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Ceratodon Moss: Agent and Recipient of Ecosystem Engineering

by

Julius T. Csotonyi ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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Abstract

Bryophytes such as *Ceratodon purpureus* sometimes form biological crusts on the surface of soils. By creating and modifying this stable soil habitat they function as ecosystem engineers. On an erodible lakeshore soil in Jasper National Park, I assessed (1) this bryophyte's soil-stabilizing role, and (2) its response to ecosystem engineering by ungulates. A layer of moss reduced both water erosion and penetration of the soil by ungulate hooves but it also reduced the soil's infiltration rate. Second, this moss responded favourably to hoof prints and other microrelief generated by ungulate trampling because of the sheltered microhabitats that microrelief provides. While these beneficial effects are only present at low to moderate trampling intensity, they imply that the very agents of disturbance facilitate the recovery of the soil-stabilizing organism that they disturb.

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Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

Overview

Ecosystem engineering is the creation or modification of habitats by organisms that cause physical state changes in materials (Jones et al. 1994). This results in the modulation of resources to other organisms (Jones et al. 1994). For example, beavers create aquatic ecosystems by flooding tracts of forest using dams (Jones et al. 1994). In this way, they control the availability of nutrients and living space to other organisms. Organisms that facilitate soil accretion and mechanically stabilize the accumulated sediments accomplish this as well. Important groups of ecosystem engineers in the soil are communities of algae, cyanobacteria, fungi, lichens and bryophytes that consolidate the surface of the soil into a distinct hard layer, called a biological soil crust. Because they often colonize soils too dry or nutrient-poor for vascular plants to inhabit, biological soil crusts can be crucial stabilizers of erodible soils. Because they remain part of the soil structure that they create, they are considered autogenic ecosystem engineers (Jones et al. 1994). They may, however, simultaneously experience the activity of allogenic ecosystem engineers, organisms that are not an intrinsic part of the habitats they create or modify (Jones et al. 1994). For example, ungulates alter the distribution of light and moisture in the soil by creating microtopographic relief in the form of hoof prints. The poikilohydric organisms in biological soil crusts may respond strongly to the altered moisture regime created by ungulate trampling. This has important implications for their own performance as ecosystem engineers.

Bryophytes are an important component of many biological soil crusts. However, their radically different morphology and physiology implies that the ecological roles they play and their response to disturbance are often distinct from those of algae or lichens. It is therefore surprising that their ecology in a soil crust context has been addressed only tangentially (Evans and Johansen 1999). I studied the soil-stabilizing influence of the moss *Ceratodon purpureus* (Hedw.) Brid. in a successionally young environment in Jasper National Park, Alberta, and the response of this bryophyte to disturbance in the form of ungulate trampling.

This first chapter (1) reviews the ecological roles of biological soil crusts and their response to disturbance, framing this knowledge in the concept of ecosystem engineering (Jones et al. 1994) and (2) highlights the role of bryophytes in biological soil crusts. An introduction to ecosystem engineering and biological soil crust diversity sets the stage for analysis of both their impact on the soil environment, and their response to disturbance. I then introduce the system that my project focuses on.

Biological Soil Crusts

Biological soil crusts are soil surface complexes of organisms and the organic matter that they produce. The living component consists of nonvascular organisms from many taxonomic groups. These are cyanobacteria (Ali 1972, Ashley et al. 1985), heterotrophic bacteria (Steppe et al. 1996, Wheeler et al. 1993), free-living fungi (States and Christensen 2001, Went and Stark 1968), lichenized fungi (Eldridge 1996, Rogers and Lange 1971, St. Clair et al. 1993), algae (Ashley et al. 1985, Fritsch 1922, Grondin and Johansen 1993, Johansen et al. 1983) and bryophytes (Downing and Selkirk 1993, Eldridge and Tozer 1996, Seppelt and Green 1998). Small vascular plants such as the

Lycophyta (club mosses) are traditionally excluded from soil crusts. The nonliving component of biological soil crusts consists of organic byproducts such as polypeptides and polysaccharides that many fungi, lichens and bacteria secrete as protective mucilaginous sheaths (Campbell 1979). Together the living and nonliving components fix soil particles in place chemically and/or physically, forming the hardened layer of soil that gives this community its name (West 1990). This crust may be a few mm to several cm thick (Belnap et al. 2001). Because biological soil crusts typically occur in arid regions on loose Regosolic soils, the hardened upper layer that they create differs clearly from the less structured soil below. The soil structure that they create is a manifestation of their ecosystem engineering activity.

