

Identification, measurement and interpretation of tree rings in woody species from mediterranean climates

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ABSTRACT

We review the literature dealing with mediterranean climate, vegetation, phenology and ecophysiology relevant to the understanding of tree-ring formation in mediterranean regions. Tree rings have been used extensively in temperate regions to reconstruct responses of forests to past environmental changes. In mediterranean regions, studies of tree rings are scarce, despite their potential for understanding and predicting the effects of global change on important ecological processes such as desertification. In mediterranean regions, due to the great spatio-temporal variability of mediterranean environmental conditions, tree rings are sometimes not formed. Often, clear seasonality is lacking, and vegetation activity is not always associated with regular dormancy periods. We present examples of tree-ring morphology of five species (*Arbutus unedo*, *Fraxinus ornus*, *Quercus cerris*, *Q. ilex*, *Q. pubescens*) sampled in Tuscany, Italy, focusing on the difficulties we encountered during the dating. We present an interpretation of anomalies found in the wood structure and, more generally, of cambial activity in such environments. Furthermore, we propose a classification of tree-ring formation in mediterranean environments. Mediterranean tree rings can be dated and used for dendrochronological purposes, but great care should be taken in selecting sampling sites, species and sample trees.

Key words: mediterranean tree rings, mediterranean climate, mediterranean vegetation, phenology, ecophysiology, wood anatomy, dendrochronology, dendroecology, *Arbutus unedo*, *Fraxinus ornus*, *Quercus cerris*, *Quercus ilex*, *Quercus pubescens*.

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I. INTRODUCTION

In a changing environment, the analysis of how forest ecosystems may react under scenarios involving changing climatic conditions is of major importance (Bazzaz, 1996). A prerequisite for such analyses is the knowledge of how forests have reacted to past climatic and anthropogenic events and trends. Proxies, such as tree rings, enable the responses of forests to environmental changes to be reconstructed for many regions. In temperate climates, cambial activity of trees and shrubs stops during the cold season, and annual tree rings, which can be used to reconstruct the climatic characteristics of the growing season, are formed (Fritts, 1976; Schweingruber, 1988, 1996). For the Mediterranean region and mediterranean (Mediterranean-type) ecosystems in general, information about past environmental conditions is scarce (Bonatti, 1966; Beug, 1977; Meiggs, 1982; Suc, 1984; Cubasch *et al.*, 1996). Such information would be very useful for understanding the effects of global change on important ecological processes such as desertification (Spaulding, 1991; Chbouki, Stockton & Myers, 1995; Meko, Stockton & Boggess, 1995; Le Houérou, 1996; Touchan & Hughes, 1999; Touchan, Meko & Hughes, 1999; Grove & Rackham, 2001). The typical mediterranean climate at low elevations is characterized by temperature and precipitation regimes that are very different from temperate climates. Vegetative activity does not always and everywhere have a regular dormancy period, so that annual tree rings are not always formed. In this respect, it is probably best to consider the summer quiescent period as a period of 'drought-

imposed rest' (Borchert, 1991, 1994) rather than true dormancy.

In the humid tropics, where climate is only slightly seasonal, trees mostly fail to form wood with distinct yearly growth layers (e.g. Sass, Killmann & Eckstein, 1995). The lack of seasonality in the tropics has long been documented and the occurrence in many species of indistinct rings or rings that are not annual is a major reason that tropical regions have been neglected in dendrochronology. Recently, however, the understanding of cambial activity in the tropics has improved (Eckstein *et al.*, 1981; Boninsegna *et al.*, 1989; Jacoby, 1989; Worbes, 1995; Vetter & Wimmer, 1999). For example, annual tree rings have been detected in *Tectona grandis* L. in northern Thailand (Pumijumng, Eckstein & Sass, 1995), and interest in tropical tree rings has consequently increased, particularly in areas with marked seasonality. When analysing tree rings in regions with unclear seasonality, such as in areas with mediterranean climates, dendroecological and wood anatomical studies in tropical regions may provide useful methodological examples (Devall, Parresol & Wright, 1995; Gourlay, 1995*a, b*; Belingard *et al.*, 1996; Gillespie, Sym & Rogers, 1998; Martínez-Ramos & Alvarez-Buylla, 1998; Pumijumng *et al.*, 1998; Bhattacharyya & Yadav, 1999; Eshete & Ståhl, 1999; Stahle, 1999; Worbes, 1999; Worbes & Junk, 1999; Callado *et al.*, 2001; Ogata *et al.*, 2001).

The presence of annual rings has long been reported in coastal mediterranean trees. Early reports came from Israel for *Pinus halepensis* Mill. (Oppenheimer, 1945) and maquis trees (Fahn, 1953), and from Italy for *P. halepensis* (Messerli, 1948,

1953) and *Pinus pinea* L. (Buli, 1949) [see Corona (1983) and Serre-Bachet (1985) for previous reviews of Mediterranean dendrochronological studies]. The presence of annual tree rings has also been detected in shrubs, e.g. in *Arctostaphylos* spp., *Ceanothus* spp. and *Heteromeles arbutifolia* (Lindl.) M. J. Roem from southern California (Keeley, 1993), and in *Cistus ladanifer* L. from Extremadura in the Iberian Peninsula, Spain (Patón *et al.*, 1993; Patón, Azocar & Tovar, 1998). Recently, the annual nature of phellogen activity (cork-ring formation) has been documented in *Quercus suber* L. from natural stands of southwestern Spain (Caritat, Molinas & Gutierrez, 1996), and cork-ring width has been related to climate (Caritat, Gutiérrez & Molinas, 2000). Mediterranean tree rings in wood and charcoal found in archaeological sites have been used to date archaeological remains (Serre-Bachet, 1982; Liphshitz & Biger, 1988) and ships (Guibal, 1996), and to reconstruct climate (Mariolopoulos, 1962) and historical events such as volcanic eruptions (Kuniholm *et al.*, 1996). Nevertheless, when dating tree rings in mediterranean regions, difficulties caused by the lack of seasonality have often been reported (Serre-Bachet, 1985; Liphshitz & Lev-Yadun, 1986; Zhang & Romane, 1991; Bellot *et al.*, 1992; Keeley, 1993; Panaïotis, Carcaillet & M'Hamedi, 1997; Enright & Goldblum, 1998; Rigg, Enright & Jaffré, 1998). Tree rings are often indistinct [see Schweingruber (1993) for a description of those few species that have been used in dendrochronology and that do not present difficulties] and, as a result, the practical application of dendrochronological methods in mediterranean regions is lacking.

II. AIMS

Our purpose is to demonstrate, on the basis of the available literature in different related fields, that tree rings in mediterranean environments can be used as a tool for dendroclimatic and dendroecological applied research. This review gives an overview of studies that may provide answers to some of the existing uncertainties. The difficulties in dating tree rings are induced by the wood-anatomical, physiological and phenological responses of trees to mediterranean climatic conditions. It is therefore useful to analyse the characteristics of climate, vegetation, phenology and ecophysiology in mediterranean environments.

After the overview, we present examples of tree

ring analyses in a mediterranean region. We first describe the ring definition of five mediterranean tree species (three broad-leaved deciduous, one sclerophyllous evergreen, one laurophyllous evergreen) at one site (same climatic conditions and same site characteristics, but different species-specific ecophysiological adaptations and phenological behaviour). We then examine the same species at two contrasting sites to assess whether they form annual tree rings and if they are therefore suitable for tree-ring studies. Finally, we build ring-width chronologies for each species and detect, describe and explain anomalies in their wood structure, such as indistinct ring boundaries and intra-annual rings (so-called false rings or double rings).

III. MEDITERRANEAN CLIMATIC CONDITIONS

The Mediterranean area is very sensitive to the climatic variations of Europe, North Africa and Asia. The Mediterranean climate consists of a temperate climate characterized by sunny, hot and dry summers, dependent on the seasonal shift of the desert regime, and by cool winters, with a pronounced rainfall maximum (in most areas) that is the result of the displacement of northerly cyclonal activity (Köppen, 1923; Walter & Lieth, 1960). This climatic regime depends on the existence of cold ocean currents (Canary Current) (Bagnouls & Gausson, 1957; Daget, 1977). Meteorological conditions during summer in the Mediterranean area are dominated by two large, semi-permanent weather systems: to the west, the Azores anticyclone; to the east, a low pressure system that extends from the Middle East to southwestern Asia, i.e. the monsoon system (Meteorological Office, 1962).

In the majority of areas, water is abundant in the cool winter, but during the rainless summer it becomes a limiting resource for most organisms. Annual precipitation maxima occur in winter, or autumn and winter, over much of the Mediterranean, but some areas, such as the east coast of Spain, southern France and most of Italy have autumn maxima (Huttary, 1950). Away from the coast, and in, for example, central southern Turkey, rainfall maxima may occur in winter and spring (Huttary, 1950). Further inland, for example in the Atlas Mountains and central Turkey, the rainfall maximum occurs in the spring.

Despite these variations, summer drought is the most important ecological factor influencing vegetation in mediterranean ecosystems, although win-

ter cold may also play a role (e.g. Trumble, 1939; Specht, 1981). The duration of the dry season and the amount of summer rainfall are thus of major importance for the differentiation between mediterranean and non-mediterranean regions, and for the identification of transitional areas. Depending on latitude and temporal annual variability, summer drought may be intermittent, or may persist for up to 5 months (Walter & Lieth, 1960). Leaf temperature may reach 50 °C in summer and drop to below freezing in winter. A secondary consequence of the dry conditions is that nutrient availability is low (di Castri, Goodall & Specht, 1981).

Mediterranean climates grade into dry climates to the south and into cool, humid climates to the north. Mediterranean lands are therefore transitional zones with indistinct borders that may vary from year to year between moist and arid ecosystems, and between temperate and tropical regions. Given that mediterranean-type climates progressively intergrade with mesic climates to the north and hot desert climates to the south, the Mediterranean basin is not a distinct biogeographical unit (Blondel & Aronson, 1995), and a division of the Mediterranean area into subzones (e.g. Köppen, 1923; Mazzoleni, Lo Porto & Blasi, 1992) may be useful for understanding the cambial activity of trees. The mediterranean bioclimatic zone can be divided into different regions, e.g. very arid, arid, semi-arid, subhumid, humid and superhumid, some variants of which are very cold and extremely cold (such as the semi-arid zones of the Anatolian Plateau) (Nahal, 1981). For a concise explanatory bioclimatic description of the Mediterranean region, see Blondel & Aronson (1999, pp. 16–25). The monthly rainfall patterns play a key role in determining the tree-ring structure, but the temperature conditions of the dry season also play an important role.

The types of vegetation and of tree-ring formation found at a particular site reflect the climatic conditions there as well as their biogeographical and evolutionary histories. Given the high variability of climatic conditions within the mediterranean area, a great variability in cambial activity (and in tree rings) within this region should be expected.

IV. MEDITERRANEAN VEGETATION

The typical woody vegetation in mediterranean regions is characterized by the predominance of hard-leaved evergreen shrubs and dwarf and short trees, with small, stiff, leathery and thick leaves.

These leaves, termed sclerophyllous, often show convergent anatomical modifications, including thick cuticles, well-developed palisade mesophyll cells, small stomatal pore area per unit leaf area and the enclosure of stomata within small pits or grooves (crypts). These are often partially occluded by hair or wax tubules (Margaris, 1981). The functional significance of sclerophylly commonly has been related to water conservation and to the resistance to negative turgor pressures, but the selective advantage of sclerophylly as protection against herbivore attacks seems also to play an important role (Salleo & Nardini, 2000). Each species has a mechanism to cope with water shortage that is to a great extent related to its structure as a whole and to its habit (Castro-Díez *et al.*, 1997). Many studies have described the major syndromes of growth form and physiology in mediterranean regions, not only within one region, but also the convergent patterns found in different regions and taxa (e.g. Naveh, 1967; Mooney & Dunn, 1970*a, b*; Mooney, 1982; Raven, 1973; Parsons & Moldenke, 1975). However, in some areas, such as southern and southwest Australia, scleromorphic plant forms have developed primarily as a response to nutrient limitation, rather than water stress (Beard, 1983). Besides the evergreen scrub-vegetation type, an overstorey of small trees is sometimes present, and an understorey of herbs may be present or absent. This vegetation type can assume various aspects resulting from different combinations of height (high, middle and low), cover (dense, discontinuous and scattered) and structure. Moreover, the dynamics of such ecosystems and their relations with other ecosystems (e.g. deserts) are very complex and still unclear (Tomaselli, 1981). With increasingly drier conditions, the dominant woody plants may become semi-deciduous, seasonally dimorphic, semi-succulent or succulent (Specht & Moll, 1983).

There are a variety of plant communities in mediterranean regions, ranging from high forests to annual grasslands. Scrublands are the dominant type. Of the forest and scrub types, evergreen forests are found in the wettest habitats, followed by evergreen scrub, and then subliguous scrub on the driest or most disturbed habitats. The forest types have the highest leaf area indices, the lowest root/shoot ratios and the greatest litter and total above-ground productivity (Mooney, 1981).

The typical vegetation of the Mediterranean basin and the more xeric and more human-disturbed scrub formations that occur when the typical vegetation is disturbed are called, respectively,

macchia and *gariga* in Italy, *maquis* and *garrigue* in France, *monte bajo* and *tomillares* in Spain, *choresh* and *batha* in Israel, *xerovuni* and *phrygana* in Greece, and *gatha* and *nabati* in Syria and Lebanon. Ecological analogues of such vegetation types are the mediterranean (Mediterranean-type) ecosystems that are found in different regions of the world between latitudes 40° and 30°, north and south of the equator, i.e. in California (*chaparral* and *coastal sage*), in Chile (*espinal*, *matorral* and *jaral*), in South Africa (*Afromontane forest*, *renosterveld*, *strandveld* and *fynbos*), and in southwestern and southern Australia (*kwongan*, *mallee* or *mallee open-scrub* and *heathland*) (Mooney & Dunn, 1970a; di Castri *et al.*, 1981).

Although superficially similar, there are some major differences in these mediterranean-type vegetation formations. For example, the South African fynbos and Australian kwongan are similar, but differ from other types in having not only a layer of large-leaved shrubs forming a dense canopy, but also a lower layer of ericoid shrubs and restioids. They also have many geophytes but few annuals (terophytes), very high levels of serotiny, and few shrub species that re-sprout after fire. One reason that these two types may be so different from the others is that the soils in which they grow are typically very poor in nutrients, which has been related to high vegetation flammability and a greater number of fires than in other mediterranean vegetation types (Cowling & Richardson, 1995). Soil nutrition appears to play a critical role in determining the nature of the understory in mediterranean ecosystems (Specht & Moll, 1983).

Many other differences also exist. For example, the deeper-rooted proteoids of the South African fynbos show relatively little drought stress in summer (although the shallow-rooted restioids and ericoid shrubs show summer declines in xylem pressure potential – Stock, van der Heyden & Lewis, 1992), and water availability is not considered to be a major factor determining the distribution of individual species within the fynbos. Trees are not a major feature of South African mediterranean vegetation, although they may have been more common in the past (Moll, McKenzie & McLachlan, 1980) and a number of species can attain substantial size if protected from fire, e.g. *Euclea racemosa* Murray, *Leucadendron argentea* (L.) R. Br., *Maytenus oleoides* (Lam.) Loes., *Olea europea* L. ssp. *africana* (Miller) P. S. Green, *Protea nitida* Miller, *Protea laurifolia* Thunb., *Widdringtonia cedarbergensis* Marsh and *Widdringtonia schwarzii* (Marloth) Mast.

The Californian chaparral is superficially similar

to the other mediterranean-type vegetation groups. However, it is characterized by extremely severe summer drought stress as a result of high temperatures and very low rainfall. Chaparral shrubs regularly reach xylem water potentials of –6 MPa in summer (Dunn *et al.*, 1976; Miller & Poole, 1979).

Mediterranean ecosystems have a very restricted distribution, but they are a major vegetation type in some countries. Moreover, as the intermediate stage between temperate and tropical forests, they play an important role against desertification processes (Le Houérou, 1996). Little information is available about the responses of these ecosystems to global change (Scarascia-Mugnozza *et al.*, 2000), although in such regions key roles are played by climate (Moreno & Oechel, 1995), air pollution (Bussotti & Ferretti, 1998), and land-use (Vita-Finzi, 1969; di Castri & Mooney, 1973; Mooney, 1977; Margaris & Mooney, 1981; Pons & Quézel, 1985; Scarascia-Mugnozza *et al.*, 2000; Cramer, 2001; Giovannini *et al.*, 2001; Grove & Rackham, 2001; Vilà *et al.*, 2001). For the Mediterranean basin, for example, landscapes have been largely determined by deforestation, overgrazing and recurrent fires in ancient times (Vita-Finzi, 1969; Meiggs, 1982; Le Houérou, 2000).

It is thus possible to have a range of different vegetation formations growing in mediterranean climates, including sclerophyllous forests (in more mesic habitats), coniferous forests, heathlands (in oligotrophic soil), and arid shrublands. Annual and seasonal water availability are the most important factors controlling the distribution of the different physiognomic forest types (Gavilán & Fernández-González, 1997). In higher-rainfall zones, tree growth improves and shrublands merge into evergreen woodlands and forests, whereas at the other extreme they merge into the arid shrublands (more open and scattered) bordering on the hot deserts (di Castri *et al.*, 1981). This pattern is illustrated particularly well in South Africa, where fynbos grades into renosterveld as precipitation decreases (fynbos generally requires more than 600 mm annual rainfall), with succulent karoo occurring when rainfall is less than 250 mm. Under wetter conditions (> 800 mm precipitation), the fynbos grades into afromontane forest, often with a very abrupt, fire-determined, boundary.

At the species level, a high proportion of mediterranean plants show marked intraspecific variation: many subspecies and ecotypes can be found (Blondel & Aronson, 1995). Thus, a high

variability can be expected in the tree-ring response of different species to the same climatic conditions (Tretiach, 1993; Damesin, Rambal & Joffre, 1998) or of the same species, and of different ecotypes within the same species, to different climatic conditions (Castro-Díez *et al.*, 1997). In relation to the status of soil nutrients, climatic determinants, biotic characteristics and fire susceptibility, the vegetation of the Mediterranean region appears to lie between that of South Africa–Australia and Chile–California (di Castri, 1990). Consequently, it could be expected to show the greatest range of responses.

