Great Basin Naturalist

Volume 45 | Number 1 Article 2

1-31-1985

Cryptogamic soil crusts: seasonal variation in algal populations in the Tintic Mountains, Juab County, Utah

Jeffrey R. Johansen
Brigham Young University

Samuel R. Rushforth
Brigham Young University

CRYPTOGAMIC SOIL CRUSTS: SEASONAL VARIATION IN ALGAL POPULATIONS IN THE TINTIC MOUNTAINS, JUAB COUNTY, UTAH

Jeffrey R. Johansen[1] and Samuel R. Rushforth[1]

Abstract.— The soil algae in the Tintic Mountains, Juab County, Utah, was studied over a one-year period in 1982 and 1983. Fluorescence microscopy was used to measure algal density in samples directly from the field. A total of 30 algal taxa was observed, blue-green algae being most abundant both in terms of density and number of species. Algal density showed peaks in late fall and late spring. Minima were present in September 1982 and July 1983. Several weak correlations between algal density and climatic data existed. In general algae correlated positively with precipitation and negatively with temperature. A combination of low precipitation and hot temperatures was likely responsible for the low density observed in July. The Chrysophyta followed slightly different trends than the other algal groups, having minima in early October 1982 and late August 1983. Field observations indicated that the degree of algal crusting varied noticeably over a period of one year, with highest abundance of hummocking in spring. Heavy summer thunderstorms destroyed algal crusting during July and August of 1983, though absolute density of algae increased during this time in response to the extra moisture.

Soil algae have received considerable study during the last half century (Metting 1981, Starks et al. 1981). Arid land soil algae are an important component of desert ecosystems for several reasons. Algae in association with lichens and mosses form crusts that stabilize the soil surface against wind and water erosion. Improved infiltration of rainwater in crusted soils further reduces erosion by lessening the amount of runoff (Brotherson and Rushforth 1983). Fixation of atmospheric nitrogen by blue-green algae, both free living in the soil and associated with soil lichens, has been well documented. Vascular seedling development tends to be facilitated in areas where crust development is pronounced (St. Clair et al. 1984).

Floristic studies of soil algae have primarily been conducted through the use of enrichment and unialgal cultures (Metting 1981). Recent studies of soil algae in the Great Basin and Colorado Plateau have been performed using distilled water wetting and/or standard culture methods (Anderson and Rushforth 1976, Ashley and Rushforth 1984, Johansen, Rushforth, and Brotherson, 1981, Johansen, Javakul, and Rushforth 1982). Studies of soil algal biomass have been done using several different methods, including chlorophyll *a* content, dilution counts, enrichment counts, plate counts, and direct counts (Metting 1981).

Direct counts of soil algae are difficult to make, since algae are often scarce in uncultured samples and identification of many species without prolonged culture and study of life cycles is often nearly impossible. However, direct counts are more indicative of natural conditions because biomass and diversity estimates are based upon data from communities that have not been modified by culturing. Fluorescence microscopy can greatly aid in examination of soil algae. Although the value of this technique was pointed out more than 30 years ago (Tchan 1952), it has not been widely used. In the present study, direct counts using fluorescence microscopy were used to measure seasonal changes in abundance of arid land soil algae. We recognize that some sacrifice in taxonomic resolution was made in exchange for ecological data based on a less modified algal community.

Methods

The study site was located in the Tintic Mountains, 7 km west of Tintic Junction, Juab County, Utah, T10S R4W S35. Several well-developed algal crusts were lo[illegible]ted on a hill crest, 1950-m elevation, in [illegible]niperus

[1]Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

osteosperma-Artemisia tridentata vascular plant community. The soil at the locality was examined and classified using standard references (Soil Conservation Service 1972, Soil Survey Staff 1951, 1975). The soil was classified as Aridic Calcixeroll, fine clayey, mixed, mesic. The surface horizon was a dark greyish brown, sandy clay loam. Other soil characteristics are listed in Table 1.

Samples were collected nine times over a period of one year beginning September 1982 (Table 2). Five samples were collected each time, except 31 October 1982, when 10 samples were collected and processed. One sample collected 15 June 1983 was lost; thus only 4 samples were available for that collection.

