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Transplant Survivorship of Bryophyte Soil Crusts in the Mojave Desert

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Abstract

Patches of the dominant biological soil crust moss (*Syntrichia caninervis*) in the Mojave Desert were subjected to transplant experiments to test the survivability of crustal transplantation due to source or destination microhabitat. After a period of 27 months, all the reciprocally transplanted and replanted sections had survived. However, percent cover of the reciprocally transplanted patches declined 20–50% relative to initial cover compared to a decline in cover of 36–52% for the replanted patches. Similarly, shoot density declined an average of 26% in the transplants and replants. Shoot mortality was essentially negligible through the first 21 months of the study and then declining across all treatments to approximately 5–10 dead shoots/cm^2. However, this shoot death was also observed in equivalent densities in the host patches, indicative of a community-wide decline in plant health that was probably related to a regional rainfall deficit over this period. A tendency existed for plants moved from a shaded site to have reduced shoot density in the new site, and plants moved into exposed sites lost significantly more cover than plants moved into shaded sites. These seemingly conflicting trends result from one of the transplant treatments, the shaded to exposed, exhibiting a greater loss in shoot density and decline in cover than its reciprocal transplant, exposed to shaded. For soil restoration of disturbed bryophyte crusts, we recommend using as source material both the exposed and the shaded portions of the crust but avoiding moving *Syntrichia* from a shaded site into an exposed site.

Key words: biological soil crust, bryophyte, crust mortality, mosses, *Syntrichia*, transplants.

Introduction

The biological soil crust found in arid lands is highly diverse, containing elements of four kingdoms. It is also known as the cryptobiotic, desert, cryptogamic, microbiotic, or microphytic crust. Nearly all desert soil crusts harbor cyanobacteria, eubacteria, algae (photosynthetic protistans), and fungi, although well-developed crustal communities also contain lichens, mosses, and liverworts as dominant species (West 1990). The soil crust varies greatly from desert to desert, probably explaining the variety of attributed names. It can be categorized by the dominant species (e.g., a *Microcoleus* crust) or by the dominant morphological group (e.g., scaly lichens; Eldridge & Rosentreter 1999). Succession of a crustal community typically progresses from cyanobacteria and algae toward associations of lichens and mosses, with stability associated with the latter two groups (Dunne 1989; Eldridge 1993; Belnap & Eldridge 2001).

The biological soil crust enhances soil quality by aggregating soil particles, increasing soil surface temperature, improving infiltration balance, and increasing soil fertility (Belnap & Lange 2001; Bowker 2007). High wind gusts are typical of southwestern U.S. deserts, and the presence of biological soil crusts protects the soil from wind erosion (Williams et al. 1995; Belnap & Gillette 1997). Recovery rates of disturbed biological crusts depend on the component parts of the crust, the substrate involved (e.g., sandstone- vs. gypsum-derived soils), soil texture, the availability of inoculant material, the temperature and moisture conditions that follow the disturbance event, and the recovery parameter used. In the higher elevation Mojave (1,500 m), estimates of early successional recovery for cyanobacteria are about a century or more, whereas bryophytes may take over 500 years to fully reestablish (Belnap 1993; Belnap & Eldridge 2001). Such long estimates for bryophyte recovery are based on observations of percent cover several years after crust removal followed by inoculation of crumbled scalped material. Some observations revealed no bryophyte recovery at all, whereas those that showed growth projected several centuries to fully reestablish (Belnap 1993). Although chlorophyll content of disturbed soils (disturbed by raking, scalping, and tracked vehicles) did not differ from undisturbed controls, nitrogenase activity exhibited significant reductions, from 23 to 100%, indicating that this physiological measure of soil health is very slow to recover (Belnap et al. 1994;

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Belnap 1996). Such findings justify a conservative approach to managing surface soil disturbances on arid lands and perhaps suggest alternative avenues be investigated for the reestablishment of bryophyte components of the crust.

