

1 **Plant-soil interactions in Mediterranean forest and shrublands: impacts of**
2 **climatic change.**

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4 Sardans J^{1,2*}, Peñuelas J^{1,2}

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6 ¹CSIC, Global Ecology Unit CREAM-CEAB-UAB. 08913 Cerdanyola del Vallés.

7 Catalonia, Spain.

8 ²CREAF, 08913 Cerdanyola del Vallés. Catalonia, Spain.

9 *Corresponding author. Facultat de Ciències, Universitat Autònoma de Barcelona.

10 08913 Bellaterra. Spain. Tel 34 93 581 29 34. Fax. 34 93 581 41 51. E-mail:

11 j.sardans@creaf.uab.cat

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24 **Abstract**

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

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

37 *Conclusions* The large plant diversity that characterizes Mediterranean ecosystems is
38 associated to the success of coexisting species in avoiding competition for soil
39 resources by differential exploitation in space (soil layers) and time (year and daily).
40 Among plant and soil traits, high foliar nutrient re-translocation and large contents of
41 recalcitrant compounds reduce nutrient cycling. Meanwhile increased allocation of
42 resources to roots and soil enzymes help to protect against soil erosion and to improve
43 soil fertility and capacity to retain water. The long-term evolutionary adaptation to
44 drought of Mediterranean plants allows them to cope with moderate increases of
45 drought without significant losses of production and survival in some species. However,
46 other species have proved to be more sensitive decreasing their growth and increasing
47 their mortality under moderate rising of drought. All these increases contribute to
48 species composition shifts. Moreover, in more xeric sites, the desertification resulting
49 from synergic interactions among some related process such as drought increases,

50 torrential rainfall increases and human driven disturbances is an increasing concern. A
51 research priority now is to discern the effects of long-term increases in atmospheric
52 CO₂ concentrations, warming, and drought on soil fertility and water availability and on
53 the structure of soil communities (e.g. shifts from bacteria to fungi) and on patching
54 vegetation and root-water uplift (from soil to plant and from soil deep layers to soil
55 superficial layers) roles in desertification.

56

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

59 **Introduction**

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

72 Some important chemical and physical properties of the soils, such as nutrient
73 availability, erodibility, moisture content, infiltration capacity, the quantity and nutritional
74 quality of soil organic carbon (SOC), cation exchange capacity, and pH, are strongly
75 determined by vegetative cover. Changes in these important soil variables can, in turn,

76 affect plant cover. Close and very broad relationships, with multiple feedbacks, thus
77 exist between plant communities and soil structure and function in this type of
78 ecosystem.

79 Although some of these plant-soil interactions are well understood, other plant-
80 soil interactions present some contrasting results such as the impact of increased
81 atmospheric CO₂ concentrations on plant litter and soil activity and others interactions
82 remain poorly studied such as the role of roots in water transport among different soil
83 layers. Consequently, a review of these main interactions is clearly needed. Current
84 predictions suggest that drought and warming will increase in Mediterranean areas
85 (IPCC 2007). Prolonged drought coupled to less predictable torrential rainfall (Frei et al.
86 1998) opens a scenario of shifts in the feedbacks and equilibrium within the plant-soil
87 system. Several studies have explored the effects of increasing atmospheric CO₂,
88 drought, and warming on Mediterranean soils and plants, observing diverse responses,
89 some of which involve feedback mechanisms between plants and soils. Some of these
90 studies report contradictory results. Most results suggest that the impacts of global
91 change threaten to increase the degradation and desertification process. In this context,
92 the current knowledge suggests that plant-soil feedbacks can play an outstanding role
93 in the capacity of these ecosystems to adapt to future scenarios. It is thus urgent to
94 review and ordinate the current knowledge to highlight the best known characteristic
95 mechanisms underlying Mediterranean plant-soil feedbacks and to identify the
96 processes that merit further research to reach a better understanding of the plant-soil
97 feedbacks and their capacity to cope with future global change scenarios.

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

103 needed to improve our knowledge of the plant-soil system in changing Mediterranean
104 environments.

105

106 **Mediterranean plants and soils**

107 Mediterranean plants: an evolution under low water and nutrient availabilities.

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

119 Mediterranean plants have acquired a set of morphological and physiological
120 adaptations in response to deficits of soil water (Table 1). The development of deep
121 and extensive root systems is among the most characteristic traits of plants in
122 Mediterranean ecosystems. Deep root systems enable the uptake of water from deep
123 soil layers in drought seasons when the upper layers are water depleted (Veneklaas
124 and Poot 2003; Padilla and Pugnaire 2007; Baldocchi and Xu 2007; Hernández-
125 Santana et al. 2008). Moreover, in Mediterranean plant communities, plant species with
126 root-systems that tend to occupy different soil layer usually coexist avoiding the root
127 systems overlapping and consequently diminishing the competition intensity, and also

128 allowing to exploit the sources throughout all the soil depth (Castells et al. 1994; Silva
129 and Rego 2003; Lefi et al. 2004; Mattia et al. 2005; Moreno et al. 2005; Filella and
130 Peñuelas 2003b; Silva and Rego 2003; Mattia et al. 2005; Mereu et al. 2009). Plants
131 with deep-roots have proved to resist better drought events than species with shallow-
132 root systems (Padilla et al. 2007; West et al. 2012). Furthermore, Mediterranean plants
133 have high root plasticity in the early stages of life (Padilla et al. 2007). At the foliage
134 morphological level, Mediterranean plants improve their capacity of drought avoidance
135 increasing their foliar sclerophylly by developing thick cuticule and increasing leaf mass
136 area (LMA) (Table 1), high density of foliar trichomes (Table 1), and high plasticity of
137 foliar morphology and size (Table 1).

138 General adaptations to drought by Mediterranean plants at physiological level
139 include a large capacity to maintain water flux and hydraulic lift (water conduction from
140 soil to plant tissues) in the soil-plant continuum (Table 1), including a large resistance
141 to xylem cavitation (Table 1) and high stomatal control (Table 1). Thus, Mediterranean
142 plants also respond to drought by both decreasing xylem cavitation vulnerability and
143 adapting and protecting leaf function and structure (De Mico and Aronne 2009;
144 Vilagrosa et al. 2010). Some studies suggest that these two responses are coordinated
145 (Vilagroasa et al. 2010). Drought changes woody architecture of woody plants
146 increasing vessel density, decreasing total hydraulic diameter (Corcuera et al. 2004;
147 Gea-Izquierdo et al. 2012), increasing vessel wall thickness (De Mico and Aronne 2009)
148 and decreasing cambial activity (de Luís et al. 2011). Other general adaptation
149 strategies to drought include the accumulation of metabolites and/or water soluble
150 sugars in tissues to increase turgor (Table 1), a large capacity to reduce metabolic
151 activity during drought periods (Table 1), and efficient photoprotective and antioxidant
152 mechanisms (Table 1). Moreover, antioxidant mechanisms to cope with summer
153 drought have already been listed (Table 1). The desiccation tolerance strategy
154 observed in some Mediterranean species allows maintaining high stomatal

155 conductance despite very low water potentials (Fotelli et al. 2000; Volaire et al. 2009)
156 In these drought tolerant species the predawn leaf relative water content decreases
157 simultaneously with stomatal closure as drought progresses (Gulías et al. 2002).
158 However, the most stress-tolerant plant species are able to develop very low water
159 potentials with markedly reduced stomatal aperture (Fotelli et al. 2000).

160 Apart from water availability, the capacity of the soil nutrient supply has often
161 been shown to be an important factor in the growth, structure, and distribution of plant
162 communities (Kruger, 1979; Specht, 1979; Carreira et al. 1992; Sardans, et al. 2004;
163 Henkin et al. 1998). Mediterranean plants share characteristics such as slow growth,
164 sclerophylly, and low nutrient contents that are present in plants of other non-
165 Mediterranean ecosystems adapted to poor soils (Bussotti et al. 2000). The importance
166 of nutrients has been appreciated in many experiments of nutrient manipulation by
167 fertilization in different Mediterranean zones of the world, for example in Californian
168 chaparral (McMaster et al. 1982), South African fynbos (Witkowski et al. 1990;
169 Herppich et al. 2002), Australian jarrah and *Eucalyptus* forests (Dell et al. 1987), and
170 the Mediterranean Basin (Mayor and Rodà 1992; Henkin et al. 1998; Sardans and
171 Peñuelas 2004; Sardans et al. 2004, 2005a, 2005b). Mediterranean plants frequently
172 change foliar chemical and physical traits in response to both water deficit and nutrient
173 stress (Gratani et al. 2003; Sardans et al. 2006a; 2008a, 2008b). Proteaceae plant
174 communities that dominate several Mediterranean climatic regions of South Africa and
175 southwestern Australia have the capacity to accumulate more or less P in seedlings
176 when P is most limiting (Groom and Lamont 2010). Due to the prevalence of soils with
177 low nutrient content in Mediterranean areas, Mediterranean plants have high levels of
178 investment in root systems to enhance nutrient uptake, in addition to the C invested for
179 adaptation to low water availability (Martínez et al. 1998; Sardans et al. 2005a, 2006b).
180 Resprouting capacity is also determined by the availability of soil nutrients (Sardans et
181 al. 2006c). A higher retranslocation of nutrients from leaves before falling is another

182 characteristic of Mediterranean plants helping them to achieve a higher nutrient use
183 efficiency (NUE) (Schlesinger and Hasey 1981; Fioretto et al. 2003; Sardans et al.
184 2005a) and having a further effect on soil organic matter quality as commented below.
185 García-Palacios et al. (2012) in an experiment of Mediterranean grasslands growing at
186 different levels of soil N availability heterogeneity observed that soil N availability
187 heterogeneity modulated the effects of root length, LMA and nutrient availability on
188 ecosystem function. The nutrient content of soil is thus a key factor for the structure
189 and function of Mediterranean plants that, in turn, influence nutrient content by their
190 adaptations that improve NUE.