V. PHENOLOGICAL BEHAVIOUR, ECOPHYSIOLOGICAL ADAPTATIONS, AND WOOD-ANATOMICAL CHARACTERISTICS OF MEDITERRANEAN TREES

The occurrence of evergreen leaves in a hot, dry climate seems like an ecological mismatch because dropping the leaves during drought could save potential water loss from the leaf surfaces. The reason to maintain leaves is that evergreen shrubs and trees can resume activity as soon as environmental factors are no longer limiting. Evergreens tend to dominate sites where resources are difficult to obtain, such as dry environments (Tretiach, 1993; Damesin *et al.*, 1998). Mediterranean species cope with drought in two ways, a drought-avoidance strategy (e.g. by shedding their leaves in summer) or a drought-tolerance strategy, continuing their growth during the dry season (de Lillis & Fontanella, 1992) – see Table 1. Such a distinction also occurs in sub-tropical dry forests, where some of the trees at a given site may be dry-season deciduous, some are evergreen and a few species bear leaves primarily during the dry season (e.g. Holbrook, Whitbeck & Mooney, 1995).

The seasonal growth pattern of the principal plant life forms found in Californian mediterranean-climate regions can be related to their rooting depths, and thus presumably to when water first becomes available to them (Mooney & Kummerow, 1981). In the autumn when the first rains begin, the long summer drought is broken first in the upper soil layers. At this time, the annuals and shallow-rooted perennial herbs and subshrubs start their seasonal growth cycle. Growth of the deeper-rooted evergreen shrubs generally does not begin until spring. Although moisture becomes available to the deeply-rooted shrubs by midwinter, stem elongation does

not start until spring (Table 1), when the danger of low-temperature damage to new tissue is reduced. However, photosynthesis occurs year-round, stem cambial growth may occur during winter, and root growth may occur in the autumn (Mooney & Kummerow, 1981).

Root systems among chaparral species vary considerably in their depth, and below-ground niche segregation may be a means of reducing competition for water resources, possibly facilitating the co-existence of chaparral species (Kummerow, 1981; Redtfeldt & Davis, 1996). Nardini, Lo Gullo & S. Salleo (1999), measuring leaf conductance in relation to water vapour, water potential and relative water content as well as seasonal changes in root hydraulic conductance per unit leaf surface area, found that *Quercus suber* and *Q. cerris* L. did not really compete for available water. *Q. suber* is a drought-avoiding sclerophyllous species that reduces leaf conductance to water vapour through an efficient stomatal control of transpiration, whereas *Q. cerris* is a drought-tolerant soft-leaved deciduous species that strongly reduces root hydraulic conductance per unit leaf surface area. In summer, when *Q. suber* was extracting water from the soil to maintain high leaf hydration, *Q. cerris* had restricted water absorption, consequently suffering drought but tolerating its effects. Thus, plants may adopt different strategies to withstand drought stress. *Q. suber* was more competitive than *Q. cerris* during water shortage, as it continued to extract sufficient water from the soil to maintain leaf hydration whereas *Q. cerris* was unable to do the same and suffered dehydration.

Lo Gullo & Salleo (1988) studied carob trees (*Ceratonia siliqua* L.) and wild olive trees (*Olea oleaster* Hoffmgg. et Link) growing at the same dry site. The carob tree was able to compensate for water loss so that the leaves maintained relative water contents as high as 95%, whereas the leaves of the wild olive tree lost more than 25% of their moisture and reached the turgor loss point. Their wild olive tolerated this pronounced dehydration, but it had a lower growth rate than the carob tree.

Studies of the controlling factors responsible for the cessation of stem growth in early summer and the resumption of growth during the cold season have established that it is probably not only depletion of soil moisture that ends the growing season. Seasonal growth of chaparral shrubs has been related to root types, but low air temperature has also been proposed as a controlling factor (di Castri *et al.*, 1981). Growth does not stop abruptly. Rather, there is an acclimation process during which growth rates

Table 1. Seasonal shoot growth (G) and leaf fall (F) of characteristic mediterranean shrubland-heathland species (from Specht et al., 1983)

Species	Winter	Spring	Summer	Autumn
Dark Island heathland, S. Australia (strongly leached soils)				
<i>Banksia ornata</i>			G	G
			F	F
<i>Casuarina pusilla</i>		G	G	G
		F	F	F
<i>Hakea</i> spp.		G	G	G
		F	F	F
Tutanning heathland, W. Australia (strongly leached soils)				
Microphanerophytes			G	G
		F	F	F
Nanophanerophytes		G	G	G
		F	F	F
Chaparral, California, USA (moderately leached soils)				
<i>Adenostoma fasciculatum</i>	G	G	G	G
				F
				F
<i>Heteromeles arbutifolia</i>	G	G	G	G
				F
				F
<i>Rhamnus crocea</i>	G	G	G	G
				F
				F
				F
				F
Sclerophyllous forest, shrublands, Montpellier, France				
<i>Pinus pinea</i>			G	G
			F	F
<i>Quercus ilex</i>		G	G	
			F	F
<i>Quercus coccifera</i>		G	G	
		F	F	

decline and there is increased stomatal closure (Pereira & Chaves, 1995). Water stress may not be the only factor involved: there is evidence from *Arbutus unedo* L. that photoinhibitory processes may be associated with the midday maximum in light intensity (Demmig-Adams *et al.*, 1989).

In mediterranean ecosystems, carbon gain is limited by summer drought and winter cold. The evergreen-sclerophyll plants fix carbon throughout the year, although at reduced levels during the summer and drought periods and during the short winter days (Mooney, 1977). The first studies of this pattern were carried out in California. *Heteromeles arbutifolia*, often used as a model for the Californian evergreen vegetation type (although how widely this assumption holds is questionable, Mauffette & Oechel, 1987), initiates its cambial activity in winter and continues growth through spring. Although *H. arbutifolia* has a reduced photosynthetic activity during the summer drought, it has the capacity to maintain photosynthesis at quite low water

potentials. For example, active photosynthesis has been noted even when pre-dawn water potentials are -2.7 MPa (Mooney, 1981). During periods of drought *H. arbutifolia* may close its stomata in the middle of the day. During severe droughts, stomata may be open only during the early morning hours. Stem elongation takes place rapidly in the spring, and is followed by an increase in the canopy biomass throughout the summer. The biomass of the fruits develops during late summer and into the autumn. Allocation of carbon to the roots also occurs during this period. Thus, at various times of the year photosynthetic carbon is moved into diverse locations (Mooney, 1977). In spring and summer, carbon is moved predominantly into compounds important in primary metabolism, and into cell-wall material (Mooney & Chu, 1974). Although *H. arbutifolia* fixes carbon year-round, the carbon is apportioned non-uniformly to various plant parts and functions, presumably to best meet the demands of the internal as well the external environment.

Canopy development presumably puts priority demands on carbon in the spring, in response to competitive constraints on access to sunlight, leaving little carbon for root development, storage, or predator protection. In autumn and winter, however, when there is no canopy development, considerable carbon is moved into these functions.

Mediterranean woody plants exhibit a great variety of growth forms and phenological traits. They may form proper resting buds (dormant) or not, and therefore they may grow during the winter or not. The ecophysiological responses of mediterranean species to the mediterranean climatic regime are well known (e.g. Mooney & Chu, 1974; Larcher, De Moraes & Bauer, 1981; Thomas & Davis, 1989; Pitacco, Gallinaro & Giulivo, 1992; Gavilán & Fernández-González, 1997; Gucci *et al.*, 1999). Duhme & Hinckley (1992), studying 26 species in southern France, identified seven different summer–autumn patterns of stomatal behaviour: (1) summergreen (deciduous) non-mediterranean, e.g. *Pyrus amygdaliformis* Vill., (2) summergreen sub-mediterranean, e.g. *Crataegus monogyna* Jacq., (3) summergreen mediterranean, e.g. *Pistacia terebinthus* L., (4) evergreen laurel type, e.g. *Pistacia lentiscus* L., *Quercus ilex* L., (5) evergreen sclerophyll, e.g. *Quercus coccifera* L., (6) drought deciduous, e.g. *Cistus albidus* L., and (7) evergreen conifer, e.g. *Juniperus oxycedrus* L. and *J. phoenicea* L. Type (1) shows no stomatal closure during the summer, whereas changes from type (1) to type (5) result in increasing stomatal reactions over the course of the day, i.e. increasing stomatal closure, particularly in the afternoon. A shift from the first type to the last types is accompanied by an increase in stomatal control, hence the ability to control stomata appears to be associated with leaf persistence, with the least control occurring in the deciduous species and the most control in the evergreen species.

In their phenological survey carried out in Central Italy near Rome, de Lillis & Fontanella (1992) separated three groups of plants with different modulation of growth activity. Evergreen sclerophyllous species (e.g. *P. lentiscus*, *Phillyrea media* L., *A. unedo*, *Ruscus aculeatus* L.) limit their growth activity to a brief period before aridity increases; a similar growth pattern is exhibited by those species (e.g. *Quercus ilex*, *Erica arborea* L., *Smilax aspera* L.) that stop producing new leaves and branches during the driest season and that recover after the first rain. Drought-deciduous species (e.g. *Calicotome villosa* (Poiret) Link) have a drought-avoidance strategy with two vegetative periods interrupted by a phase

during which they completely shed their leaves. Semi-deciduous species (*Cistus monspeliensis* L.) with mesophytic leaves have an intermediate response, even growing in the dry and cold season.

In mediterranean regions, water is usually the limiting factor. Wood anatomy, plant architecture, leaf anatomy, life history, and physiology are all related to one another, and whereas there are adaptations to aridity in each of these factors, many plants exhibit suites of co-occurring characteristics (e.g. Margaris & Papadogianni, 1977; Salleo, Nardini & Lo Gullo, 1997; Lo Gullo & Salleo, 1988; Davis *et al.*, 1999). Perhaps because all the parts of the plant system can compensate for one another, we still do not have good predictive capabilities regarding the physiology of a plant given its wood structure or *vice versa* (Gartner, 1995). The ratio of leaf area to sapwood area is generally lower in arid regions than more mesic ones (e.g. Callaway, DeLucia & Schlesinger, 1994; Mencuccini & Grace, 1995), but the response of cambial activity to foliar phenology varies greatly by species (Avila *et al.*, 1975; Liphshitz & Lev-Yadun, 1986). In addition to adaptive changes in leaf area (e.g. Villar-Salvador *et al.*, 1997), there are also anatomical (e.g. Castro-Díez *et al.*, 1997) and physiological adaptations (e.g. Sparks & Black, 1999) that control canopy transpiration. Borghetti *et al.* (1998) term the reduction of transpiration by stomatal closure 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) is a ‘plastic’ acclimation response. Some evergreen species show higher minimum leaf resistances and stomatal closure with increasing drought. This results in a decrease of summer transpiration to a level of approximately 20% of that during the winter (Margaris, 1981). The structure of the cork cambium, the cork and the phelloderm, may also be important in controlling the rate of water loss from the stem directly to the air, but there is very little published research on bark adaptations. Rooting pattern can certainly be important, with phenological, hydraulic, and reproductive strategy often tied to the species’ pattern of rooting depth (Kolb & Davis, 1994; Jarbeau, Ewers & Davis, 1995; Davis *et al.*, 1999).

There are various suites of xylem characteristics that commonly are found in woody plants of mediterranean regions [see Carlquist & Hoekman (1985), Baas & Schweingruber (1987), and Carlquist (1988) for more information and interpretation]. Two characteristics not related directly to water

transport are the structure of the cambium and wood density. The area of the cambial surface occupied by ray initials can be lower in mediterranean plants than plants of other regions. This pattern causes a reduction in the number of intercellular spaces through which water vapour diffusion can occur, with a resulting conservation of xylem water (Margaris & Papadogianni, 1977). The wood of trees in areas prone to drought tends to be denser than the wood of trees from more humid areas (Barajas-Morales, 1985). The ecological and physiological meaning of wood density in general is poorly understood (Castro-Díez *et al.*, 1998), although there is a general negative relationship at the species level between total wood density (including both earlywood and latewood) and the tension at which the wood loses half its conductivity (Hacke *et al.*, 2001). Because the ultrastructure of cell walls appears to be adaptive for resisting transverse tension (Booker & Sell, 1998), and because many mediterranean plants operate with extremely negative water potentials (Kolb & Davis, 1994), it would not be surprising if the tendency toward high wood density in mediterranean plants derives from thicker cell walls in the vessels and/or tracheids. Alternatively, the higher wood density could result from wide latewood bands that could develop in ring-porous species in favourable growth years. Although sometimes observed (e.g. Gartner, 1991*a, b*; Tyree, Davis & Cochard, 1994; Wagner & Davis, 1998), there is no requisite tradeoff between wood density and water transport in hardwoods, in which different cells hold primary responsibility for mechanical support and water transport. In softwoods, more of a tradeoff is apparent (Mencuccini, Grace & Fioravanti, 1997) although plants can compensate for lower mechanical strength or water transport capacity by making more of the needed tissue rather than increasing the capacity of a unit of wood for that function (Spicer & Gartner, 1998*a, b*). Thus, the need for high water transport or of a secondary system of vessels (see below) is not related directly to wood density.

Most of the special characteristics associated with xylem of mediterranean plants are xeromorphic traits related to water transport and vulnerability to cavitation. First, woody plants in mediterranean regions can experience very high transpiration rates because for extended periods, particularly in the spring, they have high insolation and moist soils. Thus, structural features are important that favour rapid water transport. Secondly, because of the seasonality of growth relative to the climate,

conditions in the mediterranean are favourable to formation of embolisms (air blockages) both due to drought and to freezing: plants transpire during periods of high evaporative demand and little availability of soil water (summer), and they may transpire shortly after freeze-thaw events (autumn, winter, and spring). Cavitated conduits, although initially vapour-filled, quickly fill with air as gas diffuses from surrounding air spaces. These conduits are then non-conductive even at atmospheric pressure, thus increasing hydraulic resistance in the stem. As a result of drought-induced embolism, hydraulic conductance and then plant productivity are reduced. Freezing-induced cavitation could be particularly important for evergreen shrubs and trees of mediterranean regions as intermittent freezes may reduce water transport and thus the ability of plants to take advantage of the combination of evergreen phenology and mild winter temperatures (Lo Gullo & Salleo, 1993; Pockman & Sperry, 1997). Thus, structural features are important that minimize cavitation and/or permit the plant to survive even after substantial cavitation.

The fundamental 'problem' for the design of their xylem is that structures that aid rapid water transport tend to make the plant more vulnerable to cavitation, and *vice versa*. For this reason, it is inferred, many mediterranean plants have two sets of conduits, one specialized for water transport without compromise for risk of cavitation, and another that operates with lower transport rates but that is not very vulnerable to cavitation (see below). The larger the conduit, the more efficient it is for water transport (water transport is related to conduit radius to the fourth power), but also the more vulnerable it is to both freeze-induced and drought-induced cavitation. In drought-induced cavitation, it is thought that air is pulled into a conduit at the water potential determined by the size of the largest pore in the conduit wall [thought of as a hole in the pit membrane, i.e. Zimmermann (1983), Jarbeau *et al.* (1995)]. Within an individual and within a species, the wider conduits would tend to have wider pores, and thus cavitate at less negative water potentials. However, this relationship is not particularly robust (Jarbeau *et al.*, 1995), although it is strong enough to be of some evolutionary significance (Tyree *et al.*, 1994). In freeze-induced cavitation, the conduit with the largest volume [which is strongly correlated with diameter, because vessel length and diameter are strongly correlated, Zimmermann & Potter (1982)] will have the largest bubble upon thawing, and larger bubbles will take longest to re-

dissolve. If the conduit experiences xylem tension with a bubble in it, the conduit will cavitate (reviewed in Zimmermann, 1983). Thus, conduits with larger volumes are at increased risk of freeze-induced cavitation (Cochard & Tyree, 1990; Sperry & Sullivan, 1992; Lipp & Nilsen, 1997). The wide early-wood vessels of the ring-porous and semi-ring porous species are therefore particularly vulnerable to freeze-induced embolism (i.e. Lechowicz, 1984; Cochard *et al.*, 1992; Sperry & Sullivan, 1992; Cochard *et al.*, 1997).

Species differ widely in their vulnerability to drought- and freeze-induced embolism (Tyree & Ewers, 1991). A high level of drought-induced xylem embolism has been observed in several mediterranean tree species during the growing season, even under non-stress conditions (e.g. Lo Gullo & Salleo, 1988; Hargrave *et al.*, 1994; Kolb & Davis, 1994; Tognetti & Borghetti, 1994; Tognetti, Longobucco & Raschi, 1998), particularly in older xylem. In practice, cavitations in plants should be considered as normal events (Milburn, 1993), and although in many situations the conduits refill, the method of refilling is still poorly understood (Tyree, Salleo & Mosca, 1999). The aspect and microsite occupied by members of the flora often can be related to hydraulic architecture, with the species that are more vulnerable to cavitation living in less xeric sites (Salleo & Lo Gullo, 1993) or having access to deep water (Jarbeau *et al.*, 1995; Davis *et al.*, 1999).

The frequent appearance of numerous vessels with narrow, short elements, small intervessel pits (Zimmermann, 1978; Carlquist & Hoekman, 1985; Sperry, Tyree & Donnelly, 1988; Lindorf, 1994), and helical thickenings in the vessels (Carlquist & Hoekman, 1985; Carlquist, 1988) in arid zone species has been interpreted as a strategy for conductive safety. Many mediterranean ecosystems are dominated by shrubs or branchy wood plants. Shrubs tend to have narrower, shorter vessels than do trees (reviewed in Wilson, 1995), and branches have narrower (Fegel, 1941), shorter (Zimmermann & Potter, 1982) vessels than main stems, so short narrow vessels will be common in the wood of mediterranean species. However, we still do not have a good functional explanation for why vessels are narrower and shorter in branches and shrubs than in trees.