A few studies have carried out reciprocal transplantation of nondesert bryophytes, with most finding that individual plants transplant well (e.g., Lewis & Smith 1977; Longton 1981; Kallio & Saarnio 1986). In the grassland communities of southeast Australia, crusts of mosses and liverworts were transplanted successfully (Scarlett 1994). However, no study to date has attempted experimental transplantation of whole segments of the desert bryophyte crust. Given that (1) some desert crusts are characterized by a rich cover of mosses from the genus *Syntrichia* (family Pottiaceae; Bowker et al. 2000) and (2) crumbled crust fragments used as inoculant easily blow away from the reestablishment area, the principal purpose of the present study was to determine if transplantation of segments of the *Syntrichia*-dominated bryophyte crust is feasible in the Mojave Desert. An additional purpose was to determine if the microhabitat of the *Syntrichia* crust (shaded and exposed) is a factor in transplantation success, both from a source and a destination perspective. Given the highly clonal nature of *Syntrichia* and its high level of desiccation tolerance (Mishler 1988), we hypothesized that patch transplantation survival would be independent of microclimate, that is, exposed and shaded patches would not significantly differ in their transplantation success.

Methods

Biology of *Syntrichia caninervis*

Syntrichia caninervis is a species of cold and hot deserts, occurring in western North America, southwest and central Asia, and North Africa. In the Mojave Desert, *S. caninervis* Mitt. (also known as *Tortula caninervis* (Mitt.) Broth. and *T. desertorum* Broth.) occupies the xeric portion of an elevational gradient that extends to two closely related species: *S. ruralis* (Hedw.) Web. & Mohr at intermediate elevations and *S. norvegica* Web. at the highest elevations (Oliver et al. 1993). *Syntrichia caninervis* is differentiated from its close relatives in the *S. ruralis* complex by its appressed leaves when dry, bistratose leaves, and substereid costal cells of these leaves (Flowers 1973; Kramer 1980; Mishler 2007). At low to middle elevations in the Mojave Desert, *S. caninervis* is a dominant species, exhibiting the third highest percent cover of all plants in the *Coleogyne* community (6%), a vegetation belt that constitutes one of the most widespread vegetation zones in the southwestern United States (Lei & Walker 1997; Smith et al. 1997; Bowker et al. 2000). Large patches of *S. caninervis* are often situated along the north-facing bases of *Coleogyne* shrubs, whereas smaller and more diffuse patches occur in exposed microhabitats. This is a perennial, acrocarpous species capable of clonal growth to shoot heights of 2.5 cm, and where mature individuals may not have expressed sex, that is, neither sex expression nor sexual reproduction is required for survival over the near term.

Study Site

A 100 × 120–m section of a 10-ha area was selected near White Rock Spring in the Spring Mountains of southern Nevada, U.S.A., elevation 1,494 m, as described in Bowker et al. (2000). Average annual precipitation is 25.23 ± 9.80 cm/yr ($\bar{X}$ ± 1 SD), range 16.13–41.91 (National Weather Service 1994). The site was selected due to its homogeneity with respect to vascular plant vegetation, with the general area dominated by Blackbrush (*Coleogyne ramosissima* Torr.). The study site was bordered by major washes on three directions and by an unpaved parking lot separated by a buffer zone of 100 m to the north. Soils at the site are primarily derived from sandstone. The total percent cover of bryophytes and lichens at the site is 18%, with 11% mosses, 7% lichens, and 6% *S. caninervis* (Bowker et al. 2000). The study community corresponds to the morphological group "Mosses," with the growth form erect (acrocarpous; sensu Eldridge & Rosentreter 1999).

Preliminary Trials

The lack of data on bryophytic crust manipulations dictated a set of preliminary field trials to explore the preferred size of the core to be used, the coring device best suited, and the optimum hydration state of moved patches (wet vs. dry). Therefore, a preliminary test series of transplants was carried out in the fall of 1998 in which we determined that the dominant moss at the site, *S. caninervis*, transplanted best when the crust segment was hydrated and that the smaller the core (20–40 mm), the easier it was to move the core of plants while preserving their integrity (spatial location within the patch). Polyvinyl chloride (PVC) corers were found to function adequately in removing sections of the bryophyte crust. We transplanted cores directly, rather than using individual plants, in order to preserve the natural patch structure.

