AN ABSTRACT OF THE THESIS OF

Jeanne M. Ponzetti for the degree of Master of Science in Botany and Plant Pathology presented on June 7, 2000. Title: Biotic Soil Crusts of Oregon's Shrub Steppe.

Abstract approved: Redacted for privacy

Bruce P. McCune

This research examines the community composition of biotic soil crusts at nine sites in central and eastern Oregon, U.S.A. At each site, data were collected in one pair of livestock-grazed and excluded transects. Variables recorded included: cover of biotic soil crusts and vascular plant species, soil surface pH, electrical conductivity, soil surface roughness, surface rock, gravel, bare ground, organic litter, and cowpies.

Using Non-metric Multidimensional Scaling, we extracted the primary environmental gradients controlling biotic crust community composition among sites. The strongest gradient was related to soil chemistry. Total crust cover, lichen cover, and bryophyte cover were inversely related to soil pH, electrical conductivity, and CIV (Calcareous Index Value; site scores on a scale representing relative soil calcium carbonate content). Total crust cover was also positively associated with temperature, and inversely related to elevation. Biotic crust composition was related to moisture and aspect; cooler, north-facing slopes with greater precipitation and *Festuca idahoensis* cover were compositionally distinct from flat sites with greater heat exposure.

The weakest pattern in these data appears to represent a disturbance gradient, with bare ground inversely related to exclosure age. Transect scores on this gradient were different between currently grazed and exclosure transects ($p = 0.01$, blocked MRPP). On average, bare ground was greater in the grazed transects, while total crust cover, cover of nitrogen-fixing lichens, biotic soil surface roughness, and species richness were greater within the exclosures ($p \leq 0.02$ for all, two-tailed paired t-tests). Differences in vascular plant cover, richness, and composition were not detected.

CIV was one of the strongest variables related to biotic crust composition. CIV is based on a calcareous index that uses the presence of certain lichen species as indicators

of calcareous soils. Using weighted averaging and the abundances of these indicators in our data, we revised this index, incorporating new indicators and removing poor ones.

We conclude that 1) biotic soil crusts are sensitive indicators of disturbance, 2) there are strong compositional differences in shrub steppe crust communities of Oregon, which are related to regional soil and climate differences, and 3) lichens can be used as sensitive indicators of soil chemistry.

Biotic Soil Crusts of Oregon's Shrub Steppe

by

Jeanne M. Ponzetti

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Master of Science

Presented June 7, 2000

Commencement June 2001

Master of Science thesis of Jeanne M. Ponzetti presented on June 7, 2000

APPROVED:

Redacted for privacy

Major Professor, representing Botany and Plant Pathology

Redacted for privacy

Chair of Department of Botany and Plant Pathology

Redacted for privacy

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Jeanne M. Ponzetti, Author

ACKNOWLEDGMENTS

The Prineville District Bureau of Land Management, the Northwest Scientific Association, the Nature Conservancy of Oregon supplied the financial support that made this work possible.

Numerous personnel in the Prineville, Lakeview and Burns Districts of the Bureau of Land Management assisted with locating suitable research sites and provided access to information. In particular, we thank Dan Tippy, Lucille Housley, Dave Pachioretti, Nora Taylor, Rick Hall, Curt Leet, Sandra McGuinness, and Ron Halverson. Jeff Rose and Tony Svecar, of the Eastern Oregon Agricultural Research Center, supplied information and access to the exclosures at the Northern Great Basin Experimental Range.

I thank Roger Rosentreter, John Christy, and Dan Norris for help with identifications. Pat Muir graciously allowed the use of her lab and equipment for an extended period of time. Abbey Rosso and David Wilderman assisted with lab work and data entry, and also provided valuable advice at many stages of this project. I also thank experts in the Oregon State University Department of Crop and Soil Science for their advice on soil testing methods, including Dean Hanson, Barbara Koepsell, and Will Austin.

Thanks to Pat Muir, David Pyke, Roger Rosentreter, and David Wilderman for reviewing portions of this manuscript. Their comments and insights greatly improved the final product.

Finally, I extend special thanks to Bruce McCune. This research would not have been possible without his ideas, experience, patience and support.

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Biotic Soil Crusts of Oregon's Shrub Steppe

Introduction

Visitors to the arid and semi-arid steppe regions of central and eastern Oregon are often impressed by the vast, open landscapes of rolling hills, and flat, sagebrush-covered basins, and the splashes of color from spring wildflower displays. Many will notice the bright yellows and oranges of lichen patches on basalt cliffs. But for the truly passionate observers of life, those willing to crawl on the ground on their hands and knees, entire communities of diminutive organisms await their discovery.

The diversity of life forms that comprise biotic soil crust communities is astounding. Mosses form short, cushion-like mats over the soil surface, and range in color from dark brown, green, rusty-orange, and silvery-white when dry and dormant. After a rain, they display various shades of bright green, as their leaves swell with water and resume photosynthesis. Terricolous lichens exhibit a dramatic range of sizes, colors and growth forms, including pinkish-brown hemispherical mounds, up to 10 cm in diameter, with convoluted, brain-like surfaces, to scattered bright yellow disks no larger than 2 mm across. Some lichens form leaf-like thalli covering the soil surface, and some form upright, goblet-shaped cups, from 1 to 5 cm tall. Liverworts can be dark, stringy species with minute leaves, or bright green, prostrate "thalloid" species that appear ephemerally with the spring wet season. With the aid of a microscope, algae, nitrogen-fixing cyanobacteria, fungi, bacteria and a host of microfauna can also be found living within the first few centimeters of the soil surface.

Biotic soil crusts are found in most arid and semi-arid deserts, steppes, and grassland ecosystems around the world, as well as arctic tundra and alpine sod (USDI 2000). They can usually be found where soils are too thin or the climate is too harsh to support many vascular plants. Biotic crusts have been found to reduce soil erosion, contribute nitrogen and organic matter to the soil, and influence soil-water relations (Belnap and Harper 1995, Graetz and Tongway 1986, Verrecchia et al. 1995, Williams 1993), and thus perform important ecosystem functions. However, examination of biotic crust composition, function, and responses to disturbance has been minimal in Oregon and the Pacific Northwest.

This research explores the ecology and composition of terricolous lichen and bryophyte crust communities in Oregon's steppe and juniper savannas, and looks closely at the capacity of lichens as soil chemistry indicators. The recovery of biotic crusts after removal of livestock disturbance is examined with the use of pre-existing fenced livestock exclosures. The purpose of this work is to improve our understanding of what factors control the composition of Oregon's biotic soil crusts.

Objectives

My objectives for this thesis were to:

1) determine the primary environmental variables influencing the distribution and abundance of biotic crust lichens and bryophytes;

2) determine if there is a general relationship between biotic crust composition and livestock activity in Oregon's shrub steppe; and

3) explore the use of lichen composition as an indicator of soil chemistry.

Review of Relevant Literature

Distribution and Composition. Biological soil crusts occur in a variety of biomes around the world, including arctic, alpine, subalpine, and arid to semi-arid grassland, steppe and desert (Anderson and Bliss 1998, Pérez 1997, USDI 2000). The relevant characteristics that unite these diverse ecosystems include limited vascular vegetation and low organic matter inputs to the soil surface. Due to the sessile, prostrate habit of most biotic crust organisms, they are vulnerable to excessive light competition from vascular vegetation or organic litter (Kaltenecker 1997, Ponzetti et al. 1998, Ponzetti et al. 2000). Unlike plants with roots, these organisms obtain nutrients and water from direct contact with soil and atmospheric inputs such as rain, fog, and dew; these inputs may also be reduced by accumulations of organic litter. Thus, soil crusts usually occur in sites where environmental conditions are relatively limiting to vascular plants, such as low precipitation, thin or nutrient-poor soils, or extreme temperatures.

Beyond the structural similarities among the ecosystems where they are found, the particular composition of biotic crusts varies greatly among biomes, and even among ecoregions within biomes. Pérez (1997) found liverworts and mosses to be the dominant organisms in an alpine soil of the Andes, but notes that cyanobacteria are dominant in Antarctica's crusts, and some Arctic crusts include a mixture of lichens, bryophytes and algae. Semi-arid rangelands in eastern Australia are home to a diverse array of lichens and bryophytes (Eldridge and Tozer 1997), while cyanobacteria and cyanophilous lichens dominate Israel's Dead Sea Valley (Danin et al. 1998). In western North America, mosses and lichens are abundant in the semi-arid sagebrush steppe and grasslands of the Great Basin and Columbia Basin, while cyanobacteria and nitrogen-fixing lichens are dominant in the Colorado Plateau and Sonoran Desert (USDI 2000). Flechtner et al. (1998) found the soil algal community of the Central Desert of Baja, Mexico to be distinctly different from that of other desert regions. Likewise, Nash et al. (1977) found different lichen and moss communities in representative sites from the Chihuahuan, Mohave and Sonoran deserts, which they largely attributed to differences in substrate ecology.

Substrate ecology has long been known to impact lichen and bryophyte community composition. In particular, limestone and limestone-derived substrates have relatively high pH and calcium levels; they support different biotic crust organisms than acidic substrates (Nash 1996a). Variation in pH was an important factor influencing soil-dwelling lichen and bryophyte composition in arid and semi-arid Australia (Downing and Selkirk 1993, Eldridge and Tozer 1997), and in Canadian subarctic forest-tundra (Robinson et al. 1989). Soil pH was also correlated with cyanobacterial distribution in the Central Desert of Baja, Mexico (Flechtner et al. 1998). Lichen community composition is known to be affected by calcium carbonate levels (Asta and Lachet 1978, Gilbert and Fox 1986, Eldridge and Tozer 1997), with some lichens and mosses growing predominantly on calcareous or gypsiferous substrates (Downing and Selkirk 1993, Guerra et al. 1995, Insarov and Insarov 1995).

Functional Attributes. The primary functions of biotic soil crusts in arid and semi-arid environments have been reviewed extensively by a number of authors (Eldridge and Greene 1994, Evans and Johansen 1999, Ladyman and Muldavin 1996, Williams 1994, West 1990). Many researchers have demonstrated that soils with biotic soil crusts are less susceptible to soil erosion, have higher organic matter contents, and more available nitrogen.

Biotic soil crusts reduce soil erosion through a variety of mechanisms, including increased binding of soil particles and protection from erosive forces. Soil algae, cyanobacteria, and fungi increase soil aggregate stability by binding soil particles with polysaccharide secretions (Belnap and Gardner 1993, Bailey et al. 1973, Schulten 1985). Many soil-dwelling lichens bind soil with deeply penetrating fungal hyphae or rhizines, used for anchoring the lichen to the substrate (Büdel and Scheidegger 1996, Schulten 1985). Schulten (1985) also found a web of rhizoids binding soil particles beneath the ubiquitous moss *Ceratadon purpureus*. Mosses of the Negev Desert trap airborn sediments, resulting in an accumulation of loess (Danin and Ganor 1991). As early as 1902, a field agent of the U.S. Department of Agriculture recognized the moss *Tortula ruralis* as a sand binder in northern Nevada and eastern Oregon (Griffiths 1902). By most accounts, biotic soil crusts improve soil aggregate stability and soil structure (Mücher et al. 1988, Booth 1941, Bailey et al. 1973, Neuman and Maxwell 1999, Williams 1995b). In one exception, Eldridge and Kinnell (1997) found no effect of biotic crust cover on aggregate stability; however, they also found biotic crusts to be associated with a significant reduction in soil erosion.

Lichens and bryophytes covering the soil surface physically protect it, reducing the erosive effects of water and wind. Many researchers have found that biotic crusts minimize soil erosion associated with raindrop impact and water flow (Eldridge and Kinnell 1997, Eldridge 1993, Kinnell et al. 1990, Williams 1993). The presence of biotic crusts has been demonstrated to reduce the erosive forces of wind, by increasing the threshold velocity required to move soil particles (Williams 1995a, Leys and Eldridge 1998, Neuman and Maxwell 1999). Possible mechanisms responsible for these effects include direct physical protection from wind and water, interception of raindrop energy, water absorption, improvements to soil structure, and increases in surface roughness of the soil (Eldridge and Kinnell 1997). Soil surface roughness slows the movement of water over soil, reducing detachment and transport of soil particles (Johnson and Blackburn 1989, Lehrsch et al. 1988).

Researchers have reported conflicting results regarding effects of biotic crusts on water infiltration. Some researchers have found biotic crust cover to be associated with increased infiltration rates (Eldridge 1993, Loope and Gifford 1972, Yair 1990), while others have found that crusts decrease infiltration and increase runoff (Brotherson and Rushforth 1983, Graetz and Tongway 1986). A few have found no effect of biotic crusts on infiltration (Booth 1941, Williams 1995b). In the Negev Desert, Verrecchia et al. (1995) found that swelling of cyanobacterial crusts increased runoff but also reduced evaporative water loss. Using a rainfall simulator in southern Utah, Williams (1995b) found that biological soil crusts rested from grazing for two to three years did not affect infiltration or effective hydraulic conductivity relative to areas from which crusts had been scalped or chemically killed. He determined that the presence of biotic crusts reduced time to ponding and runoff relative to scalped treatments, but also decreased erosion. Similarly, in the badlands of southeastern Spain, Alexander and Calvo (1990) found that plots with well-developed lichen cover had the most rapid time to ponding and time to runoff, but the lowest total sediment concentration associated with that runoff. They also determined that infiltration rates were influenced by lichen type, with *Collema* and *Toninia* species creating a more porous crust than other species. Brotherson and Rushforth (1983) found moss crusts to have greater infiltration than lichen and algal crusts. Thus, some of these investigations may be confounded by the effects of differing biotic crust composition (Brotherson and Rushforth 1983, Eldridge 1993, Graetz and Tongway 1986).

Biotic crusts contribute organic matter to the soil through accumulation of biomass following death and secretion of carbon compounds into the soil (Ladyman and Muldavin 1996). In the southwestern United States, researchers have found higher levels of carbon (Beymer and Klopatek 1991) and organic matter (Kleiner and Harper 1977a, Harper and Pendleton 1993, Graetz and Tongway 1986, Belnap and Harper 1995) in soils with greater biotic crust cover. Many researchers have demonstrated that crusts with cyanobacteria and nitrogen-fixing lichens contribute nitrogen to arid ecosystems (Jeffries et al. 1992, Shields et al. 1957, Evans and Belnap 1999). In addition, there is evidence that soils with biotic crusts have greater availability of other nutrients necessary for plant growth, including phosphorus, potassium, manganese and magnesium (Graetz and Tongway 1986, Harper and Pendleton 1993, Kleiner and Harper 1977a, Belnap and Harper 1995, Ridenour and Callaway 1997).

Biotic crusts in arid and semi-arid regions of the Pacific Northwest have some degree of cracking or discontinuity, either from frost-heaving, naturally occurring patchiness, or native rodent burrowing. Seedling emergence is often associated with these cracks, small disturbances, and areas of soil pinnacles and surface roughness (Eckert et al. 1986, personal observations of the author). Differences in biotic crust communities, types of disturbances, individual species life history strategies, and seed morphologies all influence the availability of seed germination sites, and seedling establishment potentials. A number of researchers have demonstrated that biotic crusts enhance seedling survival for some plants

(Eckert et al. 1986, Harper and Pendleton 1993, Lesica and Shelly 1992, Keizer et al. 1985, St. Clair et al. 1984). There is increasing evidence that the presence of biotic crusts inhibits seed germination of *Bromus tectorum*, an aggressive exotic annual grass (Larsen 1995, Kaltenecker et al. 1999a). These crusts may, in fact, limit germination for other undesirable ("weedy") species that require disturbed soil for seed burial and germination (USDI 2000, Eckert et al. 1986).

Disturbance and Recovery. There is considerable evidence that various forms of physical disturbance are detrimental to soil crusts. Studies report that cover of algal, cyanobacterial, lichen and moss crusts are reduced by off-road vehicle use and tank tracks (Belnap et al. 1994, Watts 1998), hikers (Cole 1990), and mechanical disturbance caused by livestock trampling (Anderson et al. 1982b, Beymer and Klopatek 1992, Jeffries and Klopatek 1987, Johansen and St. Clair 1986, Kaltenecker et al. 1999b). Likewise, livestock disturbance reduces species richness of crust organisms (Anderson et al. 1982b, Hodgins and Rogers 1997, Johansen and St. Clair 1986). In addition, nitrogen-fixation is suppressed by disturbance of these crusts (Belnap et al. 1994, Evans and Belnap 1999, Jeffries et al. 1992).

However, the effects of physical disturbance on crusts may vary from site to site in relation to vascular plant communities, climatic variables, soil texture, and season of livestock use. In crested wheatgrass (*Agropyron desertorum*) pastures in Idaho, Memmott et al. (1998) found total crust cover and moss cover in winter-grazed pastures to be nearly identical to ungrazed controls, but reduced in spring- and summer-grazed pastures. They found lichen cover to be significantly reduced for all grazing seasons. In a sheep-grazed three-tip sagebrush (*Artemisia tripartita*) steppe in Idaho, Bork et al. (1998) found higher moss cover within exclosures, but no difference in lichen cover under fall- and spring-grazing systems. In Utah, Marble and Harper (1989) found early-winter grazing to be less detrimental to crust cover and richness than a combination of early- and late-winter grazing. Kaltenecker et al. (1999b) found significant recovery of crust cover after removal of livestock grazing in Wyoming big sagebrush (*Artemisia tridentata* ssp.

wyomingensis) and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities, but no recovery in low sagebrush (*Artemisia arbuscula*) sites. They attribute this lack of recovery to inherently poor condition for crust development in the low sagebrush sites, including a gravelly soil surface, and dominance of rhizomatous grasses.

Biotic crust recovery rates after physical disturbance vary widely by crust organisms, community type, ecoregion, and severity of disturbance. On the Colorado Plateau of southern Utah, complete algal recovery was estimated to take 40 years, with lichen recovery estimated at 45 to 85 years (Belnap 1993). Nitrogen fixation rates in cyanobacterial crusts may take longer than 30 years to recover to pre-disturbance levels (Evans and Belnap 1999). However, in central and eastern Utah, cryptogams and algae of *Atriplex*-dominated sites were almost fully recovered from grazing after 14 to 18 years (Anderson et al. 1982b). Recovery of algal and cyanobacterial crusts generally occurs before recolonization by mosses and lichens (Belnap 1993, Johansen and St. Clair 1986, USDI 2000). Recovery is thought to be most rapid in areas of high effective precipitation, and on relatively stable, finer-textured soils (USDI 2000).

A number of studies in arid and semi-arid ecosystems have documented decreases in terricolous lichen and bryophyte cover and algal biomass in response to fire (Greene et al. 1990, Kinnell et al. 1990, Johansen et al. 1984 and 1982, Shulten 1985, West and Hassan 1985). Greene et al. (1990) report a recovery of total crust cover after four years in an Australian semi-arid woodland, but did not examine compositional recovery. Shulten (1985) found only one species of lichen beginning to recover 16 months after fire in an Iowa prairie, and observed mosses colonizing spaces previously occupied by lichens. In Utah, crust recovery five years after wildfire was not complete in terms of biomass or composition, with only three species recolonizing the burned site (Johansen et al. 1984). A few researchers have reported rapid post-fire recovery of algal biomass, from 12 to 24 months (Johansen et al. 1984, 1993, Ponzetti et al. 1998). Bryophytes have generally been found to recover faster than lichens (Kaltenecker 1997, Johansen et al 1984, Shulten 1985). However, three years after a cool-season prescribed fire in Oregon, bryophytes appeared to be recovering more slowly than lichens, largely due to relatively poor recovery of *Tortula ruralis* (Ponzetti et al. 1999). In this case, species richness had recovered to pre-burn levels, while total crust cover had not (Ponzetti et al. 1999).

These conflicting reports illustrate that crust recovery after fire is complex. Recovery is thought to be influenced by fire intensity and frequency, local climate, propagule sources, and the nature of the pre-disturbance crust and vascular plant communities (USDI 2000). Rosentreter (1986) suggests that areas that escape fire may act as refugia for biotic crust species, providing propagules that allow for more rapid recovery of nearby burned areas. If so, the nature of the fuels and fire intensity could greatly influence recovery rates.

Summary. Biotic soil crusts are complex communities of diverse organisms, occurring in a variety of biomes. In arid and semi-arid desert, steppe and grasslands, dominant organisms vary by geographic ecoregion, soil type and chemistry, climate, and other site-specific variables. Because of these differences, generalizations about disturbance effects and recovery rates do not necessarily apply across regions. However, most of the ecological functions performed by crusts are similar worldwide, particularly those regarding soil stabilization. Appropriate management of biotic soil crusts requires that we improve our site-specific knowledge of crust organisms, as well as our understanding of the differences between crusts from region to region.

Community Composition in Relation to Soil Chemistry, Climate, and Livestock Activity

Jeanne M. Ponzetti and Bruce P. McCune

Submitted to *The Bryologist*
American Bryological and Lichenological Society, Fairfax VA,
May 7, 39 pp.

Abstract

We examined biotic soil crust cover and composition at nine shrub steppe sites in central and eastern Oregon, U.S.A. One pair of livestock-grazed and excluded transects was established at each site. Data were collected on the cover of biotic soil crust and vascular plant species, soil surface pH and electrical conductivity, and other environmental variables. Using gradient analysis, we found that differences in community composition among sites were most strongly related to soil pH, electrical conductivity (EC), and Calcareous Index Value (CIV; a scale representing the relative calcium carbonate content of soils). Other important variables included precipitation, elevation, aspect and temperature. We found total crust cover to be highest at sites with lower pH, EC, and CIV. Dominant species differed markedly between the more calcareous sites with higher pH, and the less calcareous, lower pH sites. Livestock exclusion was not an important gradient in the ordination of these data, being overshadowed by the strong soil chemistry and climate gradients. However, overall community composition of soil crust species was different between currently grazed and exclosure transects ($p = 0.02$, Blocked Multi-Response Permutation Procedure).

Comparison of currently grazed and exclosure transects revealed lower cover of biotic crusts, nitrogen-fixing lichens, crust-dominated soil surface roughness, and lower species richness in the grazed transects. On average, there was more bare ground in the grazed transects ($p \leq 0.02$ for all, two-tailed paired t-tests). Our results suggested that total bunchgrass cover was higher within exclosures, but conclusive evidence was lacking ($p = 0.1$, two-tailed paired t-test). Vascular plant composition, cover, richness, shrub cover, electrical conductivity and pH were not different between the grazed and exclosure transects. Thus, reductions in cover and richness of biotic soil crusts were apparent while significant impacts to vascular plants were not obvious. We conclude that biotic soil crusts are sensitive indicators of disturbance, and that there are strong compositional differences correlated to regional soil and climate gradients in shrub

steppe crust communities of Oregon.

