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Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change

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Abstract

Background—In the Mediterranean climate, plants have evolved under conditions of low soil-water and nutrient availabilities and have acquired a series of adaptive traits that, in turn exert strong feedback on soil fertility, structure, and protection. As a result, plant-soil systems constitute complex interactive webs where these adaptive traits allow plants to maximize the use of scarce resources.

Scope—It is necessary to review the current bibliography to highlight the most know characteristic mechanisms underlying Mediterranean plant-soil feed-backs and identify the processes that merit further research in order to reach an understanding of the plant-soil feed-backs and its capacity to cope with future global change scenarios. In this review, we characterize the functional and structural plant-soil relationships and feedbacks in Mediterranean regions. We thereafter discuss the effects of global change drivers on these complex interactions between plants and soil.

Conclusions—The large plant diversity that characterizes Mediterranean ecosystems is associated to the success of coexisting species in avoiding competition for soil resources by differential exploitation in space (soil layers) and time (year and daily). Among plant and soil traits, high foliar nutrient re-translocation and large contents of recalcitrant compounds reduce nutrient cycling. Meanwhile increased allocation of resources to roots and soil enzymes help to protect against soil erosion and to improve soil fertility and capacity to retain water. The long-term evolutionary adaptation to drought of Mediterranean plants allows them to cope with moderate increases of drought without significant losses of production and survival in some species. However, other species have proved to be more sensitive decreasing their growth and increasing their mortality under moderate rising of drought. All these increases contribute to species composition shifts. Moreover, in more xeric sites, the desertification resulting from synergic interactions among some related process such as drought increases, torrential rainfall increases and human driven disturbances is an increasing concern. A research priority now is to discern the effects of long-term increases in atmospheric CO₂ concentrations, warming, and drought on soil fertility and water availability and on the structure of soil communities (e.g. shifts from bacteria to fungi) and on patching vegetation and root-water uplift (from soil to plant and from soil deep layers to soil superficial layers) roles in desertification.

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Keywords

Drought; Warming; Nitrogen; Phosphorus; Soil enzymes; Root system; C:P; C:N; N:P; Soil erosion; Plant growth; Desertification

Introduction

Mediterranean climates occur in five occidental coastal regions of the continents between latitudes 34-45° in both hemispheres, i.e. the Mediterranean Basin, California, central Chile, the Cape region of South Africa, and southwestern and southern Australia (Di Castri and Mooney 1973; Di Castri 1981). Moderately wet and cold winters are coupled with dry and hot summers, but the intensity of the drier periods, increasing from high to low latitudes within these areas, can vary widely (Di Castri and Mooney 1973; Di Castri 1981). Several studies have improved our understanding of the functional and structural traits of Mediterranean plant communities, eg. Sclerophylly, low growth rate and nutrient concentrations, and high presence of sprouting species (Kruger 1979; Specht 1979; Mooney 1989). The typical Mediterranean communities are mostly dominated by woody plants with conservative traits, such as slow growth and high sclerophylly associated with low water and nutrient availabilities.

Some important chemical and physical properties of the soils, such as nutrient availability, erodibility, moisture content, infiltration capacity, the quantity and nutritional quality of soil organic carbon (SOC), cation exchange capacity, and pH, are strongly determined by vegetative cover. Changes in these important soil variables can, in turn, affect plant cover. Close and very broad relationships, with multiple feedbacks, thus exist between plant communities and soil structure and function in this type of ecosystem.

Although some of these plant-soil interactions are well understood, other plant-soil interactions present some contrasting results such as the impact of increased atmospheric CO₂ concentrations on plant litter and soil activity and others interactions remain poorly studied such as the role of roots in water transport among different soil layers. Consequently, a review of these main interactions is clearly needed. Current predictions suggest that drought and warming will increase in Mediterranean areas (IPCC 2007). Prolonged drought coupled to less predictable torrential rainfall (Frei et al. 1998) opens a scenario of shifts in the feedbacks and equilibrium within the plant-soil system. Several studies have explored the effects of increasing atmospheric CO₂, drought, and warming on Mediterranean soils and plants, observing diverse responses, some of which involve feedback mechanisms between plants and soils. Some of these studies report contradictory results. Most results suggest that the impacts of global change threaten to increase the degradation and desertification process. In this context, the current knowledge suggests that plant-soil feedbacks can play an outstanding role in the capacity of these ecosystems to adapt to future scenarios. It is thus urgent to review and ordinate the current knowledge to highlight the best known characteristic mechanisms underlying Mediterranean plant-soil feedbacks and to identify the processes that merit further research to reach a better understanding of the plant-soil feedbacks and their capacity to cope with future global change scenarios.

By gathering data and reviewing the published studies (in the international literature) over the last two decades, this review aims (i) to characterize the functional and structural plant-soil relationships and feedbacks in Mediterranean regions, (ii) to review the impacts of increasing atmospheric CO₂, drought, and warming on the Mediterranean plant-soil system, and (iii) to suggest directions for future research needed to improve our knowledge of the plant-soil system in changing Mediterranean environments.

Mediterranean plants and soils

Mediterranean plants: an evolution under low water and nutrient availabilities

Mediterranean plant communities are generally dominated by sclerophyllous woody plants with an herbaceous or shrubby understory (Specht 1969; Orshan 1983). When large data sets of Mediterranean plants have been studied across climatic gradients, mean annual precipitation has been the most determinant climatic variable associated with plant growth and community distribution (Sardans et al. 2011). From humid to semi-arid regions, understory vegetation grades from annual and perennial grasses and herbs (savanna understory) to evergreens and sclerophylls (heathland understory). The most specific structural characteristics of Mediterranean plants are those related to conservative mechanisms linked to the avoidance of water stress but frequently also to the scarcity of soil nutrients. The lack of soil resources has led to a narrow evolution of plant-soil systems.

Mediterranean plants have acquired a set of morphological and physiological adaptations in response to deficits of soil water (Table 1). The development of deep and extensive root systems is among the most characteristic traits of plants in Mediterranean ecosystems. Deep root systems enable the uptake of water from deep soil layers in drought seasons when the upper layers are water depleted (Veneklaas and Poot 2003; Padilla and Pugnaire 2007; Baldocchi and Xu 2007; Hernández-Santana et al. 2008). Moreover, in Mediterranean plant communities, plant species with root-systems that tend to occupy different soil layer usually coexist avoiding the root systems overlapping and consequently diminishing the competition intensity, and also allowing to exploit the sources throughout all the soil depth (Castells et al. 1994; Silva and Rego 2003; Lefi et al. 2004; Mattia et al. 2005; Moreno et al. 2005; Filella and Peñuelas 2003b; Silva and Rego 2003; Mattia et al. 2005; Mereu et al. 2009). Plants with deep-roots have proved to resist better drought events than species with shallow-root systems (Padilla et al. 2007; West et al. 2012). Furthermore, Mediterranean plants have high root plasticity in the early stages of life (Padilla et al. 2007). At the foliage morphological level, Mediterranean plants improve their capacity of drought avoidance increasing their foliar sclerophylly by developing thick cuticle and increasing leaf mass area (LMA) (Table 1), high density of foliar trichomes (Table 1), and high plasticity of foliar morphology and size (Table 1).

General adaptations to drought by Mediterranean plants at physiological level include a large capacity to maintain water flux and hydraulic lift (water conduction from soil to plant tissues) in the soil-plant continuum (Table 1), including a large resistance to xylem cavitation (Table 1) and high stomatal control (Table 1). Thus, Mediterranean plants also respond to drought by both decreasing xylem cavitation vulnerability and adapting and protecting leaf function and structure (De Mico and Aronne 2009; Vilagrosa et al. 2010).

Some studies suggest that these two responses are coordinated (Vilagroasa et al. 2010). Drought changes woody architecture of woody plants increasing vessel density, decreasing total hydraulic diameter (Corcuera et al. 2004; Gea-Izquierdo et al. 2012), increasing vessel wall thickness (De Mico and Aronne 2009) and decreasing cambial activity (de Luís et al. 2011). Other general adaptation strategies to drought include the accumulation of metabolites and/or water soluble sugars in tissues to increase turgor (Table 1), a large capacity to reduce metabolic activity during drought periods (Table 1), and efficient photoprotective and antioxidant mechanisms (Table 1). Moreover, antioxidant mechanisms to cope with summer drought have already been listed (Table 1). The desiccation tolerance strategy observed in some Mediterranean species allows maintaining high stomatal conductance despite very low water potentials (Fotelli et al. 2000; Volaire et al. 2009) In these drought tolerant species the predawn leaf relative water content decreases simultaneously with stomatal closure as drought progresses (Gulías et al. 2002). However, the most stress-tolerant plant species are able to develop very low water potentials with markedly reduced stomatal aperture (Fotelli et al. 2000).