Hypotheses and Experimental Design

Our general hypothesis was that microhabitat source and destination (shaded and exposed sites) will not affect bryophyte transplant success, owing to the high degree of clonality and desiccation tolerance exhibited by *Syntrichia* (Barker et al. 2005). Therefore, a series of reciprocal transplant treatments was established to include exposed to exposed, shaded to shaded, exposed to shaded (and shaded to exposed), and replant controls. Each treatment contained 6 replicate patch pairs, that is, 12 patches per treatment and 48 total patches. For example, the exposed to shaded treatment consisted of six exposed patches and six shaded patches from which cores were reciprocally transplanted, and the replant controls consisted of six exposed and six shaded replanted cores (Fig. 1). "Shaded" is defined to be a patch of *S. caninervis* located directly under or intersecting the canopy line of a *Coleogyne* shrub. "Exposed" is defined to be a patch at least 30 cm from the nearest canopy line of a *Coleogyne* shrub (also known as the intershrub or interspace region). "Replants" are those transplants that test for the effect of moving the core without changing its location: a section of crust (a patch) is cored, uplifted, and reinserted into its original location. A "patch" in this study is defined as a cluster of *S. caninervis* plants separated by at least 3 cm from the nearest cluster of *S. caninervis* plants and is based on projected sperm dispersal distances (Anderson & Lemmon 1974; Wyatt 1977). Patches used in this experiment were generally larger than the cored region, and therefore, the cores actually represent a section of an individual patch; however, for convenience, we refer to these cored sections as patches. In addition, the host patch peripheral to (2.5 cm immediately outside) the transplanted/replanted core was assessed for percent cover and shoot survival beginning with the December 1999 sampling. These patches were used to assess background changes in percent cover and mortality. Only female patches were used in this study owing to the extreme rarity of male and mixed-sex patches at this site (Bowker et al. 2000).

Within the 100 × 120–m site, four random coordinates were generated, separated from one another by a 20 m radius (to prevent overlap of the four treatment areas), and the nearest *Coleogyne* shrub was located at each coordinate, the "focal shrub." The nearest 6–12 *Coleogyne* shrubs to the focal shrub that harbored suitably sized patches of *S. caninervis* (minimum diameter of 40 cm) without evidence of sexual reproduction (no sporophytes) were selected and flagged.

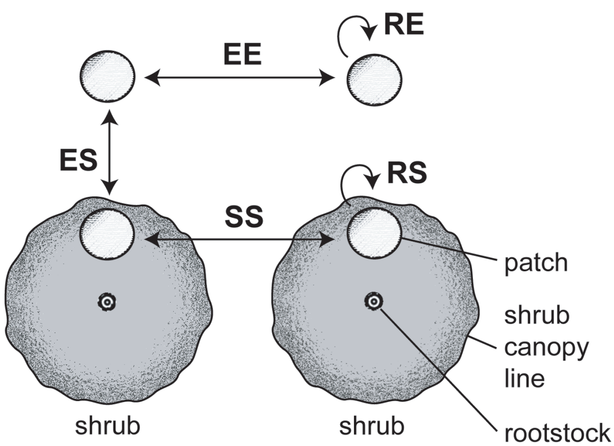

Figure 1. Experimental design of the bryophyte reciprocal transplants. EE, exposed to exposed; SS, shaded to shaded; ES, exposed to shaded and shaded to exposed; RE, replanted exposed; and RS, replanted shaded *Syntrichia cores*. This figure appears in color in the online version of the article [doi: 10.1111/j.1526-100X.2008.00445.x].

