7 ac	54.7 b

Table 3. SLA values between site. Letters refer to the significance of one-way ANOVA: different letters correspond to significantly different values (p < 0.05).

	Alà dei Sardi	Sette Fratelli	Capocaccia	Piscinas
Q. ilex	44.7 a	60.0 ns	52.7 ab	44.7 a
A. unedo	39.3 a	74.0 ns	43.3 a	48.7 a
P. lentiscus	83.3 b		40.0 a	54.7 ab
P. angustifolia	42.3 a	74.7 ns	44.7 a	49.3 a
C. monspeliensis	54.7 a	47.7 ns	61.7 b	71.7 b

Species with a long life span of the leaf tend to invest a lot of resources to protect, grow

more slowly than species with leaves less durable and retain their nutrients inside longer.

Lambers et al. (1992) suggested that a lower SLA of slow-growing species results from a

relatively thick cell structure and high concentration of secondary compounds, leading to a

lower photosynthetic rate per unit leaf dry weight. They proposed that a lower SLA,

mainly due to secondary compounds, reflects the need for protection against detrimental

abiotic and biotic factors.

We did not find large differences in water use among the populations distinct differences in

their SLA.

Despite differences in the leaf area:sapwood area ratio among species we did not find a

consistent trend in the ratio between individual from wet and dry sites. In general, this ratio

depends on vapour pressure deficit at a site, and thus tends to decrease towards drier sites

since trees avoid damaging effects of low water potentials by reducing leaf area

(Whitehead et al., 1994; Mencuccini et al., 1993). As the ratio is environmentally

determined, higher leaf area:sapwood ratios in the species from dry sites, classified drier

sites based on their annual vapour pressure deficit, appear to reflect their intrinsically

slower growth.

4.7. Wood anatomy

Significant correlations with climatic factors are shown in Tables 4-7. The highest

correlation value has been found for Q. ilex in Alà dei Sardi site.

Q. ilex is negatively correlated with temperatures in March, June and November while it is

positively correlated with the temperature in July. It is positively correlated with

precipitation in January, February, June and the precipitation values of the winter months

(October, November and December). It is also well correlated (r = 0.69) with the total

annual precipitation. With regard to the correlations with seasonal values is correlated with

rainfall for the period from January to February and precipitation for the period from

September to December.

In the site of Piscinas A. unedo has a positive correlation with the temperature in March

and negative values of correlations with rainfall in February, July and August (r = -0.60)

As regards the site of Sette Fratelli there is no significant correlation for any species.

In the site of Capocaccia there is a negative correlation with the temperature of December.

While for the precipitation A. unedo is positively correlated with the values of precipitation

in March, May, October, November and December.

It is also positively correlated with the amount of annual rainfall (r = 0.80). As for the

seasonal values of precipitation of January-April, March-August and September-October

have a positive effect with the average diameter of the vessels.

Table 4. Significant (p<0.05) correlations (r) of vessel diameter in the site of **Alà dei sardi** with monthly and seasonal mean temperature and precipitation sum.

		Q. ilex	A. unedo	P. lentiscus	P. angustifolia	C. monspeliensis
	Jan	0.18	0.15	-0.19	-0.13	0.22
	Feb	-0.20	0.25	-0.30	-0.04	-0.34
	Mar	-0.57 *	0.00	-0.06	-0.04	-0.13
	Apr	-0.14	0.38	-0.44	-0.20	0.00
	May	-0.40	-0.04	0.05	-0.13	0.36
Tomporaturo	Jun	-0.58 *	-0.18	0.13	-0.04	0.15
Temperature	Jul	0.53 *	-0.21	0.29	0.14	0.12
	Aug	-0.25	0.12	-0.09	-0.15	0.22
	Sep	-0.17	0.18	-0.15	-0.13	0.09
	Oct	-0.38	0.34	-0.40	-0.23	0.06
	Nov	-0.64 *	-0.09	0.04	-0.06	0.06
	Dec	0.47	-0.03	0.08	0.18	-0.40
	Jan	0.60 *	-0.09	0.16	0.18	-0.24
	Feb	0.57 *	-0.20	0.26	0.22	-0.21
	Mar	0.23	0.24	-0.27	-0.13	0.14
	Apr	-0.29	-0.30	0.31	0.12	-0.05
	May	0.39	0.19	-0.22	-0.05	0.02
	Jun	0.55 *	0.25	-0.23	0.03	-0.23
Precipitation	Jul	0.45	-0.03	0.05	0.18	-0.41
	Aug	-0.32	-0.21	0.18	0.07	-0.07
	Sep	-0.08	-0.36	0.39	0.05	0.35
	Oct	0.65 *	0.05	0.01	0.13	-0.26
	Nov	0.67 *	0.08	-0.04	0.12	-0.29
	Dec	0.68 *	0.00	0.05	0.16	-0.30
	total	0.69 *	-0.05	0.11	0.17	-0.25
	TGF	-0.27	0.29	-0.38	-0.14	-0.13
Temperatures	TMA	-0.33	-0.08	0.11	-0.10	0.36
sum	TSD	0.18	0.12	-0.08	0.10	-0.41
	PGA	0.67 *	-0.13	0.20	0.19	-0.19
Precipitation	PMA	0.35	0.04	-0.07	0.09	-0.26
•	PSD	0.69 *	-0.05	0.11	0.17	-0.23
sum	POct Mar	0.34	0.18	-0.13	0.39	-0.55 *

Table 5. Significant (p<0.05) correlations (r) of vessel diameter in the site of **Piscinas** with monthly and seasonal mean temperature and precipitation sum.