Ecosystem Engineering

Jones et al. (1994) coined the term "ecosystem engineering" to describe the creation or modification of habitats by one organism from another's perspective. Ecosystem engineers accomplish this by controlling the flow or availability of resources instead of contributing their biomass in more conventional trophic interactions. As a result, they may have disproportionately large influences on ecosystems for their body sizes or populations (Jones et al. 1997), and in this sense they are very similar to keystone species (Paine 1966). The oft-cited example is that of the beaver (*Castor canadensis*), which floods large tracts of land using strategically placed dams (Jones et al. 1997). The beaver's activity is an example of deliberate engineering, with strong feedback on its own fitness.

Many organisms, however, engineer the environment 'accidentally'. Ungulates, for example, generate hoof prints simply by walking. These hoof prints provide sheltered microhabitats that other organisms then colonize (West 1990). Ungulate trampling is referred to as allogenic engineering (Jones et al. 1994), because the engineer does not remain an integral part of the physical structure (the hoof print) that it creates. Autogenic engineers, on the other hand, contribute their own biomass (though not trophically) to the habitats that they create (Jones et al. 1994). Biological soil crust organisms are examples of autogenic ecosystem engineers. By growing throughout the soil surface, they add mechanical strength to it.

The notion that all organisms alter their environment to some extent may appear self-evident. However, the relative contribution of engineers is more significant in stressful environments (Bertness and Leonard 1997, Jones et al. 1997). Biological soil crust organisms, then, are prominent ecosystem engineers because they inhabit environments too harsh for most other forms of life to invade.

Adaptations for Survival: Prerequisites for Ecosystem Engineering

In order to alter an environment to create habitat space, a species must first survive there. The soil surface may be a particularly harsh environment because of large fluctuations in temperature and moisture, especially at small scales. Soil crust organisms have evolved a remarkable suite of characters to cope with the challenges of living in harsh conditions. Understanding how soil crust organisms respond to stressful environments is a useful prelude to discussion of their response to disturbance. Because the diversity of their adaptations parallels their taxonomic diversity, I discuss their adaptations on a taxon-by-taxon basis.

Biological soil crusts are not a taxonomic unit but a polyphyletic collection of organisms sharing similar habitat requirements and levels of climatic tolerance. They vary greatly in appearance depending on species composition. Their composition varies in response to soil temperature and composition, moisture content, radiation and disturbance (Belnap et al. 2001, St. Clair et al. 1993), reflecting a gradient of tolerance among the taxa, which is expressed in the order in which they colonize bare ground. Open spaces are usually pioneered by algae and cyanobacteria, followed by lichens and finally by bryophytes (West 1990).

Eukaryotic Algae

Microorganisms are usually the first colonists of newly exposed ground. Eukaryotes such as green algae (Chlorophyceae), golden-brown algae (Xanthophyceae) and diatoms (Bacilliariophyceae) are especially common under slightly acidic soil conditions (Johansen et al. 1983, Rayburn et al. 1982). Algae cope with moisture stress either by maintaining a high cytoplasmic solute concentration to resist desiccation or by tolerating cellular desiccation (Fritsch 1922). They include some taxa least sensitive to high soil temperatures (Johansen and Rushforth 1985). However, because algae are inconspicuous on the soil surface and require microscopic observation or culturing to detect, they have received very little attention (Johansen 1993).

Cyanobacteria

Heterotrophic bacteria, while present in soil crusts, are comparatively little studied (but see Wheeler et al. 1993). On the other hand, the bulk of research on biological soil crusts has usually focused on cyanobacteria. Cyanobacteria are abundant in calcium-rich, basic soils worldwide (Belnap et al. 2001) and are among the hardiest phototrophic organisms on earth. Cyanobacteria were the first organisms observed to colonize the bare volcanic island of Surtsey (Brock 1973). Most soil crust cyanobacteria secrete sheaths containing hydrophilic polysaccharides and proteins that slow dehydration and prolong metabolism between brief rains (Campbell 1979, Ladyman and Muldavin 1996, Shields and Durrell 1964). The sheath may be heavily pigmented to protect against ultraviolet radiation, to which they are exposed on the soil surface (Belnap et al. 2001). Species lacking photochemical protection are often motile, escaping damage by retreating below the surface during drought (Garcia-Pichel and Pringault 2001). Their motility also allows them to escape inundation by aeolian sediment, resulting in a gradual subterranean buildup of abandoned sheaths.

