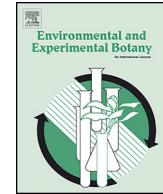




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The challenge of Mediterranean sclerophyllous vegetation under climate change: From acclimation to adaptation

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ABSTRACT

Forecasting models for climate change in southern Europe differ from those proposed for central and northern regions mainly with regard to precipitation. In fact, a strong reduction in average rainfall, mainly caused by decrease frequency of rainy events, is believed to occur in the Mediterranean basin in the forthcoming hundred years. Increased frequency of drought events will be paralleled and exacerbated by warming. Differently from areas where plant growth is limited by sub-optimal temperature (i.e. boreal and most temperate forests) and where warming has been reported to increase carbon assimilation and growth, plants growing in the Mediterranean basin are currently near their temperature optimum, and warming may contribute (e.g. with drought) to impair photosynthesis and depress growth and survival. Rising atmospheric CO₂ has been found to increase growth, photosynthesis water use efficiency, and may partially alleviate the deleterious effects of warming and drought. However, in areas where severe and prolonged drought episodes occur, severe photoinhibition and metabolic limitation to photosynthesis may prevent Mediterranean sclerophylls to take advantage of higher atmospheric CO₂, and may slow down recovery after the end of the dry season. The most sensitive forest types consist in tree species which are, in the Mediterranean basin, at the southernmost limit of their distribution range. In contrast, thermophilic trees are expected to have a greater diffusion both in southern and central Europe, as winter cold stress will be reduced by warming. Yet due to great variability of ecological features, the alleged substitution of tree species can follow a natural pattern from south to north and from low to high altitudes, without considering obstacles deriving from urbanization. For these reasons, research on the performance and ecologic plasticity of different genotypes, on species selection, and on planting and management techniques can have strategic importance for adaptive forest management.

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1. Introduction

After oscillating between 180 and 300 ppm for over 2-million years, in the last 200 years global atmospheric CO₂ concentration has risen from the 280 ppm of the pre-industrial age to the present 400 ppm (National Oceanic and Atmospheric Administration, 2012) and models predict a further increase in atmospheric CO₂ concentration to reach 600 ppm within this century (Christensen et al., 2007). This rapid change in atmospheric CO₂ concentration has been driving a profound change in climate worldwide (Christensen et al., 2007). Climate change manifests itself in two fundamentally different ways: as a change in the average yearly temperature and/or rainfall, and as a change in the frequency and intensity of rain pulses and heat waves (Rumukainen, 2012). The Mediterranean environment appears more affected by climate change than most of other climatic zones: at global level, an increase of air temperature

between 1.3 and 1.8 °C is expected within 2050, and an increase of 2–3 °C is foreseen for southern Europe (Christensen et al., 2007). Furthermore, climatic models indicate that the Mediterranean basin will be one of the areas subject to the most drastic reductions in precipitation (Petit et al., 2005; Christensen et al., 2007). The decline of average rainfall per year is mainly due to thermodynamic factors (i.e. reduced relative humidity resulting from larger continental warming compared to surrounding sea areas and reduced soil moisture due mainly to spring warming causing earlier snowmelt), and will be paralleled by a change in the frequency and intensity of rainy events. In fact, the average intensity of rainy events is predicted to increase, but their frequency will decrease to a greater extent, particularly during spring and summer months. This is likely to result in extreme drought events during summer, when low water availability is paralleled by heat and high sunlight radiation.

Climate has already changed in the past and plants are known to be able to adapt to changing climate through responses at morpho-anatomical, physiological, and molecular levels (Petit et al., 2005; Ahuja et al., 2010; Reyer et al., 2013). To survive and grow in the

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difficult climatic conditions of the Mediterranean environment, plants have developed a wide range of adaptive traits, including a "fine tuning" of phenological phases to maximize carbon gain while avoiding frost damage in winter (Cleland et al., 2007), and specific morpho-physiological characteristics which allow survival during summer drought (Lo Gullo and Salleo, 1988; McDowell et al., 2008; De Micco and Aronne, 2012). The real concern regarding the 21st century is the rate at which climate is changing, leading to a growing understanding that the current rate of climate change may exceed the rate of evolutionary changes, genetic adaptation or migration in Mediterranean trees (Klein et al., 2012). Mediterranean sclerophyllous vegetation may be particularly threatened as evergreen species are considered slow in the adaptation to changing environmental conditions (Reyer et al., 2013), thus, these species may respond to climate change by migration rather than by evolution.

Modeling current and future tree distribution as a function of climate, several authors have proposed scenarios concerning tree species migration and vegetation changes in the Mediterranean region (Benito-Garzón et al., 2008; Gaucherel et al., 2008; Attorre et al., 2011; Vitale et al., 2012; Cheaib et al., 2012). Evergreen tree species, like *Quercus ilex* L., are recognized to have a great potential for migration and their future range includes xeric regions now occupied by deciduous oaks and mountainous areas. Conversely mountain conifers such as *Pinus sylvestris* L. and *Abies alba* Mill., and temperate deciduous species such as *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl., are predicted to suffer a reduction of the distribution specially at the southernmost part of their range.

The previsions above described, concerning possible vegetation changes and shifts, collide against a principle of persistency of the forests, that are long living formations (Lloret et al., 2012). The homeostatic properties of forest ecosystems induce stabilization processes, that include attenuation of the mortality of adult trees caused by site quality variability, genotypic variability, phenotypic plasticity, and facilitative interactions. Despite of evidences reporting that seedling emergence is reduced and seedling mortality is increased by global warming (Lloret et al., 2004a), compensation may also occur by increasing future survival due to beneficial effect of reduced competition resulting from lower density in affected stands, for instance as a consequence of gap openings after event-caused mortality (Lloret et al., 2012).

The role of Mediterranean vegetation, forests and shrubland in the uptake and accumulation of carbon was highlighted by Garbulski et al. (2008). That capacity is reduced during events of extreme drought accompanied by abnormal heat waves, as highlighted by long term eddy covariance observation (Ciais et al., 2005) and experiments simulating increased heating and drought (Ogaya et al., 2011).

The sensitivity of Mediterranean species to climate change factors (increased CO₂, temperature, drought, tropospheric ozone, UV radiations and their interactions) was tested from the scientific community by mean of several controlled and field experiments. The present paper aims to verify, based on the current state of the scientific literature, the physiological effects of the above cited factors (single and in combination) on evergreen sclerophyllous woody species typical of Southern Europe. The insights obtained from experimental research will be then reconsidered in the light of the ecological consequences of climate change in the "real world", revealed both by observations made in case studies and extensive field surveys (ICP-Forests programme, see Müller-Edzards et al., 1997). While in controlled experiments plants are acclimated to certain environmental conditions, field observations have been primary focused on plants born and grown under modified conditions (e.g. near CO₂ springs), which were therefore able to adapt to environmental changes.

The hypothesis to be tested is that, despite the alleged tolerance of Mediterranean evergreen sclerophyllous species (both trees and shrubs) to increasing drought and temperature, these factors are expected to exert a harmful action, potentially able to trigger desertification processes.

2. Photosynthesis and growth: experimental evidence in a global-change scenario

2.1. Carbon dioxide

Plant responses to elevated CO₂ have been well documented on a wide range of tropical, temperate and boreal species, while research on the Mediterranean ones has been restricted to only a limited number of genera (e.g. the evergreen oaks *Q. ilex* and *Quercus suber* L., see Table 1): decreases in stomatal conductance and increased growth and photosynthesis are the most relevant responses in temperate trees, particularly if water and nutrients are not limiting (Saxe et al., 1998; Maroco et al., 2002; Luo et al., 2004; Ainsworth and Long, 2005; Ghannoum and Way, 2011). Short-term experiments showed that elevated CO₂ concentration increases photosynthesis by increasing the carboxylation rate of Rubisco ($V_{c,max}$) and by decreasing photorespiration (Saxe et al., 1998). Long-term exposure to elevated CO₂ may result in a down-regulation of net photosynthesis (Wolfe et al., 1998; Ainsworth and Long, 2005; Leuzinger et al., 2011) because of: (1) increased demand for reducing power for CO₂ fixation, in the absence of a parallel increase in light availability and/or nutrient availability (Tognetti et al., 2000; Griffin et al., 2001); (2) reduced investment in Rubisco and chlorophyll and lower nitrogen concentration per unit leaf area, resulting in lower photosynthetic potential (A_{max} = net photosynthesis at a near-saturating CO₂ concentration) (Rogers and Humphries, 2000; Smith et al., 2012); (3) reduced stomatal density and conductance, resulting in lower carbon dioxide in the sites of carboxylation (Saxe et al., 1998); (4) increased respiration in the light and altered stroma to grana thylakoids (Griffin et al., 2001); and (5) overproduction of sugars relative to sink strength, insufficient phloem loading and decreased expression of photosynthetic genes induced by carbohydrate accumulation in the leaf (Körner et al., 1995; Paul and Foyer, 2001).

Plant responses to CO₂ are species-specific and findings obtained on temperate or tropical plants cannot be directly extended to the Mediterranean ecosystems for several reasons (Saxe et al., 1998). First, Mediterranean vegetation is largely dominated by slow-growing, evergreen, sclerophyllous vegetation, which has been reported to be slower in the adaptation to high CO₂ (e.g. long-term down-regulation of photosynthesis, reduced stomatal density) than herbs, legumes and deciduous trees (Saxe et al., 1998; Ainsworth and Long, 2005; Petit et al., 2005; Reyer et al., 2013). Second, photosynthesis of evergreen sclerophylls is greatly limited by mesophyll diffusion conductance to CO₂, making carbon assimilation of these species less sensitive to the decreases in stomatal opening induced by high CO₂ (Niiinemets et al., 2011). In addition, the Mediterranean environment is characterized by severe summer drought and enhanced atmospheric CO₂ may be critical in increasing water use efficiency and growth in water limited ecosystems (Osborne et al., 2000). Finally, contrarily to that observed in most boreal and temperate forests, Mediterranean vegetation often experiences excess light stress (Tattini et al., 2005; Guidi et al., 2008, 2011) and increased substrate availability may increase the amount of radiation used for CO₂ fixation and decrease excess excitation energy (Griffin et al., 2001). These findings are consistent with the significant CO₂-induced enhancement of growth and carbon gain observed in several Mediterranean evergreen trees (Jones et al., 1995; Hattenschwiler et al., 1997; Peñuelas

Table 1

Effects of elevated CO₂ on growth, photosynthesis and defence compounds in Mediterranean sclerophyllous vegetation. Abbreviations used in the table: APX = ascorbate peroxidase; A_{sat} = net photosynthesis at saturating light; CAT = catalase; g_m = mesophyll conductance to CO₂; g_s = stomatal conductance to CO₂; J_{max} = apparent contribution of electron transport to ribulose regeneration; leaf N_{area} = leaf nitrogen per unit leaf area; leaf N_{mass} = leaf nitrogen per unit leaf mass; leaf TNC = leaf total non-structural carbohydrates; LMA = leaf mass per area; R_{day} = respiration in the light; SOD = superoxide dismutase; POX = guaiacol peroxidase; V_{c,max} = apparent carboxylation rate by Rubisco.

