Chapter 6

PLANT EFFECTS ON SOILS IN DRYLANDS: IMPLICATIONS FOR COMMUNITY DYNAMICS AND ECOSYSTEM RESTORATION

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INTRODUCTION

Almost 50% of the emerged land (6.15 10^6 ha) are considered drylands (Reynolds and Stafford Smith, 2002). They are distributed in four continents, covering from 31% (South America) to 75% (Australia) of the continental land area. Drylands encompass areas with a wide range of conditions in relation to the ratio Precipitation/Evapotranspiration (P/E), from hyperarid (P/E<0.03) to Dry Subhumid (0.5<P/E<0.75) (UNESCO, 1977). Throughout the text, we will use the term drylands in a broad sense, meaning areas where precipitation is so scarce that it becomes the main factor controlling biological processes. This definition corresponds to what Noy Meir (1973) refers to as arid ecosystems

In areas like the Mediterranean, drylands have been subjected to a long history of land use (Hillel, 1992; Grove and Rackham, 2001). But this is not always the case, as different dryland areas have supported extremely contrasted human population densities. The boundary between subhumid to semiarid conditions may be particularly sensitive to disturbances, and population buildup in subhumid and semiarid zones have probably favoured the expansion of areas characterized by discontinuous vegetation cover. This process is not recent, as population density was relatively high in areas such as the Mediterranean basin 2000 years ago (Grove and Rackham, 2001). For example, Butzer (1990) suggests that population density in the Iberian Peninsula was close to the carrying capacity for agricultural systems several times since 2,000 BP. Phases of economic welfare and social integration correspond to higher demands for resources, including land, leading to defor-

estation and, eventually, land degradation. The 20th century has shown an unprecedented increase in population density in many drylands (Le Houérou, 1992). But, unlike what happened in the past, population density has mainly concentrated in coastal areas. As a result, recent population increase has been paralleled by a reduction in the intensity of inland land use (and an increased demand for resources overseas).

Changes in land use are relevant in the context of species effect on soil properties for two reasons. First, land use, together with natural factors, have favoured land degradation in vast areas. For example, alpha grass (*Stipa tenacissima*) steppes, once covering more than 8 million ha in the Maghrib, are being destroyed at a rate of 1% per year (Aïdoud, 1989; Le Houérou, 2001). Past disturbances may interact with plant species to generate unexpected effects. For example, litterfall inputs may not be the same if individuals are established in a slope that had either been terraced or left aside. Second, with few exceptions, most individual plants may have established in their present locations not long ago. Examples of changes in land use dating less than 50 years are common (Grove and Rackham, 2001; Bonet, 2004). In contrast, the effect of land uses such as agriculture or grazing on ecosystem structure and functioning may last for centuries (Bruun et al., 2001; Maestre 2004). Changes in soil phosphorus content in the surroundings of Roman farms have been detected up to 2,000 years after abandonment (Dupouey et al., 2002). These changes were large enough to affect P concentration in oak leaves. Thus, information accumulated in soils for centuries adds noise to the interpretation of species effect on soil properties (Cortina, 1992).

There are many ways in which plants may affect soils. They can modify soil properties directly, e.g. through inputs of organic matter and nutrients, and indirectly, by affecting abiotic and biotic conditions that influence soil properties. For example, symbiosis with specific strains of mycorrhizal fungi can be relevant for the establishment of their own progeny or for the colonization by other species (Palenzuela et al., 2002; Azcón-Aguilar et al., 2003). Under dry conditions, shade may affect litter decomposition directly (Duguay and Klironomos, 2000; Verhoef et al., 2000), and as a result of changes in microclimatic conditions (Jackson and Caldwell, 1992; Cortina and Vallejo, 1994). Sometimes, changes in soil properties affect plant composition and growth, generating positive feedbacks (Northrup et al., 1995; Morehead et al., 1998). On the other hand, plants may affect soil properties in ways that may appear subtle to us, but may be rather evident to other organisms (Bais et al., 2003, 2004). This complex network of interactions hampers the interpretation of plant-soil relations. Unfortunately, our knowledge is still quite broad, and surprises arise too often.

Despite the intrinsic variability in soil properties and the complexity of soil-plant interactions, plant effects on soils play a major role in population, community and ecosystem dynamics in drylands. Several features of drylands may contribute to this. By definition, climatic conditions are harsh and soil

conditions are unfavourable for plant growth due to salinity, low organic matter, P immobilisation, etc. Thus, any slight modification of microclimate or soil properties may have disproportionate effects on other organisms (e.g., Pugnaire et al., 1996a; Moro et al., 1997; Maestre, 2003). Furthermore, xerophytes are commonly small and isolated, as compared to plants from temperate and tropical areas. This may favour litterfall, throughfall, stemflow and fine root inputs accumulating underneath the canopy, and thus intensifying plant effects. Finally, isolated plants act as obstacles for runoff carrying organic matter, nutrients and sediments (Greene et al., 2001). Thus, it is not surprising that certain plants and vegetation patches have higher infiltration rates, improved soil structure and nutrient content, and higher biological activity, creating "hotspots" of favorable soil conditions that have been referred to as "fertile islands" or "resource islands" (Whitford, 2002).

As we just mentioned, plant alteration of soil and microclimate conditions may affect other organisms to the point of controlling the composition and function of the whole ecosystem (West, 1989; Schlesinger and Pilmanis, 1998; Montaña et al., 2001). Identifying these interactions is crucial to understand and to manage dryland ecosystems. In this review, we will describe the way plants affect soil properties in drylands, and how these feedbacks, together with changes in microclimatic conditions, affect plant-plant interactions and community dynamics. In the last section, we will discuss the use of this knowledge for the restoration of degraded dryland ecosystems.

PLANT EFFECTS ON WATER DYNAMICS AND USE

In drylands, water scarcity controls plant effects on soils in several ways. Biological processes, including plant productivity, are strongly limited by water. Water limitation results in discontinuous plant cover, which is often arranged as a two-phase mosaic of vegetated and bare ground patches (Valentin et al., 1999). Spatial patterns of vegetation, together with morphological and physiological attributes of plants greatly affect water fluxes and availability (Bromley et al., 1997, Cerdà, 1997). Indeed, the spatial pattern of plant patches is essential to maintain ecosystem composition and function in drylands (Noy Meir, 1973; Tongway et al., 2001), and can be used as an indicator of the degradation status of arid and semiarid lands (Wu et al., 2000; Bastin et al, 2002; Maestre and Cortina, 2004a).