Another wood anatomical adaptation to the mediterranean environment is the low incidence of scalariform perforations (the shared wall between adjacent stacked vessel elements) (Carlquist, 1975,

1988; Baas & Schweingruber, 1987). The bars in scalariform perforations are thought to increase resistance to water flow, and thus to be rare in species that have periodically high transpiration rates (Baas, 1976; Baas & Schweingruber, 1987). However, an alternative functional explanation for scalariform perforations is that they help plants avoid embolism after freeze-thaw events by preventing the coalescence of bubbles during the thaw of sap. The smaller bubbles would have a large surface area/volume, and would therefore have an increased chance to re-dissolve (Tyree *et al.*, 1994).

There is an elevated proportion of species in mediterranean regions with vessels grouped in multiples and high numbers of vessels per mm² transverse area (Carlquist & Hoekman, 1985; Baas & Schweingruber, 1987; Carlquist, 1988; Lindorf, 1994). Ring porosity and the presence of different vessel size classes in general are of importance for the combined efficiency (wide vessels) and safety (narrow vessels or tracheids in high numbers) of xylem sap transport at different times in or throughout the growing season. Wide earlywood vessels are prone to embolism at times of water stress, which probably irreversibly incapacitates them for sap transport. Narrow vessels can then take over water transport, albeit at a much-reduced rate due to the high resistance to flow. As with other xeric species, many mediterranean species exhibit this dual strategy of wide and narrow vessels, guaranteeing a relatively efficient as well as safe hydraulic system (Baas & Schweingruber, 1987). Ring-porous species constitute approximately 40% of the woody species of floras for which the mean annual temperature is 10–23 °C, but only approximately 28% of the flora where mean annual temperature is < 10 °C and 5% of the flora at temperatures > 23 °C (Wiemann, Manchester & Wheeler, 1999). Carlquist (1988, chapter 11) reported that in southern California, 61% of the woody flora that do not have tracheids in addition to vessels have evolved alternative safe conduits, either vasicentric tracheids or vascular tracheids. Plants with vasicentric tracheids (defined as very narrow vessels that follow the three-dimensional network of the vessels) have evergreen leaves because if the vessels embolize, Carlquist hypothesizes, the vasicentric tracheids can still provide sufficient water transport to maintain the foliage. Of 84 families Carlquist listed with vasicentric tracheids, 82 have simple perforation plates, lending support to the argument that simple plates are part of the xeromorphic strategy as well. Vascular tracheids (small vessels that form at the end

of the growth rings) are hypothesized to safeguard the cambium during the dry season, and plants with vascular tracheids are often drought-deciduous (Carlquist, 1988).

In conclusion, physiological adaptations may modify the cambial response to climate at the species and at the tree level (Baas, 1976), so that different responses of cambium activity between species and between individuals of the same species may be found.

VI. CAMBIAL ACTIVITY AND TREE RINGS IN MEDITERRANEAN REGIONS

Despite the rich availability of archaeological and historical wood material that may enable proxy chronologies to be built (Attolini *et al.*, 1990; Kuniholm *et al.*, 1996) and despite the increasing interest in dendroclimatic reconstructions for the Mediterranean region (Chbouki *et al.*, 1995; Le Houérou, 1996; Conway *et al.*, 1997; Touchan *et al.*, 1999), mediterranean tree rings have seldom been used for dendroecological, dendroarchaeological or dendroclimatological purposes (Serre-Bachet, 1985). The few dendroecological and -climatological studies carried out in the region mostly have been restricted to high elevation trees, e.g. *Cedrus atlantica* (Endl.) Carr. from the Atlas Mountains of Morocco (Berger *et al.*, 1979; Serre-Bachet & Guiot, 1987; Till & Guiot, 1990; Serre-Bachet, Guiot & Tessier, 1992; Chbouki *et al.*, 1995). The main reason for this deficiency is the inability in many cases to identify clearly and date tree annual rings. Although the verification of the annual nature of tree rings is necessary for dendrochronological studies, the seasonal patterns of wood production are not yet well understood in plants lacking annual rings (Gartner, 1995), and cambial activity and its relations to ecophysiological processes in mediterranean environments are still unclear. For example, many authors state that mediterranean vegetation may continue transpiration and photosynthesis under drought stress, and may stop such processes by stomatal closure in extreme dry conditions (e.g. Zhang & Romane, 1991). During summer, only slight early morning and late afternoon stomatal opening has been observed, e.g. in *Quercus coccifera* (Duhme & Hinckley, 1992). However, it is unclear whether cambial activity stops during drought conditions when stomatal closure occurs.

Avila *et al.* (1975) studied seasonal cambial

development of four Chilean and four Californian evergreens. Two of the species, one in California and one in Chile, exhibit year-round cambial activity. *Heteromeles arbutifolia* in California and its Chilean ecological analogue *Kageneckia oblonga* Ruiz et Pavon exhibit cambial activity during winter with a maximum in spring. The other four species were trees with a very similar pattern, with cambial activity restricted mostly to spring and early summer. All the species reach a spring peak of cambial activity, even those that pursue year-round activity, and the tree species show a sharper activity peak than the shrub species. There is a partitioning of resources over time with the partitioning schedule being correlated with growth form: the herbs, then the drought-deciduous shrubs, and, finally, the evergreen shrubs, progressively initiate growth activity following the breaking of the drought by the winter rains. Cambial activity of the drought-deciduous species starts soon after the winter rains commence. The drought-deciduous types evidently utilize the water in the uppermost soil layers for their growth. Within growth forms, however, there is generally a strong synchronization of vegetative growth (Mooney, 1977). In the Mediterranean basin, several studies have also shown that the maximum photosynthetic rate occurs in spring, e.g. in phrygic formations in Greece (Margaris & Papadogianni, 1978) and in *Q. ilex* at Castelporziano near Rome (Gratani, 1997).

Cambial activity may stop not only when temperature becomes prohibitive (at these latitudes, during the winter) (Larcher, 1981), as in temperate regions, but also when periods of drought occur (during the hot, dry summer). This is the so-called characteristic Mediterranean 'double stress' (Susmel, Viola & Bassato, 1976; Mitrakos, 1980; Terradas & Savé, 1992) that triggers the formation of false or double rings. A double ring is caused by the interruption of the normal course of growth during a season; one of the zones of growth of such a ring is known as a false ring (Tingley, 1937; Schulman, 1938). In mediterranean environments, this phenomenon happens irregularly in space (at different sites at the same time) and in time (in different years at the same site), so that it is difficult to assign a date to the formation of rings.

A strong intra-annual variability in primary production in relation to water availability, has also been observed using litterfall amount as a measure of production (Bellot *et al.*, 1992). In *Cupressus arizonica* Greene in Texas, Reed & Glock (1939) detected no less than five growth rings per year. Double rings

Table 2. *Species of tropical, semi-arid and arid regions in which double rings have been detected*

Species	Location	Reference
<i>Pinus radiata</i> D. Don	Monterey Bay, California, USA	Schulman (1938)
<i>Pinus ponderosa</i> Dougl. ex Laws.	Texas, USA	Schulman (1939)
<i>Taxodium distichum</i> (L.) Rich.	Alabama, Mississippi and Georgia, USA	Beaufait and Nelson (1957)
<i>Dacrydium cupressinum</i> Lamb.	South westland terrace forests in New Zealand	Franklin (1969)
<i>Pisonia grandis</i> R.Br.	Coral island in the Pacific Ocean	Eckstein <i>et al.</i> (1981)
<i>Gmelia arborea</i> Roxb.	Nigeria	Akachuku (1985)
<i>Pinus</i> spp.	Mexican highlands	Telewski and Lynch (1991)
<i>Calocedrus decurrens</i> (Torr.) Florin	Baja California, Mexico	Dobry and Kyncl (1992)
<i>Juniperus excelsa</i> Bieb.	Arabian peninsula	Fisher (1994)
<i>Pinus occidentalis</i> Swartz	La Celestina, Dominican Republic	van der Burgt (1997)

have been reported in several species in tropical, semi-arid and arid regions (Table 2).

Villalba & Veblen (1996) found false rings in *Austrocedrus chilensis* (D. Don) Endl. from the forest-steppe ecotone in northern Patagonia (Argentina), and they show that drought can result in the formation of latewood-like cells soon after the initiation of cambial activity following the normal dormancy period. False rings in Austrian pine (*Pinus nigra* Arn.) were used to reconstruct early growing-season precipitation (Wimmer, Strumia & Holawe, 2000). On an experimental basis, Barnett (1976) induced false rings (rings of collapsed or crushed tracheids, whose thin walls have secondary thickening but lack lignin) in *Pinus radiata* D. Don trees grown in containers and subjected to periodic drought.

In the Mediterranean basin double rings have been detected in *Quercus pubescens* Willd. and *Q. ilex* from Tuscany in Italy (Maugini, 1949), in *Q. ithaburensis* (Decne.) Boiss. and *Q. calliprinos* Webb. from the maquis of Israel (Fahn, 1953), in *P. halepensis* on the slopes of the Saharian Atlas mountains in Algeria (Safar, 1994) and in Provence, Southern France (Nicault *et al.*, 2001), and in *Phillyrea latifolia* L. and *Fraxinus ornus* L. from Corsica (Panaïotis, Loisel & Paradis, 1995). In a study of the effects of double stress on tree physiology and wood formation of *Q. ilex* in Sardinia, Susmel *et al.* (1976) found evidence of vegetative activity (cambial activity) from the beginning of November to the beginning of October. The winter stop lasted 1 month. Other short stops in cambial activity were observed at the end of March and during the hot dry August. Fahn (1953) also observed cambial dormancy in August in some species. Summer precipitation was found to trigger false ring formation in *Q. ilex* from southern France (Zhang & Romane,

1991). In *Q. coccifera* at a site near Montpellier (France), leaf water potential in October was observed to be rather similar to that observed in spring, but stomata were more open in the autumn than in spring (Duhme & Hinckley, 1992). However, no observations of cambial activity were made. In central Italy, near Rome, chlorophyll content and water relations of *Q. ilex* demonstrated a second period of vegetative growth if favourable climatic conditions predominated during the autumn (Gratani, Marzi & Crescente, 1992).

According to Liphshitz & Lev-Yadun (1986), two types of cambial activity are present in Mediterranean environments: (1) the temperate Mediterranean type, in which cambial activity takes place during spring and summer, and (2) the adapted Mediterranean type, in which the activity of the cambium commences in autumn when temperatures drop and the rainy season starts, and lasts until the beginning of summer.

In conclusion, mediterranean plants must face two different types of stress, winter cold and summer drought. Drought stress is the climatic factor responsible for restriction of productivity and growth of woody plants in mediterranean environments, but low temperature effects in marginal districts, particularly in the northern and eastern parts of the Mediterranean basin and near the altitudinal limit of the macchia vegetation, should not be neglected (Larcher, 1981). Such effects include frost damage during severe winters, and reduced dry matter production and decreased vigour of the plants due to the depression of metabolic activities by suboptimal temperatures in December and January (Larcher, 1981). The decreased winter vigour is caused by low temperatures, which may be adequate for photosynthesis but not for growth (Miller, 1981), and by decreased water transport ability with freeze-

induced embolisms (Lo Gullo & Salleo, 1993). Photosynthesis and dry-matter production depend on solar irradiance. As solar energy varies in space and time, summer drought has a latitudinal variability and varies from year to year in its length. Moreover, the intensity of winter cold and the length of summer drought depend on topographic and soil conditions. Consequently, climatic conditions, vegetation type, ecophysiological response, and phenological phase all play a key role in tree-ring formation.

VII. TREE-RING MORPHOLOGY: A CASE STUDY FROM TUSCANY (ITALY)

(1) Site description

The study area is located in Lajatico (43° 26' N, 10° 42' E), in a hilly region near Pisa (Tuscany, Italy), approximately 50 km from the coast of the Tirrenian (Mediterranean) sea. The site is on a north-facing slope (20%), at an elevation of 210 m. The soils are brown loamy-clay developed from calcareous marl, and covered by a thick litter layer (Raiesi, 1998; Raiesi Gahrooe, 1998).

The climate is typical Mediterranean (subhumid region), characterized by a mild winter and summer drought. At the Saline meteorological station (72 m elevation and approximately 12 km from the site), the average total annual precipitation was 897 mm (1950–95), with a maximum in October and March, and a minimum in July. The dry period extends from June to September. The mean annual temperature was 13.6 °C. The maximum and minimum monthly temperatures were 33 °C and –4 °C.

The area is covered by a typical coastal Mediterranean macchia, an oak–ash mixed coppice (6 m mean height, and 11 cm mean diameter at 1.3 m height) composed of *Q. ilex* and *A. unedo*, with *E. arborea*, *F. ornus*, *Q. pubescens* and *Q. cerris*. *Cistus salviifolius* L., *Cytisus scoparius* L., *Genista* sp., *Juniperus communis* L., *Ligustrum vulgare* L., *Myrtus communis* L., *P. latifolia*, *P. lentiscus* and *S. aspera* are present in the shrub layer.

Additional sampling was carried out at a site near Rapolano (Siena, Italy) (43° 17' N, 11° 36' E), 73 km southeast of Lajatico, at an elevation of 270 m, approximately 100 km from the coast of the Mediterranean sea. The soils are rich in organic matter and developed from a calcareous substratum. A detailed description of this site can be found in Miglietta *et al.* (1993).

Table 3. Numbers of trees, total samples (cores and cross sections) and cross sections taken at Lajatico (43° 26' N, 10° 42' E; 210 m a.s.l.), Italy

Species	No. of trees	No. of total samples	No. of cross-section
<i>Arbutus unedo</i>	20	38	14
<i>Fraxinus ornus</i>	19	33	7
<i>Quercus cerris</i>	19	30	—
<i>Quercus ilex</i>	16	32	10
<i>Quercus pubescens</i>	20	37	—
Total	94	170	31

(2) Sampling methods

We selected the largest-diameter trees at the site for five species (*A. unedo*, *F. ornus*, *Q. cerris*, *Q. ilex*, and *Q. pubescens*). *Arbutus unedo* and *Q. ilex* are evergreen, do not form resting buds and may grow opportunisticly during the winter. *Fraxinus ornus*, *Q. cerris*, and *Q. pubescens* shed their leaves and form dormant buds. We selected both evergreen and deciduous species, to assess if there is a difference between tree rings formed by species having different vegetation habit. Recent studies on fossil coniferopsid species suggest that it may be possible to distinguish between evergreen and deciduous species using wood anatomical characteristics (Falcon-Lang, 2000a). *Arbutus unedo* and *Q. ilex* are diffuse- to semi-ring-porous species, *F. ornus*, *Q. cerris* and *Q. pubescens* are ring porous.

Trees were sampled during autumn 1997 and spring 1998. In 1997, trees were cored at 1 m height. To avoid reaction (tension) wood, two cores were taken uphill at the same height at 120° (on a horizontal cross section) to each other with an increment borer 0.5 cm in diameter. Cores were mounted on channelled wood, seasoned in a fresh-air dry store and sanded a few months later. In 1998, cross sections were taken at 1 m height for species that were found during pilot studies to be difficult to date using cores. We took 14 cross sections for *A. unedo*, 10 for *Q. ilex* and seven for *F. ornus*. In all, we analysed 170 samples from 94 trees at the site (Table 3). In Rapolano, 20 cross sections of *Q. ilex* (10 trees) were sampled, as this was the only species sufficiently represented in the stand.

(3) Dendroecological analysis

Tree rings of each specimen were identified and dated by counting them from bark to pith with the help of a stereomicroscope (magnification 6.4–40×,

Wild M3Z Leica, Germany). Because tree-ring boundaries were particularly difficult to identify, we marked each tree ring on the stem disk and then repeated the counts of tree rings series until three successive counts provided identical results. Photographs were taken of all the anomalies found in the wood-anatomical structure using the stereomicroscope or 10–20- μm thick microsections stained with Safranin.

Ring-width measurements were made to the nearest 0.01 mm on the cores and on two radii (subjectively selected as the most regular) on each of the crosssections, using TSAP measurement equipment and software package (Time Series Analysis and Presentation, Frank Rinn, Heidelberg, Germany). The results were examined using the DENS-software package (Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland). The raw ring widths of the single curves of each dated tree were plotted and single curves were checked visually and then synchronized by the *Gleichläufigkeit* (there is no English equivalent to this term), which is a measure of the year-to-year agreement between the interval trends of two chronologies based upon the sign of agreement, and Student's *t*-test, which determines the degree of correlation between the curves.

Mean sensitivity, an indicator of the responsiveness of the trees to environmental factors such as climate, was analysed for all the averaged chronologies and for all the single trees within a specific chronology. Sensitivity is defined as the mean percentage change from each measured ring-width value to the next, namely the average relative difference in width from one ring to the next, calculated by dividing the absolute value of the differences between each pair of measurements by the average of the paired measurements, then averaging the quotients for all pairs in the tree-ring series.

For all the mean chronologies, we analysed the interval trend, i.e. the number of intervals of individual ring width exhibiting the same tendency, expressed as a percentage of ascending intervals (100% indicates that all the intervals are ascending, whereas 0% indicates that all are falling).

Skeleton plots were used to determine stem age and the life history of the trees. Analyses were carried out using the methods described by Stokes & Smiley (1968) and Schweingruber *et al.* (1990). During the skeleton plot analyses, the age of the innermost rings (situated immediately next to the pith) and the presence of any abrupt growth changes was

recorded. An abrupt growth change is defined as a sudden change (increase or decrease) in increment at least 40% above or below the average increment over the previous four years.

The influence of climate on tree-ring width at the site was assessed using meteorological data recorded at the Saline meteorological station. In a first step, any ageing effect (long-term trends included) was removed by modelling the ring-width series (dependent data) as a Hegershoff function of cambial age (independent data) and indexing procedure used (Fritts, 1976). Afterwards, stepwise regressions and response functions were performed with the Precon5[®] software package to assess the influence of climate on ring-width growth. Prior growth was also taken into account to check for any autocorrelation effects (Fritts, 1976).

(4) Results and discussion

(a) Ring-width chronologies

Mean ring-width chronologies are given in Fig. 1 for each of the five Mediterranean species (*A. unedo*, *F. ornus*, *Q. cerris*, *Q. ilex*, and *Q. pubescens*) at Lajatico and a mean ring-width chronology for *Q. ilex* at Bossoleto, near Rapolano.