Non-lichenized fungi

While Schulten (1985) attributed the comparative absence of non-lichenized fungi in Iowa's sandy prairie soils to low soil nutrient status, States and Christensen (2001) turned up numerous microfungi in desert grasslands of Utah and Wyoming, especially in association with other biological soil crust taxa. Went and Stark (1968) found mycelial mats nutritionally supported by leaf litter of *Prosopis* shrubs on sand dunes near Death Valley. Although their filamentous hyphae suggest soil-stabilizing capabilities, their functional roles in biological soil crusts are relatively poorly known and await further research.

Lichens

Once stabilized by cyanobacteria, soil is often colonized by lichens, which may enhance the microtopography of the surface (Johansen 1993), endowing it with mounds up to 15 cm wide and 7 cm tall on the Colorado Plateau (George et al. 2000). Lichens are more sensitive to climatic and edaphic factors than cyanobacteria, but some are highly resistant to heat and drought (Rogers 1977), capable of maintaining net carbon gain at temperatures of 31°C (Nash et al. 1982). These symbiotic organisms often harbour cyanobacteria within their thalli, which fix atmospheric nitrogen, allowing lichens to inhabit low nutrient environments (Rychert and Skujins 1974).

Bryophytes

Bryophytes are the only plant members of biological soil crusts. Unlike vascular plants, most mosses are poikilohydric, i.e. their cellular water content approaches thermodynamic equilibrium with their environment (Vitt 1989). This led to the idea that bryophytes require a constant supply of external water to survive, a view that is currently changing (Vitt 1990). Most bryophytes can tolerate periods of drought (Vitt 1990). However, their coping strategy is fundamentally different from that of vascular plants. Mosses accomplish physiologically what vascular plants do by morphological means (Vitt 1990). Vascular plants maintain cell turgor and physiological activity even under dry conditions by tapping into long-lasting subterranean water with their roots (Raven et al. 1992). Transpiration and water conduction ensure a steady supply of water to tissues while multiple layers of leaf and stem cells and a waxy cuticle inhibit unnecessary water loss. This endohydric strategy grants vascular plants desiccation *avoidance* (Vitt 1989).

Mosses, in contrast, are desiccation *tolerant* (Vitt 1989), like cyanobacteria and algae. Their rhizoids function mainly to secure them to the soil, and they exchange moisture with the environment through stems and leaves (Frahm et al. 2000). They rehydrate and resume photosynthesis very quickly (Proctor and Smirnoff 2000), and therefore to exploit environments in which precipitation is brief and sporadic (Ladyman and Muldavin 1996). However, rapid uptake of water also means rapid water loss as the environment dries. Their cells soon lose turgidity, requiring mosses to endure desiccation at the cellular level without injury. Some species, such as *Ceratodon purpureus*, concentrate sugars such as sucrose in their cells to maintain cell membrane integrity during desiccation (Robinson et al. 2000).

Their morphology, however, buffers mosses from swings in moisture content. Soil crust bryophytes are short and mat-like, presenting a low evaporative surface area to the atmosphere. Furthermore, their habit of growing in dense cushions creates an aerodynamically smooth surface to the wind, reducing turbulence and thus evaporative water loss (Proctor 2000). Hair-like leaf tips in some taxa extend this boundary layer of dead air (Proctor 2000). These adaptations allow mosses to maintain high humidity among their stems and therefore remain physiologically active even in arid environments, where their habitat modification roles are crucially important.

Ecological Roles of Biological Soil Crusts: Mechanisms of Ecosystem Engineering

The advantage of their poikilohydric lifestyle in stressful environments allows biological soil crusts to account for up 70 percent of living cover (Belnap et al. 2001). This extensive growth has a significant impact on the soil environment. Reflecting their taxonomic diversity, the mechanisms by which these organisms engineer their environment are equally diverse and taxon dependent. They range from stabilization and accumulation of soil, to altered hydrology, nutrient status and temperature regimes.

