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Evidence of a threshold in soil erodibility generating differences in vegetation development and resilience between two semiarid grasslands

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The typical patchy structure of dryland vegetation is a result of soil–plant feedbacks occurring in water-limited areas. The resilience of dryland ecosystems depends largely on the persistence of fertility islands associated with vegetated patches, which determines the efficiency of the vegetation regarding recolonising the gaps that result from disturbances. In this study, we investigated the mechanisms underlying soil–plant interactions throughout the process of the growth and senescence of alpha grass (*Macrochloa tenacissima*) and the subsequent disintegration of islands of fertility and microtopography formed during the process at two nearby alpha grass communities exhibiting different degrees of development. The life cycle of alpha grass and the rise and disintegration of the underlying microrelief were accompanied by feedback changes in the content of soil C fractions presenting different times of cycling and incorporation to the soil, the collection of particles from splash erosion, redistribution phenomena related to particles of different sizes, and erosion of the most easily erodible materials. Despite their ecological and geographical proximity, the study sites differ with respect to the persistence, after plant death, of fertility islands, which almost disappear in one case, while they remain in the other, constituting a resource for the growth of new plants and resulting in greater development and resilience in the community. A subtle erodibility threshold emerges as a cause of the considerable differences in vegetation between the two sites.

1. Introduction

The possibility of minimising the effects of global change through land management depends on our capacity to identify different states of degradation or development and to determine the thresholds of the main associated processes. Ecosystem dynamics are complex processes including many variables, which are almost always strongly related to each other, and exhibiting thresholds and nonlinearities (Groffman et al., 2006). Drylands are particularly vulnerable to global change because many of the species inhabiting these areas are near their tolerance limits (Watson et al., 1998). Because of this, drylands are appropriate sites for studying ecological thresholds, resistance, and resilience, as small changes in land use or climate can produce relatively large effects (Stafford Smith et al., 2009).

The interaction between plants and soil is crucial for ecosystem functioning. Vegetation and soils develop together, generally through a typical feedback process (Ehrenfeld et al., 2005). Variations in climate and biogeochemical cycles affect the mechanisms underlying soil–plant interactions, which in turn may lead to large-scale feedbacks that affect the magnitude of change itself (Ehrenfeld et al., 2005). In drylands, the mechanisms underlying soil–plant interactions are mainly based on the enhanced infiltration rates of soils under plants, which act as sinks for runoff generated in bare areas, and on the accumulation of organic matter, especially its most labile fractions, which fuel microbial activity and indirectly increase the formation of aggregates and the bioavailability of nutrients (Ehrenfeld et al., 2005; Schlesinger and Pilmanis, 1998). Because both enhanced infiltration and organic matter accumulation promote plant growth and are therefore feedback mechanisms, they result in a mosaic-like distribution of vegetated patches (which become so-called islands of fertility) and unvegetated interspaces. In some cases, such mosaics are associated with a characteristic microtopography of mounds occurring under plants. These mounds result from the interception by plants of runoff-transported sediments (Sánchez and Puigdefábregas, 1994), air-transported dust (Barth and Klemmedson, 1978) and soil particles detached by splash from bare areas (Parsons et al., 1992), the genesis of soil pedestals due to the erosion of the

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surrounding soil (Martínez-Turanzas et al., 1997; Parsons et al., 1992), and increased porosity and decreased soil bulk density due to bioturbation by roots and burrowing (Biot, 1990). After plant death, in the absence of positive feedbacks, it has been reported that islands of fertility diminish (Butterfield and Briggs, 2009; Tiedemann and Klemmedson, 1986).

Information concerning the feedback mechanisms that regulate the genesis and the removal or preservation of fertility islands is of enormous interest related to the management and conservation of drylands. The resilience of these ecosystems depends on the efficiency with which species recolonise gaps resulting from disturbance (Schlesinger and Pilmanis, 1998; Vitousek and Reiners, 1975), and fertility islands are more favourable sites for the establishment of new plant individuals (Aguilera and Lauenroth, 1993). Some studies have addressed the persistence or disintegration of fertility islands by analysing the effects of experimental plant removal (Schlesinger and Pilmanis, 1998). Less research has been aimed at the investigation of declines of fertility islands following natural plant mortality and decay, mainly due to the long time scales required to measure these effects. The substitution of space for time, e.g., through sequences of microsites representing state transitions, as used by Butterfield and Briggs (2009), seems feasible for this purpose.

Alpha grass (*Macrochloa tenacissima* (L.) Kunth = *Stipa tenacissima* L.) is a perennial grass native to the Mediterranean area that is abundant in southeast Spain. Alpha grasslands typically exhibit a mosaic pattern comprised of bare soil patches alternating with patches of tussock grass. Under the tussocks, mounds develop which are smaller and approximately symmetric in flat and slightly sloping areas (<30%), and become larger, accumulate material upslope, and take on the shape of terraces or bands on steep terrain (Bochet et al., 2000; Sánchez and Puigdefábregas, 1994). Few studies have investigated the dynamics over time of fertility islands in alpha grasslands. Lesschen et al. (2008) suggested that a very slow genesis of soil spatial heterogeneity, on the order of at least 40 years, occurs during tussock development, and Goberna et al. (2007) pointed to the death of tussocks and their conversion to bare areas as a mechanism that contributes to homogenising the content of soil organic matter.

In this study, we focused on two experimental sites in patchy-vegetated semiarid alpha grasslands in southeast Spain. Both sites are highly similar in their location, climate, soils, land use, and vegetation-type. However, there are marked differences in terms of vegetation cover and composition, and soil quality and depth. Rey et al. (2011) suggested that these sites are actually representative of different degradation levels of the same ecosystem. The present study was aimed at determining why the two sites exhibit different vegetation types and soils and at inferring long-term progressive or regressive trends in the vegetation and soil evolution. Our hypothesis was that the differences observed between the two sites may be due to inherent differences in the processes of vegetation and soil development and disintegration.

On this basis, we performed a preliminary survey seeking evidence of recent land use changes that could explain the differences between the study sites. Then, we analysed functionally important properties of the soils during the cycle of formation and disintegration of the tussocks of alpha grass (*M. tenacissima*, the dominant plant species) at both sites. To this end, we employed a space-for-time sampling strategy using six different types of microsites to represent the main stages involved in the plant–soil feedback processes occurring in the investigated ecosystem, from the initial genesis of tussocks as individual plants growing in bare areas to the disintegration of the mounds formed under the tussocks.

