

Small-scale spatial patterns of two soil lichens in semi-arid Mediterranean steppe

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Abstract: Biological crusts are a common feature of the soil surface in arid and semi-arid ecosystems, where they play a major role in ecosystem functioning. In recent years, there has been an increasing interest in the ecophysiology, floristics, and dynamics of crust-forming lichens but little is known about the effect of vascular plants on their small-scale spatial distribution. To increase our understanding about the interactions between crust-forming lichens and vegetation in semi-arid areas, the spatial pattern and interaction of two soil lichens, *Cladonia convoluta* and *Squamarina cartilaginea*, at two microsites in semi-arid *Stipa tenacissima* steppe of south-eastern Spain are evaluated. The aim of this study was to determine if the microsite provided by *Stipa* tussocks promoted changes in the individual patterns and in the spatial covariation of these soil lichens. Spatial analysis by distance index (SADIE) coupled with correlation analysis was used to explore the individual patterns and the spatial relationships between the two species. SADIE detected a significant clumped pattern in the spatial distribution of both species, but *Stipa* tussocks promoted changes only in the spatial pattern of *Cladonia*. Correlation analysis revealed the presence of significant relationships between the two species, particularly close to *Stipa* tussocks. The results show that the microenvironment provided by *Stipa* is able to modify the small-scale spatial pattern of soil lichens in semi-arid steppe, and suggest the presence of facilitation between *Stipa* and *Cladonia*.

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Key words: biological crusts, *Cladonia convoluta*, local association, SADIE, spatial pattern, *Stipa tenacissima*, *Squamarina cartilaginea*, soil lichens.

Introduction

Biological crusts composed of bacteria, cyanobacteria, algae, mosses, liverworts, fungi, and lichens are a common feature of soil surfaces in arid and semiarid areas throughout the world (West 1990; Eldridge & Greene 1994). These crusts are an important source of soil organic carbon (Beymer & Klopatek 1991), fix atmospheric nitrogen (Evans & Ehleringer 1993), reduce wind and water erosion (Eldridge & Kinnell 1997), increase soil stability (Belnap & Gardner 1993), and have an important effect on soil-water interactions (Eldridge

et al. 2000b). In addition to indirect effects promoted by changes in soil stability, nutrient content and hydrology, biological soil crusts can directly affect the establishment (Prasse & Bornkamm 2000), survival (Eckert *et al.* 1986), nutrient status (Harper & Belnap 2001), and water relations (DeFalco *et al.* 2001) of vascular plants. Despite the increased knowledge about the dynamics and ecological role of biological crusts achieved in recent years, the effects of small-scale environmental heterogeneity promoted by plant growth on their distribution, and the consequences that these spatial arrangements can have for vegetation dynamics, are still poorly understood (Belnap *et al.* 2001a).

Soil lichens are an important constituent of biological crusts, and usually represent a

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later stage in their development (Lange *et al.* 1997). At regional and landscape levels, climatic factors and soil properties greatly influence the distribution of crust-forming lichens (Eldridge 1996; Eldridge & Tozer 1997; Eldridge & Koen 1998). On a smaller scale, environmental modifications promoted by plants, such as lower soil surface temperatures, reduced radiation, and decreased wind speed on the soil surface (Breshears *et al.* 1998; Belnap *et al.* 2001a), may determine their spatial distribution (Eldridge & Tozer 1997; Eldridge 1999). Quantifying the spatial distribution of lichens is of great interest (Dale 1995), and is important due to their function as constituents of biological crusts. However, few studies so far have studied small-scale variations in the distribution of soil lichens in semi-arid areas (Eldridge 1999; Maestre *et al.* 2002; Maestre & Cortina 2002).