Introduction

The deserts and semi-arid grasslands of western North America are often noted for their vast, open landscapes, and vibrant spring wildflowers. Few visitors notice the remarkable diversity of diminutive organisms growing on the soil surface, in the spaces between and under the bunchgrasses, shrubs and forbs. These organisms include lichens and bryophytes covering the soil surface, and microscopic algae, fungi, nitrogen-fixing cyanobacteria, and microfauna living within the first few centimeters of the soil. Collectively, these organisms make up biotic soil crusts, also known as microbiotic, cryptogamic or microphytic crusts.

Interest in biotic soil crusts has grown markedly as our awareness of their ecological importance has increased. In addition to providing biological diversity and color, these crusts contribute to nutrient cycling and improve soil stability and structure in some locations. Lichens and bryophytes increase resistance to erosive forces by providing soil surface cover, trapping and binding soil particles, and creating rough surface microtopographies (Danin et al. 1998, Danin and Ganor 1991, Eldridge and Kinnell 1997, Kinnell et al. 1990, Mücher et al. 1988, Schulten 1985, Williams 1993). Soil algae, cyanobacteria and fungal hyphae increase aggregate stability of the soil by binding soil particles with polysaccharide exudates (Bailey et al. 1973, Belnap and Gardner 1993, Booth 1941, Schulten 1985). Crusts composed of free-living and lichenized cyanobacteria contribute fixed nitrogen to arid and semi-arid ecosystems (Belnap et al. 1994, Evans and Ehleringer 1993, Jeffries et al. 1992, Shields et al. 1957, Starks et al. 1981). Collectively, biotic crust organisms supply nitrogen or other minerals to vascular plants, and contribute to soil organic matter content (Belnap and Harper 1995, Harper and Pendleton 1993, Pérez 1997, Snyder and Wullstein 1973). Research in a variety of arid systems indicates that biotic crusts help reduce soil erosion and maintain richer, finer soils. However, biotic crusts are sensitive to disturbances, including mechanical disturbances from domestic livestock (Anderson et al. 1982a and b, Beymer and Klopatek 1992, Hodgins and Rogers 1997, Johansen and St. Clair 1986) and human recreational activities (Belnap 1996, Cole 1990).

Thus far, most biotic crust research has focused on their ecological functions and response to disturbances. While this has made a critical contribution to our understanding, there has been little differentiation between types of soil crust communities and study of how their differences might affect their functional ecology. In western North America, the distribution and composition of crust communities in relation to environmental and biotic variables is poorly understood, both within and across ecosystems. Only a few community characterizations are available for the Chihuahuan, Sonoran, and Mohave deserts (Nash et al. 1977, Nash and Moser 1982), Colorado Plateau and Intermountain Region (Anderson et al. 1982a, St. Clair et al. 1993), and Snake River Plain of Idaho (Rosentreter 1986, Kaltenecker 1994). Floristic and ecological information has been gathered for terricolous lichens and bryophytes in the northern Great Basin and Columbia Basin of Oregon (McCune 1994, 1992; Hammer 1995; Christy and Harpel 1997), but comparative community research is generally lacking. However, Johansen et al. (1993) found shrub steppe algal communities in the Columbia Basin of Washington to be distinctly different from those in the Great Basin and Colorado Plateau.

In this study, we explored terricolous lichen and bryophyte soil crust communities at nine sites in central and eastern Oregon. To assess potential effects of livestock activity on biotic crusts composition, we chose sites with pairs of currently grazed and exclosure areas. We examined patterns of variation in crust cover and community composition, and the physical and biological factors that were correlated with those patterns. The goal of this research was to better understand how the presence of livestock and other biotic and abiotic factors influence the abundance and distribution of soil crust organisms. This information is critical to making sound land management decisions in Oregon's shrub steppe communities.

Methods

Selection of Research Sites. To address our question regarding livestock effects on crust composition, we searched central and eastern Oregon for upland steppe and shrub steppe research sites with fenced livestock exclosures. We required that the exclosures be adjacent to actively grazed pastures of the same native vascular plant community type, and with approximately the same slope and aspect between the grazed pasture and exclosure. These criteria were critical for isolating potential cattle-related effects from other, possibly confounding site factors. We did not include sites with poorly maintained exclosure fences. We found nine sites that satisfied these criteria (Figure 2.1). Mean annual precipitation and temperature data were obtained from the nearest Oregon Climate Service (1997) weather stations or county soil surveys. Field data were collected in 1995, when exclosures ranged from 11 to 58 years old.

Field Methods. Field work was conducted from April to July, 1995. At each site, a 100-m transect was placed inside the exclosure, and another matching transect was placed in the grazed pasture. Within a suitable research area defined by the above criteria, we selected a randomly-chosen fencepost, and placed the transects a random distance perpendicular to fence at that point. We placed the transects parallel to the fenceline at the majority of sites, where the topography was essentially flat. At two sites with significant slopes, we placed the transects along the elevational contour, at an angle to the fenceline. This step was necessary to match slope position between transects, and to avoid placing transects on top of erosional gullies. Transects were not closer than 10 m from the exclosure fence, trails or roads, so that concentrated cattle trampling and vehicle disturbance would not influence our results. There was one exception, where the size of the exclosure required that we locate the exclosure transect 2 m from the fence (Great Basin Experimental Range Exclosure No. 7). However, at this site, both transects were placed perpendicular to the fence, minimizing potential fenceline-related trampling

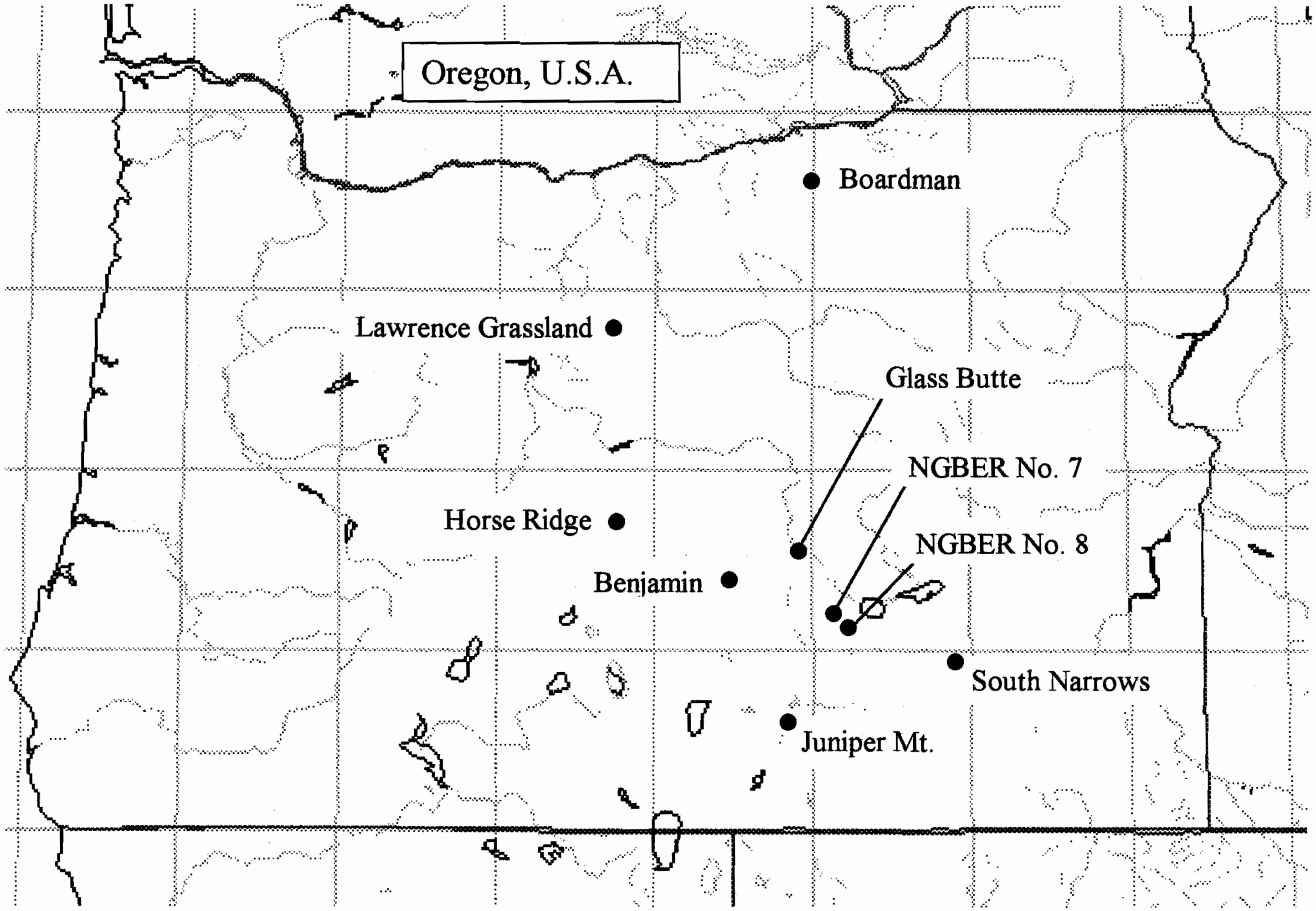

FIGURE 2.1. Locations of research sites. Each solid circle represents one site with a pair of transects.

effects. We permanently marked the transects by placing metal stakes at each end of the 100-m line.

We randomly located 45 quadrats along the length of each transect, using a quadrat size of 20- X 50-cm. Within each quadrat, we estimated cover using the following eight cover classes: <1%, 1-4%, 4-10%, 10-25%, 25-50%, 50-75%, 75-95%, 95-100%. We recorded estimates of cover for all biotic crust lichen and bryophytes to the species level when possible, or by genera or morphological groups when field identification was not possible. Morphological groups consisted of superficially similar species that were difficult to distinguish in the field. For convenience, we refer to all biotic soil crust species and morphological groups as "species" throughout this paper. We obtained voucher specimens at all sites and confirmed identifications in the laboratory; specimens are deposited at the Oregon State University Herbarium (OSC). Except where otherwise noted, nomenclature follows Esslinger and Egan (1995) for lichens, Anderson et al. (1990) for mosses, and Stotler and Crandall-Stotler (1977) for liverworts. We obtained voucher specimens from outside the quadrats, minimizing disturbance to the permanently marked transect areas, so that they may be reexamined in the future.

Cover estimates of site variables were also recorded, including vascular plants, rock (>25 mm at largest diameter), gravel (< 25 mm at largest diameter), bare ground, non-persistent litter, woody debris, and cowpies. In addition, we estimated cover of biotic soil surface roughness (roughness). Because roughness breaks down flow patterns, it is important in reducing soil erosion. For this study, we defined roughness as any soil microtopography that was dominated by lichens or bryophytes, and exhibited a minimum of a 5 mm vertical rise over a 10 mm horizontal distance. These soil pillars might be entirely covered or merely capped by lichens or bryophytes. Our criteria excluded roughness caused by rock, gravel, or pedestalled bunchgrasses, so that we assessed only that roughness associated with biotic crusts. Both wind and water erosion are reduced by rough surfaces in general and rough biotic crust microtopographies in particular (Eldridge and Kinnell 1997, Mücher et al. 1988, Williams 1993).

We recorded slope for each transect using a hand-held clinometer. Aspect was recorded in degrees east of true north. To estimate the relative amount of solar exposure at the sites, we converted the aspect azimuths to a simple heat-load scale, as follows: 1 = NE aspects, 2 = N and E aspects, 3 = SE and NW aspects and flat topography, 4 = S and W aspects, and 5 = SW aspect. Thus, heat-load increases with increasing solar exposure.

We used a "calcareous index" developed by McCune and Rosentreter (1995) to give each transect a "calcareous index value" (CIV). Lichenologists have traditionally considered lichens found growing primarily on calcareous soils to be "calciphiles." This index is based on the known affinities of certain common lichens for free calcium carbonates in surface soil. Ten species frequent on soils with low calcium carbonate content have an index value of -1, while ten species that frequent soil with high calcium carbonate content have an index value of +1. Transect CIV scores were calculated by simply summing the index values of the species present in each transect. The index ranges from -10 for the least calcareous sites to +10 for the most calcareous sites.

Soil surface samples were collected adjacent to every fifth quadrat, resulting in nine samples per transect. Because our purpose in characterizing the surface soil was to describe the lichen and bryophyte substrate, we obtained soil samples from the spaces between vascular plants, where most of the lichens and bryophytes were found. After scraping off any surface biotic crust and plant litter, we removed the top 2 cm of soil from an 8- X 8-cm area.

Soil Analyses. We pre-treated all 162 soil surface samples by passing them through a 2 mm sieve to remove the coarse fragments. We measured pH of the samples with a 1:2 soil-water ratio, placing the electrode in the supernatant rather than in the soil slurry (McLean 1982). For each transect, all nine sample pH values were averaged. We measured electrical conductivity (EC) with a digital conductivity meter, using standard methods described by Rhoades (1982). For each transect, the nine sample EC values were averaged, after excluding outliers greater than two standard deviations from the mean. For both of these measurements, we calibrated our instruments with soils of known pH and EC, obtained from the Oregon State University soil testing laboratory. We determined soil textures from field observations and various sources, including county soil surveys and landowner management files.

Statistical Analyses. All statistical analyses were applied to raw cover class data, aggregated to the transect level by averaging values from the 45 quadrats. The cover classes we used are narrow at the extreme values and broad in the middle ranges, thus approximating an arcsine square root transformation. Such a transformation is usually desirable for proportion data. By analyzing cover classes directly, these data need not be transformed to improve normality and homogeneity of variances. Multivariate analysis of raw percent cover data tends to emphasize only the most dominant species at the expense of other less abundant species. While cover class data seldom have this problem, it reappears if cover classes are transformed to the midpoints of their ranges (adapted from McCune 1996). Note that, while the cover classes we used are appropriate for the analyses performed here, the cover class averages cannot be used to approximate percent cover.

We used both univariate and multivariate approaches to explore potential effects of grazing and site variables on biotic crust cover and composition. For site variables, we used two-tailed paired t-tests to determine differences between grazed pastures and exclosures. We also tested for overall compositional differences between grazed and exclosure transects, using Blocked Multi-Response Permutation Procedure (MRBP; Mielke 1991). For this test and gradient analysis (NMS, discussed below), we pre-treated the aggregated data by deleting species occurring in only one transect, and relativizing by biotic crust species' maxima to equalize the influence of common and infrequent species.

MRBP is a non-parametric permutation technique that tests for compositional differences between groups in a multivariate distance matrix. The blocked version of this technique was needed to control for the relatively large differences among the research sites. We defined our nine sites as blocks, and the groups by grazed or exclosure transects. We used Euclidean distance as the distance measure and aligned the medians to zero for all blocks (the median for each variable in each block is subtracted from the raw data for each block). The MRBP test statistic is the average of pairwise distances between blocks within treatments. A value for the chance-corrected within-group agreement ("A") is calculated, where A = 1 - (observed difference /expected difference). Thus, A equals 1 when all items are identical within groups, and A equals zero when the heterogeneity within groups is what is expected by chance (McCune and Mefford 1999). A p-value is obtained by finding the proportion of all possible values that are less than or equal to the observed test statistic, using a Pearson type III distribution. The null hypothesis assumes that all permutations of the data are equally likely. Thus, the p-value represents the likelihood of obtaining the observed degree of clustering within treatment groups after accounting for block differences. More details on this method are available in Mielke (1984, 1991), Mielke and Berry (1982), Mielke and Iyer (1982).

We used Indicator Species Analysis (Dufrêne and Legendre 1997) to determine if any crust species were characteristically found in either the grazed or exclosure transects. With this method, a value of percent group indication is calculated for each species, based on pre-defined groups. Each species' relative frequency and relative abundance are combined to calculate these values; a species receives the maximum value of 100% indication when it occurs within all sample units of only one group. A Monte Carlo procedure tests for significance of the indicator value for each species.

Finally, we explored biotic crust species composition among transects with the multivariate ordination method Non-metric Multidimensional Scaling (NMS), an iterative method based on ranked distances. NMS seeks to minimize "stress" in the relationship between dissimilarity in the original space and the reduced ordination space. Our version of this method is based on Mather (1976), using the computational algorithm of steepest descent to find minimum stress (Kruskal 1964). We used the quantitative version of Sørensen's distance for the analysis presented here. We used the NMS and MRBP programs in the software package PC-ORD (McCune and Mefford 1999).

Results

Site Characteristics. Site characteristics are displayed in Table 2.1. The exclosures were established between 20 and 58 years prior to sampling, with the exception of Benjamin, which had been completely fenced for only 11 years prior to sampling. Boardman is unique among the sites in having an unusually low elevation, the lowest mean annual precipitation, and the highest mean annual temperature. Boardman was also the only site without some species of *Artemisia* in the transects, although it was present nearby. For the currently grazed pastures, we've synthesized available recent grazing histories and presented them in Table 2.2. However, note that stocking rates, grazing systems, seasons of use, and even pasture sizes are variable over time; this information represents a snapshot of the years immediately prior to our data collection.

Soil characteristics and results are displayed in Table 2.3. Four of the nine sites had a sandy loam soil texture, and only one had greater than 20% clay content. Electrical conductivity values were all relatively low, and pHs ranged from a low of 5.9 to a high of 7.2. In general, the soils at all of the sites were neutral to slightly acidic, and were not high in calcium carbonates or other soluble salts.

Effects Attributable to Livestock Exclusion. We recorded abundance of 51 terricolous lichen and bryophyte species in the 18 transects. Overall community composition of the biotic crust communities differed between grazed and exclosure transects ($A = 0.037$, $p = 0.02$, MRBP). On average, biotic crust species richness was higher within exclosures, with a mean difference of 2.6 species per transect ($p = 0.02$, two-tailed paired t-test; Table 2.4). All of the sites had between one and six more taxa inside the exclosures than in the grazed pastures, with the exception of Juniper Mountain, which had three more species in the grazed transect.

TABLE 2.1. Characteristics of the nine research sites. Each site has one transect in a grazed pasture and one transect in a livestock exclosure. Age of exclosure indicates how long the exclosure had been established prior to our field research. BLM = USDI Bureau of Land Management, ARS = USDA Agricultural Research Service, TNC = The Nature Conservancy, NGBER = Northern Great Basin Experimental Range. RNA = Research Natural Area, ACEC = Area of Critical Environmental Concern.

Site Name	Land Owner	Age of Exclosure (years)	Elevation (m)	Mean Annual Precipitation (mm)	Mean Annual Temperature ($^{\circ}$ C)	Dominant Vascular Plants
Benjamin RNA/ACEC	BLM	11	1507	292	6.7	*Juniperis occidentalis, Artemisia tridentata, Chrysothamnus viscidiflorus, Festuca idahoensis, Poa secunda, Koeleria cristata*
Boardman RNA	US Navy	53	240	221	11.9	*Agropyron spicatum, Stipa comata, Poa secunda, Bromus tectorum, Gutierrizia sarothrae*
Glass Butte Ecological Area	BLM	35 (+?)	1410	292	6.7	*Juniperus occidentalis, Artemisia tridentata, A. arbuscula, Chrysothamnus viscidiflorus, Festuca idahoensis, Poa secunda, Sitanion hystrix*
Horse Ridge RNA/ACEC	BLM	20	1340	297	7.9	*Juniperis occidentalis, Artemisia tridentata, Agropyron spicatum, Festuca idahoensis, Koeleria cristata*
Juniper Mt. Exclosure	BLM	57	1612	279	7.2	*Artemisia arbuscula, A. tridentata, Poa secunda, Sitanion hystrix*
Lawrence Memorial Grassland Preserve	TNC/ BLM	20	1040	299	9.2	*Artemisia rigida, Poa secunda, Festuca idahoensis, Agropyron spicatum*
NGBER Exclosure 7	ARS	58	1479	273	7.7	*Juniperis occidentalis, Artemisia tridentata, Agropyron spicatum, Stipa thurberiana, Festuca idahoensis, Poa secunda, Koeleria cristata*
NGBER Exclosure 8	ARS.	58	1400	273	7.7	*Artemisia tridentata, Chrysothamnus viscidiflorus, Poa secunda, Stipa thurberiana, Sitanion hystrix*
South Narrows ACEC	BLM	20	1353	259	8.2	*Artemisia tridentata, Poa secunda, Bromus tectorum, Sitanion hystrix*
Averages	N.A.	37	1263	276	8.1	N.A.

TABLE 2.2. Recent management history of grazed pastures. This information reflects available grazing history up to 18 years prior to data collection. Boardman was grazed by cattle and sheep; all other sites were grazed by cattle only.

Site Name	Pasture Size (ha)	Stocking Rate (ha/AUM*)	Grazing System	Season of Use	Utilization **	Distance from Grazed Transect to Water
Benjamin	4393	3.6	Rest rotation: rested every 5th year	Variable, spring to fall	average = 50% range = 30 to 70%	1.2 km (¾ mile)
Boardman †	unknown	unknown	Annual	Spring	unknown	1.6 km (1 mile)
Glass Butte Ecological Area	4192	4.2	Rest-rotation: rested every 5th year	Winter use 1993 and 1994. non-use 1992 and 1991. Prior to 1989, variable spring, summer and fall use.	average = 39% range = 25 to 50%	> 3.2 km (> 2 miles)
Horse Ridge††	1356	1.8	Variable	Spring use 1989 –1990, winter use 1983 – 1988.	average = 37% range = 20 to 60%	unknown; "pasture requires water hauling"
Juniper Mt.	7514	5.7	Unknown; occassional rest	Spring and summer.	average = 30% range = 9 to 53%	1.2 km (¾ mile)
Lawrence Memorial Grassland Preserve	approx. 775	2.6	Variable	Early spring to late summer.	unknown	1.6 km (1 mile)
NGBER Exclosure 7	810	10.1	Annual, approx. 3 months/ year.	Variable spring, summer (March - August).	unknown	1.6 km (1 mile)
NGBER Exclosure 8	65	Variable	Used as drop pasture, bull pasture	Variable	unknown	approx. 0.4 km (¼ mile)
South Narrows	745	1.3	Annual	Primarily spring (April - June), occasional summer	average = 56% range = 39 to 70%	unknown; > 0.8 km (> ½ mile)

* AUM = Animal Unit Month. The amount of forage required by one animal unit for one month. An animal unit is equivalent to one 455kg cow.
** Based on Bureau of Land Management Records
† not grazed from 1942 - 1978. †† not grazed since November 1991.

TABLE 2.3. Soil characteristics of transects. Soil texture was the same for the currently grazed and exclosure transects at each site. pH, EC, and CIV are presented individually for the grazed ("G") and exclosure ("E") transects. EC = electrical conductivity expressed in deciSiemens per meter (dS/m). CIV = Calcareous Index Value, ranging from -10 for the least calcareous transects to +10 for the most calcareous transects.