2. Materials and methods

2.1. Study area

The study was conducted at two experimental sites, Amoladeras (AM) and Balsa Blanca (BB), both of which are located in the Cabo de Gata Natural Park in southeast Almeria (Spain). The climate is semiarid Mediterranean, very similar in both areas. The mean annual temperatures oscillate around 18–19 °C. The mean annual rainfall is approximately 220 mm y^{-1}, with large inter- (greater than 30%) and intra-annual variations and 9–12 months in which precipitation is not sufficient to compensate for potential evapotranspiration. The relative humidity can be high in all months due to the proximity to the sea, and dew events are frequent. In both cases, the slope is gentle (3–10%). The soils, classified as Lithic Leptosols (Calcaric) at AM and Mollic Lithic Leptosols (Calcaric) at BB, are shallow (almost always <25 cm at BB and often <12 cm at AM) and stony, having developed over strongly calcareous alluvial fans (Rey et al., 2011).

The vegetation of both sites is dominated by *M. tenacissima*, but BB has higher cover than AM. At BB, the grassland has frequent individuals of certain shrub species, such as *Phlomis purpurea* and *Ulex parviflorus*, as well as sparse individuals of species related to the climax vegetation of the area, including *Chamaerops humilis* L., *Olea europaea* L. var. *sylvestris* Brot., *Pistacia lentiscus* L., *Rhamnus lycioides* L., and *Quercus coccifera* L. Plant species typical of disturbed sites or opportunistic species are infrequent. In contrast, the vegetation at AM frequently includes typical semiarid dwarf shrubs (*Hammada articulata*, *Helianthemum almeriense*, *Thymus hyemalis*, *Sideritis pusilla*, and others) and species characteristic of disturbed sites (*Artemisia barrelieri*, *Frankenia corymbosa*, and *Asphodelus* spp.) as well as seasonal annual plants (*Stipa capensis*, *Bromus rubens*, *Aizoon hispanicus*, *Asphodelus tenuifolius*, and others), whereas very few species characteristic of the climax vegetation remain (*C. humilis* and *Whitania frutescens*).

M. tenacissima gives rise in both sites to mounds about 10 cm height, which is less than the height of 20 cm reported by Bochet et al. (2000). The diameters of the mounds are typically between 40 and 80 cm in AM and between 50 and 130 cm in BB, whereas the bare areas have diameters ranging from 1 to 4 m in AM and from 0.5 to 2 m in BB.

2.2. Evaluation of the temporal evolution of the vegetation

The changes that may have occurred in the vegetation over the past five decades were studied by analysing aerial photographs collected at both experimental sites in 1956 and 2006. The images from 1956 are panchromatic digital ortho-photographs at a scale of 1:10,000 with a 1 m resolution obtained from the Spanish national photogrammetric black and white flight performed in 1956–1957 by Spanish-USA Air Forces. The images from 2006 are digital RGB, infrared, and panchromatic, 1:10,000 scale, 0.5 m resolution aerial photographs from the Consejería de Medio Ambiente de la Junta de Andalucia (Environmental Department of the Andalusian Autonomous Government).

We compared the total vegetation cover and the general appearance of the two sites over time. For this purpose, we analysed the images using the free software program CobCal (version 1.0, Martín Ferrari, Estación Experimental Agropecuaria INTA Concepción del Uruguay, Argentina), which allows automatic calculation of the plant cover of selected areas. Twenty-four circular areas with a diameter of 100 m were randomly selected in each image to sample the plant cover.

2.3. Soil sampling and analysis

Six types of microsites were defined, representing the complete cycle of the formation and disintegration of alpha grass tussocks: (i) inter-plant spaces (IS) without vascular vegetation, except for some occasional annual herbs; (ii) isolated young plants (YP) associated with little or no microtopographic relief; (iii) fully developed adult plants (AP) showing no signs of decline; (iv) senescent plants (SP) that were conspicuously devitalised associated with an accumulation of dead leaves and stems and presence of gaps; (v) intact, well-preserved mounds (PM) with or without plant residues; and (vi) residual, eroded mounds (EM) being actively dismantled by erosion. Four microsites of each of these types were studied at both experimental sites. Soil core samples were collected at each microsite in points with a northern exposure that were approximately equidistant from the centre and the edge of the unit, at 0–5 cm depths. Two samplings were performed: the first took place in February, during the humid season, and the second occurred in August, coinciding with the summer drought period ($6 \times 4 \times 2 \times 2 = 96$ samples in total). Soil properties that were expected to show seasonal variations (water content, labile organic fractions, electric conductivity, and pH) were studied in both winter and summer. The other soil properties studied were determined only in winter.

Our soil analysis focused on the soil organic matter and physical properties (structure and particle size distribution) that are particularly relevant to soil–plant feedbacks (Ehrenfeld et al., 2005) and that determine soil erodibility (Wischmeier et al., 1971). In particular, we analysed various fractions of soil organic carbon (SOC) that are known to have different origins and turnover times in the soil (Von Lützow et al., 2007) and contribute differently to the development of soil structure (Tisdall and Oades, 1982). The study of these parameters during the formation and disintegration of alpha grass tussocks should inform us regarding the rates of accumulation or loss of organic matter from different sources and the influence of these parameters on other functionally important soil properties.

We determined the following soil properties: water content, bulk density, and the contents of coarse fragments, clay, silt, and fine and coarse sand (Gee and Or, 2002); the water-stable microaggregation indexes CDR (clay-dispersion ratio) and ASC (aggregated silt and clay) (Igwe et al., 1999); the macroaggregate stability index CND (counting the number of drops) of dry and moist aggregates (Imeson and Vis, 1984); the pH and electric conductivity; and the contents of total organic C (TOC) (Walkley and Black, 1934), water-soluble C (WSC), hot-water extractable C (HWC) and polysaccharides (PSs) (Ghani et al., 2003), microbial biomass C (MBC) (Vance et al., 1987), particulate organic C (POC) (Cambardella and Elliott, 1992), and NaOCl-resistant C (Zimmermann et al., 2007). Further explanation of the methods used in the soil analyses is provided in Appendix 1.

WSC, HWC, MBC, and POC are considered labile SOC forms and show typical turnover periods of a few weeks, several months, a few years, or several years, respectively. In contrast, NaOCl-resistant C is representative of the recalcitrant pool of SOC, with a turnover time of hundreds to thousands of years (Von Lützow et al., 2007). To estimate the kinetic pools of SOC, total labile SOC was calculated using the following expression (Eq. (1)):

$$\text{Labile SOC} = \text{WSC} + \text{HWC} + \text{POC} \tag{1}$$

which is based on the formula suggested by García et al. (2005) (Eq. (2)):

$$\text{Labile SOC} = \text{WSC} + \text{MBC} + \text{LF-OC} \tag{2}$$

assuming that HWC includes MBC and the non-complexed organic macromolecules (light fraction organic C = LF-OC) not included in POC due to having a diameter below 50 μm. Slow (intermediate) SOC was estimated as the difference between the TOC and the sum of labile and recalcitrant SOC (Eq. (3)):

$$\text{Slow SOC} = \text{TOC} - (\text{Labile SOC} + \text{NaOCl-resistant C}) \tag{3}$$

Following the estimation of the kinetic pools, we calculated their relative contributions to the SOC by dividing their levels by that of the TOC.

