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Lichens and Their Ecological Significance in Headwaters State Park, Gallatin County, Montana

Abstract

Seventy-eight species of lichens were collected from all substrates in Headwaters State Park. Of the lichens collected, 46% had a foliose growth form, 41% were crustose, and 13% were squamulose; 50% of the lichens collected grew on rock, 22% on soil, 12% on wood and bark, 12% on moss, and 3% on woody plant litter on soil. The soil lichen crusts were more conspicuous than many other crusts because of their orange, yellow, rust and white colors. On Fort Rock in Headwaters State Park, dominant crust species were Buellia elegans, Catapyrenium *spp.,* Collema tenax, Fulgensia bracteata, Diploschistes muscorum, Psora decipiens, Psora *spp., and* Toninia sedifolia. *Crusts away from trails and foot traffic were better developed than those adjacent to trails. Lichen crusts are important in inhibiting wind and water erosion, contributing nitrogen and fixed carbon to the soil, improving soil texture and providing food and habitat for soil microinvertebrates.*

Key Words: Lichens, Headwaters State Park, soil crusts

Introduction

Headwaters State Park is historically significant as the site where Lewis and Clark recognized and named the three forks of the Missouri River in 1805. It had been an informal state park since the 1940s, when 30 acres were given to the State of Montana by the Founders Club, a group of interested citizens. It became a Registered National Historic Landmark in 1962, and was formally dedicated as the Bicentennial Site for Montana in 1975.

The park is roughly triangular, bounded on the west by the Madison River, on the northwest by the merged Madison and Jefferson rivers, and on the east and northeast by the Gallatin River. The location at which the Gallatin River joins the other rivers is the north point of the park, and the Missouri River continues its flow northward.

Most of the park's lower elevation roadside areas have been farmed and grazed. Camping areas along the Missouri River are in uncultivated grassy sites with adjacent cottonwood (*Populus balsamifera L.*), willows (*Salix* spp.), and other shrubs. In the main visitor area, about 1223 m in elevation, picnic tables are on mowed grounds near the Gallatin River with *P. balsamifera* , and planted *Pinus ponderosa* Dougl. and *Picea* sp. Trails climb upward to a flat limestone ridge (Fort Rock) at an elevation of 1236 m. The dominant native grasses are *Pseudoroegneria spicata* (Pursh) A. Love, *Heterostipa comata* (Trin. & Rupr.) Barkworth, and *Bouteloua gracilis* (H.B.K.) Lag., and the dominant shrubs are *Artemisia cana* Pursh, *A. tridentata* Nutt., and *Atriplex gardneri* (Moq.) Dietr. *Juniperus scopulorum* Sarg. is common on the north-facing slopes. Fort Rock is being invaded by *Agropyron cristatum* (L.) Gaertn., *Melilotus officinalis* (L.) Pallas, and *Centaurea maculosa* Lam.

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The top of Fort Rock has roughly parallel limestone outcrops that extend northeast to southwest; conspicuous lichen crusts have developed on shallow soils adjacent to these outcrops. Deeper soil in slight depressions between the outcrops supports the grass-forb communities, including most of the *Melilotus officinalis*.

The objectives of this study were to survey the lichen flora of the entire park and to characterize the unique lichen crusts on Fort Rock.

Study Area

Headwaters State Park occupies about 4 km² in sections 8,17, 18, 20, T2N, R2E, in northwest Gallatin County, Montana (45°55'N, 111°W). Elevations range from 1223 m along the rivers to 1236 m on the oval-shaped limestone ridge (Fort Rock), which is about 300 x 900 m, and extends northeast to southwest. Annual precipitation averages 18-28 cm, with most of the precipitation coming in March through May. Mean annual temperature is approximately 7°C, with ranges between -26° and 38°C (National Oceanic and Atmospheric Administration 1995). Soils are shallow and calcareous; outcrops are Carboniferous Mission Canyon limestone (Three Forks Area Historical Society 1983).

Methods

Lichens were collected from all substrates, including tree bark, wood, rock, cement, and soil throughout the park. Identifications were made using standard morphological and chemical techniques (Wetmore 1967, Goward et al. 1994, McCune and Goward 1995). Voucher specimens are deposited in the Montana State University Herbarium (MONT). Nomenclature for lichens and most of the vascular plants follows Esslinger and Egan (1995) and Dorn (1984).