Site Name	**Soil Texture**	**Transect Location**	**pH**	**EC (dS/m)**	**CIV**
Benjamin RNA/ACEC	Silt loam	G	6.7	0.274	3
		E	6.3	0.270	0
Boardman RNA	Sandy loam	G	6.2	0.208	-3
		E	6.1	0.181	-3
Glass Butte Ecological Area	Sandy loam	G	6.5	0.252	1
		E	6.3	0.246	-1
Horse Ridge RNA/ACEC	Loamy sand	G	5.9	0.125	-4
		E	6.0	0.331	-3
Juniper Mt. Exclosure	Sandy clay loam	G	7.2	0.392	2
		E	7.0	0.448	1
Lawrence Memorial Grassland Preserve	Silt loam	G	6.3	0.224	-2
		E	6.3	0.189	-4
NGBER Exclosure 7	Loam	G	6.3	0.275	0
		E	6.4	0.240	-1
NGBER Exclosure 8	Sandy loam	G	6.5	0.387	1
		E	6.6	0.364	2
South Narrows ACEC	Sandy loam	G	6.9	0.338	3
		E	6.7	0.350	2
Averages			**6.5**	**0.283**	**-0.3**

Frequencies of the crust variables, broken down by transect grazing history, are displayed in Table 2.5. Seven species were present only in the exclosure transects, and four species were present only in the grazed transects (Table 2.5). The lichen *Megaspora verrucosa* was found to be a potential indicator of exclosure transects (60% of perfect indication, $p = 0.08$, Indicator Species Analysis). However, no other biotic crust species were reliable indicators of either the currently grazed or exclosure group.

There is conclusive evidence that total crust cover and biotic soil s
roughness were greater within the exclosures, and that there was more ba
in the grazed transects ($p < 0.01$, paired t-tests; Table 2.4). On average, crust cover was 29% lower (C.I. $_{95\%}$: 12 - 44% lower), and soil surface roughness was 25% lower (C.I. $_{95\%}$: 11 - 39% lower) in the grazed transects. There was an average of 29% greater cover of bare ground in the grazed transects (C.I. $_{95\%}$: 21 - 38% more). The mean cover of nitrogen-fixing lichens was 31% lower in the grazed transects (C.I. $_{95\%}$: 11 - 51% lower) ($p < 0.01$, two-tailed paired t-test; Table 2.4).

Overall, vascular plant community composition was not different between exclosures and grazed transects ($A = -0.0013$, $p = 0.53$, MRBP). Total vascular plant species richness, cover, and shrub cover were not different between grazed and exclosure transects (Table 2.4). There were suggestive, but inconclusive differences in the cover of organic litter, bunchgrasses, and cowpies ($p < 0.1$, two-tailed paired t-test; Table 2.4). On average, bunchgrass cover and organic litter were both 11% greater within the exclosures, and cowpie cover was higher outside the exclosures.

Electrical conductivity and pH did not differ between grazed and exclosure transects. CIV was suggestive of a difference ($p < 0.1$, paired t-test), with the exclosure transects having a negative average value and the grazed transects having a slightly positive average value (Table 2.4). Cover of surface rock and gravel did not differ between grazed and exclosure pastures.

TABLE 2.4. Variables tested for differences based on transect grazing history. Results of two-tailed paired t-tests, means, and standard deviations (SD) are displayed for grazed transects, exclosure transects, and differences between the two groups. Unless otherwise noted, units are cover classes (not percent cover). Note that cover class values cannot be converted to percent cover estimates. N = 9 pairs for all variables.

Variable	p-value	Exclosure Transects Mean (SD)	Grazed Tramsects Mean (SD)	Difference (E - G) Mean (SD)
Biotic Crust Cover (sum of averages of all biotic crust species)	< 0.01	9.7 (2.7)	6.9 (1.8)	2.7 (2.0)
Roughness	< 0.01	3.4 (0.9)	2.5 (0.8)	0.9 (0.6)
Bare Ground	< 0.01	3.0 (1.1)	3.9 (1.0)	-0.9 (0.3)
Nitrogen-fixing Lichens (sum of averages of all nitrogen-fixing lichens)	< 0.01	1.5 (0.6)	1.0 (0.5)	0.5 (0.4)
Biotic Crust Richness (no. of species)	0.02	22.6 (3.5)	20 (2.3)	2.6 (2.7)
Cowpies	0.09	0.1 (0.1)	0.2 (0.1)	-0.1 (0.2)
Calcareous Index Value†	0.09	-0.8 (2.2)	0.1 (2.6)	-0.9 (1.4)
Organic Litter	0.10	3.8 (0.4)	3.4 (0.9)	0.4 (0.7)
Perennial Bunchgrasses (sum of averages of all perennial bunchgrass species)	0.10	5.5 (2.2)	4.8 (2.1)	0.6 (1.0)
Soil Surface pH	0.17	6.4 (0.3)	6.5 (0.4)	-0.1 (0.2)
Vascular Plants (sum of averages of all vascular plant species)	0.18	15.5 (2.5)	14.5 (2.6)	1.0 (2.0)
Surface Rock	0.37	1.2 (1.2)	1.3 (1.3)	-0.1 (0.3)
Surface Gravel	0.47	1.8 (1.2)	1.7 (1.1)	0.1 (0.5)
Vascular Plant Richness (no. of species)	0.47	25.1 (6.2)	24.4 (5.3)	0.7 (4.3)
Electrical Conductivity (dS/m)	0.62	0.29 (0.09)	0.28 (0.09)	0.02 (0.08)
Shrubs (sum of averages of all shrub species)	0.88	2.4 (1.8)	2.3 (1.1)	0.1 (0.9)

† units range from -10 (least calcareous) to +10 (most calcareous)

Environmental Gradients Affecting Biotic Soil Crust Communities. Of the 51 species we recorded in the field, ten were found in only one of the 18 transects. We excluded these "rare" species from the data for gradient analysis.

Our NMS ordination resulted in three dimensions, explaining a total of 88% of the variation in the data. Axis 1 explained 68%, Axis 2 explained 13%, and Axis 3 explained 7% of the variation. Ordination graphs are displayed in Figure 2.2, crust species codes are included in Table 2.5, and correlations of environmental variables with ordination axes are displayed in Table 2.6. The environmental variables most strongly related to crust composition were CIV, pH, electrical conductivity, elevation, heat load, temperature, and precipitation (Fig. 2.2A; Table 2.6). Total crust cover was positively associated with Axis 1 and average annual temperature, and inversely related to CIV, pH, EC, and elevation. Bunchgrass cover was positively associated with Axis 1 and total crust cover, while shrub cover, bare ground, and organic litter were negatively correlated with Axis 1 (Fig. 2.2A; Table 2.6).

Total lichen, total bryophyte, and total nitrogen-fixing lichen cover was positively associated with Axis 1. Species positively associated with Axis 1 (and total crust cover) include the mosses *Ceratodon purpureus* and *Bryum argenteum*, and the lichens *Leptochidium albociliatum*, *Leptogium* spp., *Cladonia* spp., *Diploschistes muscorum*, and *Arthonia glebosa* (Fig. 2.2B; Table 2.5). Species negatively related to Axis 1 include the lichens *Aspicilia hispida*, *Candelariella terrigena*, *Phaeorrhiza sareptana*, *Caloplaca tominii*, and the moss *Pterygoneuron ovatum* (Fig. 2.2B, Table 2.5).

The nitrogen-fixing lichens *Leptogium* spp., *Peltigera* spp., and *Leptochidium albociliatum* were positively related with Axis 1 (Fig. 2.2B; Table 2.5). The nitrogen-fixing lichen groups "Black Crust" and *Collema* spp. were negatively associated with Axis 1 and thereby associated with higher CIV sites (Table 2.5).

Site variables that were positively correlated with Axis 2 include precipitation, cover of *Festuca idahoensis* and *Koeleria cristata*, and slope (Fig.

2.2A; Table 2.6). *Aspicilia reptans*, *Caloplaca cerina*, and the moss *Encalypta rhaptocarpa* were positively associated with Axis 2 (Fig. 2.2B). Heat load and total vascular plant cover were negatively correlated with Axis 2, along with the lichen *Psora cerebriformis*.

The moss *Tortula ruralis*, bare ground, precipitation, and *Festuca idahoensis* were positively associated with Axis 3, the weakest axis. Total vascular plant cover, total lichen cover, and exclosure age were negatively associated with Axis 3, along with *Bryum* spp., the group "Black Crust," and *Endocarpon pusillum* (Tables 2.5 and 2.6). In addition, transect scores on Axis 3 were significantly different between grazed and exclosure transects, according to blocked MRPP ($A = 0.213$, $p = 0.01$). Transect scores on Axis 1 and 2 were not significantly different between grazed and exclosure transects.

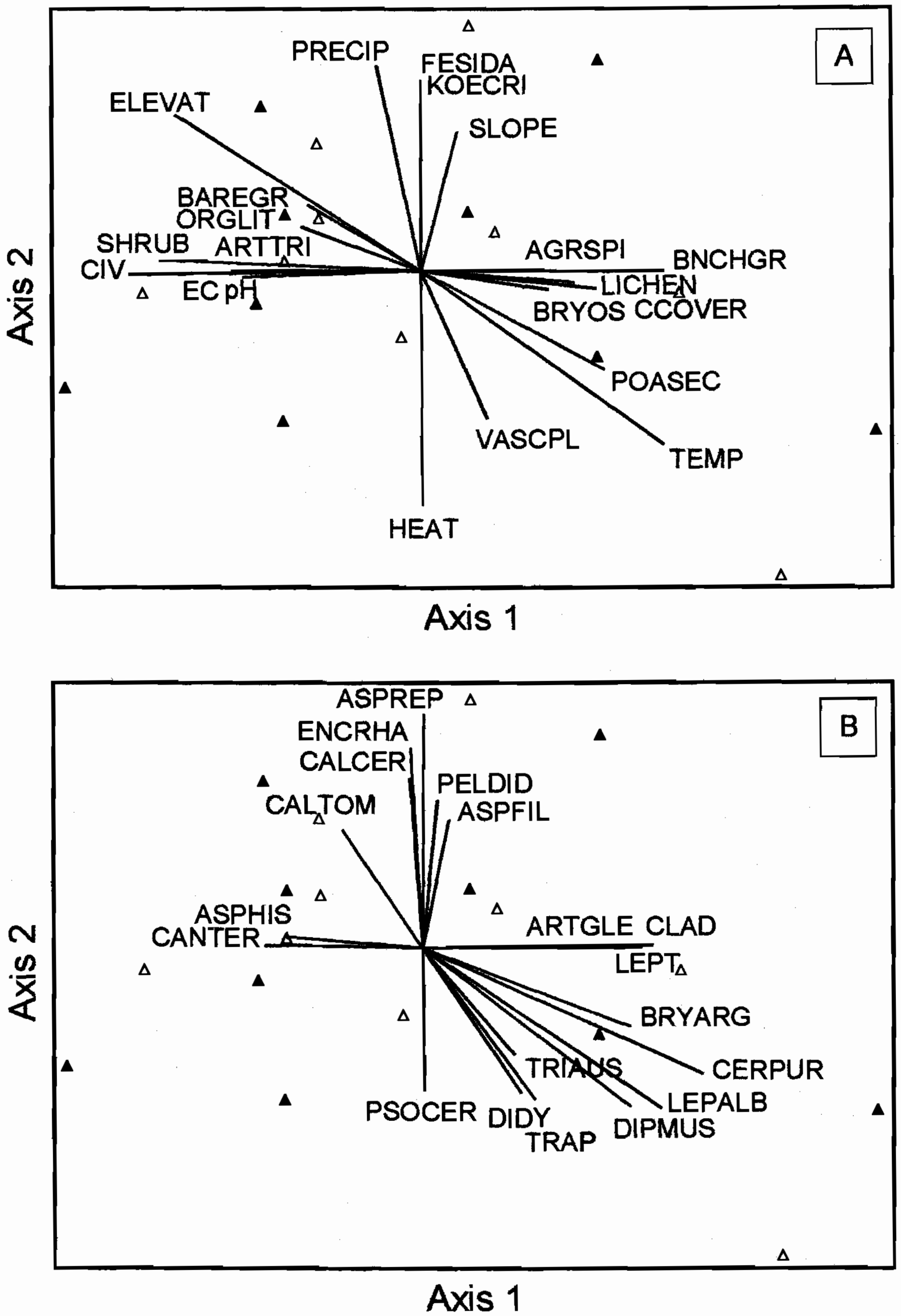

FIGURE 2.2. Ordination graphs of transects in biotic crust species space. Solid triangles represent grazed transects; open triangles represent ungrazed transects. Graph A displays overlays of environmental and vascular plant variables, along with total lichen, total bryophyte, and total crust cover. Graph B displays overlays of biotic crust species. See Tables 2.5 and 2.6 for variable codes.

TABLE 2.5. Biotic crust variable codes, their constituent species, frequencies, and correlations with ordination axes (r). Organisms were identified to species when possible; morphological groups were created for taxa that were difficult to distinguish in the field. Frequency is the number of transects in which that species was found, broken down by exclosure ("E") and grazed ("G") transects. Correlations with the NMS ordination axes are presented only for variables that occurred in more than one transect.

Code	Frequency (no. of transects)		Constituent Taxa	Correlations with Ordination Axes		
	E	G		Axis 1	Axis 2	Axis 3
ACASCH	1	0	*Acarospora schleicheri*	—	—	—
ALG	7	5	Undifferentiated algal and fungal crusts binding the soil surface.	-0.213	0.313	-0.377
AMAPUN	4	2	*Amandinea punctata*	0.198	0.485	-0.079
ARTGLE	8	4	*Arthonia glebosa*	0.586	-0.023	-0.271
ASPFIL	2	2	*Aspicilia filiformis* Rosentreter (1998)	0.25	0.561	0.354
ASPHIS	6	5	*Aspicilia hispida*	-0.578	0.163	0.22
ASP	7	6	*Apicilia* spp.	0.075	-0.527	-0.508
ASPREP	3	3	*Aspicilia reptans*	0.049	0.755	0.31
BLACK	8	7	Black Crust. This group includes free-living cyanobacteria, *Placynthiella uliginosa*, *P. oligotropha*, and poorly developed *Collema* species.	-0.354	0.083	-0.646
BRAALB	0	1	*Brachythecium albicans*	—	—	—
BRYARG	8	8	*Bryum argenteum*	0.715	-0.436	-0.247
BRYUM	8	7	*Bryum* spp., including *B. caespiticium*	-0.052	0.219	-0.658
BUEGEO	1	0	*Buellia geophila*	—	—	—
CALCER	6	7	*Caloplaca cerina*	-0.181	0.641	0.194
CALJUN	0	3	*Caloplaca jungermanniae*	0.194	0.303	0.356
CALO	0	1	*Caloplaca* sp.	—	—	—
CALTOM	6	6	*Caloplaca tominii*	-0.445	0.537	-0.393
CANTER	7	7	*Candelariella terrigena*	-0.625	0.088	-0.398

TABLE 2.5 continued

Code	Frequency E	Frequency G	Constituent Taxa	Correlations with Ordination Axis 1	Axis 2	Axis 3
CATSQU	1	1	*Catapyrenium squamulosum*	0.311	-0.052	0.228
CEPDIV	1	1	*Cephaloziella divaricata*	0.356	-0.097	0.385
CERPUR	7	8	*Ceratadon purpureus*	0.832	-0.553	-0.146
CLAD	8	7	*Cladonia* spp., including *C. cariosa*, *C. fimbriata*, *C. pocillum*, *C. pyxidata* and *C. verruculosa*. These were most often encountered as sterile squamules.	0.753	0.084	0.018
COLL	5	5	*Collema tenax* group	-0.296	-0.076	-0.46
DIDY	1	1	*Didymodon* spp., including *D. vinealis*	0.493	-0.592	-0.143
DIPMUS	3	2	*Diploschistes muscorum*	0.714	-0.622	-0.148
ENCRHA	8	8	*Encalypta rhaptocarpa*	-0.167	0.696	-0.058
ENDPUS	2	3	*Endocarpon pusillum*	-0.185	-0.194	-0.558
ENDCAT	3	2	Sterile, unidentified *Endocarpon* spp. and *Catapyrenium* spp. group.	-0.165	-0.246	0.025
LECA	8	7	*Lecanora* spp., including *L. zosterae*, *L. beringii*, and *Rinodina mucronatula*	-0.272	0.259	-0.498
LECEPI	0	1	*Lecanora epibryon*	—	—	—
LEPSUB	1	0	*Leprocaulon subalbicans*	—	—	—
LEPALB	2	3	*Leptochidium albociliatum*	0.766	-0.625	-0.084
LEPT	7	5	*Leptogium* spp., including *L. intermedium*, *L. subaridum*, and *L. tenuissimum*	0.734	-0.022	0.546
MASCAR	1	0	*Massalongia carnosa*	—	—	—
MEGVER	8	4	*Megaspora verrucosa*	-0.287	0.165	-0.173
OCHUPS	1	0	*Ochrolechia upsaliensis*	—	—	—
PELDID	1	1	*Peltigera didactyla*	0.188	0.598	0.307
PELT	2	1	*Peltigera* spp., including *P. ponojensis* and *P. rufescens*	0.349	-0.089	0.357
PHASAR	2	2	*Phaeorrhiza sareptana*	-0.465	-0.198	-0.278
PLACYN	1	0	*Placynthiella* spp., including *P. uliginosa* and *P. oligotropha*	—	—	—
PSOCER	3	1	*Psora cerebriformis*	0.058	-0.59	-0.278

TABLE 2.5 continued

Code	Frequency E	Frequency G	Constituent Taxa	Correlations with Ordination Axis 1	Axis 2	Axis 3
PSOGLO	1	0	*Psora globifera*	—	—	—
PSOMON	3	4	*Psora montana*	0.495	-0.19	0.053
PSORA	2	1	Poorly-developed sterile squamules, including *P. montana* and *Phaeorrhiza sareptana.*	0.09	0.135	-0.518
PTEOVA	8	8	*Pterygoneuron ovatum*	-0.435	0.119	-0.473
TORRUR	9	9	*Tortula ruralis*	-0.129	0.172	0.604
TORCAN	9	8	*Tortula caninervis*	0.356	-0.021	-0.224
TRAP	1	1	*Trapeliopsis bisorediata* sp. nov. (McCune, in edit).	0.526	-0.607	-0.151
TRIAUS	2	1	*Trichostomopsis australasiae*	0.476	-0.507	-0.01
UNKNBR	3	4	Small, poorly developed mosses, not identified.	0.073	-0.214	0.225
UNKNLI	8	9	Small, poorly developed lichens, not identified.	0.038	0.198	0.482

TABLE 2.6. Codes for site variables. Of the variables we recorded, those listed below were most strongly correlated with one or more of the biotic crust ordination axes. Figure 2 displays these variables in conjunction with the biotic crust ordination graphs.

		Correlations with Ordination Axes (r)		
Code	Variable	Axis 1	Axis 2	Axis 3
AGRSPI	*Agropyron spicatum*	0.553	-0.027	-0.169
ARTTRI	*Artemisia tridentata*	-0.682	-0.04	-0.208
BAREGR	Bare ground	-0.53	0.405	0.493
BNCHGR	Total Bunchgrass Cover	0.775	-0.054	-0.033
BRYOS	Total Bryophyte Cover	0.558	-0.215	-0.121
CCOVER	Total Crust Cover	0.656	-0.214	-0.333
CIV	Calcareous Index Value	-0.848	-0.097	-0.304
CLAY	Percent clay content of soil	-0.357	-0.036	-0.297
EC	Electrical Conductivity	-0.659	0.012	-0.407
ELEVAT	Elevation	-0.779	0.618	-0.053
EXLEN	Age of exclosure	0.132	-0.101	-0.405
FESIDA	*Festuca idahoensis*	-0.012	0.686	0.538
HEAT	Heat load	0.055	-0.761	-0.085
KOECRI	*Koeleria cristata*	-0.016	0.682	0.135
LICHEN	Total Lichen Cover	0.614	-0.174	-0.449
NFIXER	Total Nitrogen-fixing Lichens	0.536	-0.29	-0.315
ORGLIT	Organic Litter	-0.545	0.329	-0.276
pH	Soil Surface pH	-0.661	-0.123	-0.404
POASEC	*Poa secunda*	0.671	-0.491	-0.165
PRECIP	Mean Annual Precipitation	-0.327	0.711	0.569
SAND	Percent sand content of soil	0.023	0.195	-0.262
SHRUB	Total Shrub Cover	-0.804	0.156	-0.253
SILT	Percent silt content of soil	0.414	0.113	-0.207
SLOPE	Slope	0.299	0.584	0.207
TEMP	Mean Annual Temperature	0.773	-0.655	-0.07
VASCPL	Vascular Plant Cover	0.404	-0.602	-0.543

Discussion

Grazed Versus Exclosure Areas. Biotic crust responses to removal of livestock grazing in Oregon appear similar to those of other arid and semi-arid ecosystems. Our data demonstrate grazing-related differences in crust composition despite the relatively low statistical power associated with nine replicates. These results are particularly compelling because they are based on means from nine different sites across wide geographic and environmental ranges. Therefore, they demonstrate overall effects of grazing (and recovery from grazing) on lichen and bryophyte soil crusts of Oregon, rather than merely site-specific responses.

For example, we found slightly lower mean species richness in the currently grazed pastures. This is consistent with findings of researchers in other parts of the West and Australia, who have also documented grazing-related reductions in crust richness (Anderson et al. 1982b, Johansen and St. Clair 1986, Hodgins and Rogers 1997). While the difference we found might be considered minor at any single site, it is meaningful as an average difference between grazed and long-ungrazed sites. We can infer from these results that, in general, shrub steppe habitats in Oregon are likely to develop greater species richness if they are protected from livestock grazing. However, the magnitude of that difference and the years of protection required to realize an increase in richness remain unknown, and may vary from site to site.

Our finding of lower crust cover in grazed sites is consistent with research in the southwestern United States (Anderson et al. 1982b, Beymer and Klopatek 1992, Johansen and St. Clair 1986) and Australia (Andrew and Lange 1986, Graetz and Tongway 1986, Hodgins and Rogers 1997), but has not been documented for the Columbia Basin and Northern Great Basin before. Since biotic crusts are known to increase soil stability (Greene et al. 1990, Williams 1993), any reduction in biotic crust cover and surface roughness increases the potential for soil loss. Other functional attributes of crusts may be affected by reduced cover, including contributions of nutrients and soil organic matter (Graetz and Tongway 1986, Evans and Ehleringer 1993, Harper and Pendleton 1993).

We demonstrated compositional differences between grazed and exclosure sites using the multivariate technique MRBP, but describing the nature of those differences remains a challenge. Only one species was found to be a significant indicator of the transects within exclosures, according to the Indicator Species Analysis program. However, this program does not take into account the paired design of the study. While 41 of the 52 species were more abundant in the exclosure transects, the differences were often slight or the species occurred infrequently, making them unsuitable indicators. Because there was also considerable species overlap between grazed and exclosure groups, it is likely that overall compositional differences between the groups were due primarily to differences in species abundances, rather than presence or absence.