2.4. Statistical analyses

Plant cover values determined from aerial photographs were tested for differences between sites and years using a multi-factor analysis of variance (ANOVA). The results of the soil analyses were subjected to an ANOVA with site and microsite as between-subjects factors and season as a within-subjects factor. Some variables were transformed to fulfil the requirements of normality and homoscedasticity for the ANOVA. Pair-wise post-hoc comparisons were performed using least significant differences (LSD) tests. The Pearson correlation was used to assess the relationships between the soil aggregation measurements and various soil features. All of these tests were conducted using SPSS for Windows (v.17, SPSS Inc., Chicago IL, USA). We also performed a principal component analysis (PCA) to explore the joint variation of the soil features and to facilitate the interpretation of the relationships between such variation and microsites or development stages. PCA was performed using Canoco for Windows (version 4.5, Centre for Biometry, Wageningen, The Netherlands).

3. Results

3.1. Plant covers evolution over time

According to the results of the analysis of the aerial photographs, the plant cover was much greater at BB (mean ± SE: 56.8 ± 2.1% in 1956 and 55.2 ± 1.0% in 2006) than at AM (30.7 ± 1.4% in 1956 and 29.6 ± 1.6% in 2006), but the differences between 1956 and 2006 were negligible. Additionally, the general appearance of each site was quite similar in both years, and some large shrubs or groups of shrubs could be recognised as persisting at apparently the same points after the elapsed time period.

3.2. Effects of site, microsite, and season on soil properties

The statistical results of the ANOVA examining differences in the studied soil properties among sites, microsites, seasons, and moisture conditions are shown in Appendix 2.

The soil water content was significantly higher under patches of alpha grass compared to bare soil at both sites, even in summer, when the humidity of all the microsites was very low (Fig. 1a). The soil bulk density decreased during plant growth and increased after the death of the plants, although it decreased slightly again when the degradation of the mound began (Fig. 1b), probably as a result of loss of the surface crust through erosion. This cyclical variation of the bulk density was significantly more pronounced at AM than at BB. Similarly, the content of coarse fragments decreased during tussock growth, and showed some trend to increase again after plant death (Fig. 1c).

Particle size analysis showed significant differences between the two study sites (Fig. 1d–f). The contents of silt and coarse sand were higher at AM, where the soil texture was sandy-loam, sandy-clay-loam, or loam. Fine sand was more abundant at BB, where all of the soils exhibited a sandy-loam texture. Tussock growth coincided with an increase in silt content and decreases of coarse sand and