(b) Age

The age of the innermost ring on the stem disk taken at 1 m gives an approximate age of each tree. At this site trees grow fast and typically reach 1 m height when they are 2–5 years old (P. Cherubini and R. Tognetti, personal observations). Thus, the error caused by the cores and cross sections being taken at 1 m height rather than at the stem base is approximately 2–5 years and for our purposes may be considered negligible. The age given by the innermost ring of stem disks taken at 1 m height can therefore be considered as approximately the actual age of each tree.

Germination occurred mostly after 1935, indicating a common origin, probably triggered by coppicing (this occurred in 1935 or shortly before). Unfortunately, no written records, such as forest management plans, are available for this area. Two trees, one *Q. cerris* and one *Q. pubescens*, germinated earlier (in 1927). They were probably present in the understory before the coppicing and survived the harvesting operations. Stems continued to become established until 1972, showing that stem development in such stands is not restricted to a few years following the coppicing, but is possible for some

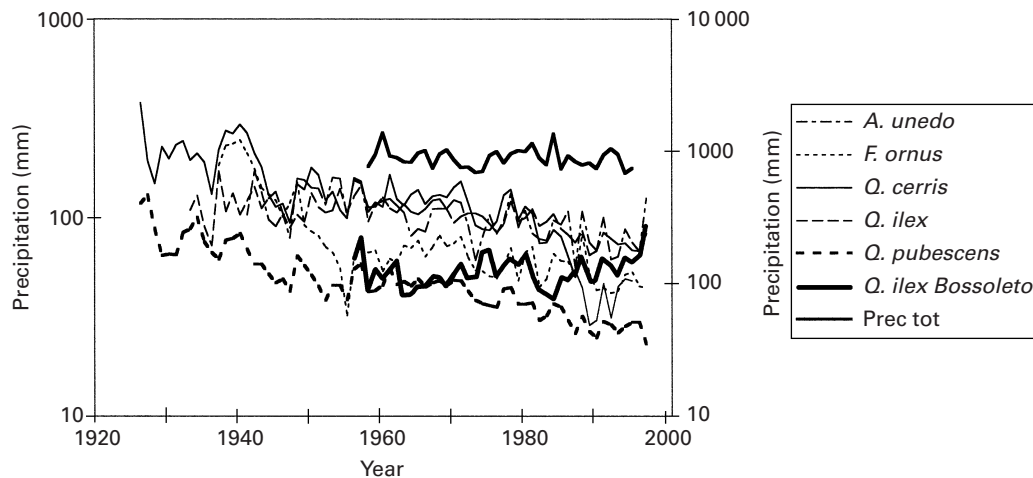


Fig. 1. Mean ring-width chronologies of each species (*Arbutus unedo*, *Fraxinus ornus*, *Quercus cerris*, *Quercus ilex*, *Quercus pubescens*) at Lajatico, and of *Q. ilex* at Bossoleto, and total annual precipitation (Prec tot) at the meteorological station of Saline for the period 1958–95. Note logarithmic scales.

decades under the canopy, probably until the canopy is closed and too dense for further stem establishment. No positive abrupt growth change, i.e. growth releases after suppression, occurred, so any major stand disturbances (such as natural tree fall or harvesting activity) after coppicing in 1935 can be excluded. All the trees showed a similar life history.

(c) Dating tree rings

All the tree rings of each specimen sampled at Lajatico and Rapolano were dated. The synchronous occurrence of pointer years, i.e. years in which particularly narrow (e.g. 1947, 1955, 1979, 1982, 1983, 1987, 1990, 1996) or wide (e.g. 1956, 1957, 1971, 1978, 1980, 1988, 1991, 1994) rings are formed, in the mean ring-width chronologies for all species (Fig. 1) indicates that, despite the difficulties that we found while cross-dating the ring-width series, tree rings were exactly dated.

Our data indicate that in the Mediterranean environment, cross-dating and synchronization of ring-width time series is difficult and time-consuming, but possible. When comparing the mean chronologies built for each species with one another, we found highly significant *Gleichläufigkeit* values (always higher than 73%), and correlation coefficients (r) that show a good synchronization, the highest r being 0.88 between *F. ornus* and *Q. pubescens*, and the lowest 0.39 between *A. unedo* and *F. ornus*. Further r values, in decreasing order, were 0.86 between *F. ornus* and *Q. cerris*, 0.80 between *Q. cerris* and *Q. pubescens*, 0.66 between *A. unedo* and both *Q. cerris* and *Q. pubescens* (showing the similarity of

ecological characteristics in the latter two species), 0.63 between *A. unedo* and *Q. ilex*, 0.61 between *Q. cerris* and *Q. ilex*, 0.48 between *Q. ilex* and *Q. pubescens*, and 0.46 between *F. ornus* and *Q. ilex*. Furthermore, our data show that the development of chronologies is possible using only a stereomicroscope. However, whole stem disks should be sampled. Dating of tree rings on cores usually fails because of missing (locally absent) rings and unclear ring boundaries that often make it impossible to assign a date to each tree ring. Analyses should therefore be restricted to whole stem disks, as for tropical trees (e.g. in Malaysia – Sass *et al.*, 1995), because cambial activity varies significantly around the circumference of the stem. This variation is possibly due to an uneven distribution of water in the tree, either from sectoral transport (e.g. Larson, Doubt & Matthes-Sears, 1994) or from relatively drier and wetter zones within an annual ring, an area that has been little researched (Cherubini, Schweingruber & Forster, 1997).

Nevertheless, even when analysing cross sections, many difficulties were found. An annual periodicity in cambial activity is present, but often is obscured by the presence of many intra-annual rings. False rings can be identified by carefully studying xylem cells and observing whether the transition from the thin band of latewood cells to earlywood is gradual, diffuse, or hazy, and not as abrupt or sharp as in a tree-ring boundary (Schulman, 1939; Kramer & Kozlowski, 1979; Telewski & Lynch, 1991; Villalba & Veblen, 1996). Trees that do not experience a distinct period of cambial quiescence exhibit a diffuse boundary between growth rings making interpret-

ation of a distinct annual ring pattern difficult, if not impossible (Telewski, 1998).

The type of boundary between earlywood and latewood within a growth ring is genetically controlled (and probably the markedness of tree rings is inversely related to leaf longevity – Falcon-Lang, 2000*b*), although it can be modified by external environmental factors. Microscopic analyses of the wood structure may help. If all the specimens show the suspected ring as sharply bounded, it can usually be assumed to be a true annual ring. Susmel *et al.* (1976) could not distinguish the wood formed by *Q. ilex* in autumn from that formed in spring, but were able to separate annual rings by observing microscopically a layer of narrow cells (fibres) that were strongly lignified at the end of the annual ring. Gourlay (1995*a, b*) distinguished the ring boundaries by the fine marginal parenchyma bands that were easily distinguished from the frequent intra-seasonal banded parenchyma by their fineness, by the more irregular spacing between the broader bands, and by the evenness of appearance in contrast to the more irregular, wavy, confluent bands. Moreover, in the transverse section, false rings are often not uniformly present along the circumference of an annual tree-ring and can therefore be identified (Fahn, 1953). However, some difficulties may still be encountered as false rings can sometimes be sharply bordered (Glock, 1951).

Another method that has commonly been used to assess the annual nature of tree rings is to relate precipitation to ring widths. If a good correlation between mean ring width and annual rainfall is found, then the annual nature of tree rings is demonstrated (Worbes, 1995). This method has been applied widely in recent times, e.g. for dating invasive shrubs in Australia (Kirschbaum & Williams, 1991), Californian chaparral shrubs (Keeley, 1993), and shrubs in the arid karoo of South Africa (Milton, Gourlay & Dean, 1997). A further problem is that false rings can sometimes be cross-dated (Dobbs, 1942). The annual nature of tree rings can therefore only be demonstrated unequivocally when trees of known age are used (e.g. in plantations).

Our results show that when using microsections the actual boundaries of tree rings can be identified easily (Fig. 2). However, the preparation of microsections is time-consuming, so we tried to avoid it while determining whether it was possible to establish a method that would be applied easily in environmental studies. It is possible to date rings without using microsections but one must make a

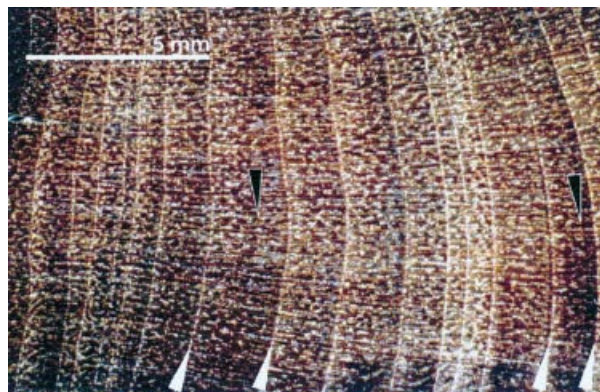


Fig. 2. Cross section of *Arbutus unedo* grown at Lajatico. The actual boundaries of tree rings (white arrows), as well as false rings (black arrows), can easily be identified.

series of repeated detailed analyses of the ring structure using a stereomicroscope. A range of magnification between approximately 10 \times and 30 \times was the most efficient for dating. In many cases 6.5 \times was insufficient magnification to separate ring boundaries, whereas 40 \times was too high a magnification as it draws attention to too many intra-annual density fluctuations and other wood-anatomical details, making an overview of the whole tree-ring structure impossible.

(d) *The effect of climate*

The synchronous occurrence of pointer years, i.e. very narrow and very wide tree rings, in the different species indicates that a climatic signal may be present in the growth patterns. In mediterranean environments, tree-ring growth is mainly limited by soil water availability, and precipitation plays a major role in determining cambial activity. However, low correlation coefficients (r) between total annual precipitation (1958–95) and specific ring-width chronologies were found (0.23 for *A. unedo*, 0.02 for *F. ornus*, 0.14 for both *Q. cerris* and *Q. pubescens*, 0.32 for *Q. ilex*). Although a strong correlation between ring width and total annual precipitation was not found, some dry periods (1972–5, 1982–3, 1989–90) did influence growth, as shown by the ring widths and climatic records (Fig. 1).

The mean sensitivities for all mean chronologies and for all the single trees within a specific chronology are shown in Table 4. A comparison of the sensitivity of the different species indicated that *A. unedo* has the highest values. This species has the shallowest root system amongst the species studied. Shallow rooting trees are sensitive to rainfall, as they are unable to reach a more permanent water table

Table 4. Mean sensitivity for all mean chronologies (*) and mean sensitivity for all trees (†) of each species. See text for details

Species	Period	Length (years)	Mean sensitivity (*)	Mean sensitivity (†)
<i>Arbutus unedo</i>	1941–97	57	0.256	0.440
<i>Fraxinus ornus</i>	1937–97	61	0.193	0.321
<i>Quercus cerris</i>	1933–97	65	0.187	0.262
<i>Quercus ilex</i>	1933–97	65	0.165	0.371
<i>Quercus pubescens</i>	1933–97	65	0.182	0.275

(see, e.g. Gourlay, 1995b). *Quercus pubescens* was overall very complacent (i.e. characterized by low sensitivity). *Quercus* species and *F. ornus* have deeper root systems than *A. unedo* and are therefore less affected by the precipitation regime.

The interval trend for all the mean chronologies was 100% in 1967, 1977, 1984, 1988 and 1991, whereas it was 0% in 1979, 1987 and 1989. It was not possible to explain consistently all these data using total annual precipitation (e.g. 1967 was a very dry year). Within each species, the interval trend was analysed for all trees for the period 1950–1996. *Quercus ilex* showed the lowest values (always less than 80%) and *A. unedo* the highest (21% of the years more than 80%). These results indicate that the highest climatic response (to rainfall) was shown by *A. unedo*, and confirm the results obtained by the sensitivity analysis, and by other studies (Arianoutsou-Faraggitaki, Psaras & Christodoulakis, 1984).

The high responsiveness of *A. unedo* to climate is also confirmed by the absence of any significant influence of prior growth on the ring-width series for this species, as shown by the autocorrelation. Prior growth explained more than 20% of the variance for radial growth of *F. ornus*, more than 30% for *Q. ilex*, more than 50% for *Q. cerris*, and more than 60% for *Q. pubescens*, but did not affect growth of *A. unedo*.

The precipitation regime of one main period (May) significantly (at $P \leq 0.05$) affected radial growth of all species at Lajatico. The analysis of all significant (at $P \leq 0.05$) results obtained using the different models for all species indicated that only the precipitation in May influenced the ring width of all species. However, some other periods significantly affected the growth of individual species.

For all *Quercus* species, which may reach water stored deep in the soil (Terradas, 1999; Werner, Correia & Beyschlag, 1999), winter precipitation also influences growth (December of previous year for *Q. cerris*, February for *Q. ilex*, and January for *Q. pubescens*).

Precipitation during August of the current year plays a significant (at $P \leq 0.05$) positive role only on tree-ring growth for *Q. cerris* and *Q. pubescens*. These species do not have a summer dormant period. They profit from the whole vegetative period because they shed their leaves during autumn, whereas *Q. ilex*, which is evergreen, may also profit from autumnal rainfall.

Quercus ilex is the only species that reacts significantly (at $P \leq 0.05$) to late-summer or early-autumnal precipitation (September) of the current year. In contrast to our results, a *Q. ilex* coppice stand in southern France near Montpellier was found to react primarily to rainfall occurring in late spring and early summer (June–July) (Zhang & Romane, 1991; Cartan-Son *et al.*, 1992). This difference may be explained by the milder autumnal temperatures that occur at our site and which may enable cambial activity in September–October. This seems to be confirmed by previous phenological observations near Rome (Central Italy) (de Lillis & Fontanella, 1992).

At Lajatico, *Q. cerris* does not react significantly to autumn precipitation, as also observed near Rome by Romagnoli & Codipietro (1996). However, Corona, Romagnoli & Torrini (1995) found that growth of this species in Gargano (southern Italy) was related to both spring and autumn rainfall. Our interpretation is that, at our site, *Q. cerris* benefits from summer precipitation, whereas in southern Italy extreme dry conditions during the summer may stop cambial activity, which then resumes in autumn, stimulated by the autumnal rainfall and associated with the milder temperatures.

The growth of *A. unedo* is significantly (at $P \leq 0.05$) influenced by precipitation in April, May and June of the current year, confirming phenological observations by de Lillis & Fontanella (1992). In comparison with other Mediterranean woody species, the greater efficiency in hydraulic transport by the xylem of *A. unedo* shoots during the spring months (higher specific hydraulic conductivity), and

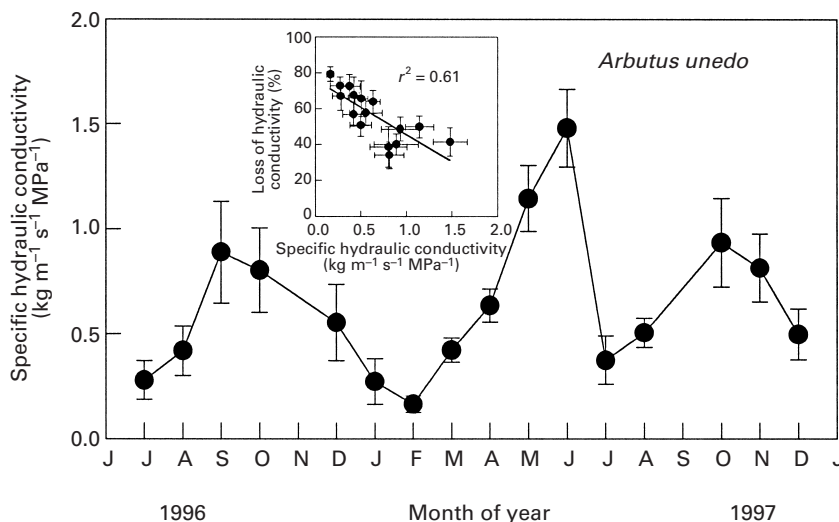


Fig. 3. Specific hydraulic conductivity of branch segments ($n = 10\text{--}12$) from the upper crown ($n = 12$ trees) (following Tognetti *et al.*, 1998). Percentage embolism was negatively correlated with specific hydraulic conductivity by linear regression (see inset, $r^2 = 0.61$, $P < 0.0001$). The seasonal course of specific hydraulic conductivity reflected that of percentage of embolism. Minimum values of specific hydraulic conductivity occurred in mid-summer and in winter (below $0.5 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$); maximum values occurred in late spring (up to $1.5 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$).

particularly the recovery of hydraulic conductivity associated with new functional xylem observed in late spring (Fig. 3), may permit higher transpiration rates, thus facilitating rapid growth and higher rates of photosynthesis. More efficient xylem may be a prerequisite for sustaining the metabolically more active laurophyllous leaves of arcto-boreal species in comparison to metabolically more conservative leaves of other Mediterranean sclerophyllous species (Larcher, 1995; Kolb & Davis, 1994). *Arbutus unedo* is a species less tolerant to prolonged drought in comparison with sclerophyllous species, as also shown by the wood structure, where evidence of a summer cessation of cambial growth was found (see below).

For *A. unedo*, growth was also significantly (at $P \leq 0.05$) positively affected by precipitation in August of the previous year. This result is difficult to explain. August precipitation of the previous year may play a positive role on water availability for the next vegetation period; all *Quercus* species have precipitation of the previous August as a factor influencing growth (although not significantly). However, *A. unedo* with its shallow root system should not be strongly influenced by deep water storage. We believe that *A. unedo*, which is the first of the species that we studied to break bud (usually at the end of February or at the beginning of March), is able to use soil water that, early in spring, is still strongly influenced by rainfall of the previous year.

Another alternative is that trunk capacitance replenished in August may influence growth the following year.

When analysing the total r^2 of climate-growth models, *Q. ilex* shows the lowest value (61%), i.e. a very low sensitivity to climate. All the other species show values for r^2 of approximately 70% (*A. unedo* 68%, *Q. cerris* 69%, *Q. pubescens* 70%, *F. ornus* 71%). Looking at the climate signal itself, without prior growth as a predictor, the model for *Q. cerris* is the weakest, with 25%, and *A. unedo* is the strongest, with 62%. Once again, *A. unedo* is the most sensitive species to rainfall.