In order to characterize the soil lichen crusts, three areas were chosen that best represented the development of the crusts along the limestone outcrops; a fourth area adjacent to a trail was included to estimate effects of heavy trampling. A 50-m cord was placed through the center of each crust area, and percent cover for all lichen species was determined in a series of 20 2 x 5 dm quadrats per crust area. Along the trail, 2 x 5 dm quadrats were placed every 5m along the sides of the main compacted path, with the quadrats placed perpendicular to the trail. Midpoints of six cover classes (0, 1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 85%, 6 = 97.5%) (Daubenmire 1959, Eversman 1995) were averaged for each crust area, giving a percent cover for each lichen species. Other percent cover categories included moss, all vascular plants and litter combined, bare ground/bare rock, and rock with lichen.

Results and Discussion

Table 1 lists lichen species by substrate and form. Of the 78 species identified, 39 species (50%) grew on rock, 17 (22%) on soil, 10 (12%) on moss or plant debris on soil or rock; 10 (12%) on wood and bark, and 2 (3%) on woody plant debris on the soil. Thirty-six species (46%) had a foliose growth form, 32 species (41%), were crustose, and 10 species (13%) were squamulose. All of the species were lichens regularly found in montane and steppe regions of the northwest or western Great Plains (Wetmore 1967, McCune and Goward 1995). Rare or infrequently collected species were *Agonimia tristicula* on soil and *Caloplaca variabilis* and *Lichenella nigritella* on rock.

Bark

In this relatively dry climate, lichens on trees were generally at the base of the trunks and on branches. Lichens collected from bark were mostly small crustose or foliose species such as the orange *Xanthoria fallax* and *X. polycarpa*, and dark brown *Phaeophyscia nigricans*.

Table 1. *Lichen species identified from Headwaters State Park; species names are arranged by substrate and growth form (crustose, squamulose, foliose). Squamulose lichens are those with thalli composed of many small separate scales, intermediate in appearance between crustose and small foliose lichens.*

WOOD AND BARK

Crustose

Candelariella aurella (Hoffm.) Zahlbr.

Foliose

Phaeophyscia kairamoi (Vain) Moberg
Phaeophyscia nigricans (Floerke) Moberg
Physcia adscendens (Fr.) H. Olivier
Physcia dimidiata (Arnold) Nyl.
Physcia dubia (Hoffm.) Lettau
Physcia stellaris (L.) Nyl.
Physcia tenella (Scop.) DC.
Xanthoria fallax (Hepp) Arnold
Xanthoria polycarpa (Hoffm.) Rieber

ROCK

Crustose

Acarospora strigata (Nyl.) Jatta
Aspicilia calcarea (L.) Mudd
Aspicilia caesiocinerea (Nyl. ex Malbr.) Arnold
Caloplaca epithallina Lynge
Caloplaca feracissima H. Magn.
Caloplaca holocarpa (Hoffm. ex Ach.) M. Wade
Caloplaca sideritis (Tuck.) Zahlbr.
Caloplaca variabilis (Pers.) Muell. Arg.
Candelariella aurella (Hoffm.) Zahlbr.
Dimelaena oreina (Ach.) Norman
Diploschistes muscorum (Scop.) R. Sant.
Lecania nylanderiana A. Massal.
Lecanora argopholis (Ach.) Ach.
Lecanora crenulata Hook.
Lecanora dispersa (Pers.) Sommerf.
Lecanora marginata (Schaerer) Hertel & Rambold
Lecanora novomexicana H. Magn.
Lecanora rupicola (L.) Zahlbr.
Lecanora symmicta (Ach.) Ach.
Lecidella patavina (Massal.) Knoph & Leuckert
Lecidella stigmatea (Ach.) Hertel & Leuckert
Rhizocarpon geminatum Koerber
Rinodina bischoffii (Hepp.) A. Massal.
Verrucaria compacta (Mass) Jatta complex
Verrucaria glaucovirens Grummann