Overall, we found no significant difference in vascular plant composition between grazed and exclosure transects, and no differences in vascular plant species richness or total cover. There was only a suggestion of lower perennial bunchgrass cover in the grazed transects. Since the average age since exclosure establishment was 37 years, we assumed that enough time had elapsed for recovery from grazing to occur. Because others have documented grazing-related effects on the dominant native plants of this region (Daubenmire 1970, Franklin and Dyrness 1973, Rickard et al. 1975), we expected to see obvious average differences between the grazed and exclosure transects. However, since only strong differences would be detected with our sample size of nine pairs, it is possible that there were relatively small but real differences in vascular plant composition that we were not able to detect. This suggests that recent average grazing pressure at the study transects had been light to moderate, resulting in slight or no differences in plant composition.

Grazing and utilization records for these sites are consistent with the idea that average grazing intensity has been light to moderate in recent years (Holechek et al. 1989). Unfortunately, the quality and level of detail available in grazing records are highly variable among the sites. However, we know that a few of the exclosures in this study were originally established because of the unusually good ecological condition of their vascular vegetation. These tend to be located in high-elevation areas, far from water, and historically have received less grazing pressure than lower-elevation areas near water sources. Range managers are instructed to not include lands further than two miles from water in calculations of cattle stocking rates since cattle may not travel that distance from water to use those lands (Holechek et al. 1989). In some cases, the grazed pastures are so large and the transects are so far from water that stocking rates are not likely to reflect the grazing pressure at the transects accurately. In addition, a couple of the sites are using flexible grazing management that allows variation in livestock use and season from year-to-year (Table 2.2). This information suggests that overall, the sites have not been heavily grazed in the recent past.

We detected clear livestock-related differences between grazed and exclosure biotic crust communities and cover, but not between vascular plant communities or cover. Thus, biotic soil crusts demonstrated recovery after removal of grazing, despite the fact that recovery of vascular plants was not as obvious. Based on this information, we generalize that within our study region, biotic soil crust communities are more sensitive to livestock disturbance than vascular plant communities.

Differences Among Sites. Biotic crust cover and community composition are strongly related to soil chemistry differences among our sites. Lichen and bryophyte abundance and distribution are known to be particularly responsive to substrate calcium carbonate content, electrical conductivity and pH (Eldridge and Tozer 1997, Anderson et al. 1982a, Gilbert and Fox 1986, Asta and Lanchet 1978). Since electrical conductivity is a measure of soluble salts in the soil solution, and pH roughly correlates with levels of base-forming cations held by soil colloids (Brady 1990), both are general indicators of the calcium content of soils. The CIVs for each transect were strongly correlated with pH and EC, indicating that all three are good surrogate measurements for relative calcium carbonate content for this study area.

We found that total crust cover was higher at our low-CIV sites. This is consistent with results from Eldridge and Tozer (1997), who studied crust distribution from 87 sites in eastern Australia, ranging from pH 6.0 to 8.5. They found that sites with high pH and calcium carbonate levels had lower, less continuous crust cover than sites with lower pH and calcium carbonate. However, we have informally observed that strongly calcareous sites in western North America often have locally high crust cover. In Idaho, Rosentreter (1986) claimed that well-developed lichen soil crusts favor high sodium slick spots over low sodium soils. Anderson et al. (1982a) found that percent crust cover increased with electrical conductivity and pH in southern Utah. Our results and observations, and the work of others, suggest a bimodal distribution of crust cover in relation to soil chemistry. We hypothesize that total crust cover is highest on neutral to slightly acidic soils and on highly calcareous soils, and lowest on slightly to moderately calcareous soils. The soils at our research sites range from slightly acidic to neutral, with only slight calcareousness or calcareous patches at some locations. Therefore, research across a broader range of soil conditions is needed to determine if this bimodal pattern holds true.

Overall crust community composition was considerably different between sites with low pH, EC, and CIV scores (Boardman, Lawrence Grasslands, Horse Ridge) and those with high CIV, pH, and EC scores (all other sites). Although there is considerable overlap of species presence among sites, differential abundances were evidence of strong regional shifts in species. For example, the lichens *Leptochidium albociliatum*, *Leptogium* spp., and *Peltigera* spp. were the dominant nitrogen-fixing species in non-calcareous soils, while *Collema* spp. and *Nostoc*-dominated black lichen crusts were more abundant at sites with higher CIV scores. Likewise, cover of *Cladonia* spp. and *Arthonia glebosa* was greater in non-calcareous, low pH sites, while cover of *Aspicilia hispida*, *Candelariella terrigena*, *Caloplaca tominii*, and *Pterygoneuron ovatum* was greater at the more calcareous, higher pH sites. Since these differences were pronounced over a range of only 1.3 pH units, we conclude that the composition of Oregon's biotic crusts are sensitive to subtle changes in soil chemistry.

Axis 2 represents another important gradient in these data, but the compositional differences are less clear. Cool north-facing slopes, with higher precipitation and greater cover of *Festuca idahoensis*, are positively associated with Axis 2. Conversely, hotter, relatively flat sites, with greater direct solar radiation are negatively associated with this axis. Species associated with cooler sites include *Encalypta rhaptocarpa* and *Aspicilia reptans*. However, many of the species negatively associated with this axis are abundant at only one site (Boardman); these include *Diploschistes muscorum* and *Leptochidium albociliatum*. In addition, none of our sites were situated on a south or southwest-facing slope.

Boardman has the hottest average annual temperature, the lowest elevation, and the lowest measurable precipitation of all the sites. However, it is also had the highest total crust cover; this was unexpected, since crust cover and recovery is thought to be greater at high elevation, low temperature sites with greater effective precipitation (USDI 2000). The positive relationship we found between high total crust cover and high temperature was partially driven by the Boardman site. A combination of environmental factors may be underlying this correlation between high crust cover and temperature. In particular, this site, and the lower Columbia Basin in general, have higher winter temperatures occurring in combination with the majority of the annual precipitation for this region. In addition, parts of the Columbia Basin receive a relatively maritime climatic influence, resulting in more moisture in the form of dew, fog, and higher relative humidity; this additional moisture can be utilized by biotic crusts. We hypothesize that higher winter temperatures coincident with winter precipitation and greater humidity at Boardman may be responsible for the high crust cover we observed. Conversely, the continental climate at the majority of the other sites include drier, colder winters, resulting in less optimal condition for crust growth and lower total crust cover. The effect of more continental climates limiting crust cover is similar to that observed by Nash and Moser (1982), who found that lichen biomass increased near the Pacific Ocean, Baja California, in relation to atmospheric moisture, rather than precipitation. Additional data would be needed to confirm this hypothesis.

Site scores on Axis 3 were significantly different based on grazing history, but site scores on the other two axes were not, according to our MRBP results. The effects of livestock activity on crust composition were largely contained by Axis 3, which explained only 7% of the variation in the data. Thus, grazing-related differences were not critical factors in the ordination analysis, relative to the strong relationships between crust composition and environmental and site factors.

Conclusion

This soil chemistry gradient was by far the strongest explanatory factor for the compositional differences among research sites. In the ordination of these data, the compositional effects of grazing were overwhelmed by the stronger soil chemistry and climate gradients. However, grazing-related differences were clearly discernable with statistical methods that accounted for the blocked design of the study. Thus we detected a general pattern in biotic soil crust response to cessation of grazing, despite broad compositional, climatic and edaphic differences among research sites. Land managers concerned with biotic soil crusts should be aware that Oregon's crusts appear to be more sensitive to livestock disturbance than vascular plants, and that there are significant differences in the cover and composition of Oregon's crusts based on regional edaphic and climatic factors.

Terricolous Lichens as Indicators of Surface Soil Chemistry in Shrub Steppe Habitats

Jeanne M. Ponzetti and Bruce P. McCune

Oregon State University
Department of Botany and Plant Pathology
Corvallis, OR 97331

Abstract

Substrate chemistry has long been considered an important influence on lichen distribution and community composition. In a study of terricolous lichens in central and eastern Oregon, U.S.A., we found strong relationships among lichen communities, soil pH, electrical conductivity, and calcareous index values (CIVs; site scores on an index of calcareous soil indicator species). Using weighted averaging, we refined the original calcareous index, incorporating new indicator species and removing poor indicators. We found both of these indices to be good indicators of soil chemistry, and recommend further testing and refinement of the index to incorporate a wider range of soil conditions and parameters.

Introduction

In much of the arid and semi-arid western United States, soil salinity is an important factor affecting the distribution and abundance of plants and soil organisms. Salt-affected soils contain soluble salts, which may include chlorides, sulfates, and carbonates of calcium, magnesium, sodium and potassium (Brady 1990). These salts accumulate at the soil surface in areas with high evapotranspiration rates and insufficient rainfall to flush them out. Soils may be classified as normal, saline, saline-sodic, or sodic, depending on the relative amounts of neutral soluble salts and sodium ions present. Saline soils are sometimes referred to as "white alkali;" these usually contain a high concentration of calcium and magnesium ions, have an electrical conductivity greater than 4 dS/m, and pH less than 8.5. Sodic soils are known as "black alkali" or "slick spots;" they are dominated by sodium ions, and typically have an electrical conductivity less than 4 dS/m and pH greater than 8.5. Saline-sodic soils have characteristics between those of saline and sodic soils, while normal soils are characterized by low conductivity (less than 4 dS/m) and a pH range between 6.5 and 7.2 (Brady 1990).

Substrate chemistry has long been known to affect lichens and lichen communities (Brodo 1973). Although some lichens appear to be non-preferential, many exhibit strong substrate specificities. Studies have demonstrated distinct differences in lichen composition and higher diversity associated with high-calcium rock types (Gilbert and Fox 1986, Asta and Lachet 1978, Insarov and Insarov 1995). Some lichens favor certain types of salt-affected soils. For example, well-developed lichen communities occur on gypsiferous soils (St. Clair et al. 1993), a type of saline soil high in calcium and sulfate. A number of lichens are found exclusively on gypsiferous substrates (Guerra et al. 1995, USDI 2000). In addition, lichenologists have traditionally employed the term "calciphile" to refer to lichens typically found on calcareous soils.

To date, however, there has been little quantification of these relationships between soil chemistry and lichen distribution and community composition. Studies comparing arid and semi-arid sites in Utah have found biotic crust cover and diversity to be positively related to electrical conductivity and pH (Anderson et al. 1982a, 1982b). However, in Australia, Eldridge and Tozer (1997) found soil lichen cover to be inversely related to pH and electrical conductivity.

With this research, we investigated whether lichen communities can be reliable indicators of soil chemistry, specifically soil pH, electrical conductivity, and by inference, calcium carbonate content. We used lichen indicator species to develop and refine a calcareous index for the arid and semi-arid intermountain region of the Pacific Northwest.

Methods

Sampling. Our research sites were all upland shrub steppe, grassland, or juniper savannah communities with a significant perennial bunchgrass component.

Since the sites were originally chosen to examine a different research question (see Chapter 2), they were not selected based on soil type or soil chemistry. We used nine sites throughout central and eastern Oregon, locating two samples (transects) at each site.

For each sample, terricolous lichen and bryophyte community data were collected along a 100-m transect, in 45 randomized 20- X 50-cm quadrats. Transects were not closer than 10 m from fence lines, trails or roads, so that concentrated cattle trampling and vehicle traffic would not influence our results. Lichens and bryophytes were recorded by species when possible, or by genera or species groups when field identification was not practical. We obtained numerous voucher specimens to confirm identifications; they are deposited at the Oregon State University Herbarium (OSC). Lichen nomenclature follows Esslinger and Egan (1995).

Soil surface samples were collected adjacent to every fifth quadrat in each transect, resulting in nine subsamples per transect. We obtained these samples from the spaces between vascular plants, where soil crust organisms tend to be abundant. After scraping off any surface biotic crust and organic litter, we collected the top 2 cm of soil from an 8- X 8-cm area.

Further details of our field methods are presented in Chapter 2.

Soil Analyses. We pre-treated all 162 soil surface samples by passing them through a 2 mm sieve to remove coarse fragments. We measured pH of the samples with a 1:2 soil-water ratio, placing the electrode in the supernatant rather than in the soil slurry (McLean 1982). For each transect, all nine sample pH values were averaged. We measured electrical conductivity (EC) with a digital conductivity meter, using standard methods described by Rhoades (1982). The samples were averaged for each transect, after excluding outliers greater than two standard deviations from the mean. In addition to standard instrument calibration methods, we verified our laboratory methods with soils of known pH and EC obtained from the Oregon State University Soil Testing Laboratory.

Calcareous Index. We used a calcareous index developed by McCune and Rosentreter (1995) to calculate a Calcareous Index Value (CIV) for each site (Table 3.1). The index was developed for arid and semiarid intermountain rangelands of the Pacific Northwest, including portions of Oregon, Washington, Idaho, and Montana. It is based on the apparent affinities of selected common lichens to free calcium carbonates in soil. Ten species frequent on soils with low calcium carbonate content have an index value of "-1," while ten species that frequent soil with high calcium carbonate content have an index value of "+1." CIVs were calculated for each transect by summing the index values of the species present in that transect. The potential site CIVs range from "-10" for the least calcareous sites to "+10" for the most calcareous sites.

TABLE 3.1. Soil calcareous index based on species presence. CIVs are calculated by summing the index values of the species present at a given site; they represent estimates of the relative abundance of free calcium carbonates on the soil surface. This index was developed by McCune and Rosentreter (1995).

Non-calciphiles Index value = - 1	Calciphiles Index value = + 1
Acarospora schleicheri	*Aspicilia fruticulosa*
Arthonia glebosa	*Aspicilia hispida*
Aspicilia reptans	*Buellia elegans*
Cladonia borealis	*Caloplaca tominii*
Diploschistes muscorum	*Collema tenax*, sensu lato
Leptochidium albociliatum	*Fulgensia bracteata*
Megaspora verrucosa	*Psora cerebriformis*
Ochrolechia upsaliensis	*Psora decipiens*
Placynthiella spp.	*Psora tuckermanii*
Xanthoparmelia wyomingica	*Toninia sedifolia*

To develop a refined calcareous index, we used a form of weighted averaging (Whittaker 1967, Curtis and McIntosh 1951) on the lichen portion of our data. Twelve of the 20 original indicator species from McCune and Rosentreter (1995) appeared in our study transects. We used the abundances of these species to calculate site calcareous scores (v) for each transect (i), according to the following formula,

$$v_i = \sum_{j=1}^{p} a_{ij} w_j \,/ \sum_{j=1}^{p} a_{ij}$$

where a = species abundances, j = species, p = the 12 indicator species, and w = species indicator weights (either 1 or -1). From these site scores, we calculated species weights for all the lichen species occurring in our transects,

$$w_j = \sum_{i=1}^{n} a_{ij} v_i \,/ \sum_{i=1}^{n} a_{ij}$$

where n = all 18 sample units. We revised the soil calcareous index based on these new species weights, by dropping poor indicators and adding new indicators to the list. Species were considered poor indicators if their revised weight was between -0.20 and + 0.20. Two criteria were used to select new indicator species: 1) indicator weights were required to be greater than 0.5 or less than -0.5, and 2) the species must have occurred in more than two transects. For each site, revised CIV scores were calculated based on the new calcareous index.

Statistical Analyses. We used Non-metric Multidimensional Scaling (NMS) to explore the relationships between lichen and bryophyte community composition and environmental variables among sample units. NMS is a multivariate gradient analysis technique available in the software package PC-ORD (McCune and Mefford 1999). It is an iterative method based on ranked distances, which seeks to minimize "stress" in the relationship between dissimilarity in the original space and the reduced ordination space. The PC-ORD version of this method is based on

Mather (1976), using the computational algorithm of steepest descent to find minimum stress (Kruskal 1964). We used the quantitative version of Sørensen's distance for the distance measure.

In addition, we calculated correlations among the following variables: soil pH, EC, original CIVs, revised CIVs, site scores on Axis 1 and Axis 2 of the ordination, and non-calcareous salinity (residuals from the regression of EC on pH). Non-calcareous salinity was included to examine the effect of soluble salts that have little influence on pH in these data. If non-calcareous salinity has an important influence on biotic crust composition in our sample, then the residuals from the regression of EC on pH would most likely be correlated with one or more variables in our ordination analysis. Conversely, if salinity in our sample is primarily caused by salts that do affect pH, we would expect small residuals.

Results

Soil chemistry data are displayed in Table 3.2. The average pH per transect ranged from a low of 5.9 to a maximum of 7.2, and electrical conductivity ranged from 0.13 to 0.45 dS/m. Transect CIVs based on the original index ranged from -4 to +3. The revised calcareous index produced transect CIVs ranging from -6 to +4 (Table 3.2).

Using weighted averaging, site calcareous scores (v) were calculated from the abundances of the12 indicator species that occurred among the sites. New species weights were calculated from these site scores (Table 3.3). *Megaspora verrucosa* had a nearly neutral revised indicator weight of 0.07, and therefore was dropped from the index. Five new indicators were added to the revised index, including *Aspicilia filiformis* Rosentreter (1998), *Caloplaca jungermanniae*, *Leptogium* spp., *Peltigera rufescens*, and *Phaeorrhiza sareptana*. The new index has a total of 24 indicator species, with 12 indicator species each indicating high and low calcium carbonate levels. Thus, the revised calcareous index has a potential range of - 12 for the least calcareous sites and +12 for the most calcareous sites (Table 3.4).

NMS gradient analysis resulted in three dimensions explaining 88% of the variation in the lichen and bryophyte community data. The strongest dimension is represented by Axis 1, explaining 68% of the variation. Electrical conductivity, pH, and CIV are among the most important environmental variables explaining biotic soil crust composition, and these tend to co-vary. For example, high total crust cover is positively associated with Axis 1 ($r = 0.66$), while CIV ($r = -0.85$), pH ($r = -0.66$), and electrical conductivity ($r = -0.66$) are inversely related to Axis 1 (Fig. 3.1). More details of the NMS ordination are presented in Chapter 2.

Electrical conductivity, pH, CIV, revised CIV, and site scores on Axis 1 are correlated with each other ($p \leq 0.01$ for all, Table 3.5). The revised CIV site scores demonstrate slightly improved correlations with pH and EC relative to the original CIV scores. Non-calcareous salinity was not significantly correlated with Axis 1 scores, original CIV scores, or the revised CIV scores ($p > 0.3$ for all; ANOVA). Non-calcareous salinity was correlated with organic matter ($r = 0.44$; $p = 0.07$, ANOVA), but not significantly correlated with the other two axes or other variables in the NMS ordination. Figure 3.2 displays scatterplots of correlations among selected variables.

TABLE 3.2. Soil analyses and transect Calcareous Index Values (CIVs). Electrical conductivity (EC) is expressed in deciSiemens per meter (dS/m). Original CIVs were based on the original soil calcareous index, having possible scores ranging from -10 for the least calcareous sites to +10 for the most calcareous sites. Revised CIVs are based on the revised calcareous index, having possible scores ranging from - 12 to + 12.

Transect No., Site Name	pH	EC	Original CIV	Revised CIV
01, Boardman RNA	6.2	0.208	-3	-4
02, Boardman RNA	6.1	0.181	-3	-4
03, South Narrows ACEC	6.9	0.338	3	5
04, South Narrows ACEC	6.7	0.350	2	4
05, Glass Butte Ecological Area	6.5	0.252	1	0
06, Glass Butte Ecological Area	6.3	0.246	-1	-1
07, NGBER No. 7	6.3	0.275	0	0
08, NGBER No. 7	6.4	0.240	-1	-1
09, Horse Ridge RNA/ACEC	5.9	0.125	-4	-4
10, Horse Ridge RNA, ACEC	6.0	0.331	-3	-5
11, NGBER Range No. 8	6.5	0.387	1	2
12, NGBER Range No. 8	6.6	0.364	2	3
13, Lawrence Memorial Grassland Preserve	6.3	0.224	-2	-3
14, Lawrence Memorial Grassland Preserve	6.3	0.189	-4	-6
15, Benjamin RNA/ACEC	6.7	0.274	3	2
16, Benjamin RNA/ACEC	6.3	0.270	0	0
17, Juniper Mt. Exclosure	7.2	0.392	2	4
18, Juniper Mt. Exclosure	7.0	0.448	1	2
Averages	6.5	0.283	-0.3	-0.3

TABLE 3.3: Revised calcareous indicator species weights for 12 species occurring in McCune and Rosentreter's (1995) original calcareous index. New species weights were calculated from weighted averages of transect calcareous scores. These species weights were used to determine the relative strength of the species as calcareous soil indicators.

Species	New Weight	Species	New Weight
Acarospora schleicheri	- 0.82	*Diploschistes muscorum*	- 0.88
Arthonia glebosa	- 0.23	*Leptochidium albociliatum*	- 0.91
Aspicilia hispida	+ 0.45	*Megaspora verrucosa*	0.07
Aspicilia reptans	- 0.38	*Ochrolechia upsaliensis*	- 0.24
Caloplaca tominii	+ 0.32	*Placynthiella* spp.	- 0.97
Collema tenax	+ 0.48	*Psora cerebriformis*	+ 0.36

TABLE 3.4. Revised calcareous index. One species was dropped and five species were added to the index, based on weighted averaging results (Table 3.3). Potential CIVs range from -12 for non-calcareous sites to +12 for the most calcareous sites.

Non-calciphiles Index value = - 1	Calciphiles Index value = + 1
Acarospora schleicheri	*Aspicilia fruticulosa*
Arthonia glebosa	*Aspicilia hispida*
Aspicilia filiformis	*Buellia elegans*
Aspicilia reptans	*Caloplaca jungermanniae*
Cladonia borealis	*Caloplaca tominii*
Diploschistes muscorum	*Collema tenax*, sensu lato
Leptochidium albociliatum	*Fulgensia bracteata*
Leptogium spp.	*Phaeorrhiza sareptana*
Ochrolechia upsaliensis	*Psora cerebriformis*
Peltigera rufescens	*Psora decipiens*
Placynthiella spp.	*Psora tuckermanii*
Xanthoparmelia wyomingica	*Toninia sedifolia*

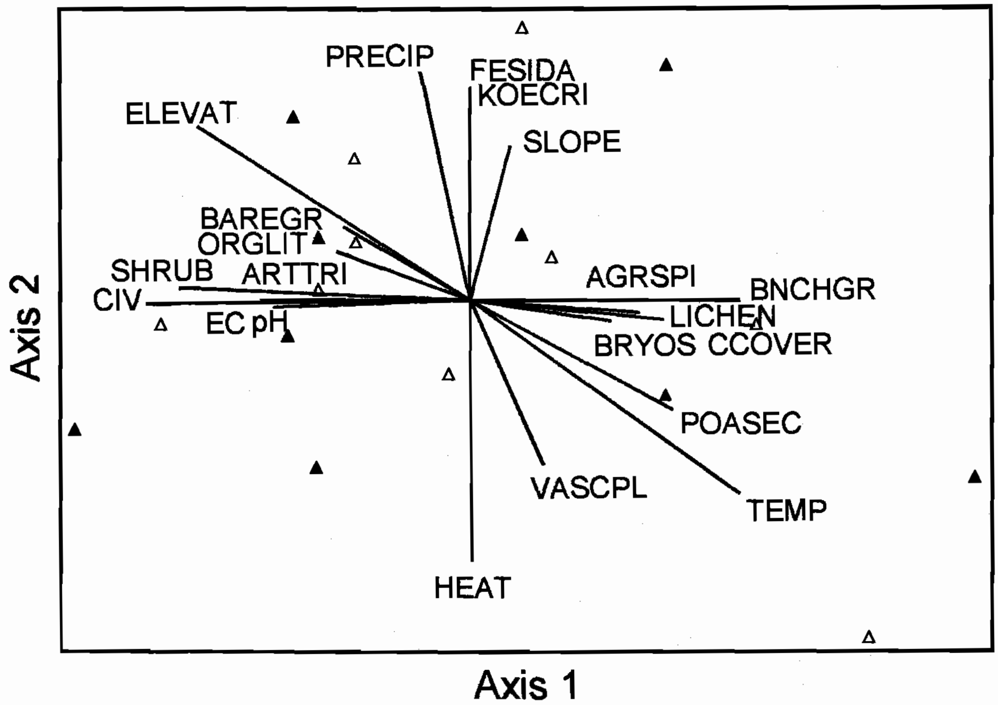

FIGURE 3.1. Ordination graph of transects in biotic crust species space. Solid triangles represent grazed transects; open triangles represent long-ungrazed transects. Vectors represent overlays of site variables and broad biotic crust groups. CCOVER = total crust cover, LICHEN = total lichen cover.