With the aim to increase our understanding about the interactions between crust-forming lichens and vegetation in semi-arid areas, the effects of the microsite provided by *Stipa tenacissima* L. on the small-scale spatial pattern of the lichens *Squamarina cartilaginea* (With.) P. James and *Cladonia convoluta* (Lam.) P. Cout. in steppe of SE Spain are evaluated in this paper. Recent research has shown that the microsite provided by *Stipa* improves microclimate (Maestre *et al.* 2001), soil structure and nutrient content (Puigedfàbregas & Sánchez 1996; Bochet *et al.* 1999), water infiltration (Cerdá 1997; Maestre *et al.* 2002), and retention after rainfall (Maestre *et al.* 2001) compared with adjacent bare ground. The presence of soil lichens increases with increasing soil moisture and stability (Eldridge & Tozer 1997), and the environmental modifications provided by *Stipa* tussocks favour the development of lichen communities that would not normally survive in the harsh environmental conditions of inter-tussock areas (Martínez-Sánchez *et al.* 1994). Thus, it is hypothesized that the microsite provided by *Stipa* is able to modify the spatial pattern of *Squamarina* and *Cladonia*, as well as their spatial relationships. The main objectives of this study were (i) to

characterize the spatial pattern of these two soil lichens in semi-arid steppe, and (ii) to test if environmental modifications generated by *Stipa* tussocks can promote changes in the spatial pattern of individual lichen species, and in the spatial relationships between them.

Materials and Methods

Study area and species evaluated

Research was conducted at three experimental sites close to Sax (38°32'N, 0°49'W, 500 m a.s.l.), in the province of Alicante (SE Spain). The three sites, Colominas (UTM coordinates: 30SXH9173), La Cueva (UTM coordinates: 30SXH9172), and La Torre (UTM coordinates: 30SXH9172), are located on SW exposures with slopes less than 8°. The climate is semi-arid Mediterranean; the 1986–1995 record for Sax meteorological station gives a mean annual temperature of 16.5°C (January 8.4°C, August 26.2°C), and a mean annual rainfall of 315 mm (August 4 mm, October 45 mm), falling mainly during the spring (Maestre 1999). The vegetation is spatially discontinuous with a cover of 40–50%, and is dominated by *Stipa*, but also includes Mediterranean shrubs and trees such as *Rosmarinus officinalis* L., *Globularia alypum* L., *Anthyllus cytisoides* L. and *Pinus halepensis* Miller.

Cladonia convoluta is a desiccation-tolerant lichen with well-developed basal squamules that have a green algal photobiont (*Trebouxia*). *Squamarina cartilaginea* is a large, greenish lichen that has a rosulate thallus with overlapping, prominent lobes that adhere to the substrate by medullar hyphae. Both species can be found in most of the steppe located in the semi-arid areas of SE Spain (Martínez-Sánchez *et al.* 1994), and are the most abundant lichens in the study area.

Field sampling

To evaluate the effect of *Stipa* tussocks on the spatial pattern of lichens, a stratified random design (Webster & Oliver 1990) was used. Two microsites were studied: tussock and open. The tussock microsite was located upslope and adjacent to *Stipa* tussocks; the open microsite was located in the inter-tussock areas with sparse vegetation cover. During the spring of 2000, five 0.25 m² (50 × 50 cm) squares were randomly selected per microsite at each site (10 squares per site). Each square was divided into one hundred 5 × 5 cm sampling quadrats, and the cover of *Cladonia* and *Squamarina* within each of these quadrats was evaluated following the Braun-Blanquet (1964) scale: (0=0%; 1=<6%; 2=6–25%; 3=25–50%; 4=50–76%; 5=>76%). One and two squares located at tussock microsites in La Torre and La Cueva sites respectively, had no *Squamarina*.

Spatial analysis of individual species

To characterize the spatial pattern of the individual species, spatial analysis by distance indices (SADIE, see