Soil Stabilization

The most consistent effect of biological soil crusts on their environment is consolidation of the soil and protection from wind and water erosion. This is especially important in deserts, where vascular plant cover is sparse, and where unprotected soil is subjected to torrential rainstorms that result in severe gulley erosion (Thornes 1994, Williams et al. 1995). Soil crusts protect the soil by two major mechanisms: particle fixation and surface shielding (Harper and Marble 1988).

Particle fixation is the mechanical or chemical entrapment of soil particles (Malam Issa et al. 2001, Zhigang et al. 1996). Mosses bind particles mechanically by entangling them in their rhizoids and filamentous immature phase (Lange et al. 1992, Schulten 1985). Lichens and fungi not only entwine particles among their hyphae, but they also secrete adhesive extracellular polysaccharides and polypeptides to fix particles chemically (Schulten 1985). Prokaryotic and eukaryotic algae are superior soil stabilizers because their thick polysaccharide-rich mucilaginous sheaths chemically adhere to soil particles and persist long after their inhabitants have left (Anderson and Rushforth 1976), gluing together even coarse sand grains more than a millimeter in diameter (Belnap and Gardner 1993).

However, the ability to shield the surface against raindrop bombardment may give moss- and lichen-dominated soil crusts the overall edge in soil stabilization (Eldridge and Kinnell 1997) because raindrops deliver 8 to 25 times as much erosive energy as surface flow (West 1990). In mosses, rehydration expands the exposed leaf area, and therefore the size of the protective shield above the soil (Eldridge and Kinnell 1997). Their stem flexibility also makes mosses effective barriers because raindrop energy is presumably absorbed upon bending.

Soil Accretion

In addition to stabilizing existing soil, biological soil crusts accrete more airborne and waterborne sediment, of which up to 30 percent may be organic material (Mamane et al. 1982). They accomplish this by disrupting air or water currents. The higher the surface area exposed, the more effectively they capture sediment (Shachack and Lovett 1998). Undulating crusts of cyanobacteria and lichens may detain runoff water in small depressions, allowing soil particles to settle out (Brotherson and Rushforth 1983). However, much sediment in arid regions is delivered by wind. Mosses, with a high leaf area index (Simon 1987), are most effective at trapping sediment among their stems (Danin and Ganor 1991, Watt 1938). The rapid growth of species such as *Ceratodon purpureus* after burial by sand (Forbes 1995, Martinez and Maun 1999) further increases the rate of sediment accretion by continually regenerating the rough surface/air interface.

Soil Hydrology

The infiltration of water into the soil is important for two reasons: it influences (1) the amount of soil water available to soil crust organisms and vascular plants, and (2) the likelihood that erosive runoff will occur. The net influence of biological soil crusts on hydrology is a function of soil crust composition and microtopography.

Influence of Biological Soil Crust Composition on Hydrology

The taxonomic composition of the crust plays a major role in influencing the infiltration rate of the soil. Cyanobacterial soil crusts seal the soil because their polysaccharide sheaths may expand in volume up to thirteen-fold upon wetting (Shields and Durrell 1964). However, once the surface is sealed, evaporation may be inhibited for the same reason (Brotherson and Rushforth 1983). Fungi may either reduce infiltration by secreting hydrophobic exudates (Williams et al. 1995), or increase it by mechanically holding soil pores open with their hyphae (Eldridge 1993). Effects are likely species- and site-specific (Belnap et al. 2001). Mosses imbibe water rapidly, for which they have been compared to sponges (Brotherson and Rushforth 1983). However, much of this imbibed water may not reach the soil beneath, partly because the silt and clay that they accumulate impedes infiltration (Brotherson and Rushforth 1983), and partly because they detain water in capillary spaces on and between their leaves and stems (Proctor 2000).

Influence of Microtopography on Hydrology

Microtopography, or the roughness of the soil surface, is probably the most important factor governing moisture content of soil beneath biological soil crusts, overriding taxonomic effects. Soil crusts may contain mounds up to 7 cm high (George et al. 2000), which cause water to pool (West 1990), increasing the time available for it to enter the soil (Harper and Marble 1988). This effect compensates for the fact that cyanobacteria slow infiltration by sealing the soil surface.