Foliose

Caloplaca cirrochroa (Ach.) Th.Fr.
Caloplaca saxicola (Hoffm.) Nordin
Caloplaca trachyphylla (Tuck.) Zahlbr.
Dermatocarpon lorenzianum Anders.
Dermatocarpon miniatum (L.) Mann
Lecanora garovaglii (Koerber) Zahlbr.
Lecanora muralis (Schreber) Rabenh.
Leptogium cyanescens (Rabenh.) Koerb.
Lichenella nigritella (Lettau) Moreno & Egea
Massalongia carnosa (Dickson) Koerber
Rhizoplaca chrysoleuca (Sm.) Zopf
Rhizoplaca melanophthalma (DC.) Leuckert & Poelt
Xanthoparmelia mexicana (Gyelnik) Hale
Xanthoria elegans (Link) Th.Fr.

SOIL

Crustose

Diploschistes muscorum (Scop.) R. Sant.
Toninia sedifolia (Scop.) Timdal

Squamulose

Catapyrenium daedalum (Kremp.) B. Stein
Catapyrenium lacinulatum (Ach.) Breuss
Catapyrenium squamulosum (Ach.) Breuss
Cladonia sp.
Psora decipiens (Hedwig) Hoffm.
Psora globifera (Ach.) A. Massal.
Psora himalayana (Church. Bab.) Timdal
Psora luridella (Tuck.) Fink
Psora russellii (Tuck.) A. Schneider
Psora tuckermanii R. Anderson ex Timdal

Foliose

Agonimia tristicula (Nyl.) Zahlbr.
Buellia elegans Poelt
Collema tenax (Sw.) Ach.
Fulgensia bracteata (Hoffm.) Rasanen
Xanthoparmelia chlorochroa (Tuck.) Hale

MOSS ON ROCK OR SOIL

Crustose

Chrysothrix chlorina (Ach.) J. R. Laundon
Mycobilimbia lobulata (Sommerf.) Hafellner

Foliose

Phaeophyscia constipata (Norrl. & Nyl.) Moberg
Phaeophyscia endococcina (Koerber) Moberg
Phaeophyscia sciastra (Ach.) Moberg
Physcia biziana (Mass.) Zahlbr.
Physcia dimidiata (Arnold) Nyl.
Physconia muscigena (Ach.) Poelt
Xanthoria candelaria (L.) Th.Fr.
Xanthoria elegans var. *splendens* (Darbish.) M.S. Christ.

WOODY PLANT LITTER ON SOIL

Crustose

Lecanora beringii Nyl.
Phaeorrhiza nimbosa (Fr.) Mayr. & Poelt

Small light gray thalli of *Physcia adscendens*, *P. dubia*, and *P. stellaris* also were on bark and wood. The bark of *Populus balsamifera* along the rivers supported more lichen growth than other trees and shrubs in the park although it was not unusual to find species of *Xanthoria* and *Physcia* on *Artemisia tridentata* bark. Lichens on wood and bark accumulate metals from atmosphere or from water flowing over them; the metals leach out into the ecosystem when the lichens die. Organic compounds such as ribitol leach out and serve as food for microorganisms and invertebrates in the system (Hale 1983). Ticks, insects, and mites frequently live or hide under foliose species on bark (personal observations).

Rock

The most conspicuous lichens on the rock near the parking areas were yellow-green foliose *Xanthoparmelia mexicana*, *Rhizoplaca melanophthalma*, and *R. chrysoleuca*; yellow-green crustose *Dimelaena oreina* and *Lecanora novomexicana*; and brownish-gray *Rhizocarpon disporum* and *Aspicilia* spp. The calcareous boulders had less lichen growth than the granitic boulders moved in from an area other than this calcareous park; *Dimelaena oreina* grows only on non-calcareous rock. The calcareous rocks along the trails and on the top and sides of Fort Rock were covered in places with bright orange *Xanthoria elegans* and *Caloplaca saxicola*, and black *Verrucaria glaucovirens* and *V. compacta*. Small colonies of *Xanthoria elegans* were also on old cement structures. Because of their requirements for nitrogen, the orange species of *Xanthoria* and *Caloplaca* on rock are considered indicators of animal or bird activity (Hale 1974). While there is some disagreement on how important lichens are to rock weathering, colonized rock usually feels softer and more crumbly under the lichen thalli than rock without lichen growth. Hyphae of the fungal component of lichens extend between rock particles and loosen them, and carbon dioxide mixes with water to produce dilute carbonic acid that dissolves rock, especially limestone. As lichens wet and dry, they expand and contract, pulling up little pieces of rock from the surface, weakening rock surface structure.