Species	Reference	Type of experiment	Treatments	Results
<i>Quercus ilex</i> (evergreen), <i>Quercus pubescens</i> (deciduous)	Körner and Miglietta (1994)	Mature vegetation in the natural environment	Lifetime exposure to high CO ₂ (CO ₂ spring, [CO ₂] = 500–1000 ppm)	Elevated CO ₂ reduced leaf N _{mass} ; leaf TNC increased in the deciduous species and were unaffected in the evergreen species
<i>Arbutus unedo</i>	Jones et al. (1995)	Mature vegetation in the natural environment	Lifetime exposure to high CO ₂ (CO ₂ spring, [CO ₂] = 2214 ppm approx.)	Elevated CO ₂ increased A _{sat} and decreased g _s , while V _{c,max} , J _{max} and R _{day} are unaffected.
<i>Quercus ilex</i>	Hattenschwiler et al. (1997)	Mature vegetation in the natural environment	Long term (30 years) CO ₂ enrichment (CO ₂ spring, [CO ₂] = 650 ppm approx.)	Elevated CO ₂ increased stem growth, particularly in young trees and when light availability is high (i.e. no canopy closure)
<i>Citrus aurantium</i>	Peñuelas et al. (1997)	Seedlings in open top chambers	Long-term (85 months) exposure to approx. 700 ppm CO ₂ .	Elevated CO ₂ increased both above- and below-ground biomass; leaf N _{area} and leaf N _{weight} concentrations decreased; leaf Mn, Ca, Mg concentrations initially decrease, then gradually recovered.
<i>Quercus ilex</i> (evergreen), Q. <i>pubescens</i> (deciduous)	Schwanz and Polle (1998)	Mature vegetation in the natural environment	Lifetime exposure to high CO ₂ (CO ₂ spring). 3 different [CO ₂] were compared: 360, 650, 1200 ppm.	Elevated CO ₂ decreased the activities of antioxidant enzymes (CAT, SOD, APX, POX), and the effect persists over time. However, lipid peroxidation did not increase.
<i>Quercus ilex</i> , <i>Phillyrea angustifolia</i> , <i>Phillyrea lentiscus</i>	De Angelis et al. (2000)	Natural vegetation in open top chambers	3 years exposure to elevated (710 ppm) or ambient (350 ppm) CO ₂	Elevated CO ₂ increased litter C and structural compounds and decreased litter nutrient content. Maximum litter decomposition rate decreased under leaves grown under elevated CO ₂ .
<i>Citrus aurantium</i>	Idso and Kimball (2001)	30-cm-tall clones, ground planted in OTC	13 years of exposure to elevated (700 ppm) or ambient (400 ppm) CO ₂	Elevated CO ₂ increased plant biomass. Early stimulation (first 20 months) was very strong (3-fold increase); longer-term measurements (60–160 months) resulted in a 2-fold stimulation of growth.
<i>Quercus ilex</i>	Loreto et al. (2001)	Young (about 5 years) field-grown plants in open top chamber	7 years exposure to elevated (700 ppm) or ambient (350 ppm) CO ₂	Elevated CO ₂ , in the absence of persistent environmental stresses, increased A _{sat} and reduced monoterpene emission, because of the inhibition of monoterpene synthase.
<i>Quercus ilex</i>	Marek et al. (2001)	Natural vegetation in open-top chambers	5 years exposure of sun and shade leaves to ambient (350 ppm approx.) or elevated (ambient + 350 ppm) CO ₂	Elevated CO ₂ increased A _{sat} in both sun and shade leaves.
<i>Quercus ilex</i>	Staudt et al. (2001)	Container-grown (4-L containers) seedlings in greenhouses under controlled conditions	10 months exposure to elevated (700 ppm) or ambient (350 ppm) CO ₂	Elevated CO ₂ increased leaf area growth, LMA and emission of monoterpenes
<i>Quercus ilex</i> (evergreen), Q. <i>pubescens</i> (deciduous)	Rapparini et al. (2004)	Mature vegetation in the natural environment	Lifetime exposure to elevated CO ₂ (CO ₂ spring). Samplings at different distance from the spring, with [CO ₂] ranging between 350 and 1400 ppm.	Basal emission rate of isoprene and monoterpenes was reduced in both species by elevated CO ₂ because of the inhibition of isoprene synthase.
Several deciduous and evergreen species	Niinemets et al. (2011)	Meta-analysis investigating the effects of elevated CO ₂ on photosynthesis in different functional groups	3 different [CO ₂]: 280, 390, 780 ppm	Evergreens are likely to be favored by rising CO ₂ over deciduous species because of lower sensitivity of A _{sat} to g _s in plants with low g _m
<i>Quercus suber</i>	Vaz et al. (2012)	Container-grown (10-L containers) seedlings in greenhouses under controlled conditions	15 months exposure to elevated (700 ppm) or ambient (350 ppm) CO ₂	6 months at elevated CO ₂ increased growth and A _{sat} , and reduced g _s . Differences between treatments disappeared after 15 months exposure to elevated CO ₂

et al., 1997; Marek et al., 2001; Staudt et al., 2001; Vaz et al., 2012) and with the increase of net primary productivity of Mediterranean sclerophyllous vegetation being around twice that estimated for the global total (Osborne et al., 2000). If the primary metabolism of Mediterranean evergreens is likely to be enhanced by elevated-CO₂, evidences of a down-regulation of secondary metabolism have also been reported. A suppressive effect of elevated CO₂ on the activity of ROS-scavenging enzymes, such as ascorbate peroxidase, catalase and superoxide dismutase, and detoxifying enzymes and metabolites, such as GSH-S transferase, has been reported

for Mediterranean plants exposed over the long-term to high CO₂ (Schwanz and Polle, 1998; Marabottini et al., 2001). The decline of antioxidant enzymes under elevated CO₂ conditions may be counterbalanced by enhanced flavonoid biosynthesis (Jaafar et al., 2012). Flavonoids (dihydroxy B-ring substituted in particular) have been reported to be effective in counteracting oxidative damage (Brunetti et al., 2013), particularly when the activity of antioxidant enzymes is impaired (Fini et al., 2011a). However, research about the impact of high CO₂ on flavonoid biosynthesis on Mediterranean sclerophylls is still lacking (Lindroth, 2012).

Similarly to that observed for antioxidant enzymes, emission of volatile organic compounds (VOCs) per unit leaf area has been generally reported to decrease under elevated-CO₂ (Rapparini et al., 2004; Possell and Hewitt, 2010), because of the down-regulation of monoterpene synthases (Loreto et al., 2001). VOCs have been reported to confer resistance to short-term heat stress and to oxidative stress (Loreto et al., 1998; Loreto and Schnitzler, 2010) and their importance may be crucial for Mediterranean evergreens. In fact, isoprene and monoterpenes have been proposed: (1) to contribute, with their biosynthesis, to the dissipation of excess energy; (2) to act as a thermoprotective molecules which stabilize chloroplast membranes during high temperature events; and (3) to have a relevant antioxidant action (Loreto and Schnitzler, 2010). In contrast to most species worldwide which emit isoprene, evergreen Mediterranean vegetation typically emits monoterpenes (Loreto, 2002; Welter et al., 2012), which are less volatile than isoprene and may better exert their protective functions inside the leaves of plants growing in hot and arid areas (Loreto, 2002). Monoterpene-emitting species of the genus *Quercus* have been favored by evolution in occupying Mediterranean-like climates (Loreto, 2002). For example, the trait of light-dependent monoterpene emission was gained by cork oak (*Quercus suber*) after the species radiated to the Mediterranean environment (Staudt et al., 2004; Monson et al., 2013). How the reduction in VOC emission induced by elevated CO₂ will deprive the leaves of their protective function against stresses and how this will affect the ecological performance of emitter Mediterranean species in relation to non-emitters deserves further research.

To accurately describe how elevated CO₂ will modulate plant responses and affect stress tolerance in a changing climate, long-term experiments applying realistic rises of carbon dioxide are needed. In fact, up to date most CO₂-enrichment experiments are carried out by imposing (artificially or using natural CO₂ springs) much greater CO₂ concentrations (usually 750 to over 1000 ppm) than those predicted for the next 100 years. Moreover, while CO₂ will gradually increase, in most experiments high CO₂ is abruptly imposed, which may lead to over-estimation of its impact of rising CO₂ on trees (Klironomos et al., 2005).

The main experiments on the effects of CO₂ on Mediterranean plants, and their effects, are summarized in Table 1.

2.2. Temperature

Temperature imposes a double constraint to plants growing in the Mediterranean environment: cold-induced photoinhibition of PSII during winter (Oliveira and Peñuelas, 2004; Silva-Cancino et al., 2012) and leaf over-heating during summer, particularly when water shortage limits transpirational leaf cooling (Larcher, 2000; Allen et al., 2010) (Table 2). An increase in mean air temperature is inextricably linked to rising CO₂ (Christensen et al., 2007) and, in the Mediterranean basin, the average temperature is expected to rise by 1.5–2.5 °C and by 3–4.5 °C during winter and summer, respectively (Christensen et al., 2007). Understanding how the increase of both winter and summer average temperature will affect plant growth and distribution and how it will modulate plant responses to increased atmospheric CO₂ is still largely unknown and it has been described as a priority for research on climate change (Ghannoum and Way, 2011). During winter, reductions of the maximum quantum yield of PSII photochemistry (F_v/F_m), enhancement of photoprotection through anthocyanins and red carotenoids, and excess excitation energy dissipation through the xanthophyll cycle have been reported in Mediterranean sclerophyllous vegetation (Garcia-Plazaola et al., 1997, 1999; Larcher, 2000; Hughes, 2011). Anthocyanins, responsible of winter leaf reddening in some species/genotypes, act as an alternative photoprotective strategy to increased xanthophyll pool (VAZ) to chlorophyll ratio

in avoiding photoinhibition (Hughes, 2011). It is unclear, however, why some species/individuals remain green while other, co-occurring, species or individuals show leaf reddening. Recent papers found that species or individuals displaying extensive winter leaf redness (thus greater cold-induced increase in anthocyanin to chlorophyll ratio) were highly susceptible to cold-induced photoinhibitory risk (Nikiforou and Manetas, 2010), but the matter deserves further investigation (Hughes et al., 2012). Global warming may reduce the occurrence of winter photoinhibition and frost injuries in sclerophyllous vegetation by increasing minimum temperature in the colder season (Ogaya and Peñuelas, 2003). This is consistent with higher winter photosynthesis observed in Mediterranean trees exposed to warmer winter day and/or night temperatures (Saxe et al., 2001; Prieto et al., 2009). The effects of reduced photoinhibition and cold-related damage due to global warming will differ across species. Southern Mediterranean species, such as *Ceratonia siliqua* L., *Myrtus communis* L., *Nerium oleander* L., *Pistacia lentiscus* L., and *Phillyrea latifolia* L., generally show a greater degree of winter photoinhibition than other sclerophyllous plants with a broader distribution range (*Laurus nobilis* L., *Rhamnus alaternus* L., *Viburnum tinus* L., *Arbutus unedo* L., *Q. ilex* L.) (Larcher, 2000; Ogaya and Peñuelas, 2003; Ogaya et al., 2011). In response to a similar increase in winter air temperature, F_v/F_m was found to increase more in the cold-sensitive *P. latifolia* than in *Q. ilex*, indicating that warming will reduce winter photoinhibition much more in the former than in the latter species (Ogaya et al., 2011). Therefore, higher winter temperatures may favor cold-sensitive species over the dominant cold-tolerant species and this may result in an altered forest structure and in land cover change from forest to shrubland (Ogaya et al., 2011).