TABLE 3.5. Correlation coefficients (r) among soil chemistry variables and ordination scores on Axis 1 and 2. Asterisks indicate significant correlations ($p < 0.01$, $n = 18$).

	pH	EC	Original CIV	Revised CIV	Axis 1 Scores	Axis 2 Scores
pH	1	--	--	--	--	--
EC	*0.76	1	--	--	--	--
Orginal CIV	*0.83	*0.72	1	--	--	--
Revised CIV	*0.85	*0.74	*0.96	1	--	--
Axis 1 scores	*-0.66	*-0.66	*-0.85	*-0.84	1	--
Axis 2 scores	0.12	0.01	0.10	0.11	0.28	1
Non-calcareous salinity	< 0.01	*0.65	0.14	0.15	0.24	0.16

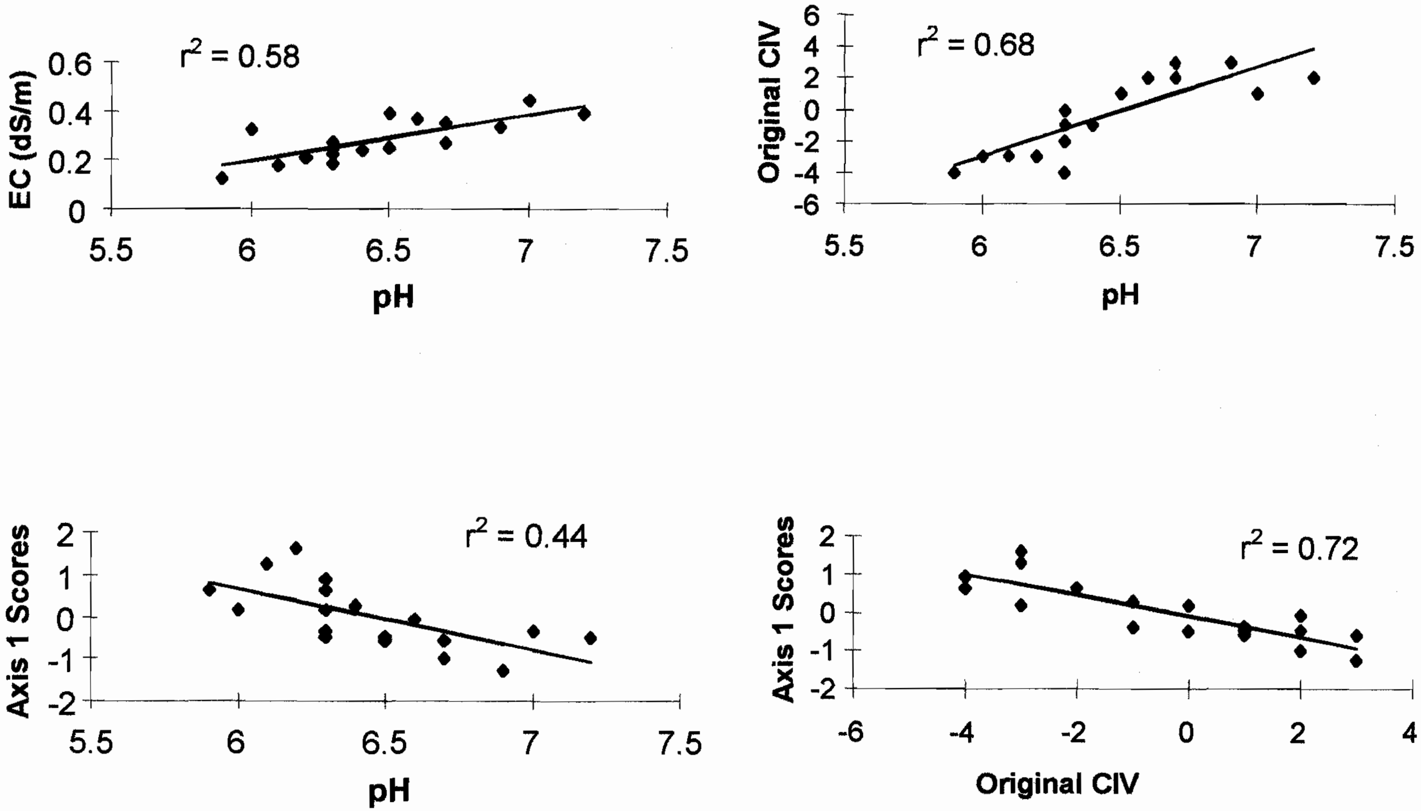

FIGURE 3.2. Scatterplots illustrating relationships among selected soil chemistry variables and transect scores on Axis 1.

Discussion

Our data demonstrate strong linear relationships among transect scores on ordination Axis 1, site CIV scores, pH and EC. Therefore, we conclude that lichen community composition can be an effective predictor of these soil parameters. However, because our samples ranged from pH 5.9 to 7.2, this result applies only to normal soils within this pH range. This study did not address truly saline, saline-sodic, or sodic soils.

Typically, pH is correlated with the percentage of base saturation in a soil, and the common base-forming cations in soils of arid and semi-arid regions are calcium and magnesium ions (Brady 1990). The exception to this situation is in highly sodic soils, where the pH may reach as high as 9 or 10, and the exchange sites of the soil colloid are dominated by sodium ions. Since the maximum pH of our soils was 7.2, sodic soils are not a factor in this study. Thus, we assume that the gradient in pH values in our samples roughly correlates with an increase in the base saturation of calcium and magnesium ions. Electrical conductivity, as a measure of soluble salts in a soil solution, reflects the amounts of calcium, magnesium, sodium and potassium salts present in the soil. In this study, EC was closely correlated with pH and CIVs. Because residuals from the regression of EC on pH were small and unrelated to the ordination axes, we conclude that non-calcareous salinity was not an important influence on biotic crust composition in our sample. Although we did not measure calcium or magnesium carbonate content directly, we can infer from our results that these compounds are primarily responsible for the relationships among pH, EC, transect CIV scores, and transect scores on Axis 1.

Because the range of soil conditions at our research sites is relatively narrow, with no transects representing high pH or EC conditions, it is unclear if the relationships demonstrated here will be maintained over a wider range of conditions. We do not expect the strong positive correlation between EC and pH to be universal for all soils, because very high pH soils generally have low conductivities (e.g. sodic soils). However, with further research, we expect to find the strong correlation between CIV, pH, and EC found in this study to extend to saline and perhaps saline-sodic soils. In addition, since there are reports that some lichens favor sodic slick spots (Rosentreter 1986), the correlations we found between CIV and pH (but not EC) might be valid over an even wider range of soil conditions.

The revised calcareous index presented here is preliminary, and should be tested at a variety of sites and revised further. Future research might include a closer look at the soil chemistry underlying this CIV gradient, particularly lichen composition in relation to calcium, magnesium, sodium, potassium, sulfate, carbonate and chloride ions, as well as the percent base saturation of the soil. The lichen communities in this study are clearly influenced by a strong soil chemistry gradient related to these variables.

Conclusion

We have demonstrated that the terricolous lichen communities of our central and eastern Oregon research sites are strongly related to a soil chemistry gradient. In particular, lichen composition of neutral soils was related to soil surface pH, electrical conductivity, and CIV; we infer that lichen composition is influenced by soil calcium and magnesium carbonate. Further research is needed to clarify the relationship of terricolous lichen communities to soil parameters not specifically tested in this study. The calcareous index presented here effectively uses lichens as indicators of soil chemistry, and could be refined further to incorporate a wider range of soil conditions.

Summary

Gradients Related to Biotic Crust Composition

Biotic crust composition is influenced by a number of interrelated variables. Soil chemistry parameters such as pH, soluble salt content, and calcium carbonates affect species distributions, but quantification of these relationships are few. Our understanding of the relationship between soil chemistry and crust composition is in its infancy. Soil texture has been found to be important to biotic crust distribution and abundance by other researchers. Various climatic conditions, such as precipitation, humidity, and temperature all influence crust cover and composition. Understanding these individual gradients, and how they work together, is crucial to understanding biotic soil crust distribution and abundance.

Soil Chemistry. Biotic soil crust cover and composition are strongly influenced by soil pH and salinity, and are correlated with the site calcareous index values (CIVs) presented in Chapter 3. These results are consistent with those of others working in Australian rangelands (Eldridge and Tozer 1997; Rogers 1972) and the western United States (Anderson et al. 1982a, 1982b; Rosentreter 1986). Our results suggest that lichens can be quite sensitive indicators of certain soil chemistry parameters, responding to relatively subtle differences in soil conditions. Because some lichens and bryophytes are known to prefer strongly calcareous substrates, these findings are likely to apply to an even wider range of soil chemical conditions than those sampled here.

We found that crust cover was highest on relatively low pH, low CIV, and low EC sites. Our observations suggested a bimodal pattern of crust cover, with high cover being common on neutral and strongly calcareous soils, and lowest cover on soils of moderate calcareousness. Additional research will be needed to confirm the generality of this pattern, and to further develop the calcareous index presented in Chapter 3, improving its applicability as an indicator of soil chemistry.

Climate. Elevation, temperature, and precipitation are strong, interrelated factors influencing biotic crusts. In general, other researchers have found that biotic crust cover increases with elevation and precipitation, until vascular plant cover precludes their growth by occupying the available space (USDI 2000). Since temperature is generally inversely related to elevation and precipitation, it is assumed that crust cover will be inversely related to temperature. Thus, our results are unusual in that we found total crust cover to be correlated with higher temperatures, and inversely related to elevation and, to a much lesser extent, precipitation.

There are a number of possible explanations for the unusual pattern of these results. The first possibility was mentioned in Chapter 2: one site, Boardman, is contributing significantly to the strength of this pattern. This site has higher annual average temperature and a lower elevation than the other sites; it also has somewhat lower precipitation than the other sites. However, it also is quite similar to other typical Columbia Basin steppe sites, in that it has higher crust cover and greater moss cover than the central Oregon sites (Ponzetti et al. 2000). Examination of the data without the Boardman transects revealed similar gradient patterns, with the exception that precipitation was not related to crust cover or temperature, and only weakly inversely related to elevation. Total crust cover was still correlated with higher temperatures and inversely related to elevation, albeit less strongly so. Thus, the Boardman transects are not solely responsible for the observed positive correlation between crust cover and temperature, but may be responsible for crust cover being somewhat inversely related to precipitation.

From the perspective of biotic soil crusts, precipitation is not the best measure of available moisture. Total crust cover may be attributable to another, unmeasured variable, such as total atmospheric moisture (Nash 1982). There appear to be differences in atmospheric moisture between the sites in the Columbia Basin ecoregion, which experience greater oceanic influence, and the sites in the northern Great Basin ecoregion, which have a more continental climate. The Columbia Basin is generally warmer than the Great Basin and High Lava Plains of

Oregon during the wet season (Jackson 1993), when optimal lichen and bryophyte growth occurs. Most lichens are photosynthetically active between temperatures of 0 to 20° C (Nash 1996b), and growth for lichens and bryophytes is directly related to the amount of time they are wet and physiologically active (Vitt 1990). The northern Great Basin and High Lava Plains of central and eastern Oregon have relatively dry, cold winters, with more precipitation occurring as snow (USDI 2000, Jackson 1993). Northern Great Basin sites also have a slightly greater proportion of their precipitation occurring in summer (Jackson 1993), when high evaporative rates result in less optimal growth conditions for biotic crusts.

The relationships of total crust cover with temperature, elevation and precipitation are complex. The weak relationship of crust cover with precipitation is likely due to the limitation of precipitation as a predictor of available moisture for crust growth. Effective moisture is clearly an important factor in crust cover; and it is modified by the form and timing of precipitation, wintertime temperatures, aspect, and atmospheric moisture. The positive relationship of crust cover to temperature appears to be a real phenomenon among our Oregon sites, with or without the Boardman transects. This relationship may be due to the fact that the warmer, lower elevation Columbia Basin is simply a more "crusty" place, as a result of other factors. However, it is likely that higher winter temperatures coincident with available moisture may be a critical part of the generally higher crust cover observed in the Columbia Basin. Additional sites in the Columbia Basin would be needed to explore these relationships further.

Soil Texture. Other researchers have found soil texture to be a significant factor in crust cover and composition. Generally, crust cover is higher on finely-textured soils, particularly those high in silt (Anderson et al.1982b, Kaltenecker et al. 1999b, Kleiner and Harper 1972, 1977a). Our study sites, however, revealed no strong relationships between biotic crusts and soil texture variables. Percentage silt was weakly correlated with Axis 3 and high precipitation cites, while percentage clay was weakly correlated with high pH and CIV cites (see Chapter 2, Table 6). However, these correlations may have been weakened because our soil texture data were derived from regional soil surveys rather than site-specific measurements. Soil texture in Oregon's shrub steppe is likely to be a more important factor than our results indicate.

Livestock Exclusion. One of the primary objectives of this research was to determine if Oregon's shrub steppe biotic crust communities were affected by physical disturbance due to livestock grazing. Our study examined the condition of crusts after livestock exclusion across a variety of vascular plant communities, soil types, and grazing regimes. On average, we found significantly higher crust cover, soil surface roughness, nitrogen-fixing lichens, and less bare ground in the exclosures. Also, there were compositional differences between treatments. Thus, we infer that mechanical disturbance from livestock grazing limits the development of biotic crust communities in Oregon's shrub steppe. In this sense, Oregon's biotic crust communities are similar to other arid and semi-arid biotic crusts in western North America, which have been shown to be sensitive to physical disturbance (Anderson et al. 1982b, Belnap et al. 1994, Beymer and Klopatek 1992, Graetz and Tongway 1986, Kaltenecker et al. 1999b).

Actual species richness is difficult to determine in most ecological studies. Richness measurements are dependent on plot size, the skill of the observers, and the intensity of observer effort (McCune and Lesica 1992, McCune et al. 1997). Biotic crust organisms are small, and can be patchy or easily hidden by other vegetation. Some are difficult to distinguish in the field, even for experts. Thus, species richness as measured in this study includes some morphological groups, and thus is really a measure of "field-observable" species richness. However, despite these limitations, we found a higher average species richness within the exclosures, suggesting that in general, Oregon's crust communities will increase in diversity in response to reductions of livestock disturbance. Note, however, that the primary livestock-related compositional differences appear to be related to relative abundance of species, rather than large differences in the particular species present in each group.

We observed general trends in the apparent recovery of biotic crusts after removal of grazing, but the magnitude of these trends will vary considerably from site to site. Factors such as the intensity, duration and timing of livestock grazing, and regional differences in crust communities related to soil and climate variables, are all likely to modify potential livestock-related effects. For example, moister, warmer sites more conducive to crust growth will likely recover more quickly from disturbances (USDI 2000). Future management-related research should concentrate on elucidating these relationships.

Scope of Inference

This study included all of the upland exclosures meeting our pre-defined search criteria in central and eastern Oregon, with the exception of lands within the Vale District of the BLM (easternmost portion of the state). Thus, our results are applicable to most arid and semi-arid shrub steppe communities within central and eastern Oregon (primarily within the Burns, Lakeview, and Prineville District boundaries of the BLM). Because our findings attributable to livestock grazing are similar to those of other researchers throughout the West, our results are likely to be applicable to most of the arid and semi-arid shrub steppe ecosystems of Oregon and Washington. Inferences regarding relationships among soil chemistry variables and crust communities are limited at this time to soils with pH between 5.9 and 7.2. Because the soil chemistry of our sites spans only a typical range, more research is needed on extreme soils, such as saline, sodic or gypsiferous soils.

Rangeland Health

Biotic soil crusts show promise as indicators of rangeland health, and are increasingly being recognized as important components of arid and semi-arid communities. Rangeland health is defined as the degree to which the integrity of the soil, vegetation, water, air, and ecological processes of rangeland ecosystems are sustained (National Research Council 1994, USDA 1997). Biotic crusts improve the sustainability of rangeland ecosystems by increasing soil stability and contributing to nutrient cycles (Williams 1993, Belnap and Harper 1995). They appear to limit germination of *Bromus tectorum*, an invasive exotic annual grass (USDI 2000). Biotic crusts in the arid and semi-arid West do not appear to limit vascular plant cover; greater crust cover often accompanies greater plant cover, or is unrelated to plant cover (Johansen and St. Clair 1986, Jeffries and Klopatek 1987, Graetz and Tongway 1986, Kleiner and Harper 1972). In this research, we found no relationship between total vascular plant cover and crust cover, but there was a positive correlation between crust cover and perennial bunchgrass cover (Chapter 2). Bare ground is often inversely related to crust cover, suggesting that a decline in crust cover produces an increase in bare soil, rather than an increase in vascular vegetation (Beymer and Klopatek 1992, Chapter 2). In addition, biotic crusts may serve as an early warning system, since they appear to be more sensitive to disturbance from livestock than vascular plant communities (Chapter 2, Anderson et al. 1982a).

In the National Range and Pasture Handbook, the Natural Resource Conservation Service (NRCS) identified cryptobiotic crusts as one of seventeen rangeland health ecological attributes, to be used as an indicator of rangeland health (USDA 1997). Crusts are considered important to soil and site stability, watershed and hydrologic cycles, and soil and plant community integrity. Site assessments of biotic crusts involve a determination of the amount and distribution that would be expected for a healthy site (USDA 1997). Reference sites that are used as benchmarks of late-seral vascular plant communities will be useful for determining expected biotic crust characteristics. However, this research and the work of others suggests that biotic crusts respond to their environment in a manner distinct from that of vascular plants; crust cover and composition are more sensitive to soil chemistry and disturbance, as well as atmospheric inputs of moisture and nutrients.

Further research will be needed to determine accurately "expected values" for biotic crust abundance and composition at various sites.

In Australia, Eldridge and Koen (1998) found crust cover on its own to be a poor indicator of rangeland health. Instead, they found total numbers of lichen and bryophyte taxa to be associated with better range condition. They found some species to be characteristic of degraded sites with eroded soils, some were characteristic of healthy, stable sites, and many had no apparent preference. Rogers and Lange (1971) found some species to be sensitive to their proximity to livestock watering holes, while others were less so. In the research presented here, lichen and bryophyte preferences for livestock-grazed or excluded sites were not obvious, but this study did not include a wide variety of rangeland condition classes. A study of species composition in relation to range condition in the western United States might reveal a gradient from disturbance-tolerant to disturbance-intolerant biotic crust species, similar to that found by Eldridge and Koen (1998) and Rogers and Lange (1971). It may be possible to create a "disturbance index" based on species presence, in much the same way that we've developed the calcareous index presented in Chapter 3. Preliminary information for such an index is available in recent work by Ponzetti et al. (2000) in Washington's Horse Heaven Hills. They found a strong gradient in biotic crust composition between relatively undisturbed, high-condition plots and disturbed, low-condition plots. Although they found that most biotic crust species decreased with increasing disturbance, some species appeared more resilient than others.

Monitoring Recommendations

Monitoring trends in total biotic crust cover will be an important part of incorporating these organisms into ecological health assessments. Total crust cover expected for a given ecological site will vary, but over time, cover can reasonably be expected to stay the same or improve with good management practices. Crust diversity may prove to be a useful indicator of rangeland health, but species richness of biotic crusts is difficult to measure reliably over time, even for skilled observers (Ponzetti et al. 2000).

Use of morphological groups for crust monitoring may be a more efficient approach than species richness (Eldridge and Rosentreter 1999), and provides more information than total cover estimates alone. Using morphological groups involves grouping species that look similar under field conditions. The level of grouping can be adjusted to match monitoring or research objectives, or can be matched to the skill of the observers. For example, morphological groups might be simply broken down into measurements of total lichen and total moss, in addition to total crust cover. This approach may be suitable when repeatability is important, such as long-term trend monitoring where observers will probably change over time. The relative proportions of lichen and bryophyte cover could be a useful indicator of trend, because in some cases, greater lichen cover coincides with later successional stages (Kaltenecker 1997).

Morphological groups can be designed around specific monitoring objectives and can incorporate increasing levels of detail. In Australia, Eldridge and Koen (1998) used ten morphological groups based on color and growth form; they found two of these groups to be positively associated with indices of healthy rangelands. Morphological groups have been used successfully in Idaho to assess crust responses to fire (Kaltenecker 1997) and recovery after grazing (Kaltenecker and Rosentreter 1997). In Oregon, morphological groups, including a functional group of nitrogen-fixing lichens, were used to assess prescribed-fire effects on biotic crusts (Ponzetti et al. 1999). However, caution should be used with assigning functions to morphological groups. For example, the group "black lichen" is generally considered to represent nitrogen-fixing lichens, but in many communities, all "black lichens" are not nitrogen-fixers, and all nitrogen-fixers are not black (Ponzetti et al. 1998). In addition, voucher specimens of common organisms in each morphological group are recommended to increase the interpretability of results.

Monitoring methods for biotic crusts should reflect research or monitoring objectives. To detect treatment effects or track change over time, repeatability and accuracy of cover estimates are critical. Studies with many small plots (such as point-intercept or line-intercept) are less likely to be affected by differences between observers or over time (McCune and Lesica 1992, McCune et al. 1997). However, while more accurate for the common species, point-intercept methods generally do not detect rare species (McCune and Lesica 1992). Thus, if diversity measurements, community dynamics, or regional differences are of interest, ocular assessments of cover with larger plots will provide greater species capture (McCune and Lesica 1992). With proper training of field personnel, ocular estimates can be also be repeatable, accurate, and they have the added advantage of being relatively fast, thus allowing for larger samples (Meese and Tomich 1992, Dethier et al. 1993). A compromise among these approaches will be needed to develop a standardized methodology allowing comparisons across regions or researchers.