The stem growth of individual species occurs at different times of the year. There is a partitioning schedule for the growing season for each species, as observed by Avila *et al.* (1975) in California, and by Arianoutsou-Faraggitaki *et al.* (1984) in Greece. Root:shoot biomass ratios of mature plants in mediterranean ecosystems tend to be higher than in more temperate ecosystems, possibly as an adaptation to the summer dry season (Hilbert & Canadell, 1995; Lloret, Casanovas & Peñuelas, 1999). We consider that each species has a different growing-strategy, based on the nature of its root system and the rate and typology of carbohydrate storage. Our data suggest that resources at Lajatico are partitioned sequentially over the year between species, i.e., *A. unedo* in early spring, *Q. cerris* and *Q. pubescens* in August, *Q. ilex* in September.

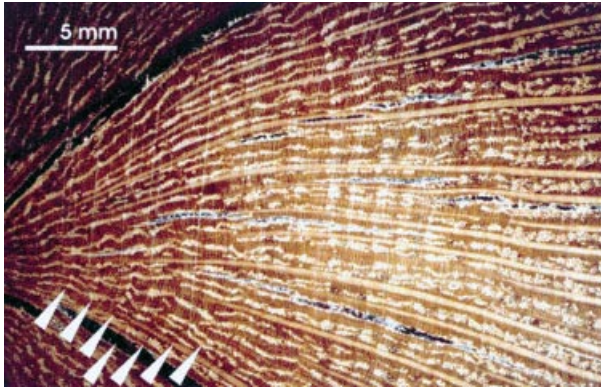


Fig. 4. Cross section of *Quercus ilex* grown at Rapolano: the identification of ring boundaries was easy and there were no difficulties in dating (some examples are shown by white arrows).

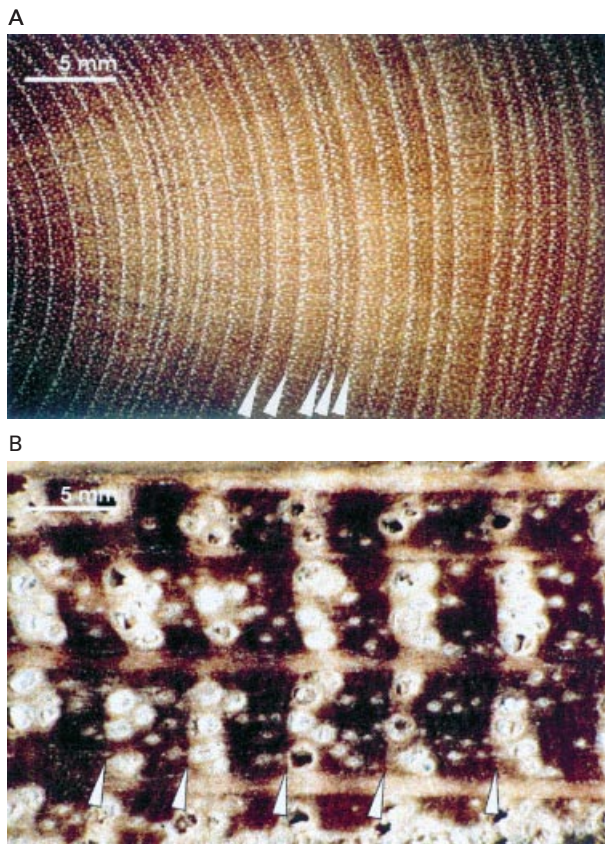


Fig. 5. The wood structure of *Fraxinus ornus* (A) and *Quercus pubescens* (B) at Lajatico shows that deciduous species form distinct tree rings that are easy to date (white arrows).

Tree rings of *Q. ilex* at Lajatico differed morphologically from those at Rapolano. At Rapolano, the identification of ring boundaries was easy and there were no difficulties in dating (Fig. 4). This was not the case at Lajatico. The difference between Lajatico

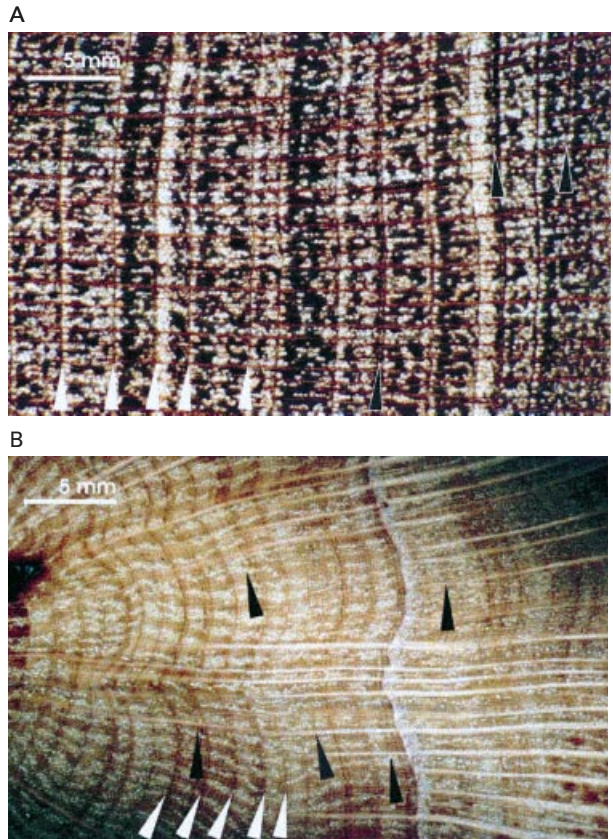


Fig. 6. Cross sections of *Arbutus unedo* (A) and *Quercus ilex* (B) at Lajatico: the annual tree rings (white arrows) were obscured by intra-annual rings (black arrows).

and Rapolano may be explained by different climatic conditions, although effects brought about by differences in resource availability cannot be excluded. Rapolano is at a similar latitude, but is more continental (i.e. winter temperatures are much lower than at Lajatico) and, as a result, *Q. ilex* cambial activity at Rapolano stops during the winter, resulting in the formation of clear annual tree rings.

(e) *The effect of the vegetation habit*

The deciduous species *F. ornus* (Fig. 5A) *Q. cerris* and *Q. pubescens* (Fig. 5B) form distinct tree rings that are easy to date at Lajatico. All have a clear winter dormant phase, during which they are leafless, and they have no summer dormancy, probably because of their deep root systems. These phenomena result in the formation of distinct tree rings, as also recently observed in tropical trees (Callado *et al.*, 2001). It was possible unambiguously to identify individual annual growth rings.

With *A. unedo* (Fig. 6A) and *Q. ilex* (Fig. 6B) at Lajatico (but not at Rapolano), it is difficult to

decide which rings should be categorized as intra-annual and which annual. On some specimens the inside ring was so diffuse as to leave no doubt that both components were laid down in the same year, but in many other cases the annual periodicity was obscured by intra-annual rings. The presence of intra-annual rings is a characteristic already described for evergreens growing in dry environments.

In the literature, there is evidence for different strategies and rhythms of cambial activity in mediterranean trees (Avila *et al.*, 1975; Arianoutsou-Faraggitaki *et al.*, 1984). Two extremes of foliage adaptation to water stress are the drought-avoiding behaviour of soft and relatively thin leaves versus the sclerophyllous strategy. The sclerophyllous strategy consists of adaptations to decrease transpiration, and is comprised mainly of modifications of the leaf anatomy such as smaller cell size, higher stomatal resistance to water vapour diffusion, and thicker cell walls and cuticle (Catarino *et al.*, 1981; Margaris & Mooney, 1981). Two tree-ring types are formed in response to such extremes in foliar adaptation: annual rings and potentially no rings (growth zones without a seasonality) (Liphshitz & Lev-Yadun, 1986). Differences in the reactions of different species in the same environment have been shown in several studies carried out in Israel. There, *Pinus pinea* enters a true winter dormancy but has no summer quiescent phase (Liphshitz *et al.*, 1984). In *Cupressus sempervirens* L. and *Pistacia lentiscus* there is a summer cessation in cambial activity (Liphshitz, Lev-Yadun & Waisel, 1981, 1985). In *Pinus halepensis* a double stop occurs, with a quiescent period being present in mid-winter and the ring border being formed in summer (Liphshitz *et al.*, 1984). Differences also exist between environments. For example, in contrast to in Israel, *P. halepensis* in Italy forms the ring border in autumn (Messeri, 1948), and *Ceratonia siliqua* in Israel is active throughout the year (Liphshitz & Lev-Yadun, 1986), whereas in northern Italy *C. siliqua* is inactive in winter, probably because of low temperatures (Scaramuzzi, Porcelli-Armenise & de Gaetano, 1971).

(f) *Phenological behaviour and ecophysiological responses of evergreen species*

Of the studied species, and thus also in comparison with the other evergreen species considered in this study (i.e. *Q. ilex*, sclerophyllous), the laurophyllous *A. unedo* presents many anomalies in the wood structure and is more difficult to date. *Arbutus unedo*

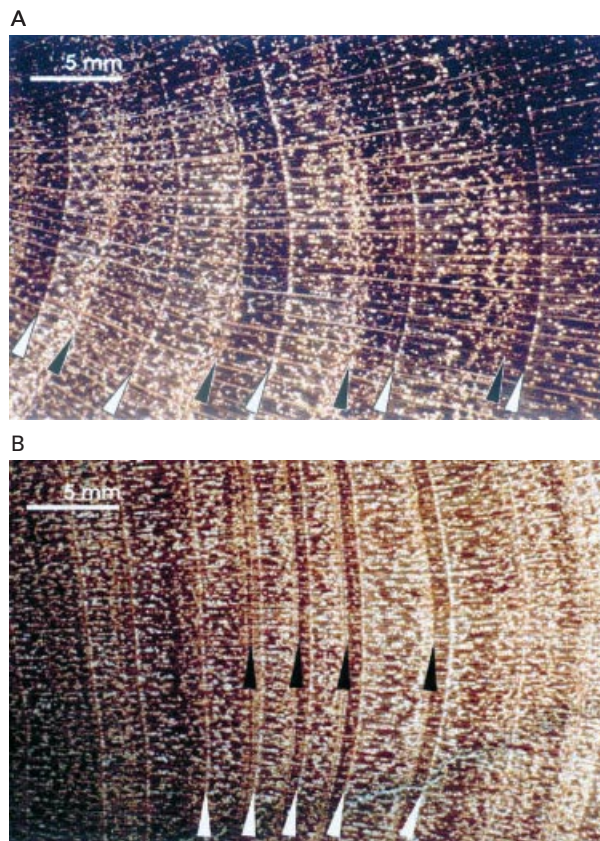


Fig. 7. Stereo-photographs of cross sections of *Arbutus unedo* grown at Lajatico (A): Rings often were formed with two distinct sectors separated by unclear boundaries (black arrows), probably caused by summer drought. (B): The two sectors are formed during different seasons of the vegetative period, see text for details. White arrows show clear annual boundaries caused by the winter cold season, whereas black arrows show growth cessation caused by the summer drought.

appeared to have intermittent examples of clear rings, and unclear ring boundaries were often found. In some cases such boundaries can be abrupt and have the appearance of an annual ring boundary (false rings).

We found that it is possible to avoid the use of microsections by using a stereomicroscope. In *A. unedo* at Lajatico, rings were often formed with two distinct sectors (Fig. 7). The first sector, which may be formed by three sub-parts has a lighter colour and consists of relatively large vessels. The second sector is formed by a band of slightly denser wood with poorly defined margins at its beginning (Fig. 7). It was difficult to date this dense wood, i.e. to assign it to the beginning of the vegetative season of the next tree ring, or to the end of the previous tree ring. A more careful analysis of the two sectors of the tree rings showed that typically the whole tree rings were

formed by a first part characterized by a row of large vessels, a second larger part with smaller vessels, then large vessels again followed by a poorly defined tree-ring boundary, and a part with very small-sized vessels followed by a clear, sharp tree-ring boundary which represented the end of the vegetative season.

We hypothesize that (1) the first part of the ring that is characterized by large vessels is the earlywood and was formed during the mild and wet beginning of spring; (2) the dark part is attributable to increasingly dry conditions; (3) the part with large vessels results from increased cambial activity that produces new functional xylem, which may be related to the partial recovery of hydraulic conductivity observed in late spring; (4) the poorly defined boundary is caused by the summer stop; (5) the dark part is the 'autumnal wood' arising from more soil moisture associated with favourable temperatures; and (6) the clear tree-ring boundary is caused by cold conditions (winter dormancy).

The evergreen habit of *A. unedo*, together with its demonstrated sensitivity to precipitation that is assured by the shallow root system, probably enables this species to react to sudden favourable environmental conditions by growing very early during the spring, when temperature conditions rapidly become favourable. The control of stomatal response in *A. unedo* by atmospheric factors and water stress has been thoroughly studied (Tenhunen *et al.*, 1980; Tenhunen, Lange & Braun, 1981; Tenhunen, Lange & Jahner, 1982; Lange, Tenhunen & Beyschlag, 1985; Beyschlag, Lange & Tenhunen, 1986, 1987, 1990; Castell, Terradas & Tenhunen, 1994; Jones *et al.*, 1995; Werner *et al.*, 1999). The seasonal pattern of photosynthesis and transpiration in *A. unedo* is strongly influenced by drought stress in summer, and plants may respond to extreme water stress by closing their stomata at midday (e.g. Duhme & Hinckley, 1992). Stomata remained closed during most of the day in mid-summer to reduce transpirational water loss, and leaf gas exchange rates were depressed. At Lajatico, leaf transpiration net photosynthetic rate and leaf gas exchange of *A. unedo* showed a two-peaked diurnal curve with a morning maximum peak and a midday depression during mid-summer and under drought stress (Barták, Raschi & Tognetti, 1999). At Rapolano, stomatal closure occurs at midday, and in the autumn, when stress is relieved, leaf conductance increases (Jones *et al.*, 1995).

Water stress during the dry summer period affects *A. unedo* more than the sclerophyllous species (Beyschlag *et al.*, 1986). The reduced photosynthetic

carbon gain during summer probably results in a summer stop in cambial activity, and, as a result, false rings may be formed. Consistent impairment of the xylem hydraulic efficiency during the growing season has been observed in *A. unedo* at Lajatico (Tognetti *et al.*, 1998). Unlike other Mediterranean species such as *Ceratonia siliqua*, *Olea europaea* var. *oleaster* L. and *Q. suber*, all of which can tolerate water potential values below the turgor loss point with only minor losses of hydraulic conductivity (Salleo & Lo Gullo, 1993), *A. unedo* shows losses of hydraulic conductivity of over 60% during the summer drought. Xylem dysfunction caused by embolism at modest tension may reduce the rates of water extraction and prolong water availability during drought (Sperry & Saliendra, 1994). Furthermore, rainfall at the beginning of autumn may have consistently reduced embolism levels in *A. unedo*, and a mechanism for the partial and gradual recovery of xylem function after early-autumn rainfall could be the construction of new xylem tissue (Kolb & Davis, 1994).

We suggest that during summer, cambial activity of *A. unedo* either is very reduced or it stops. The use of sensitive dendrometers (e.g. Downes, Beadle & Worledge, 1999) followed by later destructive sampling would help solve some of these issues.

VIII. MEDITERRANEAN TREE RINGS: CONCLUSIONS

(1) In this review we present the first tree-ring chronology for a widespread Mediterranean species (*A. unedo*) (selected data from this time series has been used in a separate study on the effect of elevated CO₂ concentrations on tree-ring growth: Tognetti, Cherubini & Innes, 2000). Dating was very difficult but possible. Furthermore, we present four chronologies for other mediterranean species. It was possible to cross-date unequivocally the samples for *Fraxinus ornus*, *Q. cerris* and *Q. pubescens*. Dating *A. unedo* was very difficult, whereas dating *Q. ilex* was difficult at Lajatico, but easy at Rapolano.

(2) Difficulties in dating are the result of false rings induced by climatic conditions (*Q. ilex* at Rapolano does not form false rings, but at Lajatico it does), vegetation type (the deciduous *F. ornus*, *Q. cerris* and *Q. pubescens* do not form false rings, but the evergreen *A. unedo* and *Q. ilex* do), ecophysiological response and phenological characteristics (the laurophyllous *A. unedo* was more difficult to date than the sclerophyllous *Q. ilex*).

(3) Whole stem disks are preferable when sampling because of missing rings and unclear ring boundaries. Microsections are ideal tools to detect false rings, but their preparation is time-consuming. It is possible to avoid the use of microsections by using a stereomicroscope.

(4) Tree-ring formation in mediterranean environments can be classified into four groups:

- (a) Trees with a winter dormancy in cambial activity: a temperate mediterranean type found in northern areas and at upper elevations, typical for annual vegetation, such as deciduous trees and shrubs that have leaves functioning with high photosynthetic capacity as long as soil moisture is available. *F. ornus*, *Q. cerris* and *Q. pubescens* at Lajatico form distinct tree rings that are easy to date. These three species have a clear winter stop, during which they are without leaves, and they have no summer stop.
 - (b) Trees with a summer stop in cambial activity: found in southern areas and at very dry sites where summer-deciduous shrubs have a drought-avoiding behaviour involving leaf desiccation or folding at the end of the growing season (the so-called malacophyllous species, such as *Salvia officinalis* L., *Rosmarinus officinalis* L. and *Cistus* sp.). If precipitation occurs during the dry season, old leaves will be rapidly unfolded and growth will resume (Gucci *et al.*, 1997).
 - (c) Trees with a double stop, in winter and in summer: an adapted mediterranean type, typical for evergreen sclerophyllous and laurophyllous vegetation, in which the activity of the cambium coincides with the climatic rhythm, with evidence of double rings, as a consequence of winter cold stress and water stress that triggers dormancy during the summer. At Lajatico, *A. unedo* showed a partial summer stop and a very clear winter stop.
 - (d) Trees with cambial activity characterized by no stops: a moist mediterranean type in which water supply enables continuous vegetation growth throughout the year and annual rings are not formed. It is found in wet, coastal sites where water is not limiting or where air humidity (fog) may supply the necessary water for vegetation. At Lajatico, *Q. ilex* showed a very unclear winter stop. Elsewhere, *P. latifolia* probably shows a similar pattern as research indicates that it maintains a positive carbon balance even under conditions of severe drought stress (Rhizopoulou & Mitrakos, 1990).
- (5) Our review of the literature and our data on

ring-width growth at two sites in Tuscany led us to believe that dendrochronological, dendroecological and dendroclimatological studies in mediterranean regions are possible, but only if great care is given to sampling strategies. Major emphasis should be given to site and species selection because of the great spatio-temporal variability in climate, vegetation types, and phenological and ecophysiological conditions.