All samples were collected from an area approximately 10 m^2 in size. Exact sample localities were subjectively chosen in crusted areas between shrubs. For each collection period, the upper 2 cm of five adjacent algal crust hummocks were collected and returned to the laboratory for immediate analysis. Samples were homogenized with a metal spatula. Six 1-gm subsamples were taken from each of the samples. One subsample was reserved for direct microscopic analysis. The other five were oven dried at (105 C) and weighed again to calculate percent soil moisture (Table 2).

The subsample reserved for microscopic analysis was wetted immediately prior to examination. The soil was placed in a volumetric cylinder, and distilled water was added to a total volume of 10 ml. The sample was then agitated vigorously by hand for 60 seconds. A 1-ml subsample was pipetted from the solution and placed in a dilution tube containing 4 ml of distilled water. This final dilution was used for direct examination under a Zeiss RA microscope with dark field and fluorescence optics. A counting chamber with a depth of 0.18 mm and field length of 10 mm was constructed as suggested by Tchan (1952) and used in all counts. Fluorescing (living) algal cells and colonies were counted under 400X magnification. All algae in 10 transects across the chamber were counted for each sample. Algae were identified to species when possible, or to genus or division when necessary. Some algae were not identifiable and were classified as unknown coccoid algae or unidentifiable algae. Moist plate cultures using Bold's Basal Medium (Bold and Wynne 1978) were started at the initiation of the study to aid in species identification.

Temperature and moisture data were taken from weather records for Eureka, Utah, the nearest weather station (National Oceanic and Atmospheric Administration 1982, 1983). The average daily temperature and precipitation for the two weeks previous to each collection date were calculated (Table 2).

An importance index for all living algal taxa was calculated by multiplying density by percent presence (Ross and Rushforth 1980). This method is often used in studies of terrestrial vascular vegetation (Warner and Harper 1972) and has the value of considering both absolute density data as well as frequency of occurrence. Species with importance values greater than 1.0 were designated prevalent species and were used in subsequent analyses of variance.

Multivariate analysis of variance adapted for a fixed-effect, unbalanced design following the methods of Bryce et al. (1980) was used to analyze differences between treatments (months) and blocks (species). The variance of each taxon was related to the mean. To satisfy the homogeneity of variance

TABLE 1. Soil properties for the Aridic Calcixeroll at the Tintic Mountain site. Soil for tests taken from A1 horizon, 0–28 cm depth, 3 October 1982.

Property		
Sand	55.6%	
Silt	20.4%	
Clay	24.0%	
Gravel	0.9%	
Lime content	2.0%	
Organic matter	8.4%	
Pore space	35.8%	
Bulk density	1.7	g/cm^3
Soluble salts	240	ppm
NH_4	100	ppm
P	155	ppm
NO_3	7	ppm
Ca	3.4	meq/liter
Mg	1.2	meq/liter
Na	1.0	meq/liter
HCO_3 and CO_3	3.9	meq/liter
Cl	0.5	meq/liter
K	0.2	meq/liter
pH, saturated paste	7.4	

assumption of analysis of variance, a log (x + 1) transformation was used (Bartlett 1947). In each analysis of variance, standardized residuals were plotted against normal scores. In every case the probability plot thus generated was subjectively judged to be normal or close to normal. The Duncan multiple range test was used to determine significance of differences between means when analysis of variance showed significance (Duncan 1955). Unless otherwise stated, the alpha value used for this test was 0.01.

Shannon-Wiener diversity indices were calculated (Shannon and Weaver 1949, Patten 1962) for each subsample for each collection date. Similarity indices for all 49 subsamples collected on the nine collection dates were determined following the methods of Ruzicka (1958). Such indices were also calculated for the nine collection dates using arithmetic averages of subsamples. Similarity indices were then clustered (Sneath and Sokal 1973) to determine the relationships between collection periods. Correlation analysis (Snedecor and Cochran 1980) was performed to determine relationships between algal abundance and precipitation and temperature data.

Results and Discussion

Description of the Flora

A total of 30 algal taxa was identified during this study (Table 3). Fifteen of these were blue-green algae, 9 were chrysophytes (including diatoms), 3 were green algae, and 3 were placed in the categories flagellates, unknown coccoid algae, and unidentifiable algae. The latter 3 categories were necessary since some of the algae encountered with the fluorescent microscope could not be placed with confidence into known divisions.