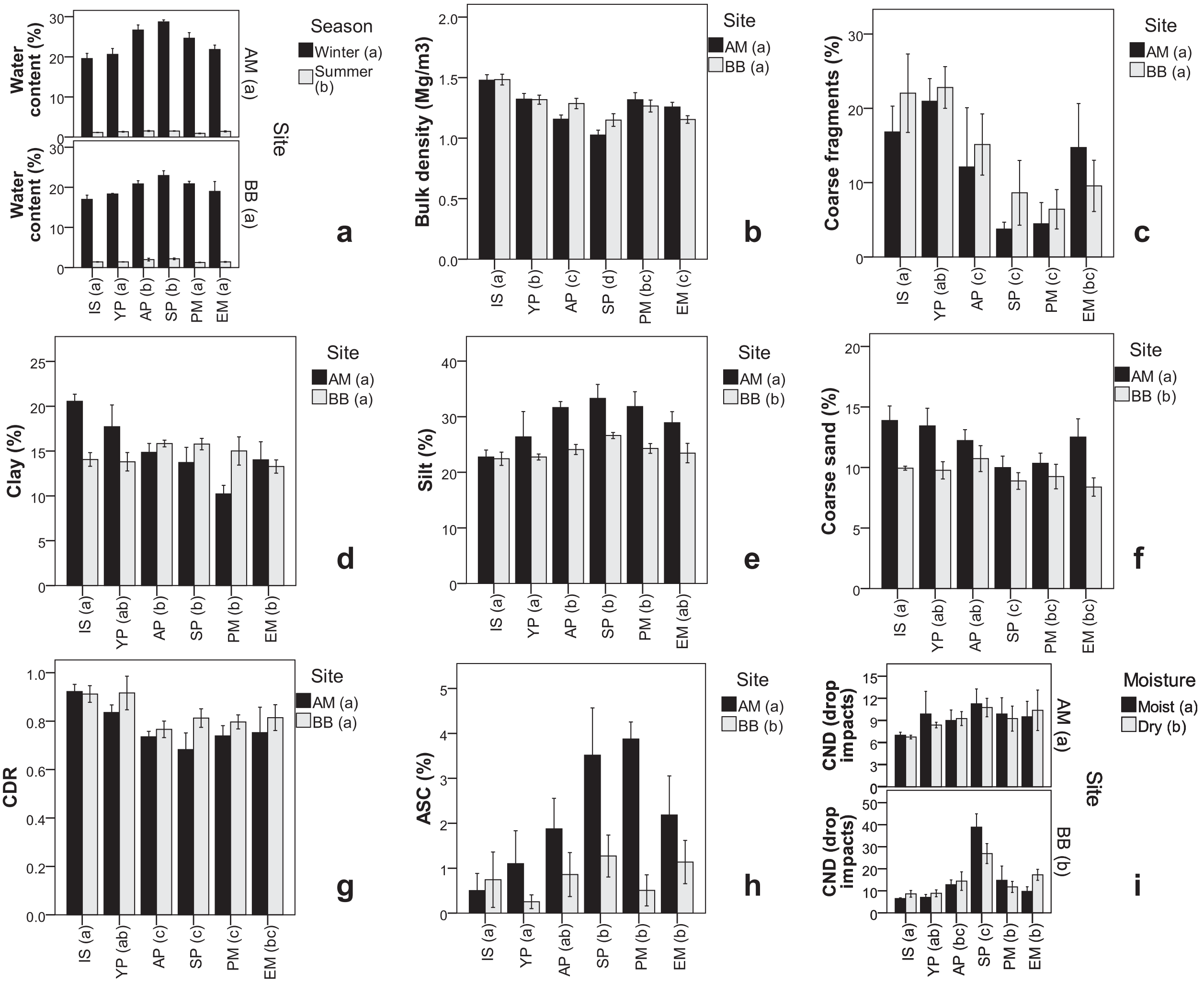

Fig. 1. Investigated soil physical properties (±SE) in relation to the site, the microsite, the season, and the moisture conditions. (a) Water content. (b) Bulk density. (c) Coarse fragments. (d) Clay. (e) Silt. (f) Coarse sand. (g) Clay-dispersion ratio (CRD). (h) Aggregated silt and clay (ASC). (i) Water drop test (CND). AM = Amoladeras, BB = Balsa Blanca, IS = inter-plant spaces, YP = young plants, AP = adult plants, SP = senescent plants, PM = well-preserved mounds (PM), EM = eroded mounds. Significant differences ($P \leq 0.05$) between the sites, the microsites, the seasons, or the moisture conditions are denoted by different letters following the labels in the corresponding axes, legends, and panels.

fragments. This variation was more pronounced at AM, where mound formation also coincided with a decrease in clay. After plant death and the subsequent disappearance of a mound, all of the cited components reverted, except for coarse sand at BB, which remained unchanged.

Soil microaggregation increased markedly as alpha grasses and the underlying mounds developed and decreased when the plants died and the mounds were eroded (Fig. 1g and h). Although this trend was evident in both of the indices employed in this study, it was much more pronounced in the ASC index. The stability of macroaggregates (Fig. 1i) also increased significantly during the formation and disintegration of tussocks and was particularly high under senescent alpha grasses. The water state (dry/moist) of the soil aggregates affected their stability, with moist aggregates being more stable than air-dried aggregates. The soils at BB showed higher macroaggregate stability, whereas the soils of AM were significantly richer in microaggregates.

Soil electric conductivity was low at the two sites, with the detected levels being well below those affecting the growth of nonhalophytes, though they were significantly higher at AM than at BB, probably due to the closer proximity of AM to the coast and greater exposure to saline spray of marine origin. Soil pH decreased (Fig. 2a) with the growth of plants and tended to increase again with the disintegration of the mound. Additionally, the soil pH was significantly higher in summer than in winter and showed little difference between the locations.

All of the SOC fractions studied exhibited similar behaviour in relation to the type of microsite: they progressively increased as a tussock grew, presented their highest values under senescent alpha grasses, and decreased as the mound dissolved (Fig. 2b–h). The SOC fractions showing the most pronounced variations between microsites were the TOC, the HWC, and PSs. The content of NaOCl-resistant C showed different patterns at the two sites: at AM, it increased until plant senescence occurred and then decreased, whereas at BB, it increased and then remained relatively stable. According to the ANOVA results, only the TOC and the NaOCl-resistant C were significantly higher at BB than at AM. However, all of the SOC fractions showed higher mean values at BB than at AM at microsites representing the initial (IS) and final (EM) stages of the process. Thus, although there was little difference detected in SOC contents in terms of mean values, remarkable differences existed in the range of variation, which was significantly greater at AM than at BB. Moreover, the SOC values presented by the mounds (PM, EM) at AM tended to approach the values of inter-plant spaces,