Soil Nutrient Status

The impact of biological soil crusts on soil nutrient status is dependent on the dominant taxa of the crust. While soil crust organisms fix much carbon, nitrogen usually limits primary production in arid environments (Belnap et al. 2001). A large body of literature addresses nitrogen fixation by cyanobacteria in soil crusts (Evans and Belnap 1999, Evans and Ehleringer 1993, Reddy and Giddens 1975, Rychert and Skujins 1974, West and Skujins 1977 and many others). Cyanobacteria and lichens may contribute 75 to 90 percent to the annual pool of fixed nitrogen in deserts (Belnap et al. 2001, Harper and Marble 1988). They are responsible for practically all the nitrogen fixed in some polar deserts (Gold and Bliss 1995). Furthermore, their sticky sheaths attract ionic nutrients by chemically adhering to negatively charged silt and clay particles (Pallis et al. 1990).

The enormous surface area of bryophytes makes them potent nutrient interceptors (Eckstein 2000). Bryophytes even intercept nutrients that leak through cyanobacterial and algal membranes that are compromised during desiccation (Schofield 1985). They also retain these resources effectively (Svensson 1995), so efflux of nutrients from mosses is very small (Eckstein 2000).

This does not mean that bryophytes do not contribute to soil nutrition at all, however. First, mosses trap fine soil particles, which may carry nutrients such as nitrogen (Pallis et al. 1990). Second, their leaves provide colonization sites for nitrogen fixing bacteria (Snyder and Wullstein 1973). Third, while their litter has a high C:N ratio, their relative carbon contribution is important in nutritionally poor arctic ecosystems (Gold and Bliss 1995, Sharrat 1997), where primary production by moss-sedge mires is up to 140 times greater than that of surrounding barren lands (Gold and Bliss 1995).

Soil Temperature

Pigments such as carotenoids and anthocyanins make many biological soil crusts darker than the substrate on which they grow (Lewis Smith 1999). This low albedo can increase soil temperature up to 44°C even in Antarctica (Lewis Smith 1999). This is particularly important because nitrogen fixation is temperature limited (Coxson and Kershaw 1983). On the other hand, the low thermal conductivity of peat may insulate the permafrost beneath mosses, preventing it from melting in the summer (Hinzman et al. 1991).

With few exceptions, the net effect of biological soil crusts on the soil environment is therefore generally positive for soil hydrology, nutrient status, temperature regime, accretion and especially stability. Biological soil crust organisms are smaller than vascular plants, but in stressful environments it takes little effort to increase habitability significantly (Bertness and Leonard 1997). However, in fragile ecosystems, it also takes little effort to cause damage, and not all ecosystem engineers have positive effects (Jones et al. 1997).

Trampled Biological Soil Crusts: Response to Ecosystem Engineering

Allogenic Ecosystem Engineering by Animals: Disturbance

While biological soil crusts increase soil stability, animals usually engineer their environment via disturbance. Sessile organisms are more likely to provide structure and living space as they grow. Trees and oysters are good examples of this (Edwards et al. 1999, Lenihan and Peterson 1998). Most animals, however, are motile. This allows them to rearrange the structure of their habitat over very short time. Prairie dogs (*Cynomys ludovicianus*), for instance, move tremendous amounts of soil by digging burrows (Ceballos et al. 1999). This activity may destroy one habitat while creating another because slow growing sessile species may not react quickly enough to adjust to altered environmental conditions. Trampling by ungulates and humans crushes soil crust organisms.

Response of Biological Soil Crusts to Mechanical Disturbance

Biological soil crusts are most widespread in ecosystems that evolved in the absence of frequent or intense soil disturbance (Belnap et al. 2001). Most research demonstrates that the net effect of trampling on biological soil crusts is negative (Evans and Johansen 1999). Trampling pulverizes the soil (Butler 1995) and loosens soil crust organisms, making them vulnerable to erosion (Belnap et al. 2001). Cole (1990) reports that human trampling immediately obliterated algal and lichen mounds in Grand Canyon National Park.

Biological soil crusts often require decades to recover from trampling. Algae, the quickest to recover, still take 1 to 5 years to reach pre-disturbance cell densities (Anderson et al. 1982). Even then, the crust does not yet posses the mature mounded structure that causes water to pool (Johansen 1993). Lichens may take 10 to 20 years to recover (Johansen 1993). Worst of all, Belnap (1993) estimates that without inoculant application, mosses in the American southwest require over 250 years to reestablish. This conclusion, however, is conditional on both climate and the trampling regime.