Handling of Transplants

In October 1998, the reciprocal transplants and replants were performed. Due to the small dimensions of available patches, an even distribution of core sizes was not possible, with most transplant dimensions of 20 mm diameter (only 9 patches were suitably sized to allow a 40-mm-diameter core, with a 20-mm-diameter core used on the remaining 39 patches). The PVC core was positioned over the source patch, and an atomizer was used to hydrate the patch inside the core using water from the nearby spring (White Rock Spring). The patch was allowed to hydrate, along with the soil beneath the patch, for several minutes prior to executing the transplant. This allowed the soil and plants to soften and yet remain intact when moved. The patch within the core along with approximately 1 cm of underlying soil was gently removed. The above procedure was repeated for the recipient patch (in reciprocal transplants, both patches are source and recipient patches). Transplants of equal diameter were inserted to ground level of the receiving patch, and disturbance about the circumference of the PVC core was minimized, although unavoidable. Prior to inserting the transplant, the number of shoots was counted. Following the transplants, the patches were visually assessed for percent cover of *S. caninervis* to the nearest 10%. During transplantation, the directional aspect of each patch was preserved (the original north-facing side of each patch was oriented to the north upon transplantation).

Assessing Cover, Density, and Mortality

In June 1999, December 1999, July 2000, and January 2001, transplanted patches were assessed for cover and shoot survivorship. Each patch was manually hydrated using an atomizer with water from the nearby spring (except on the June 1999 sampling, when patches were previously hydrated from a rain event), and after several minutes, the percent surface cover of living plants was assessed to the nearest 10% and the number of dead shoots counted. Shoots were considered dead that turned a burnt orange color. However, the mortality determination in the field may overlook a viable apical meristem that is surrounded by browned/dead leaves, and our dead shoot counts could not include shoots that died and left the patch (e.g., were blown or carried away). Over the course of the experiment, four transplanted or replanted patches were lost, presumably removed by rodents; these patches were dropped from the analyses. The number of shoots could not be accurately determined without removing the transplants; this measure was not reassessed during the study but was assessed at the conclusion of the study.

Analyses

We used the initial and final surveys to assess differences in percent cover change: $(C_f - C_i)/C_i \times 100$, where $C_f =$ final cover and $C_i =$ initial cover. Initial and final shoot densities (per cm^2) were used to calculate percent density change: $(D_f - D_i)/D_i \times 100$, where D_f = final density and D_i = initial density. Mortality was low in the first three intervals. Consequently, we used the fourth interval (month 27) to test for mortality effects. To determine the general pattern of change in percent cover and mortality at the site, we used the host patches in the one-way analysis of variance (ANOVA) with microhabitat as the independent variable and percent cover or mortality as the dependent variable. We used paired t tests to determine if replanted cores versus host patches differed in total percent cover and mortality for the same interval (1999–2001) across the two microhabitats. We used a two-way ANOVA to determine if replants differed from the within-microhabitat transplants in percent cover, mortality, and shoot density. With the transplants, we used two-way ANOVAs to test for source versus destination microhabitat effects on mortality and percent change in density and cover. Interactions between source and destination microhabitat effects were not found and dropped from the models. All ANOVAs were carried out using PROC GLM of SAS/STAT software (SAS 9.1.3; SAS Institute, Inc., Cary, NC, U.S.A.).

Results

Background Patterns

There was no difference in mortality between the host patches in the exposed versus the shaded sites (Table 1; analysis not shown). Among all the host patches, percent cover increased in the exposed sites (58.2 ± 13.8%) and decreased in the shaded sites by 17.4 ± 9.7 ($df = 1$, $F = 20.9$, $p < 0.0001$). Mortality during the last interval did not differ between the replanted cores versus the host patches ($n = 10$, $t = 1.29$, $p = 0.23$; Table 1). Percent cover of the replanted cores (43.4 ± 13.4%) decreased, whereas host patches (30.2 ± 25.8%) gained cover ($n = 10$, $t = 1.29$, $p = 0.021$). Replants did not differ from transplants for mortality or shoot density (analyses not shown); however, replants (45.9 ± 12.4%) tended to have greater reduction in percent cover than transplants (25.2 ± 5.4%; $df = 1$, $F = 3.14$, $p = 0.087$; Fig. 2).