Apart from water availability, the capacity of the soil nutrient supply has often been shown to be an important factor in the growth, structure, and distribution of plant communities (Kruger, 1979; Specht, 1979; Carreira et al. 1992; Sardans, et al. 2004; Henkin et al. 1998). Mediterranean plants share characteristics such as slow growth, sclerophylly, and low nutrient contents that are present in plants of other non-Mediterranean ecosystems adapted to poor soils (Bussotti et al. 2000). The importance of nutrients has been appreciated in many experiments of nutrient manipulation by fertilization in different Mediterranean zones of the world, for example in Californian chaparral (McMaster et al. 1982), South African fynbos (Witkowski et al. 1990; Herppich et al. 2002), Australian jarrah and *Eucalyptus* forests (Dell et al. 1987), and the Mediterranean Basin (Mayor and Rodà 1992; Henkin et al. 1998; Sardans and Peñuelas 2004; Sardans et al. 2004, 2005a, 2005b). Mediterranean plants frequently change foliar chemical and physical traits in response to both water deficit and nutrient stress (Gratani et al. 2003; Sardans et al. 2006a; 2008a, 2008b). Proteaceae plant communities that dominate several Mediterranean climatic regions of South Africa and southwestern Australia have the capacity to accumulate more or less P in seedlings when P is most limiting (Groom and Lamont 2010). Due to the prevalence of soils with low nutrient content in Mediterranean areas, Mediterranean plants have high levels of investment in root systems to enhance nutrient uptake, in addition to the C invested for adaptation to low water availability (Martínez et al. 1998; Sardans et al. 2005a, 2006b). Resprouting capacity is also determined by the availability of soil nutrients (Sardans et al. 2006c). A higher retranslocation of nutrients from leaves before falling is another characteristic of Mediterranean plants helping them to achieve a higher nutrient use efficiency (NUE) (Schlesinger and Hasey 1981; Fioretto et al. 2003; Sardans et al. 2005a) and having a further effect on soil organic matter quality as commented below. García-Palacios et al. (2012) in an experiment of Mediterranean grasslands growing at different levels of soil N availability heterogeneity observed that soil N availability heterogeneity modulated the effects of root length, LMA and nutrient availability on ecosystem function. The nutrient content of soil is thus a key factor for the structure and function of Mediterranean plants that, in turn, influence nutrient content by their adaptations that improve NUE.

A positive interaction has been observed between soil-water and nutrient availabilities (Matías et al. 2011). Increases in the availability of water increases plant-production capacity, produces more litter of higher nutritional quality (Dirks et al. 2010), and protects the soil better. All these enhancements further enable higher microbial activity and availability of nutrients (Dirks et al. 2010). In fact, the competition for soil resources is a very important and widespread phenomenon in Mediterranean plant communities (Vilà and Sardans 1999), suggesting a significant interdependence of soil-plant systems, mainly to improve water and nutrient availability and the capacity to withstand limitations.

Species-specific adaptations of plant species and communities to resist drought

The capacity of Mediterranean plants to withstand drought varies for the different species within and between plant communities. For example, Californian perennial grasses are more tolerant of drought than annuals of the Mediterranean Basin but less tolerant than perennials of the Mediterranean Basin, despite the more intense summer drought of California's Central Valley compared to the Mediterranean Basin (Vaughn et al. 2011). Other studies have observed better adaptation to drought in evergreen oaks of the Mediterranean Basin compared to those of California (Grünzweig et al. 2008). Different morphological and physiological adaptive strategies to drought have been observed in comparisons between typical groups of Mediterranean plants (Medrano et al. 2009). Different growth forms display specific morphological adjustments in response to shortages of water. Different coexisting species of the same community can also respond differently. When drought is enhanced, some species survive and grow less well than others in the short and medium terms (Ogaya et al. 2003; Ogaya and Peñuelas 2007a) due to species differences in some of the previously mentioned traits for resisting drought and increasing water use efficiency (WUE). Species also differ in their phenotypic capacity to change some traits (Lloret et al. 2004; Ogaya and Peñuelas 2008; Bell et al. 2007). Significant differences in the capacity to take up water from different soil depths (Filella and Peñuelas 2003b; Lefi et al. 2004), a trait that is especially important in severe droughts, are frequently observed. Moreover, coexisting species in the same community have different strategies for the uptake of water, from plants with leaf water potentials depending on soil water status and evaporative demands (isohydric) to plants whose leaf water potentials do not depend on soil water status and evaporative demand (anisohydric). This combination of hydraulic strategies and also different strategies to capture of water at different times allows plants to avoid competition for water (Peñuelas et al. 2011; Quero et al. 2011).

Mediterranean species also differ in their capacity to regenerate. In Mediterranean ecosystems, some species are able to regenerate by sprouting, and others can only regenerate from seeds. These two strategies are widely represented in Mediterranean communities and frequently coexist in competitive equilibrium. The high cost of biomass production together with high levels of natural disturbance (severe dry periods, recurrent fires, and herbivore pressure) are proposed as general explanations for the elevated number of species with resprouting capacity (Mooney and Dunn 1970; Lloret et al. 1999) that adds complexity and diversity to Mediterranean plant communities.

Mediterranean soils

Mediterranean areas have a large variety of soils, but they generally have medium-low fertility (Yaalon 1997). The Mediterranean region of central Chile is relatively nutrient rich, the vegetation is mainly limited by water and leaf turn-over rates is relatively high (Miller 1981). California and Europe Mediterranean areas are less nutrient rich and climate is the most limiting factor but nutrients have proved to exert some importance, and in Mediterranean areas of Australia and South-Africa soils are old and nutrient-poor, nutrients thus having an outstanding role in ecosystems structure and function (Miller 1981). The most frequent soil types range from Alfisols (*Luvisols*) in the wetter regions with mesic environments to Inceptisols and Entisols in more xeric and semi-arid environments or on slopes. A majority of calcareous rock allows the formation of *Xerolls* (Mollisols under xeric environments) due to the protection of humic organic matter by the aggregates formed with Ca^{2+} (Yaalon 1997). In extreme xeric conditions in the transition to sub-desertic environments, the arid conditions and the salinization of the upper horizon can form Aridisols. Rubefication (by the precipitation of Fe_2O_3 during summer drought from the Fe^{2+} released by the weathering of minerals during wetter seasons) and incomplete lixiviation of carbonates and nutrients (due to the lack of sufficient rainfall) from exchangeable complexes (clays and humus) are general features of Mediterranean soils (Yaalon 1997).

Apart from the limiting water content during summer drought, Mediterranean soils are often poor in nutrients (Specht 1973; Di Castri 1981; Carreira et al. 1991). Along with nitrogen (Mayor and Rodà 1994), phosphorus is a frequent limiting nutrient in Mediterranean ecosystems (McMaster et al. 1982; Witkowski et al. 1990; Lebourgeois et al. 1997; Henkin et al. 1998; Sardans et al. 2004, 2005a, 2006d). Soil moisture and nutrient supply and their availability for plant growth thus strongly interact in Mediterranean ecosystems (Everard et al. 2010).

The large variation in soil moisture throughout the year significantly impacts soil chemistry and activity, causing large seasonal changes in the activities of soil enzymes (Sardans and Peñuelas 2005 and 2010; Sardans et al. 2006d, 2008c and 2008d). A comparison of studies from the last two decades that have used similar methods to estimate activities of extracellular soil enzymes indicates that the activities of several important extracellular enzymes, such as urease, protease, β -glucosidase, and acid and alkaline phosphatases, in Mediterranean soils are similar to those of other temperate ecosystems, such as temperate grasslands, temperate wet forests, and tropical forests (Figure 1, Table S1 in the supplementary material). Soil enzyme activity is considered one of the best proxies of health and activity of soils (Dick 1977), so the similar activities suggest that even though Mediterranean ecosystems are generally less productive than other temperate and tropical ecosystems, they invest similar amounts of resources to produce soil enzymes. For example, the activity of root phosphatases in Mediterranean shrubs is equal to or even higher than in shrubs of other temperate areas of Europe (Estiarte et al. 2008). These similarities are probably related to the limiting role of nutrients and to the advantage provided by nutrient availability to improve WUE. For example, higher N availability improves the mechanisms of stomatal control reducing the unproductive water losses allowing a higher biomass production by unit of water absorbed (Brueck 2008).

Soil enzyme activity in Mediterranean soils is mainly determined by moisture. Many studies have reported decreased activity with decreasing soil moisture, both throughout the year (Grierson and Adams 2000; Quilchano and Marañón 2002; Criquet et al., 2002; Bell and Adams 2004; Sardans et al., 2008c; 2008d; Rutigliano et al. 2009; Sardans and Peñuelas 2010) and along gradients of soil moisture or experimental drought (García et al. 1994; Sardans and Peñuelas 2005 and 2010; Sardans et al. 2006d, 2008c and 2008d). Long summer droughts decrease soil enzyme activity and plant uptake and change soil C:N:P stoichiometry relative to other seasons (Aponte et al. 2010). Moreover, soil enzyme activity depends more on soil moisture than on SOC nutritional quality (Sardans and Peñuelas 2010), although both are important factors controlling rates of mineralization (García-Pausas et al. 2004; Rutigliano et al. 2009; Incerti et al. 2011). For example, the C:N and C:P ratios of litter are inversely correlated with rates of decomposition (Bengston et al. 2012). Similar results are observed when soil activity has been measured by soil respiration. Positive relationships are found between soil respiration and soil moisture (Rey et al. 2002 and 2011; Inghima et al. 2009; Carbone et al. 2011). In Mediterranean ecosystems when volumetric soil water content dropped below certain values, ranging from 13% (Rey et al. 2011) to 20% (Xu and Qi 2001; Rey et al. 2002) depending on reports, there is a strong soil respiration limitation. However, litter decomposition rates of Mediterranean forests are similar to those of temperate deciduous forest (Van Wesemael 1992). The values are very variable, ranging from 0.12 to 2.22 yr⁻¹ depending on the species (Van Wesemael, 1993; Fioretto et al. 2003; Rodríguez-Pleguezuelo et al. 2009). Frequently N concentration increases during decomposition process (Gallardo and Merino 1992; Fioretto et al. 2003), specially in the first months of decomposition (Gallardo and Merino 1999). Thereafter, during more advanced stages of decomposition, N release can decrease increasing litter N concentration (Maisto et al. 2011), observing in some cases a shift from N limitation to P limitation throughout litter decomposition process (Gallardo and Merino 1999). Not all studies have detected this trend in N concentrations during decomposition process (Fioretto et al. 2001). N litter concentration is also correlated with litter decomposition rates (Moro and Domingo 2000; García-Pausas et al. 2004), but lignin content and leaf mass area (LMA) of litter are also determinant in Mediterranean plants litter decomposition rates (Cortez et al., 1996, 2007; Karakov et al. 2007). Furthermore, plant species of early succession stages with low LMA, and high growth rate and litter N content have faster litter decomposition rates and N release from litter than species of later successional stages with opposite traits (García-Pausas et al. 2004; Kazakou et al. 2006 and 2009). Litter resulting from mixing litter of different species have proved to decompose at different rates (in general faster) than that expected from the decomposition rates observed by each species litter alone (De Marco et al. 2011). The importance and changes of P concentration during litter decomposition process has been less studied than those of N. Some studies have observed a decrease of P concentrations during litter decomposition (Gallardo and Merino 1999; Fioretto et al. 2001) with the consequent increases in litter N:P ratio (Gallardo and Merino 1999). In addition to litter quality, soil temperature and moisture have also an outstanding role in litter decomposition rates in Mediterranean ecosystems (Fioretto et al. 2000; Dirks et al. 2010; Incerti et al. 2011). Dirk et al. (2010) observed that litter decomposition is related with atmospheric humidity during summer, showing that during dry periods a significant part of water to leaf litter decomposition can come from atmosphere. The community density of soil

macroinvertebrate decomposers is also related to precipitation through its effects on the physical properties of soil and the quality of plant litter (Morón-Ríos et al. 2010). These studies demonstrate that in Mediterranean ecosystems water availability is the most important factor determining soil biological functioning.