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APPENDICES

Appendix A

Research Site and Transect Location Information

Benjamin RNA/ACEC

County. Lake Co., Oregon.

Legal Location of Research Area. T. 23 S., R. 20 E., Sec. 7, Willamette Meridian.

Directions to Research Area. From the northeast corner of the RNA (section 7), walk south along fence-line to the 15th fencepost, about 100 m. The fencepost was labeled with a round metal tag reading, "BLM 200; Ponzetti '95, #15 and #16."

Directions to Grazed Transect. The transect is 100 m due east of the labeled fencepost. The transect marker rebar is labeled with a round metal tag reading, "BLM 190; Ponzetti #15." The transect line runs 180 degrees from this marker rebar. I read the west side of the transect line.

Directions to Exclosure Transect. Go to the sixth metal fencepost to the south of the 15th labeled fencepost (described above). Then proceed 25 m due west, into the exclosure. The transect marker rebar is labeled with a round metal tag reading, "BLM 182; Ponzetti #16." The transect line runs 180 degrees from this marker rebar. I read the west side of the transect line.

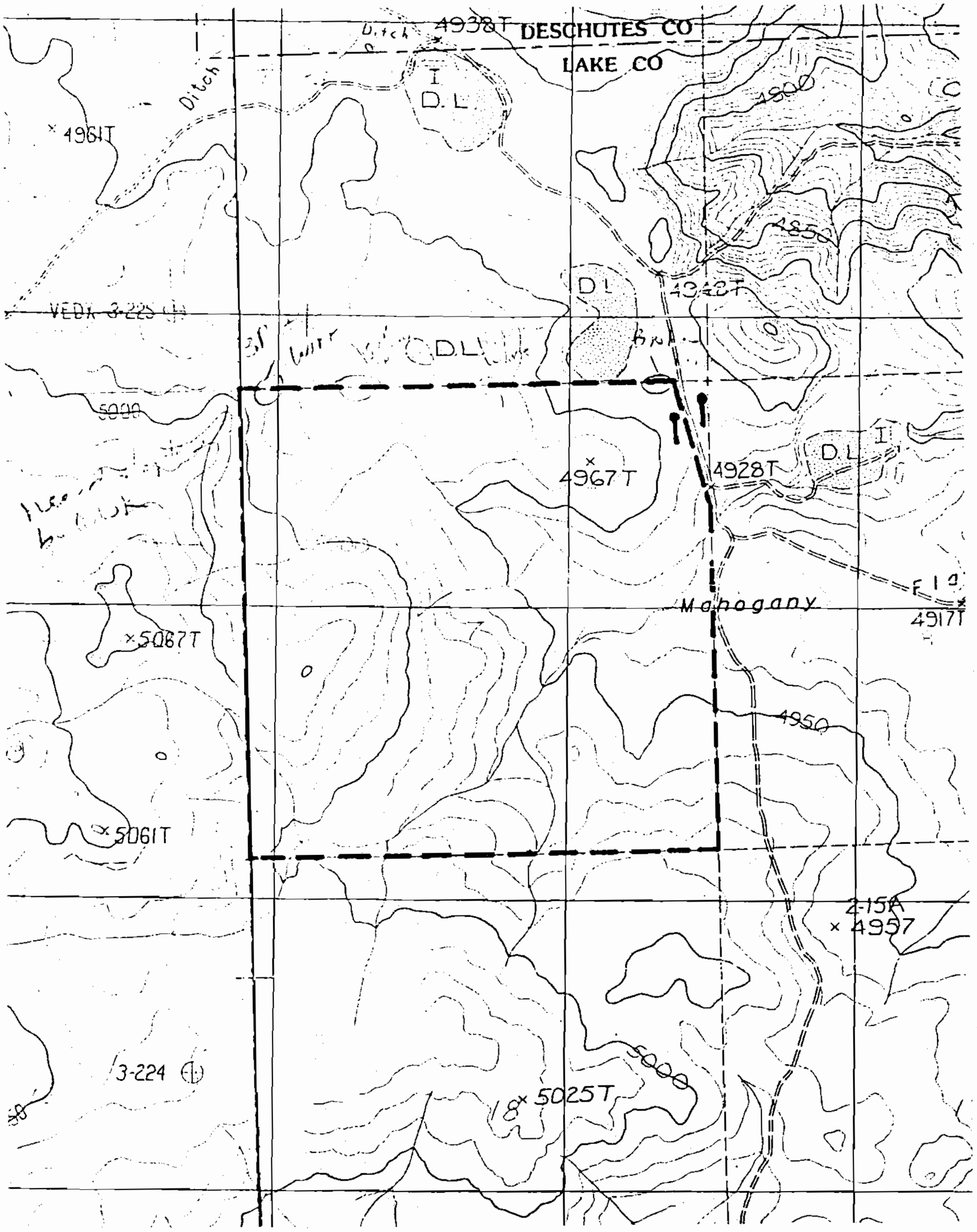

Figure A1. Benjamin RNA/ACEC. Lake Co., Oregon. T. 23 S., R. 20 E., Sec. 7, Willamette Meridian. ●— = transect location.

Boardman RNA

County. Morrow Co., Oregon.

Legal Location of Research Area. T. 2 N., R. 25 E., Sec. 3, Willamette Meridian.

Directions to Research Area. From the southeast corner of RNA "C," go 200 m west along the east-west fenceline. Fencepost number 42, counted from the southeast corner, is painted with orange paint, but not labeled.

Directions to Grazed Transect. From the orange painted fencepost, travel due south for 73 m. Transect marker rebar is in a swale at the north end of a patch of sagebrush. The transect marker rebar is low to the ground, painted orange, and marked with a red flag with a white stem. The transect line runs 265 degrees from this marker rebar. I read the south side of the transect line.

Directions to Exclosure Transect. From the orange painted fencepost, go due north 50 m. The transect marker rebar is not painted orange, but is marked with a red flag with a white stem. The transect line runs 268 degrees from this marker rebar. I read the south side of the transect line.

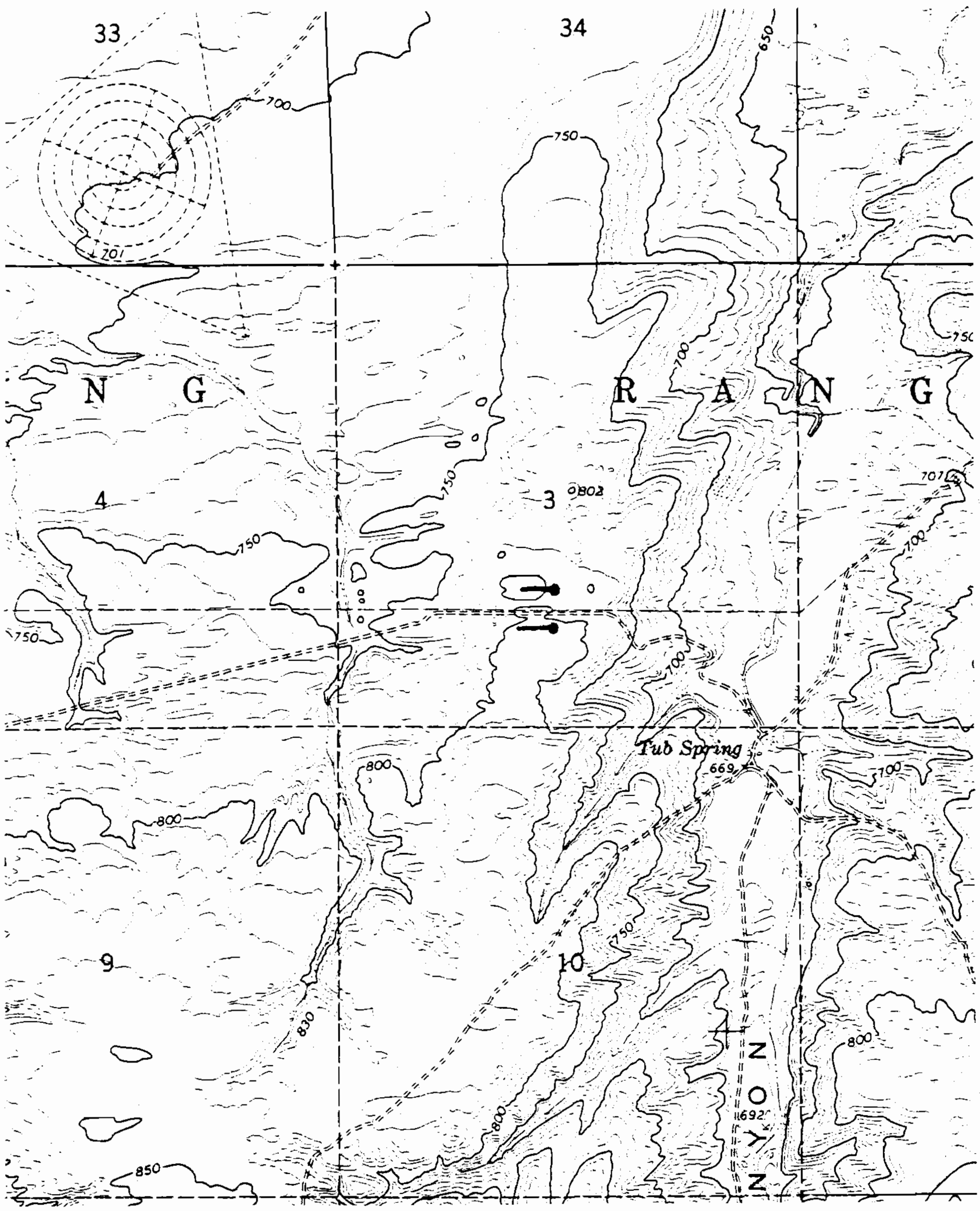

Figure A2. Boardman RNA. Morrow Co., Oregon. T. 2 N., R. 25 E., Sec. 3, Willamette Meridian. ●— = transect location.

Glass Butte Ecological Area

County. Lake Co., Oregon.

Legal Location of Research Area. T. 23 S., R. 23 E., Sec. 15, Willamette Meridian.

Directions to Research Area. From Brothers, Oregon, take Highway 20 east to just before milepost 81. Pull off on the south side of the road. Follow the fenceline south, past a very large juniper tree in the fence, about 120 m, to and orange painted fencepost. The fencepost is labeled with a round metal tag reading, "BLM 872; Ponzetti 5/95."

Directions to Grazed Transect. From the labeled fencepost, go due west exactly 50 m. The transect marker rebar is in the ground next to a large sagebrush. It's labeled with a metal tag reading, "BLM 862; Ponzetti 5/95, #5." The transect runs north from this marker rebar; I read the east side of the transect line.

Directions to Exclosure Transect. From the labeled fencepost, go due east 50 m. The transect marker rebar is labeled with a metal tag reading, "BLM 902; Ponzetti 5/95 #6." The transect runs north from this marker rebar; I read the east side of the transect line.

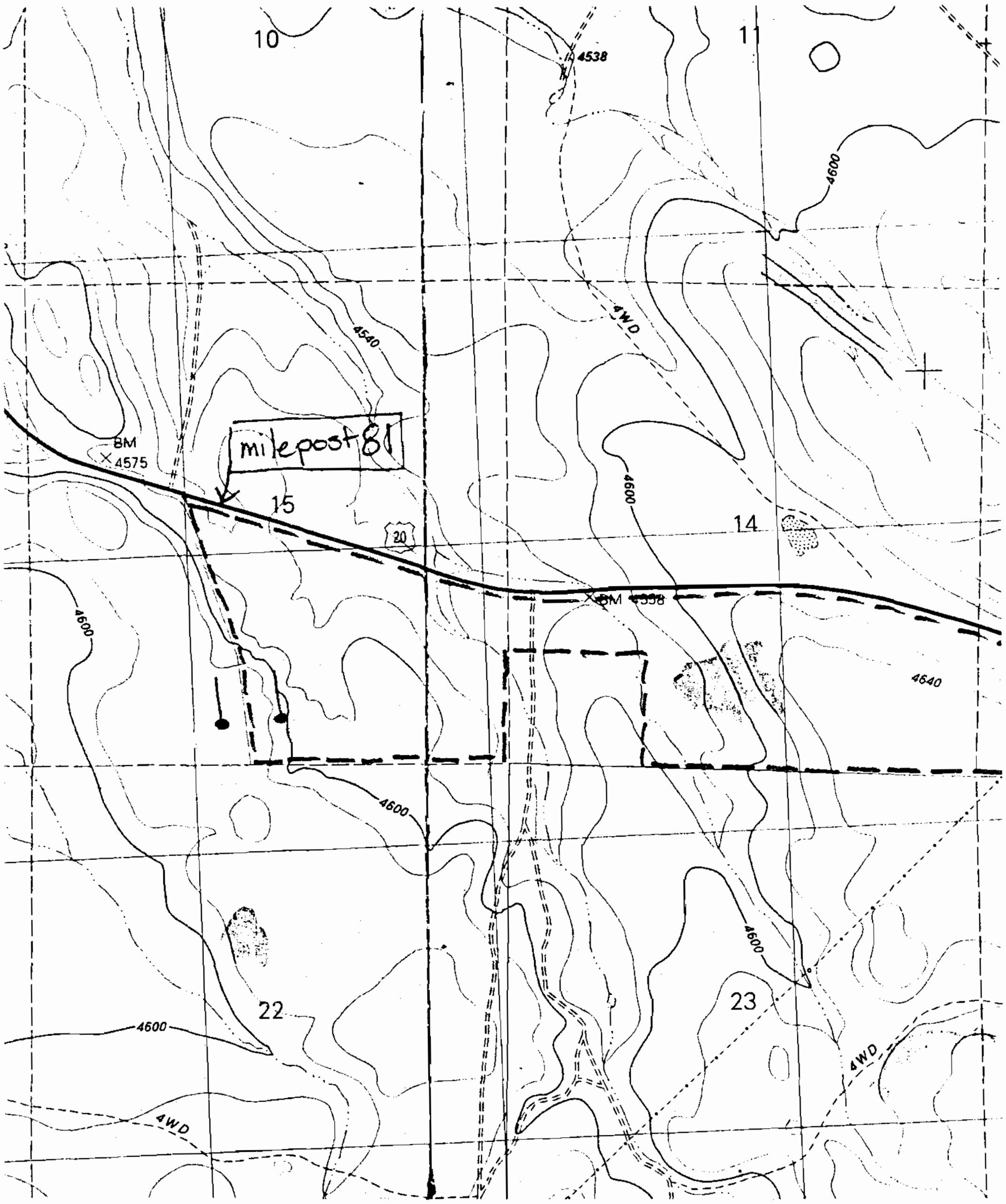

Figure A3. Glass Butte Ecological Area. Lake Co., Oregon. Hat Butte 7½' Quad, USGS. T. 23 S., R. 23 E., Sec. 15, Willamette Meridian. ●— = transect location.

Horse Ridge RNA/ACEC

County. Deschutes Co., Oregon.

Legal Location of Research Area. T. 19 S., R. 14 E., Sec. 15, Willamette Meridian.

Directions to Research Area. Take the old highway to the northeast road into Horse Ridge RNA. Follow the road to the RNA fenceline, in section 15. Walk up the fenceline (uphill, to the south) approx. 200 m to where there is a juniper tree incorporated into the fence. The next fencepost to the south is labeled with a round metal tag reading, "BLM 891; Ponzetti 6/95."

Directions to Grazed Transect. This transect is separated into two segments. For segment 1, go 90 degrees from the labeled fencepost for 25 m. The transect marker rebar is labeled with a metal tag reading, "BLM 822; Ponzetti #9 S. 1." For segment 2, go 25 m at 90 degrees from the juniper tree in the fence, one "post" directly to the north of the labeled fencepost. The transect marker rebar is labeled with a metal tag reading, "BLM 804; Ponzetti # 9 S. 2." The transect runs 110 degrees from this marker rebar. I read the south side of these segments.

Directions to Exclosure Transect. This transect is separated into two segments. For segment 1, go 265 degrees from the labeled fencepost for 25 m. The transect marker rebar is labeled with a metal tag reading, "BLM 903; Ponzetti #10 S. 1." Segment 1 extends 300 degrees from this marker rebar. To find segment 2, go 270 degrees for 25 m from the juniper tree in the fence, one "post" directly north of the labeled fencepost. The transect marker rebar is labeled with a metal tag reading, "BLM 870; Ponzetti #10 S. 2." Segment 2 extends 310 degrees from this marker rebar. I read the south side of these segments.

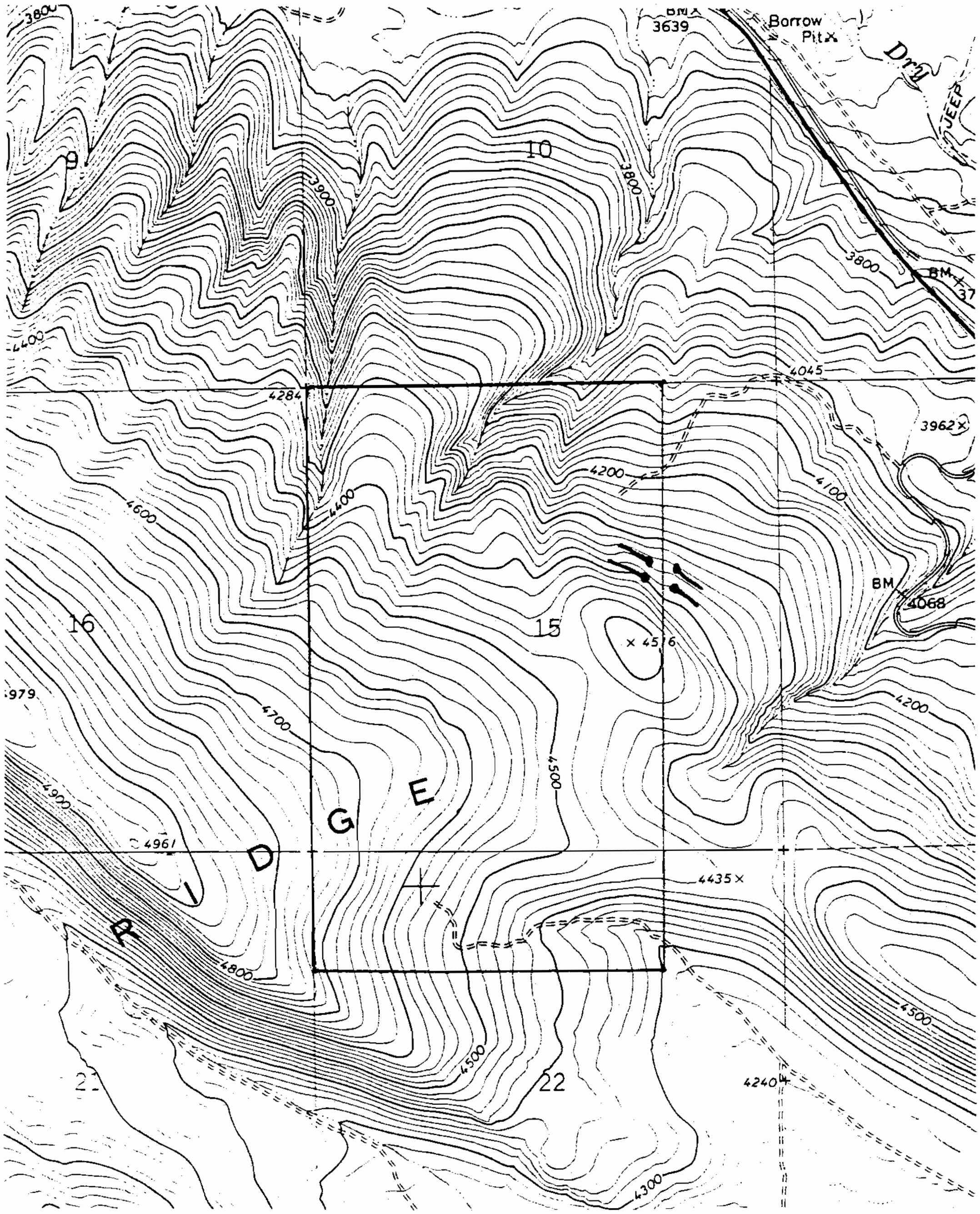

Figure A4. Horse Ridge RNA/ACEC. Deschutes Co., Oregon. Horse Ridge 7½' Quad, USGS. T. 19 S., R. 14 E., Sec. 15, Willamette Meridian. ●— = transect location.

Juniper Mountain Exclosure

County. Harney Co., Oregon.

Legal Location of Research Area. T. 30 S., R. 24 E., Sec. 17 and 18, Willamette Meridian.

Directions to Research Area. From the road at the north end of the exclosure, walk 100 m east of the northwest exclosure corner. A metal fencepost is flagged with orange, and labeled with a metal tag reading, "BLM 183; '95 Ponzetti #17 & #18."

Directions to Grazed Transect. From the labeled fencepost, walk northeast (32 degrees) for 50 m. The transect marker rebar is labeled with a metal tag reading, "BLM 910; Ponzetti # 17." This marker is about 20 m south of a section corner post. The transect extends at 130 degrees from the rebar labeled with the metal tag. I read the south side of the transect.

Directions to Exclosure Transect. From the labeled fencepost, walk 50 m perpendicular to the fenceline (212 degrees). Transect marker rebar is labeled with a metal tag reading, "BLM 164; Ponzetti #18." The transect extends at 130 degrees from this marker. I read the south side of the transect.