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

200

201 Species-specific adaptations of plant species and communities to resist drought
202 The capacity of Mediterranean plants to withstand drought varies for the different
203 species within and between plant communities. For example, Californian perennial
204 grasses are more tolerant of drought than annuals of the Mediterranean Basin but less
205 tolerant than perennials of the Mediterranean Basin, despite the more intense summer
206 drought of California's Central Valley compared to the Mediterranean Basin (Vaughn et
207 al. 2011). Other studies have observed better adaptation to drought in evergreen oaks

208 of the Mediterranean Basin compared to those of California (Grünzweig et al. 2008).
209 Different morphological and physiological adaptive strategies to drought have been
210 observed in comparisons between typical groups of Mediterranean plants (Medrano et
211 al. 2009). Different growth forms display specific morphological adjustments in
212 response to shortages of water. Different coexisting species of the same community
213 can also respond differently. When drought is enhanced, some species survive and
214 grow less well than others in the short and medium terms (Ogaya et al. 2003; Ogaya
215 and Peñuelas 2007a) due to species differences in some of the previously mentioned
216 traits for resisting drought and increasing water use efficiency (WUE). Species also
217 differ in their phenotypic capacity to change some traits (Lloret et al. 2004; Ogaya and
218 Peñuelas 2008; Bell et al. 2007). Significant differences in the capacity to take up water
219 from different soil depths (Filella and Peñuelas 2003b; Lefi et al. 2004), a trait that is
220 especially important in severe droughts, are frequently observed. Moreover, coexisting
221 species in the same community have different strategies for the uptake of water, from
222 plants with leaf water potentials depending on soil water status and evaporative
223 demands (isohydric) to plants whose leaf water potentials do not depend on soil water
224 status and evaporative demand (anisohydric). This combination of hydraulic strategies
225 and also different strategies to capture of water at different times allows plants to avoid
226 competition for water (Peñuelas et al. 2011; Quero et al. 2011).

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

234 Lloret et al. 1999) that adds complexity and diversity to Mediterranean plant
235 communities.

236

237 Mediterranean soils

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

256 Apart from the limiting water content during summer drought, Mediterranean
257 soils are often poor in nutrients (Specht 1973; Di Castri 1981; Carreira et al. 1991).
258 Along with nitrogen (Mayor and Rodà 1994), phosphorus is a frequent limiting nutrient
259 in Mediterranean ecosystems (McMaster et al. 1982; Witkowski et al. 1990;

260 Lebourgeois et al. 1997; Henkin et al. 1998; Sardans et al. 2004, 2005a, 2006d). Soil
261 moisture and nutrient supply and their availability for plant growth thus strongly interact
262 in Mediterranean ecosystems (Everard et al. 2010).

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

282 Soil enzyme activity in Mediterranean soils is mainly determined by moisture.
283 Many studies have reported decreased activity with decreasing soil moisture, both
284 throughout the year (Grierson and Adams 2000; Quilchano and Marañón 2002; Criquet
285 et al., 2002; Bell and Adams 2004; Sardans et al., 2008c; 2008d; Rutigliano et al. 2009;
286 Sardans and Peñuelas 2010) and along gradients of soil moisture or experimental
287 drought (García et al. 1994; Sardans and Peñuelas 2005 and 2010; Sardans et al.

288 2006d, 2008c and 2008d). Long summer droughts decrease soil enzyme activity and
289 plant uptake and change soil C:N:P stoichiometry relative to other seasons (Aponte et
290 al. 2010). Moreover, soil enzyme activity depends more on soil moisture than on SOC
291 nutritional quality (Sardans and Peñuelas 2010), although both are important factors
292 controlling rates of mineralization (García-Pausas et al. 2004; Rutigliano et al. 2009;
293 Incerti et al. 2011). For example, the C:N and C:P ratios of litter are inversely correlated
294 with rates of decomposition (Bengston et al. 2012). Similar results are observed when
295 soil activity has been measured by soil respiration. Positive relationships are found
296 between soil respiration and soil moisture (Rey et al. 2002 and 2011; Inglima et al.
297 2009; Carbone et al. 2011). In Mediterranean ecosystems when volumetric soil water
298 content dropped below certain values, ranging from 13% (Rey et al. 2011) to 20% (Xu
299 and Qi 2001; Rey et al. 2002) depending on reports, there is a strong soil respiration
300 limitation. However, litter decomposition rates of Mediterranean forests are similar to
301 those of temperate deciduous forest (Van Wesemael 1992). The values are very
302 variable, ranging from 0.12 to 2.22 yr⁻¹ depending on the species (Van Wesemael,
303 1993; Fioretto et al. 2003; Rodríguez-Pleguezuelo et al. 2009). Frequently N
304 concentration increases during decomposition process (Gallardo and Merino 1992;
305 Fioretto et al. 2003), specially in the first months of decomposition (Gallardo and
306 Merino 1999). Thereafter, during more advanced stages of decomposition, N release
307 can decrease increasing litter N concentration (Maisto et al. 2011), observing in some
308 cases a shift from N limitation to P limitation throughout litter decomposition process
309 (Gallardo and Merino 1999). Not all studies have detected this trend in N
310 concentrations during decomposition process (Fioretto et al. 2001). N litter
311 concentration is also correlated with litter decomposition rates (Moro and Domingo
312 2000; García-Pausas et al. 2004), but lignin content and leaf mass area (LMA) of litter
313 are also determinant in Mediterranean plants litter decomposition rates (Cortez et al.,
314 1996, 2007; Karakov et al. 2007). Furthermore, plant species of early succession
315 stages with low LMA, and high growth rate and litter N content have faster litter

316 decomposition rates and N release from litter than species of later successional stages
317 with opposite traits (García-Pausas et al. 2004; Kazakou et al. 2006 and 2009). Litter
318 resulting from mixing litter of different species have proved to decompose at different
319 rates (in general faster) than that expected from the decomposition rates observed by
320 each species litter alone (De Marco et al. 2011). The importance and changes of P
321 concentration during litter decomposition process has been less studied than those of
322 N. Some studies have observed a decrease of P concentrations during litter
323 decomposition (Gallardo and Merino 1999; Fioretto et al. 2001) with the consequent
324 increases in litter N:P ratio (Gallardo and Merino 1999). In addition to litter quality, soil
325 temperature and moisture have also an outstanding role in litter decomposition rates in
326 Mediterranean ecosystems (Fioretto et al. 2000; Dirks et al. 2010; Incerti et al. 2011).
327 Dirk et al. (2010) observed that litter decomposition is related with atmospheric
328 humidity during summer, showing that during dry periods a significant part of water to
329 leaf litter decomposition can come from atmosphere. The community density of soil
330 macroinvertebrate decomposers is also related to precipitation through its effects on
331 the physical properties of soil and the quality of plant litter (Morón-Ríos et al. 2010).
332 These studies demonstrate that in Mediterranean ecosystems water availability is the
333 most important factor determining soil biological functioning.