Topographic factors, due to solar incidence and slope variation, and soil texture, due to water-infiltration capacity, have key roles in plant cover by determining the retention and storage of soil water, soil enzyme activity, and rates of soil erosion (Bastida et al. 2008). Soils with sandy structures are particularly critical in Mediterranean regions because of their high permeability and low capacity to retain water (Kooijman et al. 2005; Prieto et al. 2010). Soil organic matter (SOM) plays a key role in soil-water content by allowing the formation of stable aggregates that decrease the index of soil erosion (Barthes and Roose 2002). Calcareous Mediterranean soils have some singular differences from other soils regarding soil fertility. These soil types severely immobilize phosphate due to precipitation with Ca^{2+} (Carreira and Lajtha 1997), which is frequently critical because of the natural low P content of Mediterranean soils. On the other hand, calcareous soils have a good capacity to physically stabilize the SOM (Rovira and Vallejo 2003; Rovira et al. 2010), which should be beneficial due to the importance of stable soil aggregates in preventing soil erosion (Barthes and Roose 2002). Mediterranean soils have a low-moderate humification index (Simón et al. 1994) as a result of lower plant production and soil microbial activity imposed by summer drought and cold winters in continental and alpine areas (Simón et al. 1994). Soils of Mediterranean woodlands normally contain considerable amounts of SOC, with moder the main frequent type of humus (Vacca 2000; van Wesemael and Verstraten 1993; Sevink et al. 1989), although mull humus is also widely represented (Peltier et al. 2001; Sadaka and Ponge 2003; Andretta et al. 2011 and 2012). The constraints and feedback processes resulting from the long and highly variable summer droughts have large effects on humus properties (Sevink et al. 1989; van Wesemael and Verstraten 1993; Vacca 2000; Peltier et al. 2001; Ponge 2003; Andretta et al. 2011) and microbial communities (Monakrouses et al. 2004; Goberna et al. 2005; Aponte et al. 2010) in Mediterranean areas. Amounts of SOM in Mediterranean ecosystems depend on levels of precipitation (Boix-Fayos et al. 1998; Gómez-Rey et al. 2010) and type of plant community (Lucas-Borja et al. 2010). Rewetting events during summer droughts are particularly important by suddenly increasing the mineralization of the SOC, ecosystem carbon fluxes (Jarvis et al. 2007) and the release of nutrients (Rey et al. 2005; Almagro et al. 2009).

Plant-soil relationships in Mediterranean ecosystems

Several studies have observed a strong interdependence between changes in plant community and changes in soil properties in Mediterranean ecosystems (García et al. 2002; Goberna et al. 2007a, 2007b; Estríngia et al. 2010; Dias et al. 2011). These close relationships are observed through both time and space. We here discuss the most relevant plant-soil relationships summarized from the literature. Most feedbacks between Mediterranean plant communities and soils are linked to their mutual protection.

Plant cover: avoiding competition for soil resources and improving the physical protection of soil

Despite the low water content and nutrient availability of Mediterranean soils, Mediterranean plant communities frequently have a notable cover and species diversity, reflecting the large capacity of coexisting species to avoid competition for soil resources. The avoidance of overlapping structures of the root system has been widely observed among different types of plants, such as between trees and grasses (Silva and Rego 2003; Lefi et al. 2004; Mattia et al. 2005; Moreno et al. 2005) or among more similar types, such as between woody evergreens (Filella and Peñuelas 2003b; Silva and Rego 2003; Mattia et al. 2005; Mereu et al. 2009). This differential capacity of plant species to exploit soil sources at different depths of soil has beneficial effects for the coexistence of species. Filella and Peñuelas (2003b) observed higher water uptake in evergreen shrubs growing under large pine trees than in those growing under smaller pines or in those separated from large pine trees, an effect very likely linked to the hydraulic lift, driven by a deep root system of big trees, from deep soil layers to shallower layers, effect that improves the water status of shrubs that grew under big pine trees (Filella and Peñuelas 2003a). The possibility that the deep roots can pump water to the surface layers, thereby helping to maintain higher moisture levels in the upper richer soil layers, is a phenomenon that needs to be investigated in depth. The extensive and deep root systems of Mediterranean plant communities also protect the soil against erosion from torrential rain (Andreu et al. 1998; Chirino et al. 2006), mainly on slopes (Mattia et al. 2005; De Baets et al. 2007 and 2008). This widespread presence of roots throughout the soil layers has several other notable effects on soil properties and traits, such as decomposer fauna and physical soil texture (Maestre and Cortina 2002, 2003). The presence of Mediterranean plant communities with more diverse species compositions improves soil quality and structure (higher levels of SOM, microbial biomass, and nutrient content; more stable aggregates; a more equilibrated texture; and greater permeability) (Andreu et al. 1998; Pinzari et al. 1999; Chirino et al. 2006).

Plant cover and soil fertility and water availability

Most studies suggest a significant positive and rapid feedback between soil properties linked to fertility (water-storing capacity, permeability, nutrient availability, depth) and plant cover (Gallardo et al. 2000; Johnson-Maynard et al. 2002; Castaldi et al. 2009; Ochoa-Hueso et al. 2011). An increase in plant cover thus has a direct positive effect on soil porosity, which increases water-infiltration capacity and decreases runoff (Johnson-Maynard et al. 2002; Goberna et al. 2007a; Garcia-Estringana et al. 2010). This capacity to improve water infiltration generally occurs in different types of plant community but is higher in grasses and angiosperm evergreen shrub and tree communities than in pine forests (Johnson-Maynard et al. 2002; Garcia-Estringana 2010). These differences are probably linked to the observed differences in the formation of sand-sized organic matter in different communities, such as between evergreen shrubs and pines (Quideau et al. 1998). A positive feedback between plant cover and soil properties is consequently established. The improvement of soil quality generated by plant cover improves soil moisture and water availability, fertility (Gallardo et al. 2000), and soil enzyme activity (García et al. 2002). These effects are related to the improvements in the physical and chemical properties of soil and thus to higher water availability that, in turn, has a positive effect on Mediterranean plants (Sadaka and Ponge

2003; Ruiz-Sinoga et al. 2011). This relationship between plant cover and soil protection and fertility tends to be stronger in dry areas than in wetter areas (Ruiz-Sinoga et al., 2011).

Mediterranean plants, by having some of their typical properties linked to mechanisms of stress avoidance, can affect soil properties linked to nutrient cycling and availability. A reduction in nutrient losses in litterfall could be a strategy employed by sclerophyllous plants adapted to poor soils (Aerts 1995) and could partially compensate for decreased nutrient uptake in dry conditions. This conservative use of water and nutrients, though, can also retard nutrient cycling as a result of the larger content of structural compounds and the more recalcitrant litter that also has lower nutrient concentration due to a high level of retranslocation. Mediterranean plants can cover up to 84% of the N demand throughout leaf expansion from retranslocation from old tissues (Silla and Escudero 2003). High levels of N, P and K retranslocation from senescing leaves have been widely observed in Mediterranean plants (Grubb 1977; Pugnaire and Chapin 1993; Fioretto et al. 2003; Milla et al. 2005; Sardans et al. 2005a; Fife et al. 2008). Sclerophyllous leaves are moreover rich in structural compounds (Rundel 1982; Gallardo and Merino 1992; Turner 1994) that also produce litter of low nutritional quality and lower rates of litter decomposition, which can then lead to more occluded humic compounds that retain nutrients in unavailable forms to plants in the soil. However, photodegradation could contribute to decrease lignin concentration in litter of Mediterranean soils such as observed in other semiarid environments (Austin and Vivanco, 2006; Austin and Ballaré 2010; Ballaré et al. 2011). A fast release of N under high UV radiation intensity allowing increases in soil microbial activity is one of the probable mechanisms underlying this effect (Foereid et al. 2010). Mediterranean plants are rich in secondary metabolites such as phenolics (Castells and Peñuelas 2003; Hernandez et al. 2004; Skerget et al. 2005; Coulis et al. 2009; Bettaieb et al. 2011), compounds that decrease N mineralization rates in litter (Castells and Peñuelas 2003; Castells et al. 2004) and retard decomposition (Castaldi et al. 2009). Foliar extracts of *Arbutus unedo* rich in phenolic compounds strongly inhibit soil nitrification (Castaldi et al. 2009). Mediterranean plants have higher levels of N and P retranslocation (Nuñez-Oliveira et al. 1993; Fioretto et al. 2003; Sardans et al. 2005a) that lead to leaf litter with low nutrient concentrations. This strategy of retranslocation has further consequences on the rates of litter decomposition because the concentrations of litter N and P appear to be determinants in the rates of litter decomposition (Schlesinger and Hasey 1981) and in the community structure of soil decomposers (Almagro and Martínez-Mena 2012). More retranslocation should thus lead to a low release of N and P from litter and lower availability of soil N and P. The high capacity for erosion of Mediterranean rain may have further favored the evolution of plants toward higher retranslocation to assure better control of nutrient stocks, thereby improving the capacity of the plant-soil system to retain nutrients. The high retranslocation is related to the observed higher percentage of nutrients in the stand biomass of Mediterranean forests compared with other forest types (Rodà et al. 1999a,b; Sardans and Peñuelas 2012; Sardans et al. 2012a).