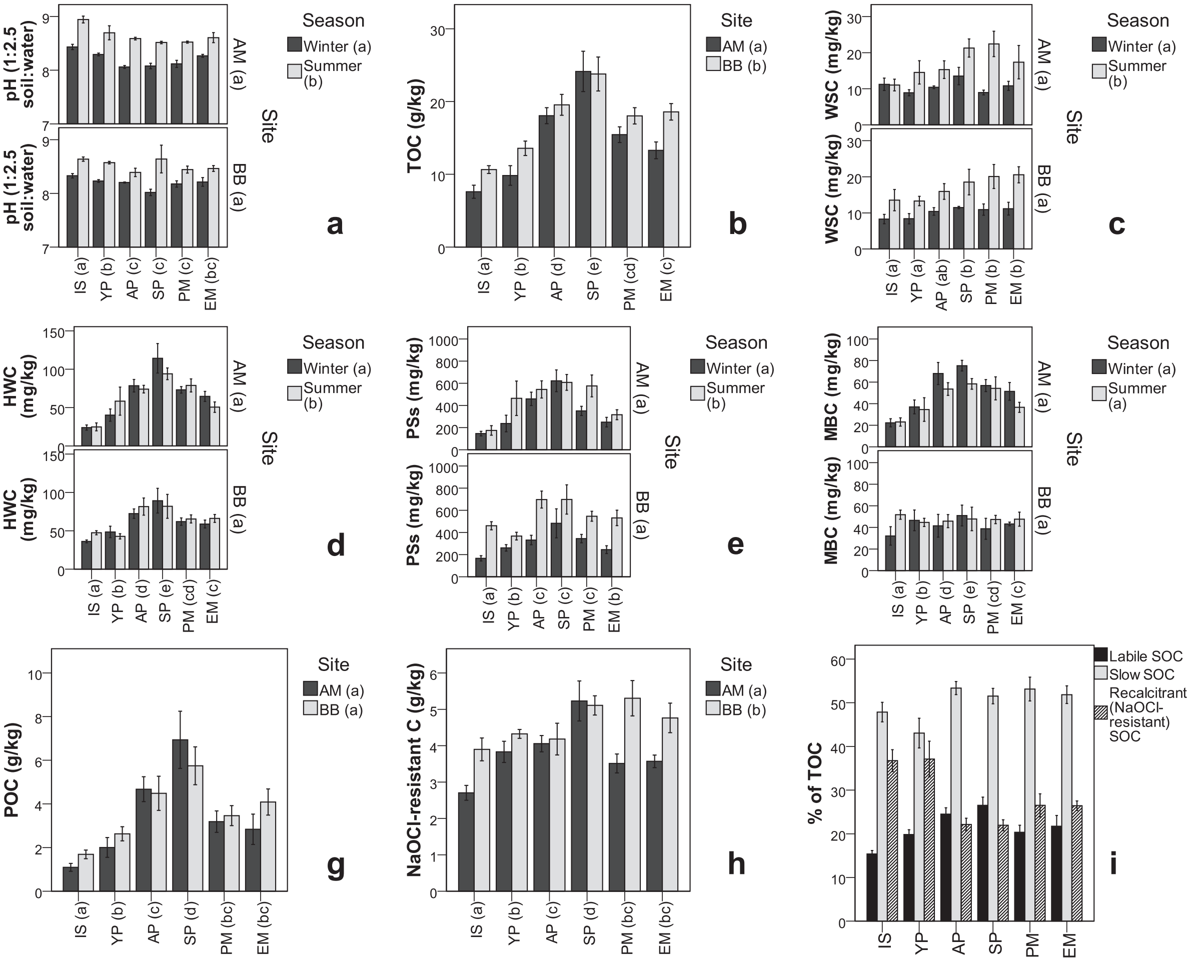

Fig. 2. Investigated soil chemical properties (±SE) in relation to the sites, the microsites, and the seasons. (a) pH. (b) Total organic C (TOC). (c) Water-soluble C (WSC). (d) Hot-water extractable C (HWC). (e) Polysaccharides (PSs). (f) Microbial biomass C (MBC). (g) Particulate organic C (POC). (h) NaOCl-resistant C. (i) Contribution of recalcitrant, slow and labile C pools to TOC. AM = Amoladeras, BB = Balsa Blanca, IS = inter-plant spaces, YP = young plants, AP = adult plants, SP = senescent plants, PM = well-preserved mounds (PM), EM = eroded mounds. Significant differences ($P \le 0.05$) between the sites, the microsites, or the seasons are denoted by different letters following the labels in the axes, legend, and panels.

returning to the starting point. However, at BB, there was little change (WSC, WSC, PSs, MBC) or even a slight increase (TOC, POC) in most SOC fractions in eroded mounds compared to preserved ones, which suggests that the mounds remain uncolonised for a shorter period of time at BB than at AM.

The contents of the WSC (Fig. 2c) and PSs (Fig. 2e) were significantly higher in summer than in winter. The HWC (Fig. 2d) and the MBC (Fig. 2f) did not show seasonal differences, but in the case of MBC, this was due to opposite trends at the two sites, with higher values being observed in winter at AM and in summer at BB. We observed that the increase of PSs in summer was significantly more intense at BB, coinciding with the higher content of MBC found at this site.

3.3. Relationships of particle size and SOC fractions with soil erodibility

Principal component analysis (Fig. 3) allowed the visualisation of the covariation of particle size, SOC fractions, and soil aggregation. The first PCA axis represented more than 40% of the total variance and was associated with the formation and disintegration of tussocks and mounds. The microsites were ordered along this axis following the progressive sequence IS < YP < EM = PM = AP < SP ($F_{g.l.=5} = 25.6$, $P = 0.000$, ANOVA/LSD) as bulk density, pH, clay dispersion, and coarse fragments decreased, and SOC content and the stability of macro- and microaggregates increased. The second axis discriminated the samples from the two sites ($F_{g.l.=1} = 63.0$, $P = 0.000$), mainly due to the higher electric conductivity and contents of coarse sand and clay at AM and the higher contents of fine sand and recalcitrant SOC at BB.

As can be seen in Table 1, the ASC and the CDR were significantly correlated with each other, but not with the CND. The ASC was correlated with the fractions of clay, silt, and sand, although silt appeared to play a greater role in the formation of microaggregates. The ASC and the CDR presented a good correlation with different fractions of SOC, especially with the HWC. The CND showed the highest correlation with slow SOC and was the only index that showed correlations with recalcitrant SOC.

4. Discussion

4.1. Soil–plant feedback changes

The development and degeneration of tussocks of *M. tenacissima* are associated with complex soil processes involving the selective accumulation and loss of soil particles of different sizes (Fig. 1c–f)

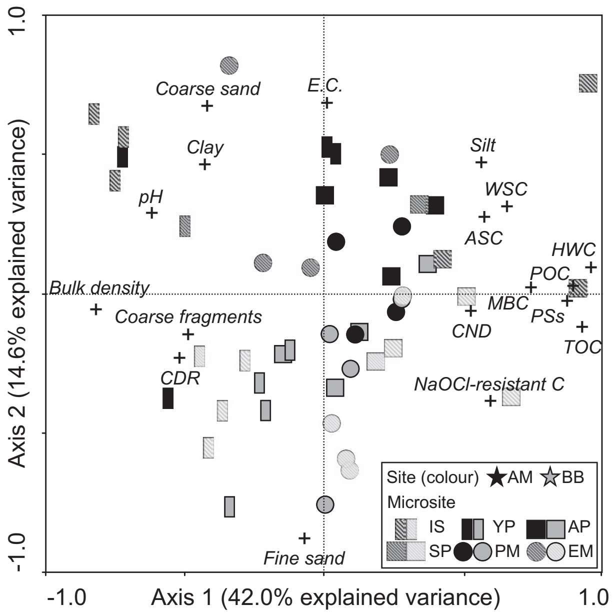

Fig. 3. Principal component analysis (PCA) of the investigated soil properties. Crosses represent soil properties. Other symbols refer to the distinct stages during tussock growth, with the colour representing the study site. AM = Amoladeras, BB = Balsa Blanca, IS = inter-plant spaces, YP = young plants, AP = adult plants, SP = senescent plants, PM = well-preserved mounds (PM), EM = eroded mounds, CDR = clay-dispersion ratio, ASC = aggregated silt and clay, CND = water drop test, TOC = total organic carbon, WSC = water-soluble carbon, HWC = hot-water extractable carbon, PSs = polysaccharides, MBC = microbial biomass carbon, POC = particulate organic carbon.

and SOC fractions (Fig. 2b–i) with different turnover rates, which in turn, give rise to differing soil erodibility, as seen with respect to aggregate stability (Fig. 1i). These processes are positively fed-back during plant growth because they enhance the growth itself, and tend to revert when the plant dies and the feedback ceases.

The formation of a tussock coincided with a build-up of labile, slow, and recalcitrant SOC. However, the three kinetic SOC pools did not accumulate at the same rate (Fig. 2i). The labile SOC accumulated rapidly, showing a progressively increasing contribution to the TOC. This increase was largely due to the enrichment of POC, which was the major component of the labile SOC, indicating an increasing accumulation of plant material with little processing. Recalcitrant SOC accumulated slowly, with a sharp decrease in its contribution to the TOC, while slow SOC tended to exhibit continued importance. After plant death, the labile fraction responded more quickly again with a pronounced decrease, while recalcitrant SOC increased only very slowly, and slow SOC remained constant. This behaviour coincides with that described by Kelly and Burke (1997) in the steppe grasslands of North America, where a rapid loss of labile SOC following the death of plants was not observed to be accompanied by an analogous loss of the other fractions of SOC.

Table 1
Correlation (Pearson's r) of soil aggregation indexes with particle size and SOC fractions. ASC = aggregated silt and clay, CDR = clay-dispersion ratio, CND = water drop test, EC = electric conductivity, HWC = hot-water extractable carbon, MBC = microbial biomass carbon, POC = particulate organic carbon, PSs = polysaccharides, SOC = soil organic carbon, TOC = total organic carbon, WSC = water-soluble carbon. $^*P \leq 0.05$, $^{**}P \leq 0.01$.