Soil

The soil crusts, also called cryptogamic or microbiotic crusts, are referred to here as lichen crusts because lichens were the dominant visible organism. On Fort Rock the lichen crusts were superficially similar to each other in appearance, developing in narrow strips adjacent to the parallel limestone outcrops surrounded by the grass-forb communities; however, they were slightly different in detail (Table 2). Crust 1 was chosen because it seemed to be the most exemplary, undisturbed crust. Crust 2 had no evidence of trampling and was on coarser, more gravelly soil than the other crust strips. Crust 3 was adjacent to the highest point of Fort Rock on the north end, and parts of it had more foot and dog-paw prints than the other crust strips. Crust 4 was trampled. Except for *Diploschistes muscorum*, absent from crust 4, all the lichen crusts had the same species visible in field examinations (Table 2). The most conspicuous vascular plants in the crusts were *Bouteloua gracilis* (H.B.K.) Lag. and *Opuntia polyacantha* Haw.

Soil in crusts 1, 2 and 3 averaged 45% lichen cover (Table 2), although crust 3 had lower lichen cover and higher moss cover than the other two less disturbed crusts. Trampling, as in soil crust 4, resulted in less lichen cover, only about 20% cover compared to 34 to 52% in other crusts, and more bare rock and soil, 45% cover compared to 10 to 28% in other crusts.

The soil crusts were unusual on Fort Rock compared to many other locations because they were relatively colorful and conspicuous; soil crusts tend to be

Table 2. *Analysis of soil crust sites in Headwaters State Park. Percent cover was determined by adding midpoints of 20 quadrats for each crust site and dividing by 20. Composite was determined by adding midpoints of 60 quadrats (20 from each site) and dividing by 60. Crusts 1-3 were strips of well-developed crust area along parallel limestone outcrops away from established trails; crust 4 was immediately adjacent to a trail.*

LICHEN SPECIES IN CRUSTS	CRUST 1	CRUST 2	CRUST 3	COMPOSITE	CRUST 4
Buellia elegans	10.5	14.0	8.0	10.8	1.6% cover
Catapyrenium spp.	13.3	11.0	6.0	10.1	11.9
Collema tenax complex	11.6	5.4	10.4	9.1	1.8
Fulgensia bracteata	6.9	2.8	5.6	5.1	2.0
Diploschistes muscorum	3.4	10.0	1.3	4.9	0
Psora decipiens	3.4	3.9	1.3	3.0	1.5
Psora spp.	1.6	0.9	0.9	1.1	0.3
Toninia sedifolia	0.9	1.4	0.8	1.0	0.3
Other	0.1	0.4	0	0.2	0
Lichen total	51.7	49.8	34.3	45.3	19.4
Bare rock and bare soil	10.0	28.4	19.4	17.8	45.4
Vascular plants including litter	30.9	20.7	36.4	29.3	44.2
Rock with lichen growth	1.4	1.5	0.4	1.1	0.4
Moss	1.6	2.6	7.6	4.0	5.3

an inconspicuous dark brown and black. The only other colorful soil crusts observed by the first author have been in the Colstrip area in southeastern Montana, also on calcareous soils. The major soil crust lichen species in Headwaters State Park were white foliose *Buellia elegans*, orange foliose *Fulgensia bracteata*, brown species of the squamulose genus *Catapyrenium* (primarily C. *lacinulatum* and C. *squamulosum*), white crustose *Diploschistes muscorum*, black inconspicuous *Collema tenax*, orange-red *Psora decipiens*, and other brown species of *Psora* (primarily *P. tuckermanii*). *Toninia sedifolia*, with tiny gray squamules, was very inconspicuous. Other lichens identified from the crusts but not distinguishable in the field were *Agonimia tristicula*, *Catapyrenium daedalum*, *Psora globifera*, *P. himalayana*, and *P. russellii*. *Caloplaca holocarpa* and *Phaeorrhiza nimbosa* grew on woody plant debris on soil. A notable genus missing from the crusts, and rare in the park in general, was *Cladonia*; only one small mat of sterile squamules was observed. Cyanobacteria, primarily *Nostoc* but also filamentous forms, were visible in nearly every microscopic examination of the crust. Moss species were present but were not identified because they lacked capsules.