IX. ACKNOWLEDGEMENTS

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X. REFERENCES

- AKACHUKU, A. E. (1985). Intra-annual variation in wood density in *Gmelina arborea* from X-ray densitometry and its relationship with rainfall. *Tree-Ring Bulletin* **45**, 43–53.
- ARIANOUTSOU-FARAGGITAKI, M., PSARAS, G. & CHRISTODOULAKIS, N. (1984). The annual rhythm of cambial activity in two woody species of the Greek 'maquis'. *Flora* **175**, 221–229.
- ATTOLINI, M. R., CALVANI, F., GALLI, M., NANNI, T., RUGGIERO, L., SCHAEER, E. & ZUANNI, F. (1990). The relationship between climatic variables and wood structure in *Pinus halepensis* Mill. *Theoretical and Applied Climatology* **41**, 121–127.
- AVILA, G., LAJARO, M., ARAYA, S., MONTENEGRO, G. & KUMMEROW, J. (1975). The seasonal cambium activity of Chilean and Californian shrubs. *American Journal of Botany* **62**, 473–478.
- BAAS, P. (1976). Some functional and adaptive aspects of vessels member morphology. In *Wood Structure in Biological and Technological Research* (eds P. Baas, A. J. Bolton and D. M. Catling), pp. 157–181. Leiden Bot. Series 3, Leiden University, The Hague, The Netherlands.
- BAAS, P. & SCHWEINGRUBER, F. H. (1987). Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. *IAWA Bulletin n.s.* **8**, 245–274.
- BAGNOULS, F. & GAUSSEN, H. (1957). Les climats biologiques et leur classification. *Annales de Géographie* **355**, 193–220.
- BARAJAS-MORALES, J. (1985). Wood structural differences between trees of two tropical forests in Mexico. *IAWA Bulletin n.s.* **6**, 355–364.
- BARNETT, J. R. (1976). Rings of collapsed cells in *Pinus radiata* stemwood from lysimeter-grown trees subjected to drought. *New Zealand Journal of Forestry Science* **6**, 461–465.

- BARTÁK, M., RASCHI, A. & TOGNETTI, R. (1999). Photosynthetic characteristics of sun and shade leaves in the canopy of *Arbutus unedo* L. trees exposed to *in situ* long-term elevated CO₂. *Photosynthetica* **37**, 1–16.
- BAZZAZ, F. A. (1996). *Plants in Changing Environments. Linking Physiological, Population, and Community Ecology*. Cambridge University Press, Cambridge, United Kingdom.
- BEARD, J. S. (1983). Ecological control of the vegetation of Southwestern Australia: Moisture versus nutrients. In *Mediterranean-type Ecosystems. The Role of Nutrients* (eds. F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis), pp. 66–73. Springer Verlag, Berlin, Germany.
- BEAUFAIT, W. R. & NELSON, T. C. (1957). Ring counts in second-growth baldcypress. *Journal of Forestry* **55**, 588.
- BELINGARD, C., TESSIER, L., DE NAMUR, C. & SCHWARTZ, D. (1996). Dendrochronological approach to the radial growth of okoume (Congo). *Comptes rendus de l'Académie des sciences Paris, Sciences de la vie* **319**, 523–527.
- BELLOT, J., SÁNCHEZ, J. R., LLEDÓ, M. J. & MARTÍNEZ ESCARRÉ, A. (1992). Litterfall as a measure of primary production in Mediterranean holm-oak forest. *Vegetatio* **99/100**, 69–76.
- BERGER, A. L., GUIOT, J., MATHIEU, L. & MUNAUT, A. V. (1979). Tree-rings and climate in Morocco. *Tree-Ring Bulletin* **39**, 61–75.
- BEUG, H.-J. (1977). Vegetationsgeschichtliche Untersuchungen im Küstenbereich von Istrien (Jugoslawien). *Flora* **166**, 357–381.
- BEYSLAG, W., LANGE, O. L. & TENHUNEN, D. J. (1986). Photosynthese und Wasserhaushalt der immergrünen mediterranen Hartlaubpflanze *Arbutus unedo* L. im Jahreslauf am Freilandstandort in Portugal. I. Tagesläufe von CO₂-Gaswechsel und Transpiration unter natürlichen Bedingungen. *Flora* **178**, 409–444.
- BEYSLAG, W., LANGE, O. L. & TENHUNEN, D. J. (1987). Photosynthese und Wasserhaushalt der immergrünen mediterranen Hartlaubpflanze *Arbutus unedo* L. im Jahreslauf am Freilandstandort in Portugal. II. Charakteristische Gaswechselfparameter von CO₂-Aufnahme und Transpiration. *Flora* **179**, 399–420.
- BEYSLAG, W., LANGE, O. L. & TENHUNEN, D. J. (1990). Photosynthese und Wasserhaushalt der immergrünen mediterranen Hartlaubpflanze *Arbutus unedo* L. im Jahreslauf am Freilandstandort in Portugal. III. Einzelfaktorenanalyse zur Licht-, Temperatur- und CO₂-Abhängigkeit der Netto-photosynthese. *Flora* **184**, 271–289.
- BHATTACHARYYA, A. & YADAV, R. R. (1999). Climatic reconstructions using tree-ring data from tropical and temperate regions of India – a review. *IAWA Journal* **20**, 311–316.
- BLONDEL, J. & ARONSON, J. (1995). Biodiversity and ecosystem function in the Mediterranean basin: human and non-human determinants. In *Mediterranean-type Ecosystems. The Function of Biodiversity* (eds. G. W. Davis and D. M. Richardson), pp. 43–119. Springer Verlag, Berlin, Germany.
- BLONDEL, J. & ARONSON, J. (1999). *Biology and Wildlife of the Mediterranean Region*. Oxford University Press, Oxford, UK.
- BONATTI, E. (1966). North Mediterranean climate during the last Würm glaciation. *Nature* **209**, 984–985.
- BONINSEGNA, J. A., VILLALBA, R., AMARILLA, L. & OCAMPO, J. (1989). Studies on tree rings, growth rates and age-size relationships of tropical tree species in Misiones, Argentina. *IAWA Bulletin n.s.* **10**, 161–169.
- BOOKER, R. E. & SELL, J. (1998). The nanostructure of the cell wall of softwoods and its functions in a living tree. *Holz als Roh- und Werkstoff* **56**, 1–8.
- BORCHERT, R. (1991). Growth periodicity and dormancy. In *Physiology of Trees* (ed. A. S. Raghavendra), pp. 221–245. John Wiley & Sons, New York, USA.
- BORCHERT, R. (1994). Induction of rehydration and bud break by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees: Structure and Function* **8**, 198–204.
- BORGHETTI, M., CINNIRELLA, S., MAGNANI, F. & SARACINO, A. (1998). Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. *Trees: Structure and Function* **12**, 187–195.
- BULI, U. (1949). *Ricerche climatiche sulle pinete di Ravenna*. Consiglio Nazionale delle Ricerche, Centro di Studi per la Geografia Fisica, Tipografia Mareggiani, Bologna, Italy.
- BUSSOTTI, F. & FERRETTI, M. (1998). Air pollution, forest condition and forest decline in Southern Europe: an overview. *Environmental Pollution* **101**, 49–65.
- CALLADO, C. H., DA SILVA NETO, S. J., SCARANO, F. R., BARROS, C. F. & COSTA, C. G. (2001). Anatomical features of growth rings in flood-prone trees of the Atlantic rain forest in Rio de Janeiro, Brazil. *IAWA Journal* **22**, 29–42.
- CALLAWAY, R. M., DELUCIA, E. H. & SCHLESINGER, W. H. (1994). Biomass allocation of montane and desert ponderosa pine: an analog for response to climate change. *Ecology* **75**, 1474–1481.
- CARITAT, A., GUTIÉRREZ, E. & MOLINAS, M. (2000). Influence of weather on cork-ring width. *Tree Physiology* **20**, 893–900.
- CARITAT, A., MOLINAS, M. & GUTIERREZ, E. (1996). Annual cork-ring width variability of *Quercus suber* L. in relation to temperature and precipitation (Extremadura, southwestern Spain). *Forest Ecology and Management* **86**, 113–120.
- CARLQUIST, S. (1975). *Ecological Strategies of Xylem Evolution*. University of California Press, Berkeley, California, USA.
- CARLQUIST, S. (1988). *Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood*. Springer Verlag, Berlin, Germany.
- CARLQUIST, S. & HOEKMAN, D. A. (1985). Ecological wood anatomy of the woody southern California flora. *IAWA Bulletin n.s.* **6**, 319–347.
- CARTAN-SON, M., FLORET, C., GALAN, M. J., GRANDJANNY, M., LEFLOC'H, E., MAISTRE, M., PERRET, P. & ROMANE, F. (1992). Factors affecting radial growth of *Quercus ilex* L. in a coppice stand in southern France. *Vegetatio* **99/100**, 61–68.
- CASTELL, C., TERRADAS, J. & TENHUNEN, J. D. (1994). Water relations, gas exchange, and growth of resprouts and mature plant shoots of *Arbutus unedo* L. and *Quercus ilex* L. *Oecologia* **98**, 201–211.
- CASTRO-DÍEZ, P., VILLAR-SALVADOR, P., PÉREZ-RONTOMÉ, C., MAESTRO-MARTÍNEZ, M. & MONTERRAT-MARTÍ, G. (1997). Leaf morphology and leaf chemical composition in three *Quercus* (Fagaceae) species along a rainfall gradient in NE Spain. *Trees: Structure and Function* **11**, 127–134.
- CASTRO-DÍEZ, P., PUYRAVAUD, J. P., CORNELISSEN, J. H. C. & VILLAR-SALVADOR, P. (1998). Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia* **116**, 57–66.
- CATARINO, F. M., CORREIA, O. A., WEBB, E. & DAVID, M. (1981). Morphological and physiological responses of the Mediterranean evergreen sclerophyll, *Ceratonia siliqua*, to different light intensities. In *Components of Productivity of*

- Mediterranean-climate Regions. Basics and Applied Aspects* (eds. N. S. Margaris and H. A. Mooney), pp. 5–15. Dr W. Junk Publishers, The Hague, The Netherlands.
- CHBOUKI, N., STOCKTON, C. W. & MYERS, D. E. (1995). Spatio-temporal patterns of drought in Morocco. *International Journal of Climatology* **15**, 187–205.
- CHERUBINI, P., SCHWEINGRUBER, F. H. & FORSTER, T. (1997). Morphology and ecological significance of intra-annual radial cracks in living conifers. *Trees: Structure and Function* **11**, 216–222.
- COCHARD, H., BREDI, N., GRANIER, A. & AUSSENAC, G. (1992). Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl, *Q. pubescens* Willd, *Q. robur* L.). *Annales des Sciences Forestières* **49**, 225–233.
- COCHARD, H., PEIFFER, M., LE GALL, K. & GRANIER, A. (1997). Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. *Journal of Experimental Botany* **48**, 655–663.
- COCHARD, H. & TYREE, M. T. (1990). Xylem dysfunction in *Quercus*: vessel size, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology* **6**, 393–407.
- CONWAY, D., BROOKS, N., BRIFFA, K. R., DESTA, S., MERRIN, P. D. & JONES, P. D. (1997). *Exploring the potential for dendroclimatic analysis in Northern Ethiopia*. Final Report, Natural Environment Research Council (contract: GR9/02164), Climatic Research Unit, University of East Anglia, Norwich, United Kingdom.
- CORONA, E. (1983). Dendrocronologia in Italia. *Dendrochronologia* **1**, 21–35.
- CORONA, P., ROMAGNOLI, M. & TORRINI, L. (1995). Stem annual increments as ecobiological indicators in Turkey oak (*Quercus cerris* L.). *Trees: Structure and Function* **10**, 13–19.
- COWLING, R. & RICHARDSON, D. (1995). *Fynbos. South Africa's Unique Floral Kingdom*. Institute for Plant Conservation and Fernwood Press, Vlaeberg, South Africa.
- CRAMER, W. (2001). Fire ecology, Mediterranean forests and global change. *Forest Ecology and Management* **147**, 1–2.
- CUBASCH, U., VON STORCH, H., WASZKEWITZ, J. & ZORITA, E. (1996). Estimates of climate change in Southern Europe derived from dynamical climate model output. *Climate Research* **7**, 129–149.
- DAGET, P. (1977). Le bioclimat méditerranéen: caractères généraux, modes de caractérisation. *Vegetatio* **34**, 1–20.
- DAMESIN, C., RAMBAL, S. & JOFFRE, R. (1998). Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. *Acta Oecologica* **19**, 195–204.
- DAVIS, S. D., EWERS, F. W., WOOD, J., REEVES, J. J. & KOLB, K. J. (1999). Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Écoscience* **6**, 180–186.
- DE LILLIS, M. & FONTANELLA, A. (1992). Comparative phenology and growth in different species of the Mediterranean maquis of central Italy. *Vegetatio* **99/100**, 83–96.
- DEMMIG-ADAMS, B., ADAMS, W. W., WINTER, K., MEYER, A., SCHREIBER, U., PEREIRA, J. S., KRUGER, A., CZYGAN, F. C. & LANGE, O. L. (1989). Photochemical efficiency of photosystem II, photon yield of CO₂ evolution, photosynthetic capacity and carotenoid composition during the midday depression of net CO₂ uptake in *Arbutus unedo* growing in Portugal. *Planta* **177**, 377–387.
- DEVAL, M. S., PARRÉSOL, B. R. & WRIGHT, S. J. (1995). Dendroecological analysis of *Cordia alliodora*, *Pseudobombax septenatum* and *Annona spraguei* in Central Panama. *IAWA Journal* **16**, 411–424.
- DI CASTRI, F. (1990). An ecological overview of the five regions of the world with mediterranean climate. In *Biogeography of Mediterranean Invasions* (eds. R. H. Groves and F. di Castri), pp. 3–15. Cambridge University Press, Cambridge, UK.
- DI CASTRI, F., GOODALL, D. W. & SPECHT, R. L. (1981). *Mediterranean-type shrublands*. Ecosystems of the world 11. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- DI CASTRI, F. & MOONEY, H. A. (1973). *Mediterranean-type Ecosystems. Origin and Structure*. Ecological Studies 7, Springer Verlag, New York, USA.
- DOBBS, C. G. (1942). A false-ring pattern in larch. *Nature* **3804**, 377–379.
- DOBRY, J. & KYNCL, J. (1992). Tree-ring density profiles in Cupressaceae. In *Tree Rings and Environment: Proceedings of the International Symposium, Ystad, Sweden (3–9 September 1990)* (eds. T. S. Bartholin, B. E. Berglund, D. Eckstein, F. H. Schweingruber and O. Eggertsson), pp. 83–84. Lundqua Report 34, Lund, Sweden.
- DOWNES, G., BEADLE, C. & WORLEDGE, D. (1999). Daily stem growth patterns in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Trees: Structure and Function* **14**, 102–111.
- DUHME, F. & HINCKLEY, T. M. (1992). Daily and seasonal variation in water relations of macchia shrubs and trees in France (Montpellier) and Turkey (Antalya). *Vegetatio* **99/100**, 185–198.
- DUNN, E. L., SHROPSHIRE, F. M., SING, L. C. & MOONEY, H. A. (1976). The water factor in convergent evolution in mediterranean-type vegetation. In *Water and Plant Life* (eds. O. L. Lange, L. Kappen and E. D. Schulze), pp. 492–505. Springer Verlag, New York, USA.
- ECKSTEIN, D., OGDEN, J., JACOBY, G. C. & ASH, J. (1981). Age and growth rate determination in tropical trees: the application of dendrochronological methods. In *Age and Growth Rate of Tropical Trees: New Directions for Research* (eds. F. H. Bormann and G. Berlyn), pp. 83–106. School of Forestry and Environmental Studies Bull. 94, Yale University, Yale, USA.
- ENRIGHT, N. J. & GOLDBLUM, D. (1998). Stand structure of the emergent conifer *Agathis ovata* in forest and maquis, Province Sud, New Caledonia. *Journal of Biogeography* **25**, 641–648.
- ESHETE, G. & STÄHL, G. (1999). Tree rings as indicators of growth periodicity of acacias in the Rift Valley of Ethiopia. *Forest Ecology and Management* **116**, 107–117.
- FAHN, A. (1953). Annual wood ring development in maquis trees of Israel. *Palestine Journal of Botany, Jerusalem series* **6**, 1–26.
- FALCON-LANG, H. J. (2000a). A method to distinguish between woods produced by evergreen and deciduous coniferopsids on the basis of growth ring anatomy: a new palaeoecological tool. *Palaeontology* **43**, 785–793.
- FALCON-LANG, H. J. (2000b). The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for palaeoclimatic studies. *Palaeogeography, Palaeoclimatology, Palaeoecology* **160**, 317–328.
- FEGEL, A. C. (1941). *Comparative Anatomy and Varying Physical Properties of Trunk, Branch, and Root Wood in Certain Northeastern Trees*. Bulletin of the New York State College of Forestry at Syracuse University. Technical Publication 55, 14, 5–20.
- FISHER, M. (1994). Is it possible to construct a tree-ring chronology for *Juniperus excelsa* (Bieb.) subsp. *polycarpus* (K.