	CDR	ASC	CND
CDR	1	−0.493**	−0.079
ASC	−0.493**	1	0.094
CND	−0.079	0.094	1
Clay	0.173	0.393**	0.014
Silt	−0.195	0.594**	0.117
Fine sand	0.132	−0.256	0.000
Coarse sand	−0.167	−0.067	−0.264
Sand	0.074	0.305*	−0.113
TOC	0.487**	0.407**	0.636**
POC	0.447**	0.426**	0.507**
WSC	−0.247	0.460**	0.305**
HWC	0.560**	0.533**	0.419**
PSs	0.474**	0.393**	0.416**
MBC	0.354*	0.501**	0.115
Recalcitrant (NaOCl-resistant-) SOC	−0.123	0.152	0.420**
Slow SOC	0.514**	0.372*	0.660**
Labile SOC	0.465**	0.447**	0.513**

We found seasonal patterns for certain labile SOC fractions: WSC (Fig. 2c) and PSs (Fig. 2e), which showed their highest values in summer. An increase of PSs in summer was reported by Steinberger et al. (1999) in a semiarid region of Israel and was attributed to oscillations in the amount and activity of microbial biomass. A summer increase in the WSC agrees with what has been observed in other semi-arid soils of southern Spain (Bastida et al., 2006; Goberna et al., 2007). Because the alpha grass root system is the main source of WSC in these ecosystems (García et al., 2005), it is likely that the increase in WSC resulted from its accumulation during the season of maximum plant activity (spring), as suggested Bastida et al. (2006). If this is the case, the WSC exhibited a residence time of at least several months in our study, which is considerably longer than the turnover time of a few weeks assumed initially.

The accumulation of SOC and bioturbation by roots and soil fauna during tussock development are probably responsible for decreasing soil bulk density (Fig. 1b) and increasing infiltration rates. Our results point to decreased bulk density as an important mechanism for the formation of mounds under alpha grasses. This process reverted after plant death, which is consistent to the tendency for increased bulk density that was observed by Tiedemann and Klemmedson (1986) in the decades following experimental shrub removal. Bioturbation is consistent with the observed variation in the content of coarse fragments (Fig. 1c), which could gradually shift to the periphery of the tussock due to the swelling and genesis of a protruding microrelief.

We found differences in microsite humidity levels (Fig. 1a) in agreement with those observed by Puigdefábregas et al. (1996), who reported higher moisture under patches of alpha grass than under bare soil, whereas Goberna et al. (2007) did not find any differences, and Maestre et al. (2001) found such differences only at certain times of year. As well, we found lower pH values under alpha grass tussocks than under bare ground (Fig. 2a), similar to those reported Martínez-Sánchez et al. (1994), who related these lower values to higher biological activity and the accumulation of organic acids. However, García et al. (2005), Goberna et al. (2007), and Maestre et al. (2001) found no such significant differences. It seems unlikely in our case that decreased soil pH was due to the accumulation of organic acids, because the lower pH values were observed in winter (Fig. 2) coinciding with the lowest values in those labile SOC fractions showing seasonal variations (PSs, WSC; Fig. 2c and e). More plausibly, both the higher soil moisture and lower pH are due to increased infiltration and leaching occurring under alpha grass patches.

Our observation of the coarse sand content decreasing during tussock development (Fig. 1f) differs from that by Sánchez Barrionuevo (1995) in steep areas of the same region, who reported sand accumulation under tussocks and related it to the interception of runoff-transported material. This difference may be explained by mechanisms such as raindrop splash, which should be of greater importance than sediment capture in flat areas similar to the ones studied in the present investigation (Bochet et al., 2000), as well as to differences in parent materials, as the soils in the area studied by Sánchez Barrionuevo (1995) develop over mica schist rocks. Goberna et al. (2007) found that soils under tussocks showed higher contents of clay on gypsum materials, higher contents of sand on alluvial materials, and similar properties on marlstones compared to bare soils, which were all loamy textured in their investigation. Concerning the differences between the sites, the coarser texture of the soils at AM may be due to relatively more intense erosion occurring there, which has been described as being responsible for the loss of fine soil particles in other arid ecosystems (Rodríguez Rodríguez et al., 2002, 2005).

Finally, our findings concerning macroaggregate stability in relation to tussock growth (Fig. 1i) are consistent with the results of several studies (Cammeraat and Imeson, 1998; Cantón et al., 2009; Lesschen et al., 2008) reporting a higher stability of macroaggregates under alpha grass patches than in bare soil. However, our results regarding microaggregation (Fig. 1g and h) are disparate from those of Cammeraat and Imeson (1998) and Lesschen et al. (2008), who failed to detect differences in microaggregation.

4.2. Soil aggregation model

Several studies have investigated the stability of soil structure in alpha grasslands and have highlighted the cementing roles of soil organic matter (Bochet et al., 1999; Boix-Fayos et al., 2001; Cammeraat and Imeson, 1998; Cantón et al., 2009), calcite (Boix-Fayos et al., 2001; Cammeraat and Imeson, 1998), and gypsum (Bochet et al., 1999). Boix-Fayos et al. (2001) found a correlation between macroaggregate stability and organic matter only when the content of the latter parameter exceeded a certain threshold, but no correlation was detected between organic matter and microaggregation, which was correlated with clay content. Cantón et al. (2009) observed a correlation of the stability of macroaggregates with organic matter content, but not with particle size composition. With respect to specific fractions of SOC, Rillig et al. (2003) could not link an increase in glomalin (glycoproteins) to a higher aggregate stability, whereas García et al. (2005) observed a positive correlation of aggregate stability with soluble carbohydrates.

Tisdall and Oades (1982) proposed a widely accepted model for the formation of soil aggregates, according to which microaggregates are formed from associations of free particles via persistent unions, such as associations of humic matter with clay minerals or Fe or Al complexation. Subsequently, microaggregates combine and form macroaggregates through temporary cementing, such as via fungal hyphae, roots, and PSs derived from plants and microorganisms. Because of this hierarchy in cementing agents, microaggregates contain more slow and recalcitrant SOC, whereas macroaggregates are proportionally richer in labile SOC. Oades (1984) proposed an alternative to this model, under which microaggregates can also be formed through transient cementing within macroaggregates and released when the macroaggregates eventually disintegrate.