		Q. ilex	A. unedo	P. lentiscus	P. angustifolia	C. monspeliensis
	Jan	-0.05	-0.21	-0.02	-0.02	0.10
	Feb	0.01	0.08	-0.11	-0.11	0.05
	Mar	0.27	0.56 *	-0.45	-0.45	-0.01
	Apr	-0.04	0.13	0.09	0.09	-0.07
	May	-0.08	-0.24	0.22	0.22	-0.05
Tomporatura	Jun	-0.08	-0.09	0.28	0.28	-0.13
Temperature	Jul	0.01	0.22	0.14	0.14	-0.18
	Aug	0.06	-0.02	-0.05	-0.05	-0.01
	Sep	-0.10	-0.15	0.31	0.31	-0.13
	Oct	-0.23	-0.39	0.45	0.45	-0.09
	Nov	-0.10	-0.12	0.31	0.31	-0.14
	Dec	-0.10	-0.07	0.32	0.32	-0.16
	Jan	0.02	-0.26	-0.07	-0.07	0.10
	Feb	-0.17	-0.53 *	0.18	0.18	0.11
	Mar	-0.09	-0.48	0.03	0.03	0.15
	Apr	-0.02	-0.28	0.01	0.01	0.06
	May	0.01	-0.23	-0.17	-0.17	0.18
	Jun	0.19	0.18	-0.35	-0.35	0.09
Precipitation	Jul	-0.15	-0.60 *	0.19	0.19	0.10
	Aug	-0.26	-0.66 *	0.37	0.37	0.07
	Sep	-0.14	-0.47	0.28	0.28	0.00
	Oct	-0.08	-0.48	0.03	0.03	0.14
	Nov	0.05	-0.17	-0.21	-0.21	0.16
	Dec	-0.07	-0.46	0.01	0.01	0.15
	total	0.20	0.25	-0.42	-0.42	0.12
T	TGF	0.02	0.07	-0.11	-0.11	0.05
Temperatures	TMA	-0.03	-0.03	0.19	0.19	-0.11
sum	TSD	-0.15	-0.20	0.37	0.37	-0.14
	PGA	-0.06	-0.44	0.02	0.02	0.13
Precipitation	PMA	0.01	-0.26	-0.17	-0.17	0.18
sum	PSD	-0.06	-0.43	0.00	0.00	0.14
	POctMar	0.09	-0.05	-0.16	-0.16	-0.09

Table 6. Significant (p<0.05) correlations (r) of vessel diameter in the site of **Sette Fratelli** with monthly and seasonal mean temperature and precipitation sum.

		Q. ilex	A. unedo	P. angustifolia	C. monspeliensis
	Jan	-0.03	-0.14	0.03	0.18
	Feb	-0.18	-0.23	0.14	-0.29
	Mar	0.15	-0.03	-0.34	0.02
	Apr	-0.09	0.35	0.48	-0.21
	May	0.13	0.42	0.15	0.22
Temperature	Jun	0.09	0.43	0.25	0.05
remperature	Jul	0.08	0.29	0.02	-0.06
	Aug	0.13	-0.08	-0.21	0.36
	Sep	0.17	0.15	-0.08	0.57
	Oct	0.04	0.33	0.22	0.22
	Nov	0.07	0.34	0.12	0.07
	Dec	0.11	0.30	-0.03	-0.23
	Jan	0.05	-0.35	-0.45	-0.06
	Feb	-0.10	-0.23	-0.10	-0.53
	Mar	0.03	-0.02	0.03	0.24
	Apr	0.01	-0.09	-0.13	-0.27
	May	-0.13	-0.44	-0.14	-0.05
	Jun	-0.12	-0.35	-0.15	-0.25
Precipitation	Jul	-0.01	0.37	0.26	-0.26
	Aug	0.01	0.38	0.23	-0.26
	Sep	0.17	0.19	-0.22	0.01
	Oct	0.01	-0.26	-0.16	0.55
	Nov	-0.10	-0.45	-0.23	-0.04
	Dec	-0.03	0.11	0.13	0.10
	total	0.00	-0.43	-0.42	-0.05
	TGF	-0.13	-0.11	0.21	-0.17
Temperatures	TMA	0.16	0.39	0.08	0.21
sum	TSD	0.10	0.38	0.11	0.11
	PGA	0.02	-0.26	-0.30	-0.19
Precipitation	PMA	-0.14	-0.37	-0.11	-0.18
sum	PSD	0.03	-0.30	-0.34	0.22
	POctMar	-0.02	-0.23	-0.28	-0.26

Table 7. Significant (p<0.05) correlations (r) of vessel diameter in the site of **Capocaccia** with monthly and seasonal mean temperature and precipitation sum.

