Alga- and Lichen-Stabilized Surface Crusts as Soil Nitrogen Sources

ALGA- AND LICHEN-STABILIZED SURFACE CRUSTS AS SOIL NITROGEN SOURCES[1]

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ALGAE AND LICHENS contribute significantly to soil formation in a variety of ecological habitats. Algae have been investigated from the standpoint of nitrogen nutrition in desert (Fogg, 1947) and semidesert soils (Robbins, 1912; Fletcher and Martin, 1948), as a source of oxygen (Harrison and Aiyer, 1913) and nitrogen (Watanabe et al., 1951) in rice fields, and with respect to their possible value as pioneer vegetation in volcanic deposits (Treub, 1888). Soil algae are also recognized as an important agency in stabilizing surface crust in areas denuded of macro-vegetation by drought (Piercy, 1917; Drouet, 1937) or erosion (Elwell et al., 1939; Osborn, 1950) and in improving water infiltration (Booth, 1941).

The present study investigates (a) the seasonal incidence of algal species in alga- and lichen-stabilized soil crusts from several semi-arid habitats and (b) the amino nitrogen and combined nitrite and nitrate of these surface strata compared to subsurface levels. Observations are based mainly on soil samples collected from the Tularosa Basin in Lincoln and Otero Counties, southcentral New Mexico, from two strikingly contrasting xeric habitats. One, the Alamogordo White Sands (fig. 1), a deposit of drifting, 97 per cent gypsum, lies in the lowest part of the basin, covering an area approximately 28 miles long and 8 to 10 miles wide to a depth of 1000 ft. (Potter, 1938). The other, a recent lava flow, the Carrizozo "malpais" (fig. 2), extends northward along the main axis of the basin, filling a narrow valley ½ to 5 miles wide and 44 miles long to a depth of around 70 ft. toward the center and 10 to 20 ft. along the margins. In addition, samples were collected from that part of the Tularosa Basin immediately surrounding the gypsum sand deposit and the lava flow. This section of the basin floor varies from semidesert, alkaline plain adjacent to the gypsum deposit to typical overgrazed range land adjoining the lava flow on either side. Average annual precipitation in the Tularosa Basin, ranging from approximately 8 in. in the White Sands to 11 in. at the northern tip of the lava flow, is correlated mainly with altitude. The depth of the water table varies from 2 to 3 ft. in the gypsum flats to well over a hundred feet in parts of the surrounding basin floor.

METHOD.—Soil crust and subsurface samples were collected in the dried condition from widely separated sections of the gypsum sand, the lava flow, and the surrounding basin floor. In the field, these samples were placed directly on moistened filter paper in sterile Petri dishes to minimize fungal contamination. These cultures were maintained in indirect light at room temperature for several weeks for microscopic observation and the identification of algal and lichen species. A portion of each sample was dehydrated for the determination of amino nitrogen by Allen's method (1951) for semi-micro-Kjeldahl analysis. Total nitrite and nitrate determinations were made on each sample by a modification of the Bray method (1945). Small amounts of soil were introduced into nitrogen-free mannitol media to check for nitrogen fixation by azotobacter and into inorganic ammonium sulfate media selective for nitrifying organisms.

OBSERVATIONS.—1. *Alga and lichen floras of gypsum sand.*—An alga-stabilized surface crust covers flats of the gypsum sand throughout except in the immediate vicinity of seed plants. This surface stratum retards wind and water erosion by binding together an otherwise mobile substrate. It separates readily from subsurface layers in pieces 6 to 11 in. across and usually ranging from 5 to 10 mm. in thickness (fig. 3). The crust consists of gypsum particles consolidated mainly by gelatinous masses of the ensheathed, unicellular green alga, *Palmogloea protuberans* (Sm. and Sow.) Kutz., parasitized by fungal hyphae, and associated occasionally with *Plectonema nostocorum* Born. and rarely also with *Nostoc* spp. *Palmogloea* and the associated organisms form a bright green seam 2–5 mm. below the surface as well as a black-green patchy surface growth (fig. 4, 5) which becomes conspicuously darkened following several rains.

Table 1 indicates the incidence at different seasons of the 3 algal species which throughout the year contribute to stabilizing the surface crust of the gypsum flats.

Palmogloea protuberans (fig. 6), along with the associated fungus, appeared in 56 out of 68 algal crust samples collected from widely separated sites in the gypsum deposit. *Plectonema nostocorum* was present in 8 and *Nostoc* spp. in only 4 of the algal crusts. Samples from the surface of peripheral gypsum flats one to 3 dunes removed from the surrounding plain ordinarily contained, in addition to the above species, 2 or more of the following: *Microcoleus vaginatus* (Vauch.) Gom., *M. paludosus* (Kutz.) Gom., *Schizothrix californica* Dr., *S. lamyi* Gom. and *Scytonema hofmannii* Ag. These species, characteristic of the surrounding Tularosa Basin floor and of the lava soils, do not appear in the gypsum sand except in these