Table 2. Soil moisture for each collection date and mean high and low temperature and precipitation for two-week period previous to collection date.

Date	Temperature (degrees C)	Precipitation (cm)	Soil moisture (g/kg)
24-IX-1982	8-20	2.4	37.4
3-X-1982	6-16	10.7	205.6
31-X-1982	0-11	4.4	240.9
29-XI-1982	-6- 4	1.0	275.1
14-I-1983	-6- 6	0.0	178.0
15-V-1983	1-16	2.4	35.9
15-VI-1983	6-24	1.6	1.2
29-VII-1983	15-28	2.1	19.2
26-VIII-1983	13-26	4.7	25.9

Algal taxa in the Tintic locality with an importance index greater than 1.0 included *Microcoleus vaginatus* (importance value = 351.56), *Nostoc* species (258.92), unidentifiable algae (162.36), unknown coccoids (161.05), *Phormidium minnesotense* (141.97), unknown coccoid Chlorophyta (118.72), unidentified Chrysophyceae (64.27), *Navicula mutica* (58.16), *Hantzschia amphioxys* (56.64), *Anabaena* cf. *variabilis* (33.01), *Synechococcus aeruginosus* (26.37), *Tolypothrix tenuis* (10.15), unknown Chlorosarcinales (5.81), unknown Chroococcaceae (4.25), and *Pinnularia borealis* (2.17).

Multivariate analysis of variance of prevalent species density data showed that significant ($p < .001$) differences existed between taxa. Duncan's multiple range test showed that *Microcoleus vaginatus* was significantly more abundant than all other species or categories. *Nostoc* species were more abundant than all other less common taxa. Unidentifiable algae, unknown coccoid algae, *Phormidium minnesotense*, and unknown coccoid Chlorophyta formed a group, of which each was more abundant than less common taxa. Chrysophyte cysts, *Navicula mutica*, *Hantzschia amphioxys*, and *Anabaena* cf *variabilis* formed a second group, of which each was more abundant than less prevalent taxa.

The Tintic algal flora is similar in most respects to that we have observed from other localities in the Great Basin and Colorado Plateau (Anderson and Rushforth 1976, Ashley et al. in press, Johansen et al. 1981, 1982, 1984). It is dominated by filamentous blue-green algae, particularly *Microcoleus vaginatus*, *Nostoc* species, and *Phormidium* species. In addition, diatoms are more diverse and often more abundant than green algae. One conspicuous difference between our soil crusts and several others we have examined was the absence of an obvious moss and lichen component. Some lichens were present in our crusts, but they were rare. This is likely due to the fact that the study area is regularly grazed, and grazing is known to cause severe damage to the moss and lichen components of crusts (Anderson et al. 1982, Brotherson et al. 1983).

Diversity and Similarity

Shannon-Wiener diversity indices varied between 2.285 and 3.399 for the individual subsamples. Average Shannon-Wiener diversity for each collecting period ranged between 2.690 and 3.229. These figures are similar to or higher than other Shannon-Wiener values for soil algal studies we have made in other regions of the Great Basin (Johansen and St. Clair in review, Johansen et al. 1982, 1984). The rather low range of diversity for these samples was borne out by species richness figures. Total number of taxa observed per collecting period varied between 14 and 19. Even though variability in diversity was rather low in comparison to other systems we have studied, analysis of variance showed that diversity was significantly different between months. Duncan's multiple range test showed that the diversity in collections from cooler months (especially January and June) was significantly higher than diversity in warmer months (especially August and September).

Stand similarity on the basis of species density data was high, averaging 68% for the winter stands and 50% for the remaining stands. When these data were clustered, only winter stands (31 October, 29 November, 14 January, and 15 May) formed a discrete group. Stand similarity on the basis of species presence or absence was even higher, with an average similarity of 74%. When these data were clustered, the same winter months formed a group, except that the samples from early October and July were included.

TABLE 3. Taxa present at the Tintic Mountain site together with importance values (PFI) and density for each collection date. Unit value for density is 1000 organisms/g dry weight soil.