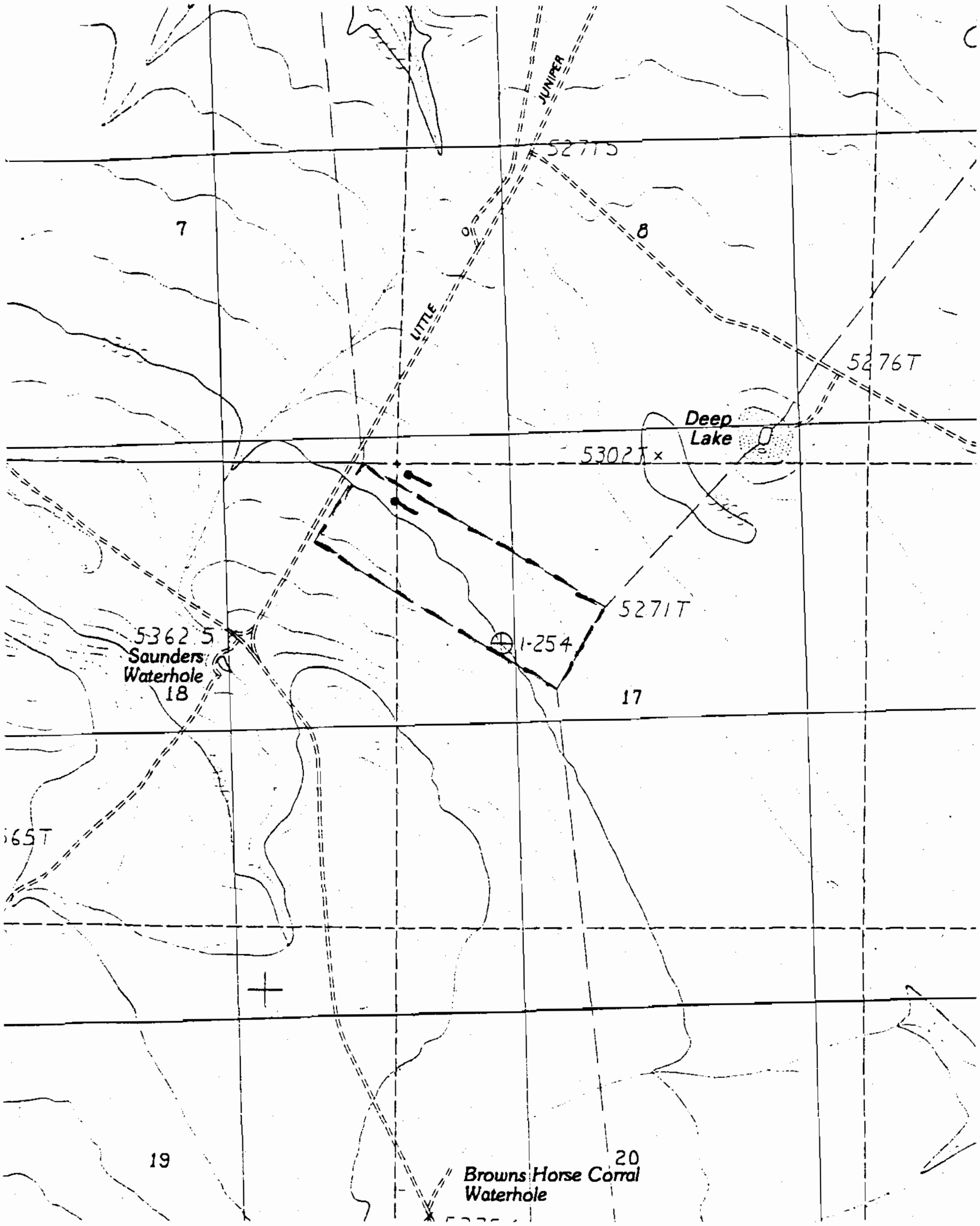

Figure A5. Juniper Mt. Exclosure. Harney Co., Oregon. Juniper Mt. 7½' Quad, USGS. T. 30 S., R. 24 E., Sec. 17 and 18, Willamette Meridian. •— = transect location.

Lawrence Memorial Grassland Preserve

County. Wasco Co., Oregon.

Legal Location of Research Area. T. 7 S., R. 16 E., Sec. 22 and 23, Willamette Meridian.

Directions to Research Area. From the southeast corner of the preserve, walk north along the north-south fenceline about 130 m. A metal fencepost is labeled with a metal tag reading, "BLM 187; Ponzetti '95 #13 & #14." This fencepost is just before the fenceline dips into a swale dominated by *Pseudoroegneria spicata*.

Directions to Grazed Transect. From the labeled fencepost, go approx. 125 meters due east. The transect marker rebar is at the north end of a mound, labeled with a metal tag reading, "BLM 162; Ponzetti #13." The transect line extends north from this marker. I read the west side of the transect line.

Directions to Exclosure Transect. From the labeled fencepost, go 140 m at 276 degrees. The transect marker rebar is at the north end of a mound, and labeled with a metal tag reading, "BLM 188; Ponzetti #14." The transect line extends north from this marker. I read the west side of the transect line.

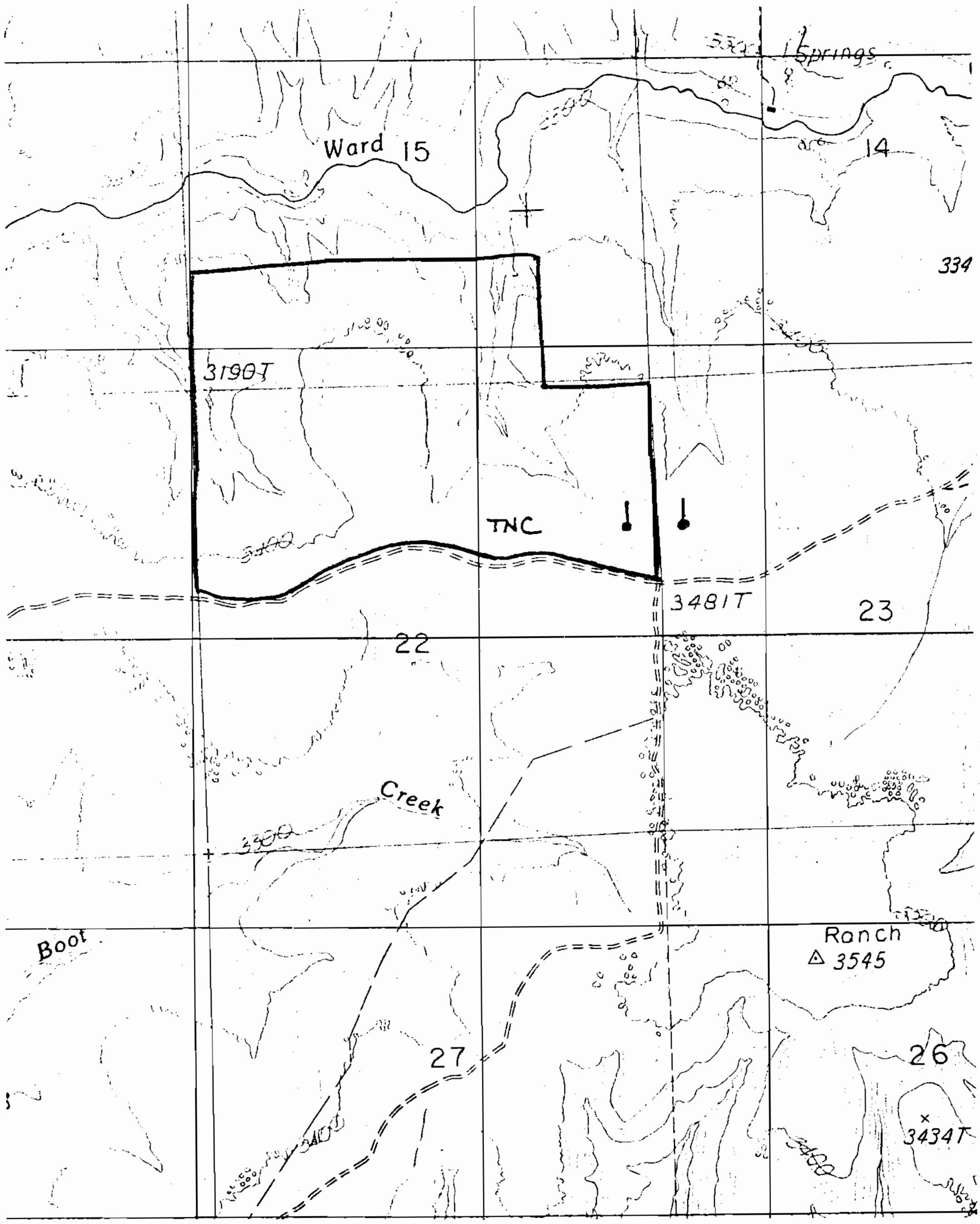

Figure A6. Lawrence Memorial Grassland Preserve. Wasco Co., Oregon. Shaniko Summit 7½' Quad, USGS. T. 7 S., R. 16 E., Sec. 22 and 23, Willamette Meridian. ●— = transect location.

Northern Great Basin Experimental Range Exclosure No. 7

County. Harney Co., Oregon.

Legal Location of Research Area. T. 24 S., R. 25 E., Sec. 3, Willamette Meridian.

Directions to Research Area. Use the north entrance to the Northern Great Basin Experimental Range, from Highway 20. Go 0.5 mile south from the entrance. The exclosure is on the west side of the road, about 200 m away. Walk up the south border of the exclosure to a labeled fencepost about 200 m from the road. The fencepost is labeled with a metal tag reading, "BLM 897; Ponzetti 95."

Directions to Grazed Transect. This transect is divided into two segments. Segment 1 beings 10 m south of the labeled fencepost. The transect marker rebar is labeled with a metal tag reading, "BLM 935; Ponzetti #7 S. 1." For the second segment, go one fencepost north (downslope) from the labeled fencepost. From that fencepost go exactly10 m south. The transect marker rebar is labeled, "BLM 819; Ponzetti #7 S. 3." These transects run south from their marker rebar. I read the west side of the transect.

Directions to Exclosure Transect. This transect is divided into two segments. Segment 1 begins 2 m north of the labeled fencepost. The rebar marker is labeled, "BLM 914; Ponzetti #8 S. 1." To find segment 2, go one fencepost uphill (west) of the the labeled fencepost. Segment 2 begins 2 m north of that fencepost. Both segments run north from their marker rebar. I read the west side of the transect line.

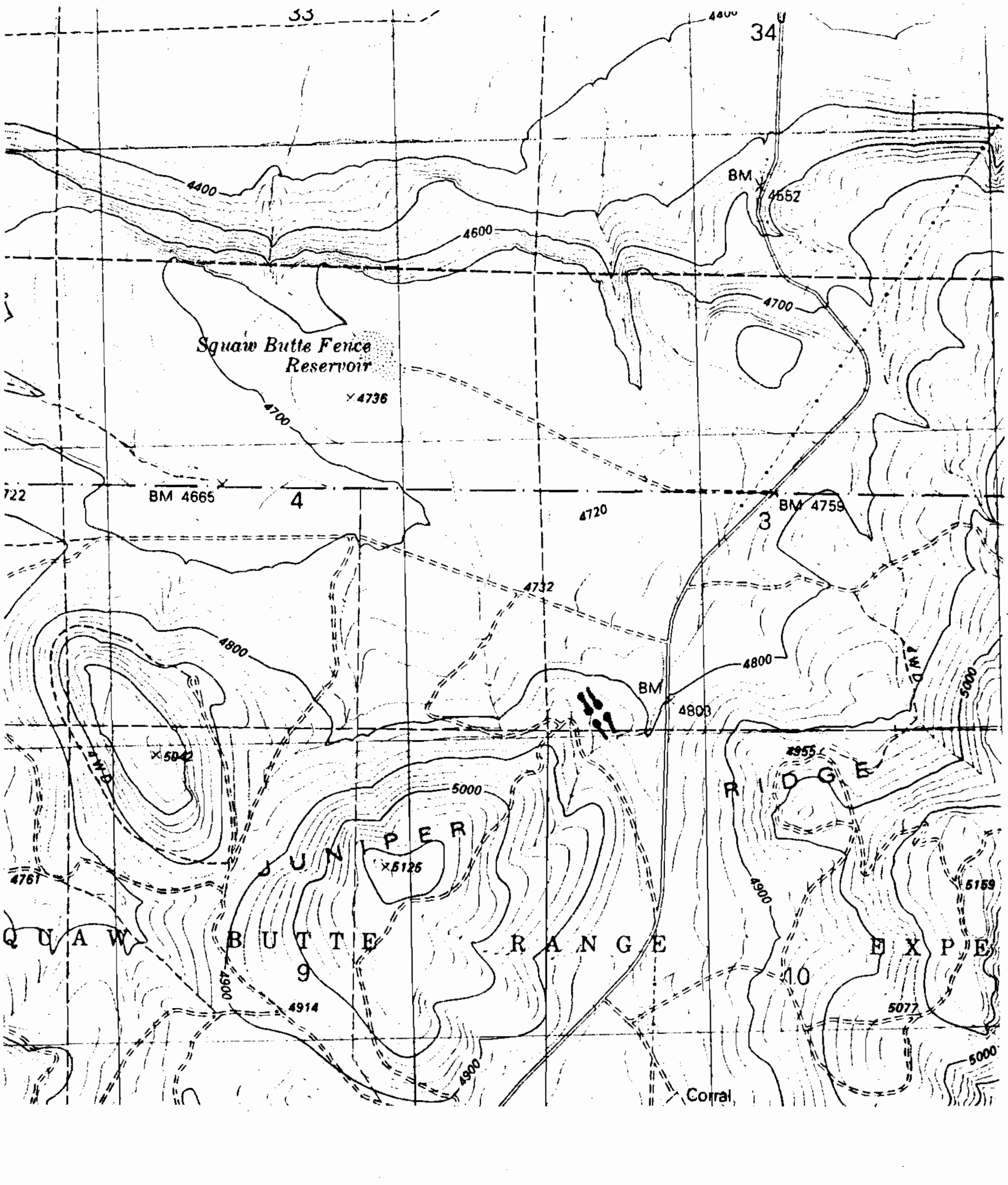

Figure A7. Northern Great Basin Experimental Range Exclosure No. 7. Harney Co., Oregon. Suntex 7½' Quad, USGS. T. 24 S., R. 25 E., Sec. 3, Willamette Meridian. ●— = transect location.

Northern Great Basin Experimental Range Exclosure No. 8

County. Harney Co., Oregon.

Legal Location of Research Area. T. 24 S., R. 25 E., Sec. 22, Willamette Meridian.

Directions to Research Area. From the Great Basin Experimental Range Headquarters, drive south, the east to Range No. 8. Go to the eastern edge of the old exclosure (with orange fenceposts). The fenceline runs north - south on the eastern edge of the exclosure. From the northeast corner post, go four fenceposts to the south (this was three metal fenceposts). The fourth fencepost is labeled with a metal tag reading, "BLM 850; Ponzetti '95 #11 & #12."

Directions to Grazed Transect. This transect is separated into two segments. Segment 1 is exactly 40 m due east of the labeled fencepost. The marker rebar is labeled, "BLM 828; Ponzetti #11 S. 1." Segment 2 is exactly 50 m due east of the labeled fencepost. The segment 2 marker rebar is labeled, "BLM 855; Ponzetti #11 S. 2." The transects run south from the marker rebar; I read the west side of the transect line.

Directions to Exclosure Transect. This transect is separated into two segments. Segment 1 begins exactly 20 m due west from the labeled fencepost. The transect marker rebar is labeled, "BLM 873; Ponzetti #12 S. 1." Segment 2 is exactly 30 m west of the labeled fencepost, with a marker rebar labeled, "BLM 861; Ponzetti #12 S. 2." The transects run south from the marker rebar; I read the west side of the transect line.

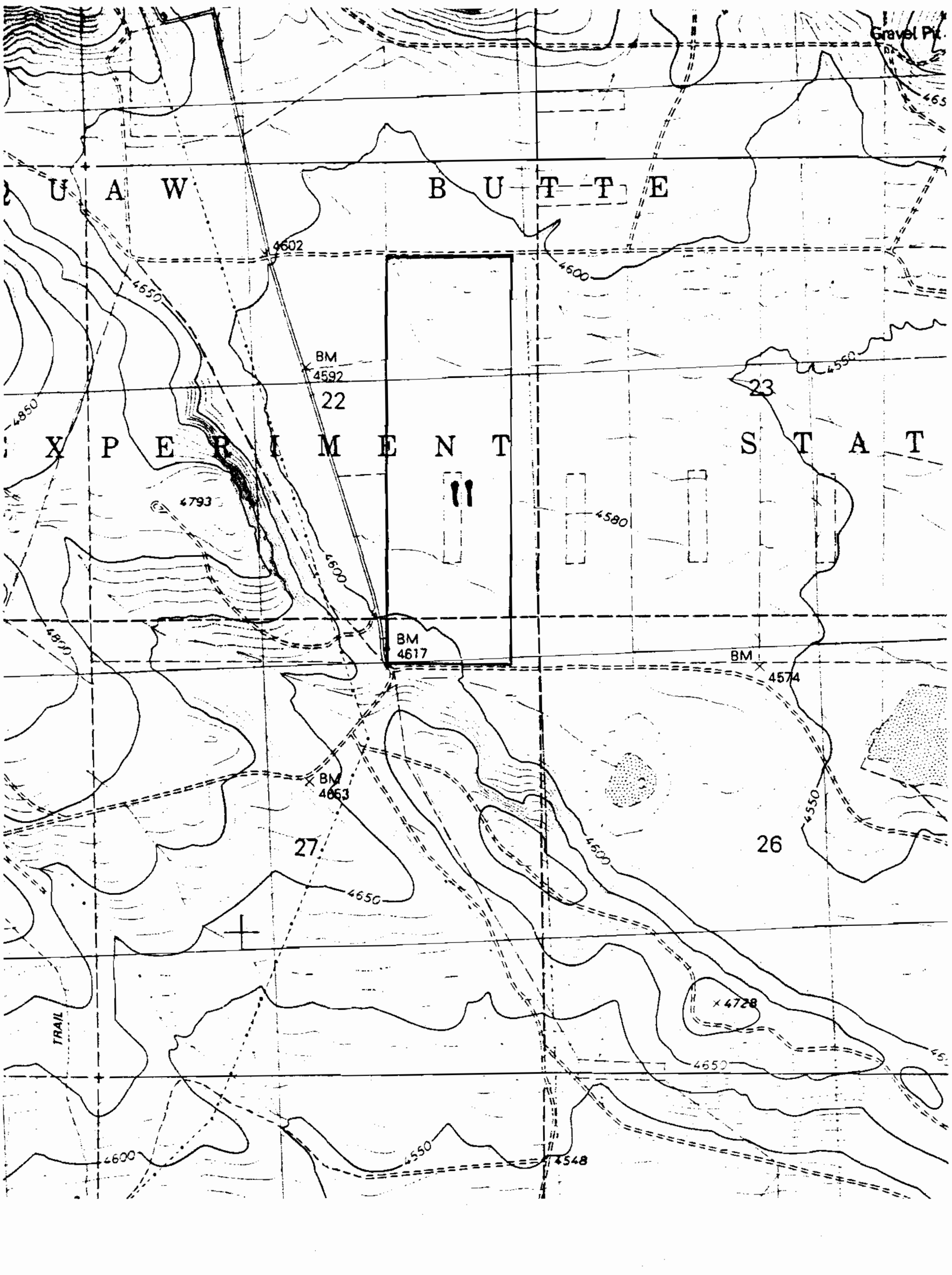

Figure A8. Northern Great Basin Experimental Range Exclosure No. 8. Harney Co., Oregon. Squaw Butte 7½' Quad, USGS. T. 24 S., R. 25 E., Sec. 22, Willamette Meridian. ●— = transect location.

South Narrows ACEC

County. Harney Co., Oregon.

Legal Location of Research Area. T. 27 S., R. 30 E., Sec. 11 and 12, Willamette Meridian.

Directions to Research Area. From Burns, Oregon, head south on Highway 205. Just past milepost 25, take the dirt road on the west side of the road. Go through the metal gate to the BLM ACEC interpretive sign. From the second set of stairs over the fence, go west along the fenceline about 120 m, to a white fencepost with an orange-painted top. This fencepost is labeled with a metal tag reading, "BLM 806; Ponzetti 5/95."

Directions to Grazed Transect. From the labeled fencepost, go 100 m at 330 degrees. The transect marker rebar is labeled with a metal tag reading, "BLM 856; Ponzetti 5/95 #3." This transect runs 40 degrees from the rebar marker. I read the south side of the transect line.

Directions to Exclosure Transect. From the labeled fencepost, go 125 m at 150 degrees. The transect marker rebar is labeled, "BLM 821; Ponzetti 5/95 #4." The transect runs 110 degrees from this marker rebar. I read the south side of the transect line.

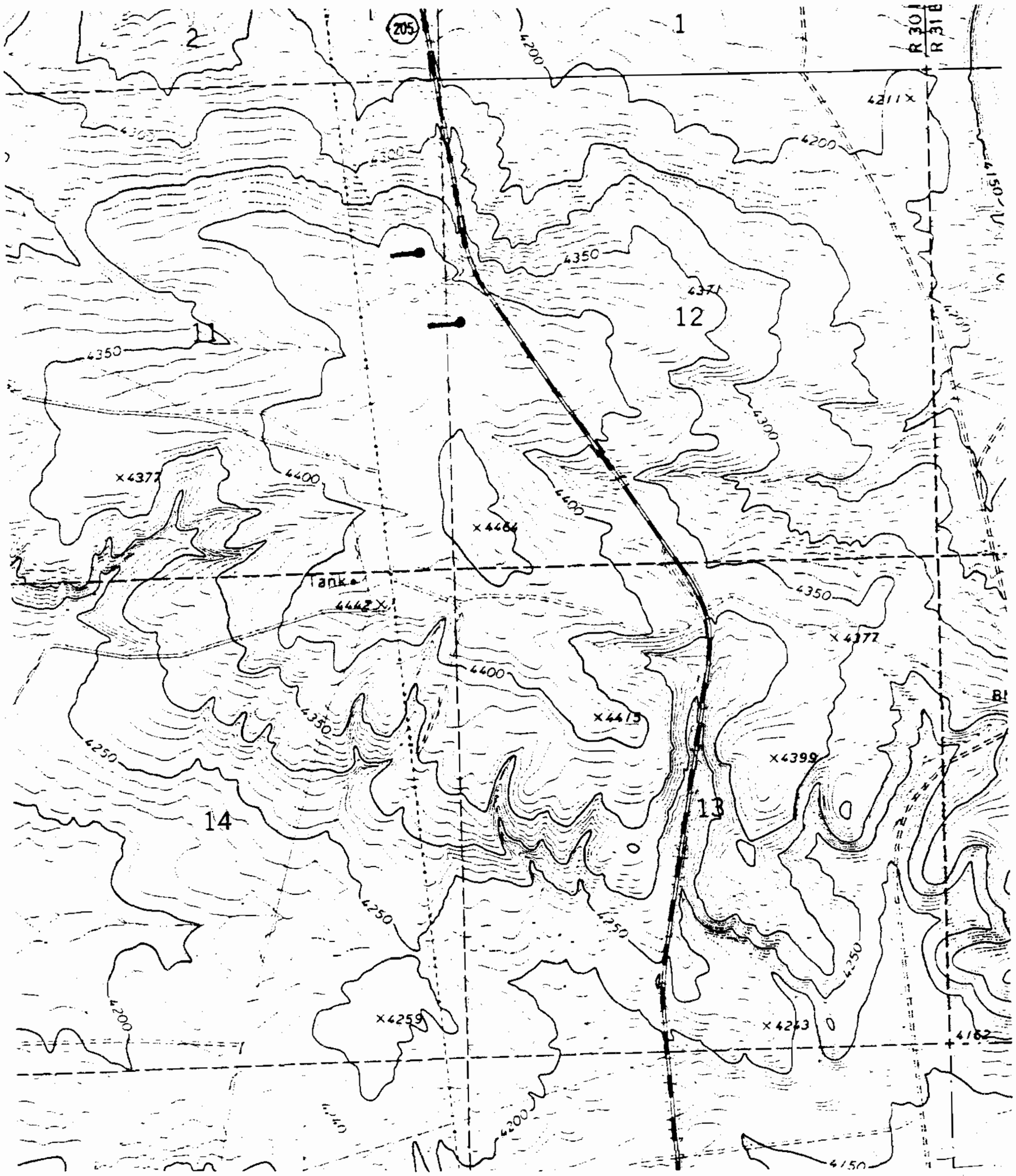

Figure A9. South Narrows ACEC. Harney Co., Oregon. Coyote Buttes 7½' Quad, USGS. T. 27 S., R. 30 E., Sec. 11 and 12, Willamette Meridian.