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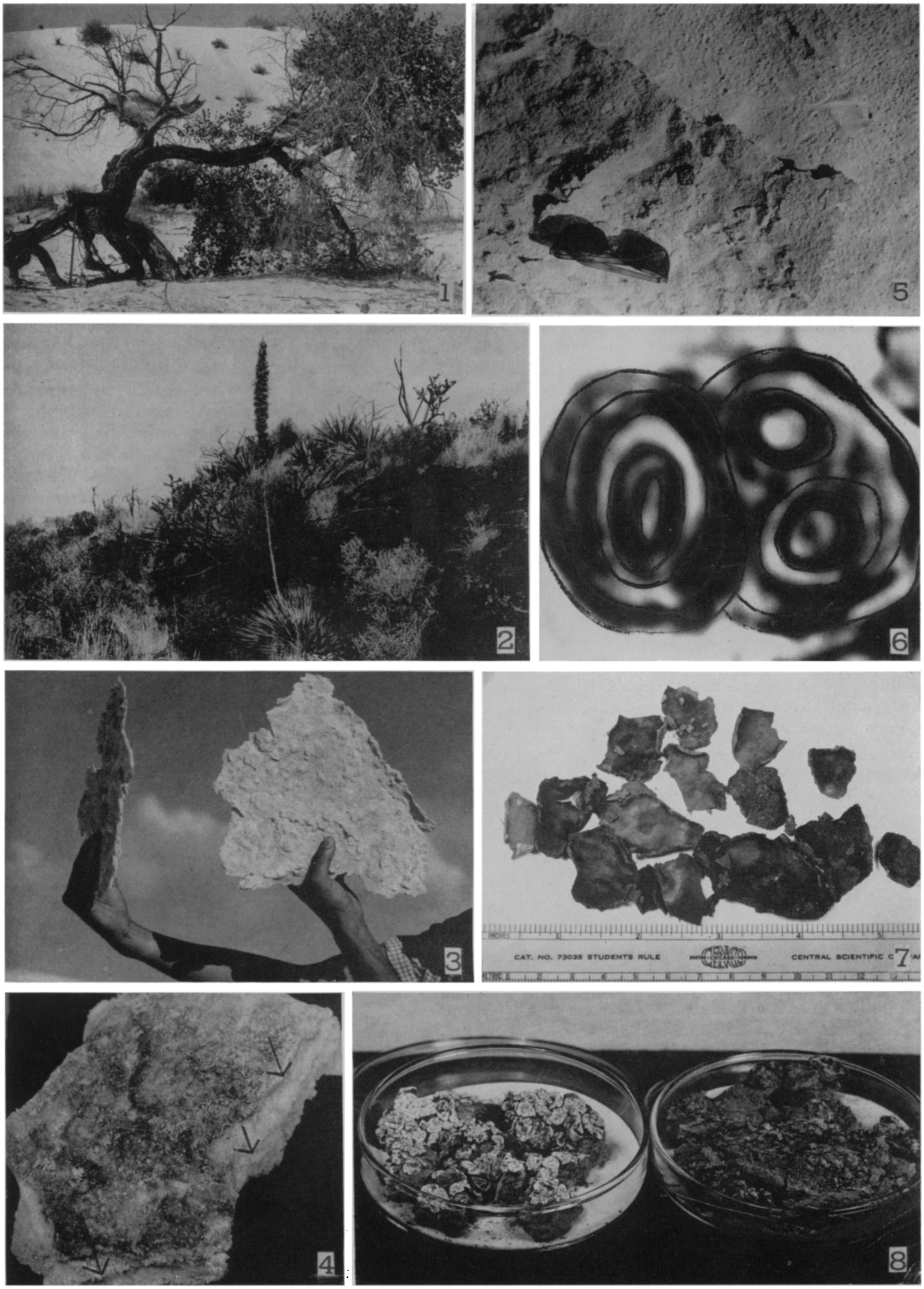
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TABLE 1. *Average amino nitrogen content and incidence of algal species in stabilized surface crust on gypsum sand, Alamogordo, New Mexico*

		Total number of samples	*Nostoc* spp.	*Palmogloea protuberans* (Sm. & Sow.) Kutz.	*Plectonema nostocorum* Born.	Average for all samples in collection series
June	Average amino nitrogen of crust samples (p.p.m., range 147–227)		—	212	207	212
	Number of samples in which this alga appeared	20	0	16	4	
July	Average amino nitrogen of crust samples (p.p.m., range 51–425)		—	252	175	245
	Number of samples in which this alga appeared	22	0	20	2	
November	Average amino nitrogen of crust samples (p.p.m., range 80–535)		417	277	299	297
	Number of samples in which this alga appeared	26	4	20	2	
		68				256 (Av. for all samples)

marginal areas. *Palmogloea protuberans*, on the other hand, was found in no samples from outside the gypsum deposit.

In the gypsum and other soils examined algae were present below the surface crust only where drifting sand had buried earlier algal growth. Occasionally successively-formed surface crusts are covered by intermittent wind action, resulting in stratification of algal layers at about 2-in. intervals down to a depth of 6 to 8 in. Algal growth and activity, however, are limited to the surface inch of soil, the organisms not surviving to any appreciable extent after burial. This, along with the lack of adequate moisture, explains the absence of algae from the drifting dunes which alternate with the narrow gypsum flats.

In most samples the algae, particularly *P. protuberans*, are in various stages of parasitism or lichenization, but lichen crusts are characteristic of only the peripheral flats where a surface growth mainly of *Heppia* and *Dermatocarpon* spp. form black, warty hummocks one-half inch to several inches across. Such lichen growth is characteristic of the alkaline plain immediately surrounding the gypsum sand.