Taxa	PFI	9/24	10/3	10/31	11/29	1/14	5/15	6/15	7/29	8/26
CYANOPHYTA										
Anabaena cf *variabilis*	33.01		20	15	23	155	7	96	15	52
Chroococcus pallidus	0.08							13		
Chroococcus species	0.02		3							
Gloeocapsa aeruginosa	0.73							57	15	
Gloeocapsa punctata	0.01						1			
Gloeothece linearis var. *composita*	0.56	1	10	3	12	2				
Merismopedia punctata	0.01									3
Microcoleus vaginatus	351.56	240	153	241	275	249	502	514	281	639
Nostoc species	258.92	131	267	234	296	188	235	710	48	305
Oscillatoria geminata	0.18							10		
Phormidium minnesotense	141.97	19	84	138	213	121	266	270	50	98
Synechococcus aeruginosus	26.37	123	30	36	6	22	36	82	20	23
Tolypothrix tenuis	10.15			33	10	16	38	18	12	11
Tolypothrix species	0.33			2						14
Unknown Chroococcaceae	4.25	1	15	47	47	3		7		
CHLOROPHYTA										
Oocystis species	0.02									4
Chlorosarcinales	5.81			3	2			56	36	37
Unknown coccoids	118.72	15	58	124	164	137	124	304	56	99
CHRYSOPHYTA										
Achnanthes species	0.02					3				
Caloneis bacillum	0.01			1						
Hantzschia amphioxys	56.64	81	26	43	87	52	84	46	44	40
Navicula mutica	58.16	71	23	64	87	80	66	75	45	28
Navicula species	0.02							2		1
Pinnularia borealis	2.17	7	6	8	4	6	8	4	3	
Pinnularia species	0.01								1	
Unknown pennate	0.01					2				
Chrysophyceae	64.27	33	48	64	54	69	67	182	36	28
OTHER UNIDENTIFIABLE ALGAE										
Flagellates	0.03	1					3			
Unknown coccoids	161.05	15	100	32	256	175	231	445	67	201
Unidentifiable algae	162.36	72	153	226	274	173	137	167	35	150

Climatic Factors

Our original hypothesis was that precipitation and total soil algal growth would be positively correlated during all seasons. However, when we ran correlation analyses, we discovered that precipitation and algal growth were almost always negatively correlated, although values were not significant. When we discovered this, we divided total algae into several categories for separate analyses. These categories included Cyanophyta, Chlorophyta, Chrysophyta, and other algae. The negative correlation we noted for total algal growth held for all of these categories whether the period of precipitation prior to collection date used in the analysis was for 3, 7, 14, 21, or 28 days.

In view of these negative correlations, we computed the net increase or decrease in abundance for each algal group for each collection interval. We then correlated these data with climatic data. The results of this correlation of incremental algal growth with precipitation were low, but positive for all algal groups (Table 4).

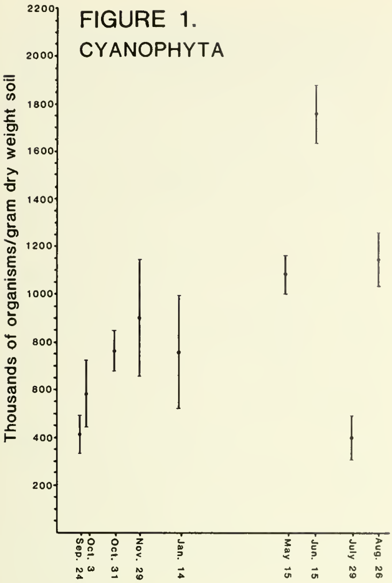
As a whole, our data indicate that algal growth was not related in a linear manner to precipitation. It seems probable that when a minimum amount of moisture is present in the soil, algal growth will not be limited and moisture beyond this threshhold does not enhance growth and may in fact reduce algal density. Stokes (1940) found that soil algae in New Jersey grew best at 40%–60% soil moisture and that growth was strongly curtailed in saturated soil. On the other hand, low moisture is often a limiting factor for algal growth in desert regions (Lynn and Cameron 1973). For instance, Brock (1975) found that the depletion of soil moisture to −7 bars began to deter the growth of *Microcoleus* in desert crusts.