At the patch level, canopies differ in their capacity to intercept water. For small rains, which normaly account for a large number of rain events, interception can be high (Martínez-Meza and Whitford, 1996; González-Hidalgo and Bellot, 1997; Bellot et al., 2001), and may promote the formation of dry shadows (Valladares and Pearcy, 2002). Stemflow and throughfall are strongly dependent on plant architecture (Martínez-Meza and Whitford, 1996, Domingo et al., 1998). Funnel-like structures, as found in many shrubs, favour moisture concentration around the base of the stems (West, 1989; Martínez-Meza and Whitford, 1996), whereas tussock grasses may concentrate throughfall inputs around the canopy edge (Puigdefábregas et al., 1999). Rainfall redistribution may affect deep soil moisture content as well, as water fluxes at the base of the stem may circulate down the soil profile following the roots and root pores (West, 1989; Martínez-Meza and Whitford, 1996; Ryel et al., 2003). These fast tracks for water fluxes may explain why increases in moisture content following a rainfall event are not necessarily sequential, from top to bottom, but water may saturate deeper soil profiles earlier than shallow ones (González-Hidalgo et al.,2003). Species with the highest stemflow, and with deep roots may favour the recharge of deep soil horizons (Martínez-Meza and Whitford, 1996). These traits are common in some desert and Mediterranean plants (Cannon, 1911; Kummerov, 1981). On the other hand, hydraulic lift −water translocation to upper or lower parts of the soil profile through the rooting system − has been described in drylands worldwide (Caldwell et al., 1998; Burguess et al., 1998; Filella and Peñuelas, 2003; Gutiérrez and Squeo, 2004). This movement of water may affect N mineralization and microbial activity as well (Caldwell et al., 1998). The
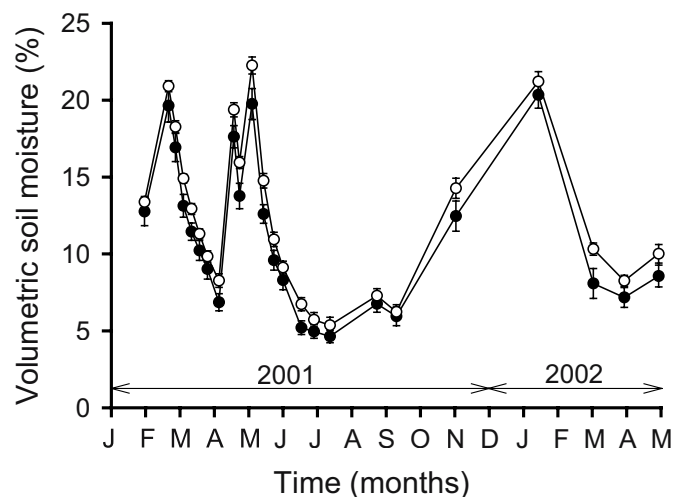

Figure 1. Moisture content of the 0-20 cm soil underneath *Stipa tenacissima* tussocks that were either left undisturbed (black dots) or bended to suppress shadow (white dots) in a steppe located in SE Spain. Data represent means and standard errors (n = 6). Redrawn from Appendix A in Maestre et al. (2003a).

shade provided by plant canopies, together with litter accumulation, influence the soil water balance in the surroundings of plant patches (Fig. 1). It is important to note that shade may not only affect soil moisture content, but may also influence individual plant performance and plant community composition by modifying evaporative demand, and light quantity and quality (Valladares, 2003).

Stormy rains are common in some drylands, such as the Mediterranean and West Peru (De Luís et al., 1997; Arntz and Fahrbach, 1996). For example, in Spain, more than 100 rain events with intensity higher than 100 mm in 24 h, including seven rain events higher than 500 mm in 24 h, were recorded between 1901 and 1989 (Olcina, 1994). There is increasing evidence that the amount and frequency of large vs. small rainfall events may control ecosystem function and composition in drylands (Ehleringer et al., 1999). One of the consequences of rainfall concentration is that part of the water does not accumulate in soils, but is either drained or exported as runoff (Bellot et al., 2001; De Luís et al., 2001). Surface runoff can have strong effects on plant-soil interactions because it may transport sediments and organic matter within or beyond the slope, and because it favours the increase in soil fertility and water availability under plant canopies (Cerdà, 1997; Puigdefábregas et al., 1999). Structures in contact with the surface soil (lower branches, multiple stems, litter, tussock plants, etc.) favour runoff retention (Rostagno, 1989; Bromley et al., 1997), and attributes of plant patches like size, width parallel to the slope, and spatial pattern are critical to define the ability of an ecosystem to retain and use those resources transported by runoff (Ludwig et al., 1999).

Most of the water inputs in drylands are lost by evapotranspiration. Thus, in Mediterranean watersheds, annual evapotranspiration, and not drainage, is well correlated with precipitation (Piñol et al., 1991). Vegetation management, involving shifts from woody to herbaceous vegetation, partial clearing and formation of stone pavements, etc. has been used to collect more drainage water (Hillel, 1992; Lavee et al., 1997; Burch et al., 1987). In general, evapotranspiration is proportional to LAI, and suppression of woody vegetation commonly results in increasing soil moisture availability, seepage drainage or watershed runoff (Burch et al., 1987; Bellot et al., 2001), although exceptions exist (Dodd et al., 1998). On the contrary, increases in woody cover (e.g. such as shrub encroatchment) may lead to a reduction in surface water availability or groundwater levels (Puigdefábregas and Mendizábal 1998; Ohte et al., 2003; Bellot et al., 2004) (Fig. 2). The increase in the cover of woody invasive species can have important economic consequences (Le Maitre et al., 2002). Species identity may also be relevant for water losses. Obvious examples are summer-deciduous or semi-deciduous species (e.g. *Cistus salviifolius*, *Cistus albidus*, *Euphorbia dendroides*, etc.), that reduce evapotranspiration losses by leaf shedding (Ne'eman and Goubitz, 2000). The difference between drought escapers, drought avoiders and drought tolerant

species (Levitt, 1980), could be helpful in this context. Comparisons in water use between pairs of species are frequent. For example, pines commonly close stomata at relatively high water potential, and thus may reduce water losses during drought as compared to other species. *Pistacia lentiscus* and *Quercus coccifera*, two coexisting shrubs common in the western Mediterranean basin,
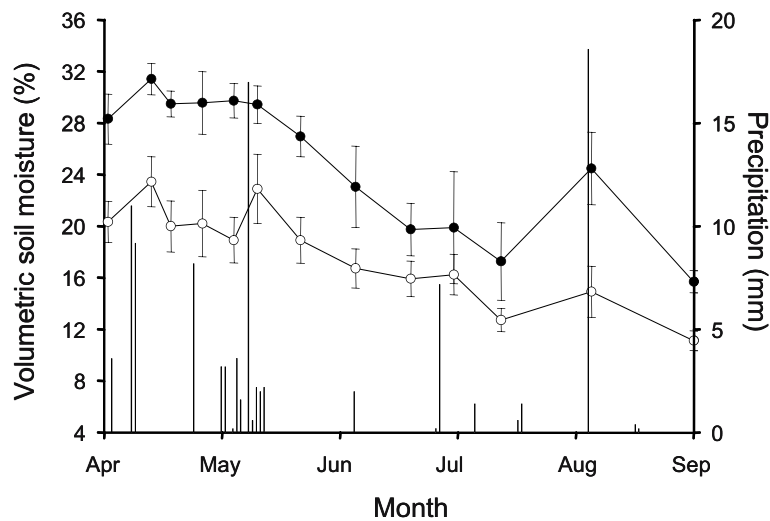

Figure 2. Changes in moisture content of the surface soil (0-10 cm depth) of adjacent Mediterranean semiarid grasslands with (white circles) and without (black circles) a dense cover of *Pinus halepensis* (3470 trees ha^{-1}). Bars correspond to rainfall events recorded during the period of study (April-September 1996). Soil moisture data represent means and standard errors (n = 5). Redrawn from Bellot et al. (2004).
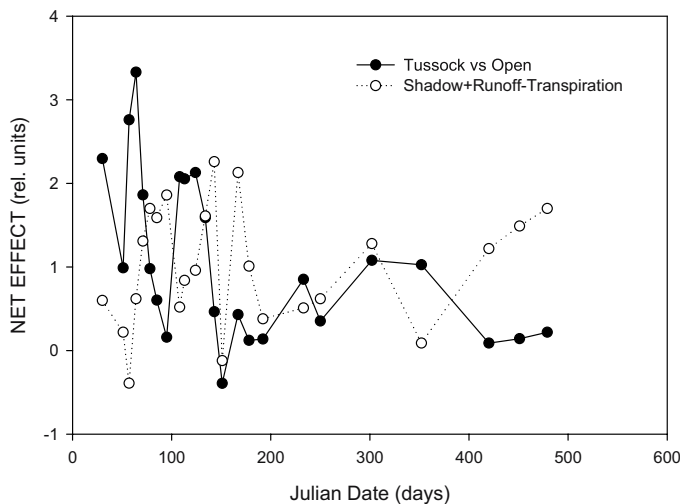

Figure 3. Net effect of the tussock grass *Stipa tenacissima* on soil moisture content (0-20 cm depth) as compared to the arithmetic addition of the net effects of transpiration, runoff and shadow in a Mediterranean semiarid steppe of SE Spain. Net effects are calculated from the standardized differences in moisture content between tussock and open microsites (net tussock effect), tussock and herbicided tussock (net transpiration effect), tussock with and without runoff (net runoff effect) and standing and bended tussock (net shadow effect). From original data in Maestre et al. (2003a).

show contrasted water use strategies (Vilagrosa et al., 2003). Other factors being equal, the water spender *P. lentiscus* is likely to deplete soil moisture sooner after a rain that *Q. coccifera*. But, to our knowledge, no attempt to systematically relate plant strategy to withstand drought, and water dynamics at a plot and catchment scale has been made so far.