		Q. ilex	A. unedo	P. lentiscus	P. angustifolia	C. monspeliensis
	Jan	0.16	0.00	0.24	-0.01	-0.15
	Feb	0.05	-0.25	0.22	0.04	-0.20
	Mar	0.16	-0.13	0.21	0.09	0.17
	Apr	0.08	-0.14	0.07	-0.36	-0.12
	May	0.26	0.28	-0.06	-0.44	0.19
Temperature	Jun	-0.08	0.12	-0.26	-0.60	-0.30
remperature	Jul	-0.18	0.10	-0.33	-0.53	-0.21
	Aug	0.29	0.28	0.03	-0.14	0.34
	Sep	0.19	0.32	-0.18	-0.55	0.18
	Oct	-0.20	-0.03	-0.19	-0.39	-0.56 *
	Nov	-0.06	0.19	-0.29	-0.59	-0.15
	Dec	-0.06	0.17	-0.32	-0.70 *	-0.11
	Jan	0.06	0.18	0.01	0.43	0.45
	Feb	0.00	-0.16	0.02	-0.24	-0.04
	Mar	-0.07	-0.13	0.23	0.72 *	-0.18
	Apr	0.37	0.27	0.01	-0.26	0.67 *
	May	-0.14	-0.25	0.26	0.83 *	-0.11
	Jun	0.08	0.11	0.02	0.37	0.54 *
Precipitation	Jul	0.00	0.00	0.00	0.00	0.00
	Aug	-0.12	-0.15	-0.11	-0.44	-0.25
	Sep	0.10	0.29	-0.18	-0.38	0.10
	Oct	0.02	-0.14	0.29	0.78 *	0.15
	Nov	-0.09	-0.10	0.16	0.77 *	0.16
	Dec	-0.08	-0.12	0.23	0.77 *	-0.13
	total	-0.03	-0.07	0.21	0.80 *	0.12
T	TGF	0.12	-0.19	0.20	-0.08	-0.14
Temperatures	TMA	0.09	0.27	-0.23	-0.60	0.02
sum	TSD	-0.07	0.16	-0.28	-0.61	-0.22
	PGA	0.11	0.04	0.21	0.67 *	0.34
Precipitation	PMA	-0.11	-0.21	0.21	0.77 *	0.04
sum	PSD	-0.06	-0.06	0.19	0.78 *	0.05
	POctMar	0.03	0.21	-0.05	0.32	0.43

5. Discussion

5.1. Dendrochronology

In regards to the different climatic variables, the main element that unites all species is the increased importance of precipitation compared to the temperatures towards ring width, in accordance with what has been reported for other species in other studies (Cherubini, 2003). In particular, abundance of rain in the period of growing season does not seem to exert a direct influence on the activity of exchange. Indeed, it is the period in which they are concentrated most of the annual precipitation, which are those of fundamental importance for the reconstruction of the water table after the period of summer drought it is the main water resource for the growth. However, unlike the results obtained for the Q. ilex the age of the plant in A. unedo seems to have an important role in modulating the response to different parameters incremental monthly.

C. monspeliensis shows particular characteristics than the others, as its annual growth seems to be determined by the abundance of rainfall in January-February and November-December. This difference is probably due to the different ability of plants of different ages to use groundwater resources (He et al, 2005). These are easily explored from the deeper root systems of the trees mature, depending on two factors: 1) the low water retention capacity of the soil, due to the almost complete lack of structure and sandy texture, involves a rapid drainage rainwater to greater depths, 2) the presence of a long taproot that pressed to absorb the water from deeper layers.

So the younger plants whose underground system has not yet reached its maximum development in depth, can take advantage of the sun mainly water resources made available by the rains of the months closer to or coincident with the beginning of the vegetative, showing indifferent the most abundant rain fall. More difficult to interpret is

the lack of a relationship with the autumn rain, obtained for *Q ilex* species. Some literature

data (Battipaglia et al., 2010) show opposite results globally, indicating a positive

influence of the rains in September, subject mainly to the characteristics of the substrate or

other microstational variables.

In particular (Battipaglia et al., 2010) refers to the importance of these precipitation in the

formation of wood. In the examined case is possible, however, that in dependence of non-

defined specific stational situations, the first rains in September after the summer

vegetative interruption can reactivate metabolic processes that involve an expenditure of

reserve substances, but failed to result in a further increase ring already formed, thus

reducing the potential for growth in the next season. On the other hand, the presence of

false rings, usually indicators of growth processes polycyclic, was entirely negligible in the

analyzed material.

The positive influence of high temperatures in April was not observed in any of the studies

of species of the Mediterranean. His action, however, concerns only the older plants,

moreover, are not exposed in this time of year to water supply problems. This could be

interpreted in terms of anticipation of phenological processes associated with the start

cambial activity, resulting in a lengthening of the phase of active growth and then a thicker

ring annually. Even the absent relationship between the growth of the plants and the

temperature of June is unsatisfactory in the site of Sette Fratelli and Piscinas, especially in

reference to the fact that a response of positive sign would have been more consistent with

the characteristics of the species and the environment.