Perry 1998 and Perry *et al.* 1999 for a complete description of the method) was used. This technique is based on the 'distance to regularity' (D), which measures the distance that the values of the variable evaluated (cover in this study) would need to move to achieve an arrangement where all sampling units had the same value. To calculate D , SADIE uses the transportation algorithm (Kennington & Helgason 1980). To assess the magnitude of D , SADIE performs a randomization test where the observed value of D is compared with the corresponding values of randomizations where the data are randomly arranged amongst the sampling units. Division of the observed value of D by the mean value from randomizations gives an index of aggregation, I_a . This index gives information on the overall spatial pattern in the data set; a clumped spatial pattern is indicated by $I_a > 1$, a random pattern has a I_a close to 1, and a regular pattern has a $I_a < 1$. A formal test for the non-randomness in the spatial distribution of data can be obtained by calculating the proportion of values in the frequency distribution that are as large or larger than the observed value of D . Another index provided by SADIE is the index of clustering (v), which measures the degree of clustering of the data into patches (areas with above-average cover) and gaps (areas with below-average cover). This dimensionless index quantifies the degree to which each sample contributes to the overall clustering of the data. Sampling units included within areas of high cover (patches) have values of v (by convention v_p) higher than 1.5, while those located in regions of low cover (gaps) present values of v (by convention v_g) below -1.5 (Perry *et al.* 1999). This index is a continuous variable and, if contoured on a two-dimensional map, it shows the spatial distribution of patches and gaps in the data. To test for the presence of significant patches and/or gaps in the data, the mean value of the clustering index for patches, V_p , is usually compared with its expectation of 1 and, separately, the mean value for gaps, V_g , is compared with its expectation of -1 using randomization tests as described above. Despite being initially developed for the spatial analysis of data in the form of integer counts, SADIE can also handle binary data, semi-quantitative data and continuous data if previously categorized (Perry 1998; Perry *et al.* 1999). Furthermore, to use SADIE, data do not need to follow any particular distribution, and results are specifically conditioned by the heterogeneity of the data set (Bell 1998).

SADIE analyses were performed separately for each species using 2340 randomizations. The proportion of sampling squares that significantly departed from randomness in the two microsites was analysed using hierarchical log-linear models (Agresti 1990). In these analyses, the data were compared in a three-way table (Significant departure from randomness, Microsite and Site). The analysis was performed using an unsaturated model containing two-order terms after backward elimination of three-order non-significant terms (Agresti 1990). SADIE indices were tested for significance between microsites by using a two-way ANOVA, with microsite as a fixed factor and site as a random

factor. SADIE indices were log-transformed before statistical testing to correct for heterogeneity of variances (Underwood 1997). All the statistical analyses were performed with the SPSS for Windows 9.0 package (SPSS, Chicago, Illinois, USA). Contour maps of SADIE index of clustering were made by using SURFER 5.0 (Golden Software, Boulder, Colorado, USA).

Spatial association between species

A measure of spatial association should (1) be based on a clear comparison of the spatial properties of each species so that spatial features that match between the two species contribute to association, and those that mismatch contribute to dissociation, and (2) take into account the spatial pattern of each of the individual sets (Perry 1997; Perry & Dixon 2002). A correlation analysis between the values of v for the two species satisfies these two properties. Sampling units where indices of both species show a patch or a gap will contribute strongly and positively to the correlation, while those where one set shows a patch and the other a gap contribute strongly and negatively. Sampling units with small values of v will contribute weakly to the correlation. This analysis satisfies the second property because in the formation of v the spatial pattern of the species has been already accounted for (Perry & Dixon 2002). As the values of v were non-normally distributed in all cases (Kolmogorof-Smirnov test, $P < 0.05$), the significance of the correlation coefficient was tested using a randomization test in which the values of v of each species were randomly reassigned amongst the sampling units.

Another type of information of interest that can be obtained with SADIE is the measurement of local association using a local indicator of spatial association (LISA) approach (Anselin 1995). A LISA analysis can reveal characteristics of the spatial association between two species undiscovered by the analysis of their overall association (Anselin 1995; Cressie & Collins 2001). With SADIE, this analysis can be done by using the contribution of each sampling unit towards the overall correlation coefficient of the values of v (Perry & Dixon 2002). In practice, if the values of v for *Cladonia* are denoted v_1 , with mean q_1 and those of *Squammarina* are denoted v_2 , with mean q_2 , a measure of local spatial association for a sampling unit i (χ_i) is given by (Winder *et al.* 2001; Perry & Dixon 2002):

$$\chi_i = \frac{n(v_{i1} - q_1)(v_{i2} - q_2)}{\sqrt{\sum_i (v_{i1} - q_1)^2 (v_{i2} - q_2)^2}}$$

where n is the number of sampling units (100 in this study). Positive values of χ indicate the presence of coincidences of patches or gaps in both species, while negative values indicate the presence of a patch in one species and a gap in the other. It is interesting to note that the mean of χ is the correlation coefficient between the values of v of both species. As χ is a continuous variable, it can also be mapped and contoured to display