Finally, plants may affect water availability by favouring the formation of calcite and laterites, and thus modifying soil volume (Viles, 1990). Water uptake from the vadose zone may lead rhizoconcretion precipitation around particular roots, whereas phreatophytes may favour different forms of calcite precipitation in the zone of capillary rise (Thomas, 1988). These processes result in the reduction of root absorptive capacity, root death, and finally the decrease in available soil.

Given the diversity of effects of plants on water fluxes, it is not surprising that the effect of plants on water availability, a critical soil property in drylands, may substantially vary according to plant community composition and structure. Furthermore, it is difficult to explain variations in moisture content as the additive effect of changes in single fluxes (Fig. 3). On the other hand, plant effects on soil moisture content may be short-lived, being restricted to the lapse between a rainfall event (and, eventually, homogeneous high moisture content), and soil dessication, or to particular periods of the year (Belsky et al., 1993) (Fig. 4). This is particularly true for shallow soils and surface soil horizons.

ORGANIC MATTER AND NUTRIENTS: ISLANDS OF FERTILITY

Litterfall inputs are relatively low in drylands due to constrains in plant productivity (Berg et al., 1999; Breckle, 2002), but they may be substantially higher immediately underneath the canopy. Variability in litter decomposition rates is very high, ranging from some of the lowest rates recorded (0.07 yr^{-1}; Hart et al., 1992), to relatively high values (Gallardo and Merino, 1992). For Mediterranean ecosystems, Aerts (1997) found that short term decay rates were largely variable, averaging 0.35 $years^{-1}$. These values were very close to those of temperate ecosystems (0.36 $years^{-1}$), and substantially lower than decay rates in tropical areas (2.33 $years^{-1}$). Within a given site, variability in litter decomposition rates can be very high (Gallardo and Merino, 1992), suggesting that species identity may control soil organic matter (SOM) dynamics and nutrient availability. In Mediterranean ecosystems litter decay rates are related to actual evapotranspiration (AET) and litter quality (Aerts, 1997), but the amount of variability explained by single climatic or chemistry parameters is very low. In desert ecosystems, AET underestimates decomposition rates, probably due the activity of soil fauna (Whitford et al., 1981). The relationship between litter decay rates and a widely used index of
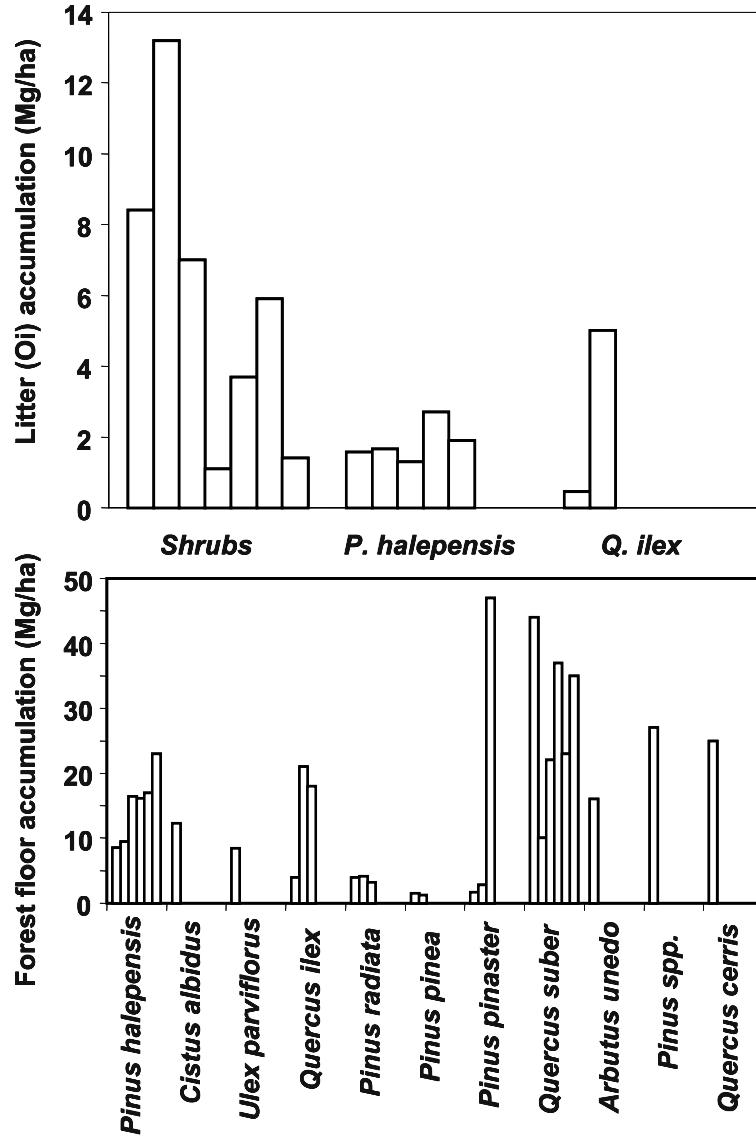
Figure 5. Litter (upper graph) and forest floor (lower graph) accumulation in Mediterranean forests and shrublands dominated by different woody species. Data from Fons (1995), Ferran (1996), Huesca et al. (1998), Serrasolsas and Vallejo (1999), Cortina (1992), Berg et al. (1993), Sevink et al. (1989), and Van Wesemael and Veer (1992). Only maximum values were taken from studies reporting measurements at several locations.

recalcitrance, the lignin to nitrogen ratio, is often poor in drylands (Gallardo and Merino, 1992; Aerts, 1997). The resistance of the external layers of leaves and needles may be more important drivers of decomposition rates in these environments than the quality of the whole tissue (Gallardo and Merino, 1992; Cortina and Vallejo, 1994).