Habitat-Specific Transplanting Effects

Mean shoot mortality rate over the first 21 months of the transplanted cores was 0.24 shoots/cm^2 (range 0–6.69; Table 1). In the fourth interval (27 months), mean shoot mortality was 6.29 shoots/cm^2 (range 0–22.93; Table 1). Only mortality in this last interval was tested and was not related to source ($df = 1$, $F = 0.14$, $p = 0.707$) or destination microhabitat type ($df = 1$, $F = 1.47$, $p = 0.235$). Initial and final shoot densities are given in Table 2. There was no statistically significant destination microhabitat effect on percent change in shoot density ($df = 1$, $F = 0.0$, $p > 0.99$). However, there was a tendency for cores transplanted from the shade to have a greater reduction in shoot density (34.9 ± 9.2) than cores transplanted from exposed sites (10.4 ± 10.15; $df = 1$, $F = 2.74$, $p = 0.11$; Table 2). The reduction in cover of plants transplanted into the exposed sites (36.3 ± 6.29%) was greater than plants transplanted into the shaded sites (21.2 ± 5.6%; $df = 1$, $F = 4.69$, $p = 0.038$; Fig. 2). There was no statistical source microhabitat effect on percent change in cover ($df = 1$, $F = 1.77$, $p = 0.19$).

Discussion

Although all transplanted cores of *Syntrichia caninervis* survived, at least in part, to the conclusion of the study,

Table 1. Shoot mortality as the number of dead shoots per square centimeter in *Syntrichia* crust transplants, including data from the host patch (surrounding the transplants) from the 8-month mark on.

Treatment	*Initial Mean Shoot Mortality (± 1 SD)*	*Mean Shoot Mortality: 8 Months (± 1 SD)*	*Mean Shoot Mortality: 14 Months (± 1 SD)*	*Mean Shoot Mortality: 21 Months (± 1 SD)*	*Mean Shoot Mortality: 27 Months (± 1 SD)*
Shaded to shaded, $n = 12$	0.58 ± 1.11	0.03 ± 0.09	0.03 ± 0.09	0.61 ± 0.69	5.09 ± 8.01
Intact host patch		0.00	0.00	0.01 ± 0.03	5.27 ± 5.69
Exposed to exposed, $n = 11^a$	0.56 ± 1.93	0.41 ± 0.75	0.35 ± 1.15	0.38 ± 1.05	8.77 ± 5.41
Intact host patch		0.00	0.08 ± 0.24	0.01 ± 0.04	5.40 ± 3.25
Exposed to shaded, $n = 5^a$	0.00	0.00	0.00	0.00	3.95 ± 3.99
Intact host patch		0.00	0.00	0.00	4.73 ± 5.88
Shaded to exposed, $n = 6$	0.00	0.00	0.00	0.00	6.08 ± 4.57
Intact host patch		0.00	0.00	0.00	8.20 ± 7.64
Replants					
Shaded, $n = 6$	0.00	0.00	0.00	0.00	5.09 ± 5.08
Intact host patch		0.00	0.00	0.00	6.17 ± 6.36
Exposed, $n = 4^b$	0.00	0.00	0.00	0.00	19.59 ± 10.91
Intact host patch		0.00	0.00	0.00	10.92 ± 5.92

[a] One transplant was disturbed and lost in these treatments.
[b] Two transplants were disturbed and lost in this treatment.