84

Dr. Matteo Cabras – Titolo: Ecological implications of wood anatomy, ring growth and shoot allometry of Mediterranean maquis species.

The correlation of Q. ilex site Piscinas with the temperatures of November and with the

temperature seasonally of September-December was seen as a positive response of plant

growth to a mild winter.

P. angustifolia, especially sensitive to frost, show a good radial growth throughout the

growing season in the absence of very low temperatures and long periods of freezing

during the winter season. The site of Ala dei Sardi has a low average minimum

temperatures from December to March: the periods of winter frost could cause stress that

would lead to a decrease in strength and potential growth of the tree, and mortality is a de

root system end. The correlation of February following the direct with temperatures in

March: the period before the resumption of cambial activity. In this period P. angustifolia

prepare the hatching of the buds and fruit production, which at the end of April are ripe and

ready for dissemination. In this sense, the correlations of the species associated with these

months may be due to microclimatic conditions and phenological both.

A. unedo during the growing season the species reveals a direct relationship with rainfall in

March in the sites of Capocaccia and Piscinas (dry sites), period in which needed for water

intake during the active life. The month of May sees the return of the species in full swing.

The availability of water in this part of the growing season as well as stimulate the activity

of the exchange, ensuring a good cell turgor and the synthesis of proteins, processes that

have a positive effect on growth rings. The same applies to the leaf area which makes it

grow by increasing the amount of photosintetate products and for further growth. For the

month of April are also positive correlations with temperatures of spring are generally

attributable to the ecology of the species are becoming more meaning when read to match

the amount reported for the rain: in the presence of high temperatures, the rate of

vegetative plant system requires an adequate water supply.

5.2. Wood anatomy

Correlation analysis showed that precipitation has been a more important factor affecting

vessel formation than precipitation. Current year winter monthly mean precipitation had

the most important role in vessel formation showing the highest correlation coefficients

and occurring in Alà dei Sardi for *Q. ilex* and Capocaccia site for *P. angustifolia*.

Q. ilex has shown significant correlations only in the site of Alà dei Sardi and no

significant correlation in the other three sites suggests that other endogenous or exogenous

factors can influence the formation of the vessel. Arbutus unedo also has a significant

correlation only site in the site Piscinas in regard to precipitation. The only significant

correlation for *P. angustifolia* is found on the site.

C. monspeliensis correlation with previous year mean precipitation in Ala dei Sardi site

might be explained by nutrient reserve formation for next season Affecting vessel

formations.

Species in this study did not have extremely sensitive to climatic factors especially in the

growing season. Precipitation, with respect to temperature, appear to play a more important

role. The greater climatic response is more evident in for Q. ilex in the site of Alà dei Sardi

and for *P. angustifolia* in the site of Capocaccia.

The fact that for the other species not significant correlations have been found with the

values of temperature and precipitation suggests that other endogenous or exogenous

factors can influence the formation of the vessel. This type of research should therefore be

investigated. You might as well get a larger database on which to identify possible

response patterns that go beyond the inevitable differences due to individual peculiarities

of the subjects analyzed.

6. Conclusions

The analysis of the woody growths according to a dendrochronological approach in Mediterranean scrubs has shown that the cambial activity is sensitive to climatic factors

(temperature and precipitation).

The growth of the wood showed a general decreasing trend in the time and a significant

irregularities linked to interannual variations in climate. The series of annular growth of the

wood have been strongly influenced by precipitation.

Precipitations had only a delayed effect in the time on the growth of wood for the area of

Piscinas and Capocaccia, characterized by low water retention of soils (sandy soils at the

site of Piscinas and limestone at the site of Capocaccia) while the area of Ala dei Sardi and

the area of Sette Fratelli with a silicate soils had an effect in the short term.

In the latter case, precipitations has influenced the cambial activity in the months from

May until September. Precipitation has assumed a positive influence on the cambial

activity and the summer drought becomes the limiting factor, as it shown the high and

negative correlation in the months of May and June (Sette Fratelli site).

Even the temperatures have affected the cambial activity. In particular, in the site of

Piscinas temperatures relatively higher during the cooler months of the summer (June and

September) were the only climatic variables for the period of vegetative activity.

For the site of Alà dei Sardi, the temperatures lowest combined with precipitation of

greater magnitude during the period of vegetative activity have had a greater influence on

the cambial activity.

As regards wood anatomy our results suggests that among the studied species, there are not

substantial differences on regards to periods of drought. It remains unclear whether the

Mediterranean species can take an advantage of its conduction system. Although the

number of cell number and tree-ring width clearly reduced, species of dry sites showed deviant responses in cell size from that described in the wettest sites (Sette Fratelli and Ala dei Sardi). This highlights that the process of formation of the wood to the site is not understood in detail, yet. Further investigations should focus on wood anatomical studies using, for example, the pinning method, which allows accurate analysis of the climate/cell ratios growth with high temporal resolution. In addition, controlled irrigation experiments allow a verification of the current theory about the influence of drought on cell division and differentiation.

7. Reference

Acherar M, Rambal S., 1992. Comparative water relations of four Mediterranean oak species. Vegetatio, 99–100, 177–184.