2. *Nitrogen content of gypsum sand.*—The high amino nitrogen found in the surface crust from gypsum flats is identified with the stabilizing algal layer. Amino nitrogen of the algal crust, ranging in individual samples from 147 to 227 p.p.m. in June, 51 to 425 p.p.m. in July and 80 to 535 p.p.m. in November (table 1), varies both with the thickness of the algal seam and the extra-algal fraction. The higher amino nitrogen of the surface crusts containing *Nostoc*, averaging 417 p.p.m. (table 1), suggests that this may be a nitrogen-fixing species,

Fig. 1–8.—Fig. 1. Typical encrusted gypsum flat and drifting dune, Alamogordo White Sands, New Mexico.—Fig. 2. A more densely vegetated section of a recent lava flow, Carrizozo, New Mexico.—Fig. 3. Gypsum crust consolidated by the unicellular green alga, *Palmogloea protuberans,* and associated organisms. Crust samples 5–10 mm. thick and up to 11 in. across separate readily from subsurface layers.—Fig. 4. Gypsum crust showing subsurface algal seam and darkened surface growth.—Fig. 5. Alga-stabilized crust of gypsum flat.—Fig. 6. Photomicrograph of ensheathed *Palmogloea protuberans,* which with associated organisms stabilizes the surface crust and constitutes the ultimate nitrogen source of the gypsum sand.—Fig. 7. Typical surface crust from lava soil, stabilized by three species of filamentous blue-green algae, *Microcoleus paludosus, M. vaginatus* and *Schizothrix californica.*—Fig. 8. Typical lichen crusts from lava soil, *Lecidea rubiformis* (left) and *Dermatocarpon hepaticum.*

either *N. commune* Vauch. or *N. muscorum* Ag. Samples from a depth of 6 in. showed amino nitrogen only in scattering sites where water had stood recently or where stratification of soil layers containing algae indicated burial of previous algal crusts by wind action. The contrast between surface and subsurface levels of amino nitrogen is most apparent in the difference in amino nitrogen of the gypsum crust, averaging 212 p.p.m. in June, 245 p.p.m. in July and 297 p.p.m. in November (table 1), and amino nitrogen of samples taken at a depth of 6 in., averaging 10 p.p.m. in June (table 4, 1), with rare traces of amino nitrogen at the 12-in. level. Soil samples from the dunes were negative for amino nitrogen, nitrite and nitrate. Only the peripheral flats, where the gypsum substrate is contaminated by soil from the neighboring plain, support a microflora which is a rich source of amino nitrogen, the lichen crust in this area averaging 1178 p.p.m. (table 4, 1).

Total nitrite and nitrate average 2.1 p.p.m., ranging from 0.5 to 8 p.p.m. (table 4, 1) for samples of gypsum sand from depths of 3 to 6 in. in the vicinity of young absorbing roots where the greatest amounts of organic material and microbial activity presumably occur. In the algal crusts, however, total nitrite and nitrate for 20 samples collected in June (table 4, 1) average 5.6 p.p.m., or more than 10 times the average concentration of 0.45 p.p.m. 6 in. below the algal crust.

Neither nitrogen fixation activity nor the organism *Azotobacter* could be demonstrated in the gypsum substrate with media selective for this organism. In ammonium sulfate inorganic media, positive tests for nitrite and nitrate were obtained after 6 months in 56 per cent of 107 gypsum sand cultures taken in essentially equal numbers from the surface, 6-in. and 12-in. levels. The subsurface inocula ordinarily were obtained from the vicinity of absorbing roots. The usual nitrifying organisms, however, could not be isolated in fluid media nor on silica gel.

3. *Alga and lichen floras of lava soils.*—The relatively unweathered lava lacks any accumulation of soil except in scattering surface depressions, which support around 130 species of seed plants. Surface crust from soil pockets in the lava were commonly smaller and thinner samples than those separating naturally from flats in the gypsum sand. The high amino nitrogen of the alga-stabilized crusts is identified largely with the presence of several filamentous blue-green algae, mainly species of four genera: *Microcoleus, Porphyrosiphon, Schizothrix* and *Scytonema.*

Table 2 gives the incidence of the 13 algal species found in March, June and November in alga- and lichen-stabilized surface crusts on lava soil. The most widely distributed species is *Microcoleus vaginatus.* It appears in 40 out of 50 alga- and in 31 of 59 lichen-stabilized crusts, or in 71 of the total 109 samples. *Porphyrosiphon fuscus* Gom., the second most abundant species, appears in 19 of 50 algal and in 27 of 59 lichen crusts, or in 46 of 109 samples. Within the Tularosa Basin this species was found only in lava soils. *Schizothrix californica* appeared in 24; *Scytonema ocellatum* Lyngb., in 19; *S. hofmanii,* in 16; *Schizothrix giuseppei* Dr., in 15; *Microcoleus paludosus,* in 13; and *Nostoc* spp. in 10 of the 109 samples from widely separated sections of the lava, while 3 algal species occurred in only one sample each, and 2 were found in fewer than 10 samples (table 2). *Microcoleus vaginatus* was less prominent in algal crusts in March, appearing in 11 out of 27 samples, than in those of the June and November collection series, in which it occurred in 24 out of 40 and 36 of 42 samples, respectively (table 2).