During summer, global warming may exacerbate the deleterious effects of leaf over-heating and may affect a wide number of metabolic processes, including photosynthesis, respiration, meristem initiation, water transport and phenology (Battaglia et al., 1996; Atkin and Tjoelker, 2003; Ghannoum and Way, 2011). Pioneer studies predicted that warming, coupled with increased CO₂ concentration, will increase growth and carbon gain (Long, 1991). However, most experiments were carried on temperate forest, or on genotypes from the northern part of species distribution ranges, where sub-optimal temperatures often limit metabolic processes (Lin et al., 2010; Way and Oren, 2010; O'Sullivan et al., 2013). These findings may not apply to species, such as Mediterranean ones, which are currently living near their optimum temperature range (Saxe et al., 2001; Lloyd and Farquhar, 2008; Werten et al., 2011). Because respiration reaches its maximum at a temperature (T_{max}) higher than the temperature at which photosynthesis starts to decline (T_{crit}), leaf temperatures between T_{crit} and T_{max} lead to a lower photosynthesis to dark respiration ratio, minimum carbon gain and reduced growth potential (Lloyd and Farquhar, 2008; Ghannoum and Way, 2011). Acclimation of respiration is slower in evergreens than in deciduous trees and herbs (Atkin and Tjoelker, 2003). In fact, acclimation of respiration can occur through altered sensitivity to temperature (i.e. dynamic variations of the proportional change in respiration per a 10 °C temperature increase, Q_{10}) or through variation of basal respiration, with the second mechanism, which requires new leaves to be formed, having a greater impact (Loveys et al., 2003; Bruhn et al., 2007). T_{crit} for some Mediterranean evergreen species ranges between 35 and 55 °C (Larcher, 2000), values which are somewhat higher than the average maximum air temperature in the Mediterranean basin (about 35 °C). Leaf temperature may be, however, up to 8–10 °C higher than air, especially in the thick leaves of sclerophylls, and particularly when transpiration is limited by summer drought (Larcher, 2000; Nobel, 2005). If we consider the 3–4 °C increase in air T predicted in summer for Mediterranean regions (Christensen et al., 2007), it is conceivable that T_{crit} will be exceeded in many cases.

Table 2

Effects of temperatures on growth, photosynthesis and defense compounds in Mediterranean sclerophyllous vegetation. Abbreviations used in the table: A_{sat} = net photosynthesis at saturating light; F_0 = basal fluorescence of dark adapted leaves; F_v/F_m = maximum quantum yield of PSII photochemistry; NPQ = non-photochemical quenching; $Q_{10,\text{short-term}}$ = proportional change of respiration per 10 °C rise in temperature; R = mitochondrial respiration; R_0 = basal respiration; T_{air} = air temperature; T_{crit} = critical temperature for photosynthesis (i.e. T at which F_0 start abruptly to increase); T_{leaf} = leaf temperature; T_{max} = temperature at which respiration is maximum; VAZ = violaxanthin + anteraxanthin + zeaxanthin.

Species	Reference	Plant material and growing conditions	Treatments	Results
Winter temperatures				
<i>Quercus suber</i>	Garcia-Plazaola et al. (1997)	Mature stand in the natural environment	Seasonal variation of A_{sat} , F_v/F_m , NPQ, VAZ in sun and shade leaves.	NPQ and VAZ pool peaked in January and June, when A_{sat} was limited by cold and drought, respectively. F_v/F_m reached the minimum in January. <i>Q. suber</i> is better adapted to tolerate excess light at high T_{air} than low T_{air} .
<i>Quercus ilex</i>	Garcia-Plazaola et al. (1999)	Open woodland covered by <i>Q. ilex</i> and <i>Q. faginea</i>	Physiological and biochemical leaf parameters measured in winter and in summer on sun and shade leaves	F_v/F_m declined greatly while VAZ and antioxidant pool increased during winter in sun leaves. Sun leaves are capable of reducing oxidative damage during winter by decreasing photosynthetic efficiency and by an extraordinarily efficient antioxidant system.
<i>Nerium oleander</i> , <i>Myrtus communis</i> , <i>Pistacia lentiscus</i> , <i>Ceratonia siliqua</i> , <i>Viburnum tinus</i> , <i>Laurus nobilis</i> , <i>Rhamnus alaternus</i> , <i>Olea europaea</i> , <i>Arbutus unedo</i> , <i>Quercus ilex</i>	Larcher (2000)	Field-grown plants in a botanical garden (Arco Arboretum, Italy)	Comparative study of cold tolerance in several Mediterranean sclerophyllous species	All Southern Mediterranean species (<i>C. siliqua</i> , <i>M. communis</i> , <i>N. oleander</i> , <i>P. lentiscus</i>) were more photoinhibited during winter than most of widespread maquis species (<i>L. nobilis</i> , <i>R. alaternus</i> , <i>V. tinus</i>). The lower degree of winter photoinhibition was found on <i>O. europaea</i> , <i>A. unedo</i> and <i>Q. ilex</i>
<i>Quercus ilex</i> , <i>Phillyrea latifolia</i>	Ogaya and Peñuelas (2003)	3–4 m tall natural vegetation	Seasonal variation of gas exchange and chlorophyll fluorescence in sun and shade leaves	<i>P. latifolia</i> had higher optimum temperature for A_{sat} than <i>Q. ilex</i> in both summer and winter. <i>Q. ilex</i> was more tolerant of winter cold than <i>P. latifolia</i>
<i>Cistus albidus</i> , <i>Quercus ilex</i>	Oliveira and Peñuelas (2004)	Container-grown seedlings (<i>C. albidus</i>) and saplings (<i>Q. ilex</i>) grown outdoor or in greenhouses under controlled T and irradiance	During winter, plants were grown in "warm" ($T_{\min} = 9.3^{\circ}\text{C}$, $T_{\text{avg}} = 18.8^{\circ}\text{C}$), "moderate cold" ($T_{\min} = 1.3^{\circ}\text{C}$, $T_{\text{avg}} = 9.3^{\circ}\text{C}$), "extreme cold" ($T_{\min} = -4.2^{\circ}\text{C}$, $T_{\text{avg}} = 6.1^{\circ}\text{C}$) conditions	Plants exposed to cold displayed lower growth, survival, A_{sat} and F_v/F_m . The two species displayed different mechanisms to cope with moderate and extreme cold stress.
<i>Erica multiflora</i> , <i>Globularia alypum</i> , <i>Pinus halepensis</i>	Prieto et al. (2009)	Natural vegetation in a dry calcareous shrubland	Night-time warming (about 1 °C) using reflective curtains	Warming increased A_{sat} in the three species, mostly in the cold season
<i>Quercus ilex</i> , <i>Phillyrea latifolia</i>	Ogaya and Peñuelas, 2011	Undisturbed vegetation in the natural environment	Seasonal variation of F_v/F_m in the two species and rain exclusion experiment	Lowest F_v/F_m found in winter in both species. In a warming climate, the less cold-tolerant and more heat and drought tolerant species <i>P. latifolia</i> will be favored over <i>Q. ilex</i>
<i>Cistus albidus</i> , <i>Buxus sempervirens</i> , <i>Arctostaphylos uva-ursi</i>	Silva-Cancino et al. (2012)	Cut twigs from natural vegetation. After being collected, twigs were maintained at $T = 24/20^{\circ}\text{C}$	Recovery from winter photoinhibition was compared in the three species	<i>Buxus</i> showed the strongest chronic photoinhibition, <i>Cistus</i> the least. During relief, recovery of F_v/F_m , pigments and chloroplast ultrastructure is a species-specific
Summer temperature				
<i>Eucalyptus globulus</i>	Battaglia et al. (1996)	Container-grown plant in controlled-temperature greenhouses	Seedlings were acclimated to different day/night T_{air} : 15/10, 23/18, 30/25 °C. After 3 weeks of acclimation, were put at constant temperature: 10, 20 or 30 °C	A_{sat} was higher at 20 °C than at 30 °C, particularly in plants which were not acclimated to high T_{air} .
<i>Quercus ilex</i> , <i>Pinus halepensis</i>	Méthy et al. (1997)	Mature vegetation in the natural habitat	F_0/T curves over a 5–55 °C temperature range. Heat stress was imposed in different ways and with different duration	Long-term exposure to heat induced damage to thylakoid membranes at 40 °C (pine) or at 45 °C (oak). Holm oak recovered faster after heat exposure than pine.
<i>Quercus ilex</i>	Loreto et al. (1998)	Container-grown plants in controlled-temperature greenhouses and growth chambers	Short-term heat stress (T_{air} raised up to 55 °C) and relief on leaves exposed to either ambient or low O_2 air, fumigated or not with selected monoterpene	Monoterpene emission is maximum at 35 °C and it is higher in non-photorespiratory conditions. Fumigation with monoterpenes improves thermotolerance and facilitate recovery from short-term heat stress.
<i>Quercus ilex</i>	Larcher (2000)	Field-grown plants in a botanical garden (Arco Arboretum, Italy)	Heating of mature leaves at a rate of 1 °C/min.	T_{crit} was found to be 47–48 °C for holm oak leaves. During summer, at high PPFD, T_{leaf} is 4–8 °C warmer than T_{air} .

Table 2 (Continued)

Species	Reference	Plant material and growing conditions	Treatments	Results
Several herbaceous and woody species	Loveys et al. (2003)	Hydroponic culture of plantlets and seedlings	Long-term exposure to different growth temperatures (18, 23, 28 °C).	Prolonged exposure to high T_{air} resulted in the acclimation of both A_{sat} and R , with A/R ratio re-established. For maximal acclimation, development of new leaves was required
Several early-successional Mediterranean species	Lloret et al. (2004a)	Natural vegetation in a dry shrubland	Passive, night-time warming using reflective aluminum curtains	Warming increased seedling mortality. Species currently producing fewer recruits are more likely to disappear in a warmer climatic scenario.
<i>Eucalyptus pauciflora</i>	Bruhn et al. (2007)	Seedlings in PVC pipes buried the field	10 months exposure to night-time warming with a FATI system ($T_{ambient}$, $T_{ambient} + 0.3$; $T_{ambient} + 1.3$; $T_{ambient} + 2.2$)	Old leaves showed limited acclimation to warming. The primary mechanisms of R acclimation to warming is the change in R_0 , rather than in $Q_{10,short-term}$
<i>Erica multiflora, Globularia alypum</i>	Lluisà et al. (2009)	Natural vegetation in a dry shrubland	Passive, night-time warming using reflective aluminum curtains	Night-time warming increased isoprene and monoterpene emissions in <i>E. multiflora</i> in spring and summer, and decreased it in summer.
<i>Eucalyptus pauciflora</i>	O'Sullivan et al. (2013)	3-year-old container grown saplings and mature, field-grown trees	Temperature response curves in contrasting environments and at different rates of air T increase	During summer, T_{crit} is 8–10 °C lower than T_{max} . T_{crit} in winter is higher than T_{crit} in summer.

Temperature limits photosynthesis directly through modulation of the rate of photosynthetic enzyme activity, and indirectly through changes in the leaf to air vapor pressure deficit, a key factor in setting stomatal conductance. Most of the direct limitation of temperature on photosynthesis is due to a reversible decline in the maximum rate of electron transport (June et al., 2004) and to the release of a manganese-stabilizing extrinsic 33 kDa protein of PSII, causing the reversible inactivation of PSII reaction centers (Yamane et al., 1997). Isoprenoids, whose emission usually increases with temperature until T_{crit} (because they are produced from newly-assimilated carbon) have long been known to increase thermotolerance (Loreto et al., 1998; Lluisà et al., 2009). In the context of global warming, the monoterpene load from Mediterranean forests will therefore increase, particularly if emitter species are favored in the long-term over non-emitter species (Staudt et al., 2001).