TABLE 1. Frequency of sampled squares* that showed a non-random spatial pattern ($I_a \neq 1$, $P < 0.05$)

Species	Frequency (%)					
	Colominas		La Cueva		La Torre	
	Tussock	Open	Tussock	Open	Tussock	Open
<i>Cladonia convoluta</i>	100	80	100	60	100	60
<i>Squamarina cartilaginea</i>	60	100	0†	60	50‡	40

* $n=5$ except when indicated; † $n=3$; ‡ $n=4$.

graphically the areas of local positive or negative association. A 95% confidence interval for χ under the null hypothesis of no association may be derived from the randomizations performed to test the significance of the overall correlation between the two species (Winder *et al.* 2001; Perry & Dixon 2002). To do that, the lower 2.5th centile and the upper 97.5th centile of the ordered correlation coefficients, which indicate the limits of the confidence interval for the overall correlation, were multiplied by \sqrt{n} (Perry & Dixon 2002).

Correlation and local association analyses were performed by using 10 000 randomizations with the program Genstat for Windows, 5th edition (VSN International, Oxford, UK). The proportion of sampling squares where the relationship between the two species was significant ($P < 0.05$) was analysed using hierarchical log-linear models. The data were compared in a three-way table (Significant association, Microsite, and Site) as described above. Contour maps of local association were performed with SURFER 5.0 (Golden Software, Boulder, Colorado, USA).

Results

The overall spatial pattern of *Cladonia* was generally non-random, because 100% and 60–80% of sampled squares in tussock and open microsites, respectively, had I_a values significantly different from 1 (Table 1). The spatial pattern of this species was affected by microsite, as the number of sampled squares in which I_a showed any significant deviation from randomness was significantly higher in the tussock microsite (Log-linear analysis, $G^2_{\text{Microsite} \times \text{Significant departure from randomness}} = 8.05$, $df=1$, $P=0.004$). Mean values obtained for I_a were higher than 1.3 in both microsites and for all sites, suggesting the presence of a clumped pattern in the distribution of this species (Table 2). The significant values of V_i and V_j also suggest

the presence of patches and gaps in the data (Table 2). All SADIE indices for this species showed higher mean values at tussock microsite than those in the open microsite, and these differences were significant (Table 3). In the case of *Squamarina*, the number of sampled squares with a I_a significantly different from randomness ranged from 0% to 60% in tussock microsite, and from 40% to 100% in open microsite (Table 1). These differences were not statistically significant (Log-linear analysis, $G^2_{\text{Microsite} \times \text{Significant departure from randomness}} = 2.72$, $df=1$, $P=0.099$). Values of I_a and V_i were generally lower than those obtained for *Cladonia* (Table 2). *Squamarina* did not show any significant differences between microsites for any of SADIE indices (Table 3).

Contour maps of the index of clustering visually indicate the spatial distribution of the main patches and gaps within the sampled squares (Fig. 1). Two major features of the spatial pattern of *Cladonia* can be inferred from these maps. This species shows generally a higher degree of clustering in the tussock microsite, and the degree of clustering in this microsite decreases with distance from the canopy edge of *Stipa* tussocks. In the open microsite, this tendency towards an aggregation in a specific part of the sampled squares is not evident. Maps of *Squamarina* clearly reflect the lack of significant differences in the spatial pattern of this species between the two microsites. The degree of clustering is similar in both microsites, and there is no