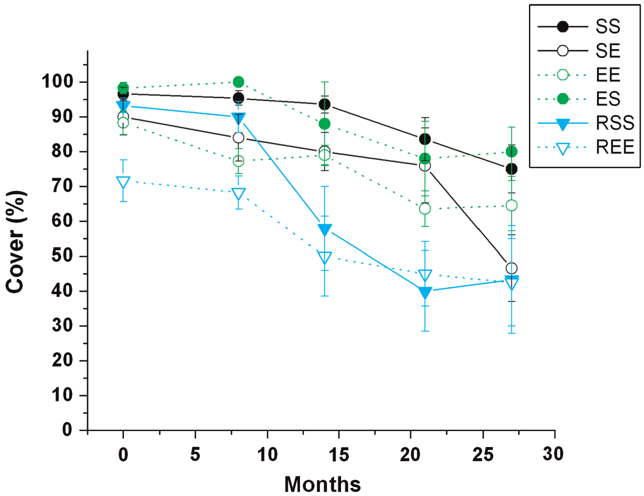

Figure 2. Percent cover ($\overline{X}$ and SEs) for the transplants and replants over the course of 27 months. Circles, transplants; squares, replants; open symbols, exposed during study; dark symbols, shaded during study; dashed line, original microhabitat is exposed; solid line, original microhabitat is shaded. This figure appears in color in the online version of the article [doi: 10.1111/j.1526-100X.2008.00445.x].

percent cover declined markedly, and mortality was evident across all treatments. The greatest decline in cover was observed in shaded plants moved into an exposed habitat (50%). When exposed plants were moved into shaded habitats, higher cover values were present after 27 months (a reduction of 13%). This pattern was reflected in shoot density, with a nearly 10-fold decline in shoot density at the conclusion of the experiment in the shaded to exposed treatment compared to the exposed to shaded treatment. Clearly, shaded plants, when reciprocally transplanted with exposed plants, did not adapt as well as their reciprocals, although these tendencies were not statistically significant. When exposed plants were relocated to exposed habitats, the effect on cover after 27 months was similar to that of shaded plants relocated into shaded habitats (declines of 29 vs. 22%, respectively). Coupling the tendency of better density if the source is from an exposed site with the significant decline in cover if the destination is to an exposed site, our recommendation is that the one combination to be avoided when moving sections of crust containing *Syntrichia* is using shaded source material and transplanting it into exposed sites; all other combinations will work comparatively well.

Several nondesert bryophyte species have been subjected to transplantation, although most such studies were not a part of an explicit test of transplantation success rate under field conditions. Experiments were carried out to detect fertilization in *Climacium* (both sexes into greenhouse pots; Bedford 1938) and *Pleurozium* (male stems into female patches and female stems into male patches; Longton & Greene 1969), in both cases demonstrating successful fertilization. In a study of gamete dispersal distances, 54 patches of *Weissia controversa* Hedw. were reciprocally transplanted along a road shoulder in Florida, with 74% (40) of these transplants surviving to reproduce sexually (Anderson & Lemmon 1974). Similarly, tufts (9 cm^2) of *Tetraphis pellucida* Hedw. were reciprocally transplanted along a decaying log in New York (U.S.A.) in a study of the change in allocation of sporophytic versus gemmiferous shoots (Kimmerer 1991). Transplants were left in place for 15 months, with little or no mortality. *Pogonatum dentatum* was successfully reciprocally transplanted between upland and lowland habitats in Sweden in a study of life history traits (Hassel et al. 2005). Patches of the pleurocarpous *Hylocomium splendens* (Hedw.) B.S.G. were successfully reciprocally transplanted when dry between contaminated and uncontaminated sites, including treatments of moss turf and moss turf with associated organic layers (Brūmelis et al. 2000). The aquatic *Fontinalis antipyretica* Hedw. was transplanted from one stream into another in Portugal by moving stones to which the plants were attached, for a period of 27 days, to test metal accumulation from mine effluent (Sérgio et al. 2000). Finally, reciprocal transplants of shaded and exposed patches of the semiarid grassland moss *S. ruralis* (Hedw.) Web. & Mohr were successfully executed with desiccated plants, but monitoring was only for a period of 8 days in order to assess photosynthetic efficiency (Hamerlynck et al. 2002).

Table 2. Initial and final shoot densities in *Syntrichia* crust transplants.