Influence of Climate on Soil Crust Recovery

Most studies on the response of biological soil crusts to disturbance are done in the stressful, arid climate of the southwest United States (e.g., Anderson et al. 1982, Kleiner and Harper 1972, Jeffries and Klopatek 1987, Johansen and St. Clair 1986). Here the impact of trampling may be especially severe because lichens and mosses may barely balance respiratory carbon losses with photosynthetic carbon gains (Evenari 1985). In mosses and lichens, rehydration causes re-initiated of respiration *before* photosynthesis (Evans and Johansen 1999), leading to a temporary loss of carbon after rewetting. If they dry before balancing their carbon budget, they experience a net loss of carbon. Therefore, below a critical frequency or duration, rains may actually damage or kill soil crusts by depriving them of carbon (Belnap et al. 2001). Soil crusts in mesic higher latitudes should respond less negatively to disturbance. A change in the dominant soil crust species may also accompany increase in latitude. Weedy species that more efficiently capitalize on increased moisture and nutrient regimes of higher latitudes increase in prevalence.

Influence of Trampling Regime on Soil Crust Recovery

Variation in the trampling regime, i.e. the distribution and intensity of trampling, may reduce or even reverse the negative impact of herbivores on crusts. Savory (1988) notes that when animals confine their movements to well-used game trails they cause less damage to soil crusts than when they spread out in herds (Savory 1988). The effects of trampling intensity are similarly straightforward; more animals cause worse damage. In Utah and Arizona, biological soil crust covered 21% of the land on an ungrazed site, but only 12% on lightly grazed soil, and as little as 7% on a heavily grazed site (Jeffries and Klopatek 1987).

Perhaps most important to the recovery of soil crust biota, but least studied (Butler 1995), are the microclimatic effects of microtopography caused by hoof prints. Microtopography enhances microclimatic heterogeneity (Alpert 1991). Mosses respond positively to microhabitats where they are shaded from desiccation (Alpert 1982, 1985, 1991). Hence they should benefit from ecosystem engineering that increases structural complexity. Hoof prints also accumulate water from runoff (Ross, 1995) much like the depressions between the mounds of undulating soil crusts, leading to colonization of hoof prints by algae (West 1990). Similarly, lichen reestablishment may be 20 times quicker on sites with shade than in locations exposed to direct sun (Belnap et al. 2001).

However, persistence of hoof prints depends on soil texture. In sandy soils, hoof prints do not persist for long, probably because of the soil's lower moisture capacity (Belnap et al. 2001), and therefore its inability to preserve form. Coarse soil texture may therefore inhibit the positive effects of trampling because of the quick reversion of microtopography to a flat surface. Soil crusts are usually studied on sandy soils, with sand contents of up to 87 to 99 percent (Jeffries and Klopatek 1987). This may explain the consistently negative response of biological soil crusts to trampling in these studies. In regions with finer soils trampling may benefit soil crust organisms, or at least it may reduce some of its own negative effects, by creating microtopography that shelters the plants from desiccation.

Research Questions and Study System

Alpert (1991) has investigated the positive influence of microtopography on moss growth in the absence of disturbance. Others have examined the negative impact of disturbance on biological soil crust bryophytes (e.g. Belnap 1993). What is missing is an investigation of how microtopography generated by trampling influences the recovery of moss soil crusts in an environment in which we expect to see positive ecosystem engineering effects of trampling. I studied the response of the moss *Ceratodon purpureus* to ungulate trampling on silt-rich soils in Jasper National Park, Alberta. This moss forms extensive crusts on the fragile soils of this ecosystem. Because these soils are heavily exposed to the erosive agents of wind, water and ungulate trampling, I also investigated the role of this moss in soil stabilization.

Ceratodon purpureus is a mat forming acrocarpous moss with a worldwide distribution, from the high Arctic (Schofield 1985) to as far south as 83°S in Antarctica (Seppelt and Green 1998). This bryophyte is commonly reported from recently disturbed sites (Vitt et al 1988) and has many adaptations for survival in stressful environments. In continental Antarctica, *C. purpureus* is one of the most drought-tolerant mosses (Robinson et al. 2000). It also possesses red pigments that shield it from ultraviolet radiation (Lewis Smith 1999). *Ceratodon purpureus* is very tolerant of toxic soils (Jules and Shaw 1994) and it is known as a "fire moss" for its habit of invading recently burned sites containing ash that is high in alkaline chemicals (Bates 2000). *Ceratodon purpureus* is also commonly found on sand dunes, where it responds to constant sand burial by rapid vertical growth, emerging from under seven times its own height in sand (Martinez and Maun 1999).