Aronne G., De Micco V. 2001. Seasonal dimorphism in the Mediterranean *Cistus incanus* L. subsp. incanus. Annals of Botany 87: 789-794.

Aschmann H., 1973. Distribution and peculiarity of mediterranean ecosystems. In: Di Castri F., Mooney H.A. (eds.); Mediterranean type ecosystems - origin and structure: 11-19. Springer-Verlag, Berlin.

Battipaglia G., De Micco V., Brand W.A., Linke P, Aronne G., Saurer M. and Cherubini P 2010. Variations of vessel diameter and d13C in false rings of *Arbutus unedo* L. reflect different environmental conditions. New Phytologist - 188: 1099–1112.

Bernetti G., 1997. La vegetazione forestale del bacino del Mediterraneo e le altre vegetazioni di tipo Mediterraneo. Italia Forestale e Montana LII (6): 469-471.

Blondel, J., and Aronson, J., 1999. Biology and Wildlife of the Mediterranean Region, Oxford University Press, Oxford.

Boyer, J.S., 1982. Plant productivity and environment. Science 218, 443–448.

Camarda I., 2004 - La macchia mediterranea come ecosistema forestale complesso. Italus Hortus, 11(4): 8-15.

Castro-Diez P, Villar-Salvador P, Perez-Rontome C, Maestro-Martinez M, Montserrat-Martì G., 1997 Leaf morphology and leaf chemical composition in three *Quercus* (Fagaceae) species along a rainfall gradient in NE Spain. Trees 11:127-134.

Chaves M.M., Pereira J.S., Maroco J., Rodrigues M.L., Ricardo C.P.P., Osòrio M.L., Carvalho I., Faria T., Pinheiro C., 2002. How Plants Cope with Water Stress in the Field? Photosynthesis and Growth Annals of Botany. 89: 7. pp 907-916.

Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., and Innes, J.L., 2003. Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. Biol. Rev. Camb. Philos. Soc. **78**(1): 119–148. doi:10. 1017/S1464793102006000. PMID:12620063.

Cook, E. & Briffa, K., 1990. Data analysis. In: Methods of Dendrochronology. Applications in the Environmental Sciences (Eds. E.R. Cook and L.A. Kairiukstis). Kluwer, Dordrecht, pp 97- 162.

Clemente A.S, Rego F.C., Correia O.A., 1996. Demographic Patterns and Productivity of Post-Fire Regeneration in Portuguese Mediterranean Maquis International Journal of Wildland Fire 6(1) 5 – 12.

Cornelissen J.H.C., Lavorel S., Garnier E., Diaz S., Buchmann N., Gurvich D.E., Reich P.B., Ter Steege H., Morgan H.D., Van Der Heijden M.G.A., Pausas J.G. Poorter H., 2003 A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Juornal of Botany 51, 335-338. CSIRO Publishing.

Correia O.A., Catarino F.M., 1994. Seasonal changes in soil-to-leaf resistance in *Cistus* sp. and *Pistacia lentiscus*. Acta Oecol., 15 1994, pp. 289–300.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.T.K & Arianoutsou, M., 1996. Plant diversity in Mediterranean-climate regions. Trends in Ecology and Evolution 11: 362-366.

Damesin C., Rambal S., 1995. Field study of leaf photosynthetic performance by a Mediterranean deciduous oak tree (*Quercus pubescens*) during a severe summer drought. NewPhytol 131: 159–167.

Di Castri F, Mooney H.A., 1973. Mediterranean-type ecosistems: Origin and structure. Ecological Studies, vol. 7, Springer-Verlag, New York, NY, pp. 405.

Di Castri F., Goodall D.W., Specht R.L. 1981. (Eds), Mediterranean-type shrublands. Ecosystems of the World 11. Elsevier, Amsterdam.

Demetzos C., Harvala C., Philianos S.M., Skaltsounis A.L., 1990. A new labdane type diterpene and other compounds from the leaves of *Cistus incanus* subsp. *Creticus* J. Nat. Prod., 53, pp. 1365–1368.

Ephrat Y., 1971. Periderm development and the annual rythm of phellogen and cambial activity in *Quercus suber* and *Quercus calliprinos*. M. Sc. Thesis, Tel-Aviv University.

Epron D., 1997. Effects of drought on photosynthesis and on the thermotolerance of photosystem II in seedlings of cedar (*Cedrus atlantica* and *C. libani*). J Exp Bot 48: 1835–1841.

Fahn A., 1962. Xylem structure and the annual rhythm of cambial activity in woody species of the East Mediterranean regions. Int. Assoc. Wood Anat. Bull. 1961/2:2-6.

Fantechi, F. & Margaris, N.S., 1986. Desertification in Europe. Dordrecht: D. Reidel Publishing Co.pp 231.

Filella I.; Llusià J.; Piñol J.; Peñuelas J., 1998. Leaf gas exchange and fluorescence of *Phillyrea latifolia*, *Pistacia lentiscus* and *Quercus ilex* samplings in severe drought and

high temperature conditions Environmental and Experimental Botany Volume: 39, Issue: 3, June 1, pp. 213-220.