Certain of the species which appear less frequently are in only one collection series, but none of these soil algae show a cleancut seasonal succession. The number of algal species per algal crust sample ranged from 1 to 4. The average number for March, June and November was, respectively, 2.8, 2.1 and 2.1. Sample 39, collected in November (fig. 7), is typical of one form of algal crust which separates from the lava soil in drying, curling away from the subsurface strata. The areas of darker coloration are identified with the growth of *Microcoleus paludosus, M. vaginatus* and *Schizothrix californica.* The average of several amino nitrogen determinations on this crust was 1872 p.p.m.

Within the lava flow lichens form encrusted gray, black or white growths on most of the surface soil pockets. The lichen body, together with a loosely held and highly porous soil mass, separates from subsurface strata as an encrusted unit (fig. 8). These lichens are of different species and usually also of different genera than those on the adjacent basalt rock with which they superficially appear to be continuous. Rock and soil lichens are each inclined to grow on only the one particular substratum. The colorful display of lichens on rough basalt surfaces, particularly those tilted toward the vertical, are frequently predominantly mixed bright yellow-green, gray-green and reddish-brown species of *Acarospora.* Solid areas of any one species are rare.

The lichens characteristic of lava soil are listed in table 3.[2] These lichen growths extend from the somewhat sheltered and presumably more moist rock bases outward into the soil pockets. Like the soil algae, the lichens ordinarily do not grow about the base of seed plants, with the exception of *Sporobolus* spp. and other bunchgrasses.

Of the total of 59 samples of surface crust from lava soil showing lichen growth, *Dermatocarpon squamellum, Heppia despreauxii* and *Collema coccophorum* appeared most frequently, occurring in

[2] The authors are indebted to Dr. Grace Howard, University of Washington, for the determinations of the lichen species.

TABLE 2. *Amino nitrogen content and incidence of algal species in stabilized surface crust on lava soil, Carrizozo, New Mexico*

		Total number	*Microcoleus paludosus* (Kutz.) Gom.	*M. vaginatus* (Vauch.) Gom.	*Nostoc* spp.	*Plectonema nostocorum* Born.	*Porphyrosiphon fuscus* Gom.	*Schizothrix acutissima* Dr.	*S. californica* Dr.	*S. giuseppei* Dr.	*S. macbridei* Dr.	*S. stricklandii* Dr.	*Scytonema ocellatum* Lyngb.	*S. hofmannii* Ag.	*Symploca muscorum* (Ag.) Gom.
March	Average amino N (p.p.m.)		——	1283	1579	——	1328	——	1575	——	——	——	1202	1592	——
	Algal (range 616–1941)		2144	1379	——	——	1317	——	1594	894	1626	1188	1451	1146	——
	Lichen (range 626–2784)														
	Algal crusts containing this species	11	3	6	1	0	8	0	5	0	0	0	3	2	0
	Lichen crusts containing this species	16	3	5	0	0	4	0	3	3	1	1	6	2	0
June	Average amino N (p.p.m.)														
	Algal (range 822–1913)		1525	1473	1525	——	——	——	1525	1729	——	——	——	——	——
	Lichen (range 1271–3059)		1718	2231	2389	——	2209	——	——	2125	1561	1585	2412	2283	——
	Algal crusts containing this species	11	1	10	1	0	0	0	2	3	0	0	0	0	0
	Lichen crusts containing this species	29	4	14	5	0	17	0	0	9	2	0	1	11	0
November	Average amino N (p.p.m.)														
	Algal (range 914–2355)		1636	1778	2309	——	1695	1665	1778	——	2406	——	1818	——	1844
	Lichen (range 1810–3267)		——	2644	2725	2944	2428	2705	2489	——	——	——	2891	2357	——
	Algal crusts containing this species	28	2	24	1	0	11	5	11	0	1	0	5	0	1
	Lichen crusts containing this species	14	0	12	2	1	6	3	3	0	0	0	4	1	0
	Total	109	13	71	10	1	46	8	24	15	4	1	19	16	1

20, 12 and 9 samples respectively (table 3). *Heppia guepini* and *Solorina saccata* were found in only one crust sample each. The only lichen crusts lacking a growth of algae independently of the lichen were 4 samples of *Dermatocarpon squamellum.*

On lava soil the same algal species are characteristic of the extra-lichen fraction of the lichen crusts as of algal crusts (tables 2, 3). The number of algal species within each soil crust supporting lichen growth ranged from 1 to 5 and averaged 2.5 in March, 2.4 in June and 2.7 in November. Very few of these algae are listed in the literature as lichen hosts. Since it is not known what algae the usually listed hosts of these lichens are derived from, however, they may be some of those found in this study to occur within the lichen bodies in the free state.

Microcoleus vaginatus was isolated from a greater variety of lichen crusts than any other alga, appearing in all samples of *Collema nigrescens* and in from half to most of the other lichen crusts (table 3). *Porphyrosiphon fuscus* was second highest in incidence, appearing frequently in association with all of the 8 lichen species.

Only *Microcoleus vaginatus* (in 40 algal and 31 lichen samples) and *Schizothrix californica* (in 18 algal and 6 lichen samples) appeared much more frequently in algal than in lichen crusts (table 2). *Microcoleus paludosus, Porphyrosiphon fuscus, Schizothrix acutissima* and *Scytonema ocellatum* occurred in essentially equal numbers of alga- and lichen-stabilized crusts, while *Nostoc* spp., *Schizothrix giuseppei, S. macbridei* and *Scytonema hofmannii* appeared much more frequently in association with lichens. The only specimens of lava soil in which *Schizothrix stricklandii* and *Plectonema nostocorum* appeared were lichen crusts, though *P.*

nostocorum is fairly common in the gypsum sand. *Scytonema hofmannii* and *Porphyrosiphon fuscus* are more abundant in lichen crusts in June than in either type of sample for other seasons. *Microcoleus vaginatus* is less prominent in March than in June or November.