The capacity of plants to absorb nutrients in the early phases of regeneration may be a key factor to prevent the degradation of soil. Resprouting capacity should be particularly important in nutrient-poor environments and in environments, such as Mediterranean ecosystems, where the risk of nutrient losses is high after fires or from torrential rainfall.

The sprouting capacity during the initial phases of regeneration after disturbances such as fires thus provides resprouting species with a higher competitive ability for nutrient uptake than the species that can only regenerate with seeds (Lloret et al. 2004; Sardans et al. 2004). However, in Mediterranean ecosystems sprouter-seeders strategies present clear trade off, with sprouters having higher allocation to root system and less to flowering and seed production, and seeders having higher aboveground growth capacity, higher flowering and seed production (Enright and Glodblum 1999, Bell 2001). Sprouters tend to have a higher conservative use of nutrients than seeders (Saura-Mas and Lloret 2009), but it is not clear that in general sprouters increase their cover with fires. Contrarily, regional surveys have reported an increase in the relative abundance of non-resprouters in burnt areas (Lloret et al. 2005). Nevertheless, other reports suggest that the presence of resprouters can be enhanced when the frequency of disturbances increases (Bon and Midgley 2003). However, some studies have suggested new possibilities that explain the high prevalence of sprouter plant species in Mediterranean ecosystems. Lamont and Wiem (2003) suggest that the great genet resilience associated with frequent new branching by fire, drought-rewetting and herbivore might benefit the somatic mutations in the meristematic tissues favoring ecotypic differentiation and speciation in sprouters. Moreover, within a single species resprouts have proved to better resist drought than genets grown from seeds (Peña-Rojas et al. 2004).

Plant communities with high numbers of species produce litter with higher rates of decomposition and a better capacity to retain soil N than communities with lower species diversity (Bonanomi et al. 2010; Maisto et al. 2011). This finding suggests that a mixed litter from different species constitutes a more balanced and complete source of food for the community of soil decomposers than litter from only one species. In Mediterranean ecosystems that produce litter of low nutritional quality, the mixing of species in species-rich communities is thus favored because the diversity can improve soil activity and nutrient mineralization, conferring greater stability to the soil. Baraza et al. (2009) have observed that foliar nutritional quality is highly variable among different Mediterranean plants of the same and of different communities, frequently with different nutritional properties, creating a scenario of differential nutritional supplies in space (different species) and time (seasons) in which herbivores must select their diet.

In Mediterranean arid areas with high risk of desertification, usually water infiltration capacity is higher and run-off erosion is lower in slopes with less insolation and evaporation capacity (Boix-Fayos et al. 1998; Kutiel et al. 1998). In slopes of more arid Mediterranean areas the variability of water and nutrients availability is related to the distribution of vegetation patches with respect to bare soil patches that can be considered as runoff sinks and sources, respectively (Boix-Fayos et al. 1998; Kutiel et al. 1998; Ruíz-Sinoga and Martínez-Murillo 2009; Mayor et al. 2009; Mayor & Bautista 2012; Gabarrón-Galeote et al. 2012; Merino-Martin et al. 2012). But some few studies have not observed these relationships so clearly (González-Pelayo et al. 2010). This effect of patches is crucial in the maintenance of vegetation in more arid sites. The patches of vegetation also influence hydrological and erosion behavior (Ruíz-Sinoga et al. 2011), and are related with soil properties (Ocho-Hueso et al. 2011) such as infiltration capacity and biological activity throughout the slopes (Maestre & Cortina 2002; Agra and Ne'eman 2012). When adjacent patches have different species composition, with different root depth and density, ones can

act as runoff sinks and others as runoff sources (Merino-Martin et al. 2012). Grazing, particularly from mammals, contribute to maintain plant diversity between different patches of vegetation (Golodets et al. 2011). The presence of patches with very different species composition can exert a key role in plant invasive success to maintain large soil variability (Harrison et al. 2001; Prober & Wiehl 2011). Moreover, the presence of large trees in patches exerts an important role in maintaining high level of herbaceous species richness by affecting light and water competition intensity and availability (Blank and Carmel 2012).

The Mediterranean agroforest systems (Dehesa) that cover wide areas in south Europe and constitute a particular system where human activities help to maintain the ecosystem with a particular plant cover with savanna structure (Gallardo 2003; Gallego Fernández et al. 2004) that maintain great differences in the horizontal spatial distribution of soil nutrient availability (Gallardo 2003; Gea-Izquierdo et al. 2010), soil organic content (Howlett et al. 1987) and soil water availability (Joffre et al. 1999). All these soil properties are positively related with tree canopy. Regional scale evidences of the tree density and mean annual precipitation suggest that the structure of these man-made ecosystems have adjusted over long-time and corresponds to an optimal functional equilibrium with water cycle (Joffre et al. 1999). Frequently the major problem to maintain these ecosystems and maintain tree production is the shrub competition that strongly impacts soil nutrient availability (Rolo et al. 2010).

Changes during successional events: soil properties and plant diversity

The positive feedbacks between plant cover and soil fertility properties also drive plant succession. An increase in the growth of tree seedlings is observed when shrub cover increases, with shrubs acting as nursery species for the seedlings by enhancing soil properties such as infiltration, retention capacity, and soil enzyme activity (Duponnois et al. 2011). In the driest Mediterranean areas with sparse vegetation, soil patches under vegetation present higher levels of water permeability, SOM, microbial biomass, and enzyme activity than bare soil (Goberna et al. 2007b). Moreover, when plant cover is enhanced, the SOM, soil microbial biomass, and activity linked to higher biomass production and soil moisture quickly increase (García et al. 2005; Muñoz et al. 2007; Duponnois et al. 2011; Maestre et al. 2011). The composition and activity of soil microbial communities in Mediterranean areas are strongly determined by changes in plant communities that cover the soil (Bonkowski and Roy 2012), and soil microbial activity is generally negatively affected by the degradation of the plant cover (García et al. 2002). Other studies have also observed a close relationship between the spatial distribution of plants and soil NH_4^+ concentration (Gallardo et al. 2000; Castillo-Monroy et al. 2010). More diverse plant communities are associated with soils higher in SOM and N concentration than are plant communities with fewer species (Lucas-Borja et al. 2012). In the meadow-shrubland-maquis succession in Mediterranean climates, the aboveground biomass and overall soil activity increase, although with high seasonal fluctuations (Fioretto et al. 2009). In fact, when soil properties have been studied in different plant communities from grassland to evergreen shrubland and forest, larger differences in soil variables related to soil fertility have been observed among seasons than among different plant communities (Monokrousos et al. 2004), illustrating the strong link between seasonal changes of

aboveground vegetation with seasonal changes in soil properties. Anyway, regarding nutrient availability in soils the current studies suggest a strong mechanisms of nutrient conservation during succession in Mediterranean ecosystems. Intense nutrient uptake and accumulation capacities are observed in the early successional species (Carreira and Neil 1992). The presence of legumes is high in different Mediterranean successional communities both in early successional stages with high presence of herbaceous legumes and in latter successional stages with high presence of perennial legume shrubs (Arianoutsou and Thanos 1996). Regarding drought response strategy, early successional species escape drought by dying before summer while later herbaceous species maintain a favourable water status in relation to leaf shedding during summer; finally, late successional trees with a large body allow access to a large pool of resources, producing dense leaves that can tolerate desiccation (Navas et al. 2008). In this respect, seed banks of herbaceous plants are less sensible to decrease than those of woody plants if the frequency of severe drought episodes increases (del Cacho and Lloret 2011). The protection of soil moisture and the improvement of soil texture under shrubs can facilitate tree seedling survival in most wet Mediterranean ecosystems (Gómez-Aparicio et al. 2005).

Studies during the course of succession of plant communities in Mediterranean areas show a progressive replacement of species with low leaf mass area (LMA) and high concentrations of foliar nutrients by species with opposite traits (Cortez et al. 2007). Fast-growing species are replaced by slower growing species associated with the conservative use of soil resources. This trend in Mediterranean areas is closely associated with changes in the availability of soil N and P and also with the ratio between bioavailable N and P (Dias et al. 2011). The large capacity of the fast-growing, nutrient-rich species to absorb nutrients in the first phases of succession of the plant community should be particularly important in Mediterranean areas by hindering the loss of soil nutrients by erosion and leaching.