Forest floor accumulation in drylands is commonly lower than in more mesic environments because of low litterfall, and relatively high decomposition rates and vertical transfers (Vallejo et al., 1998; Fig. 5). However, particularly dry conditions and surface accumulation of rock fragments may favour the formation of xeromoder type duff layers (Sevink et al., 1989; Fons, 1995). This is probably due to reduced transfer to lower soil horizons, as CO_2 efflux is promoted by the presence of a stone layer (Casals et al., 2000). As previously mentioned, small height and isolation may increase the potential of dryland vegetation to concentrate litterfall, and locally promote forest floor build-up. Plant species differ in forest floor accumulation, and morphology (Peltier et al., 2001), although other factors
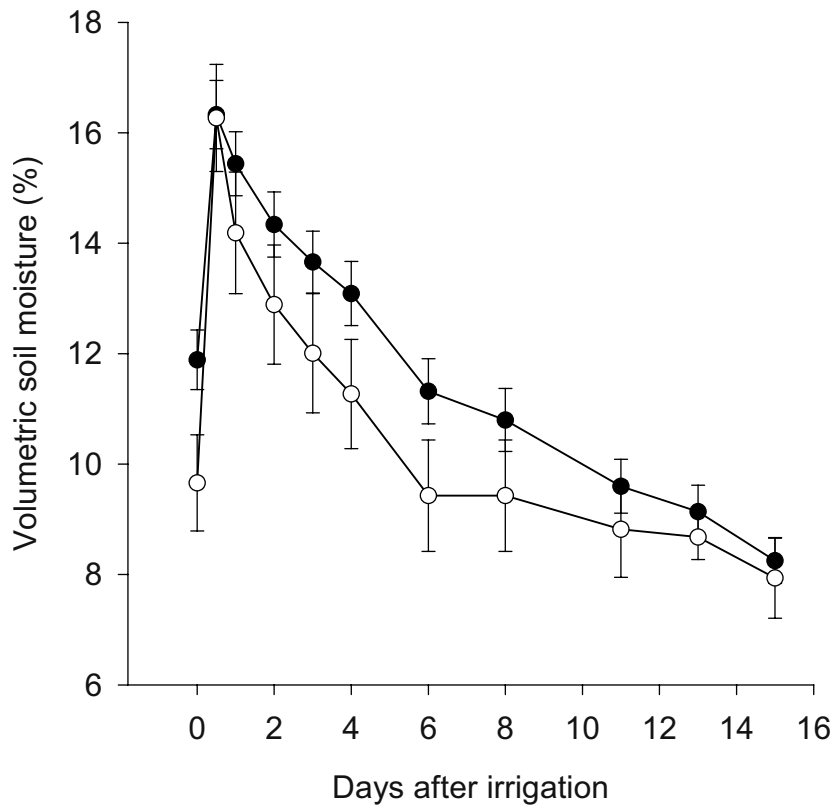

Figure 4. Changes in volumetric soil moisture content in the surface soil (0-20 cm) underneath *Stipa tenacissima* tussocks (black circles) and in open areas (white circles) after irrigation in a semiarid steppe in SE Spain. Soil moisture data represent means and standard errors (n = 10). Redrawn from Maestre et al. (2001).

such as lithology may be more important in determining forest floor properties (Sevink et al., 1989; Fons, 1995). Aphyllous species (crassulacean, many legumes, etc.), and species with no spontaneous leaf shedding (e.g. tussock grasses, palms) accumulate small amounts of litter; whereas species loosing a substantial amount of their foliage every year can create a relatively thick forest floor (Bochet et al., 1999; Peltier et al. 2001). Under Mediterranean conditions, conifers may accumulate thicker forest floor layers than hardwoods (Peltier et al., 2001).

Litter incorporation into the mineral soil and SOM stabilization can be greatly affected by soil fauna (Whitford, 2002). Soil fauna may comminute partly decomposed litter and favour SOM transport down the profile (Anderson, 1988; Bertrand and Lumaret, 1992; Romanyà et al., 2000a). It is also affected by plant species and plant cover type. For example, in New Mexico deserts, shrub cover may negatively affect the presence and activity of some mammals and promote the abundance of rabbits, but may not affect ants and termites (Krogh et al., 2002; Jackson et al., 2003). In Mediterranean environments, millipedes are more frequently found under *Quercus coccifera* than under *Q. ilex*, *Q. pubescens* or *Brachypodium ramosum* (Bertrand and Lumaret, 1992). However, Maestre and Cortina (2002) did not find any relationships between the spatial pattern of earthworm casts and the spatial pattern of grass species in a semi-arid steppe in SE Spain. Given the important effects of soil fauna on SOM dynamics, infiltration and nutrient turnover in drylands (Whitford, 2002), further studies on the interactions between plants, fauna and soils are needed.

SOM decomposition, as plant productivity, is negatively affected by water limitations (Meentemeyer, 1978), and SOM content in dryland soils is commonly low (Vallejo et al., 1998). SOM is usually higher underneath the canopy of isolated plants and vegetation patches than in open areas (see below). Organic matter accretion as shrubs increase in size has been described (Pugnaire et al., 1996a, Tirado, 2003). Fine root inputs and historical changes in the spatial pattern of vegetation distribution may, however, attenuate these differences (Puigdefábregas et al., 1999), although plant effects on SOM may last less than two decades (Burke et al., 1999; Romanyà et al., 2000b; Martínez-Mena et al., 2002). It is often difficult to evaluate species effect on SOM because the age of individuals under comparison may be very different. This is particularly true for resprouting species. For example, in a review on the effects of 20th century afforestations with *Pinus halepensis* (one of the most common tree species in the Mediterranean) on semiarid ecosystem properties, Maestre and Cortina (2004b) found that most studies on SOM dynamics reported lower SOM contents underneath pine canopies than underneath patches of relatively undisturbed shrubland. We don't know if differences arise from contrasted species properties or from time, and thus we don't know if pines will ever reach the SOM levels found under established shrubs. Contrasts in soil CO_2 efflux can be substantial under different types of vegetated patches within a given ecosystem (Maestre and Cortina, 2003; Fig.
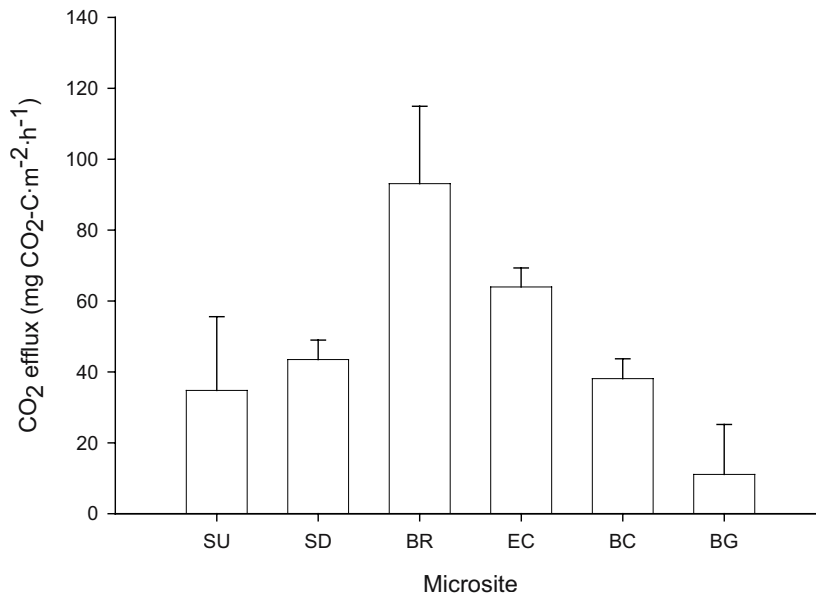
Figure 6. Soil respiration from different microsites in a *Stipa tenacissima* steppe in SE Spain. Measurements were taken on May 2001. Bars represent means and standard errors of ten replicates per microsite. SU: Upslope of *S. tenacissima* tussocks, SD: Downslope of *S. tenacissima* tussocks, BR: under the canopy of the sprouting perennial grass *Brachypodium retusum* EC: bare ground areas covered with earthworm casts, BC: bare ground areas covered with biological crusts, BG: bare ground areas covered with physical crusts. From original data in Maestre and Cortina (2003).

6), an indication that species may greatly differ in their overall effects on SOM content and quality. Plants can greatly modify nutrient accumulation and availability through mechanisms such as weathering, nitrogen fixation, runoff capture, concentration of animal feces, etc. (West, 1989; Kelly et al., 1998; Eviner and Chapin, 2003). Nitrogen fixing plants, legumes and actinorhizal plants, are widespread in drylands. This is remarkable, as soil properties that are common in drylands (such as low P availability, salinity and low water availability) may negatively affect N fixation rates (Reddell et al., 1991; Azcón and Altrash, 1997). Sprent (1987) suggested that deep rooting and adaptations to minimize water loss, such as the presence of phyllodes, may have contributed to their success. Experimental measures of N fixation rates range from less than 1 kg N ha^{-1} year^{-1} to 390 kg N ha^{-1} year^{-1} (Table 1).