Summer warming may differently affect species distribution and relative dominance, with species and provenances better adapted to tolerate higher temperatures favored. Species with steep leaf angles (resulting in lower light absorption efficiency and in structural photoprotection when high temperature and VPD reduced the amount of light used in the photosynthetic process), extensive leaf coverage by trichomes, small-sized and compound leaves (resulting in thin boundary layers and enhanced heat dissipation by convection), high capacity to dissipate excess energy through non-photochemical quenching, and emission of volatile organic compounds are likely to be better adapted to tolerate warming and heat extremes (Nobel, 2005; Pearcy et al., 2005; Lluisà et al., 2009; Welter et al., 2012; Monson et al., 2013).

The main experiments on the effects of temperatures on Mediterranean plants, and their effects, are summarized in Table 2.

2.3. Interactions between rising CO₂ and warming

Up to date, most of the studies on climate change evaluated the impact of either warming or elevated CO₂. However, in situ, temperature and carbon dioxide are changing concurrently. Thus, one of the major knowledge gap in plant responses to climate change is that the interactive effects of CO₂ concentration and warming have rarely been examined (Ghannoum and Way, 2011). Recent studies found that carbon dioxide and temperature seem to have an additive but antagonistic effect on plant growth and leaf anatomical

characteristics (Wertin et al., 2011; Dieleman et al., 2012; Smith et al., 2012; Xu et al., 2012, but see also Table 3). Leaf morpho-anatomical traits, such as leaf mass per area, leaf thickness, cell size, chloroplast number and size, and the fraction of intercellular airspaces occupied by palisade cells were increased by elevated-CO₂ and decreased by warming (Smith et al., 2012; Xu et al., 2012). Changes in these anatomical characteristics are expected to affect both photosynthesis (mesophyll conductance to CO₂ in particular and, by consequence, the amount of CO₂ effectively reaching the chloroplasts) and tolerance to some abiotic stresses (such as drought and ozone), but much will depend on whether the effect of CO₂ or temperature prevails.

The impact of CO₂ enhancement often predominates over temperature in temperate species and/or in populations growing in the northern part of a species' distribution range (Dieleman et al., 2012), but for species growing near their temperature optimum, such as in the Mediterranean, the effect of warming can prevail. For example, increasing temperature overcame the growth enhancement induced by elevated CO₂ in red oak seedlings near the southern limit of the species' range (Wertin et al., 2011).

Another important question to be answered is whether elevated CO₂ will mitigate or exacerbate the effects of warming on Mediterranean sclerophyllous. Because stomatal closure is induced by high CO₂, transpiration is reduced and this may exacerbate the effects of warming. Leaves of *Q. ilex* grown in elevated-CO₂ were warmer, if compared to ambient-CO₂ plants, when exposed to heat stress (Pintó-Marijuan et al., 2013). However, despite inherently lower stomatal conductance in elevated-CO₂ plants if compared to ambient-CO₂, stomata of the former are less responsive to temperature stress, resulting in higher carbon assimilation and growth under heat stress (Idso et al., 1993; Faria et al., 1996, 1999). Also, reduced photorespiration and increased linear electron transport induced by elevated CO₂ have been reported to increase up to 7 °C the thermal optimum of photosynthesis (Ghannoum et al., 2010; Logan et al., 2010). A recent study confirmed that exposure of *Q. ilex* to elevated CO₂ shifted T_{crit} from 35 to 45 °C (Pintó-Marijuan et al., 2013). These findings are consistent with the higher thermotolerance and the faster recovery from a sudden heat stress observed in *Q. suber* acclimated to elevated CO₂ (Faria et al., 1996, 1999). The authors also found that, despite the suppressive effect of high CO₂ on antioxidant enzymes when plants were grown in optimal conditions, SOD activity increased greatly when elevated-CO₂ plants

Table 3

Effects of elevated $[CO_2]$ and warming on growth, photosynthesis and defence compounds in Mediterranean sclerophyllous vegetation. Abbreviations used in the table: A_{sat} = net photosynthesis at saturating light; A_{max} = net photosynthesis at saturating CO_2 ; ASC = ascorbate peroxidase; J_{max} = apparent contribution of electron transport to ribulose regeneration; leaf N_{area} = leaf nitrogen per unit leaf area; leaf TNC = leaf total non-structural carbohydrates; LMA = leaf mass per area; SD = stomatal density; SOD = superoxide dismutase; T = temperature; VAZ = violaxanthin + anteraxanthin + zeaxanthin; $V_{c,max}$ = apparent carboxylation rate by Rubisco; Z = zeaxanthin.

Species	Reference	Plant material and growing conditions	Treatments	Results
<i>Citrus aurantium</i>	Idso et al. (1993)	30-cm-tall clones, planted in the field in OTC	Natural seasonal variation of T in plants grown for 2 years at elevated (700 ppm) or ambient (350 pp) CO_2 .	CO_2 -enrichment had negligible effects on leaf biomass at average $T=5^{\circ}C$. However, at $T=35^{\circ}C$, leaf area, leaf dry mass, and leaf starch content were higher in elevated- than in ambient- CO_2 .
<i>Quercus suber</i>	Faria et al. (1996)	Seedlings grown in 10-L containers in controlled glasshouses	Sudden heat shock ($T=45^{\circ}C$ for 4 h) imposed on plants acclimated to either ambient (350 ppm) or elevated (700 ppm) for 14 months	Elevated CO_2 resulted in a downregulation of A_{sat} . However, during heat stress, elevated- CO_2 plants had positive A_{sat} , while A_{sat} was negative in ambient- CO_2 . Recovery from heat stress was faster in elevated- CO_2 plants.
<i>Quercus suber</i>	Faria et al. (1999)	Seedlings grown in 10-L containers in controlled glasshouses	Sudden heat shock ($T=45^{\circ}C$ for 4 h) imposed on plants acclimated to either ambient (350 ppm) or elevated (700 ppm) for 6 months	Elevated CO_2 increased A_{sat} and plant biomass, but not A_{max} . Stomata of elevated- CO_2 plants were less sensitive to T . The effect of sudden heat shock was more pronounced in ambient- than in elevated CO_2 , because of greater SOD activity in the latter.
<i>Eucalyptus sideroxylon, Eucalyptus saligna</i>	Ghannoum et al. (2010)	Seedlings grown in 10-L containers in controlled glasshouses	3 different $[CO_2]$: 290, 400, 650 ppm; 2 different air temperatures (day/night): 26/18 °C, 30/22 °C	Elevated CO_2 increased A_{sat} , A_{max} and J_{max} , while $V_{c,max}$ was little affected. Photosynthesis acclimated to warming: A_{sat} and A_{max} were similar at the two growth T . Thermal optimum of photosynthesis increased by 7 °C under elevated CO_2 .
<i>Eucalyptus sideroxylon, Eucalyptus saligna</i>	Logan et al. (2010)	Seedlings grown in 10-L containers in controlled glasshouses	3 different $[CO_2]$: 290, 400, 650 ppm; 2 different air temperatures (day/night): 26/18 °C, 30/22 °C	Elevated CO_2 resulted in greater PSII operating efficiency and increased energy partitioning to electron transport than to energy dissipation at high T .
<i>Quercus rubra</i> ^a	Wertin et al. (2011)	Two-year-old saplings in 12-L container in wood-PVC growth chambers	One growing season at 3 different T ($T_{ambient}$, $T_{ambient}+3^{\circ}C$; $T_{ambient}+6^{\circ}C$) and at 2 different $[CO_2]$ (400 ppm, 700 ppm)	Elevated CO_2 increased biomass by 38%. Growth response to warming was negative and strong enough to negate growth enhancement by high CO_2 .
<i>Eucalyptus sideroxylon</i>	Smith et al. (2012)	Seedlings grown in 10-L containers in controlled glasshouses	3 different $[CO_2]$: 280, 400, 650 ppm; 2 different air temperatures (day/night): 26/18 °C, 30/22 °C	Rising CO_2 reduced A_{max} and leaf N_{area} and increased the number of palisade layers. Elevated T increased stomatal frequency but had no effect on A_{max} . $[CO_2]$ and T showed no interactive effect.
<i>Eucalyptus saligna</i>	Xu et al. (2012)	Seedlings grown in 10-L containers in controlled glasshouses	3 different $[CO_2]$: 290, 400, 650 ppm; 2 different air temperatures (day/night): 26/18 °C, 30/22 °C	Leaf thickness and mesophyll size were increased by elevated CO_2 , but decreased by warming. High CO_2 increased LMA because of greater accumulation of leaf TNC. Except for $[CO_2]=290$ ppm, warming reduced chloroplast number.
<i>Quercus ilex</i>	Pintó-Marijuan et al. (2013)	Resprouts from excised 2-year-old plants grown in 6-L containers in controlled greenhouses	Temperature increases from 25 °C to 45 °C and relief on resprouts grown at $[CO_2]=350$ or 700 ppm	Elevated- CO_2 plants showed downregulation of A_{sat} , higher starch, lower g_s , and similar SD, than ambient- CO_2 plants. During heat stress, elevated- CO_2 plants has higher ASC, Z/VAZ, phenolic compounds, lower photorespiration and lower stomatal sensitivity to T .

^a Deciduous temperate species.

were exposed to heat stress. These results indicate that plants acclimated to elevated- CO_2 could compensate to their constitutively lower antioxidant defences by a greater inducible upregulation of defence metabolism during heat stress, if compared to plants acclimated to ambient- CO_2 .

In conclusion, elevated CO_2 is likely to exert ameliorative effects on photosynthesis of Mediterranean sclerophyllous species during heat stress, especially in BVOC-emitter species. The main

experiments on the interactive effects of CO_2 and temperature on Mediterranean plants, and their effects, are summarized in Table 3.

2.4. Drought

High radiation, high temperature and low water availability usually co-occur during Mediterranean summer. Thus, plants challenged against drought also suffer from multiple stress conditions

Table 4

Effects of drought on evergreen sclerophylls (E) and some deciduous species (D) typical of the Mediterranean basin. Some of the species are truly-Mediterranean (M), others inhabited the area prior to the onset of Mediterranean summer drought (PM). Abbreviations used in the table: APX = ascorbate peroxidase; A_{sat} = net photosynthesis at saturating light; β -carotene_{chl} = concentration of carotene per unit chlorophyll; CAT = catalase; D = deciduous species; DPS = de-epoxidation state of xanthophyll cycle; E = evergreen species; F_v/F_m = maximum quantum yield of PSII photochemistry; g_s = stomatal conductance to CO_2 ; LAR = leaf area ratio; LMA = leaf mass per area; lutein_{chl} = concentration of lutein per unit chlorophyll; M = true-Mediterranean species; MDA = concentration of malondialdehyde; PM = pre-Mediterranean species; RWC = leaf relative water content; TLA = total leaf area; WUE = water use efficiency; WUE_i = intrinsic water use efficiency; Φ_{NPQ} = yield of regulated energy dissipation; Φ_{NO} = yield of non-regulated energy dissipation; Φ_{PSII} = actual yield of PSII photochemistry; Ψ_w = pre-dawn water potential.