Mycorrhizae and their role in Mediterranean plant-soil relationships

Mycorrhizae improve the resistance of plant communities against environmental stresses including nutrient deficiency, drought, and soil disturbance. Therefore, they play a key role in Mediterranean plant communities that frequently experience all these stresses that threaten to increase in the scenario of global change. Several studies in Mediterranean plant communities have observed that mycorrhizal fungi play an important role in the capacity of plants to take up water (Bell and Adams 2004) and nutrients (Martínez-García et al. 2011). Mycorrhizal activity in Mediterranean ecosystems is often specifically associated with an improvement in the uptake of P (Bell and Adams 2004; Domínguez-Nuñez et al. 2006; Martínez-García et al. 2011). Frequently a positive correlation between total percentage of mycorrhizal root-length colonization and soil organic matter contents and soil N concentrations has been observed in Mediterranean ecosystems (Çakan and Karatas 2006). Studies of mycorrhizal inoculation in Mediterranean plants have shown a largely improved N, P and K uptake by inoculated plants (Azcon and Barea 1997; Medina and Azcon 2010) improving plant survival, diversity and functionality of these drought-adapted plant communities (Barea et al. 2011). These studies have demonstrated that the role of mycorrhization in more dry and nutrient poor-Mediterranean ecosystems is critical to

improve the drought resistance capacity and to prevent the aggravation of desertification process.

Mycorrhizal fungal communities are sensitive to processes of soil degradation and to summer drought (Martínez-García et al. 2012). Both reduce mycorrhizal density, but the communities do not disappear, suggesting a certain degree of adaptation to stress (Barea et al. 2011).

Impacts of increased atmospheric CO₂ concentrations

Mediterranean shrublands have the lowest capacity to store C compared to other temperate-climate shrublands throughout Europe (Beier et al. 2009). However, several studies have hypothesized an increase in plant and microbial biomass under high atmospheric CO₂ in Mediterranean ecosystems (Dhillion et al. 1996). An overview of the current literature identifies three basic and direct effects of increased CO₂ concentrations on Mediterranean ecosystems: changes in plant water conductance, a trend to increase the accumulation of biomass, and a change in the chemistry of plant tissues (Table 2, Table S2 in the supplementary material).

Under elevated levels of atmospheric CO₂, the foliar conductance of water decreases and WUE increases (Bettarini et al. 1995; Tognetti et al. 1999a, 1999b, 2000; Roumet et al. 2000; Maroco et al. 2002; Morgan et al. 2004) (Table 2). Some studies (Peñuelas and Azcón-Bieto 1992; Scarascia-Sugnozza et al. 1996; Nijs et al. 2000; Morgan et al. 2004; Peñuelas et al. 2008a; Andreu-Hayles et al. 2011; Maseyk et al. 2011), and mathematical models (Osborne et al. 2000) suggest that increases in concentrations of atmospheric CO₂, by increasing WUE, can counteract the effects of the projected increase in drought in the coming decades (IPCC 2007). Long-term experiments have not tested whether Mediterranean plants could acclimate to elevated CO₂ to buffer these higher WUEs. Moscatelli et al. (2001) observed that the effects of elevated CO₂ on plant growth and microbial biomass occurred only at the beginning of their study and progressively diminished as monitoring continued. In this context, Rey et al. (1997) showed that the effects on relative growth rates (RGR) had disappeared after 4.5 years of plants exposed to increased atmospheric CO₂ concentrations and that the increased biomass accumulation was the result of an early effect of RGR. A recent study has observed that elevated atmospheric CO₂ (712 ppm) during a strong summer drought did not prevent a decline in water use and the capacity of soil to store water in the most critical dry periods (Hernández-Santana et al. 2009). Moreover, the results of other studies manipulating atmospheric CO₂ and conditions of drought have suggested that these two variables may have compensatory effects; the effects of short-term increases in CO₂ on several plant variables that improve WUE can be counteracted by enhanced conditions of drought at the levels projected by most climatic models (López et al. 1998; Nijs et al. 2000; Loreto et al. 2001; Hernández-Santana et al. 2009).

An overview of the current bibliography (Table 2) on the effects of increased atmospheric CO₂ on plant growth and photosynthetic capacity indicates a short-term enhancement of plant growth and photosynthetic rates (Scarascia-Mugnozza et al. 1996; López et al. 1998;

Nijs et al. 2000; Marek et al. 2001), but this positive effect is frequently only observed in nutrient-rich soils (Midgley et al. 1995; Cruz et al. 2003). The positive effect on growth generally decreased with time (Körner & Miglietta 1994; Jones et al. 1995; Peñuelas et al. 2008a; Andreu-Hayles et al. 2011), suggesting acclimation to increase of atmospheric CO₂ concentrations (Navas et al. 1995; Roumet et al. 2000; Sauser et al. 2003). The increased growth in the short-term is linked to increases in WUE associated with an atmosphere richer in CO₂ (Nijs et al. 2000). Moreover, increased atmospheric CO₂ concentrations can favor species that fix N₂ over those that do not (Navas et al. 1997; Grünzweig and Dumbur 2012) and can increase the nutrient uptake capacity by enhancing mycorrhizal associations (Rillig et al. 1998a). The higher production of reproductive and vegetative biomass of legumes than non N₂-fixing plants under increased atmospheric CO₂ concentrations related to higher protein synthesis capacity could give competitive advantage to legumes in a CO₂-rich atmosphere (Navas et al. 1997; Grünzweig and Dumbur 2012).

Most data from Mediterranean regions show that when plants are grown in increased atmospheric CO₂ concentrations a decrease in plant N and P concentrations is observed and consequently the C:N and C:P ratios of plant biomasses increase (Sardans et al. 2012b and Table 2). Under elevated CO₂, plant production and the C:N ratio increase, diminishing the concentrations of N and other nutrients (De Angelis et al. 2000; Peñuelas et al. 2001; Bassirirad et al. 2003; Tognetti and Peñuelas 2003) and increasing phenolic compounds (Peñuelas and Estiarte 1998; Castells et al. 2002) in foliar biomass. Mediterranean plants can partially buffer the effects of higher C:N ratios in plant tissues under increased atmospheric CO₂ concentrations by increasing the retranslocation, fixing, and mineralization of N (Peñuelas and Estiarte 1997). Despite the capacity of plants and ecosystems to increase nutrient availability under increased atmospheric CO₂ concentrations, most studies have observed higher C:N ratios and lower nutrient contents in plant tissues under increased atmospheric CO₂ concentrations than in current levels of atmospheric CO₂ concentration (Bettarini et al. 1995; Midgley et al. 1995; Gahrooe et al. 1998; Cotrufo et al. 1999; Roumet et al. 1999; De Angelis et al. 2000; Blaschke et al. 2001; Peñuelas et al. 2001; Tognetti and Peñuelas 2003; Cruz et al. 2003) (Table 2). This decrease in N concentrations could impact on plant-insect relationships (Roumet et al. 1999). The effects of increased atmospheric CO₂ concentrations can have opposite feedbacks on the capacity of soil to mineralize. The increases of plant biomass and litter and microbial biomass under increased atmospheric CO₂ concentrations suggest a possible increase in soil enzyme activity linked to higher soil microbial biomass (Dhillion et al. 1996). On the other hand, several reports have suggested a slow-down of litter decomposition and mineralization rates under increased atmospheric CO₂ concentrations in Mediterranean ecosystems (Gahrooe 1998; Cotrufo et al. 1999; De Angelis et al. 2000) linked to an increase of litter C:N and C:lignin (De Angelis et al. 2000) and C:P (Cotrufo et al. 1999) ratios that can counteract the higher soil enzyme activity. In fact, high concentrations of atmospheric CO₂ over two years had no important direct effect on soil nitrification and denitrification (Pinay et al. 2007). Higher concentrations of atmospheric CO₂ can increase the short-term turnover of C due to higher growth and litter production, but this effect decreases in the medium term by the limitation of nutrients (Cotrufo et al. 2005). Differential effects of the enhancement of atmospheric concentrations of CO₂ in different species of plants have been observed in mycorrhizal-plant

symbioses where the presence of mycorrhizae increases in the roots of some species and decreases in others (Rillig et al. 1998b) (Table 2). An increase in phenolics in leaf litter decreases N mineralization (Castells et al. 2004), also suggesting a change in the nutritional quality of plant biomass for herbivores. Nevertheless, all these chemical changes can be buffered under long-term exposure to elevated CO₂, as observed in plants in the vicinity of CO₂ springs, suggesting an evolutionary adaptive response in Mediterranean plants to changes in levels of CO₂ (Peñuelas et al. 2002b).

Climatic changes impact on plant-soil relationships

The largest effects of climatic change in Mediterranean ecosystems (IPCC 2007) may well be those related to increased drought, since water stress is already the principal constraint in the Mediterranean region (Specht 1979; Mooney 1989). Enhanced drought is expected to be accompanied by more severe torrential rainfall (Frei et al. 1998), already frequent events (Romero et al. 1998). Over the last century, temperatures have shown an overall trend toward warming (Kutiel and Maheras 1998; Peñuelas et al. 2002a). Precipitation has exhibited either a long-term downward trend, principally in the dry season (Kutiel et al. 1996; Esteban-Parra et al. 1998), or no significant change (Piñol et al. 1998; Peñuelas and Boada 2003), but potential evapotranspiration has risen in all cases.

Warming

The effects of climatic change on nutrient supply in Mediterranean areas may depend on a trade-off between warming and the effects of drought. Concentrations of nutrient in the biomass result from the balance of nutrient uptake and growth. Increased temperatures in these water-limited ecosystems will further decrease the availability of soil water by enhancing evapotranspiration (Larcher 2000), which will very likely result in a decrease in the uptake of nutrients by roots and in the movement of these nutrients to shoots (Bradford and Hsiao 1982) altogether having a general negative effect on soil activity and plant growth. Warming can also have a direct effect during cold and wetter winters by increasing soil enzyme activities (Sardans et al. 2006g), extending growth periods (Peñuelas and Filella 2001; Peñuelas et al. 2002a), and raising photosynthetic rates (Llorens et al. 2003b). This positive effect during the cold season could be counterbalanced by a lower availability of water in the summer and by shortening the growing season by extending the duration of water deficits (Llorens et al. 2003b; Peñuelas et al. in preparation). The effect of warming on plant growth depends on total annual precipitation. Warming has positive effects on growth in wetter years and no or even negative effects in drier years (Swarbreck et al. 2011). In a study analyzing long-term temporal metadata in Mediterranean areas, changes in precipitation may even have had a relatively higher importance than changes in temperature in explaining phenological shifts in some Mediterranean plant communities (Peñuelas et al. 2004). As mentioned above, some studies have observed a threshold value of temperature showing that during periods with temperatures above 20 °C soil activity is strongly dependent of soil moisture (Rey et al. 2011). In Mediterranean regions, warming only increases soil enzyme activities (Sardans et al. 2008c; Sardans and Peñuelas 2010) and SOM mineralization in the year periods in which soil moisture is high (Bottner et al. 2000; Qi and Xu 2001; Sardans et al. 2006d). The effects of warming at the levels projected by climatic

models (IPCC 2007) in arid environments such as Mediterranean areas are thus related to the indirect effect of decreasing soil-water content (Peñuelas et al. 2004; Swarbreck et al. 2011; Sardans et al. 2012b).