- Koch), Takhtajan from the northern mountains of Oman? *Dendrochronologia* **12**, 119–127.
- FRANKLIN, D. A. (1969). Growth rings in rimu from south westland terrace forest. *New Zealand Journal of Botany* **7**, 177–188.
- FRITTS, H. C. (1976). *Tree Rings and Climate*. Academic Press, London, UK.
- GARTNER, B. L. (1991a). Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobum*. *Oecologia* **87**, 180–189.
- GARTNER, B. L. (1991b). Structural stability and architecture of vines vs. shrubs of poison oak, *Toxicodendron diversilobum*. *Ecology* **72**, 2005–2015.
- GARTNER, B. L. (1995). Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. In *Plant Stems: Physiology and Functional Morphology* (ed. B. L. Gartner), pp. 125–149. Academic Press Inc., San Diego, California, USA.
- GAVILÁN, R. & FERNÁNDEZ-GONZÁLEZ, F. (1997). Climatic discrimination of Mediterranean broad-leaved sclerophyllous and deciduous forests in central Spain. *Journal of Vegetation Science* **8**, 377–386.
- GILLESPIE, R. D., SYM, S. D. & ROGERS, K. H. (1998). A preliminary investigation of the potential to determine the age of individual trees of *Breonadia salicina* (Rubiaceae) by relating xylem vessel diameter and area to rainfall and temperature data. *South African Journal of Botany* **64**, 316–321.
- GIOVANNINI, G., VALLEJO, R., LUCCHESI, S., BAUTISTA, S., CIOMPI, S. & LLOVET, J. (2001). Effects of land use and eventual fire on soil erodibility in dry Mediterranean conditions. *Forest Ecology and Management* **147**, 15–23.
- GLOCK, W. S. (1951). Cambial frost injuries and multiple growth layers at Lubbock, Texas. *Ecology* **32**, 28–36.
- GOURLAY, I. D. (1995a). Growth ring characteristics of some African *Acacia* species. *Journal of Tropical Ecology* **11**, 121–135.
- GOURLAY, I. D. (1995b). The definition of seasonal growth zones in some African *Acacia* species – a review. *IAWA Journal* **16**, 353–359.
- GRATANI, L. (1997). Canopy structure, vertical radiation profile and photosynthetic function in a *Quercus ilex* evergreen forest. *Photosynthetica* **33**, 139–149.
- GRATANI, L., MARZI, P. & CRESCENTE, M. F. (1992). Morphological adaptations of *Quercus ilex* leaves in the Castelporziano forest. *Vegetatio* **99/100**, 155–161.
- GROVE, A. T. & RACKHAM, O. (2001). *The Nature of Mediterranean Europe*. Yale University Press, London, UK.
- GUCCI, R., MASSAI, R., CASANO, S., GRAVANO, E. & LUCCHESINI, M. (1997). The effect of drought on gas exchange and water potential in leaves of seven mediterranean woody species. In *Impacts of Global Change on Tree Physiology and Forest Ecosystems* (eds. G. M. J. Mohren, K. Kramer and S. Sabaté), pp. 225–231. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- GUCCI, R., MASSAI, R., CASANO, S. & MAZZOLENI, S. (1999). Seasonal changes in the water relations of Mediterranean co-occurring woody species. *Plant Biosystems* **133**, 117–128.
- GUIBAL, F. (1996). Dendrochronological studies in the French Mediterranean area. In *Tree Rings, Environment and Humanity* (eds. J. S. Dean, D. M. Meko and T. W. Swetnam), pp. 505–513. Radiocarbon, University of Arizona, Tucson, Arizona, USA.
- HACKE, U. G., SPERRY, J. S., POCKMAN, W. T., 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.
- HARGRAVE, K. R., KOLB, K. J., EWERS, F. W. & DAVIS, S. D. (1994). Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytologist* **126**, 695–705.
- HILBERT, D. W. & CANADELL, J. (1995). Biomass partitioning and resource allocation of plants from Mediterranean-type ecosystems: possible responses to elevated atmospheric CO₂. In *Global Change and Mediterranean-type Ecosystems* (eds. J. M. Moreno and W. C. Oechel), pp. 76–101. Ecological Studies 117, Springer Verlag, Berlin, Germany.
- HOLBROOK, N. M., WHITBECK, J. L. & MOONEY, H. A. (1995). Drought responses of neotropical dry forest trees. In *Seasonally Dry Tropical Forests* (eds. S. H. Bullock, H. A. Mooney and E. Medina), pp. 243–276. Cambridge University Press, Cambridge, UK.
- HUTTARY, J. (1950). Die Verteilung der Niederschläge auf die Jahreszeiten im Mittelmeergebiet. *Meteorologische Rundschau* **3**, 111–119.
- JACOBY, G. C. (1989). Overview of tree-ring analysis in tropical regions. *IAWA Bulletin n.s.* **10**, 99–108.
- JARBEAU, J. A., EWERS, F. W. & DAVIS, S. D. (1995). The mechanism of water-stress-induced embolism in two species of chaparral shrubs. *Plant, Cell and Environment* **18**, 189–196.
- JONES, M. B., CLIFTON BROWN, J., RASCHI, A. & MIGLIETTA, F. (1995). The effects on *Arbutus unedo* L. of long-term exposure to elevated CO₂. *Global Change Biology* **1**, 295–302.
- KEELEY, J. E. (1993). Utility of growth rings in the age determination of chaparral shrubs. *Madroño* **40**, 1–14.
- KIRSCHBAUM, S. B. & WILLIAMS, D. G. (1991). Colonization of pasture by *Kunzea ericoides* in the Tidbinbilla Valley, ACT, Australia. *Australian Journal of Ecology* **16**, 79–90.
- KÖPPEN, W. (1923). *Der Klima der Erde*. Bornträger, Berlin, Germany.
- KOLB, K. J. & DAVIS, S. D. (1994). Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* **75**, 648–659.
- KRAMER, P. J. & KOZLOWSKI, T. T. (1979). *Physiology of Trees*, 2nd edn. McGraw-Hill, New York, USA.
- KUMMEROW, J. (1981). Structure of roots and root system. In *Mediterranean-type Shrublands* (eds. F. di Castri, D. W. Goodall and R. L. Specht), pp. 269–288. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- KUNIHOLM, P. I., KROMER, B., MANNING, S. W., NEWTON, M., LATINI, C. E. & BRUCE, M. J. (1996). Anatolian tree rings and the absolute chronology of the eastern Mediterranean, 2220–718 BC. *Nature* **381**, 780–783.
- LANGE, O. L., TENHUNEN, J. D. & BEYSCHLAG, W. (1985). Effects of humidity during diurnal courses on the CO₂- and light-saturated rate of net CO₂ uptake in the sclerophyllous leaves of *Arbutus unedo*. *Oecologia* **67**, 301–304.
- LARCHER, W. (1981). Low temperature effects on mediterranean sclerophylls: an unconventional viewpoint. In *Components of Productivity of Mediterranean-climate Regions. Basics and Applied Aspects* (eds. N. S. Margaris and H. A. Mooney), pp. 259–266. Dr W. Junk Publishers, The Hague, The Netherlands.
- LARCHER, W. (1995). *Plant Physiological Ecology*. Springer Verlag, Berlin, Germany.
- LARCHER, W., DE MORAES, J. A. P. V. & BAUER, H. (1981). Adaptive responses of leaf water potential, CO₂-gas exchange and water use efficiency of *Olea europaea* during drying and

- rewatering. In *Components of Productivity of Mediterranean-climate Regions. Basics and Applied Aspects* (eds. N. S. Margaris and H. A. Mooney), pp. 77–84. Dr W. Junk Publishers, The Hague, The Netherlands.
- LARSON, D. W., DOUBT, J. & MATTHES-SEARS, U. (1994). Radially sectorized hydraulic pathways in the xylem of *Thuja occidentalis* as revealed by the use of dyes. *International Journal of Plant Science* **155**, 569–582.
- LECHOWICZ, M. J. (1984). Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *American Naturalist* **124**, 821–842.
- LE HOUÉROU, H. N. (1996). Climate change, drought and desertification. *Journal of Arid Environments* **34**, 133–185.
- LE HOUÉROU, H. N. (2000). Restoration and rehabilitation of arid and semiarid mediterranean ecosystems in North Africa and West Asia: a review. *Arid Soil Research and Rehabilitation* **14**, 3–14.
- LINDORF, H. (1994). Eco-anatomical wood features of species from a very dry tropical forest. *IAWA Journal* **15**, 361–376.
- LIPSHCHITZ, N. & BIGER, G. (1988). Identification of timber and dating of historical buildings in Eretz Israel (Palestine) by dendrohistorical and dendrochronological methods. *Dendrochronologia* **6**, 99–110.
- LIPSHCHITZ, N. & LEV-YADUN, S. (1986). Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. *IAWA Bulletin n.s.* **7**, 145–153.
- LIPSHCHITZ, N., LEV-YADUN, S., ROSEN, E. & WAISEL, Y. (1984). The annual rhythm of activity of the lateral meristems (cambium and phellogen) in *Pinus halepensis* Mill. and *Pinus pinea* L. *IAWA Bulletin n.s.* **5**, 263–274.
- LIPSHCHITZ, N., LEV-YADUN, S. & WAISEL, Y. (1981). The annual rhythm of activity of the lateral meristems (cambium and phellogen) in *Cupressus sempervirens* L. *Annals of Botany* **47**, 485–496.
- LIPSHCHITZ, N., LEV-YADUN, S. & WAISEL, Y. (1985). The annual rhythm of activity of the lateral meristems (cambium and phellogen) in *Pistacia lentiscus* L. *IAWA Bulletin n.s.* **6**, 239–244.
- LIPP, C. C. & NILSEN, E. T. (1997). The impact of subcanopy light environment on the hydraulic vulnerability of *Rhododendron maximum* to freeze-thaw cycles and drought. *Plant, Cell and Environment* **20**, 1264–1272.
- LLORET, F., CASANOVAS, C. & PEÑUELAS, J. (1999). Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology* **13**, 210–216.
- LO GULLO, M. A. & SALLEO, S. (1988). Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *New Phytologist* **108**, 267–276.
- LO GULLO, M. A. & SALLEO, S. (1993). Different vulnerabilities of *Quercus ilex* L. to freeze- and summer drought-induced xylem embolism: an ecological interpretation. *Plant, Cell and Environment* **16**, 511–519.
- MARGARIS, N. S. (1981). Adaptive strategies in plants dominating mediterranean-type ecosystems. In *Mediterranean-type Shrublands* (eds. F. di Castri, D. W. Goodall and R. L. Specht), pp. 309–315. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- MARGARIS, N. S. & MOONEY, H. A. (1981). *Components of Productivity of Mediterranean-climate Regions. Basics and Applied Aspects*. Dr W. Junk Publishers, The Hague, The Netherlands.
- MARGARIS, N. S. & PAPADOGIANNI, P. (1977). The ratio of ray and fusiform initials in some plants dominating Mediterranean formations in Greece. *Flora* **166**, 219–222.
- MARGARIS, N. S. & PAPADOGIANNI, P. (1978). Cambial activity in some plants dominating phryganic formations in Greece. *Phyton (Greece)* **36**, 1–5.
- MARIOLOPOULOS, E. G. (1962). Fluctuation of rainfall in Attica during the years of the erection of the Parthenon. *Pure and Applied Geophysics* **51**, 243–250.
- MARTÍNEZ-RAMOS, M. & ALVAREZ-BUYLLA, E. R. (1998). How old are tropical rain forest trees? *Trends in Plant Science* **3**, 400–405.
- MAUFFETTE, Y. & OECHEL, W. C. (1987). Seasonal photosynthate allocation of the Californian coast live oak *Quercus agrifolia*. In *Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems* (eds. J. D. Tenhunen, F. M. Catarino, O. L. Lange and W. C. Oechel), pp. 437–444. Springer Verlag, Berlin, Germany.
- MAUGINI, E. (1949). L'evoluzione della cerchia legnosa in *Quercus pubescens* W. e in *Quercus ilex* L. nel clima di Firenze. *Nuovo Giornale Botanico Italiano n.s.* **56**, 593–611.
- MAZZOLENI, S., LO PORTO, A. & BLASI, C. (1992). Multivariate analysis of climatic patterns of the Mediterranean basin. *Vegetatio* **98**, 1–12.
- MEIGGS, R. (1982). *Trees and Timber in the Ancient Mediterranean World*. Oxford University Press, Oxford, UK.
- MEKO, D., STOCKTON, C. W. & BOGGESE, W. R. (1995). The tree-ring record of severe sustained drought. *Water Resources Bulletin* **31**, 789–801.
- MENCUCCINI, M. & GRACE, J. (1995). Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology* **15**, 1–10.
- MENCUCCINI, M., GRACE, J. & FIORAVANTI, M. (1997). Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. *Tree Physiology* **17**, 105–113.
- MESSERI, A. (1948). L'evoluzione della cerchia legnosa in *Pinus halepensis* Mill. in Bari dal luglio 1946 al luglio 1947. *Nuovo Giornale Botanico Italiano n.s.* **55**, 111–132.
- MESSERI, A. (1953). Relazioni fra clima ed accrescimento del tronco nel Pino d'Aleppo. Osservazioni nella pineta di Patemisco Gallio (Golfo di Taranto). *Nuovo Giornale Botanico Italiano n.s.* **60**, 251–287.
- METEOROLOGICAL OFFICE (1962). *Weather in the Mediterranean. Vol. 1. General Meteorology*. HMSO, London, UK.
- MIGLIETTA, F., RASCHI, A., BETTARINI, I., RESTI, R. & SELVI, F. (1993). Natural CO₂ springs in Italy: a resource for examining long-term response of vegetation to rising atmospheric CO₂ concentrations. *Plant, Cell and Environment* **16**, 873–878.
- MILBURN, J. A. (1993). Cavitation. A review: past, present and future. In *Water Transport in Plants under Climatic Stress* (eds. M. Borghetti, J. Grace and A. Raschi), pp. 14–26. Cambridge University Press, Cambridge, UK.
- MILLER, P. C. (1981). Light and energy environments of chaparral and matorral in Southern California and Central Chile. In *Components of Productivity of Mediterranean-climate Regions. Basics and Applied Aspects* (eds. N. S. Margaris and H. A. Mooney), pp. 267–276. Dr W. Junk Publishers, The Hague, The Netherlands.
- MILLER, P. C. & POOLE, D. K. (1979). Patterns of water use by shrubs in southern California. *Forest Science* **25**, 84–98.
- MILTON, S. J., GOURLAY, I. D. & DEAN, W. R. J. (1997). Shrub growth and demography in arid Karoo, South Africa:

- inference from wood rings. *Journal of Arid Environments* **37**, 487–496.
- MITRAKOS, K. (1980). A theory for Mediterranean plant-life. *Oecologia Plantarum* **15**, 245–252.
- MOLL, E. J., MCKENZIE, B. & MGLACHLAN, D. (1980). A possible explanation for the lack of trees in the Fynbos, Cape Province, South Africa. *Biological Conservation* **17**, 221–228.
- MOONEY, H. A. (1977). *Convergent Evolution in Chile and California*. Mediterranean climate ecosystems. US/IBP Synthesis Series 5, Dowden, Hutchinson & Ross, Inc., Stroudsburg, USA.
- MOONEY, H. A. (1981). Primary production in mediterranean-climate regions. In *Mediterranean-type Shrublands* (eds. F. di Castri, D. W. Goodall and R. L. Specht), pp. 249–255. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- MOONEY, H. A. (1982). Habitat, plant form, and plant water relations in Mediterranean-climate regions. *Oecologia Mediterranea* **8**, 481–488.
- MOONEY, H. A. & CHU, C. (1974). Seasonal carbon allocation in *Heteromeles arbutifolia*, a California evergreen shrub. *Oecologia* **14**, 295–306.
- MOONEY, H. A. & DUNN, E. L. (1970a). Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. *Evolution* **24**, 292–303.
- MOONEY, H. A. & DUNN, E. L. (1970b). Photosynthetic systems of Mediterranean-climate shrubs and trees of California and Chile. *The American Naturalist* **104**, 447–453.
- MOONEY, H. A. & KUMMEROW, J. (1981). Phenological development of plants in mediterranean-climate regions. In *Mediterranean-type Shrublands* (eds. F. di Castri, D. W. Goodall and R. L. Specht), pp. 303–307. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- MORENO, J. M. & OECHEL, W. C. (1995). *Global Change and Mediterranean-type Ecosystems*. Ecological Studies 117, Springer Verlag, Berlin, Germany.
- NAHAL, I. (1981). The mediterranean climate from a biological viewpoint. In *Mediterranean-type Shrublands* (eds. F. di Castri, D. W. Goodall and R. L. Specht), pp. 63–86. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- NARDINI, A., LO GULLO, M. A. & SALLES, S. (1999). Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant, Cell and Environment* **22**, 109–116.
- NAVEH, Z. (1967). Mediterranean ecosystems and vegetation types in California and Israel. *Ecology* **48**, 445–458.
- NICAULT, A., RATHGEBER, C., TESSIER, L. & THOMAS, A. (2001). Observations sur la mise en place du cerne chez le pin d'Alep (*Pinus halepensis* Mill.): confrontation entre les mesures de croissance radiale, de densité et les facteurs climatiques. *Annals of Forest Science* **58**, 769–784.
- OGATA, Y., NOBUCHI, T., FUJITA, M. & SAHRI, M. H. (2001). Growth rings and tree growth in young para rubber trees from peninsular Malaysia. *IAWA Journal* **22**, 43–56.
- OPPENHEIMER, H. R. (1945). Cambial wood production in stems of *Pinus halepensis*. *Palestine Journal of Botany, Rehovot Series* **2**, 22–51.
- PANAÏOTIS, C., CARCAILLET, C. & M'HAMED, M. (1997). Determination of the natural mortality age of an holm oak (*Quercus ilex* L.) stand in Corsica (Mediterranean Island). *Acta Oecologica* **18**, 519–530.
- PANAÏOTIS, C., LOISEL, R. & PARADIS, G. (1995). Dating natural gaps in the holm oak forest (*Quercus ilex* L.) in Fango MAB Reserve (Corsica) by reading rings of maquis components. *Annales des Sciences Forestières* **52**, 477–487.
- PARSONS, D. J. & MOLDENKE, A. R. (1975). Convergence in vegetation structures along analogous climatic gradients in California and Chile. *Ecology* **56**, 950–957.
- PATÓN, D., AZOCAR, P. & TOVAR, J. (1998). Growth and productivity in forage biomass in relation to the age assessed by dendrochronology in the evergreen shrub *Cistus ladanifer* (L.) using different regression models. *Journal of Arid Environments* **38**, 221–235.
- PATÓN, D., ZABALLOS, T., VALLE, M., ROTA, A., ROJAS, A., MARTÍN, L. & TOVAR, J. (1993). Calculo de la carga ganadera maxima por metodos dendrocronologicos en matorrales de *Cistus ladanifer*. *Archivos de Zootecnia* **42**, 415–428.
- PEREIRA, J. S. & CHAVES, M. M. (1995). Plant responses to drought under climate change in mediterranean-type ecosystems. In *Global Change and Mediterranean-type Ecosystems* (eds. J. M. Moreno and W. C. Oechel), pp. 140–160. Springer Verlag, Berlin, Germany.
- PITACCO, A., GALLINARO, N. & GIULIVO, C. (1992). Evaluation of actual evapotranspiration of a *Quercus ilex* L. stand by the Bowen Ratio-Energy Budget method. *Vegetatio* **99/100**, 163–168.
- POCKMAN, W. T. & SPERRY, J. S. (1997). Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* **109**, 19–27.
- PONS, A. & QUÉZEL, P. (1985). The history of the flora and vegetation and past and present human disturbance in the mediterranean area. *Geobotany* **7**, 25–43.
- PUMIJUMNONG, N., ECKSTEIN, D. & SASS, U. (1995). Tree-ring research on *Tectona grandis* L. in northern Thailand. *IAWA Journal* **16**, 385–392.
- PUMIJUMNONG, N., ECKSTEIN, D., SASS, U. & PARK, W.-K. (1998). Tree-ring network on teak (*Tectona grandis* L.) and its use for climatic reconstruction. In *Proceedings of the Second East-Asia Workshop on Tree-ring Analysis* (eds. W.-K. Park and J.-S. Kim), pp. 165–170. Agricultural science and technology Institute, Chungbuk National University, Cheongju, Republic of Korea.
- RAIESI, F. R. (1998). *Effects of Elevated Atmospheric CO₂ on Soil Organic Carbon Dynamics in a Mediterranean Forest Ecosystem*. Ph.D. Dissertation, Wageningen Agricultural University, Wageningen, The Netherlands.
- RAIESI GAHROOEE, F. (1998). Impacts of elevated atmospheric CO₂ on litter quality, litter decomposability and nitrogen turnover rate of two oak species in a Mediterranean forest ecosystem. *Global Change Biology* **4**, 667–677.
- RAVEN, P. H. (1973). The evolution of Mediterranean floras. In *Mediterranean-type Ecosystems: Origin and Structure* (eds. F. di Castri and H. A. Mooney), pp. 213–224. Springer Verlag, New York, New York, USA.
- REDTFELDT, R. A. & DAVIS, S. D. (1996). Physiological and morphological evidence of niche segregation between two co-occurring species of *Adenostoma* in California Chaparral. *Écoscience* **3**, 290–296.
- REED, E. L. & GLOCK, W. S. (1939). Doubling or intermittent growth in the “annual ring” of Arizona cypress. *Pan-American Geologist* **72**, 74–75.
- RHIZOPOULOU, S. & MITRAKOS, K. (1990). Water relations of evergreen sclerophylls. I. Seasonal changes in the water relations of eleven species from the same environment. *Annals of Botany* **65**, 171–178.