Species	Reference	Plant material and growing conditions	Treatments	Results
<i>Ceratonia siliqua</i> , <i>Laurus nobilis</i> , <i>Olea oleaster</i>	Lo Gullo and Salleo (1988)	20-year-old trees growing in a botanical garden	Comparison of water relation parameters among co-occurring species during summer drought	Different strategies to cope with drought were found: drought-tolerance in <i>O. oleaster</i> , drought-avoidance by water-spending in <i>C. siliqua</i> , drought avoidance by water-saving in <i>L. nobilis</i> . <i>C. siliqua</i> relies on efficient uptake of deep water from soil and efficient transport to leaves and may be unable to tolerate very dry habitats where <i>O. oleaster</i> can still survive.
<i>Olea europaea</i> (PM)	Angelopoulos et al. (1996)	Saplings in 18-L containers	4 irrigation treatments resulting in unstressed, mildly stressed, moderately stressed and severely stressed plants Withholding water (7 days) and relief	Moderate and severe drought resulted in irreversible photoinhibition of PSII. After relief, A_{sat} and F_v/F_m recovered only partially
<i>Phillyrea latifolia</i> (PM), <i>Pistacia lentiscus</i> (PM), <i>Quercus ilex</i> (PM)	Filella et al. (1998)	Saplings in 1.8-L containers in plastic tunnels		After 7 days of drought, only <i>P. latifolia</i> had positive A_{sat} . After relief, <i>Q. ilex</i> did not recover.
<i>Arbutus unedo</i> (PM), <i>Cistus monspeliensis</i> (M), <i>Erica arborea</i> (M), <i>Myrtus communis</i> (PM), <i>Phillyrea latifolia</i> (PM), <i>Quercus ilex</i> (PM)	Gucci et al. (1999)	Adult plants growing in field conditions in a coastal area	Seasonal and diurnal measurements of Ψ_w , g_s and sap flow, performed before and during summer drought	M species had higher g_s and sap flow than PM species before the onset of drought. During drought, g_s was very low in all species, but M species had more negative Ψ_w than PM species.
<i>Rosmarinus officinalis</i> (M)	Munné-Bosch and Alegre (2000)	Two-year-old rooted cuttings planted in the field	Seasonal trend of water relation, photoinhibition, and leaf pigments on plants subjected to severe drought	During drought, chl decreased, tocopherol _{chl} , β -carotene _{chl} , lutein _{chl} and DPS increased. This allowed the avoidance of irreversible damage to PSII and a prompt recovery after relief from drought.
<i>Quercus ilex</i> (E), <i>Q. pubescens</i> (D)	Marabottini et al. (2001)	20–30-year-old plants near a CO_2 spring	2 water regimes (irrigated with 20-L water/day or not irrigated) on plants grown at ambient (292 ppm) or elevated (1074 ppm) CO_2	Elevated- CO_2 constitutively depresses the activity of leaf antioxidant enzymes. However, during drought, elevated- CO_2 -trees had higher CAT and APX than ambient- CO_2 -ones, indicating a enhanced compensatory effort of the former during water shortage.
<i>Cistus</i> (M), <i>Erica</i> (M), <i>Genista</i> (M), <i>Juniperus</i> (PM), <i>Lavandula</i> (M), <i>Olea</i> (PM), <i>Pinus</i> (PM), <i>Pistacia</i> (PM), <i>Quercus</i> (PM), <i>Rosmarinus</i> (M)	Peñuelas et al. (2001)	Natural vegetation in over 190 sites in Central and Southern Spain	Response of M and PM vegetation to a severe drought (years 1994 and 1995) and to a wet year (1996)	M species were more damaged by severe drought than PM species, but recovered better after the wet 1996.
<i>Lavandula stoechas</i> (M), <i>Rosmarinus officinalis</i> (M)	Nogues and Alegre (2002)	Saplings planted in the field	2 irrigation regimes: (1) irrigated with 50 mm _{water} /month; (2) no irrigation	Gas exchange and water relation parameters decreased in both irrigated and non-irrigated plants during summer, and fully recovered in autumn.
<i>Heteromeles arbutifolia</i>	Valladares and Pearcy (2002)	Natural vegetation in an unusually dry El Niño year	Seasonal trend of gas exchange and water relation in sun and shade leaves	Drought reduced A_{sat} and Ψ_w to a much greater extent in shade than in sun leaves. During summer drought, sunflecks resulted in a strong photoinhibition of shade leaves. Little photoinhibition was found on sun leaves, because of a more efficient photoprotective system
<i>Cistus incanus</i> (M), <i>Phillyrea latifolia</i> (PM), <i>Quercus ilex</i> (PM)	Bombelli and Gratani (2003)	Natural vegetation in a dry coastal area (soil moisture between 0.5 and 8%)	Seasonal measurement of leaf gas exchange and water relations in the three species	M species had higher A_{sat} , g_s than PM species prior to drought. Drought decreased A_{sat} , g_s , Ψ_w more in M than in PM species. <i>Q. ilex</i> and <i>P. latifolia</i> are less sensitive to drought than <i>C. incanus</i> .
<i>Pinus pinaster</i> (PM)	Nguyens-Queyrens and Bouchet-Lannat (2003)	Seedling from 5 provenances grown in 12-L containers in a greenhouse	Slowly-imposed 10-weeks drought on different seed sources	Osmotic adjustment is of primary importance for drought tolerance in <i>P. pinaster</i> . Solute accumulation was 2.3 times higher in plants from the driest source than in plants from the wettest

Table 4 (Continued)

Species	Reference	Plant material and growing conditions	Treatments	Results
<i>Phillyrea angustifolia</i> (PM)	Munné-Bosch and Peñuelas (2003)	3-year-old plants in the field	Rain exclusion experiment and relief	At RWC = 60%, DPS increased by 70%. At RWC < 50%, β -carotene decreased and MDA increased. Recovery was slow and plants were still experiencing oxidative stress during recovery, and this stress was more severe as the previous drought was more intense.
<i>Quercus rotundifolia</i> (E), <i>Q. faginea</i> (D)	Mediavilla and Escudero (2004)	Mature 100-year-old trees and saplings transplanted to the field	Seasonal trend of leaf gas exchange and water relation in D and E species at the seedling and mature stage	$Q. rotundifolia$ had lower g_s and less negative Ψ_w than <i>Q. faginea</i> . Interspecific differences disappeared at the seedling stage. Seedlings of both species displayed a low stomatal sensitivity to drought than mature trees, which may result in higher mortality during drought.
<i>Quercus coccifera</i> , <i>Q. ilex</i> , <i>Pistacia lentiscus</i> , <i>P. terebinthus</i>	Valladares et al. (2005)	Saplings in 4-L containers in a controlled glasshouse	Sun- and shade phenotypes exposed to a 70-day drought under high light or low light	Shade phenotypes under drought and high light showed an earlier and larger decline in F_v/F_m than sun phenotypes, but survived longer. The degree of photoinhibition negatively correlated with survival and drought tolerance.
<i>Quercus cerris</i> (D), <i>Q. frainetto</i> (D), <i>Q. ilex</i> (E)	Manes et al. (2006)	3-year-old plants grown in containers in controlled chambers	3 irrigation regimes: (1) daily watering to CC (25 cm^3); (2) daily watering with 12 cm^3 ; (3) withholding water	D species had higher g_s and root length in well watered conditions, but were more sensitive to drought, resulting in lower g_s and Ψ_w during water stress than the E species. Root growth was also reduced by drought to a greater extent in D than in E species.
<i>Arbutus unedo</i> , <i>Pinus sylvestris</i> , <i>P. pinaster</i> , <i>Pistacia lentiscus</i> , <i>P. terebinthus</i> , <i>Quercus coccifera</i> , <i>Q. faginea</i> , <i>Q. ilex</i> , <i>Q. pyrenaica</i> , <i>Q. robur</i> , <i>Viburnum tinus</i>	Valladares and Sánchez-Gómez (2006)	Seedlings in 3-L containers grown outdoor under a polyethylene screen	Rain exclusion experiment for one growing season	<i>A. unedo</i> and <i>V. tinus</i> had higher survivorship under water stress than <i>P. terebinthus</i> . Survival was positively related to LMA, LAR and inversely related to plant dry mass and TLA. Fast growing species experienced the greatest growth reduction because of drought. Severe drought decreased WUE.
<i>Ceratonia siliqua</i> (PM)	Osorio et al. (2011)	Seedlings in 3-L containers in controlled chambers	Withholding water (15 days) and recovery (36 h) on plants acclimated for 20 days to either 25/18 °C or 32/21 °C (day/night)	Warming exacerbated the effects of drought. A_{sat} and Ψ_w decreased to a greater extent at 32/21 °C during drought. At 25/18 °C, Φ_{PSII} , Φ_{NPQ} , Φ_{NO} were not affected by drought, while they were at 32/21 °C. Lipid peroxidation was found only at 32/21 °C. After relief, recovery of A_{sat} and F_v/F_m was not complete.
<i>Anthyllis cytisoides</i> (M), <i>Chamaerops humilis</i> (PM), <i>Helianthemum syriacum</i> (M), <i>Nerium oleander</i> (PM), <i>Olea europaea</i> (PM), <i>Pinus halepensis</i> (PM), <i>Pistacia lentiscus</i> (PM), <i>Rhamnus lycioides</i> (PM), <i>Rosmarinus officinalis</i> (M)	Moreno-Gutiérrez et al. (2012)	Natural vegetation in a semi-arid, open woodland community	Comparison among co-occurring species	PM species displayed a conservative water use (low g_s , high WUE _i) and rely on deeper soil water source than M species. M species are more opportunistic (high g_s , low WUE _i) during the wet season when shallow water is available, and use avoidance mechanisms (e.g. drought deciduousness) to survive summer drought. M species may perform better under the projected climate change scenario for Mediterranean regions.
Several deep rooted and shallow rooted shrub species	West et al. (2012)	Natural vegetation in either a 8-year post-fire site or a 2-year post-fire site	3-year rain exclusion experiment comparing deep rooted and shallow rooted species. Both drought-tolerant and drought-avoider shallow rooted species were compared	Shallow rooted, drought-tolerant shrubs suffered considerable reduction in growth and flowering and increased mortality during drought. By contrast, shallow rooted drought-avoiders and deep rooted shrubs were largely unaffected by drought.

which result in lower stomatal conductance and carbon assimilation, cell dehydration, excess excitation energy, massive generation of reactive oxygen species and, eventually, cell necrosis (Flexas et al., 2004; Guidi et al., 2008; Jubani-Marí et al., 2010; Fini et al., 2012) (Table 4). It is now agreed that current Mediterranean conditions, with the characteristic summer drought and high inter-annual variability, appeared 3.2 million years ago, in the Pliocene.

While some Mediterranean genera, mainly shrubs (e.g. *Cistus*, *Erica*, *Genista*, *Hibiscus roseus*, *Lavandula*, *Rosmarinus*) evolved after that period, other species currently inhabiting the Mediterranean landscape, mainly trees, have a pre-Mediterranean origin (e.g. the genus *Ceratonia*, *Quercus*, *Pinus*, *Pistacia*, *Olea*) (Peñuelas et al., 2001; Petit et al., 2005). Consistently with their different evolutionary origins, Mediterranean plants display a wide range of mechanisms to

survive to drought (Peñuelas et al., 2011; West et al., 2012), including escape (completion of vegetative and reproductive phases before the onset of drought, typical of annual plants), avoidance (ability to avoid large decreases in leaf pre-dawn water potential and relative water content during drought) and tolerance (ability to maintain physiological and metabolic processes at decreasing pre-dawn water potential during water stress) (Levitt, 1980; Gucci et al., 1999; Valladares and Sánchez-Gómez, 2006; De Micco and Aronne, 2012). Such strikingly different mechanisms of response are at the base of species richness in Mediterranean areas. If the ongoing climate change will favor some mechanisms over the others, local species richness will be greatly reduced (Sala et al., 2000). Species richness is crucial for maintaining key ecological functions linked to nutrient cycling, carbon storage and soil fertility, thus for promoting ecosystem resistance to desertification (Maestre et al., 2012).