Some studies have observed that N mineralization is enhanced more rapidly than P mineralization under warming (Rinnan et al., 2007). This study did not refer specifically to Mediterranean ecosystems but in Mediterranean areas this could also occur, and the increases in available soil N:P ratios could further increase in some Mediterranean areas where the N deposition is increasing in the last years (Vourlitis & Pasquini 2009; Pinho et al. 2012). In fact, experiments of N fertilization in Mediterranean terrestrial ecosystems have shown an increased water-use efficiency (WUE) (Guerrieri et al. 2010), a response that could have positive effect on plant production under warming. However, other possible impacts such as changes in competitive relationships between species adapted to N-limitation and adapted to P-limitation remain to be investigated. In this respect some studies have observed that the changes in nutrient cycling in Mediterranean ecosystems under global change are strongly related to community composition shifts (Maestre et al. 2012).

Drought

The decline in total rainfall and/or availability of soil water projected for the coming decades (IPCC, 2007) may prove to be even more drastic under warmer conditions with a CO₂-rich atmosphere and higher demand for water (Piñol et al. 1998; Peñuelas et al. 2005). Some studies investigating the impact on Mediterranean ecosystems of increased atmospheric CO₂ concentrations, drought and warming suggest that most future scenarios of drought combined with warming and/or with increased atmospheric CO₂ concentrations may involve strong impacts on soil-water deficits and water use in trees of Mediterranean forests by increasing soil water deficit (Hernández-Santana et al. 2008).

Plants—Increases in drought intensity at the level projected for the coming decades (ICPP 2007) could reduce soil moisture (Sardans et al. 2008a, 2008b), plant growth and cover in the short term (Boix-Fayos et al. 1998; Goldstein et al. 2000; Beier et al. 2004; Serrano et al. 2005; Tsiafouli et al. 2005; Ogaya and Peñuelas 2007a; Sardans et al. 2008a, 2008b; Prieto et al. 2009a, 2009b; Pérez-Ramos et al. 2010; Cotrufo et al. 2011; Talmon et al. 2011) (Table 3, Table S3 in the supplementary material). Moreover, plant cover can be seriously threatened by the increase of fire risk projected in the Mediterranean area in the context of enhanced drought (Mouillot et al. 2002; Moriondo et al. 2006).

Drought also induces changes in foliar nutrient contents, with a general trend to reduce foliar N (Sardans et al. 2008a, 2008b), P (Sardans and Peñuelas 2004, 2007a; Sardans et al. 2008g), and micronutrients (Sardans et al. 2008e, 2008f), which can also change in other plant tissues (Sardans and Peñuelas 2004, 2007a, 2008b; Sardans et al. 2006b, 2008a, 2008b, 2008e, 2008f, 2008g). The nutrient content of aboveground biomass, mainly in leaves, tends to decrease with drought (Sardans et al. 2008a; 2008b), with the exception of K that increases in some aboveground tissues of some plant species (Sardans and Peñuelas 2007a; Sardans et al. 2008g). Drought increases the C:N and C:P ratios of Mediterranean shrubs and trees, associated with a protective and conservative mechanism (Inclan et al. 2005;

Sardans et al. 2008b; 2008c; 2008d; Matías et al. 2011) and with sclerophylly and increases in lignin content (Bussotti et al. 2000; Sardans et al. 2006a). Drought enhances the allocation of N to the root system, which increases the capacity to absorb water (Sardans et al. 2008a; González et al. 2010). Drought also increases the oxidative stress of Mediterranean plants (Munné-Bosch and Peñuelas 2003 and 2004). Under moderate conditions of drought, photosynthetic pigments remain more or less constant, and anti-stress compounds such as α -tocopherol increase in concentration. When stress from drought is severe, the concentration of photosynthetic pigments falls, and anti-stress pigments and secondary compounds can increase more (Munne-Bosch and Peñuelas 2004; Hernandez et al. 2004) or even decrease (Bettaieb et al. 2011) due to the loss of production capacity. Drought can induce foliar senescence that contributes to the remobilization of nutrients during stress, thus allowing the rest of the plant, including new leaves, to benefit from the nutrients accumulated during the foliar life span (Munne-Bosch and Alegre 2004). Sclerophylly is a typical and general trait of evergreen Mediterranean plants and usually increases when the environment evolves toward drier conditions (Dunn et al., 1977; Sabaté et al., 1992; Oliveira et al., 1994).

During drought, different plant species of the same community exhibit differential decreases in the growth of aboveground biomass (Mamolos et al. 2001; Ogaya and Peñuelas 2007b; Prieto et al. 2009a, 2009b), changes in foliar nutrient concentrations and contents (Peñuelas et al. 2008b; Sardans et al. 2008a, 2008b, 2008e, 2008f), and effects on hydraulic conductivity (Mereu et al. 2009) (Table 3). These differences in growth and nutrient uptake during drought are related to species differences in the capacity to maintain ecophysiological traits, such as photosynthetic rate, WUE, regulation of foliar gas exchange (Peñuelas et al. 2000; Llorens et al. 2003a, 2003b; Ogaya and Peñuelas 2003; Ozturk et al. 2010; Vilagrosa et al. 2010; Galle et al. 2011), capacity to protect against oxidative damage (Munné-Bosch and Peñuelas 2004), root depth (Padilla and Pugnaire 2007; West et al. 2012) and capacity to reabsorb N (Sanz-Perez et al. 2009).

The relationships between hydraulic architecture and leaf area are a key factor determining drought adaption success. Drought-induced mortality in Mediterranean pines has proved to be related to lower hydraulic conductivity per unit of leaf area (Martínez-Vilalta and Piñol 2002). The resistance to xylem embolism allows to maintain higher stomatal conductance and sap flow even at lower water potentials thus permitting large WUE (Martínez-Vilalta et al. 2003). The survival capacity to drought has been proved to be also related to carbon reserves (Voltaire 1995; Galiano et al. 2012). Under drought, the Mediterranean tree *Olea europea* stops growth but not photosynthetic activity that allows it to store assimilates, produce antioxidants, antiherbivore compounds, such as phenolics, and osmoprotective substances, mainly water soluble sugars allowing to maintain cell turgor (Voltaire 1995; Sofu et al. 2008). Mediterranean trees usually present lower stomatal sensitivity to drought in seedling phase than in adult phase, probably in benefit of an increase in growth under competition with understory vegetation, making them more vulnerable to drought events in initial phases of growth (Mediavilla and Escudero 2004).

Soils—As discussed above, moderate reductions in rainfall imply significant decreases in soil moisture. In addition to this direct effect, reduced rainfall can indirectly affect plants by reducing growth and increasing C:nutrient ratios. Some studies have also reported increases

in SOM (Talmon et al. 2011). Most reports recommend the differentiation between short-term and medium- and long-term effects of drought on SOM (Ogaya and Peñuelas 2006; Martí-Roure et al. 2011; Navarro-García et al. 2012). In the short term, drought can increase SOM by increasing the total amount of litterfall (Oliveira and Peñuelas 2002; Ogaya and Peñuelas 2006; Martí-Roure et al. 2011) and dead roots (Lloret et al 1999; Padilla and Pugnaire 2007). Few long-term experiments on the effect of drought on SOM have been conducted, but observational studies under prolonged and sustained drought or across environmental gradients suggest that SOM decreases by the reduction of plant cover, implying a decrease in litterfall and an increase in soil erosion by diminishing soil protection and permeability (Boix-Fayos et al. 1998; Li et al. 2011; Navarro-García et al. 2012).

SOM mineralization is very sensitive to drought in Mediterranean ecosystems (Table 3). Decreases in soil enzyme activity (Zaman et al. 1999; Fioretto et al. 2000; Li and Sarah 2003; Sardans and Peñuelas 2005, 2010; Sardans et al. 2006d; Sardans et al 2008c, 2008d; Hueso et al. 2011), soil respiration (Bottner et al. 2000; Qi and Xu 2001; Emmett et al. 2004; Asensio et al. 2007), and root enzyme activity (Sardans et al. 2007) have been widely observed under drought conditions. The decrease in soil enzyme activity is mainly due to the direct effect of the reduction in soil moisture (Sardans et al. 2008c; Sardans and Peñuelas 2010) but also to the higher C:nutrient ratio in plant litter (Wessel et al. 2004). This decrease in the nutritional quality of the SOM can have a significant effect on the rates of litter decomposition (Coûteaux et al. 2002).

Another interesting but poorly studied aspect is the effect of drought on the structure of the community of decomposers. Curiel-Yuste et al. (2011) observed that fungi became more abundant and active than bacteria when soils were drier. More associations of arbuscular mycorrhizal fungi increase the tolerance of plants to drought (Benabdellah et al. 2011). Changes in the community of soil decomposers under drought should be the focus of new studies because these changes can be very important for understanding the capacity of Mediterranean ecosystems to adapt to increasing conditions of drought. Increases in fungal biomass can increase the capacity of plants to take up water and/or of soil to retain more water but can also change the capacity of nutrient cycling. Further research is needed to fill this gap.