334 Topographic factors, due to solar incidence and slope variation, and soil texture,
335 due to water-infiltration capacity, have key roles in plant cover by determining the
336 retention and storage of soil water, soil enzyme activity, and rates of soil erosion
337 (Bastida et al. 2008). Soils with sandy structures are particularly critical in
338 Mediterranean regions because of their high permeability and low capacity to retain
339 water (Kooijman et al. 2005; Prieto et al. 2010). Soil organic matter (SOM) plays a key
340 role in soil-water content by allowing the formation of stable aggregates that decrease
341 the index of soil erosion (Barthes and Roose 2002). Calcareous Mediterranean soils
342 have some singular differences from other soils regarding soil fertility. These soil types
343 severely immobilize phosphate due to precipitation with Ca^{2+} (Carreira and Lajtha

344 1997), which is frequently critical because of the natural low P content of
345 Mediterranean soils. On the other hand, calcareous soils have a good capacity to
346 physically stabilize the SOM (Rovira and Vallejo 2003; Rovira et al. 2010), which
347 should be beneficial due to the importance of stable soil aggregates in preventing soil
348 erosion (Barthes and Roose 2002). Mediterranean soils have a low-moderate
349 humification index (Simón et al. 1994) as a result of lower plant production and soil
350 microbial activity imposed by summer drought and cold winters in continental and
351 alpine areas (Simón et al. 1994). Soils of Mediterranean woodlands normally contain
352 considerable amounts of SOC, with moder the main frequent type of humus (Vacca
353 2000; van Wesemael and Verstraten 1993; Sevink et al. 1989), although mull humus is
354 also widely represented (Peltier et al. 2001; Sadaka and Ponge 2003; Andreetta et al
355 2011 and 2012). The constraints and feedback processes resulting from the long and
356 highly variable summer droughts have large effects on humus properties (Sevink et al.
357 1989; van Wesemael and Verstraten 1993; Vacca 2000; Peltier et al. 2001; Ponge
358 2003; Andreetta et al. 2011) and microbial communities (Monakrouses et al. 2004;
359 Goberna et al. 2005; Aponte et al. 2010) in Mediterranean areas. Amounts of SOM in
360 Mediterranean ecosystems depend on levels of precipitation (Boix-Fayos et al. 1998;
361 Gómez-Rey et al. 2010) and type of plant community (Lucas-Borja et al. 2010).
362 Rewetting events during summer droughts are particularly important by suddenly
363 increasing the mineralization of the SOC, ecosystem carbon fluxes (Jarvis et al. 2007)
364 and the release of nutrients (Rey et al. 2005; Almagro et al. 2009).

365

366 **Plant-soil relationships in Mediterranean ecosystems**

367 Several studies have observed a strong interdependence between changes in plant
368 community and changes in soil properties in Mediterranean ecosystems(García et al.
369 2002; Goberna et al. 2007a,2007b; Estringa et al. 2010; Dias et al. 2011). These close
370 relationships are observed through both time and space. We here discuss the most

371 relevant plant-soil relationships summarized from the literature. Most feedbacks
372 between Mediterranean plant communities and soils are linked to their mutual
373 protection.

374

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

377 Despite the low water content and nutrient availability of Mediterranean soils,
378 Mediterranean plant communities frequently have a notable cover and species diversity,
379 reflecting the large capacity of coexisting species to avoid competition for soil
380 resources. The avoidance of overlapping structures of the root system has been widely
381 observed among different types of plants, such as between trees and grasses (Silva
382 and Rego 2003; Lefi et al. 2004; Mattia et al. 2005; Moreno et al. 2005) or among more
383 similar types, such as between woody evergreens (Filella and Peñuelas 2003b; Silva
384 and Rego 2003; Mattia et al. 2005; Mereu et al. 2009). This differential capacity of plant
385 species to exploit soil sources at different depths of soil has beneficial effects for the
386 coexistence of species. Filella and Peñuelas (2003b) observed higher water uptake in
387 evergreen shrubs growing under large pine trees than in those growing under smaller
388 pines or in those separated from large pine trees, an effect very likely linked to the
389 hydraulic lift, driven by a deep root system of big trees, from deep soil layers to
390 shallower layers, effect that improves the water status of shrubs that grew under big
391 pine trees (Filella and Peñuelas 2003a). The possibility that the deep roots can pump
392 water to the surface layers, thereby helping to maintain higher moisture levels in the
393 upper richer soil layers, is a phenomenon that needs to be investigated in depth. The
394 extensive and deep root systems of Mediterranean plant communities also protect the
395 soil against erosion from torrential rain (Andreu et al. 1998; Chirino et al. 2006), mainly
396 on slopes (Mattia et al. 2005; De Baets et al. 2007 and 2008). This widespread

397 presence of roots throughout the soil layers has several other notable effects on soil
398 properties and traits, such as decomposer fauna and physical soil texture (Maestre and
399 Cortina 2002, 2003). The presence of Mediterranean plant communities with more
400 diverse species compositions improves soil quality and structure (higher levels of SOM,
401 microbial biomass, and nutrient content; more stable aggregates; a more equilibrated
402 texture; and greater permeability) (Andreu et al. 1998; Pinzari et al. 1999; Chirino et al.
403 2006).

404

405 Plant cover and soil fertility and water availability

406 Most studies suggest a significant positive and rapid feedback between soil properties
407 linked to fertility (water-storing capacity, permeability, nutrient availability, depth) and
408 plant cover (Gallardo et al. 2000; Johnson-Maynard et al. 2002; Castaldi et al. 2009;
409 Ochoa-Hueso et al. 2011). An increase in plant cover thus has a direct positive effect
410 on soil porosity, which increases water-infiltration capacity and decreases runoff
411 (Johnson-Maynard et al. 2002; Goberna et al. 2007a; Garcia-Estringana et al. 2010).
412 This capacity to improve water infiltration generally occurs in different types of plant
413 community but is higher in grasses and angiosperm evergreen shrub and tree
414 communities than in pine forests (Johnson-Maynard et al. 2002; Garcia-Estringana
415 2010). These differences are probably linked to the observed differences in the
416 formation of sand-sized organic matter in different communities, such as between
417 evergreen shrubs and pines (Quideau et al. 1998). A positive feedback between plant
418 cover and soil properties is consequently established. The improvement of soil quality
419 generated by plant cover improves soil moisture and water availability, fertility (Gallardo
420 et al. 2000), and soil enzyme activity (García et al. 2002). These effects are related to
421 the improvements in the physical and chemical properties of soil and thus to higher
422 water availability that, in turn, has a positive effect on Mediterranean plants (Sadaka

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

426 Mediterranean plants, by having some of their typical properties linked to
427 mechanisms of stress avoidance, can affect soil properties linked to nutrient cycling
428 and availability. A reduction in nutrient losses in litterfall could be a strategy employed
429 by sclerophyllous plants adapted to poor soils (Aerts 1995) and could partially
430 compensate for decreased nutrient uptake in dry conditions. This conservative use of
431 water and nutrients, though, can also retard nutrient cycling as a result of the larger
432 content of structural compounds and the more recalcitrant litter that also has lower
433 nutrient concentration due to a high level of retranslocation. Mediterranean plants can
434 cover up to 84% of the N demand throughout leaf expansion from retranslocation from
435 old tissues (Silla and Escudero 2003). High levels of N, P and K retranslocation from
436 senescing leaves have been widely observed in Mediterranean plants (Grubb 1977;
437 Pugnaire and Chapin 1993; Fioretto et al. 2003; Milla et al. 2005; Sardans et al. 2005a;
438 Fife et al. 2008). Sclerophyllous leaves are moreover rich in structural compounds
439 (Rundel 1982; Gallardo and Merino 1992; Turner 1994) that also produce litter of low
440 nutritional quality and lower rates of litter decomposition, which can then lead to more
441 occluded humic compounds that retain nutrients in unavailable forms to plants in the
442 soil. However, photodegradation could contribute to decrease lignin concentration in
443 litter of Mediterranean soils such as observed in other semiarid environments (Austin
444 and Vivanco, 2006; Austin and Ballaré 2010; Ballaré et al. 2011). A fast release of N
445 under high UV radiation intensity allowing increases in soil microbial activity is one of
446 the probable mechanisms underlying this effect (Foereid et al. 2010). Mediterranean
447 plants are rich in secondary metabolites such as phenolics (Castells and Peñuelas
448 2003; Hernandez et al. 2004; Skerget et al. 2005; Coulis et al. 2009; Bettaieb et al.
449 2011), compounds that decrease N mineralization rates in litter (Castells and Peñuelas

450 2003; Castells et al. 2004) and retard decomposition (Castaldi et al. 2009). Foliar
451 extracts of *Arbutus unedo* rich in phenolic compounds strongly inhibit soil nitrification
452 (Castaldi et al. 2009). Mediterranean plants have higher levels of N and P
453 retranslocation (Nuñez-Oliveira et al. 1993; Fioretto et al. 2003; Sardans et al. 2005a)
454 that lead to leaf litter with low nutrient concentrations. This strategy of retranslocation
455 has further consequences on the rates of litter decomposition because the
456 concentrations of litter N and P appear to be determinants in the rates of litter
457 decomposition (Schlesinger and Hasey 1981) and in the community structure of soil
458 decomposers (Almagro and Martínez-Mena 2012). More retranslocation should thus
459 lead to a low release of N and P from litter and lower availability of soil N and P. The
460 high capacity for erosion of Mediterranean rain may have further favored the evolution
461 of plants toward higher retranslocation to assure better control of nutrient stocks,
462 thereby improving the capacity of the plant-soil system to retain nutrients. The high
463 retranslocation is related to the observed higher percentage of nutrients in the stand
464 biomass of Mediterranean forests compared with other forest types (Rodà et al.
465 1999a,b; Sardans and Peñuelas 2012; Sardans et al. 2012a).