Recent papers have pointed out that two contrasting water use strategies emerge among Mediterranean species. True-Mediterranean plants display a profligate/opportunistic water use, which is heavily dependent on highly fluctuating shallow soil water (Bombelli and Gratani, 2003; Peñuelas et al., 2011). Opportunistic species are characterized by shallow rooting, low investment in leaf tissues, high stomatal conductance and low water use efficiency, aimed at maximizing growth and carbon gain during the narrow windows of high water availability after rain pulses followed by drought-deciduousness (i.e. the capacity of abscising leaves to prevent water loss during drought, and to emit quickly new leaves after drought has been relieved) or reversible down-regulation of electron transport after the onset of drought (Hernández-Santana et al., 2011; Moreno-Gutiérrez et al., 2012). Pre-Mediterranean species display a more conservative water use, characterized by lower stomatal conductance and carbon gain than opportunistic species during the favorable season, but higher leaf gas exchange and water use efficiency during drought. Several morpho-physiological and biochemical traits involved in control of water loss have been identified in pre-Mediterranean trees, including high cuticle thickness and leaf coverage by trichomes, sunken stomata, early stomatal closure, deep rooting, osmotic adjustment, low vulnerability to cavitation and low turgor loss (Lo Gullo and Salleo, 1988; Nguyen-Queyrens and Bouchet-Lannat, 2003; Mediavilla and Escudero, 2004; Valladares et al., 2005; Valladares and Sánchez-Gómez, 2006; Manes et al., 2006; Vitale et al., 2012). These traits allow pre-Mediterranean species to benefit from occasional rain pulses and from deep soil water during the dry season, when their more shallow-rooted opportunistic competitors are drought-dormant (i.e. have shed their leaves to avoid dehydration during drought) (West et al., 2012).

There is little evidence as to whether the high-investment in leaf tissue of evergreen sclerophylls will be advantageous over the low-investment, opportunistic behavior of drought-deciduous species under the dryer and warmer conditions predicted for the 21st century, and how the different water-use patterns will affect structure and composition of Mediterranean plant communities (Niinemets et al., 2011; Moreno-Gutiérrez et al., 2012; Reyer et al., 2013). After a severe summer drought, pre-Mediterranean species with conservative water use were less damaged, but also had slower recovery after relief, than Mediterranean opportunistic species (Peñuelas et al., 2001). On the other hand, the combined effect of warming and drought greatly reduced photosynthesis and F_v/F_m , which did not fully recover after relief from drought, in *C. siliqua* (Osorio et al., 2011), while it had little effect on true-Mediterranean shrubs, which were already "drought-dormant" (Nogues and Alegre, 2002).

To get the best from their long-lived leaves it is essential for sclerophylls to keep them functional (not photoinhibited or wilted) during drought. Sclerophyll itself, a trait primarily evolved in

plants to maximize nutrient use efficiency in nutrient-poor environments and to enhance protection against pathogens, also offers some protection against wilting (De Micco and Aronne, 2012). In fact, sclerophyllous leaves undergo large decreases in water potential in response to much smaller declines in volumetric water (Niinemets et al., 2011), maintain high cell hydration when osmotic potential at full turgor is low (Bartlett et al., 2012), and are capable of full recovery from short-term partial embolism of leaf xylem (Salleo et al., 1997). These characteristics allow sclerophylls to maintain their metabolism in conditions of dehydration, which causes wilting in other leaf types, and are crucial for tolerating short-term water stresses (i.e. large but brief daily changes in leaf water potential, as occur along Mediterranean coasts or in areas characterized by high humidity of the air condensating at night), but may be less effective under more severe or prolonged droughts (Salleo et al., 1997), particularly if the photosynthetic apparatus becomes strongly photoinhibited.

Photoinhibition may occur when the usage of PAR for photosynthesis decreases because of stomatal and biochemical limitations to carbon assimilation. As also observed in several species from different functional groups (Flexas et al., 2004; Fini et al., 2013), recovery from drought of Mediterranean sclerophylls is much slower and often incomplete if leaves become severely photoinhibited during water shortage (Angelopoulos et al., 1996; Munné-Bosch and Peñuelas, 2003). In this regard, plant and leaf anatomical (i.e. leaf hairiness, changes in crown architecture and leaf orientation) and biochemical traits (i.e. content of chlorophyll, antioxidant enzymes, carotenoids, flavonoids), which depend on both the species and the environmental conditions (i.e. sunlight irradiance) at which leaves developed, are crucial for avoiding and countering oxidative damage during stress conditions (Valladares and Pearcy, 2002; Munné-Bosch and Alegre, 2000; Guidi et al., 2011). In this context, the species-specific capacity of evergreen sclerophylls to maintain leaf functionality during drought (i.e. avoid wilting, cavitation and photoinhibition) is likely to determine the relative abundance in their community in a changing climate. For example, *Phillyrea* spp. and *Pistacia* spp. will be favored by warmer and drier conditions over the codominant species *Q. ilex* because of greater water use efficiency and the lower photosynthetic imbalance during drought (Filella et al., 1998; Ogaya and Peñuelas, 2003; Ogaya et al., 2011).

Increasing atmospheric CO₂ may or may not alleviate the deleterious effects of drought on Mediterranean sclerophylls. Elevated CO₂ is expected to increase the transpiring leaf area, and root growth will be similarly promoted. Root length density, fine root biomass, fine root longevity and mycorrhizal colonization will increase under elevated-CO₂, with positive effects on water uptake (Eissenstat et al., 2000; Idso and Kimball, 2001). However, roots tend to be shallower in a high-CO₂ world, and this may affect the long-term field performance of species typically relying on deep water sources (e.g. *C. siliqua*). More negative osmotic potential, lower g_s , and higher WUE resulting from exposure to elevated CO₂ are likely to increase tolerance to mild to moderate drought events (Tognetti et al., 1996). However, during severe drought, when biochemical limitation to photosynthesis prevails (Flexas et al., 2004; Fini et al., 2012), the benefit of CO₂-enrichment is probably little. Accordingly, elevated CO₂ did not reduce drought events in *Quercus pyrenaica*, *Q. suber* and other Mediterranean species (Hernández-Santana et al., 2011; Vaz et al., 2012).

The main experiments on the effects of drought on Mediterranean plants, and their effects, are summarized in Table 4.

2.5. Air pollution and tropospheric ozone

The action of air pollutants on vegetation in Mediterranean ecosystems is a well-known topic. Mediterranean coastal regions are often home of heavily populated urban areas and industrial

Table 5

Effects of ozone in Mediterranean sclerophyllous vegetation in experimental conditions. Abbreviations used in the table: OTC = open-top chambers; FC = fumigation chambers; Gh = greenhouse facility; CF = charcoal-filtered air; NF = non-filtered air; NF+40 = non-filtered air plus O₃ 40 ppb (or 30 ppb, 80 ppb); OP = open air; Pn = photosynthesis; g_s = stomatal conductance; ChlF = chlorophyll fluorescence; Chl = chlorophyll content; POD = peroxidase activity; Foliar symptoms = visible foliar symptoms; AGB = above ground biomass; SOD = superoxide dismutase activity; RWC = relative water content; Rgsh = reduced glutathione content; F_v/F_m = photochemical maximal efficiency; δ¹³C = carbon stable partitioning; δ¹⁵N = nitrogen isotope partitioning; Vcmax = apparent carboxylation rate by Rubisco; J_{max} = apparent contribution of electron transport to ribulose regeneration; ANTOX = hydrosoluble antioxidant activity.

Species	Reference	Type of experiment	Treatment	Results
<i>Quercus ilex</i>	Manes et al. (1998)	FC, seedlings 4 year-old	O ₃ (0, 65, 175, 300 ppb) per 4 days, 6 h/day	Pn, ChlF, POD influenced in treatments at 300 ppb
<i>Quercus ilex</i> spp. <i>ilex</i> ; <i>Quercus ilex</i> spp. <i>ballota</i> ; <i>Ceratonia siliqua</i> ; <i>Arbutus unedo</i> ; <i>Olea europaea</i> spp. <i>sylvestris</i>	Inclán et al. (1999)	OTC, seedlings 2 year-old	CF; NF; NF+40, 9 h/day (10:00–18:00), 1 year	Foliar symptoms in <i>Q. ilex</i> spp. <i>ballota</i> and <i>A. unedo</i> (NFA+40). Reduction AGB in <i>Q. ilex</i> spp. <i>ballota</i> , <i>O. europaea</i> spp. <i>sylvestris</i>
<i>Arbutus unedo</i> ; <i>Hedera helix</i> ; <i>Laurus nobilis</i> ; <i>Nerium oleander</i> ; <i>Viburnum tinus</i>	Lorenzini et al. (1999)	FC, plants 1 year-old	200 ppb O ₃ for 5 h	Foliar symptoms on <i>A. unedo</i> and <i>N. oleander</i> . Reduction of Pn in all species.
<i>Arbutus unedo</i> ; <i>Myrtus communis</i> ; <i>Pistacia lentiscus</i> ; <i>Pistacia terebinthus</i>	Skelly et al. (1999)	OTC, seedlings	CF, NF, OP, one growth season	Foliar symptoms on all the species investigated, in NF and OP
<i>Arbutus unedo</i>	Bussotti et al. (2003)	FC, seedlings 2 year-old	Ozone exposure at 0, 50 and 100 ppb for 21 days, 5 h/day	Foliar symptoms at 50 and 100 ppb; structural changes in the epidermis and walls more pronounced at 100 ppb
<i>Quercus coccifera</i>	Elvira et al. (2004)	FC, seedlings 1 year-old (two ecotypes)	CF, NF+40, 6 h/day, 5 days a week, 2 years	Reduction of Pn and g _s during the first year, in autumn and winter in NF+40 in one ecotype investigated
<i>Phillyrea latifolia</i> ; <i>Arbutus unedo</i> ; <i>Laurus nobilis</i>	Nali et al. (2004)	Gh, seedlings 2 year-old	O ₃ exposition: 110 ppb and 0 ppb for 5 h/day, for 3 months	Foliar symptoms in all species. Decrease of Pn in <i>Arbutus</i> and <i>Laurus</i> ; decrease of RWC in <i>Arbutus</i> and <i>Laurus</i> ; increase of SOD and rGSH content in <i>Arbutus</i> and <i>Phillyrea</i>
<i>Pistacia lentiscus</i>	Reig-Armiñana et al. (2004)	OTC, seedlings	CF, NF+40, NF+80. Fumigation for 6 months, 8 h/day	Alteration of the foliar ultrastructural characteristics; premature leaf senescence
<i>Arbutus unedo</i>	Paoletti (2005)	FC, seedlings 2 year-old	O ₃ exposition: 110 nmol mol ⁻¹ , 900–1400 h, 90 days	Slowed stomatal response (sluggishness)
<i>Quercus ilex</i> subsp. <i>ilex</i> ; <i>Quercus ilex</i> subsp. <i>ballota</i> ; <i>Olea europaea</i> cv. <i>vulgaris</i> ; <i>Ceratonia siliqua</i>	Ribas et al. (2005a)	OTC, seedlings, 2 years	CF, NF, NF+40	Decrease of F _v /F _m in NF+40; increase of δ ¹³ C in <i>Quercus ilex</i> subsp. <i>Ilex</i> and subsp. <i>ballota</i> , <i>Ceratonia siliqua</i> in NF+40; decrease of Chl in NF+40 in all species; reduction of N foliar content and increase in δ ¹⁵ N in NF+40. Increase of LMA in all species; increase of the spongy parenchyma thickness in <i>O. europaea</i> and in <i>C. siliqua</i> . Reduction of Pn in NF+40, WW in <i>C. siliqua</i> ; reduction of the AGB in NF in <i>Q. ilex</i> and NF+40 in <i>C. siliqua</i> . Increase of the foliar δ ¹⁵ N in NF+40. Decrease in <i>Q. ilex</i> of foliar N concentration and Chl. Foliar symptoms and increase of g _s in NF+WW of <i>Q. ilex</i> .
<i>Quercus ilex</i> ; <i>Ceratonia siliqua</i>	Ribas et al. (2005b)	OTC, seedling 1-year old in pot	CF, NF, NF+40, 7:00–17:00 GMT, for 5 days/every week. Two water regime: well-watered (WW); low water supply (LW); 2 years	Reduction of Pn in NF+40, WW in <i>C. siliqua</i> ; reduction of the AGB in NF in <i>Q. ilex</i> and NF+40 in <i>C. siliqua</i> . Increase of the foliar δ ¹⁵ N in NF+40. Decrease in <i>Q. ilex</i> of foliar N concentration and Chl. Foliar symptoms and increase of g _s in NF+WW of <i>Q. ilex</i> .
<i>Pistacia lentiscus</i> , <i>Pistacia terebinthus</i> , <i>Viburnum tinus</i>	Calatayud et al. (2010)	OTC, seedlings 1–2-year old in pot	CF and NF+30, for 4 months	Foliar symptoms in <i>Viburnum tinus</i> , in <i>Pistacia terebinthus</i> and <i>P. lentiscus</i> . Reduction of Pn in <i>Viburnum tinus</i> ; reduction of Chl and F _v /F _m in <i>Pistacia terebinthus</i> ; reduction of V _{c,max} and of J _{max} in <i>V. tinus</i> . Reduction of the ANTOX and increased of the rASC in <i>V. tinus</i> NF+30, while the ANTOX decrease in <i>P. lentiscus</i> . Increase of SOD in all species in NF and NF+30
<i>Quercus ilex</i> subsp. <i>ballota</i>	Calatayud et al. (2011)	OTC, seedling 2-year old in pot	CF and NF+30, 8 h/day, 10:00–18:00 GMT for week, 2 years	<i>Quercus ilex</i> subsp. <i>ballota</i> was the species most tolerant to ozone respect the other <i>Quercus</i> sp. investigated based on Foliar symptoms, gas exchange, Chl and biomass.
<i>Quercus ilex</i> subsp. <i>ilex</i> <i>Quercus ilex</i> subsp. <i>ballota</i>	Alonso et al. (in press)	OTC, seedlings 2-year-old	CF; NF; NF+40, continuously exposed for 26 months. Two water regime: well-watered (WW); low water supply (LW)	Ozone and drought stress reduce Pn and aboveground biomass in both subspecies. In <i>Q. ilex</i> subsp. <i>ilex</i> the biomass reduction is higher with the interaction Ozone + Drought.