Fonti P., Treydte K., Osenstetter S., Frank D., Esper J., 2009. Frequency-dependent signals in multi-centennial oak vessel data. *Palaeogeogr. Palaeocl.* 275: 92–99.

Fritts H.C., 2001. Tree Rings and Climate. Blackburn Press, Caldwell, New Jersey. 567 p.

Fritts H.C., 1976. Tree rings and climate. London: Academic Press; p. 567.

García-González I., Eckstein D., 2003. Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiol.* 23: 497–504.

Gonzalez IG., Eckstein D., 2003. Climatic signal of earlywood vessels of oak on a maritime site. Tree Physiology; 23: 497–504.

Gratani L., Bombelli A., 1999. Leaf anatomy, inclination, and gas exchange relationships in evergreen sclerophyllous and drought semideciduous shrub species. Photosynthetica 37: 573-585.

Gratani L., Pesoli P., Crescente M.F., Aichner K., Larcher W., 2000. Photosynthesis as a temperature indicator in *Quercus ilex L*. Global Planet Change 24: 153–163.

Gucci R., Lombardini L., Tattini M., 1997. Analysis of leaf water relations in two olive (Olea europea) cultivars differing in tolernce to salinity. – Tree Physiol. 17:31-21.

Hacke U.G., Sperry J.S., Pockman WT, Davis S.D., McCulloh K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457–461.

Università di Sassari

Hacke U.G., Sperry J.S., Wheeler J.K., Castro L., 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiology 26: 689–701.

Harley P.C., Tenhunen J.D., Beyschlag W., Lange O.L., 1987. Seasonal changes in net photosynthesis rates and photosynthetic capacity in leaves of *Cistus salvifolius*, a European Mediterranean semideciduous shrubs. Oecologia 74: 380–388.

He J.S., Zhang Q.B., Bazzaz F.A., 2005. Differential drought responses between samplings and adult trees in four co-occurring species of New England. Trees, 19: 442-450.

Hinkley T.M., Duhme F., Hinkley A.R., Richter H., 1980. Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity Botanisches Institut, Universitat für Bodenkultur, Vienna, Austria Plant, Cell and Environment {1980} 3, 131-140.

Hsiao T.C., 1973. Plant responses to water stress. Ann. Rev. Plant Physiol., 24: 519-570.

Houghton J.T., Meira Filho L.G., Callander B.A., Harris N., Kattenberg A. and Maskell K., 1996. (Eds.) *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, Cambridge, UK.

IPCC, 2001. Climate Change 2001: the Scientific Basis. Third Assessment Report of Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Jacobsen A.L., Pratt R.B., Davis S.D., Ewers F.W., 2008. Comparative community physiology: nonconvergence in water relations among three semi-arid shrub communities. New Phytologist 180: 100–113.

Kuzucuoglu C., 1989. Fire in the Mediterranean region. Blue Plan. Ecology, 72: 371-412.

Ladjal M., Epron D., Ducrey M., 2000. Effects of drought preconditioning on

thermotolerance of photosystem II and susceptibility of photosynthesis to heat stress in

cedar seedlings. Tree Physiol 20: 1235–1241.

Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: a

search for physiological causes and ecological consequences. Advances in Ecological

Research 23, 187 - 126.

Larcher W (2000) Temperature stress and survival ability of Mediterranean sclerophyllous

plants. Plant Biosystems 134: 279–295.

Liphschitz N, Lev-Uadum S., 1986. Cambial activity of evergreen and seasonal dimorphics

around the Mediterranean. Int. Assoc. Wood Anat. Bull. 7: 145-153.

Llorens L., Penuelas J., Filella I., 2003b. Diurnal and seasonal variations in the

photosynthetic performance and water relations of two co-occurring Mediterranean shrubs,

Erica multiflora and Globularia alypum. Physiol Plant 118: 84–95.

López B., Albaladejo J., 1990F. Factores ambientales de la degradación del suelo en el

área mediterránea. J. Albadalejo, M.A. Stocking, E. Díaz (Eds.), Degradación y

Regeneración del Suelo en Condiciones Ambientales Mediterraneas, CSIC, Murcia, pp.

13–45.

Maherali H., Pockman W.T., Jackson R.B., 2004. Adaptive variation in the vulnerability of

woody plants to xylem cavitation. Ecology 85: 2184–2199.

Meeus, J., Wijermans, M.P., and Vroom, M. J., 1990. Agricultural landscapes in Europe

and their transformation. Landscape and Urban Planning 18: 289–352.

Mencuccini M., Grace J., 1993. Climate influences the leaf area/sapwood area ratio in

Scots pine. Tree Physiology 15, 1-10.

Mulas M., Abeltino P., Brigaglia N., 1998. Evaluation of *Pistacia lentiscus* L. genetic

resources to select ecotypes having high efficiency in the colonization of marginal lands.

ISHS Acta Horticulturae 457: Symposium on Plant Biotechnology as a tool for the

Exploitation of Mountain Lands. Acta Hort. 457, ISHS.