4. *Nitrogen content of lava soil.*—Table 2 indicates the range in amino nitrogen for a total of 50 algal and 59 lichen samples collected in March, June and November. Both the upper and lower limits of the range of amino nitrogen were lower for algal than for lichen crusts. The amino nitrogen of the lichen crust averaged slightly higher in March, almost one-fourth higher in June, and more than one-third higher in November than that of the algal crust (table 4, 2). For all 3 collection series, amino nitrogen averaged 1545 p.p.m. for the 50 algal and 1985 p.p.m. for the 59 lichen crusts. Total nitrite and nitrate for the same samples averaged 7.9 p.p.m. and 6.2 p.p.m., respectively. The amino nitrogen of the lichen crusts averaged 22.2 per cent higher and the total nitrite and nitrate 21.5 per cent lower than in alga-stabilized surface strata. Average amounts of nitrite and nitrate of the algal crust show less seasonal variation than amino nitrogen. For lava soil samples from depths of around 3 in. in the vicinity of young absorbing roots total nitrite and nitrate averaged 1.87 p.p.m. and ranged from 0.5 to 11.5 p.p.m. (table 4, 3). The relatively high amino nitrogen of the few samples of lava surface soil lacking algae or lichens, averaging 866 p.p.m. (table 4, 3), might be explained by leaching from adjacent areas in the same soil pocket, by the accumulation of organic material over a long period, as at the base of trees or shrubs, or by the presence of a non-photosynthetic microflora. Only 10 such samples were among the 125 surface specimens collected within the lava flow. Algal crusts, however, are 78 per cent higher in amino nitrogen and lichen crusts 85 per cent higher than these lava surface layers lacking such growth. The amino nitrogen of the imported yellow clay along the main highway across the lava, averaging 422 p.p.m. (table 4, 3), also appears to come from the cover of macrovegetation or from a microflora lacking chlorophyll.

The amino nitrogen content of lichen crusts varies with the luxuriance of growth rather than with any particular combination of algal and lichen species (table 3). Even the lichens which may contain *Nostoc* as the algal host, as *Collema nigrescens* or *Solorina saccata* var. *spongiosa*, are not significantly higher in amino nitrogen, where at all higher. Amino nitrogen of lichen crust formed by a particular species may vary widely with the substrate or when growing in association with a moss. The amino nitrogen of *Collema nigrescens* growing on soil at the base of sandstone rocks on an island in the lava flow averaged 836

TABLE 3. *Lichen species forming surface crust on lava soil, algal host in lichen, associated algal species most commonly found in soil samples, and average p.p.m. amino nitrogen for surface crust with included lichen and algae*

Lichen	Algal host	Number samples	Algal species in soil with lichen [a]	Average p.p.m. amino N
1. *Collema nigrescens* (Huds.) D.C.	*Nostoc*	5	B in all, E in 2, G in 1, L in 1	836 on sand, 2838 on lava soil
2. *Collema coccophorum* Tuck.	?	9	A in 2, B in 6, C in 3, E and K in 3, H in 4, I in 3, J in 1	1958 on lava soil
3. *Dermatocarpon squamellum* (Nyl.) Herre	*Pleurococcus*	20	A in 1, B in 3, C in 1, E in 9, H in 2, K in 6, L in 5	932 with moss, 1797 with algae
4. *Heppia despreauxii* (Mont.) Tuck.	blue-green, usually *Pleurococcus*	12	A in 2, B in 6, C in 1, D in 1, E in 6, F in 1, G in 1, H in 1, K in 3, L in 4	2093
5. *H. guepini* (Del.) Nyl.	same as above	1	B, E, F, G	2030
6. *Lecidea decipiens* F. *dealbata* (Mass.) Jatta	*Protococcus*, *Gloeocapsa*, or *Pleurococcus*	6	A in 1, B in 6, C in 2, E in 4, G in 3, H in 4, L in 1	2203
7. *L. rubiformis* Wahl.	same as above	5	A in 1, B in 3, E in 1, F in 1, H in 1, K in 2	2721
8. *Solorina saccata* var. *spongiosa* Nyl.	*Palmella* or *Nostoc*	1	B and E	2542
	Total	59		

[a] Key to algal species in column 4 above:

A. *Microcoleus paludosus*	E. *Porphyrosiphon fuscus*	I. *S. macbridei*
B. *M. vaginatus*	F. *Schizothrix acutissima*	J. *S. stricklandii*
C. *Nostoc* sp.	G. *S. californica*	K. *Scytonema hofmannii*
D. *Plectonema nostocorum*	H. *S. giuseppei*	L. *S. ocellatum*

TABLE 4. *Nitrite, nitrate and amino nitrogen (p.p.m.) at different seasons for soil types in the Tularosa Basin, New Mexico*