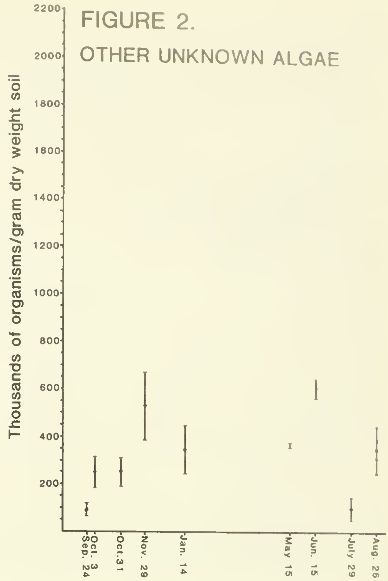
Incremental growth of algal groups was also correlated with air temperature. All correlations were negative, and the largest coefficients were obtained when median temperature rather than maximum temperature data were used (Table 4). Generally, the best correlations occurred when temperature data for the three-day period prior to collection were used rather than data for longer periods. This indicates rapid negative algal response to high air temperatures.

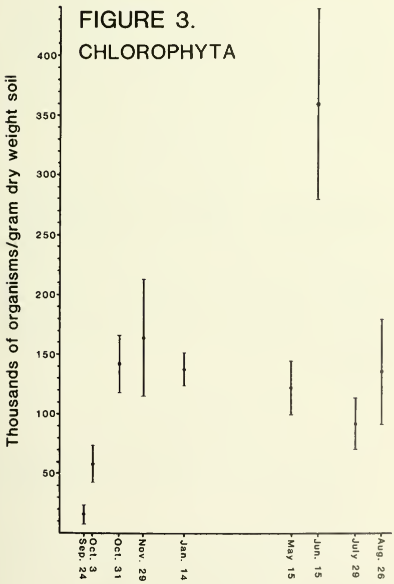
Abundance of blue-green algae was more negatively correlated with temperature than all other groups. This was surprising since many species of blue-green algae are known thermophiles and have been demonstrated to tolerate high temperatures in the laboratory

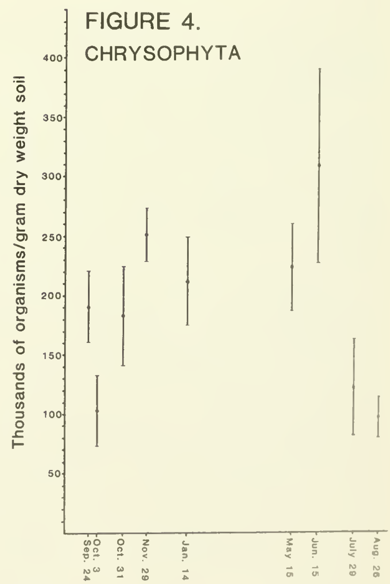
TABLE 4. Correlation coefficients for incremental algal growth versus climatic factors. Climatic factors include mean daily precipitation (PRECIP), mean maximum temperature (MAX-T), and mean midtemperature (MID-T). Means were computed for the 3-, 7-, 14-, 21-, and 28-day periods prior to the collection dates. Significant correlations are asterisked ($\alpha < .05$°, $\alpha < .01$°°).

Algal group	Climatic factor	Days 3	7	14	21	28
	PRECIP	.033	−.077	.026	.063	.317°
CYANOPHYTA	MAX-T	−.315°	−.322°	−.342°	−.301°	−.306°
	MID-T	−.429°°	−.382°°	−.386°°	−.321°	−.324°
	PRECIP	.181	.039	.041	.066	.118
CHLOROPHYTA	MAX-T	−.283	−.249	−.236	−.175	−.199
	MID-T	−.375°	−.297°	−.287	−.208	−.234
	PRECIP	.312°	−.137	−.189	−.206	−.016
CHRYSOPHYTA	MAX-T	−.260	−.199	−.240	−.193	−.218
	MID-T	−.285	−.231	−.275	−.217	−.248
	PRECIP	.000	.113	.236	.251	.331°
OTHER ALGAE	MAX-T	−.248	−.257	−.199	−.124	−.123
	MID-T	−.309°	−.278	−.210	−.116	−.118
	PRECIP	.129	.060	.169	.212	.332°
TOTAL ALGAE	MAX-T	−.254	−.234	−.190	−.120	−.130
	MID-T	−.334°	−.266	−.226	−.133	−.147









Figs. 1–4. Mean density and standard deviation of algal groups during collection year: 1, Cyanophyta. 2, Other algae of unknown division. 3, Chlorophyta. 4, Chrysophyta. Note the lows 31 October and 26 August in Chrysophyta, although other groups had minima on 24 September and 29 July.