- RIGG, L. S., ENRIGHT, N. J. & JAFFRÉ, T. (1998). Stand structure of the emergent conifer *Araucaria laubensfelsii*, in maquis and rainforest, Mont Do, New Caledonia. *Australian Journal of Ecology* **23**, 528–538.
- ROMAGNOLI, M. & CODIPIETRO, G. (1996). Pointer years and growth in Turkey oak (*Quercus cerris* L.) in Latium (central Italy). A dendroclimatic approach. *Annales des Sciences Forestières* **53**, 671–684.
- SAFAR, W. (1994). *Contribution à l'étude dendroécologique du Pin d'Alep (Pinus halepensis Mill.) dans une région semi-aride d'Algérie: l'Atlas saharien (Ouled Nail – Aurès – Hodna)*. Thèse de doctorat, Université de Droit, d'Économie et des Sciences d'Aix-Marseille III, Faculté des Sciences et Techniques Saint-Jérôme, Laboratoire de Botanique Historique et Palynologie, Marseille, France.
- SALLEO, S. & LO GULLO, M. A. (1993). Drought resistance strategies and vulnerability to cavitation of some Mediterranean sclerophyllous trees. In *Water Transport in Plants under Climatic Stress* (eds M. Borghetti, J. Grace and A. Raschi), pp. 99–113. Cambridge University Press, Cambridge, UK.
- SALLEO, S. & NARDINI, A. (2000). Sclerophylly: evolutionary advantage or mere epiphenomenon? *Plant Biosystems* **134**, 247–259.
- SALLEO, S., NARDINI, A. & LO GULLO, M. A. (1997). Is sclerophylly of Mediterranean evergreens an adaptation to drought? *New Phytologist* **135**, 603–612.
- SASS, U., KILLMANN, W. & ECKSTEIN, D. (1995). Wood formation in two species of Dipterocarpaceae in peninsular Malaysia. *IAWA Journal* **16**, 371–384.
- SCARAMUZZI, F., PORCELLI-ARMENISE, V. & DE GAETANO, A. (1971). Recherches sur le comportement et le rythme de la callogenèse de fragments de tiges de certains arbres. *Comptes rendus de l'Académie des sciences Paris* **272**, 2544–2547.
- SCARASCIA-MUGNOZZA, G., OSWALD, H., PIUSSI, P. & RADOGLU, K. (2000). Forests of the Mediterranean region: gaps in knowledge and research needs. *Forest Ecology and Management* **132**, 97–109.
- SCHULMAN, E. (1938). Classification of false annual rings in Monterey pine. *Tree-ring Bulletin* **4**, 4–7.
- SCHULMAN, E. (1939). Classification of false annual rings in west Texas pines. *Tree-ring Bulletin* **6**, 11–13.
- SCHWEINGRUBER, F. H. (1988). *Tree Rings. Basics and Applications in Dendrochronology*. Reidel, Dordrecht, The Netherlands.
- SCHWEINGRUBER, F. H. (1993). *Trees and Wood in Dendrochronology*. Springer Verlag, Berlin, Germany.
- SCHWEINGRUBER, F. H. (1996). *Tree Rings and Environment. Dendroecology*. Paul Haupt, Berne, Switzerland.
- SCHWEINGRUBER, F. H., ECKSTEIN, D., SERRE-BACHET, F. & BRÄKER, O. U. (1990). Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia* **8**, 9–38.
- SERRE-BACHET, F. (1982). Analyse dendroclimatologique comparée de quatre espèces de pins et du chêne pubescent dans la région de la Gardiole près Rians (Var, France). *Ecologia Mediterranea* **8**, 167–183.
- SERRE-BACHET, F. (1985). La dendrochronologie dans le bassin méditerranéen. *Dendrochronologia* **3**, 77–92.
- SERRE-BACHET, F. & GUIOT, J. (1987). Summer temperature changes from tree-rings in the mediterranean area during the last 800 years. In *Abrupt Climatic Change, Evidence and Implications* (eds W. H. Berger and L. D. Labeyrie), pp. 89–97. NATO ASI Series C, Mathematical and Physical Sciences, Vol. 216, Reidel Publ. Co., The Hague, The Netherlands.
- SERRE-BACHET, F., GUIOT, J. & TESSIER, L. (1992). Dendroclimatic evidence from southwestern Europe and North-western Africa. In *Climate since AD 1500* (eds R. Bradley and P. D. Jones), pp. 349–365. Routledge, London, UK.
- SPARKS, J. P. & BLACK, R. A. (1999). Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. *Tree Physiology* **19**, 453–459.
- SPAULDING, W. G. (1991). Pluvial climatic episodes in North America and North Africa: types and correlation with global climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* **84**, 217–227.
- SPECHT, R. L. (1981). Primary production in mediterranean-climate ecosystems regenerating after fire. In *Mediterranean-type Shrublands* (eds F. di Castri, D. W. Goodall and R. L. Specht), pp. 257–267. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- SPECHT, R. L. & MOLL, E. J. (1983). Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In *Mediterranean-type Ecosystems. The Role of Nutrients* (eds F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis), pp. 41–65. Springer Verlag, Berlin, Germany.
- SPECHT, R. L., MOLL, E. J., PRESSINGER, F. & SOMMERVILLE, J. (1983). Moisture regime and nutrient control of seasonal growth in mediterranean ecosystems. In *Mediterranean-type Ecosystems. The Role of Nutrients* (eds F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis), pp. 120–132. Springer Verlag, Berlin, Germany.
- SPERRY, J. S. & SALIENDRA, N. Z. (1994). Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **17**, 1233–1241.
- SPERRY, J. S. & SULLIVAN, J. E. M. (1992). Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology* **100**, 605–613.
- SPERRY, J. S., TYREE, M. T. & DONNELLY, J. R. (1988). Vulnerability of xylem to embolism in a mangrove vs. an inland species of Rhizophoraceae. *Physiologia Plantarum* **74**, 276–283.
- SPICER, R. & GARTNER, B. L. (1998a). How does a gymnosperm branch (*Pseudotsuga menziesii*) assume the hydraulic status of a main stem when it takes over as leader? *Plant, Cell and Environment* **21**, 1063–1070.
- SPICER, R. & GARTNER, B. L. (1998b). Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood. *Tree Physiology* **18**, 777–784.
- STAHL, D. W. (1999). Useful strategies for the development of tropical tree-ring chronologies. *IAWA Journal* **20**, 249–253.
- STOCK, W. D., VAN DER HEYDEN, F. & LEWIS, O. A. M. (1992). Plant structure and function. In *The Ecology of Fynbos. Nutrients, Fire and Diversity* (ed. R. Cowling), pp. 226–240. Oxford University Press, Oxford, UK.
- STOKES, M. A. & SMILEY, T. L. (1968). *An Introduction to Tree-ring Dating*. University of Chicago Press, Chicago, USA.
- SUC, J.-P. (1984). Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* **307**, 429–432.
- SUSMEL, L., VIOLA, F. & BASSATO, G. (1976). *Ecologia della lecceta del Supramonte di Orgosolo (Sardegna Centro-orientale)*. Cedam, Padova, Italy.

- TELEWSKI, F. W. (1998). Physiology of tree-ring formation. In *Proceedings of the Second East-Asia Workshop on Tree-ring Analysis* (eds. W.-K. Park and J.-S. Kim), pp. 37–51. Agricultural science and technology Institute, Chungbuk National University, Cheongju, Republic of Korea.
- TELEWSKI, F. W. & LYNCH, A. M. (1991). Measuring growth and development of stems. In *Techniques and Approaches in Forest Tree Ecophysiology* (eds. J. P. Lassoie and T. M. Hinckley), pp. 503–555. CRC Press, Boca Raton, Florida, USA.
- TENHUNEN, J. D., LANGE, O. L. & BRAUN, M. (1981). Midday stomatal closure in mediterranean type sclerophylls under simulated habitat conditions in an environmental chamber. II. Effect of the complex of leaf temperature and air humidity on gas exchange of *Arbutus unedo* and *Quercus ilex*. *Oecologia* **50**, 5–11.
- TENHUNEN, J. D., LANGE, O. L., BRAUN, M., MEYER, A., LÖSCH, R. & PEREIRA, J. S. (1980). Midday stomatal closure in *Arbutus unedo* leaves in a natural macchia and under simulated habitat conditions in an environmental chamber. *Oecologia* **47**, 365–367.
- TENHUNEN, D. J., LANGE, O. L. & JAHNER, D. (1982). The control by atmospheric factors and water stress of midday stomatal closure in *Arbutus unedo* growing in a natural macchia. *Oecologia* **55**, 165–169.
- TERRADAS, J. (1999). Holm oak and holm oak forests: an introduction. In *Ecology of Mediterranean Evergreen Oak Forests* (eds. F. Rodà, J. Retana, C. A. Gracia and J. Bellot), pp. 3–14. Springer Verlag, Berlin, Germany.
- TERRADAS, J. & SAVÉ, R. (1992). The influence of summer and winter stress and water relationships on the distribution of *Quercus ilex* L. *Vegetatio* **99/100**, 137–145.
- THOMAS, C. M. & DAVIS, S. D. (1989). Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* **80**, 309–320.
- TILL, C. & GUIOT, J. (1990). Reconstruction of precipitation in Morocco since AD 1100, based on *Cedrus atlantica* tree-ring widths. *Quaternary Research* **33**, 337–351.
- TINGLEY, M. A. (1937). Double growth rings in Red Astrachan. *Proceedings American Society Horticultural Science* **34**, 61.
- TOGNETTI, R. & BORGHETTI, M. (1994). Formation and seasonal occurrence of xylem embolism in *Alnus cordata*. *Tree Physiology* **14**, 241–250.
- TOGNETTI, R., CHERUBINI, P. & INNES, J. L. (2000). Comparative stem-growth rates of Mediterranean trees under background and naturally-enhanced ambient CO₂ concentrations. *New Phytologist* **146**, 59–74.
- TOGNETTI, R., LONGOBUCCO, A. & RASCHI, A. (1998). Vulnerability of xylem to embolism in relation to plant hydraulic resistance in *Quercus pubescens* and *Quercus ilex* co-occurring in a Mediterranean coppice stand in central Italy. *New Phytologist* **139**, 437–447.
- TOMASELLI, R. (1981). Main physiognomic types and geographic distribution of shrub systems related to mediterranean climates. In *Mediterranean-type Shrublands* (eds. F. di Castri, D. W. Goodall and R. L. Specht), pp. 95–106. Ecosystems of the world 11, Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- TOUCHAN, R. & HUGHES, M. K. (1999). Dendrochronology in Jordan. *Journal of Arid Environments* **42**, 291–303.
- TOUCHAN, R., MEKO, D. & HUGHES, M. K. (1999). A 396-year reconstruction of precipitation in Southern Jordan. *Journal of the American Water Resources Association* **35**, 49–59.
- TRETIACH, M. (1993). Photosynthesis and transpiration of evergreen Mediterranean and deciduous trees in an ecotone during a growing season. *Acta Oecologica* **14**, 341–360.
- TRUMBLE, H. C. (1939). Climatic factors in relation to the agricultural regions of southern Australia. *Transactions of the Royal Society of South Australia* **63**, 36–43.
- TYREE, M. T., DAVIS, S. D. & COCHARD, H. (1994). Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal* **15**, 335–360.
- TYREE, M. T. & EWERS, F. W. (1991). The hydraulic architecture of trees and other woody plants (Tansley Review nr 34). *New Phytologist* **119**, 345–360.
- TYREE, M. T., SALLEO, S. & MOSCA, R. (1999). Refilling of embolized vessels in young stems of laurel: do we need a new paradigm? *Plant Physiology* **120**, 11.
- VAN DER BURGT, X. M. (1997). Determination of the age of *Pinus occidentalis* in La Celestina, Dominican Republic, by the use of growth rings. *IAWA Journal* **18**, 139–146.
- VETTER, R. E. & WIMMER, R. (1999). Remarks on the current situation of tree-ring research in the tropics. In *Tree-ring Analysis: Biological, Methodological and Environmental Aspects* (eds. R. Wimmer and R. E. Vetter), pp. 131–137. CAB International, Cambridge, UK.
- VILÀ, M., LLORET, F., OGHIERI, E. & TERRADAS, J. (2001). Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management* **147**, 3–14.
- VILLALBA, R. & VEBLEN, T. T. (1996). A tree-ring record of dry spring-wet summer events in the forest-steppe ecotone, Northern Patagonia, Argentina. In *Tree Rings, Environment and Humanity* (eds. J. S. Dean, D. M. Meko and T. W. Swetnam), pp. 107–116. Radiocarbon, University of Arizona, Tucson, Arizona, USA.
- VILLAR-SALVADOR, P., CASTRO-DÍEZ, P., PEREZ-RONTOME, C. & MONTSERRAT-MARTI, G. (1997). Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees: Structure and Function* **12**, 90–96.
- VITA-FINZI, C. (1969). *The Mediterranean Valleys. Geological Changes in Historic Times*. Cambridge University Press, Cambridge, UK.
- WAGNER, K. R. & DAVIS, S. D. (1998). Tradeoffs between hydraulic efficiency and mechanical strength stems of four co-occurring species of chaparral shrubs. *Oecologia* **117**, 53.
- WALTER, H. & LIETH, H. (1960). *Klimadiagramm-Weltatlas*. Gustav Fischer Verlag, Vienna, Austria.
- WERNER, C., CORREIA, O. & BEYSLAG, W. (1999). Two different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. *Acta Oecologica* **20**, 15–23.
- WIEMANN, M. C., MANCHESTER, S. R. & WHEELER, E. A. (1999). Paleotemperature estimation from dicotyledonous wood anatomical characters. *Palaios* **14**, 459–474.
- WILSON, B. F. (1995). Shrub stems: forms and function. In *Plant Stems: Physiology and Functional Morphology* (ed. B. L. Gartner), pp. 91–102. Academic Press Inc., San Diego, California, USA.
- WIMMER, R., STRUMIA, G. & HOLAWA, F. (2000). Use of false rings in Austrian pine to reconstruct early growing season precipitation. *Canadian Journal of Forest Research* **30**, 1691–1697.
- WORBES, M. (1995). How to measure growth dynamics in tropical trees – a review. *IAWA Journal* **16**, 337–351.
- WORBES, M. (1999). Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from

- the Caparo Forest Reserve in Venezuela. *Journal of Ecology* **87**, 391–403.
- WORBES, M. & JUNK, W. J. (1999). How old are tropical trees? The persistence of a myth. *IAWA Journal* **20**, 255–260.
- ZHANG, S. H. & ROMANE, F. (1991). Variations de la croissance radiale de *Quercus ilex* L. en fonction du climat. *Annales des Sciences Forestières* **48**, 225–234.
- ZIMMERMANN, M. H. (1978). Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany* **56**, 2286–2295.
- ZIMMERMANN, M. H. (1983). *Xylem Structure and the Ascent of Sap*. Springer Verlag, Berlin, Germany.
- ZIMMERMANN, M. H. & POTTER, D. (1982). Vessel-length distribution in branches, stem and root of *Acer rubrum* L. *IAWA Bulletin n.s.* **3**, 103–109.