466 The capacity of plants to absorb nutrients in the early phases of regeneration
467 may be a key factor to prevent the degradation of soil. Resprouting capacity should be
468 particularly important in nutrient-poor environments and in environments, such as
469 Mediterranean ecosystems, where the risk of nutrient losses is high after fires or from
470 torrential rainfall. The sprouting capacity during the initial phases of regeneration after
471 disturbances such as fires thus provides resprouting species with a higher competitive
472 ability for nutrient uptake than the species that can only regenerate with seeds (Lloret
473 et al. 2004; Sardans et al. 2004). However, in Mediterranean ecosystems sprouter-
474 seeders strategies present clear trade off, with sprouters having higher allocation to
475 root system and less to flowering and seed production, and seeders having higher
476 aboveground growth capacity, higher flowering and seed production (Enright and
477 Glodblum 1999, Bell 2001). Sprouters tend to have a higher conservative use of

478 nutrients than seeders (Saura-Mas and Lloret 2009), but it is not clear that in general
479 sprouters increase their cover with fires. Contrarily, regional surveys have reported an
480 increase in the relative abundance of non-resprouters in burnt areas (Lloret et al. 2005).
481 Nevertheless, other reports suggest that the presence of resprouters can be enhanced
482 when the frequency of disturbances increases (Bon and Midgley 2003). However,
483 some studies have suggested new possibilities that explain the high prevalence of
484 sprouter plant species in Mediterranean ecosystems. Lamont and Wiem (2003)
485 suggest that the great genet resilience associated with frequent new branching by fire,
486 drought-rewetting and herbivore might benefit the somatic mutations in the
487 meristematic tissues favoring ecotypic differentiation and speciation in sprouters.
488 Moreover, within a single species resprouts have proved to better resist drought than
489 genets grown from seeds (Peña-Rojas et al. 2004).

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

502 In Mediterranean arid areas with high risk of desertification, usually water
503 infiltration capacity is higher and run-off erosion is lower in slopes with less insolation
504 and evaporation capacity (Boix-Fayos et al. 1998; Kutiel et al. 1998). In slopes of more

505 arid Mediterranean areas the variability of water and nutrients availability is related to
506 the distribution of vegetation patches with respect to bare soil patches that can be
507 considered as runoff sinks and sources, respectively (Boix-Fayos et al. 1998; Kutiel et
508 al. 1998; Ruíz-Sinoga and Martínez-Murillo 2009; Mayor et al. 2009; Mayor & Bautista
509 2012; Gabarrón-Galeote et al. 2012; Merino-Martin et al. 2012). But some few studies
510 have not observed these relationships so clearly (González-Pelayo et al. 2010). This
511 effect of patches is crucial in the maintenance of vegetation in more arid sites. The
512 patches of vegetation also influence hydrological and erosion behavior (Ruíz-Sinoga et
513 al. 2011), and are related with soil properties (Ocho-Hueso et al. 2011) such as
514 infiltration capacity and biological activity throughout the slopes (Maestre & Cortina
515 2002; Agra and Ne'eman 2012). When adjacent patches have different species
516 composition, with different root depth and density, ones can act as runoff sinks and
517 others as runoff sources (Merino-Martin et al. 2012). Grazing, particularly from
518 mammals, contribute to maintain plant diversity between different patches of vegetation
519 (Golodets et al. 2011). The presence of patches with very different species composition
520 can exert a key role in plant invasive success to maintain large soil variability (Harrison
521 et al. 2001; Prober & Wiehl 2011). Moreover, the presence of large trees in patches
522 exerts an important role in maintaining high level of herbaceous species richness by
523 affecting light and water competition intensity and availability (Blank and Carmel 2012).

524 The Mediterranean agroforest systems (Dehesa) that cover wide areas in south
525 Europe and constitute a particular system where human activities help to maintain the
526 ecosystem with a particular plant cover with savanna structure (Gallardo 2003; Gallego
527 Fernández et al. 2004) that maintain great differences in the horizontal spatial
528 distribution of soil nutrient availability (Gallardo 2003; Gea-Izquierdo et al. 2010), soil
529 organic content (Howlett et al. 1987) and soil water availability (Joffre et al. 1999). All
530 these soil properties are positively related with tree canopy. Regional scale evidences
531 of the tree density and mean annual precipitation suggest that the structure of these

532 man-made ecosystems have adjusted over long-time and corresponds to an optimal
533 functional equilibrium with water cycle (Joffre et al. 1999). Frequently the major
534 problem to maintain these ecosystems and maintain tree production is the shrub
535 competition that strongly impacts soil nutrient availability (Rolo et al. 2010).

536

537 Changes during successional events: soil properties and plant diversity

538 The positive feedbacks between plant cover and soil fertility properties also drive plant
539 succession. An increase in the growth of tree seedlings is observed when shrub cover
540 increases, with shrubs acting as nursery species for the seedlings by enhancing soil
541 properties such as infiltration, retention capacity, and soil enzyme activity (Duponnois
542 et al. 2011). In the driest Mediterranean areas with sparse vegetation, soil patches
543 under vegetation present higher levels of water permeability, SOM, microbial biomass,
544 and enzyme activity than bare soil (Goberna et al. 2007b). Moreover, when plant cover
545 is enhanced, the SOM, soil microbial biomass, and activity linked to higher biomass
546 production and soil moisture quickly increase (Garcia et al. 2005; Muñoz et al. 2007;
547 Duponnois et al. 2011; Maestre et al. 2011). The composition and activity of soil
548 microbial communities in Mediterranean areas are strongly determined by changes in
549 plant communities that cover the soil (Bonkowski and Roy 2012), and soil microbial
550 activity is generally negatively affected by the degradation of the plant cover (García et
551 al. 2002). Other studies have also observed a close relationship between the spatial
552 distribution of plants and soil NH_4^+ concentration (Gallardo et al. 2000; Castillo-Monroy
553 et al. 2010). More diverse plant communities are associated with soils higher in SOM
554 and N concentration than are plant communities with fewer species (Lucas-Borja et al.
555 2012). In the meadow-shrubland-maquis succession in Mediterranean climates, the
556 aboveground biomass and overall soil activity increase, although with high seasonal
557 fluctuations (Fioretto et al. 2009). In fact, when soil properties have been studied in

558 different plant communities from grassland to evergreen shrubland and forest, larger
559 differences in soil variables related to soil fertility have been observed among seasons
560 than among different plant communities (Monokrousos et al. 2004), illustrating the
561 strong link between seasonal changes of aboveground vegetation with seasonal
562 changes in soil properties. Anyway, regarding nutrient availability in soils the current
563 studies suggest a strong mechanisms of nutrient conservation during succession in
564 Mediterranean ecosystems. Intense nutrient uptake and accumulation capacities are
565 observed in the early successional species (Carreira and Neil 1992). The presence of
566 legumes is high in different Mediterranean successional communities both in early
567 successional stages with high presence of herbaceous legumes and in latter
568 successional stages with high presence of perennial legume shrubs (Arianoutsou and
569 Thanos 1996). Regarding drought response strategy, early successional species
570 escape drought by dying before summer while later herbaceous species maintain a
571 favourable water status in relation to leaf shedding during summer; finally, late
572 successional trees with a large body allow access to a large pool of resources,
573 producing dense leaves that can tolerate desiccation (Navas et al. 2008). In this
574 respect, seed banks of herbaceous plants are less sensible to decrease than those of
575 woody plants if the frequency of severe drought episodes increases (del Cacho and
576 Lloret 2011). The protection of soil moisture and the improvement of soil texture under
577 shrubs can facilitate tree seedling survival in most wet Mediterranean ecosystems
578 (Gómez-Aparicio et al. 2005).

579 Studies during the course of succession of plant communities in Mediterranean
580 areas show a progressive replacement of species with low leaf mass area (LMA) and
581 high concentrations of foliar nutrients by species with opposite traits (Cortez et al.
582 2007). Fast-growing species are replaced by slower growing species associated with
583 the conservative use of soil resources. This trend in Mediterranean areas is closely
584 associated with changes in the availability of soil N and P and also with the ratio

585 between bioavailable N and P (Dias et al. 2011). The large capacity of the fast-growing,
586 nutrient-rich species to absorb nutrients in the first phases of succession of the plant
587 community should be particularly important in Mediterranean areas by hindering the
588 loss of soil nutrients by erosion and leaching.