Apparently, our findings are better explained by the latter alternative. During plant growth, a sharp increase was observed in microaggregation (Fig. 1h), which cannot be attributed to slow enrichment of recalcitrant C observed (Fig. 2h and i). A plausible explanation for this finding is that the increasing level of microaggregation reflects the accumulation of pre-existing labile SOC-rich microaggregates captured by the plant in the form of sediments and splash particles. The silt fraction appears to play a greater role than the clay fraction in the composition of the microaggregates, because the change in the content of associated silt and clay (Fig. 1h) during plant growth was more precipitous than that of aggregated clay (Fig. 1g). A microaggregation model mainly based on the aggregation of silt particles is also consistent with the observed silt enrichment (Fig. 1e). The supplies of labile SOC due to microaggregate capture augment those produced by alpha grass, which is responsible for the highest macroaggregate stability occurring under fully developed vegetation patches. After plant death, macroaggregate breakdown occurs due to mineralisation of the labile SOC that cements the macroaggregates and the impact of raindrops, thus releasing labile SOC-rich particles, which can be captured by other tussocks.

4.3. Trends inferred from soil–plant feedbacks

Seemingly, no current difference in habitat features between AM and BB appears to be sufficiently large to explain the considerable divergence in the development of vegetation observed at the two sites. Furthermore, because the vegetation changed very little in both AM and BB over the investigated 50-year period, we can rule out the existence of actively occurring degradation processes in the studied ecosystems and of differential land uses in the recent past as being responsible for the divergence between the two field sites, as both sites were already equally different in 1956. The observed differences should therefore be attributed to intrinsic differences between the sites.

The two sites investigated in the present study appear to differ in the length of their associated soil–plant feedback loops. At AM, the formation of a tussock and its related microtopography was followed by its subsequent decay and return to soil conditions that were seemingly comparable to the initial conditions for almost all of the characteristics studied. In contrast, at BB, the soil did not return to its initial conditions, facilitating earlier plant decolonisation, which in turn reinforces the maintenance of relatively good soil conditions. The situation at BB appears to represent the standard model of stabilising feedbacks that is usually assumed to occur in patchy-vegetated dryland ecosystems (Ehrenfeld et al., 2005). The conditions at AM are quite different: islands of fertility are more transient; thus, new plants could have a similar chance of thriving at sites that were previously occupied or in bare inter-plant spaces. Because persistent resource islands are not always available at AM, vegetation development requires additional effort compared to that at BB, explaining why the plant cover levels at AM remain well below those of BB, even without the occurrence of anthropogenic degradation processes.

Our interpretation of these findings is that a threshold of erodibility separates the two situations. The difference in soil erodibility at the two sites was sufficient to cause divergence between them due to different rates of soil–plant feedback. In the case of BB, erodibility remained below a certain threshold, allowing positive feedback related to vegetation and soil to occur through the progressive shortening of feedback loop lengths, whereas at AM, an erodibility threshold was reached, and erosion caused progressive soil loss and slowed the development of vegetation. The shallower soil at AM is currently limiting and forms part of the feedback loop, slowing vegetation development.

However, the ultimate cause of the differing feedback loop lengths between the sites remains unclear. It is likely that the observed divergence is ultimately due to small differences in site-characteristic microclimatic features (e.g., in the amount or timing of rainfall, which are determinant of rainfall erosivity) that are close to threshold levels, and that feedback processes have magnified the effects of small differences. The scarce available data did not allow us to elucidate this with certainty.

As can be seen from the findings presented in Section 3.1, neither of the two sites had a significant change in the vegetation (and presumably in the soils) between 1956 and 2006. At present, feedback soil–plant interactions occur without net change in any direction in both sites, as they appear to be sufficiently stable at a land management time scale. Nevertheless, if the sites were subjected to climate changes or regimes of use different to the present, they may exhibit very different responses. Because the resilience of an ecosystem depends on the ease with which the recolonisation of gaps produced by disturbances occurs, the resilience of the ecosystem at BB will be much higher than that at AM due to the longer permanency and more favourable characteristics of the resource islands available for the growth of new plants at BB.

5. Conclusions

The patchy spatial structure of alpha grasslands is governed by complex soil–plant feedbacks. The mechanisms underlying soil–plant interactions appear to include the soil dilatation produced by bioturbation (Fig. 1b), resulting in increased water infiltration and in the genesis of a protruding microrelief and gradual shift of coarse fragments to the periphery of a tussock (Fig. 1c); the accumulation and eventual release of labile SOC fractions (Fig. 2i), which are determinant of macroaggregate stability (Fig. 3, Table 1); and the redistribution of water-stable microaggregates rich in silt and labile SOC (Section 3.3).

A threshold of erodibility appears to separate the two situations investigated, and a difference in resilience (which is greater at BB) exists. A new hypothesis emerges as a result of our work: the two sites are characterised by feedback loops with different lengths, and thus, there are probably significant differences in plant colonisation efficiency, in spite of the similar low-disturbance regimes and analogous soils at the sites. At BB, the mosaic-patterned landscape of tussocks growing in islands of fertility and bare areas is more stable; resource islands tend toward permanence (in a spatial sense) and consolidate non-labile SOC (Fig. 2h); plant recruitment is likely to occur more readily; and recovery after a common small disturbance is likely to be faster. In contrast, at AM, resilience is lower as a consequence of the erosion of the nutrient pools, and common small disturbances maintain vegetation and soil at a lower level of development.

The ultimate cause of differing feedback loop lengths remains unclear but is probably related to subtle differences in the microclimate (e.g., in rainfall erosivity) at these two sites. If this is the case, a small habitat gradient appears to affect the carrying capacity of these ecosystems as well as their resilience and their future evolution. This result is relevant in the present context of global change, under which increased temperature, decreased and more concentrated rainfall, and an increased frequency of extreme events are forecasted (IPCC, 2007) for the western Mediterranean region.

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Appendix 1. Methods used in soil analyses

Soil samples were weighed, sieved (<2 mm), and held in a refrigerator (4 °C) until analysis, except for a portion of the samples that was not sieved but was air-dried for the analysis of soil macroaggregates.

The content of coarse fragments (>2 mm) was determined by sieving and weighing. The water content of fine earth (<2 mm) was determined gravimetrically by drying soil sub-samples at 105 °C for 48 h. We calculated the bulk density from the fresh weight and known volume of the soil core samples, the water content of the fine earth fraction, and the content of coarse fragments. Finally, we expressed the soil water content on a volume basis, taking into account the contents of the water in the fine earth and coarse fragments, the soil bulk density, and the sampled soil depth.

The particle size distribution of the fine earth was determined using sodium hexametaphosphate as a dispersing agent. The contents of clay (<2 μm) and silt (2–50 μm) were quantified via the Bouyoucos hydrometer method, and those of fine (50 μm–0.5 mm) and coarse sand (0.5–2 mm) were determined by sieving and weighing (Gee and Or, 2002).