TABLE 2. Summary of SADIE indices* obtained for the two species

Site	Species	Microsite	I_a	V_i	V_j
Colominas	<i>Cladonia convoluta</i>	Tussock	2.76 ± 0.17	2.51 ± 0.10	-2.62 ± 0.17
		Open	1.46 ± 0.09	1.45 ± 0.10	-1.47 ± 0.09
	<i>Squamarina cartilaginea</i>	Tussock	1.49 ± 0.10	1.31 ± 0.14	-1.50 ± 0.11
		Open	1.51 ± 0.09	1.45 ± 0.07	-1.51 ± 0.09
La Cueva	<i>Cladonia convoluta</i>	Tussock	3.21 ± 0.16	2.93 ± 0.21	-2.96 ± 0.12
		Open	1.36 ± 0.13	1.37 ± 0.14	-1.32 ± 0.10
	<i>Squamarina cartilaginea</i>	Tussock†	1.00 ± 0.03	1.04 ± 0.03	-1.00 ± 0.03
		Open	1.45 ± 0.17	1.37 ± 0.15	-1.45 ± 0.17
La Torre	<i>Cladonia convoluta</i>	Tussock	2.67 ± 0.35	2.54 ± 0.38	-2.49 ± 0.33
		Open	1.48 ± 0.17	1.48 ± 0.17	-1.48 ± 0.18
	<i>Squamarina cartilaginea</i>	Tussock‡	1.57 ± 0.36	1.62 ± 0.37	-1.57 ± 0.36
		Open	1.22 ± 0.09	1.19 ± 0.08	-1.22 ± 0.09

*Data represent mean ± 1 SE ($n=5$, except when indicated); I_a =index of aggregation; V_i =mean of the index of clustering for patches, and V_j =mean of the index of clustering for gaps.

† $n=3$; ‡ $n=4$.

TABLE 3. Results of a two-way ANOVA to assess the significance of the microsite and site effects on log-transformed SADIE indices

Species	SADIE indices*	ANOVA results								
		Microsite			Site			Microsite × Site		
		F	df	P	F	df	P	F	df	P
<i>Cladonia convoluta</i>	I_a	61.08	1,2	0.016	0.18	2,2	0.846	1.41	2,24	0.264
	V_i	61.26	1,2	0.016	0.17	2,2	0.857	1.02	2,24	0.378
	V_j	47.05	1,2	0.021	0.12	2,2	0.893	1.59	2,24	0.224
<i>Squamarina cartilaginea</i>	I_a	0.11	1,2	0.772	0.74	2,2	0.574	3.02	2,21	0.070
	V_i	0.08	1,2	0.800	0.37	2,2	0.730	2.63	2,21	0.095
	V_j	0.13	1,2	0.749	0.77	2,2	0.566	2.93	2,21	0.075

* I_a =index of aggregation; V_i =mean of the index of clustering for patches; V_j =mean of the index of clustering for gaps.

clear tendency in either of the two microsities towards a main aggregation close to the edge of *Stipa* tussocks.

The number of sampled squares that presented a significant relationship between the two species was higher in the tussock microsite at all three sites (Table 4). However, these differences were not significant (Log-linear analysis, $G^2_{\text{Microsite} \times \text{Sampled squares}}$ with significant correlation coefficient=1.89, df=1, $P=0.169$). This lack of significant differences is also reflected in the maps of χ (Fig. 2), but it is interesting to note the presence of a predominantly negative association

between the two species for most cases in the tussock microsite, decreasing as the distance from the tussocks increases.

Discussion

In semi-arid Mediterranean steppe, *Stipa* acts as an 'ecosystem engineer' (Jones *et al.* 1997) modifying the spatial patterning of resources available for other organisms. The harsh environmental conditions in these areas are ameliorated in the vicinity of the tussocks (Maestre *et al.* 2001), and other