589

590 Mycorrhizae and their role in Mediterranean plant-soil relationships

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

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

614

615 **Impacts of increased atmospheric CO₂ concentrations**

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

624 Under elevated levels of atmospheric CO₂, the foliar conductance of water
625 decreases and WUE increases (Bettarini et al. 1995; Tognetti et al. 1999a, 1999b,
626 2000; Roumet et al. 2000; Maroco et al. 2002; Morgan et al. 2004) (Table 2). Some
627 studies (Peñuelas and Azcón-Bieto 1992; Scarascia-Sugnozza et al. 1996; Nijs et al
628 2000; Morgan et al. 2004; Peñuelas et al. 2008a; Andreu-Hayles et al. 2011; Maseyk et
629 al. 2011), and mathematical models (Osborne et al. 2000) suggest that increases in
630 concentrations of atmospheric CO₂, by increasing WUE, can counteract the effects of
631 the projected increase in drought in the coming decades (IPCC 2007). Long-term
632 experiments have not tested whether Mediterranean plants could acclimate to elevated
633 CO₂ to buffer these higher WUEs. Moscatelli et al. (2001) observed that the effects of
634 elevated CO₂ on plant growth and microbial biomass occurred only at the beginning of
635 their study and progressively diminished as monitoring continued. In this context, Rey

636 et al. (1997) showed that the effects on relative growth rates (RGR) had disappeared
637 after 4.5 years of plants exposed to increased atmospheric CO₂ concentrations and
638 that the increased biomass accumulation was the result of an early effect of RGR. A
639 recent study has observed that elevated atmospheric CO₂ (712 ppm) during a strong
640 summer drought did not prevent a decline in water use and the capacity of soil to store
641 water in the most critical dry periods (Hernández-Santana et al. 2009). Moreover, the
642 results of other studies manipulating atmospheric CO₂ and conditions of drought have
643 suggested that these two variables may have compensatory effects; the effects of
644 short-term increases in CO₂ on several plant variables that improve WUE can be
645 counteracted by enhanced conditions of drought at the levels projected by most
646 climatic models (López et al. 1998; Nijs et al. 2000; Loreto et al. 2001; Hernández-
647 Santana et al. 2009).

648 An overview of the current bibliography (Table 2) on the effects of increased
649 atmospheric CO₂ on plant growth and photosynthetic capacity indicates a short-term
650 enhancement of plant growth and photosynthetic rates (Scarascia-Mugnozza et al.
651 1996; López et al. 1998; Nijs et al. 2000; Marek et al. 2001), but this positive effect is
652 frequently only observed in nutrient-rich soils (Midgley et al. 1995; Cruz et al. 2003).
653 The positive effect on growth generally decreased with time (Körner & Miglietta 1994;
654 Jones et al. 1995; Peñuelas et al. 2008a; Andreu-Hayles et al. 2011), suggesting
655 acclimation to increase of atmospheric CO₂ concentrations (Navas et al. 1995; Roumet
656 et al. 2000; Sauser et al. 2003). The increased growth in the short-term is linked to
657 increases in WUE associated with an atmosphere richer in CO₂ (Nijs et al. 2000).
658 Moreover, increased atmospheric CO₂ concentrations can favor species that fix N₂ over
659 those that do not (Navas et al. 1997; Grünzweig and Dumbur 2012) and can increase
660 the nutrient uptake capacity by enhancing mycorrhizal associations (Rillig et al. 1998a).
661 The higher production of reproductive and vegetative biomass of legumes than non N₂-
662 fixing plants under increased atmospheric CO₂ concentrations related to higher protein

663 synthesis capacity could give competitive advantage to legumes in a CO₂-rich
664 atmosphere (Navas et al. 1997; Grünzweig and Dumbur 2012).

665 Most data from Mediterranean regions show that when plants are grown in
666 increased atmospheric CO₂ concentrations a decrease in plant N and P concentrations
667 is observed and consequently the C:N and C:P ratios of plant biomasses increase
668 (Sardans et al. 2012b and Table 2). Under elevated CO₂, plant production and the C:N
669 ratio increase, diminishing the concentrations of N and other nutrients (De Angelis et al.
670 2000; Peñuelas et al. 2001; Bassirirad et al. 2003; Tognetti and Peñuelas 2003) and
671 increasing phenolic compounds (Peñuelas and Estiarte 1998; Castells et al. 2002) in
672 foliar biomass. Mediterranean plants can partially buffer the effects of higher C:N ratios
673 in plant tissues under increased atmospheric CO₂ concentrations by increasing the
674 retranslocation, fixing, and mineralization of N (Peñuelas and Estiarte 1997). Despite
675 the capacity of plants and ecosystems to increase nutrient availability under increased
676 atmospheric CO₂ concentrations, most studies have observed higher C:N ratios and
677 lower nutrient contents in plant tissues under increased atmospheric CO₂
678 concentrations than in current levels of atmospheric CO₂ concentration (Bettarini et al.
679 1995; Midgley et al. 1995; Gahrooe et al. 1998; Cotrufo et al. 1999; Roumet et al.
680 1999; De Angelis et al. 2000; Blaschke et al. 2001; Peñuelas et al. 2001; Tognetti and
681 Peñuelas 2003; Cruz et al. 2003) (Table 2). This decrease in N concentrations could
682 impact on plant-insect relationships (Roumet et al. 1999). The effects of increased
683 atmospheric CO₂ concentrations can have opposite feedbacks on the capacity of soil to
684 mineralize. The increases of plant biomass and litter and microbial biomass under
685 increased atmospheric CO₂ concentrations suggest a possible increase in soil enzyme
686 activity linked to higher soil microbial biomass (Dhillion et al. 1996). On the other hand,
687 several reportas have suggested a slow-down of litter decomposition and
688 mineralization rates under increased atmospheric CO₂ concentrations in
689 Mediterranean ecosystems (Gahrooe 1998; Cotrufo et al. 1999; De Angelis et al.

690 2000) linked to an increase of litter C:N and C:lignin (De Angelis et al. 2000) and C:P
691 (Cotrufo et al. 1999) ratios that can counteract the higher soil enzyme activity. In fact,
692 high concentrations of atmospheric CO₂ over two years had no important direct effect
693 on soil nitrification and denitrification (Pinay et al. 2007). Higher concentrations of
694 atmospheric CO₂ can increase the short-term turnover of C due to higher growth and
695 litter production, but this effect decreases in the medium term by the limitation of
696 nutrients (Cotrufo et al. 2005). Differential effects of the enhancement of atmospheric
697 concentrations of CO₂ in different species of plants have been observed in mycorrhizal-
698 plant symbioses where the presence of mycorrhizae increases in the roots of some
699 species and decreases in others (Rillig et al. 1998b) (Table 2). An increase in phenolics
700 in leaf litter decreases N mineralization (Castells et al. 2004), also suggesting a change
701 in the nutritional quality of plant biomass for herbivores. Nevertheless, all these
702 chemical changes can be buffered under long-term exposure to elevated CO₂, as
703 observed in plants in the vicinity of CO₂ springs, suggesting an evolutionary adaptive
704 response in Mediterranean plants to changes in levels of CO₂ (Peñuelas et al. 2002b).

705

706 **Climatic changes impact on plant-soil relationships**

707 The largest effects of climatic change in Mediterranean ecosystems (IPCC 2007) may
708 well be those related to increased drought, since water stress is already the principal
709 constraint in the Mediterranean region (Specht 1979; Mooney 1989). Enhanced
710 drought is expected to be accompanied by more severe torrential rainfall (Frei et al.
711 1998), already frequent events (Romero et al. 1998). Over the last century,
712 temperatures have shown an overall trend toward warming (Kutiel and Maheras 1998;
713 Peñuelas et al. 2002a). Precipitation has exhibited either a long-term downward trend,
714 principally in the dry season (Kutiel et al. 1996; Esteban-Parra et al. 1998), or no

715 significant change (Piñol et al. 1998; Peñuelas and Boada 2003), but potential
716 evapotranspiration has risen in all cases.