	Initial Mean Shoot Number (per cm^2) (± 1 SD)	*Final Mean Shoot Number (per cm^2) (± 1 SD)*	*Percent Gain or Loss After 27 Months*
Shaded to shaded, $n = 12$	34.99 ± 3.37	21.38 ± 12.62	−38
Exposed to exposed, $n = 11$[a]	39.43 ± 14.06	30.54 ± 8.33	−14
Exposed to shaded, $n = 5$[a]	37.13 ± 7.20	34.55 ± 13.79	−03
Shaded to exposed, $n = 6$	31.74 ± 11.76	22.96 ± 15.96	−29
Replants			
Shaded, $n = 6$	35.19 ± 8.14	14.70 ± 9.25	−57
Exposed, $n = 4$[b]	26.75 ± 4.17	26.11 ± 13.37	−04
Overall mean	35.18 ± 9.39	24.90 ± 12.82	−26

[a] One transplant was disturbed and lost in these treatments.
[b] Two transplants were disturbed and lost in this treatment.

The deleterious effects of large grazing animals on desert lands, and on biological crusts in particular, have long been recognized (Beymer & Klopatek 1992) but remained controversial until recently summarized (Jones 2000; Warren & Eldridge 2001). Soil-related variables (including the soil crust, bulk density of soil, soil erosion, and soil infiltration) and vegetative cover variables were found to be most sensitive to grazing in arid lands. Of the six studies that have assessed the effects of grazing on biological soil crusts, an average reduction in percent crust cover in grazed treatments was 44% (Jones 2000 and references therein). Furthermore, biological crust cover was suggested as a primary metric for rangeland managers to assess the health of arid lands.

Bryophyte patches likely have the greatest density of shoots of any plant, although estimates of this parameter are few. In *S. caninervis*, the density of organically connected individuals was estimated at $22/cm^2$ and after adjusting for the number of shoots per individual equates to approximately 41 shoots/cm^2 (Stark et al. 2001). The overall mean initial shoot density in the current study was 35 shoots/cm^2, ranging from 27 to 39 shoots/cm^2. Unfortunately, such high densities may mean that, in a single step, a large animal, including humans, can kill thousands of plants, noting, however, that ungulate footprints at low densities promoted the growth of the soil moss *Ceratodon* (Csotonyi & Addicott 2004).

In the Gurbantunggut and Tengger deserts of northern China, *S. caninervis* (as *Tortula desertorum*) has been the subject of a variety of studies in attempts to reconstruct the biological crust in the lab and field (e.g., Tian et al. 2005). Plants of *S. caninervis* respond better when cultivated from native soil and regenerate faster in the lab from detached leaf fragments (Xu et al. 2008). The latter authors determined that in China, *S. caninervis* exhibited the most vigorous asexual reproduction during the early summer and found that this species can be cultured in the lab from protonema to shoot production in about 2 months, whereupon it can be placed into the field. The related crust species *S. ruralis*, widespread in cold deserts, was found to propagate less rapidly from fragments compared to *Ceratodon* and *Bryum* (Jones & Rosentreter 2006). Due to the warmer early summer temperatures in the Mojave Desert, we suggest that the time for transplanting or moving lab explants of *S. caninervis* be in late winter or early spring to capitalize on the winter/early spring rainfall and cooler temperatures.

From a crust standpoint, two major microhabitats exist in the Mojave Desert: under shrub canopy (shaded) and in open areas (exposed). The shaded sites tend to have a higher soil moisture content, likely owing to the effect of canopy shade in retarding evaporation from the soil surface (Thompson et al. 2005). Plants of *S. caninervis* differ according to microhabitat. Shaded plants tend to be larger, express sex more frequently, undergo sexual reproduction more frequently, and are the only site in which males occur (Bowker et al. 2000). Based on studies of its close relative *S. ruralis*, which also occupies dimorphic microhabitats in arid grasslands, plants in the more exposed microsites, when compared to their shaded counterparts, were smaller and had lower tissue N and C, lower pigment concentrations, and reduced efficiencies of photosystem II, even after moving into a shaded microsite (Hamerlynck et al. 2002). Acclimation was predicted by the latter authors to occur slowly following transplantation, longer than their weeklong experiment.