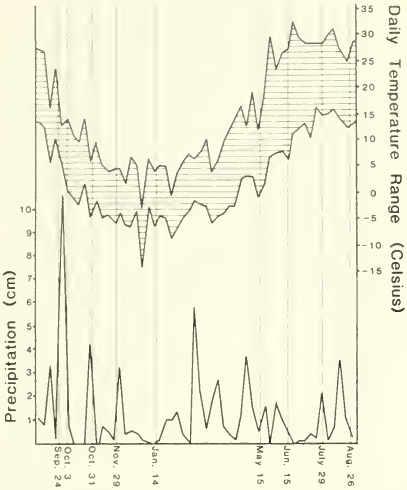


Fig. 5. Precipitation and daily temperature range for the Tintic Mountain site. Vertical lines represent sample times.

(Booth 1946, Castenholz 1969). Chrysophytes demonstrated the smallest correlation values, indicating that they were least affected by high air temperature.

To visualize algal growth throughout the collection period, mean density and standard deviation for each algal group were plotted against time (Figs. 1–4). In general, algal growth of all groups peaked in late fall and again in June. All groups showed a marked decrease in cell density in July and recovery in August. The July decrease was apparently due to high temperatures combined with low precipitation (Fig. 5). Even though a storm occurred immediately prior to the July collecting date, apparently the flora did not have time to respond to the increased moisture. Lynn and Cameron (1973), when studying soil algae of the Curlew Valley, found that algal growth was minimal between mid-July and mid-September. The July and September collections in our study were likewise low in algal density. The recovery in August is perhaps unusual and likely due to the major storms that occurred mid-July to late August (Fig. 5).

Growth curves were remarkably similar for all algal groups (Figs. 1–4). The greatest deviation from the typical pattern was demonstrated by chrysophytes (Fig. 4), which did not show the August recovery. Furthermore, the yearly minimum in Chrysophyta followed a hundred-year storm in late September (Johansen in press). Correlation analyses also demonstrated differences between chrysophytes and the other algal groups (Table 4). It was the only group without any significant negative correlations with temperature, which may indicate that these algae are not as adversely affected by high temperatures.

As a final note, we observed that the degree of hummocking or pinnacling of algal crusts at the study site varied throughout the year. Throughout the fall of 1982 crusts were abundant and well developed. After snowmelt in May 1983 we noted that crusts appeared even more abundant and well developed. At this time, algal hummocks were evident even in jeep roads adjacent to the site. By July crusting in roadways had been destroyed, though crusts elsewhere were still abundant. In late August the crusts at our study site were severely damaged and eroded by powerful rain storms, although algal numbers in the soils remained relatively high. These observations may indicate that the durability and longevity of algal crusts is much less than we had previously thought.

Acknowledgments

We thank the members of the Department of Microbiology, Brigham Young University for their assistance during our use of the transmission fluorescence microscope. Blaine Metting, Larry St. Clair, Jack Brotherson, and Bill Evenson reviewed the manuscript prior to publication and provided helpful suggestions.

Literature Cited

Anderson, D. C., K. T. Harper, and S. R. Rushforth. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. J. Range Manage. 35:355–359.

Anderson, D. C., and S. R. Rushforth. 1976. The cryptogam flora of desert soil crusts in southern Utah, USA. Nova Hedwigia 28:691–729.

Ashley, J., and S. R. Rushforth. 1984. Growth of soil algae on topsoil and processed oil shale from the Uintah Basin, Utah, USA. Reclam. Reveg. Res. 3:49–63.

Ashley, J., S. R. Rushforth, and J. R. Johansen. In press. Soil algae of cryptogamic crusts from the Uintah Basin, Utah, USA. Great Basin Nat.

Bartlett, M. S. 1947. The use of transformations. Biometrics 3:39–52.