Soil microaggregation was assessed by analysing the particle size distribution of soil samples dispersed in distilled water and comparing it to the particle sizes of soil samples dispersed using sodium hexametaphosphate. Two indices were employed for this comparison, the clay dispersion ratio (CDR) and aggregated silt and clay (ASC) (Igwe et al., 1999), using the formulas presented below:

$$\mathrm{CDR}\,(\%) = 100 * \%\mathrm{Clay}\,(\mathrm{water})/\%\mathrm{Clay}\,(\mathrm{sodium\ hexametaphosphate})$$

$$\mathrm{ASC} = \%\mathrm{Clay}\,(\mathrm{sodium\ hexametaphosphate}) + \%\mathrm{Silt}\,(\mathrm{sodium\ hexametaphosphate}) - (\%\mathrm{Clay}\,(\mathrm{water}) + \%\mathrm{Silt}\,(\mathrm{water}))$$

The stability of macroaggregates was determined by means of a water drop impact test (Imeson and Vis, 1984). Aggregates 4–4.8 mm in diameter, which are predominant in these soils, were selected (by dry sieving) because this the most widely used size in similar studies conducted in southeast Spain (Boix-Fayos et al., 2001; Cammeraat and Imeson, 1998; Cantón et al., 2009). A portion of the aggregates was moistened via capillarity action on filter paper that was in contact with deionised water. Individual aggregates were tested based on the impact of drops with a weight of 0.1 g falling from a 1 m height. We counted the number of drop impacts required for total breakdown of the aggregates (index CND, counting the number of drops). In each sample, 30–40 air-dried and moist aggregates were analysed, and the median was used as a measure of the central tendency.

The soil pH was measured in 1:2.5 soil:water suspensions, and the electrical conductivity (EC) was determined in 1:10 soil:water extracts.

Water-soluble C (WSC) was analysed in 1:10 soil:water ratio extracts obtained through shaking for 30 min, centrifugation at 3500 rpm, and filtering through nitrocellulose membranes (pore size = 0.45 μm) (Ghani et al., 2003). Hot-water extractable C (HWC) was quantified in 1:10 soil:water ratio extracts following the extraction of WSC, incubation at 80 °C for 16 h, centrifugation at 3500 rpm, and filtering through nitrocellulose membranes (pore size = 0.45 μm) (Ghani et al., 2003). Microbial biomass C (MBC) was analysed with the fumigation–extraction method (Vance et al., 1987) using the same calibration factor ($K_c = 0.38$) that has been used in other studies performed in similar ecosystems (Bastida et al., 2006; García et al., 2005; Goberna et al., 2007). Particulate organic C (POC) was assessed by analysing the carbon content in the sand fraction of soils separated by means of dispersion with sodium hexametaphosphate and sieving through a 50-μm mesh (Cambardella and Elliott, 1992). NaOCl-resistant C was determined after the oxidisation of soil organic matter using 6% NaOCl in a 1:50 soil:oxidant ratio for three periods of 18 h (Zimmermann et al., 2007).

The C content of the solid samples (TOC, NaOCl-resistant C, POC) was determined by the Walkley and Black (1934) method, consisting of oxidisation with 1 N sodium dichromate in acid and back titration using 0.5 N ammonium-ferrous sulphate. The C contents of soil extracts (WSC, HWC, MBC) were determined in aliquots of 10 mL using 0.05 N sodium dichromate and 0.05 N ammonium-ferrous sulphate. In the HWC extracts, we also determined the content of polysaccharides (PSs) using the phenol method with no acid hydrolysis (Ghani et al., 2003).

Appendix 2. ANOVA of the investigated soil properties in relation to the sites, the microsites, the seasons, and the moisture conditions.

	Site		Microsite		Site × Microsite	
	$F_{g.l.=1}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=5}$	Sig.
Bulk density	0.51	0.478	17.8	0.000	2.35	0.048
Coarse fragments	0.17	0.678	4.11	0.002	0.81	0.548
Clay	3.07	0.088	2.79	0.032	4.67	0.002
Silt	14.0	0.001	3.92	0.006	0.88	0.506
Fine sand	35.6	0.000	1.16	0.346	0.77	0.576
Coarse sand	19.7	0.000	2.16	0.081	0.99	0.436
CDR	3.82	0.059	3.82	0.007	0.41	0.837
ASC	14.4	0.001	3.19	0.017	1.37	0.258
TOC	13.7	0.001	30.0	0.000	1.19	0.335
POC	1.39	0.247	16.4	0.000	0.93	0.471
NaOCl-resistant C	16.2	0.000	6.43	0.000	2.39	0.057
Slow SOC	0.86	0.000	11.9	0.001	0.87	0.512
Labile SOC	0.25	0.621	15.2	0.000	0.87	0.514

	Moisture		Moisture × Site		Moisture × Microsite		Moisture × Site × Microsite		Site		Microsite		Site × Microsite	
	$F_{g.l.=1}$	Sig.	$F_{g.l.=1}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=1}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=5}$	Sig.
CND	6.08	0.019	3.88	0.056	1.58	0.191	1.33	0.273	5.25	0.028	5.82	0.000	1.36	0.263

	Season		Season × Site		Season × Microsite		Season × Site × Microsite		Site		Microsite		Site × Microsite	
	$F_{g.l.=1}$	Sig.	$F_{g.l.=1}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=1}$	Sig.	$F_{g.l.=5}$	Sig.	$F_{g.l.=5}$	Sig.
Water content	10,283	0.000	50.1	0.000	7.81	0.000	2.10	0.088	1.35	0.253	13.0	0.000	0.81	0.549
$EC_{1:10}$	14.7	0.000	0.43	0.517	0.65	0.666	1.15	0.351	31.9	0.000	1.63	0.177	1.60	0.185
pH	223	0.000	4.02	0.053	1.67	0.168	1.77	0.143	4.00	0.053	7.57	0.000	0.86	0.516
WSC	67.6	0.000	1.11	0.299	1.33	0.273	1.07	0.392	0.01	0.910	3.02	0.022	0.32	0.900
HWC	0.12	0.735	1.05	0.312	1.23	0.314	1.76	0.145	0.01	0.935	18.6	0.000	1.86	0.126
PSs	92.1	0.000	15.8	0.000	1.17	0.342	3.49	0.011	2.04	0.162	11.2	0.000	1.29	0.288
MBC	0.00	0.964	7.07	0.012	1.25	0.309	0.22	0.952	0.02	0.89	4.58	0.002	3.31	0.015

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