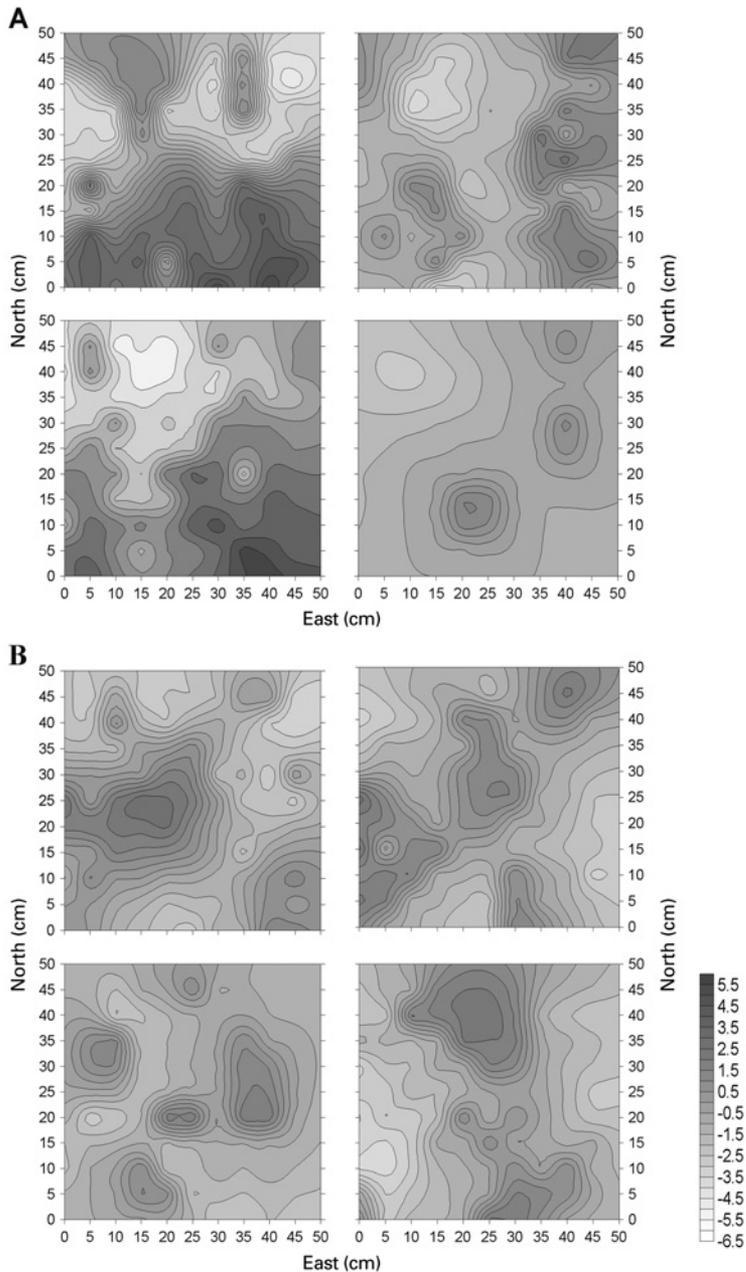


FIG. 1. Contour maps of the SADIE index of clustering in tussock (left) and open (right) microsites. A, *Cladonia convoluta*; B, *Squamarina cartilaginea*. In the tussock microsite the north axis reflects the distance from the edge of the tussock. For brevity, only selected maps from the Colominas site are shown.

organisms such as lichens and bryophytes can benefit from these changes (Martínez-Sánchez *et al.* 1994; Maestre *et al.*

2002). The use of SADIE analysis of a multiple set of sampling squares and sites supported the hypothesis that the microsite

TABLE 4. Frequency of sampled squares* in which the correlation coefficient showed a significant relationship ($P < 0.05$) between *Cladonia convoluta* and *Squamarina cartilaginea*

Frequency (%)					
Colominas		La Cueva		La Torre	
Tussock	Open	Tussock	Open	Tussock	Open
40	20	67†	40	50‡	20

* $n=5$, except when indicated; † $n=3$; ‡ $n=4$.

provided by *Stipa* promoted changes in the spatial pattern of individual lichen species, but not in the spatial correlation between them. The two species of lichens differed, however, in individual responses to the microsite, as the spatial pattern of *Squamarina* was not affected by the presence of *Stipa* tussocks. Our results agree with Maestre & Cortina (2002), who showed that the spatial pattern of biological crusts was positively related with that of *Stipa* in a 50 m × 50 m plot, and also with studies reporting a positive or nil effect of vascular plants on soil lichens (Belnap *et al.* 2001b and references therein).