We have reviewed published literature on changes in soil properties under vegetation patches in drylands. The data set includes 31 references, and more than 40 species and vegetation types covering a rainfall gradient from less than 100 mm to more than 1000 mm, with most studies in the range 200-250

Table 1. Some examples of N inputs through biological fixation in drylands.

Species	N fixation rate (kg ha^{-1} year^{-1})
Prosopis glandulosa[1]	25-30
Prosopis glandulosa[2]	150
Prosopis glandulosa[7]	45-140
Prosopis glandulosa[8]	16
Prosopis glandulosa[11]	40-50
Casuarina equisetifolia[3,4]	40-60
Ceanothus velutinus[5]	108
Ceanothus greggi[6]	0.1
Adenocarpus decorticans[9]	0.5-1
Acacia caven[10]	0.5-18
Prosopis alba[10]	0.0-1.2
Prosopis chilensis[10]	0.2-1.7
Chamaecytisus proliferus[10]	8-193
Chamaecytisus proliferus[12]	390

[1]Rundel et al. (1982), [2]Felker (1979), [3]Dommergues (1963), [4]Gauthier et al. (1985), [5]Youngberg and Wollum (1976), [6]Kummerov et al. (1978), [7]Johnson and Mayeux (1990), [8]López-Villagra and Felker (1997), [9]Moro (1992), [10]Aronson et al. (2002), [11]Sharifi et al. (1982), [12]Unkovich et al. (2000).

mm. All communities show discontinous cover of woody vegetation and herbaceous tussocks, with most studies reporting cover values ranging from 20% to 50%. Lythology and soil types are diverse, from acidic (pH 4.5) to alkaline (pH 8.5). We used the index RII (Armas et al., 2004) to compare soil properties underneath the canopy and in intercanopy areas. RII is calculated as:

$$RII=(VARc-VARi)/(VARc+VARi)$$

where VARc and VARi are the values of a given soil property for the canopy and intercanopy areas, respectively. RII ranges from –1 to +1, with positive values indicating increases in the variable under study in canopy microsites.

For the 41 comparisons of soil organic carbon content (TOC) between soils underneath vegetated patches and soils in open areas (Fig. 7), average soil depth is 10 cm (range 1-40 cm). TOC ranged from 0.1 to 10%. Vegetated patches showed an average increase in TOC up to 450%, with most values falling between 50% and 100%. In no case TOC was higher in open areas than in vegetated areas.

Results from the 31 studies comparing total N (TKN) content are similar to those of TOC (Fig 8). TKN ranged from 0.02% to 1.7%. The relative
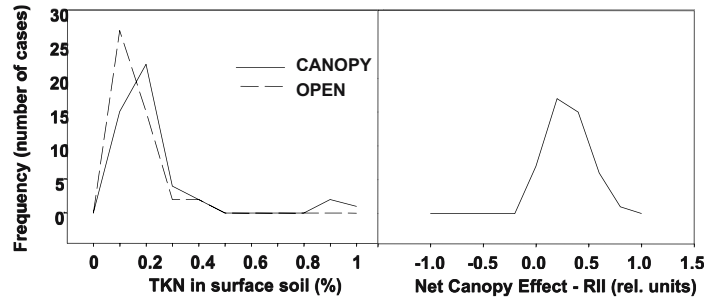
Figure 7. Left: Total organic carbon concentration in surface soils under the canopy of vegetation patches (CANOPY, solid line), and in open areas (OPEN, broken line) in several comparative studies conducted in drylands. Right: Net canopy effect (RII) on total soil carbon concentrations in surface soils. This effect was calculated as (TOCc-TOCi)/(TOCc+TOCi), where TOCc and TOCi are total carbon concentration in canopy and intercanopy areas, respectively.
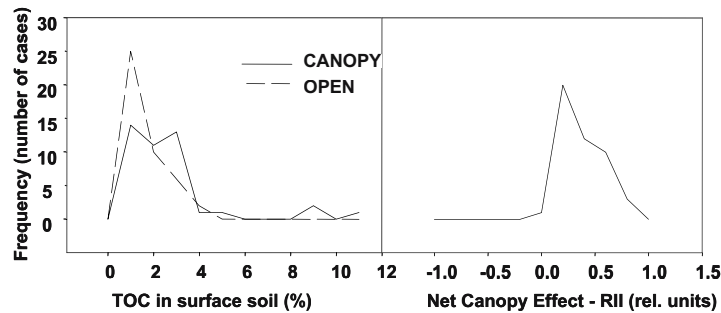

Figure 8. Left: Total organic nitrogen concentration in surface soils under the canopy of vegetation patches (CANOPY, solid line), and in open areas (OPEN, broken line) in several comparative studies in drylands. Right: Net canopy effect (RII) on total soil carbon concentration in surface soils. This effect was calculated as (TKNc-TKNi)/(TKNc+TKNi), where TKNc and TKNi are total nitrogen concentrations in canopy and intercanopy areas, respectively.
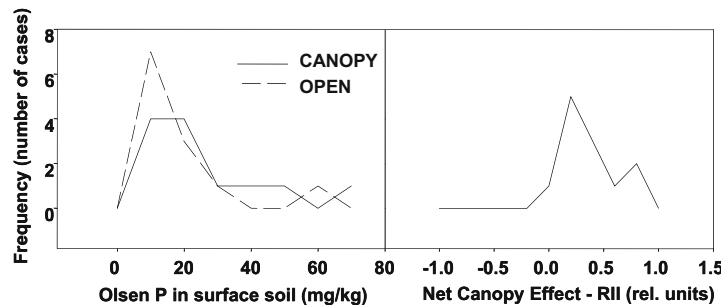
Figure 9. Left: Concentration of available phosphorus (bicarbonate extraction) in surface soils under the canopy of vegetation patches (CANOPY, solid line), and in open areas (OPEN, broken line) in several comparative studies in drylands. Right: Net canopy effect (RII) on total soil carbon concentration in surface soils. This effect was calculated as (PAVc-PAVi)/(PAVc+PAVi), where PAVc and PAVi are available phosphorus concentrations in canopy and intercanopy areas, respectively.

increses in TKN underneath vegetated patches were in the same range as for TOC. The number of studies showing higher TKN in open areas as compared to vegetated areas was very low, and of those, none showed a substantial decrease in TKN. Phosphorus availability (Olsen's bicarbonate extraction; n = 12; Fig. 9) ranged from 1-56 ppm in open areas to 2-65 ppm underneath vegetated patches. Most studies found a ca. 50% increase in P availability underneath vegetated patches.

BARE AREAS THAT ARE NOT

As mentioned before, precipitation in drylands is not high enough to maintain a continuous cover of vascular plants (Specht, 1988), leaving what are commonly, and wrongly, referred to as bare ground areas. Soil surface conditions in these areas is relevant for ecosystem functioning (Tongway and Ludwig, 1997), and its degradation may impair water fluxes to plant patches (Eldridge et al., 2000), and modify ecosystem-level processes like soil respiration (Maestre and Cortina, 2003). Bare areas are frequently covered by communities of cryptogams (mosses, lichens, cyanobacteria, liverworts and green algae), commonly referred to as biological crusts (West, 1990). Crusts are an important source of soil organic carbon (Beymer and Klopatek, 1991), fix atmospheric nitrogen (Rychert and Skuji⌊š, 1974), reduce wind and water erosion (Belnap, 1995), increase soil stability (Belnap and Gardner, 1993), and have an important effect on soil-water interactions (Eldridge et al., 2000). Biological crusts are preferentially established on fine textured slightly alkaline soils, with low content of surface rock fragments (Vitousek et al., 2002), In drylands, smooth and rugose crusts dominate (Belnap, 2001).