717

718 Warming

719 The effects of climatic change on nutrient supply in Mediterranean areas may depend
720 on a trade-off between warming and the effects of drought. Concentrations of nutrient
721 in the biomass result from the balance of nutrient uptake and growth. Increased
722 temperatures in these water-limited ecosystems will further decrease the availability of
723 soil water by enhancing evapotranspiration (Larcher 2000), which will very likely result
724 in a decrease in the uptake of nutrients by roots and in the movement of these nutrients
725 to shoots (Bradford and Hsiao 1982) altogether having a general negative effect on
726 soil activity and plant growth. Warming can also have a direct effect during cold and
727 wetter winters by increasing soil enzyme activities (Sardans et al. 2006g), extending
728 growth periods (Peñuelas and Filella 2001; Peñuelas et al. 2002a), and raising
729 photosynthetic rates (Llorens et al. 2003b). This positive effect during the cold season
730 could be counterbalanced by a lower availability of water in the summer and by
731 shortening the growing season by extending the duration of water deficits (Llorens et al.
732 2003b; Peñuelas et al. in preparation). The effect of warming on plant growth depends
733 on total annual precipitation. Warming has positive effects on growth in wetter years
734 and no or even negative effects in drier years (Swarbreck et al. 2011). In a study
735 analyzing long-term temporal metadata in Mediterranean areas, changes in
736 precipitation may even have had a relatively higher importance than changes in
737 temperature in explaining phenological shifts in some Mediterranean plant communities
738 (Peñuelas et al. 2004). As mentioned above, some studies have observed a threshold
739 value of temperature showing that during periods with temperatures above 20 °C soil
740 activity is strongly dependent of soil moisture (Rey et al. 2011). In Mediterranean
741 regions, warming only increases soil enzyme activities (Sardans et al. 2008c; Sardans

742 and Peñuelas 2010) and SOM mineralization in the year periods in which soil moisture
743 is high (Bottner et al. 2000; Qi and Xu 2001; Sardans et al. 2006d). The effects of
744 warming at the levels projected by climatic models (IPCC 2007) in arid environments
745 such as Mediterranean areas are thus related to the indirect effect of decreasing soil-
746 water content (Peñuelas et al. 2004; Swarbreck et al. 2011; Sardans et al. 2012b).

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

760

761 Drought

762 The decline in total rainfall and/or availability of soil water projected for the coming
763 decades (IPCC, 2007) may prove to be even more drastic under warmer conditions
764 with a CO₂-rich atmosphere and higher demand for water (Piñol et al.1998; Peñuelas et
765 al. 2005). Some studies investigating the impact on Mediterranean ecosystems of
766 increased atmospheric CO₂ concentrations, drought and warming suggest that most
767 future scenarios of drought combined with warming and/or with increased atmospheric

768 CO₂ concentrations may involve strong impacts on soil-water deficits and water use in
769 trees of Mediterranean forests by increasing soil water deficit (Hernández-Santana et al.
770 2008).

771

772 *Plants*. Increases in drought intensity at the level projected for the coming decades
773 (ICPP 2007) could reduce soil moisture (Sardans et al. 2008a, 2008b), plant growth
774 and cover in the short term (Boix-Fayos et al. 1998; Goldstein et al. 2000; Beier et al.
775 2004; Serrano et al. 2005; Tsiafouli et al. 2005; Ogaya and Peñuelas 2007a; Sardans
776 et al. 2008a, 2008b; Prieto et al. 2009a, 2009b; Pérez-Ramos et al. 2010; Cotrufo et al.
777 2011; Talmon et al. 2011) (Table 3, Table S3 in the supplementary material). Moreover,
778 plant cover can be seriously threatened by the increase of fire risk projected in the
779 Mediterranean area in the context of enhanced drought (Mouillot et al. 2002; Moriondo
780 et al. 2006).

781 Drought also induces changes in foliar nutrient contents, with a general trend to
782 reduce foliar N (Sardans et al. 2008a, 2008b), P (Sardans and Peñuelas 2004, 2007a;
783 Sardans et al. 2008g), and micronutrients (Sardans et al. 2008e, 2008f), which can
784 also change in other plant tissues (Sardans and Peñuelas 2004, 2007a, 2008b:
785 Sardans et al. 2006b, 2008a, 2008b, 2008e, 2008f, 2008g). The nutrient content of
786 aboveground biomass, mainly in leaves, tends to decrease with drought (Sardans et al.
787 2008a; 2008b), with the exception of K that increases in some aboveground tissues of
788 some plant species (Sardans and Peñuelas 2007a; Sardans et al. 2008g). Drought
789 increases the C:N and C:P ratios of Mediterranean shrubs and trees, associated with a
790 protective and conservative mechanism (Inclan et al. 2005; Sardans et al. 2008b;
791 2008c; 2008d; Matías et al. 2011) and with sclerophylly and increases in lignin content
792 (Bussotti et al. 2000; Sardans et al. 2006a). Drought enhances the allocation of N to
793 the root system, which increases the capacity to absorb water (Sardans et al. 2008a;
794 González et al. 2010). Drought also increases the oxidative stress of Mediterranean

795 plants (Munné-Bosch and Peñuelas 2003 and 2004). Under moderate conditions of
796 drought, photosynthetic pigments remain more or less constant, and anti-stress
797 compounds such as α -tocopherol increase in concentration. When stress from drought
798 is severe, the concentration of photosynthetic pigments falls, and anti-stress pigments
799 and secondary compounds can increase more (Munne-Bosch and Peñuelas 2004;
800 Hernandez et al. 2004) or even decrease (Bettaieb et al. 2011) due to the loss of
801 production capacity. Drought can induce foliar senescence that contributes to the
802 remobilization of nutrients during stress, thus allowing the rest of the plant, including
803 new leaves, to benefit from the nutrients accumulated during the foliar life span
804 (Munne-Bosch and Alegre 2004). Sclerophylly is a typical and general trait of
805 evergreen Mediterranean plants and usually increases when the environment evolves
806 toward drier conditions (Dunn et al., 1977; Sabaté et al., 1992; Oliveira et al., 1994).

807 During drought, different plant species of the same community exhibit
808 differential decreases in the growth of aboveground biomass (Mamolos et al. 2001;
809 Ogaya and Peñuelas 2007b; Prieto et al. 2009a, 2009b), changes in foliar nutrient
810 concentrations and contents (Peñuelas et al. 2008b; Sardans et al. 2008a, 2008b,
811 2008e, 2008f), and effects on hydraulic conductivity (Mereu et al. 2009) (Table 3).
812 These differences in growth and nutrient uptake during drought are related to species
813 differences in the capacity to maintain ecophysiological traits, such as photosynthetic
814 rate, WUE, regulation of foliar gas exchange (Peñuelas et al. 2000; Llorens et al.
815 2003a, 2003b; Ogaya and Peñuelas 2003; Ozturk et al. 2010; Vilagrosa et al. 2010;
816 Galle et al. 2011), capacity to protect against oxidative damage (Munné-Bosch and
817 Peñuelas 2004), root depth (Padilla and Pugnaire 2007; West et al. 2012) and capacity
818 to reabsorb N (Sanz-Perez et al. 2009).

819 The relationships between hydraulic architecture and leaf area are a key factor
820 determining drought adaption success. Drought-induced mortality in Mediterranean
821 pines has proved to be related to lower hydraulic conductivity per unit of leaf area

822 (Martínez-Vilalta and Piñol 2002). The resistance to xylem embolism allows to maintain
823 higher stomatal conductance and sap flow even at lower water potentials thus
824 permitting large WUE (Martínez-Vilalta et al. 2003). The survival capacity to drought has
825 been proved to be also related to carbon reserves (Volaire 1995; Galiano et al. 2012).
826 Under drought, the Mediterranean tree *Olea europea* stops growth but not
827 photosynthetic activity that allows it to store assimilates, produce antioxidants,
828 antiherbivore compounds, such as phenolics, and osmoprotective substances, mainly
829 water soluble sugars allowing to maintain cell turgor (Volaire 1995; Sofo et al. 2008).
830 Mediterranean trees usually present lower stomatal sensitivity to drought in seedling
831 phase than in adult phase, probably in benefit of an increase in growth under
832 competition with understory vegetation, making them more vulnerable to drought
833 events in initial phases of growth (Mediavilla and Escudero 2004).

834

835 *Soils.* As discussed above, moderate reductions in rainfall imply significant decreases
836 in soil moisture. In addition to the direct effect, reduced rainfall can indirectly affect
837 plants by reducing growth and increasing C:nutrient ratios. Some studies have also
838 reported increases in SOM (Talmon et al. 2011). Most reports recommend the
839 differentiation between short-term and medium- and long-term effects of drought on
840 SOM (Ogaya and Peñuelas 2006; Martí-Roure et al. 2011; Navarro-García et al. 2012).
841 In the short term, drought can increase SOM by increasing the total amount of litterfall
842 (Oliveira and Peñuelas 2002; Ogaya and Peñuelas 2006; Martí-Roure et al. 2011) and
843 dead roots (Lloret et al 1999; Padilla and Pugnaire 2007). Few long-term experiments
844 on the effect of drought on SOM have been conducted, but observational studies under
845 prolonged and sustained drought or across environmental gradients suggest that SOM
846 decreases by the reduction of plant cover, implying a decrease in litterfall and an
847 increase in soil erosion by diminishing soil protection and permeability (Boix-Fayos et al.
848 1998; Li et al. 2011; Navarro-García et al. 2012).