Bold, H. C., and M. J. Wynne. 1978. Introduction to the algae, structure and reproduction. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 706 pp.

Booth, W. E. 1946. The thermal death point of certain soil-inhabiting algae. Proc. Montana Acad. Sci. 5/6:21–23.

Brock, T. D. 1975. Effect of water potential on a *Microcoleus* (Cyanophyceae) from a desert crust. J. Phycol. 11:316–320.

Brotherson, J. D., and S. R. Rushforth. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. Great Basin Nat. 43:73–78.

Brotherson, J. D., S. R. Rushforth, and J. R. Johansen. 1983. Effects of long-term grazing on cryptogam crust cover in Navajo National Monument. J. Range Manage. 36:579–581.

Bryce, G. R., D. T. Scott, and M. W. Carter. 1980. Estimation and hypothesis testing in linear models—a reparameterization approach to the cell means model. Communications in Statistics—Theor. Meth. A9(2):131–150.

Castenholz, R. W. 1969. Thermophilic blue-green algae and the thermal environment. Bacteriol. Rev. 33:476–504.

Duncan, D. B. 1955. Multiple range and multiple *F* tests. Biometrics 11:1–42.

Johansen, J. R. In press. Response of soil algae to a hundred-year storm in the Great Basin Desert, USA. Phykos.

Johansen, J. R., A. Javakul, and S. R. Rushforth. 1982. The effects of burning on the algal communities of a high desert soil near Wallsburg, Utah, USA. J. Range Manage. 35:598–600.

Johansen, J. R., S. R. Rushforth, and J. D. Brotherson. 1981. Subaerial algae of Navajo National Monument, Arizona. Great Basin Nat. 41(4):433–439.

Johansen, J. R., and L. L. St. Clair. In review. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA.

Johansen, J. R., L. L. St. Clair, B. L. Webb, and G. T. Nebeker. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. Bryologist 87:238–243.

Lynn, R. I., and R. E. Cameron. 1973. Role of algae in crust formation and nitrogen cycling in desert soils. US/IBP Desert Biome Res. Memo. 73-40(3):2.3.4.6.-1-26.

Metting, B. 1981. The systematics and ecology of soil algae. Bot. Review 47(2):195–312.

National Oceanic and Atmospheric Administration. 1982. September—December, Utah 1982. Climatological Data, Utah 84(9–12).

———. 1983. January—August, Utah 1983. Climatological Data, Utah 85(1–8).

Ross, L. E., and S. R. Rushforth. 1980. The effects of a new reservoir on the attached diatom communities in Huntington Creek, Utah, USA. Hydrobiologia 68:157–165.

Ruzicka, M. 1958. Anwendung mathematisch-statistischer Methoden in der Geobotanik (synthetische Bearbeitung von Aufnahmen). Biologia Bratisl. 13:647–661.

Shannon, G. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. of Illinois Press, Urbana. 117 pp.

Sneath, P. H., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco. 573 pp.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. 7th ed. Iowa State Univ. Press, Ames, Iowa. 507 pp.

Soil Conservation Service. 1972. Soil survey laboratory methods and procedures for collecting soil samples. U.S. Dept. Agric. SSIR 1. U.S. Govt. Printing Office, Washington, D.C. 63 pp.

Soil Survey Staff. 1951. Soil survey manual. U.S. Dept. Agric. Handb. 18. U.S. Govt. Printing Office, Washington, D.C.

———. 1975. Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys. U.S. Dept. Agric. Handb. 436. U.S. Govt. Printing Office, Washington, D.C. 754 pp.

Starks, T. L., L. E. Shubert, and F. R. Trainor. 1981. Ecology of soil algae: a review. Phycologia 20(1):65–80.

St. Clair, L. L., B. L. Webb, J. R. Johansen, and G. T. Nebeker. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. Reclam. Reveg. Res. 3:129–136.

Stokes, J. L. 1940. The influence of environmental factors upon the development of algae and other microorganisms in the soil. Soil Sci. 49:171–184.

Tchan, Y. T. 1952. Study of soil algae. I. Fluorescence microscopy for the study of soil algae. Proc. Linn. Soc. London 77:265–269.

Warner, J. H., and K. T. Harper. 1972. Understory characteristics related to site quality for aspen in Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 16(2):1–20.