		Number samples	Average NO_2^- plus NO_3^-	Range NO_2^- NO_3^-	Average amino nitrogen	Range amino nitrogen
1. GYPSUM SAND						
June	Algal crust, inner flats	20	5.6	2.6–9.0	212	147–227
	6″ down, flats	20	0.45	0.0–1.5	10	0.0–53
	12″ down, flats	20	0.0	——	0.1	0.0–0.8
	Subsurface, 3-6″, near macrovegetation, no crust	41	2.1	0.5–8.0	no detn.	no detn.
	Lichen crust, peripheral flats	10	5.2	1.5–15.0	1178	447–2417
2. LAVA SURFACE CRUSTS						
March	Algal	11	7.9	1.5–16.0	1355	616–1941
	Lichen	16	5.9	1.5–16.5	1425	626–2785
June	Algal	11	7.2	3.2–13.6	1504	822–1913
	Lichen	29	6.1	2.0–12.0	2019	1271–3059
Nov.	Algal	28	8.2	2.0–18.0	1639	914–2355
	Lichen	14	6.8	1.5–17.5	2582	1810–3267
3. LAVA SOILS LACKING ALGAE OR LICHENS						
June	Subsurface, 1-3″, vicinity of roots	32	1.87	0.5–11.5	821	575–984
	Surface, no crust	10	1.5	0.5–4.0	866	629–1084
	Roadside, yellow clay	6	1.0	0.5–3.0	422	258–548
4. TULAROSA BASIN FLOOR						
June	Lichen crust adjacent to gypsum deposit	12	10.5	5.5–21.2	1553	1034–2271
	6″ down from above	12	5.0	0.5–16.0	199	51–372
	Algal crust adjacent to gypsum	10	8.9	3.5–20.0	1031	548–1641
	Surface soil lacking algae or lichens (mesquite-creosite bush zone)	10	2.1	1.5–2.5	225	147–314
	6″ down from above	10	2.5	1.0–3.0	270	234-328

p.p.m., less than one-third the concentration for the same species on lava soil (table 3), though the associated algal species were identical in the two substrates. Similarly, the amino nitrogen of *Dermatocarpon squamellum* intermingled with moss averaged 932 p.p.m., slightly more than one-half the concentration for the same lichen species growing alone or associated with algae, apparently because of the high content of inert cellulosic material in moss. The average amino nitrogen for all seasons for the 8 lichen species growing on lava soils alone or with associated algae ranged from 1797 to 2838 p.p.m. (table 3).

Over a period of 13 months, nitrate was formed in 17 and ammonia in 30 of 41 nitrogen-free mannitol cultures inoculated with lava soil from the vicinity of roots, demonstrating an efficient nitrogen-fixing capacity. *Azotobacter* was isolated from somewhat less than half the cultures. In ammonium sulfate inorganic media, positive tests for nitrate were obtained in 27 of 41 lava soils in 7 months and 34 in 13 months. The usual nitrifying organisms, however, could not be isolated on silica gel.

5. *Algal and lichen floras and nitrogen content of soils from the Tularosa Basin floor.*—Soil samples were collected from various parts of the basin floor surrounding the gypsum sand and the lava flow. The aridity and salinity of this alkaline plain exercise a selective action on macrovegetation and probably also on the microflora. For most of the length of the lava flow, on that part of the basin floor adjacent on either side, bare patches of soil, gravelly in places, separate the widely spaced shrubs of creosote bush, mesquite or *Atriplex* which successfully compete with semidesert herbaceous undercover for the limited moisture. Physically, the soil under mesquite and creosote bush is coarser, moisture relations are less favorable, and the surface soil is less stable than in lower parts of the basin where *Atriplex* is dominant.

In the *Atriplex* zone, immediately surrounding the gypsum sand, black lichens of the genera *Heppia* and *Dermatocarpon* form conspicuous patches on the soil surface. The algae associated with the lichen growths are filamentous, blue-green forms of the same species as found in alga-stabilized surface crust in this part of the basin. Listed in order of diminishing frequency of occurrence, these algal species are *Microcoleus vaginatus, Schizothrix lamyi, S. acutissima, S. californica, Microcoleus paludosus* and *Scytonema hofmannii.* The algal flora of the basin floor is conspicuously lackting in *Palmogloea protuberans* and *Plectonema nostocorum* characteristic of the gypsum sand and in *Porphyrosiphon fuscus,* the second most prominent species in the lava flow.

Both the range (548 to 1641 p.p.m.) and the average (1031 p.p.m.) of amino nitrogen for algal crusts from the basin floor (table 4, 4) is lower than for lava soils. The average amino nitrogen for lichen crusts (1553 p.p.m.), however, compares more favorably with that for similar lava soil crusts. Amino nitrogen of algal crust from the basin floor averages 44 per cent higher and that of the lichen crust 56 per cent higher than for surface samples in the same area lacking such growth. Total nitrite and nitrate for the 6-in. level below lichen crusts, amounting to 5 p.p.m., is relatively high, comparing more favorably with that for the surface than other subsurface samples examined. Amino nitrogen at the 6-in. level immediately below the lichen crusts, averaging 199 p.p.m. (table 4, 4), is also comparatively high.

In the creosote bush and mesquite zones, in the absence of algal or lichen growth, no surface crust exists. The average amino nitrogen of 225 p.p.m. in surface samples contrasts sharply with that of algal and lichen crusts from lower parts of the basin. This is the only collection area where amino nitrogen and total nitrite and nitrate were higher at the 6-in. level than on the surface. This nitrogen appears to come from the limited organic debris and the activity of soil microflora other than algae and lichens.