plants, which are direct source of pollutants (Table 5). These pollutants, however, act at local scale and may produce limited cases of forest decline (for review, see Bussotti and Ferretti, 1998). The main concern for the health of forests is made today by the role of tropospheric ozone, that is the most widespread pollutant in the Mediterranean region (Cristofanelli and Bonasoni, 2009) and it is believed to reduce carbon assimilation and storage (Anav et al., 2011; Ainsworth et al., 2012) via a reduction of photosynthesis connected both to stomatal and non-stomatal limitation. The deleterious actions of ozone on photosynthesis include the inactivation of Rubisco with subsequent suppression of the Calvin-Benson cycle (Fontaine et al., 2003; Inclan et al., 2005; Bussotti et al., 2011) and the induction of stomatal closure with subsequent carbon starvation (King et al., 2005). Ozone is therefore considered a factor that reduces the effectiveness of the forests to buffer the effects of the atmospheric CO₂ increase (Kitao et al., 2009). Ground levels of ozone are expected to increase in Mediterranean regions as consequence of climate change because its formation and accumulation in the atmosphere is connected to high temperature and solar radiation. Despite high levels of ozone, the results of several experiments in controlled and semi-controlled conditions (reviewed in Table 5) suggest that Mediterranean vegetation is tolerant to ozone (Bussotti and Gerosa, 2002; Paoletti, 2006). This tolerance is attributed to stomatal limitations that, during the hottest and driest periods, reduce the fluxes of ozone inside the leaves (Vitale et al., 2003; Manes et al., 2007; Fares et al., 2013). Foliar traits connected to sclerophyll, namely the density of the apoplastic component of the mesophyll, may play a key role in detoxification processes (Bussotti, 2008). Occurrence of foliar symptoms and growth reduction however, were observed in few experimental cases and field conditions (see Table 5 and Calderon Guerrero et al., 2013). Moreover, Alonso et al. (in press) suggest a possible synergistic effect on growth reduction between ozone and drought stress in *Q. ilex*.

The impact of ozone pollution on Mediterranean forests can be exacerbated by the biogenic emission of VOCs (Davison et al., 2009), the formation of which is in turn enhanced by warming (Lluisà et al., 2009). The effects of a simultaneous increasing of environmental drought and high levels of ozone on Mediterranean vegetation are unpredictable. In fact, drought-induced stomatal closure, as a consequence of the accumulation of abscisic acid (ABA) in the leaves, is counteracted by the ethylene production induced by ozone (Wilkinson and Davies, 2009, 2010). It is, therefore, a need for future research to investigate the combined effects of ozone, drought and warming on sclerophyllous evergreen vegetation.

2.6. UV radiations

The depletion of stratospheric ozone, and the resulting increase of UV radiations reaching the terrestrial ecosystems, is particularly severe in the polar regions (Newsham and Robinson, 2009). At mid latitudes, both UV-B and UV-A fluxes can be modified by environmental factors, such as clouds, aerosols and air pollution (Munakata et al., 2009). The predicted decreases in mean cloudiness of the Mediterranean basin due to climate change may lead to increases in the UV radiation reaching Mediterranean ecosystems in the near future (WMO, 2010).

The changes in plants induced by UV-A and UV-B radiation include the reduction of leaf surface, specific leaf area (SLA), plant height and aboveground biomass, DNA damage, as well as the increase of leaf thickness and UV screening compounds in the foliar epidermis (Caldwell et al., 2003; Newsham and Robinson, 2009; Ballaré et al., 2011; Verdaguera et al., 2012) (Table 6). At ecosystem level, leaf chemistry alterations affect plant-insect interactions (Rousseaux et al., 1998).

Mediterranean sclerophyllous vegetation is generally considered not sensitive to UV action (experiments were reviewed in

Table 6; see also Paoletti, 2006) because it is acclimated to an environment where natural irradiance often exceed the amount of radiation used in the photosynthetic process (excess light stress). Exposition to high light induces morpho-physiological and biochemical adjustments aimed at avoiding the generation of reactive oxygen species (e.g. VAZ to chlorophyll ratio) and provides the leaves with effective antioxidant and UV-screening compounds (flavonoids and other polyphenols) in the leaf epidermis, trichomes and mesophyll, which improve tolerance to UV (Tattini et al., 2000; Guidi et al., 2011).

With global warming many types of interactions (both beneficial and detrimental) between UV, temperature and drought are expected (for details see Caldwell et al., 2003). In the Mediterranean ecosystems the modifications induced by high UV radiation contribute to increase the water use efficiency, making plants more resistant to drought and high temperatures (Kyparissis et al., 2001). Consequently, it is predicted that increasing UV radiation is unlikely to have any significant impact on the photosynthetic productivity of Mediterranean sclerophylls (Nogués and Baker, 2000).

3. Tree mortality, reproduction and vegetation shift: what are happening in the “real” world

3.1. Mortality induced by severe drought and heat waves

According to the experimental results above reported, the climate change factors that potentially exert the greater impact on the Mediterranean region will be increasing drought and temperature. These factors are strongly correlated in Southern Europe, and extreme drought events correspond to heat waves. The effects of drought and temperature have been assessed in Mediterranean ecosystems both in cases study and extensive field surveys.

It is well known that, globally, drought leads to extensive mortality in forest stands and shrublands (Gitlin et al., 2006; Allen et al., 2010) and dieback events have been extensively reported for conifers and mesophilic species within the southern Europe and Mediterranean regions (Jump et al., 2006; Vilà-Cabrera et al., 2011). The typical sclerophyllous Mediterranean vegetation has also shown clear signs of suffering as a result of events of severe drought (Peñuelas et al., 2001). Lloret et al. (2004b) described a case of dieback in *Q. ilex* after a period of extreme aridity in the forests of Catalonia (Spain). The mortality within the stand object of study was distributed in patches in relation to the different type of geological bedrock. Shales in fact allowed greater penetration of the root system into the soil, with a more efficient provisioning of water. Recurrent episodes of aridity reduced the ability to regenerate the canopies in *Q. ilex* because of a depletion of starch reserves, which can lead to change in the vegetation shape, from tree to shrub (Lloret et al., 2004b; Galiano et al., 2012), and reduced the plant reproductive capacity (Pérez-Ramos et al., 2013).

As far as the extensive surveys are concerned, the condition of European forest trees is monitored annually by the ICP-Forests program (Müller-Edzards et al., 1997). In southern Europe, there has been a continuous increase in defoliation since 1990, in contrast to central and northern European regions where the levels of defoliation have been stable (Carnicer et al., 2011). In Spain the increase in defoliation has also coincided with an increase in mortality, and these parameters have been particularly high in the years when there have been heat waves and very strong drought in the Iberian peninsula (1990–1995, 1999–2000, and 2005–2006). During the same drought stress events, a strong reduction of insect defoliator populations has also been observed, with an alteration of the food chain (Trotter et al., 2008).

Interactions between climate change and forest pathogens may be of various kinds and, at the current state of knowledge, it seems

Table 6

Effects of UV radiation in Mediterranean sclerophyllous vegetation in experimental conditions. Abbreviations used in the table: Gh = greenhouse; Fp = field plot (UV-frame, open nursery); AM = ambient UV radiation; AM+ = ambient plus supplemental UV-B radiation; A = CO₂ assimilation rate; g_s = stomatal conductance; ACE = apparent carbon efficiency; AQE = apparent quantum efficiency; AGB = above ground biomass; LT = leaf thick; CT = cuticle thick; LMA = leaf mass per area. In the table is indicated also the period of the experiment.