Anderson and Rushforth (1976) identified 11 lichen species from soil crusts in Utah; they also identified 47 algae species including green algae and diatoms, 11 cyanobacteria, and six mosses for a total of 75 species in the cryptogamic crusts. In this study, 13 lichens were identified from the crusts, mostly the same species of *Psora, Collema, Fulgensia,* and *Diploschistes,* as in Anderson and Rushforth's collections. Two major additional crust species in Headwaters but not in the Utah study were *Buellia elegans* and *Toninia sedifolia*. A major species in southeastern Montana that was not present at Headwaters is *Squamarina lentigera* (Weber) Poelt. All of the lichen crust species at Headwaters are also components of cryptogamic crusts studied in sagebrush grasslands in southern Idaho (Kaltenecker and Wicklow-Howard 1994).

Metting (1991) distinguished among three different kinds of soil crusts. In moist microhabitats, moss and liverwort crusts are more important and tend to extend significantly above the soil surface. Within the soil, smaller crusts are dominated by algae, bacteria, cyanobacteria and fungi, and seem to be characteristic of more disturbed sites. Lichen crusts are an intermediate kind of crust that live on and immediately below the soil surface. Fungi associated with lichens extend into the soil and appear to enhance development of stable soil aggregates (Bailey et al. 1973). Soil crusts are important in arid grassland areas for several reasons (Eldridge and Greene 1994), especially in giving stability to soil in dry, windy areas. Harper and St. Clair (1985) demonstrated that physical disruption (simulated trampling) increased water runoff by 51% and increased soil loss 686% over that of control areas. Complete removal of the crust increased water runoff 92% and soil loss 1441%. The polysaccharide sheath around cyanobacterial cells is hydrophilic, attracting water that helps cell survival and binds soil particles (Harper and Marble 1988). The tiny mounds and depressions that are characteristic of soil crusts dominated by *Collema tenax*, a small nitrogen-fixing species, are very effective at increasing water absorption, and decreasing splash erosion, as water settles into the depressions (Loope and Gifford 1972, Brotherson and Rushforth 1983).

Soil crusts also contribute to the mineral content of soils. It is estimated that crusts containing free-living cyanobacteria and those in lichens such as *Collema* sp. contribute 10 kg h^{-1} y^{-1} of fixed nitrogen to grassland systems (Rychert et al. 1978). Beymer and Klopatek (1991) demonstrated that carbon fixed in photosynthesis is contributed to the soil ecosystem.

Biologically, soil crusts contribute food and habitat for small invertebrates; for example, some ants eat moss capsules (Loria and Hernstadt 1980) and a desert isopod (*Hemilepistrus reaumuri*) feeds on cryptogams directly (Steinberger 1989). Many small mites and insects are routinely collected with lichen and moss species (personal observation), although there is no evidence that they are feeding on lichens. Increased temperature stability of lichen-covered soil apparently also contributes to increased soil heterotrophic activity; soil respiration was reduced in a lichen-denuded system in Iceland due to changes in heterotrophic detritovores and fungivores in soil *Collembola* communities (Sendstad 1981). Decreased nitrogen and phosphorus were also noted in these communities.

The role of lichen crusts relative to vascular plants is not clear, and it might depend on the thickness of the lichen thalli and density of cover. Some studies have indicated that the uneven nature of some crusts such as those dominated by *Collema tenax* might provide refugia for seeds and enhance germination (Harper and St. Clair 1985, Mucher et al. 1988, Harper and Pendleton 1993). Crusts might also be beneficial to seed germination because they concentrate water and nutrients within 10 mm of the soil surface (Graetz and Tongway 1986). On the other hand, some of the denser covers of lichens at Headwaters State Park, such as the species of *Psora* spp., *Buellia elegans*, or *Diploschistes muscorum*, appeared to not provide a favorable germination site for most seeds, and vascular plants have not been routinely observed protruding from within these crusts. This is consistent with observations where dense mats of lichens in forests inhibited growth of seedlings of forest trees (Brown and Mikola 1974), although those lichens were tall fruticose species.