Depending on crust composition, net annual carbon input has been estimated between 0.4 and 37 g C m^{-2} year^{-1} (Evans and Lange, 2003). In arid areas this may represent a significant input of organic matter. These figures correspond to relatively high instantaneous rates of C fixation, up to ca. 5 ⌊mol CO_2 m^{-2} s^{-1} (García-Pichel and Belnap, 1996; Lange et al. 1997; Lange et al., 1998), as crusts remain inactive for long periods.

When biological crusts incorporate cyanobacteria and cyanolichens, they may fix substantial amounts of atmospheric nitrogen. Several studies have measured N fixation rates higher than 10 kg N ha^{-1} year^{-1} (Rychert and Skuji⌊š, 1974; Belnap, 2002; Evans and Lange, 2003), although much lower rates are reported (Jeffries et al., 1992; Aranibar et al., 2003). Part of this N may be lost by denitrification and ammonia volatilization (Vitousek et al., 2002). These estimations are, however, subjected to great uncertainty, as substantial spatial and temporal variability adds to methodological limitations. Nevertheless, N inputs in arid ecosystems coming from biological crusts can be relevant at an ecosystem scale (Evans and Ehleringer, 1993; Billings et al., 2003).

Biological crusts affect water fluxes in various ways. Increased surface roughness may favour runoff reduction and water infiltration (Warren, 2001). However, the relatively flat morphology of biological crusts in arid and semiarid areas not subjected to freezing may reduce the magnitude of this effect. The net effect of biological crusts on infiltration rate depends on soil texture, and on the identity of the organisms dominating the crusts. In sandy soils, biological crusts may increase microporosity and reduce infiltration. In soils with higher fine particle content, biological crusts improve aggregation and create macropores, thus increasing infiltration rate. Moss-dominated crusts favor infiltration, and lichen- and cyanobacteria-dominated crusts reduce it (Maestre et al., 2002a). Crusts may also affect erosion and sediment transport by altering runoff, attaching soil particles together, and physically protecting the surface soil. Accordingly, disturbance of the biological crust may favour increased sediment yield (Belnap and Gillette, 1997).

Biological crusts and vascular plants interact in a number of ways. Vascular plants usually outcompete biological crusts, but they can also take advantage of the microenvironment created by the former. Environmental modifications promoted by plants, such as lower surface soil temperatures, reduced radiation, and decreased wind speed on the soil surface, promote changes in the composition, dominance and spatial pattern of the organisms forming these crusts (Eldridge, 1999; Maestre et al. 2002a, Maestre 2003). On the other hand, biological crusts can directly affect the establishment (Prasse and Bornkamm, 2000), survival (Eckert *et al.* 1986), nutrient status (Harper and Belnap, 2001), and water relations (DeFalco *et al.*, 2001) of vascular plants by altering soil surface topography, modifying water and nutrient fluxes, chelating metals, secreting growth promoting compounds, favouring mycorrhizal abundance or increasing pH (Belnap and Harper, 1995; Belnap et al., 2001; Li et al., 2002; Pendleton et al., 2003).

PLANT RESPONSE TO DISTURBANCES MODULATE PLANT EFFECTS ON SOILS

In environments that are prone to disturbances such as wildfire or grazing, resistance and resilience against disturbance are relevant traits affecting plant species effect on soils. As previously described, species that maintain a relatively humid microclimate under the canopy will affect soil processes directly. But they will also affect the probability of ignition and fire severity (Elvira and Lara, 1989; Wheelan, 1995), and thus attenuate the effects of wildfire, including changes in plant community composition. Persistance after disturbances that remove aboveground parts, such as wildfire, is increased by resprouting. This is a common trait in Mediterranean vegetation (Kummerov, 1981), that can be crucial to ensure fast soil protection after disturbance (Vallejo and Alloza, 1998). Resprouters are likely to affect soil properties in a

given location more intensely than species that depend on the seed bank to reestablish, despite that some obligate seeders may show some degree of persistance at small spatial scales (Moreno and Oechel, 1994).

Plant architecture may also affect stability against disturbances. It is well known that trees may increase erosion by raindrop splash as compared to shrubs, due to the formation of big throughfall drops falling from more than 8-9 m above the surface soil (Viles, 1990). On the other hand, vertical continuity of the canopy may favour the combustion of all vegetation strata. Accordingly, self-pruning may influence fire effects on soils. Vertical structure can also be relevant in shrubs. *Ulex parviflorus* is a spiny leafless leguminous shrub that colonizes abandoned agricultural fields in the western Mediterranean. Senescent stems form early and, without abscission, remain as standing necromass, increasing the fuel load. When the canopy is not closed, the surface layer next to this species, devoid of forest floor, may be colonized by grasses such as *Brachypodium retusum*. *Cistus albidus* is a coexisting shrub in these areas; its leaves twist during drought and may fall as summer progresses. They usually form a relatively thick forest floor devoid of herbaceous layer, with little foliar biomass concentrating in the top of the branches. Vertical continuity of the fuel load is higher in *Ulex parviflorus*, and this may be the cause for higher combusting power underneath this species (Fig. 10).

Forest floor accumulation affects ecosystem resilience in several ways. Forest floor protects the surface soil from rainfall splash, limiting the formation of physical crusts (Thomas, 1988), and reducing the risk of erosion. This is particularly relevant in areas where plant cover has been previously removed by wildfire or clearing. For example, low severity fires may not completely destroy the forest floor (Gillon et al., 1999). Furthermore, patches of relatively thick forest floor may withstand further rains, even high intensity rains, and thus protect the underlying soil from erosion (García-Cano, 1998). Considering all factors involved in the comparison between *Ulex parviflorus* and *Cistus albidus*, soil protection after wildfire is lower in the former because it accumulates less forest floor, it shows higher combustion of surface litter, and because ashes are readily washed away after fire.

COMMUNITY DYNAMICS DRIVEN BY CHANGES IN SOIL PROPERTIES

Plant-plant interactions, resulting from the net output of positive and negative interactions, are crucial for ecosystem composition, structure and dynamics in drylands (Whitford, 2002). Most studies on negative plant-plant relations in these areas have focused on trophic interactions, resource depletion and competition, and allelopathy (Scholes and Archer, 1997; Kröpfl et al., 2002; Whitford, 2002). Other negative interactions have comparatively
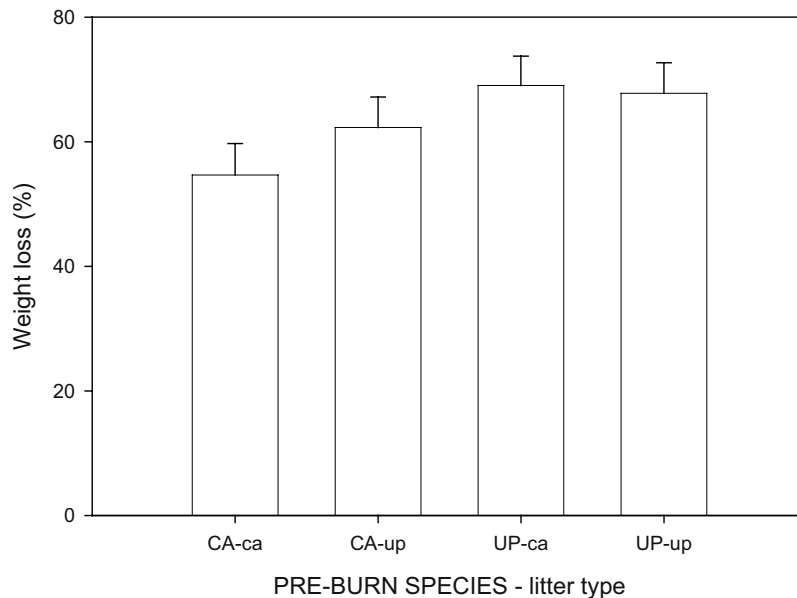
Figure 10. Weight loss through combustion of *Cistus albidus* (ca) and *Ulex parviflorus* (up) litter located underneath the canopy of individuals of *Cistus albidus* (CA) and *Ulex parviflorus* (UP) prior to an experimental fire. Bars represent means and standard errors of 30 individuals per species and litter type. Location was the only significant factor (F=88, p=0.01). Unpublished data from M.F. García-Cano.

received much less attention, probably due to the inherent experimental difficulty in differentiating trophic and non-trophic factors. Negative interactions can be the result of plant effects on soils, such as increased salinity, caliche formation, etc. (Cortina and Vallejo, 2004). On the other hand, positive interactions may result from increases in resource availability, amelioration of microclimate and soil conditions, increases in pollination and propagule dispersal rates, and defense against pathogens and herbivores (Callaway, 1995).