Species	Reference	Type of experiment	Treatment	Results
<i>Erica curvirostris</i> ; <i>E. farii</i> ; <i>E. nudiflora</i>	Musil and Wand (1993)	Gh, 4 months	UV-B exposition: 7.8 kJ/m ² /day; 9.4 kJ/m ² /day; 11.4 kJ/m ² /day	Reduction of pollen germination and pollen tube growth in all species; reduction of A in <i>E. farii</i> . Increase of ACE, AQE, and g _s in <i>E. nudiflora</i>
<i>Phlomis fruticosa</i>	Nikolopoulos et al. (1995)	Fp, seedling in pot	AM and AM+	Reduction of leaf number and total leaf area; inhibition of new leaf; premature falling of older leaves; decrease of AGB, leaf, stem and root after 1 year
<i>Nerium oleander</i>	Drilias et al. (1997)	Fp, seedlings 1 year-old in pot, 2 years	AM and AM+	Reduction of AGB in AM+ not irrigated plants. Increase of cuticle thickness.
<i>Cistus creticus</i>	Stephanou and Manetas (1998)	Fp, 1 year-old seedlings in pot, 20 months	AM and AM+	Increase of the seed number per fruit and total seed mass per plant
<i>Olea europaea</i> cv. <i>halkidiki</i>	Liakoura et al. (1999)	Seedling grown in pot in greenhouse	Absence and AM+ 4 months	Increase of abaxial CT and trichome
<i>Olea europaea</i> ; <i>Rosmarinus officinalis</i> ; <i>Lavandula stoechas</i>	Nogués and Baker (2000)	Gh, 2 year-old plants in pot	Absence and presence of UV-B radiation. Irradiation in UV: 14 h/day, 8 weeks	No significant effects on the growth or photosynthetic activities. Increase of flavonoid and anthocyanin content in <i>Olea</i>
<i>Cistus creticus</i>	Stephanou et al. (2000)	Fp, 1 year-old seedlings in pot, 2 years	AM and AM+	Increase of size of the nectary and the duration of insect visit
<i>Ceratonia siliqua</i>	Kyparissis et al. (2001)	Fp, seedlings 1 year-old in pot	AM and AM+	Reduction of leaves number; reduction of N content; increase of stem dry mass
<i>Phlomis fruticosa</i>	Levizou and Manetas (2001a)	Fp, seedlings in pot	AM and AM+	Decrease in total leaf phenolics
<i>Ceratonia siliqua</i> ; <i>Phlomis fruticosa</i>	Levizou and Manetas (2001b)	Fp, 5 month-old seedlings in pot	AM and AM+	Increase of the adaxial CT in <i>C. siliqua</i> ; increase of the petiole length, AGB and root dry weight in <i>P. fruticosa</i>
<i>Phillyrea angustifolia</i> ; <i>Pistacia lentiscus</i> ; <i>Daphne gnidium</i> ; <i>Ilex aquifolium</i> ; <i>Laurus nobilis</i>	Verdaguer et al. (2012)	Gh, seedlings 1 year-old in pot	UV-B+ UV-A; UV-A; without UV radiation	Increase of LMA and LT in UV-B+ UV-A radiation; increase of the adaxial epidermal cell thickness in UV-A; increase of the palisade-to-mesophyll ratio in UV-A and UV-B+ UV-A treatments in <i>P. lentiscus</i> and <i>D. gnidium</i>

that the greatest dangers may arise from the so-called weakness parasites, which attack plants already weakened by prolonged conditions of water stress. For example, *Quercus cerris* is threatened by *Biscogniauxia mediterranea* (De Not.) O. Kuntze, and the evergreen species *Q. ilex* is subject to *Phytophthora cinnamomi* Rands (Desprez-Loustau et al., 2006; Capretti and Battisti, 2007). *B. mediterranea* development is favored by a mechanism involving the release of the amino acid proline, which accelerates the fungal radial growth more than other amino acids (Capretti and Battisti, 2007).

3.2. Reproduction processes

Climate change affects phenology and reproductive processes (Misson et al., 2011), so altering the dynamic of the forest regeneration. Directional climate change – particularly drier conditions in Mediterranean shrublands – would result in a change in recruitment of the plant community. Mediavilla and Escudero (2004) suggest that potential adult mortality would not be compensated for by actual seedling recruitment, thus enhancing shifts in community composition (Lloret et al., 2009). There is increasing field evidence of changed phenophases (i.e. seasonal biological events) of plants in the last few decades (Peñuelas and Filella, 2001) along with climate change. Flowering date has, on average, advanced and the average growing season has been lengthened by 10.8 days in Europe for the period 1951–1996. Finally, reviewing research carried out on boreal and temperate tree species, Hanninen and Tanino (2011) observed that elevated air temperatures during the dormancy induction occurring in late summer and early autumn increases the depth of dormancy, so that more chilling is required for rest break and/or more accumulation of temperature sum for bud burst. The conclusions are that one part of the annual cycle

impacts subsequent parts and that individual seasonal responses should not be examined in isolation without taking into account the history of the plant. This concept could be applied also to Mediterranean evergreen trees, and more research in this field is required.

3.3. Vegetation shift

Concerning the changes taking place in the distribution of species and the effects of climate change on biodiversity, it was verified that the contraction of *P. sylvestris* at the lower limit of its range (Valais, Switzerland) is in favor of a greater expansion of the deciduous xero-tolerant oak species *Quercus pubescens* Willd. (Rigling et al., 2013), while in the mountains of Catalonia (Montseny mountains) *Q. ilex* tends to replace the heathlands with *Calluna vulgaris* (L.) Hull and beech forests (*F. sylvatica*) at mid altitudes (Peñuelas and Boada, 2003).

The replacement of the genotypes present with more resistant (adapted) genotypes, which are able to grow and reproduce in the new environmental conditions (Saxe et al., 2001), theoretically, may occur spontaneously by means of migrations of thermo-xeric plant species from southern to northern latitudes and from low to high altitudes. This spontaneous migration, however, can occur only over very long periods and can be hampered by the persistence of the currently present species (Lloret et al., 2012) or man-made barriers (i.e. structures of urbanization), that determine the fragmentation of forests. For these reasons the introduction "by man" of more suitable genotypes may be a desirable practice, also planting non strictly-native species and provenances in anticipation of climate change.

Current opinion encourages the planting of local provenances of native species, citing adaptation of provenances to local conditions,

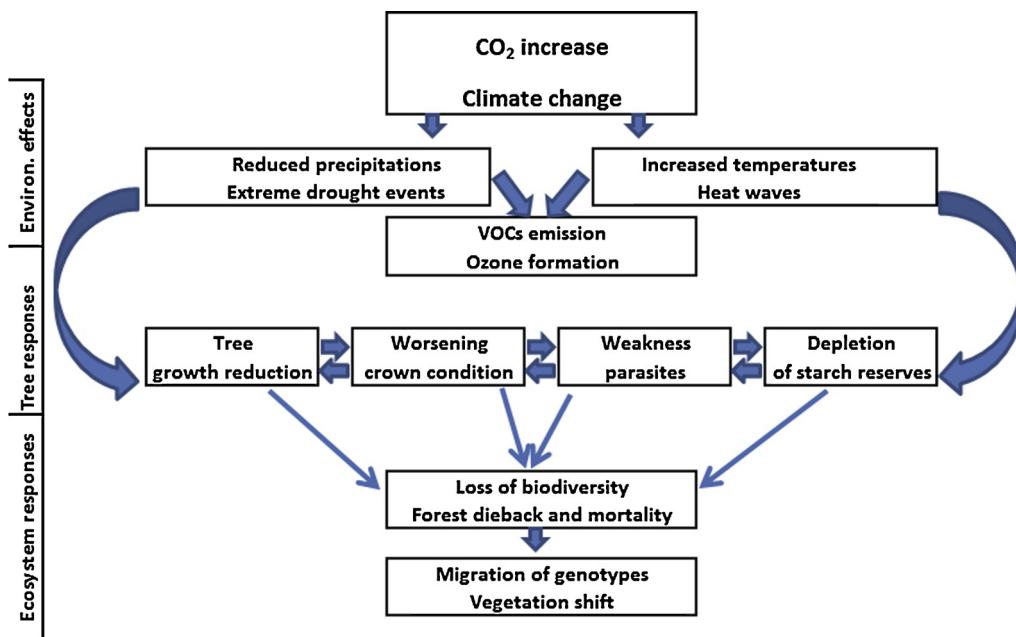


Fig. 1. Relationship between environmental changes and responses at the tree/ecosystem level in the Mediterranean region.

and the requirement to maintain biodiversity and a native genetic base. Local provenances however may not be able to adapt to a changing climate, particularly given the rate of change predicted. Sourcing planting stock from regions with a current climate similar to that predicted for the future may provide one option, although care must be taken to ensure that suitable provenances are selected that are not at risk from, for example, spring frost damage as a result of early flushing.

Studies conducted in Italy on *Q. ilex* in common gardens showed a high phenotypic plasticity of this species, for which the most xeric provenances have smaller leaves and greater leaf mass per area (Gratani et al., 2003). Smaller leaves and higher leaf mass per area were typical of xeric-provenances (Pesoli et al., 2003; Bussotti, 2008), while mesic ones displayed higher growth capacity but higher susceptibility to water stress (Martin-StPaul et al., 2012). Another aspect of genotypic adaptation strategy concerns the selection, within the same population, of genotypes with high water use efficiency (Brendel et al., 2008; Roussel et al., 2009).

3.4. Cultural practices

Based on these premises it is of paramount importance to select well-adapted evergreen species and provenances, but also to develop techniques in the nursery stage for successful establishment after planting in the open environment. It is known that exposure of plants to mild stress in the nursery phase can induce acclimation to subsequent stress events (Vilagrosa et al., 2003; Villar-Salvador et al., 2004). Thus, nursery pre-conditioning has been proposed as useful technique to increase water use efficiency and improve drought tolerance by promoting osmotic adjustment, efficient stomatal regulation and carboxylation efficiency (Fini et al., 2011b).

Planting and cultivation techniques in Mediterranean woodlands subject to climate change have not been explored thoroughly, and the current literature can lead to opposing conclusions. Gea-Izquierdo et al. (2009) analyzing a long tree-ring chronology (141 years) of *Q. ilex* from different stand conditions in the Iberian peninsula, argued that stands with high tree density can buffer the effects of climate extremes. On the other hand, Ruiz-Benito et al. (2013) re-analyzed the mortality trends by means of inventory data from

Iberian forests and concluded that water deficiency enhanced the effects of the competition within the stands, thus increasing tree mortality in dense forests. These studies suggest that the greater resilience of the population in dense forests may be detrimental to individuals as a result of the competition. Finally, as suggested by Rolo and Moreno (2011), understorey shrubs play a vital role in water exploitation due to the different characteristics of the root systems of trees and shrubs respectively.

4. Conclusions

The different climate change factors (increasing CO₂, temperature, drought and ozone pollution) have contrasting effects when considered separately in experimental conditions, and their interactive actions may be either synergistic or antagonistic. Tree responses in the field, however, seem to be driven by extreme drought events and severe heat waves. The relationships between ecological factors and tree responses are summarized in Fig. 1.

The long-term evolutionary adaptation to drought of typical sclerophyllous Mediterranean plant species allows them to cope with moderate increases of drought without significant losses of production and survival. The thermophilic oak species, particularly Mediterranean evergreen oaks, seem favored by climate change at the expense of conifers, beech and relict formations at the southern limit of their range. Recurrent episodes of extreme water stress can lead to a decline in *Q. ilex* (also with the contribution of weakness parasites) in favor of shrubby vegetation. In areas that will experience severe and prolonged dry periods because of climate change, drought-deciduous profligate/opportunistic species may be favored over sclerophylls. Migration and changes in tree species composition may be slowed down and made difficult by mechanisms of resilience of the vegetation itself, consequently the adaptation processes should be favored by the anthropic action.

The reduction of forest cover in more xeric areas can raise the albedo by increasing the flow of heat into the atmosphere and reducing the effects of transpiration on air warming (Bonan, 2008). In addition, water stress causes an increase in biogenic emissions (BVOCs) in the forests of *Q. ilex* (Peñuelas and Llusià, 2003; Lavoie et al., 2011), with unpredictable effects on atmospheric chemistry and processes of the biosphere. Finally, there is growing concern

that heat waves, and their synergistic interactions with torrential rainfall and human-driven disturbances, can trigger desertification processes (Sardans and Peñuelas, 2013).

In this review we have summarized the available knowledge on the effects of climate change on Mediterranean sclerophyllous trees and shrubs, and their functional ability to deal with it. There are still several key points that must be addressed to have a more comprehensive understanding. They include, for example, phenological responses, the interaction between biotic and abiotic stress and the resistance of typical Mediterranean plants to frost. This latter aspect could be a key factor for the acclimation of Mediterranean vegetation in mountain sites (Andivia et al., 2012; Ogaya and Peñuelas, 2007) and consequently for the true possibility of thermophilic species to survive at higher elevations. More generally, the ecological consequences of climate change and the interactions among all the biotic and abiotic factors need to be carefully investigated.

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