849 SOM mineralization is very sensitive to drought in Mediterranean ecosystems
850 (Table 3). Decreases in soil enzyme activity (Zaman et al. 1999; Fioretto et al. 2000; Li
851 and Sarah 2003; Sardans and Peñuelas 2005, 2010; Sardans et al. 2006d; Sardans et
852 al 2008c, 2008d; Hueso et al. 2011), soil respiration (Bottner et al. 2000; Qi and Xu
853 2001; Emmett et al. 2004; Asensio et al. 2007), and root enzyme activity (Sardans et al.
854 2007) have been widely observed under drought conditions. The decrease in soil
855 enzyme activity is mainly due to the direct effect of the reduction in soil moisture
856 (Sardans et al. 2008c: Sardans and Peñuelas 2010) but also to the higher C:nutrient
857 ratio in plant litter (Wessel et al. 2004). This decrease in the nutritional quality of the
858 SOM can have a significant effect on the rates of litter decomposition (Coûteaux et al.
859 2002).

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

870 Mediterranean ecosystems under drought show no clear patterns of shifts in
871 N:P ratios (Sardans et al. 2008a; 2008b; 2012b). Different compensatory effects
872 probably occur in the cycles of these two nutrients. P is frequently retranslocated more
873 than N (Sardans et al. 2005a), but the comparative changes in N and P retranslocation
874 with increasing conditions of drought is not known. On the other hand, increases of soil
875 moisture decrease the fraction of P available in soils and increase the fraction of

876 unavailable P (Sardans and Peñuelas 2004; Sardans et al. 2008g). N is also more
877 soluble and easily leached than P and can be more lixiviated from soil by typical
878 Mediterranean storms when plant cover is reduced under drought and in physically
879 degraded soils. How increases in drought will affect Mediterranean ecosystems by
880 changing N:P ratios remains unclear, but the N:P ratio is an important variable favoring
881 species having different rates of growth (Sardans et al. 2012c).

882 Reductions in water uptake, mobility of nutrients in the soil, and release of
883 nutrients from the SOM can exert a feedback contributing to reduce the capacity of
884 plants under drought to take up nutrients by slowing the cycling of nutrients (Sardans et
885 al. 2012b). Increasing nutrient concentrations in soils increase the risk of nutrient
886 losses caused by runoff during torrential rainfalls (Sardans and Peñuelas 2004; Matías
887 et al. 2011). Drought projected for the coming decades should not sufficiently change
888 the concentrations of trace elements in the medium term to constitute any
889 environmental or health problems (Sardans and Peñuelas 2007b; Sardans et al.
890 2008h).

891

892 *System adaptation capacity.* The long-term evolutionary adaptation of Mediterranean
893 plants to long dry summers allows them to cope with moderate increases of drought
894 without an important loss of their production capacity and survival (Cotrufo et al. 2011).
895 Mediterranean shrubs subject to drought increase their levels of antioxidative
896 mechanisms to prevent injuries from increased oxidative stress (Munné-Bosch and
897 Alegre 2000; Munné-Bosch and Peñuelas 2003 and 2004; Peguero-Pina et al. 2008;
898 Nogues et al. 2012). Other processes enhanced by drought can contribute to increase
899 the capacity of plants to take up water. For example, Benabdellah et al. (2011)
900 observed an increase in arbuscular mycorrhizae that increased the capacity of plants to
901 take up water. Nutrient retranslocation increased when drought increased (Correia and
902 Martínez-Louçao 1997), which increased the concentrations of nutrients in plants and
903 thus contributed to an improvement in WUE. Higher nutrient retranslocation, however,

904 should increase the C:nutrient ratio in litter and contribute to the formation of more
905 recalcitrant SOM and to the slowing of nutrient cycling. The advantages and
906 disadvantages of nutrient retranslocation under increasing conditions of drought remain
907 unclear and deserve further research.

908

909 *Additional effects on C-cycling and emissions of biogenic volatile organic compounds.*
910 Drought usually increases emissions of plant terpenes, although this effect strongly
911 depends on drought intensity (Pegoraro et al. 2005; Plaza et al. 2005; Llusia et al. 2006,
912 2008, 2010). Studies suggest that severe drought decreases the emission of terpenes
913 (Loreto et al. 2001; Pegoraro et al. 2007; Peñuelas and Staudt 2010) but reduces sink
914 strength of the soil for atmospheric isoprene (Pegoraro et al. 2007). The effects of
915 drought on the emission of terpenes from Mediterranean soils remain unclear and vary
916 for different VOC compounds (Asensio et al. 2008).

917 Rewetting events after a period of drought have a large impact on soil
918 respiration and microbial activity and increase the loss of C from soil (Navarro-García
919 et al. 2012). After rewetting events, as for example after a rain event in a drought
920 period, an increase of soil heterotrophic respiration from litter and other soil organic
921 fractions (Rey et al. 2005; Jarvis et al. 2007; Casals et al. 2011; Placella et al. 2012)
922 and increases in the activity of some soil enzymes (Zornoza et al. 2006) have been
923 widely observed. The capacity to faster resuscitation capacity of certain microbial
924 groups after wet-up of dry soils may be a phylogenetically conserved ecological
925 property in Mediterranean soils (Placella et al. 2012). This process can imply a sudden
926 increase in nutrient availability, Butterly et al. (2009) observed a 35-40% increase of
927 available P. However, this effect drops during the first days after rain (Butterly et al.
928 2009). These effects are due to the increased water availability and to the increase of
929 SOC made accessible to microorganisms by the physical destruction of soil structure
930 by drying/wetting events (Inglima et al. 2009; Unger et al. 2010; Navarro-García et al.

931 2012) and by the increases of osmoregulatory substances released from
932 microorganisms in response to hypo-osmotic stress (in order to avoid cell lyses) that
933 increases the organic source to respiration (Unger et al. 2010). In the short term,
934 rewetting causes a cascade of effects, from increases of SOC mineralization and
935 availability of nutrients (Nguyen and Marschner 2005; Inglima et al. 2009) to short
936 periods of plant growth (Xiang et al. 2008).

937

938 *Desertification.*

939 Climate change scenarios projected for the coming decades predict a reduction in total
940 precipitation and a higher frequency and severity of torrential rainfall (Frei et al. 1998;
941 Romero et al. 1998; IPCC 2007 The most threatening phenomenon for Mediterranean
942 soils, especially in the most xeric areas, is desertification linked to a continual positive
943 feedback of higher frequency and intensity of torrential rainfall (associated to climatic
944 change) with an increase of soil erosion, which in turn leads to a loss of soil fertility and
945 thus plant cover. These facts can also be aggravated by human activities (such as
946 excessive livestock pressure) and by the increasing frequency and extend of fires,
947 specially in European Mediterranean region (Shakesgy 2011), that then leads to an
948 increased risk of erosion and desertification. The increases of fires intensity and
949 frequency is a serious concern (Shakesgy 2011). Moreover the investigations of
950 community succession and soil processes after fires in Mediterranean plant
951 communities create plant patches (Baeza et al. 2007) and soil degradation, reducing
952 water infiltration (Coelho et al. 2004), all of them leading towards desertification
953 process. During the last decades, several Mediterranean areas of the EU countries
954 have been subjected to land-use change (Millan et al. 2005; Zucca et al. 2006;
955 Calatrava et al. 2011; Salvati et al. 2012), whereby unproductive areas were forested
956 or abandoned or submitted to overexploitation (Calatrava et al. 2011). It appears that
957 these processes favour a general trend towards an increased cover of semi-arid

958 shrublands, and in the worst cases to desertification (Zucca et al. 2006) and may even
959 decrease rain events (Millan et al. 2005). This cascade of positive feedbacks among
960 these four variables has been observed in some studies in southern Spain (García et al.
961 2002; Moreno-de las Heras et al. 2011; Ruiz-Sinoga et al. 2011 and 2012) and is
962 exponentially favored and accelerated by the increase in aridity (Ruiz-Sinoga et al.
963 2011). The erosion of soils in Mediterranean areas is strongly related to torrential
964 rainfall (González-Hidalgo et al. 2007). Slopes and higher erodible bedrock accelerate
965 this process (Moreno-de las Heras et al. 2011). Moreover, photodegradation of litter
966 rises when plant cover decreases (Barnes et al. 2012), thus increasing the SOM losses
967 and contributing to soil degradation. Soil erosion is becoming the primary
968 environmental concern in human economic balances in Mediterranean regions (Riera
969 et al. 2007).

970

971 **Future research directions**

972 Mediterranean plants resist moderate increases in drought without significant changes
973 in their production capacity and survival and are able to maintain levels of soil fertility.
974 These capacities are species specific. The mortality observed in some forested
975 Mediterranean areas after severely dry summers varies in different species of the same
976 community (Hernández-Santana et al. 2009). While we do not know the real level of
977 future droughts, we can expect an increasing relative cover of more drought-adapted
978 species within communities. The impact of this situation on the soil is less clear
979 because if the drought is not severe, a new equilibrium in the plant-soil system may be
980 attained. Therefore, further research is needed.