In semi-arid steppe, *Cladonia* forms continuous patches in the vicinity of *Stipa* tussocks that become sparser as the distance from the edge of the tussocks increases. In the open microsites, patches are smaller and sparse. These differences were clearly reflected in the SADIE indices, and suggest that *Stipa* tussocks facilitate the development of *Cladonia* (*sensu* Callaway 1995). These results may be explained by differences between microsites in the colonization and growth rates of this species. In the study area, *Cladonia* is able to colonize decomposing organic material, which in turn is highly abundant beneath *Stipa* tussocks. Thus, the greater development found in the tussock microsites may be due to a greater availability of microsites for colonization. But it is also likely that the observed patterns may be favoured by the reproductive strategy of *Cladonia*. No fertile *Cladonia* individuals were observed in the study area, suggesting that fragmentation is the primary means

of dispersal to new areas (Eldridge *et al.* 2000a). In semi-arid steppe, *Stipa* tussocks act as sinks of runoff water and sediments generated in the open areas (Puigdefábregas & Sánchez 1996). Thus, it is possible that colonization of tussock microsites by *Cladonia* may be enhanced with thallus detached in other microsites and deposited underneath *Stipa* tussocks by water erosion (Bailey 1976). After colonization, the improvement of microclimatic conditions in the tussock microsites may enhance physiological activity and growth of *Cladonia* compared to the open microsites. Although *Cladonia* has a compact cushion-like growth form that reduces the rate of water loss (Evans & Lange 2001) and retains its chlorophyll content and photosynthetic apparatus during desiccation (Tuba *et al.* 1996), PS II is found to be non-functional in desiccated thalli (Sass *et al.* 1996). Furthermore, loss of turgor is detected when relative water content is less than 60% (Proctor *et al.* 1998). The small-scale spatial patterns of *Cladonia* found in *Stipa* steppe do not agree with studies performed in less stressful areas of the United States, which reported reductions in the cover of *Cladonia* sp. with the increase of shading by grasses (Robinson 1959; Brodo 1961). They also contrast with studies carried out on a regional scale in semi-arid areas of Australia, where squamules of *Cladonia* sp. tended to occur in open microsites devoid of plant cover and biomass (Eldridge 1996; Eldridge & Tozer 1997).

The mechanisms underlying the small-scale spatial pattern of *Squamarina* cannot be elucidated from the results of this study. However, the lack of differences in the spatial pattern of this species between microsites may be the result of its physiological characteristics. Lange *et al.* (1997) showed how a similar species, *Squamarina lentigera* (Weber) Poelt, is able to retain its photosynthetic apparatus during desiccation periods, and to start photosynthesis with levels of moisture as low as 0.08–0.09 mm of equivalent rainfall. Furthermore, this species needs high levels of radiation (photosynthetic photon fluence rate between the wavebands