Positive and negative interactions are highly dynamic in drylands, and their balance may depend on site properties, climatic conditions, species identity and development stage (Pugnaire et al., 1996b; Maestre and Cortina, 2004c; Gómez-Aparicio et al., 2004). Bertness and Callaway (1995), and Callaway and Walker (1997) suggested that positive interactions should be more intense under high environmental stress or consumer pressure, and should depend on the size of the facilitator. Within individual shrub canopies, soil resources and microclimate show complex spatial patterns (Halvorson et al., 1994; Moro et al., 1997), and their interaction promote the emergence of different niches that increase in number and availability as shrubs increase in size (Pugnaire et al., 1996a). Increased habitat availability, together with the amelioration of the harsh climatic conditions, promote an increase in the

strength of facilitative interactions with the increase in the size of the facilitator canopy (Callaway and Walker, 1997). Other plant traits –e.g. related to the capacity to concentrate resources or to deter predators- can be considered to estimate the 'nursing' power of a given species. For example, the capacity to build up *nebkhas* or mounds of sediments underneath plant canopies has been associated with canopy compactness (density) and openess (a trait related to the presence of branches at the soil level), as well as to the degree of mycorrhization (Carrillo-García et al., 1999). According to these authors, dense canopies, whether open or closed, should be prone to *nebkha* formation, whereas only open ones would allow the presence of understorey plants. These observations are likely to depend on slope. Evidences on the superior capacity of shrubs to alter soil properties are, however, not conclusive (Mazzarino et al., 1996; Schlesinger et al., 1996). The capacity to accumulate litter may also be relevant to establish nurse-protegé interactions, although evidence on the net effect of litter on seedling emergence and establishment is contrasting (Fowler, 1988; Owens et al., 1995; Milton, 1995). Functional matrices, as those proposed by Ervine and Chapin (2003) to characterize plant capacity to alter soils, could incorporate other relevant traits to describe nursing capacity.

It has been suggested that nurse-protegé interactions are more common in arid and semiarid communities than in other environments (Flores and Jurado, 2003). According to these authors, the Fabaceae and Mimosaceae (which may be capable of fixing atmospheric N) are among the most common nurse families (20% and 7% of the reported species, respectively), suggesting that N inputs may be a major driver of positive interactions in drylands. The capacity to fix N of a potential nurse plant is not, however, solid evidence of nutritional facilitation (Barnes and Archer, 1999). Defense against grazing and trampling may also be important, as many nurse species have thorns (*Acacia* spp., *Prosopis* spp., Cactaceae, with 11%, 4% and 5% of the nurse species, respectively), and unpalatable leaves.

As previously mentioned, nurse-protegé relations are commonly the combination of independent factors, both positive and negative. However, very few studies have performed manipulative field experiments to dissect the net effects of a given plant-plant interaction into their underlying positive and negative effects (Holzapfel and Mahall, 1999; Maestre et al., 2003a). This knowledge is necessary to understand community dynamics and to develop sound management programs. We evaluated the effects of the perennial tussock grass *Stipa tenacissima* on the native late-successional shrub *Pistacia lentiscus* in semiarid Mediterranean steppes. *Stipa tenacissima* (alpha grass) is a tussock grass distributed in the western Mediterranean basin from arid to dry subhumid conditions (100-500 mm; White, 1983). It is one of the dominant species in steppes, that have been strongly affected by human activities carried out during centuries, such as wood harvesting and fiber cropping (Barber et al., 1997). After cessation of human activities, shrub patches that were once part of these steppes hardly recover because of past

management practices and inherent restrictions to plant growth. Shrub patches are, however, crucial for the composition, stability and function of semiarid steppes, despite their low contribution to the total plant cover (Maestre and Cortina, 2004a). In addition, the area covered by late-successional sprouting shrubs is the most influencing individual variable on perennial plant species richness in these steppes (Maestre, 2004).

Stipa tenacissima tussocks can retain runoff and sediments from upslope, a process that affects their own performance (Puigdefábregas et al., 1999). These tussocks also contribute to resource concentration, for example by favouring infiltration underneath the canopy (Cerdà, 1997). As a consequence of the changes in soil, microclimate and biological conditions, woody vegetation gets preferentially established close to alpha canopies (Maestre et al., 2001, 2003a), where they can withstand higher degrees of climatic stress (García-Fayos and Gasque, 2002; Maestre et al., 2003a). Previous studies had shown that *S. tenacissima* improved soil fertility (Puigdefábregas and Sánchez, 1996; Bochet et al. 1999; Aïdoud et al., 1999), but not nitrogen content (Bessah et al., 1999), reduced irradiation and soil temperature (Maestre et al., 2001), and received runoff water (Puigdefábregas et al., 1999) as compared to adjacent bare ground areas. We wanted to estimate the weight of each of these factors in increasing the survival and growth of introduced woody seedlings. We established a manipulative experiment in which we planted seedlings of a common shrub species, *Pistacia lentiscus*, upslope of alpha tussocks that were either undisturbed, herbicided or bended, or upslope of alpha tussocks where runoff had been excluded (Maestre et al., 2003a). We also planted *P. lentiscus* seedlings in undisturbed open areas. Finally, we carried out a laboratory experiment to test the effect of soil properties on *P. lentiscus* seedlings. In contrast to our expectations, runoff did not affect seedling survival. Seedlings planted in alpha soil showed a trend towards better growth and nutritional status, but the overall effect of soil type was not statistically significant. Finally, shadow was the most important factor affecting seedling establishment. So, in quantitative terms, the three factors ranked: shade>>soil fertility>runoff. No grazing on *Pistacia lentiscus* was detected.

We performed a similar experiment with *Pinus halepensis* in semiarid plantations of SE Spain. It is one of the most common tree species in the Mediterranean basin, indeed one of the few tree species that can thrive under semiarid conditions. *Pinus halepensis* forests have extended in the last decades due mainly to afforestation (Pausas et al., 2004). Under semiarid conditions, *P. halepensis* plantations show poor growth and cover, and spontaneous colonisation by sprouting shrubs is scarce (Maestre and Cortina, 2004b). Community composition (e.g. bird richness) has been related to the abundance and structure of shrubs in these forests (López and Moro, 1997). Pine canopies frequently show a relatively dense herbaceous understorey dominated by the perennial grass *Brachypodium retusum* (Bautista and Vallejo, 2002), whereas the establishment of woody seedlings in these

microsites seems to be impeded (Maestre et al., 2003b). We established a series of field and glasshouse experiments to evaluate the relative importance of direct interactions (soil fertility, allelochemicals, shadow and water availability, and competition) and indirect interactions (through pine effects on the herbaceous layer) (Maestre et al., 2004). We found that the direct effects of pine on introduced seedlings, including competition, were rather small. Thus, pine death by girdling, and the resulting decrease in belowground competition, while maintaining a protective shadow, did not affect seedling performance. In contrast, suppression of the herbaceous layer greatly increased seedling survival and growth.