981 The interaction between atmospheric CO₂ and increased drought should be
982 studied in long-term experiments, because a short-term counteracting effect has been
983 observed. At long-term, the acclimation of plants to increased atmospheric CO₂

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

998 Summarizing the information in the literature, we can identify two different
999 groups of feedbacks in Mediterranean plant-soil systems in response to the scarcity of
1000 water and nutrients in soils. Firstly, a high allocation to a deep, strong, and dense root
1001 system together with a notable plant cover and investment in soil enzyme production
1002 exerts a positive effect on soil fertility and protection capacity. Secondly but in contrast,
1003 a high nutrient retranslocation, high retention of nutrients in standing biomass, and high
1004 C:nutrient content of litter constitute constraints for a rapid release of nutrients from the
1005 SOM, lowering fertility and slowing the soil processes that produce high quality SOM.
1006 Current studies indicate that drought enhancement slows the first group of positive
1007 properties for soil fertility and protection but intensifies the second group of negative
1008 properties.

1009 Plant cover, soil biological activity, and fertility are interconnected. The causes
1010 underlying the high soil enzyme activity observed in Mediterranean ecosystems

1011 warrants future research. Most efforts to date have investigated the relationships
1012 between soil moisture, temperature, and food quality of litter in terms of lignin content
1013 or C:nutrient ratio, but Mediterranean plants may possess mechanisms for stimulating
1014 soil enzyme production. Because the current data suggest that extensive root systems
1015 can significantly impact soil enzymes, the introduction of soil genomics, proteomics,
1016 and metabolomics should be encouraged to gain knowledge of the role of plants,
1017 through rhizospheric activity and root exudates, on soil microbial communities, on soil
1018 enzyme activity, soil mineralization, and soil texture. Moreover, these studies should
1019 investigate the role of metabolites at different levels and in different processes, such as
1020 the allelopathic inhibition of growth of competing vegetation, stimulation of microbial
1021 and especially fungal growth, or changes in soil structure by contributing to the
1022 formation of soil aggregates.

1023 Studies in Mediterranean areas suggest a key role for the root system mediated
1024 by the availability of water. A more thorough knowledge of root structure and
1025 distribution of entire plant communities, from forests in mesic areas to sparse
1026 shrublands in drier areas, should be another main objective for research in this area.
1027 This research would provide a better understanding of the shifts that occur in plant
1028 communities when climate evolves to a different pattern of precipitation. The study of
1029 how root systems and particularly the deepest roots, which frequently enter fractures in
1030 the bedrock, pump water from the deepest to the upper soil layers warrants urgent
1031 research. How root systems maintain higher levels of soil mineralization and activity
1032 also warrants further research. Isotopic methods should be a useful tool in these
1033 studies by allowing the monitoring of the movement of water in soil-plant systems.

1034 We also lack knowledge of the interacting effects of drought and warming in
1035 realistic field scenarios and in different conditions, from cold alpine forested areas to
1036 dry, warm lowland areas. The presence of large gradients of water availability and
1037 temperature in Mediterranean alpine areas, frequently over short distances, constitutes

1038 an excellent playground for investigating the role of soil moisture and temperature and
1039 their interactions in modulating the active and passive mechanisms of plants that affect
1040 soil texture and fertility. Moreover, these studies could help us to better understand the
1041 capacity of response of the different Mediterranean ecosystems to the projected
1042 increase in drought. In the context of future scenarios of global change, field
1043 experiments are needed for studying the long-term effects of high concentrations of
1044 atmospheric CO₂ combined with drier conditions, because this future scenario is very
1045 likely and because the current but incomplete results strongly suggest that the effects
1046 of increasing concentrations of atmospheric CO₂ on plants could decline with time.

1047

1048

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1053

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2267 Figure legend

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2269 Figure 1. Soil extracellular activities of urease, protease, β -glucosidase, and acid and
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2271 Mediterranean soils compared with temperate and tropical soils. The reports have
2272 analyzed urease activity by the Kandeler and Gerber (1988) method or by comparable
2273 methods such as that of Tabatabai and Bremner (1969), protease activity by the Ladd
2274 and Butler (1972) method, β -glucosidase activity by the Eivazi and Tabatabai (1988) or
2275 related methods (Dick et al. 1996), and acid and alkaline phosphatase activities by the
2276 Tabatabai and Bremner (1969) and comparable methods (Tabatabai 1994). The values
2277 presented are those of controls when diverse treatments were applied to the studied
2278 soils and of the annual mean when several measurements were conducted throughout
2279 the year. The number of studies reviewed, by biome and enzyme, are depicted above
2280 the bars. The bars indicate mean (+ S.E.). For detailed information, see Table S1 in the
2281 supplementary material.

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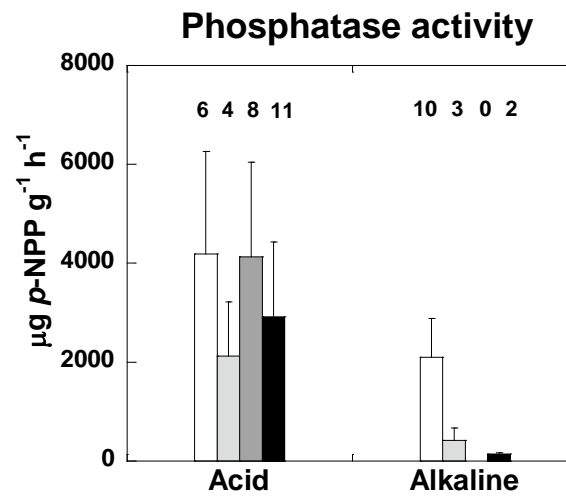
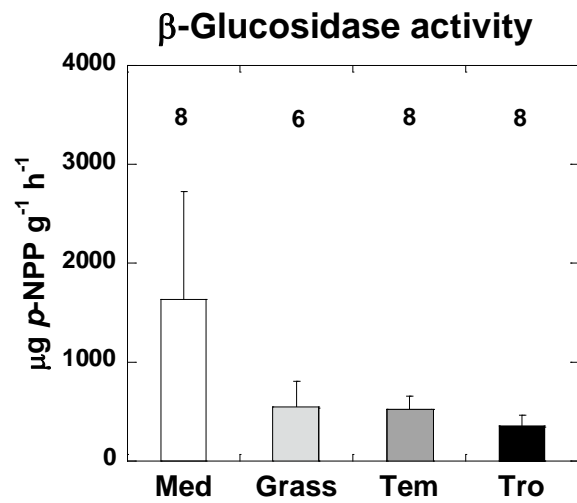
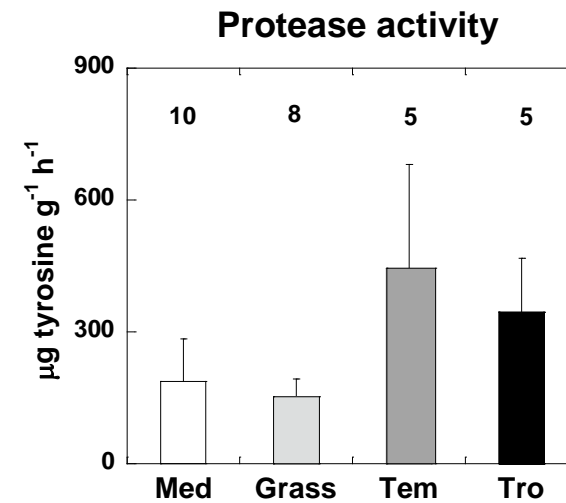
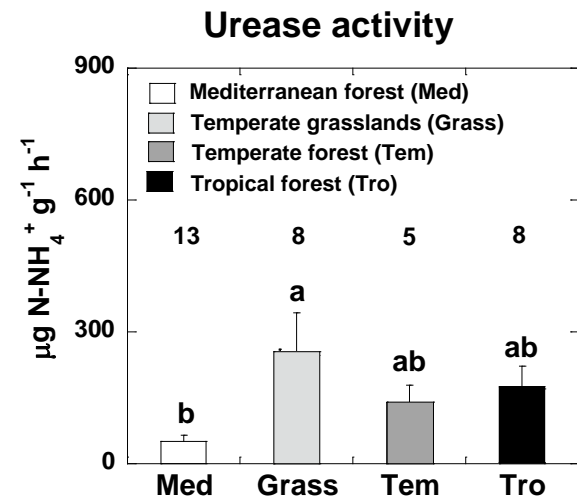


Figure 1

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 cuticule 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 [CO₂] 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
Asymmetrical species-specific effects	0	0	16
Soil permeability	4	0	0