In most reciprocal transplant experiments involving seed plants, individuals are sampled and grown in a glasshouse for a period prior to transplantation. This serves to reduce the carryover effects of, for example, stored resources and mycorrhizae (Schmid 1985). Such standardization may also allow the authors to define or grow shoots for the experiment or to determine genetic diversity of study patches (e.g., Kik et al. 1990). In mosses, however, roots do not occur, and shoots are well defined, and so there is less need for the intermediate glasshouse step in transplantation studies.

Syntrichia caninervis reproduces without the assistance of specialized asexual propagules. However, the species, like most other mosses, is capable of vegetative propagation through fragmentation due to the totipotency of most gametophytic cells. Therefore, while stepping on a patch may injure or kill the shoots, if the crushing occurs when shoots are dry (most of the time), such crushing actually may serve to disperse bits of stems and leaves that can germinate into plants elsewhere or in place. The frequency of sexual reproduction is low owing to the rarity of male plants and restricted sperm dispersal distances involved. In order for sexual reproduction to occur, male and female plants must be nearly juxtaposed because sperm dispersal distances are on the order of millimeter to a few centimeters (Anderson & Lemmon 1974).

It follows that most *S. caninervis* patches are probably established asexually through the dispersal of broken branches, buds, and leaves from parent patches. Although spreading crust inoculant is effective for some crustal components (Belnap 1993), full recovery of *S. caninervis* patches from crushed fragments or spores would take up to 15 years, given immediate establishment (unlikely), based on current age estimates of individual plants that approximate 15 years (Stark et al. 2000). The transplantation of existing patches from areas of abundance may hasten the process by providing instant source patches, which can then spread into impacted areas. Transplantation of the bryophyte crust therefore, at a minimum, has potential for small-scale reclamation projects on arid soils.

The decline in cover across treatments is mitigated by the increased mortality in the host patches. The host patches can be viewed as a control for natural, undisturbed patches that surround each transplant or replant. At the conclusion of the study, mortality in host patches ranged from 4 to 11 dead shoots/cm^2 compared to 4–9 dead shoots/cm^2 in the treatments. One outlier was the exposed replant, which had a very high mortality, 20 shoots/cm^2. Therefore, we conclude that mortality was approximately equivalent between the treatments and the host patches. That cover declined in the transplants without significant mortality during the first 21 months of the study is puzzling; a decline in cover by about 20% with no observable mortality may be in part due to sampling error associated with visually approximating cover to the nearest 10%. Alternatively, such a disparity may arise through a decrease in shoot density, perhaps through individual shoot removal or disturbance from animals. Unfortunately, we have no intermediate determinations of shoot density, only initial and final, and density counts for host patches were not assessed. The duration of the experiment occurred during a particularly harsh weather pattern with respect to the mosses. Over this period, conditions were too dry to allow a complete sexual reproductive cycle to be completed. Sporulation was last noted in this area in the summer of 1998. Sporophytes were not matured in 1999 or 2000, and we suggest that these conditions of low rainfall have negatively impacted the entire community of gametophytes. That all the transplants are at least in part still alive at the conclusion of the study is a positive result, given the abiotic conditions that accompanied this study.

Implications for Practice

- This study demonstrates, for the *Syntrichia caninervis*–dominated soil crust associated with Blackbrush communities in the Mojave Desert, that bryophyte crusts can be transplanted with a fairly high success rate and that the microhabitat of the source and destination patch (shaded or exposed) should be taken into account when undertaking transplants for restoration measures. Specifically, moving a patch of *Syntrichia* from a shaded site to an exposed site should be avoided.
- For restoring a bryophyte crust in arid lands, whole sections of patches can be used by way of making a shallow core of a resident patch and inserting the core into the area in need of restoration.
- For best results, patches under the canopy of shrubs should be transplanted to a similarly shaded region. If shrub canopy in the destination region is not available, then the source patches used should come from exposed sites.
- Transplanting should be carried out during the late winter or early spring in hot deserts and in late spring in cold deserts.

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