Mediterranean ecosystems under drought show no clear patterns of shifts in N:P ratios (Sardans et al. 2008a; 2008b; 2012b). Different compensatory effects probably occur in the cycles of these two nutrients. P is frequently retranslocated more than N (Sardans et al. 2005a), but the comparative changes in N and P retranslocation with increasing conditions of drought is not known. On the other hand, increases of soil moisture decrease the fraction of P available in soils and increase the fraction of unavailable P (Sardans and Peñuelas 2004; Sardans et al. 2008g). N is also more soluble and easily leached than P and can be more lixiviated from soil by typical Mediterranean storms when plant cover is reduced under drought and in physically degraded soils. How increases in drought will affect Mediterranean ecosystems by changing N:P ratios remains unclear, but the N:P ratio is an important variable favoring species having different rates of growth (Sardans et al. 2012c).

Reductions in water uptake, mobility of nutrients in the soil, and release of nutrients from the SOM can exert a feedback contributing to reduce the capacity of plants under drought to take up nutrients by slowing the cycling of nutrients (Sardans et al. 2012b). Increasing nutrient concentrations in soils increase the risk of nutrient losses caused by runoff during torrential rainfalls (Sardans and Peñuelas 2004; Matías et al. 2011). Drought projected for the coming decades should not sufficiently change the concentrations of trace elements in the medium term to constitute any environmental or health problems (Sardans and Peñuelas 2007b; Sardans et al. 2008h).

System adaptation capacity—The long-term evolutionary adaptation of Mediterranean plants to long dry summers allows them to cope with moderate increases of drought without an important loss of their production capacity and survival (Cotrufo et al. 2011). Mediterranean shrubs subject to drought increase their levels of antioxidative mechanisms to prevent injuries from increased oxidative stress (Munné-Bosch and Alegre 2000; Munné-Bosch and Peñuelas 2003 and 2004; Peguero-Pina et al. 2008; Nogues et al. 2012). Other processes enhanced by drought can contribute to increase the capacity of plants to take up water. For example, Benabdellah et al. (2011) observed an increase in arbuscular mycorrhizae that increased the capacity of plants to take up water. Nutrient retranslocation increased when drought increased (Correia and Martínez-Louçao 1997), which increased the concentrations of nutrients in plants and thus contributed to an improvement in WUE. Higher nutrient retranslocation, however, should increase the C:nutrient ratio in litter and contribute to the formation of more recalcitrant SOM and to the slowing of nutrient cycling. The advantages and disadvantages of nutrient retranslocation under increasing conditions of drought remain unclear and deserve further research.

Additional effects on C-cycling and emissions of biogenic volatile organic compounds—Drought usually increases emissions of plant terpenes, although this effect strongly depends on drought intensity (Pegoraro et al. 2005; Plaza et al. 2005; Llusia et al. 2006, 2008, 2010). Studies suggest that severe drought decreases the emission of terpenes (Loreto et al. 2001; Pegoraro et al. 2007; Peñuelas and Staudt 2010) but reduces sink strength of the soil for atmospheric isoprene (Pegoraro et al. 2007). The effects of drought on the emission of terpenes from Mediterranean soils remain unclear and vary for different VOC compounds (Asensio et al. 2008).

Rewetting events after a period of drought have a large impact on soil respiration and microbial activity and increase the loss of C from soil (Navarro-García et al. 2012). After rewetting events, as for example after a rain event in a drought period, an increase of soil heterotrophic respiration from litter and other soil organic fractions (Rey et al. 2005; Jarvis et al. 2007; Casals et al. 2011; Placella et al. 2012) and increases in the activity of some soil enzymes (Zornoza et al. 2006) have been widely observed. The capacity to faster resuscitation capacity of certain microbial groups after wet-up of dry soils may be a phylogenetically conserved ecological property in Mediterranean soils (Placella et al. 2012). This process can imply a sudden increase in nutrient availability, Butterly et al. (2009) observed a 35-40% increase of available P. However, this effect drops during the first days after rain (Butterly et al. 2009). These effects are due to the increased water availability and

to the increase of SOC made accessible to microorganisms by the physical destruction of soil structure by drying/wetting events (Inglima et al. 2009; Unger et al. 2010; Navarro-García et al. 2012) and by the increases of osmoregulatory substances released from microorganisms in response to hypo-osmotic stress (in order to avoid cell lyses) that increases the organic source to respiration (Unger et al. 2010). In the short term, rewetting causes a cascade of effects, from increases of SOC mineralization and availability of nutrients (Nguyen and Marschner 2005; Inglima et al. 2009) to short periods of plant growth (Xiang et al. 2008).

Desertification: Climate change scenarios projected for the coming decades predict a reduction in total precipitation and a higher frequency and severity of torrential rainfall (Frei et al. 1998; Romero et al. 1998; IPCC 2007). The most threatening phenomenon for Mediterranean soils, especially in the most xeric areas, is desertification linked to a continual positive feedback of higher frequency and intensity of torrential rainfall (associated to climatic change) with an increase of soil erosion, which in turn leads to a loss of soil fertility and thus plant cover. These facts can also be aggravated by human activities (such as excessive livestock pressure) and by the increasing frequency and extend of fires, specially in European Mediterranean region (Shakesgy 2011), that then leads to an increased risk of erosion and desertification. The increases of fires intensity and frequency is a serious concern (Shakesgy 2011). Moreover the investigations of community succession and soil processes after fires in Mediterranean plant communities create plant patches (Baeza et al. 2007) and soil degradation, reducing water infiltration (Coelho et al. 2004), all of them leading towards desertification process. During the last decades, several Mediterranean areas of the EU countries have been subjected to land-use change (Millan et al. 2005; Zucca et al. 2006; Calatrava et al. 2011; Salvati et al. 2012), whereby unproductive areas were forested or abandoned or submitted to overexploitation (Calatrava et al. 2011). It appears that these processes favour a general trend towards an increased cover of semi-arid shrublands, and in the worst cases to desertification (Zucca et al. 2006) and may even decrease rain events (Millan et al. 2005). This cascade of positive feedbacks among these four variables has been observed in some studies in southern Spain (García et al. 2002; Moreno-de las Heras et al. 2011; Ruiz-Sinoga et al. 2011 and 2012) and is exponentially favored and accelerated by the increase in aridity (Ruiz-Sinoga et al. 2011). The erosion of soils in Mediterranean areas is strongly related to torrential rainfall (González-Hidalgo et al. 2007). Slopes and higher erodible bedrock accelerate this process (Moreno-de las Heras et al. 2011). Moreover, photodegradation of litter rises when plant cover decreases (Barnes et al. 2012), thus increasing the SOM losses and contributing to soil degradation. Soil erosion is becoming the primary environmental concern in human economic balances in Mediterranean regions (Riera et al. 2007).

Future research directions

Mediterranean plants resist moderate increases in drought without significant changes in their production capacity and survival and are able to maintain levels of soil fertility. These capacities are species specific. The mortality observed in some forested Mediterranean areas after severely dry summers varies in different species of the same community (Hernández-

Santana et al. 2009). While we do not know the real level of future droughts, we can expect an increasing relative cover of more drought-adapted species within communities. The impact of this situation on the soil is less clear because if the drought is not severe, a new equilibrium in the plant-soil system may be attained. Therefore, further research is needed.

The interaction between atmospheric CO₂ and increased drought should be studied in long-term experiments, because a short-term counteracting effect has been observed. At long-term, the acclimation of plants to increased atmospheric CO₂ concentrations could diminish the compensatory effect of the increasing drought intensity. Similarly, warming can have a positive effect on ecosystems such as alpine areas by reducing the length of the cold season that can compensate the negative effects on production capacity resulting from the increased water stress during summer. These last contradictory effects have not been thoroughly studied, at least to the best of our knowledge, and should be a clear objective for further studies. If drought is more severe, and longer dry summers coincide with more severe torrential rainfall, a strong influence on soil erosion can be expected, as occurs in some areas of southeastern Spain (Ruíz-Sinoga et al. 2011 and 2012). Moreover, the projected increased drought could be even more detrimental for Mediterranean ecosystems if it occurs in spring (Allard et al. 2008). In addition to the environmental impact, an increase in the area of shrubland affected by erosion is a key concern, for several reasons. An increase of 1% in the current area of shrubland of the Mediterranean Basin could cause an enormous economic impact (Riera et al. 2007).

Summarizing the information in the literature, we can identify two different groups of feedbacks in Mediterranean plant-soil systems in response to the scarcity of water and nutrients in soils. Firstly, a high allocation to a deep, strong, and dense root system together with a notable plant cover and investment in soil enzyme production exerts a positive effect on soil fertility and protection capacity. Secondly but in contrast, a high nutrient retranslocation, high retention of nutrients in standing biomass, and high C:nutrient content of litter constitute constraints for a rapid release of nutrients from the SOM, lowering fertility and slowing the soil processes that produce high quality SOM. Current studies indicate that drought enhancement slows the first group of positive properties for soil fertility and protection but intensifies the second group of negative properties.

Plant cover, soil biological activity, and fertility are interconnected. The causes underlying the high soil enzyme activity observed in Mediterranean ecosystems warrants future research. Most efforts to date have investigated the relationships between soil moisture, temperature, and food quality of litter in terms of lignin content or C:nutrient ratio, but Mediterranean plants may possess mechanisms for stimulating soil enzyme production. Because the current data suggest that extensive root systems can significantly impact soil enzymes, the introduction of soil genomics, proteomics, and metabolomics should be encouraged to gain knowledge of the role of plants, through rhizospheric activity and root exudates, on soil microbial communities, on soil enzyme activity, soil mineralization, and soil texture. Moreover, these studies should investigate the role of metabolites at different levels and in different processes, such as the allelopathic inhibition of growth of competing vegetation, stimulation of microbial and especially fungal growth, or changes in soil structure by contributing to the formation of soil aggregates.