DISCUSSION.—Soil algae in general endure drought periods through the ability to readily absorb atmospheric vapor as well as liquid water and through the protection afforded by gelatinous sheaths, granules, fat droplets, pigments, reduced vacuoles and, in some, spore formation. In surface forms many ordinary vegetative cells endure prolonged desiccation without any appreciable outward change (Fritsch, 1922). The various above mechanisms enable a variety of soil algae during drought to compete successfully with higher plants. *Porphyrosiphon notarisii* in Brazil grows in pure stands or in association with other species on dry soil denuded of macrovegetation (Drouet, 1937). One species of *Palmogloea* is frequently one of the colonizers of burned over soils (Fritsch, 1922).

The dominance of *Microcoleus vaginatus* on soils of the lava and the Tularosa Basin floor is attributable in part to its pronounced resistance to desiccation. This species has been developed from a soil culture maintained in a dry state for 36 months (Petersen, 1935). The genera *Microcoleus, Porphyrosiphon, Schizothrix* and *Scytonema* all have gelatinous sheaths, varying from homogeneous to lamellate. The sheath in *Porphyrosiphon* is purplish red and in older specimens of certain species of *Schizothrix* is also colored.

Only *Nostoc* of the 18 algal genera identified from Utah soils (Martin, 1949), only *Nostoc* and *Microcoleus vaginatus* of 21 species isolated from cultivated Colorado soils (Robbins, 1921), and only *Nostoc* of the 5 or more genera from range soil crust in southern Arizona (Fletcher and Martin, 1948) are common to those of the Tularosa Basin.

Of the algae characteristic of lichen crusts on lava soil and on the basin floor, only *Nostoc* is named in the literature as a lichen host. However, many lichens have two hosts enwrapped in the same thallus, and more than a hundred lichen species contain, in addition to the traditional host, a second or rarely a third alga, always blue-green and always near the surface (Clements and Shelford, 1939). Circumstances influence which fungus and which alga will grow together. It has been suggested that lichens represent a symbiosis of fungi, algae and *Azotobacter,* which would explain the initial accumulation of soil nitrogen (Lazarev, 1945). Krasilnikov (1949), however, failed to isolate azotobacter from 250 lichen samples distributed in more than 40 species. He found, further, that *Azotobacter* introduced into lichen crusts did not survive. Whether or not there is a symbiosis between *Azotobacter* and any portion of a lichen remains to be established. Lichens and mosses are known to collect dust and mineral nitrogen from wind and rain (Weaver and Clements, 1929).

The concentration of amino nitrogen, nitrite and nitrate in the gypsum crust, as well as the absence of a nitrogen-fixing bacterial flora, indicates that the algal growth in this substrate constitutes the main ultimate and possibly the only source of nitrogen. The capacity for nitrification shown by the gypsum sand in inorganic ammonium sulfate media establishes the presence in this substrate of nitrifying organisms which convert ammonia from dead organic matter of the algal crust to nitrite and nitrate. While the amount of amino nitrogen of the surface crust from gypsum flats is unimpressive in comparison to that of the lava flow or the immediately surrounding basin floor, nitrite and nitrate derived from the amino nitrogen compare favorably with that of these more fertile soils.

Normally, nitrite, nitrate and ammonia together rarely account for more than one per cent of the soil nitrogen (Russell, 1937). Total nitrite and nitrate have been found to range from 2 to 20 p.p.m. in arable English soil with a total nitrogen of around 1500 p.p.m. (Russell, 1937) and from 1.0 to 15.0 p.p.m. in the Grants, New Mexico, lava flow and the surrounding range area (Lindsey, 1951). By comparison, of all the soils examined only sand from the dunes and subsurface levels of the gypsum are conspicuously deficient in nitrite and nitrate.

The amino nitrogen of the surface crust represents the bulk of nitrogen in all soils observed. Though not in a form immediately available to plants, this amino nitrogen constitutes a continually renewable source of inorganic forms which macrovegetation can utilize. The amino nitrogen of the algal and lichen surface crusts is mainly incorporated in living protoplasm. However, numbers of vegetative cells die regularly, particularly during periods of desiccation, releasing nitrogen. In agricultural soil types, rewetting after a dry period results in compete mineralization of free amino nitrogen within 2 weeks, making inorganic nitrogen available to macrovegetation. This nitrogen is readily distributed with moisture, reducing the level to such an extent that it is again difficult to detect. The low nitrite and nitrate at the 6-in. level below the algal crust of the gypsum flats appears to be explained by the highly transient nature of these forms as a result of downward movement with soil water.