•— = transect location.

Appendix B

Biotic Crust Species Lists

Benjamin RNA/ACEC

Algae
Arthonia glebosa
Aspicilia hispida
Apicilia spp.
Black Crust
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca tominii
Candelariella terrigena
Ceratadon purpureus
Cladonia spp.
Collema tenax group
Encalypta rhaptocarpa
Endocarpon/Catapyrenium group
Lecanora spp.
Leptogium spp.
Megaspora verrucosa
Psora montana
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Unknown bryophytes (small, poorly developed mosses, not identified)
Unknown lichens (small, poorly developed lichens, not identified)

Boardman RNA

Acarospora schleicheri

Arthonia glebosa
Apicilia spp.
Black Crust
Bryum argenteum
Caloplaca sp.
Ceratadon purpureus
Cladonia spp.
Didymodon spp.
Diploschistes muscorum
Endocarpon pusillum
Lecanora spp.
Leptochidium albociliatum
Leptogium spp.
Psora cerebriformis
Psora montana
Tortula ruralis
Tortula caninervis
Trapeliopsis bisorediata sp. nov. (McCune, in edit)
Trichostomopsis australasiae
Unknown lichens (small, poorly developed lichens, not identified)

Glass Butte Ecological Area

Algae
Amandinea punctata
Arthonia glebosa
Aspicilia hispida
Apicilia spp.
Aspicilia reptans
Black Crust
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca tominii
Candelariella terrigena
Ceratadon purpureus
Cladonia spp.
Encalypta rhaptocarpa
Endocarpon/Catapyrenium group
Lecanora spp.
Leptogium spp.
Megaspora verrucosa
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Unknown lichens (small, poorly developed lichens, not identified)

Horse Ridge RNA/ACEC

Algae
Amandinea punctata
Arthonia glebosa
Aspicilia filiformis Rosentreter (1998)
Aspicilia hispida
Aspicilia reptans
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca jungermanniae
Caloplaca tominii
Candelariella terrigena
Ceratadon purpureus
Cladonia spp.
Diploschistes muscorum
Encalypta rhaptocarpa
Lecanora spp.
Leprocaulon subalbicans
Leptochidium albociliatum
Leptogium spp.
Megaspora verrucosa
Ochrolechia upsaliensis
Peltigera didactyla
Peltigera spp.
Psora montana
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Unknown lichens (small, poorly developed lichens, not identified)

Juniper Mountain Exclosure

Algae
Aspicilia hispida
Apicilia spp.
Black Crust
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca jungermanniae
Caloplaca tominii
Candelariella terrigena
Ceratadon purpureus
Cladonia spp.
Collema tenax group
Encalypta rhaptocarpa
Lecanora spp.
Lecanora epibryon
Megaspora verrucosa
Psora/Phaeorrhiza group
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Unknown bryophytes (small, poorly developed mosses, not identified)
Unknown lichens (small, poorly developed lichens, not identified)

Lawrence Memorial Grassland Preserve

Algae
Amandinea punctata
Arthonia glebosa
Aspicilia filiformis Rosentreter (1998)
Aspicilia hispida
Black Crust
Brachythecium albicans
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca jungermanniae
Catapyrenium squamulosum
Cephaloziella divaricata
Ceratadon purpureus
Cladonia spp.
Diploschistes muscorum
Encalypta rhaptocarpa
Lecanora spp.
Leptochidium albociliatum
Leptogium spp.
Massalongia carnosa
Megaspora verrucosa
Peltigera spp.
Phaeorrhiza sareptana
Placynthiella spp.
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Trichostomopsis australasiae
Unknown bryophytes (small, poorly developed mosses, not identified)
Unknown lichens (small, poorly developed lichens, not identified)

Northern Great Basin Experimental Range No. 7

Algae
Amandinea punctata
Arthonia glebosa
Apicilia spp.
Aspicilia reptans
Black Crust
Bryum argenteum
Bryum spp.
Buellia geophila
Caloplaca tominii
Candelariella terrigena
Ceratadon purpureus
Cladonia spp.
Collema tenax group
Encalypta rhaptocarpa
Endocarpon pusillum
Lecanora spp.
Leptogium spp.
Megaspora verrucosa
Psora globifera
Psora/Phaeorrhiza group
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Trichostomopsis australasiae
Unknown lichens (small, poorly developed lichens, not identified)

Northern Great Basin Experimental Range No. 8

Algae
Arthonia glebosa
Aspicilia hispida
Apicilia spp.
Black Crust
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca tominii
Candelariella terrigena
Ceratadon purpureus
Cladonia spp.
Collema tenax group
Encalypta rhaptocarpa
Endocarpon/Catapyrenium group
Lecanora spp.
Leptogium spp.
Megaspora verrucosa
Phaeorrhiza sareptana
Psora cerebriformis
Psora montana
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Unknown bryophytes (small, poorly developed mosses, not identified)
Unknown lichens (small, poorly developed lichens, not identified)

South Narrows ACEC

Arthonia glebosa
Aspicilia hispida
Apicilia spp.
Black Crust
Bryum argenteum
Bryum spp.
Caloplaca cerina
Caloplaca tominii
Candelariella terrigena
Collema tenax group
Encalypta rhaptocarpa
Endocarpon pusillum
Lecanora spp.
Megaspora verrucosa
Phaeorrhiza sareptana
Psora cerebriformis
Pterygoneuron ovatum
Tortula ruralis
Tortula caninervis
Unknown bryophytes (small, poorly developed mosses, not identified)
Unknown lichens (small, poorly developed lichens, not identified)

Appendix C

Biotic Crust Species Data Matrix

TABLE A1. Biotic crust species data matrix. Data are average cover classes (not percent cover). Biotic crust species and morphological groups are in 51 columns; see Table 2.5 for explanation of column acronyms. Transects are in 18 rows; see Table 3.2 for transect identities.

	UNKNLI	ACASCH	ARTGLE	ASPHIS	ASP	CALJUN	CALTOM	CALCER	CANTER	CLAD	COLL
tran01	0.02222	0	0.4	0	0.13333	0	0	0	0	1.11111	0
tran02	0.08889	0.46667	0.04444	0	1.11111	0	0	0	0	1.51111	0
tran03	0.08889	0	0	0.04444	0.2	0	0.15556	0.02222	0.42222	0	0.04444
tran04	0.06667	0	0.02222	0.17778	0.22222	0	0.24444	0.02222	0.44444	0	0.28889
tran05	0.17778	0	0	0.13333	0.17778	0	0.44444	0.06667	0.11111	0.28889	0
tran06	0.37778	0	0.04444	0.11111	0.08889	0	0.24444	0.04444	0.11111	0.42222	0
tran07	0.04444	0	0.17778	0	0.17778	0	0.2	0	0.11111	1.11111	0.42222
tran08	0.04444	0	0.28889	0	0.24444	0	0.37778	0	0.06667	1.55556	0.44444
tran09	0.08889	0	0.17778	0	0	0.04444	0	0.13333	0.17778	1.28889	0
tran10	0.26667	0	0.15556	0.11111	0	0	0.24444	0.22222	0.28889	1.88889	0
tran11	0.22222	0	0.06667	0.06667	0.48889	0	0.02222	0.02222	0.44444	0.44444	0.24444
tran12	0.11111	0	0.28889	0.13333	0.44444	0	0.08889	0.11111	0.51111	0.82222	0.55556
tran13	0.13333	0	0	0	0	0.02222	0	0.02222	0	0.51111	0
tran14	0.48889	0	0.11111	0.02222	0	0	0	0	0	1.44444	0
tran15	0.2	0	0	0.31111	0	0	0.04444	0.02222	0.13333	0.15556	0.24444
tran16	0.08889	0	0.02222	0.26667	0.11111	0	0	0.11111	0.06667	0.15556	0.24444
tran17	0.08889	0	0	0.2	0.55556	0.02222	0.22222	0.13333	0.48889	0	0.2
tran18	0	0	0	0	0.64444	0	0.2	0.08889	0.57778	0.06667	0.11111

TABLE A1 Continued

	BLACK	BUEGEO	AMAPUN	DIPMUS	ENDPUS	ENDCAT	LECA	LECEPI	LEPT	MEGVER	PELT
tran01	0	0	0	1.08889	0.2	0	0.02222	0	0.51111	0	0
tran02	0.6	0	0	1.22222	0	0	0	0	0.62222	0	0
tran03	0.55556	0	0	0	0.26667	0	0	0	0	0.06667	0
tran04	0.8	0	0	0	0.35556	0	0.11111	0	0	0.22222	0
tran05	0.53333	0	0	0	0	0	0.08889	0	0.13333	0	0
tran06	0.93333	0	0.02222	0	0	0.04444	0.08889	0	0.17778	0.04444	0
tran07	0.91111	0	0.06667	0	0.17778	0	0.22222	0	0	0	0
tran08	1.08889	0.08889	0.24444	0	0.2	0	0.17778	0	0.06667	0.02222	0
tran09	0	0	0.06667	0	0	0	0.06667	0	0.53333	0.08889	0
tran10	0	0	0.26667	0.02222	0	0	0.04444	0	0.77778	0.04444	0.08889
tran11	0.26667	0	0	0	0	0.26667	0.15556	0	0	0.02222	0
tran12	0.6	0	0	0	0	0.4	0.04444	0	0.06667	0.06667	0
tran13	0.24444	0	0	0.02222	0	0	0	0	0.8	0	0.2
tran14	0.37778	0	0.06667	0.17778	0	0	0.04444	0	1.06667	0.2	0.6
tran15	0.4	0	0	0	0	0.08889	0.04444	0	0.04444	0	0
tran16	0.24444	0	0	0	0	0.02222	0.04444	0	0.11111	0.13333	0
tran17	1.64444	0	0	0	0	0	0.53333	0.02222	0	0.22222	0
tran18	1.8	0	0	0	0	0	0.31111	0	0	0.11111	0

TABLE A1 Continued

	PSOCER	PSOMON	PSOGLO	PHASAR	ALG	TRAP	UNKNBR	CEPDIV	CERPUR	DIDY	ENCRHA
tran01	0	0.17778	0	0	0	0.17778	0	0	1.55556	0.2	0
tran02	0.42222	0.08889	0	0	0	0.75556	0	0	1.93333	1.24444	0
tran03	0.2	0	0	0.26667	0	0	0.02222	0	0	0	0.06667
tran04	0.2	0	0	0.44444	0	0	0	0	0	0	0.15556
tran05	0	0	0	0	0	0	0	0	0.2	0	0.35556
tran06	0	0	0	0	0.62222	0	0	0	0.24444	0	0.48889
tran07	0	0	0	0	0.48889	0	0	0	0.55556	0	0.33333
tran08	0	0	0.02222	0	0.62222	0	0	0	0.71111	0	0.51111
tran09	0	0.13333	0	0	0.02222	0	0	0	0.17778	0	0.4
tran10	0	0.06667	0	0	0.2	0	0	0	0	0	0.62222
tran11	0	0.02222	0	0	0.22222	0	0.22222	0	0.08889	0	0.08889
tran12	0.02222	0.2	0	0.24444	0.28889	0	0.06667	0	0.35556	0	0.66667
tran13	0	0	0	0.02222	0	0	0	0.13333	0.37778	0	0.2
tran14	0	0	0	0	0.26667	0	0.35556	0.33333	1.42222	0	0.35556
tran15	0	0.06667	0	0	0.24444	0	0.06667	0	0.13333	0	0.26667
tran16	0	0	0	0	0.48889	0	0.06667	0	0.02222	0	0.35556
tran17	0	0	0	0	0.73333	0	0.04444	0	0.15556	0	0.37778
tran18	0	0	0	0	0.42222	0	0	0	0.17778	0	0.68889

TABLE A1 Continued

	BRYUM	BRYARG	BRAALB	PTEOVA	TORRUR	TORCAN	TRIAUS	LEPALB	CALO	ASPREP	PSORA
tran01	0	1.02222	0	0	1.15556	0.22222	0	0.93333	0.15556	0	0
tran02	0	0.71111	0	0	1.2	0.46667	0.04444	1	0	0	0
tran03	0.06667	0	0	0.13333	2.08889	0	0	0	0	0	0
tran04	0.15556	0.15556	0	0.26667	2.48889	0.04444	0	0	0	0	0
tran05	0.11111	0.24444	0	0.11111	1.84444	0.04444	0	0	0	0.35556	0
tran06	0.11111	0.15556	0	0.31111	2.33333	0.04444	0	0	0	0.33333	0
tran07	1.24444	0.42222	0	0.15556	1.04444	0.33333	0	0	0	0.08889	0.22222
tran08	1.46667	0.62222	0	0.31111	1.71111	0.64444	0.02222	0	0	0.04444	0.2
tran09	0.04444	0.15556	0	0.02222	2.04444	0.46667	0	0.04444	0	0.55556	0
tran10	0.13333	0	0	0.06667	2.06667	0.15556	0	0	0	0.33333	0
tran11	0.02222	0.22222	0	0.31111	1.17778	0.26667	0	0	0	0	0
tran12	0.42222	0.73333	0	0.44444	2.04444	0.26667	0	0	0	0	0
tran13	0	0.46667	0.06667	0.04444	3.55556	0.2	0.02222	0.11111	0	0	0
tran14	0.02222	0.97778	0	0.15556	3.22222	0.6	0	0.28889	0	0	0
tran15	0.04444	0.06667	0	0.08889	2.33333	0.26667	0	0	0	0	0
tran16	0.06667	0.13333	0	0.08889	2.73333	0.46667	0	0	0	0	0
tran17	0.57778	0.48889	0	0.71111	1.6	0.6	0	0	0	0	0
tran18	0.66667	0.55556	0	0.37778	2.28889	0.64444	0	0	0	0	0.02222

TABLE A1 Continued

	PELDID	LEPSUB	ASPFIL	OCHUPS	CATSQU	PLACYN	MASCAR
tran01	0	0	0	0	0	0	0
tran02	0	0	0	0	0	0	0
tran03	0	0	0	0	0	0	0
tran04	0	0	0	0	0	0	0
tran05	0	0	0	0	0	0	0
tran06	0	0	0	0	0	0	0
tran07	0	0	0	0	0	0	0
tran08	0	0	0	0	0	0	0
tran09	0.02222	0	0.51111	0	0	0	0
tran10	0.02222	0.02222	0.31111	0.02222	0	0	0
tran11	0	0	0	0	0	0	0
tran12	0	0	0	0	0	0	0
tran13	0	0	0.02222	0	0.02222	0	0
tran14	0	0	0.06667	0	0.28889	0.13333	0.17778
tran15	0	0	0	0	0	0	0
tran16	0	0	0	0	0	0	0
tran17	0	0	0	0	0	0	0
tran18	0	0	0	0	0	0	0

Appendix D

Codes and Descriptions of Vascular Plant and Environmental Variables

TABLE A2. Codes and descriptions of vascular plant and environmental variables. This list includes all site variables used in the ordination analysis that are not biotic soil crust "species."

CODE	DESCRIPTION
GRAZED	1 = grazed transects; 0 = exclosure transects
BLOCK	each site is one of nine blocks
FORBS	total forb cover (sum of average cover of all forb species)
RESIDS	residuals from the regression of electrical conductivity on pH
CIV	Calcareous Index Values (see text)
PRECIP	precipitation in mm
TEMP	temperature in degrees Celsius
pH	pH (transect values are averages of 9 samples per transect)
EC	electrical conductivity (dS/m)
HEAT	heatload; ranges from 1 (NE aspect) to 5 (SW aspect)
EXLENG	number of years exclosure had been established prior to data collection
GIRANK	ranking of grazed sites by grazing intensity (from 1 to 9)
CRRICH	biotic crust species richness
CCOVER	total crust cover (sum of average cover of all biotic crust variables)
VARICH	vascular plant species richness
VASCPL	total vascular plant cover (sum of average cover of all vascular plant species)
BNCHGR	total bunchgrass cover (sum of average cover of all bunchgrasses)
ELEVAT	elevation (m)
SLOPE	slope (degrees)
SAND	percent sand
SILT	percent silt
CLAY	percent clay
ROUGHN	biotic soil surface roughness (see text)
ROCK	cover of rock
GRAVEL	cover of gravel
BAREGR	cover of bare ground
ORGLIT	cover of organic litter
JUNOCC	cover of Juniperus occidentalis
ARTTRI	cover of Artemisia tridentata
ARTARB	cover of Artemisia arbuscula
CHRNAU	cover of Chrysothamnus nausosus
CHRVIS	cover of Chrysothamnus viscidiflorus
TETRAD	cover of Tetradymia spp.
SHRUB	total shrub cover (sum of average cover of all shrub species)
AGRSPI	cover of Agropyron spicatum (= Pseudoroegneria spicata)
STITHU	cover of Stipa thurberiana
POASEC	cover of Poa secunda
FESIDA	cover of Festuca idahoensis
KOECRI	cover of Koeleria cristata

Table A2 Continued

CODE	DESCRIPTION
SITHYS	cover of Sitanion hystrix
BROTEC	cover of Bromus tectorum
TAECAP	cover of Taenatherium caput-medusae
BRYOS	total bryophyte cover (sum of average cover of all bryophytes)
LICHEN	total lichen cover (sum of average cover of all lichens)
NFIXER	total nitrogen-fixing lichens (sum of average cover of all nitrogen-fixing lichens)
COWPIE	cover of cowpies
ARTRIG	cover of Artemisia rigida
GUTSAR	cover of Gutierrezia sarothrae
STICOM	cover of Stipa comata
ORYHEN	cover of Oryzopsis hendersonii
ORYWEB	cover of Oryzopsis webberi
FESMIC	cover of Festuca microstachys
ZZZGRA	cover of unknown grass spp.
CARFIL	cover of Carex filifolia
ZZZHER	cover of unknown herb spp.
ACHMIL	cover of Achillea millefolium
ALLZZZ	cover of Allium spp.
ALYALY	cover of Alyssum alyssoides
ANTDIM	cover of Antennaria dimorpha
ANTMIC	cover of Antennaria microphylla
ASTZZZ	cover of unknown Astragalus spp.
ASTCUR	cover of Astragalus curvicarpus
ASTFIL	cover of Astragalus filipes
ASTLEN	cover of Astragalus lentiginosus
ASTPUR	cover of Astragalus purshii
ZZZBOR	cover of unknown Boraginaceae family spp.
BLESCA	cover of Blepharipappus scaber
CCHZZZ	cover of Calochortus spp.
CASZZZ	cover of Castilleja spp.
CLTZZZ	cover of Claytonia spp.
CLNZZZ	cover of Collinsia spp.
CLNPAR	cover of Collinsia parviflora
CREZZZ	cover of Crepis spp.
ZZZCRU	cover of unknown Cruciferae family spp.
DESZZZ	cover of Descurania spp.
DRAVER	cover of Draba verna
EPIZZZ	cover of Epilobium spp.
ERPLAN	cover of Eriophyllum lanatum
ERIZZZ	cover of Erigeron spp.
ERGZZZ	cover of Eriogonum spp.
ERGUMB	cover of Eriogonum umbellatum var. umbellatum
EROCIC	cover of Erodium cicutarium
GAYZZZ	cover of Gayophytum spp.
HOLUMB	cover of Holosteum umbellatum
IDASCA	cover of Idahoa scapigera
LACZZZ	cover of Lactuca spp.
LTDZZZ	cover of Leptodactylon pungens

Table A2 Continued

CODE	DESCRIPTION
LEUMON	cover of Leucocrinum montanum
LITZZZ	cover of Lithophragma spp.
LTMRUD	cover of Lithospermum ruderale
LOMZZZ	cover of unknown Lomatium spp.
LOMCOU	cover of Lomatium cous
LOMMAC	cover of Lomatium macrocarpum
LOMNEV	cover of Lomatium nevadensis
LOMTRI	cover of Lomatium triternatum
LUPZZZ	cover of Lupinus spp.
MISZZZ	cover of Microseris spp.
MICGRA	cover of Microsteris gracilis
MIMNAN	cover of Mimulus nanus
PHLZZZ	cover of unknown Phlox spp.
PHLHOO	cover of Phlox hoodii
PHLLON	cover of Phlox longifolia
PLAPAT	cover of Plantago patagonica
POLDOU	cover of Polygonum douglasii
RANTES	cover of Ranunculus testicularis
SENZZZ	cover of Senecio spp.
TRIZZZ	cover of unknown Trifolium spp.
TRIMAC	cover of Trifolium macrocephalum
ZIGVEN	cover of Zigadenus venenosus
CHADOU	cover of Chaenactis douglasii
PLEZZZ	cover of Plectritis spp.
AGRCRI	cover of Agropyron cristatum
DELZZZ	cover of Delphinium spp.
ARAZZZ	cover of Arabis spp.
CRYCIR	cover of Cryptantha circumscissa
LEWRED	cover of Lewisia rediviva
AGOZZZ	cover of Agoseris spp.
ZZZCOM	cover of unknown Compositae family spp.
BALZZZ	cover of Balsamorhiza spp.

Appendix E

Archived Data Files

TABLE A3. Archived data files. The following data files have been saved to a 3.5" floppy disk, available with the library copies of this thesis.

File Name	File Type	Contents
crust51.wk1	PC-ORD spreadsheet	Biotic crust species abundances, averaged at the transect level. Matrix = 51 spp. X 18 transects. This file contains the same data as Table A1 in Appendix C, but is formatted for use in PC-ORD.
crust41.wk1	PC-ORD spreadsheet	Reduced biotic crust species matrix; deleted spp. with fewer than 2 transects. Matrix = 41 spp. X 18 transects.
crust1.txt	text file	raw crust species data; has not been averaged at the transect level. These data are in compact format, for import into PC-ORD.
vascenvt.txt	text file	raw environmental variables; has not been averaged at the transect level. These data are in compact format, for import into PC-ORD. This includes vascular plant data and other variables collected in the field at the quadrat level.
sitevars.wk1	PC-ORD spreadsheet	all environmental and vascular plant variables, averaged at the transect level. Matrix = 119 variables X 18 transects.
envtcodes	MS Word '97	acronyms and descriptions for all 119 environmental and vascular plant variables. The contents of this file is displayed in Appendix D.