In some studies, a positive correlation between microbiotic cover and vascular plant cover has been reported (Graetz and Tongway 1986, Mucher et al 1988, Tongway and Smith 1989). *Festuca octoflora* Walt. and *Mentzelia multiflora* (Nutt.) Gray growing on a soil with a crust dominated by *Collema tenax* had more N, Mg, and Fe in their tissues than plants growing on adjacent soil with no crust, although the crust seemed to compete with *M. multiflora* for soil P (Belnap and Harper 1995). This suggests a nutritional relationship between a crust and vascular plants. Other studies have reported a negative correlation between lichen crusts and vascular plants (Harper and Marble 1988, Eldridge 1993, Eversman 1995). Soil lichens grow best in meadows and fields where they are not shaded by vascular plants. At Headwaters, lichen crusts were best developed immediately adjacent to the outcrops, probably because they can out-compete most of the vascular plants in those dry sites with very shallow soils. Continued encroachment by the taller exotics at Headwaters State Park may decrease the amount of ground cover by the crusts.

The extensively developed soil crusts of Headwaters State Park indicate the stable, undisturbed nature of much of Fort Rock. Crusts are easily broken and crushed by trampling and are absent in areas of heavy foot traffic and grazing. It takes 14-18 years for lichens and mosses to double their contribution to soil crusts in Utah, and 15-20 years to reach an equilibrium (Anderson et al. 1982). Restoration of crusts disturbed or removed by grazing is fastest during late winter and early spring when the most water is available (Marble and Harper 1989). Visitor traffic in Headwaters State Park is greatest in the summer and fall when crusts are dry and metabolically inactive. Less foot traffic in late winter and early spring, when more moisture is available and metabolic activity is greater, probably allows development and repair of damaged crusts due to moderate trampling.

Conclusions

The well-developed soil crusts on Fort Rock at Headwaters State Park indicate that trampling is negligible in most places off the trails, and that grazing has not occurred on Fort Rock for many years. The ecological roles of the lichen crusts are in protecting soil from wind and water erosion, improving soil texture, contributing nitrogen and carbon to the soil, and providing habitat for microinvertebrates. Small invertebrates are routinely collected with samples of lichen crust, although it does not appear that any animals, including large grazing animals, eat the lichens either from the soil or the rocks. Lichens on the rocks are contributing to rock erosion, a first step in soil formation.

Literature Cited

Anderson, D. C., and S. R. Rushforth. 1976. The cryptogam flora of desert soil crusts in southern Utah, U.S.A. Nova Hedwigia XXVIII: 691-729.

Anderson, D. C., K. T. Harper, and S. R. Rushforth. 1982. Recovery of cryptogamic crusts from grazing on Utah winter ranges. J. Range Manage. 35: 355-339.

Bailey, D., P. A. Mazurak, and J. R. Rosowski. 1973. Aggregation of soil particles by algae. J. Phycology 9: 99-101.

Belnap, J ., and K. T. Harper. 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Res. and Rehab. 9: 107-115.

Beymer, R. J ., and J. M. Klopatek. 1991. Potential contribution of carbon by micro- phytic crusts in pinyon-juniper woodlands. Arid Soil Res. Rehab. 5: 187-198.

Brotherson, J. D ., and S. R. Rushforth. 1983. Influence of cryptogamic crusts on moisture relationships of a soil in Navajo National Monument, Arizona. Great Basin Nat. 43: 73-79.

Brown, R. T ., and P. Mikola. 1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. Acta For. Fennica 141: 5-22.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science 33: 43-64.

Dorn, R. D. 1984. Vascular Plants of Montana. Mountain West Publishing, Cheyenne, WY. 276 pp.

Eldridge, D. J. 1993. Cryptogams, vascular plants and soil hydrological relations: some preliminary results from the semi-arid woodlands of eastern Australia. Great Basin Nat. 53: 48-58.

Eldridge, D. J ., and R. S. B. Greene 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. Aust. J. of Soil Res. 32: 389-415.

Esslinger, T. L ., and R. S. Egan. 1995. A sixth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. The Bryologist 98: 467- 549.