Mulas M., Deidda P., 1998. Domestication of woody plants from mediterranenan maquis

to promote new crops for mountain lands. ISHS Acta Horticulturae 457: Symposium on

Plant Biotechnology as a tool for the Exploitation of Mountain Lands. Acta Hort. 457,

ISHS.

Naveh Z., 1990. Fire in the Mediterranean: a landscape perspective. In: J.G. Goldhammer

and M.J. Jenkins (Editors), Fire in Ecosystem Dynamics. SPB Academic Publishing. The

Hague, pp. 401-434.

Naveh, Z., Dan. J., 1973. The human degradation of Mediterranean landscapes in Israel.

Mediterranean Type Ecosystems. Eds. F. di Castri and H. A. Mooney~ Ecological Studies

7: 373-390. Springer, Heidelberg.

Naveh Z., 1995. Conservation, restoration and research priorities for mediterranean

uplands threatened by global climate change. In: Global change and mediterranean-type

ecosystems (Moreno M.J. e Oechel W., eds). Ecological Studies 117, Springer, New York.

pag. 482-507.

Pereira J.S., Chaves M.M., 1995. Plant responses to drought under climate change in

Mediterranean-type ecosystems J.M. Moreno, W.C. Oechel (Eds.), Global Change and

Mediterranean-type Ecosystems, Ecology Studies, vol. 117Springer-Verlag, Berlin (1995), pp. 140–160.

Perez-Trejo F., 1992. Desertification and land degradation in the European Mediterranean.

Report EUR 14850 EN. Brussels: European Commission, DG Science, Research and Development. 63 pp.

Pinol J., Terradas J., Lloret F., 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastaleastern Spain. Climatic Change 38, 345–357.

Rambal S., 1992. The differential role of mechanisms for drought resistance in a Mediterranean evergreen shrub: a simulation approach. Plant, Cell and Environment, 16, 35–44.

Rundel P.W., 1998. Landscape disturbance in Mediterranean-type ecosystems: an overview. In: P.W. Rundel, G. Montenegro and F. Jaksic (Editors), *Lanscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems*. Springer-Verlag. Berlin, pp. 3-22.

Rust S., Solger A., Roloff A., 2004. Bottlenecks to water transport in *Quercus robur* L.: the abscission zone and its physiological consequences. *Basic Appl. Ecol.* 5: 293–299.

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140: 543–550.

Schweingruber F.H., 1973. Der Jahrring; Methodik, Zeit und Klima in der Dendrochronologie. Bern: Haupt; 1983. p. 234.

Schweingruber, F.H., 1988. Tree Rings. Basics and Applications in Dendrochronology. Reidel, Dortrecht, The Netherlands.

Schweingruber, F.H., 1996. Tree Rings and Environment. Dendroecology. Paul Haupt, Berne, Switzerland.

Schweingruber F.H., 2007. Wood Structure and Environment. Springer, Berlin. 279 p.

Sperry J.S., Hacke U.G., Pittermann J., 2006. Size and function in conifer tracheids and angiosperm vessels. American Journal of Botany 83: 1490–1500.

Steppe K., Lemeur R., 2007. Effect of ring-porous and diffuse-porous stem wood anatomy on the hydraulic parameters used in a water and storage model. *Tree Physiol*. 27: 43–52.

Tenhunen J.D., Sala A, Harley P.C., Dougherty R.L., Reynolds J.F., 1990. Factors influencing carbon fixation and water use by Mediterranean sclerophyll shrubs during summer drought. Oecologia 82: 381–393.

Thomas F.M., Bartels C., Gieger T., 2006. Alterations in vessel size in twigs of *Quercus robur* and *Quercus petraea* upon defoliation and consequences for water transport under drought. *IAWA J.* 27: 395–407.

Tyree M.T, Zimmermann M.H., 2002. Xylem structure and the ascent of sap. Berlin, Heidelberg, New York: Springer. p. 283.

Tomaselli R., 1997. The Degradation of the Mediterranean Maquis: Ambio, Vol. 6, No. 6, The Mediterranean: A Special Issue. pp. 356-362.

Trabaud L., Prodon R., 1993. Fire in Mediterranean Ecosystems. Commission of European Communities, Brussels, 441 pp.

Valladares F., Pearcy R.W., 1997. Interactions between water stress, sun-shade

acclimation, heat tolerance and photoinhibition in the sclerophyll Heteromeles arbutifolia.

Plant Cell Environ 20: 25-36.

Vaganov E.A., 1990. The tracheidogramm method in tree-ring analysis and its application.

In: Cook ER, Kairiukstis LA, editors. Methods of dendrochronology. Applications in the

environmental sciences. Dordrecht, Boston, London: Kluwer Academic Publishers. p. 63-

76.

Werner C., Correia O.A., Beyschlag W., 1999. Two different strategies of Mediterranean

maquis plants to avoid photoinhibitory damage by excessive radiation levels during

summer drought. Acta Oecol., 20, pp. 15-23.

Whitehead D., Edwards W.R.N., Jarvis P.G., 1984. Conducting sapwood area, foliage area

and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. Canadian Journal

of Forest Research 14, 940-947.

Wimmer R., 2002. Wood anatomical features in tree-rings as indicators of environmental

change. Dendrochronologia 20: 21–36.