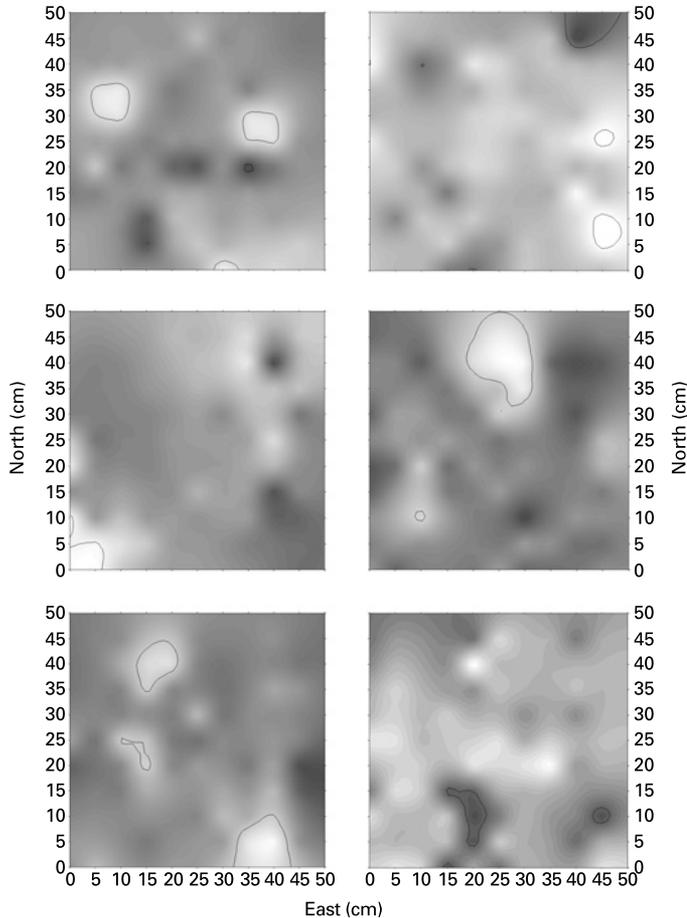


FIG. 2. Contour maps of local association between *Cladonia convoluta* and *Squamarina cartilaginea* in tussock (left) and open (right) microsites. White and grey patches represent areas of negative and positive association, respectively. Significant positive or negative association areas ($P < 0.05$) are included within a solid line. In the tussock microsite the north axes reflect the distance from the edge of the tussock. For brevity, only selected maps from the Colominas site are shown.

400–700 nm of 800 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for saturation of net photosynthesis. Thus, it is possible that *Squamarina* may not be able to develop in the shaded environment provided by *Stipa* tussocks.

Local association maps suggest the presence of negative interactions between the two species in the surroundings of the tussocks. This negative association, which decreases with the distance from the tussock, may be explained by at least two hypotheses: (1) a process of competitive exclusion (Lawrey 1991), in which *Cladonia* successfully competes against

Squamarina in the colonization of the resources, mainly the space, and (2) *Squamarina* fails to establish in the microsite provided by the tussocks. It is suggested that the first of these hypotheses could explain the observed patterns. Higher metabolic activity and carbon gain of *Cladonia* compared to *Squamarina* (Evans & Lange 2001) in the vicinity of the tussocks would enhance the growth of the former, making it more competitive for the colonization of the space within this microsite. However, further studies are needed to test the hypothesis.

The morphology of the components of biological crusts largely determines their ecological function relative to water infiltration, erosion, water retention and resilience to disturbances (Eldridge & Rosentreter 1999; Belnap *et al.* 2001a). The differences found in the spatial pattern of *Cladonia* between microsites could also have important influences on the hydrological fluxes in the steppe studied. Following the classification of Eldridge & Rosentreter (1999), in the study area *Cladonia* can be included within the morphological group of leafy lichens. Increased soil surface roughness caused by these lichens may enhance water infiltration (Belnap *et al.* 2001a), and seed-trapping (Zaady *et al.* 1997). Thus, it may be possible that the higher degree of clustering of *Cladonia* observed close to *Stipa* may improve the water status of the tussocks and create favourable microsites for vascular plant establishment. Data obtained in semi-arid steppe from Almería (SE Spain) show that cover of annuals is greatest in the first 10 cm from the edge of *Stipa* tussocks (Sánchez 1995), but no reference is made to biological crust components. Further manipulative experiments are needed to clarify the role that the spatial aggregation of *Cladonia* found may have on the development of vascular plant communities associated with *Stipa* tussocks.

Spatial pattern analysis has a long history in plant community studies, and plays an important role in generating hypotheses in ecology (Greig-Smith 1983; Dale 1999). Although its application to lichens has not been as popular as with vascular plants (Dale 1995, 1999), valuable information about the use of environmental resources by lichens, biotic interactions between them, and relationships with other organisms can be obtained from the analysis of their spatial distribution. In the steppe studied, both *Cladonia* and *Squamaria* exhibited complex small-scale spatial patterns. The results obtained in this study increase our understanding about the relationships of individual biological crust components and vascular plants in semi-arid environments. Further specific studies are needed to clarify

the mechanisms underlying the spatial patterns observed, and to elucidate the importance of these patterns for the maintenance and dynamics of vascular plants in semi-arid *Stipa* steppe.

I am indebted to Professor Joe N. Perry for his help and advice with SADIE, as well as for useful comments on the manuscript. M^a Dolores Puche helped during fieldwork, and Vicent Calatayud helped in the determination of lichens. Jordi Cortina, Eli Zaady, and David Eldridge made helpful comments and suggestions on earlier drafts of the manuscript. This work was supported by a FPU fellowship from the Spanish Ministerio de Educación, Cultura y Deporte, and by the European Commission funded REDMED project (contract number ENV4-CT97-0682).

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