Eversman, S. 1995. Lichens of alpine meadows on the Beartooth Plateau, Montana and Wyoming, U.S.A. Arctic and Alpine Res. 27: 400-406.

Goward, T., B. McCune, and D. Meidinger. 1994. The Lichens of British Columbia, Illustrated Keys. Part 1, Foliose and Squamulose Species. Ministry of Forests, Victoria, B.C., Canada. 181 pp.

Graetz, R. D ., and D. J. Tongway. 1986. Influence of grazing management on vegetation, soil structure and nutrient distribution and the infiltration of applied rainfall in a semi-arid chenopod shrubland. Aust. J. Ecol. 11: 347-360.

Hale, M. E. 1974. The Biology of Lichens. Second Edition. American Elsevier Publishing Co., New York. 181 pp.

Hale, M. E. 1983. The Biology of Lichens. Third Edition. Edward Arnold, Baltimore, MD. 190 pp.

Harper, K. T ., and J. R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. Pp. 135-169, *in*: P. T. Tueller (ed.). Vegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Boston, MA.

Harper, K. T ., and R. L. Pendleton. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? Great Basin Nat. 53: 59-72.

Harper, K. T ., and L. L. St. Clair. 1985. Cryptogamic soil crusts on arid and semiarid rangelands in Utah. Effects on seedling establishment and soil stability. Final Report, Bureau of Land Management, Utah State Office, Salt Lake City, UT. 103 pp.

Kaltenecker, J ., and M. Wicklow-Howard. 1994. Microbiotic soil crusts in sagebrush habitats of southern Idaho. Eastside Project, Columbia River Basin Ecosystem Management Plan. U.S. Forest Service, Boise, ID. 56 pp.

Loope, W. L ., and G. F. Gifford. 1972. Influence of a soil microfloral crust on selected properties of soils under pinyon-juniper in southeastern Utah. J. Soil and Water Cons. 27: 164-167.

Loria, M ., and J. Hernstadt. 1980. Moss capsules as food of the harvester ant. Messor. Bryologist 83: 524-525.

Marble, J. R ., and K. T. Harper. 1989. Effect of timing of grazing on soil-surface cryptogamic communities in a great basin low-shrub desert: a preliminary report. Great Basin Nat. 49: 104-107.

McCune, B ., and T. Goward. 1995. Macrolichens of the Northern Rocky Mountains. Mad River Press, Inc., Eureka, CA. 208 pp.

Metting, B. 1991. Biological surface features of semiarid lands and deserts. Pp. 257-293, *in*: J. Skujins (ed.). Semiarid lands and deserts: soil resource and reclamation. Marcel Dekker, New York.

Mucher, H. J., C. J. Chartres, D. J. Tongway and R. S. B. Greene. 1988. Micro-morphology and significance of the surface crusts of soils in rangelands near Cobar, Australia. Geoderma 42: 227-244.

National Oceanic and Atmospheric Administration. 1995. Climatological Data Annual Summary, Montana. Volume 98. National Climatic Data Center, Ashville, N.C. 28 pp.

Rychert, R., J. Skujins, D. Sorensen, and D. Porcella. 1978. Nitrogen fixation by lichens and free-living microorganisms in deserts. pp. 20-30, In: N. E. West and J. Skujins. (eds.). Nitrogen in desert ecosystems. Dowden, Hutchinson & Ross., Inc. Stroudsburg, PA.

Sendstad, E. 1981. Soil ecology of a lichen heath at Spitsbergen, Svalbard: effects of artificial removal of the lichen plant cover. J. Range Manage. 34: 442-445.

Steinberger, Y. 1989. Energy and protein budgets of the desert isopod Hemilepistrus reaumuri. Acta Oecologia 10: 117-134.

Three Forks Area Historical Society. 1983. Headwaters Heritage History. Artcraft Printers, Butte, MT. 698 pp.

Tongway, D. J ., and E. L. Smith. 1989. Soil surface features as indicators of rangeland site production. Aust. Rangeland J. 11: 15-20.

Wetmore, C. 1967. Lichens of the Black Hills of South Dakota and Wyoming. Publications of the Museum, Michigan State University, Biological Series 3: 4. 464 pp.