Woodcock D.W., 1989. Climate sensitivity of wood-anatomical features in a ring-porous

oak (*Quercus macrocarpa*). Canadian Journal of Forest Research; 19:639–44.

Woodward F.I., 1983. The significance of interspecific differences in specific leaf area to

the growth of selected herbaceous species from different altitudes. New Phytol 95:313-

323.

8. Appendix

Table I. Significant (p<0.05) correlations (r) of ring width of *Quercus ilex* with monthly and seasonal mean temperature and precipitation sum.

		Alà dei Sardi	Sette Fratelli	Capocaccia	Piscinas
	Jan				
	Feb				
	Mar				
	Apr				0.58
	May			0.41	
Temperatures	Jun				
Temperatures	Jul				0.41
	Aug				
	Sep				
	Oct				
	Nov				0.31
	Dec	0.57			
	Jan				
	Feb				
	Mar				
	Apr				
	May				
Precipitation sum	Jun	0.42			
1 recipitation sum	Jul	0.51			
	Aug				
	Sep				
	Oct				
	Nov	0.45			
	Dec	0.51			
	TGA				
Temperatures sum	TMA				
	TSD				0.31
	total	0.54			
	PGA				
Precipitation sum	PMA				
	PSD	0.52			
	POTMAR			0.36	

Table II. Significant (p<0.05) correlations (r) of ring width of *Arbutus unedo* with monthly and seasonal mean temperature and precipitation sum.

		Alà dei Sardi	Sette Fratelli	Capocaccia	Piscinas
	Jan				
	Feb				
	Mar				
	Apr			0.22	
	May				
Temperatures	Jun				
Temperatures	Jul				
	Aug				
	Sep				
	Oct				0.35
	Nov				
	Dec				
	Jan				
	Feb				
	Mar			0.23	0.33
	Apr				
	May			0.22	
Precipitation sum	Jun				
1 Tecipitation sain	Jul				
	Aug				
	Sep				
	Oct				
	Nov			0.33	
	Dec			0.27	
	TGA				
Temperatures sum	TMA				
	TSD				
	total			0.34	
	PGA				
Precipitation sum	PMA			0.25	
	PSD			0.35	
	POTMAR			0.49	

Table III. Significant (p<0.05) correlations (r) of ring width of *Pistacia lentiscus* with monthly and seasonal mean temperature and precipitation sum.

		Alà dei Sardi	Capocaccia	Piscinas
	Jan			
	Feb			-0.28
	Mar			
	Apr			
	May			0.28
Temperatures	Jun		-0.41	
Temperatures	Jul			
	Aug			0.27
	Sep	-0.44		
	Oct			
	Nov			
	Dec			
	Jan			
	Feb			
	Mar			
	Apr			
	May			-0.31
Precipitation sum	Jun		0.35	
	Jul	0.50	0.34	
	Aug			
	Sep			
	Oct			
	Nov			
	Dec			0.38
	TGA			
Temperatures sum	TMA			0.32
	TSD			
	total			
	PGA			
Precipitation sum	PMA		0.35	
	PSD			
	POTMAR		0.30	

Table IV. Significant (p<0.05) correlations (r) of ring width of *Phillyrea angustifolia* with monthly and seasonal mean temperature and precipitation sum.

		Alà dei Sardi	Sette Fratelli	Capocaccia	Piscinas
	Jan				
	Feb				
	Mar				
	Apr		-0.32		
	May		-0.34		
Temperatures	Jun		-0.41		
Temperatures	Jul				
	Aug				-0.23
	Sep				
	Oct				
	Nov				
	Dec				
	Jan		0.29		
	Feb				
	Mar				
	Apr				
	May		0.32		
Precipitation sum	Jun				
1 recipitation sam	Jul			0.26	
	Aug				
	Sep				
	Oct				
	Nov				
	Dec				
	TGA				
Temperatures sum	TMA				
	TSD				
	total				
	PGA				
Precipitation sum	PMA				
	PSD				
	POTMAR	0.23			

Table V. Significant (p<0.05) correlations (r) of ring width of *Cistus monspeliensis* with monthly and seasonal mean temperature and precipitation sum.

		Alà dei Sardi	Sette Fratelli	Capocaccia	Piscinas
	Jan				
	Feb		0.52		
	Mar				
	Apr	-0.66			
	May				
Tomporoturas	Jun				
Temperatures	Jul	0.75			
	Aug				
	Sep				
	Oct	-0.86	-0.65	-0.62	
	Nov	-0.56			
	Dec	0.79			
	Jan	0.90	0.70		
	Feb	0.91			
	Mar				-0.57
	Apr				
	May		0.50		
Precipitation sum	Jun			0.68	
1 recipitation sum	Jul	0.63			
	Aug				
	Sep				-0.54
	Oct	0.76			
	Nov	0.66			
	Dec	0.78			-0.54
	TGA	-0.70			
Temperatures sum	TMA				
	TSD	0.61			
	total	0.82	0.56		
	PGA	0.91	0.55		-0.58
Precipitation sum	PMA				
	PSD	0.84			
	POTMAR	0.66			