SUMMARY

A series of observations establishes the incidence of a total of 14 algal species in alga- and lichen-stabilized soil crusts from several contrasting semi-desert substrates. These observations provide the basis for evaluating such surface crusts as sources of amino nitrogen and total nitrite and nitrate. 1) On flats throughout the gypsum sand deposit the surface crust is stabilized mainly by *Palmogloea protuberans*, associated occasionally with *Plectonema nostocorum* and rarely with *Nostoc*. 2) Amino nitrogen averaged 256 p.p.m. for alga-stabilized gypsum crust and 10 p.p.m. for the 6-in. level in June. Total nitrite and nitrate averaged 5.6 p.p.m. for algal crust samples in June, 0.45 p.p.m. 6 in. below the algal crust, and 2.1 p.p.m. for samples from 3- to 6-in. levels in the vicinity of roots. 3) More than half the gypsum samples exhibited nitrifying activity, but no evidence could be found for bacterial nitrogen fixation. 4) In 109 surface crusts from lava soil, the more prominent algal species, in order of decreasing incidence, were *Microcoleus vaginatus, Porphyrosiphon fuscus, Schizothrix californica, Scytonema ocellatum, S. hofmannii, Schizothrix giuseppei, Microcoleus paludosus,* and *Nostoc* spp. The same algae appeared in the 50 algal crusts as in the 59 which were lichen-stabilized. The lichen species found on lava soils, in approximate order of diminishing frequency of occurrence, were *Dermatocarpon squamellum, Heppia despreauxii, Collema coccophorum, Lecidea decipiens* F. *dealbata, Collema nigrescens, Lecidea rubiformis, Heppia guepinii,* and *Solorina saccata* var. *spongiosa*. 5) The amino nitrogen of the lichen crusts from lava soil averaged 22.2 per cent higher (1985 p.p.m.) and the total nitrite and nitrate 21.5 per cent lower (6.2 p.p.m.) than for the alga-stabilized stratum. 6) Culture in 2 selective media demonstrated the presence of nitrifying bacteria in most lava soil samples and *Azotobacter* in somewhat less than half. The amino nitrogen averaged 866 p.p.m. for lava surface layers lacking algal or lichen growth, however, compared to 1545 and 1985 p.p.m., respectively, for strata supporting algae and/or lichens. 7) The algal species characteristic of surface crusts from the Tularosa Basin floor immediately surrounding the gypsum sand belong to the blue-green genera *Microcoleus, Schizothrix* and *Scytonema*. Amino nitrogen averaged 1031 p.p.m. for algal crusts, 1553 p.p.m. for lichen crusts, and 199 p.p.m. at the 6-in. level below lichens. 8) In the mesquite and creosote bush zones, in the absence of algal or lichen growth, amino nitrogen apparently from organic debris averaged 225 p.p.m., and total nitrite and nitrate, 2.1 p.p.m. for surface strata. Amino nitrogen averaged 270 p.p.m. and total nitrite and nitrate 2.5 p.p.m. at the 6-in. level. 9) Alga- and lichen-stabilized surface crusts, through death and decomposition of component cells, particularly during periods of desiccation, release amino and other nitrogen compounds. These are mineralized when moisture becomes available and are distributed with soil water. The surface growth of algae and lichens thus represents a continually renewable supply of soil nitrogen.

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CHITIN SYNTHESIS AND NITROGEN METABOLISM DURING DIFFERENTIATION IN BLASTOCLADIELLA EMERSONII[1,2]

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JUDGING FROM our current state of knowledge, the peculiar idiosyncrasies and distinguishing characteristics of *Blastocladiella emersonii* seem to render it quite different in a fundamental way from its many aquatic relatives. Starting with a motile spore, three developmental pathways are recognized. One of these is induced by bicarbonate. For the two that remain, the direction taken can be correlated with the distribution of a visible cytoplasmic particle in the spores from which such plants are derived. (Fig. 1; Cantino, 1956; Cantino and Horenstein, 1956a, 1956b; Emerson, 1955; and references therein.) Whether or not these apparently unique attributes of *B. emersonii* are indeed real, or simply momentary artifacts resulting from our relative lack of detailed knowledge of these other fungi at a similar level of integration can only be revealed by future investigations.

Among the most thoroughly-documented phenomena associated with the developmental history of *Blastocladiella* are these: (1) its mode of development, from uniflagellate spore to mature thallus, can occur along either of two major morphogenetic pathways. One of these gives rise to a resistant-sporangial (R.S.) plant in which the terminal cell possesses a thick, chitinous wall, extensively pitted and heavily pigmented with melanin; the other gives rise to an ordinary colorless (O.C.) plant in which the terminal cell possesses a very thin, colorless, chitinous wall bearing several conspicuous papillae at maturity. (2) the process can be controlled at will by the simple expedient of providing or not providing bicarbonate in the immediate environment of the plant as it grows; in the presence of bicarbonate R.S. plants are produced, while in its absence O.C. plants are formed instead. And (3) a good deal of detailed knowledge has now accumulated regarding the biochemical mechanisms by which the bicarbonate initiates and maintains the morphogenetic pattern.

Attempts have been made elsewhere (Cantino, 1956; Emerson, 1955) to integrate most of these numerous observations into an orderly and, hopefully, a comprehensible picture. For purposes of orientation, and in order to facilitate with a minimum of space an understanding of the bearing of the work which follows upon the problem of morphogenesis in *Blastocladiella*, a brief, select tabulation of some of our earlier, pertinent observations is shown in fig. 2.

Our most recent studies of the mechanism of differentiation in *Blastocladiella* have centered upon the fact that an R.S. plant possesses a much thicker wall than does an O.C. plant. In the past, direct microchemical tests (e.g., Nabel, 1939; Cantino, unpublished), and more recently X-ray analyses (Frey, 1950) upon members of the Blastocladiales have led to the belief that the wall material is composed of chitin and that it is essentially free of cellulose. Assuming for the moment that these conclusions are correct, and that the cell walls of both R.S. and O.C. plants consist of chitin, a major question arises: what is the underlying, biochemical mechanism by which bicarbonate induces the net synthesis of a much greater quantity of chitin during the genesis of a thick-walled R.S. plant than that which is laid down during the formation of

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