Studies in Mediterranean areas suggest a key role for the root system mediated by the availability of water. A more thorough knowledge of root structure and distribution of entire plant communities, from forests in mesic areas to sparse shrublands in drier areas, should be another main objective for research in this area. This research would provide a better understanding of the shifts that occur in plant communities when climate evolves to a different pattern of precipitation. The study of how root systems and particularly the deepest roots, which frequently enter fractures in the bedrock, pump water from the deepest to the upper soil layers warrants urgent research. How root systems maintain higher levels of soil mineralization and activity also warrants further research. Isotopic methods should be a useful tool in these studies by allowing the monitoring of the movement of water in soil-plant systems.

We also lack knowledge of the interacting effects of drought and warming in realistic field scenarios and in different conditions, from cold alpine forested areas to dry, warm lowland areas. The presence of large gradients of water availability and temperature in Mediterranean alpine areas, frequently over short distances, constitutes an excellent playground for investigating the role of soil moisture and temperature and their interactions in modulating the active and passive mechanisms of plants that affect soil texture and fertility. Moreover, these studies could help us to better understand the capacity of response of the different Mediterranean ecosystems to the projected increase in drought. In the context of future scenarios of global change, field experiments are needed for studying the long-term effects of high concentrations of atmospheric CO₂ combined with drier conditions, because this future scenario is very likely and because the current but incomplete results strongly suggest that the effects of increasing concentrations of atmospheric CO₂ on plants could decline with time.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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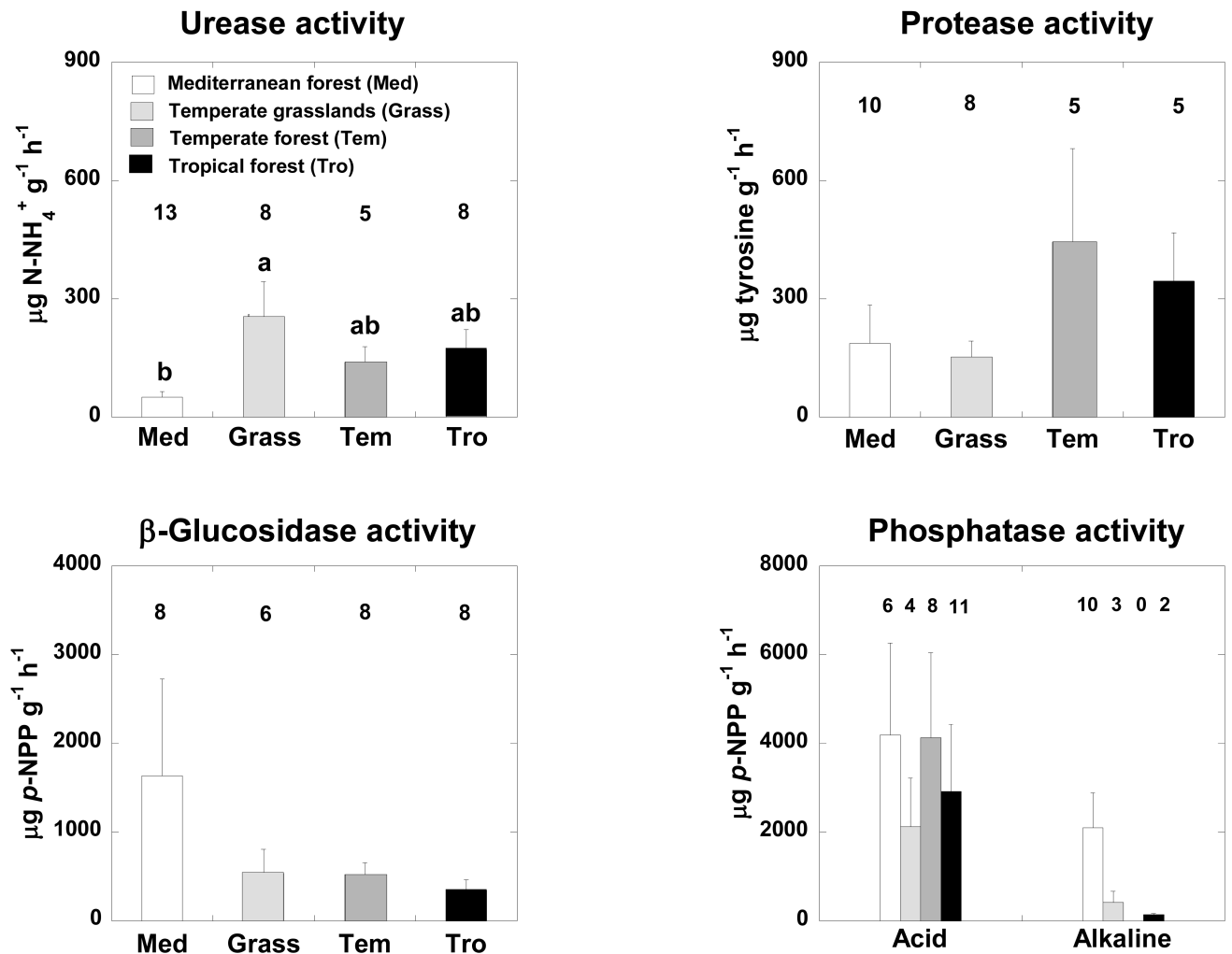


Figure 1.

Soil extracellular activities of urease, protease, β -glucosidase, and acid and alkaline phosphatases expressed in mg substrate released g^{-1} soil dry weight h^{-1} in Mediterranean soils compared with temperate and tropical soils. The reports have analyzed urease activity by the Kandeler and Gerber (1988) method or by comparable methods such as that of Tabatabai and Bremner (1969), protease activity by the Ladd and Butler (1972) method, β -glucosidase activity by the Eivazi and Tabatabai (1988) or related methods (Dick et al. 1996), and acid and alkaline phosphatase activities by the Tabatabai and Bremner (1969) and comparable methods (Tabatabai 1994). The values presented are those of controls when diverse treatments were applied to the studied soils and of the annual mean when several measurements were conducted throughout the year. The number of studies reviewed, by biome and enzyme, are depicted above the bars. The bars indicate mean (+ S.E.). For detailed information, see Table S1 in the supplementary material.

Table 1

Mediterranean morphological and physiological traits related to water stress avoidance and the bibliographic support.

Strategy level	Mechanisms	References
Water uptake capacity	Deep-root system	Baldocchi and Xu 2007 Castell et al. 1994 David et al. 2007 Filella and Peñuelas 2003b Hernández-Santana et al. 2008 Lefi et al. 2004 Mattia et al. 2005 Mereu et al. 2009 Moreno et al. 2005 Padilla and Pugnaire 2007 Silva and Rego 2003 Veneeklas and Poot 2003 West et al. 2012
	Root system plasticity	Padilla et al. 2007
Leaf mechanical structures to avoid water losses	Thick cuticle and high leaf mass area (LMA)	Bussotti et al. 2000 De Mico and Aronne 2009 Limousin et al. 2010 Sardans et al. 2006a
	High density of trichomes	Filella et al. 1999 Galmés et al. 2007b
	High plasticity of morphology and size	Hoff and Rambal 2003 Limousin et al. 2010
Control of water transport	Maintainance of water lift	Díaz-Barradas et al. 2010 Filella and Peñuelas 2003a Kurz-Besson et al. 2006 Oliveras et al. 2003 Prieto et al. 2010a,b Ripullone et al. 2009 Sofo et al. 2008
	Large resistance to xylem cavitation	Nardini et al. 2000 Martínez-Villata and Piñol 2002 Martínez-Vilalta et al. 2003 De Mico and Aronne 2009 Vilagrosa et al. 2010
	High stomatal control	Deffine et al. 2001 Fotelli et al. 2000 Galmes et al. 2007a Grant et al. 2010 Lefi et al. 2004 Lo Gullo et al. 2003 Misson et al. 2010 Peña-Rojas et al. 2004 Ripullone et al. 2009 Vaz et al. 2010
Improving water retention capacity	Increasing cell turgor capacity by enhancing the concentration of metabolites and/or water soluble sugars	Otiene et al. 2006 Rivas-Ubach et al. 2012 Sofo et al. 2004 and 2008 Vilagrosa et al. 2010 Volaire 1995
Reducing water losses	Reducing metabolic activity	Maseyk et al. 2008 Rivas-Ubach et al. 2012
Protection against oxidative stress	Antioxidant mechanisms	Hernández et al. 2004 Munné-Bosch and Lalueza 2007 Sofo et al. 2004

Table 2

Effects of increasing atmospheric [CO₂] on Mediterranean plant-soil systems. The numbers represent the number of studies in ISI's Web of Science reporting the corresponding result. For detailed information, see Table S2 in the supplementary material.

	Effects of increasing atmospheric [CO ₂] on Mediterranean plant-soil systems		
	↓	=	↑
Water-use efficiency	0	0	6
Foliar water conductance	8	0	0
Growth and photosynthetic rates	1	4	9
Nutrient concentrations	12	1	0
Assymetrical species-specific effects	0	0	4

Table 3

Effects of increasing drought on Mediterranean plant-soil systems. The numbers represent the number of studies in ISI's Web of Science reporting the corresponding result. For detailed information see Table S3 in the supplementary material.

	Drought effects on Mediterranean plant-soil systems		
	↓	=	↑
Production and growth	12	0	0
Soil activity and nutrient-cycle rates	20	0	0
Assymmetrical species-specific effects	0	0	16
Soil permeability	4	0	0