In a review of 31 studies on facilitation we found that improved soil properties, including increased nutrient availability, was the most common mechanism of facilitation that was mentioned (25 out of 31 studies). Of these, 8 studies attributed the positive interactions to higher nitrogen availability. Half of the studies mentioned shade as an important driver of positive interactions. Finally, only three studies attributed facilitation to the presence of litter. However, most of the studies reviewed were observational. On the other hand, for logistic reasons manipulative experiments commonly use simplified designs, focusing on integrated factors (such as soil fertility or shading) rather than specific processes. So our knowledge on the relative importance of the various drivers of facilitation in drylands is still very poor, and does not allow for sound generalizations.

IMPLICATIONS FOR ECOSYSTEM MANAGEMENT AND RESTORATION

Being a priority in land management in a wide variety of biomes, the restoration of degraded ecosystems is especially important in drylands, as they are being degraded and desertified at a fast rate throughout the globe (Reynolds, 2001, Abahussain et al., 2002; Reynolds and Stafford-Smith, 2002). Degraded ecosystems in drylands are usually characterised by a reduced plant cover and impoverished plant species diversity (Jauffret and Lavorel, 2003; Maestre, 2004; Cortina et al., in press). Despite the specific objectives of their restoration that may differ depending on the degree of degradation, and on climatic, biotic and socio-economic constraints, restoration programs often aim to increase plant cover by directly introducing plant individuals, primarily woody species (Whisenant, 1999; Young, 2000; Vallejo et al., 2000, Cortina et al., in press). This management action is crucial to stop further degradation, to combat desertification and to foster the recovery of the structure, composition and function of degraded ecosystems in these areas (Castillo et al., 1997; Reynolds, 2001; Cortina and Vallejo, 2004). However, if the target area is extensively degraded, restoration efforts could be initiated with actions focusing on the recovery of ecosystem structure by increasing the number of patches and reducing the downslope distance

between them. This can be done by inserting brush piles parallel to land contours. Experiments conducted in Australia have shown the effectiveness of this technique in creating fertile patches and ultimately rehabilitating degraded landscapes (Ludwig and Tongway, 1996; Tongway and Ludwig, 1996). Such brush piles would reduce soil and nutrient losses, and would act as filters rather than barriers. They would also provide suitable microsites for enhancing the establishment, growth and survival of perennial plants in the short term. Once this intervention has reduced degradation, the next step to restore these systems should be the introduction of seedlings of native woody species.

If the target area holds some plant cover, restoration efforts can take advantage of facilitative interactions among plants. Positive interactions, and among them, those mediated by changes in soil properties, can be crucial to maintain the integrity of dryland ecosystems. Accordingly, they can be very helpful if not essential for reassembling pieces of degraded ecosystems. In the previous section we have seen that there are numerous evidences of facilitative interactions in drylands. These interactions can be used to promote the establishment of species of interest, and this has been increasingly recommended as a restoration technique (Maestre et al., 2001; Castro et al., 2002; Gómez-Aparicio et al., 2004). On the other hand, a thorough understanding of the mechanistic basis of positive interactions may allow the identification of the main drivers of facilitation, and thus their use in restoration. For example, shadow may be crucial in the first stages of seedling establishment. Nurse plants may not be always available, or their use may be restricted for logistic or economic reasons. In this case, the use of ecotechnological tools to reduce incoming radiation such as treeshelters, can be a suitable alternative to improve seedling performance (Cortina et al., in press). This technique is also convenient when consumer pressure is high. Amelioration of soil fertility can be easily achieved by using various types of soil amendments. Residues with high SOM and nutrient content, such as composted domestic refuses and sewage sludge are becoming increasingly available (Valdecantos et al., 2002; Fuentes et al., 2002a, 2002b; Valdecantos et al., in press). As the quality of these products improves, they will be increasingly used for the restoration of areas where soil fertility hampers succession. Nowadays, there is a vast array of techniques used in ecosystem restoration, deriving from mechanisms like those previously described (Table 2). Further knowledge on this type of interactions will help to develop new ecotechnology in this area, and to improve the success of restoration programmes.

Table 2. Some techniques used for the restoration of degraded semiarid ecosystems and the ecosystem component and main processes that are affected. From Tongway et al. (2004).

Technique	Ecosystem component	Process	References
Branches, mulch, etc.	Sinks	Sediment, runoff and seed capture	1,2
Perches	Birds rest	Propagule concentration, eventually water and nutrients	3,4
Organic amendments and fertilisation	Islands of fertility	Local soil improvement	5,6
Stones around introduced plants	Sinks	Resource retention including moisture	-
Stone pavements	Patches with low infiltration	Runoff	7,8,9
Treeshelters	Nurse plants	Protection against incomming radiation and herbivory	10,11
Field and nursery mycrorrhizae and rhizoflora inoculation	Exo and endosimbiotic microflora	Increase in resource availability, protection against pathogens and stress	12,13,14
Site preparation (microcatchments, terracing, etc.)	Sinks	Resource capture, mainly water. Increase in available soil	15,16
Cyanobacteria inoculation	Biological crusts	Soil protection, runoff generation	17,18
Nurse species plantation	Nurse plants	Processes associated with facilitation	19

[1]Ludwig and Tongway (1996), [2]Tongway and Ludwig (1996), [3]Bonet (2004), [4]Wunderlee (1997), [5]Cortina et al. (2001), [6]Valdecantos et al. (2002), [7]E. De Simón, pers. com., [8]Hillel (1991), [9]Lavee et al. (1997), [10]Vallejo et al. (2003), [11]Bellot et al. (2002), [12]Azcón and Barea (1997), [13]Caravaca et al. (2003), [14]Maestre et al. (2002b), [15]Whisenant et al. (1995), [16]Boeken and Shachak (1994), [17]Buttars et al. (1998), [18]Belnap (1993), [19]Vilagrosa et al. (1997).

CONCLUSIONS

Throughout the 20th century drylands have been the focus of an impressive amount of research. In some cases, findings have supported traditional knowledge and practices. But very often research has provided entirely new perspectives on dryland functioning. Still, it is somewhat discouraging that some of the questions that we are trying to answer, such as those on the rooting depth of some species, or on the effects of site preparation and the use of organic amendments, were already posed more than 2,000 years ago (e.g. Theophrastus, *Peri Phyton Historia*). This delay may partly result from the vast diversity of interactions that are involved. In this review, we have seen that interactions are strongly dependent on plant identity, or as a first approach, to plant functional types (Eviner and Chapin, 2003). We have also seen that plant-plant interactions may change depending

on site properties, climatic conditions, or plant age. However, we know very little on the importance of such interactions on community dynamics and large-scale processes. In most cases, we just guess they are relevant. For example, we still don't know how important for succession is disturbance that may be followed by a short-term unfavourable climatic period. Must we asume that the interaction observed in a particular short-term study will prevail in the long-term, and will control community organization? When will facilitative interactions turn into competitive – or positive net balances turn into negative- as plants grow? It is clear that more research is needed in this area; particularly manipulative experiments, long-term studies and modelling.

This review has also shown that we can successfully estimate plant effects on background soil fertility. But as our knowledge on some areas of soil science such as soil biochemistry, soil microbiology and soil fauna increases, we realize that some plant-plant interactions that were previously attributed to other factors are actually occurring in the soil arena. This information is needed to evaluate the relative importance of soil processes on plant-plant interactions and community dynamics.

Drylands are threatened by a combination of natural factors and human activities (Reynolds and Stafford Smith, 2002). Further knowledge on the effects of plants on soils, and on the importance of such changes on long-term ecosystem dynamics will help to improve dryland management and sustainability.

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