Some of these characteristics also predispose the moss to mechanically stabilizing the silt loam soils of the Jasper Lakeshore where I conducted this study. In this ecosystem aeolian sediment is deposited from the periodically exposed bed of Jasper Lake. The resulting calcareous soils are subject to wind and water erosion, as they are sparsely vegetated (Holland and Coen 1982). Due to its low winter snow cover, this area is heavily used by ungulates for winter forage (Holroyd and van Tighem 1983), so it experiences heavy trampling, with which *C. purpureus* must also contend.

In this study I examine two questions on the involvement of *C. purpureus* in ecosystem engineering. In Chapter 2, I evaluate the role of this moss as a soil-stabilizer. Specifically, I address the hypotheses that a crust of *C. purpureus* (1) increases the resistance of the soil to penetration, (2) reduces water erosion from the surface of soils, but (3) impedes the infiltration of water into the soil below. This bryophyte's response to sediment burial should create thick crusts that impose structure on the soil, especially important because of the intensity of trampling at this site (Dekker and Bradford 2000). However, its efficiency in accreting windblown sediment may create a layer of silt and clay among its stems that inhibits infiltration of water (Blackburn 1975). A substantial reduction in infiltration capacity may lead to the production of erosive runoff during rainstorms.

In Chapter 3, I investigate how *C. purpureus* responds to ungulate trampling, a form of allogenic ecosystem engineering. My study is unique in that it examines this response at a regional scale, and at the scale of individual hoof prints and moss plants. Microtopography generated by trampling should have a beneficial influence on the growth of this bryophyte at low trampling intensity by sheltering the moss from desiccation. This beneficial effect of microtopography should buffer the moss against trampling damage when trampling intensity and frequency is low.

Finally, in Chapter 4, I review my findings and suggest avenues for future research in each area that I examined. I conclude by discussing the contribution of each ecosystem engineer to this unique system. Very few studies have addressed the question of how the activity of one ecosystem engineer impacts another. Answering this question is relevant to an understanding of ecosystem functioning. The impact of ecosystem engineers may be unexpectedly large since they do not partake in resource flows but only control them (Jones et al. 1997). The cumulative impact of two or more *interacting* engineers on the ecosystem may therefore be multiplicative instead of additive.

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Chapter 2

Soil Stabilization by *Ceratodon purpureus*

Abstract

On fragile soils, biological soil crusts of bryophytes such as *Ceratodon purpureus* (Hedw.) Brid. may be relatively important ecosystem engineers, protecting the soil from erosion and mechanical damage. I investigated three ways in which the moss *Ceratodon purpureus* contributes to soil stability near the shore of Jasper Lake in Jasper National Park, Alberta. First, I measured how effectively the moss resists mechanical damage by ungulate trampling. Soil crusts of *Ceratodon purpureus* are ten times stronger than bare soil and three times stronger than lichen crusts, making them theoretically capable of supporting the weight of an adult elk without breaking. Second, I compared erosive sediment loss from moss-crusted and uncrusted soil under flowing water. Erosion was 15 times lower on moss-covered plots than on unprotected soil. Finally, I measured the infiltration rate of moss crust to assess the likelihood that *C. purpureus* would induce erosive runoff under heavy rainfall. Although moss reduced the infiltration rate of water into the soil, runoff is unlikely to occur because the infiltration rate is still high. I conclude that *C. purpureus* adds to the stability of the soil at Jasper Lake, and may therefore facilitate vascular plant community establishment.

Introduction

Biological soil crusts significantly alter the soil surface environment that they share with vascular plants. Most consistently, these ecosystem engineers (Jones et al. 1994) impose physical structure on the soil. A growing body of research addresses small-scale soil structure because of its implications for processes such as the movement of water and air through the soil, the creation of living space for microbes and therefore the availability of nutrients to plants (Hartge and Stewart 1995).

The creation of soil structure is highly beneficial in loose, erodible soils, and where processes such as trampling mechanically disturb the soil. Soil crusts with a bryophytic component are especially effective soil stabilizers because of the complex, raised stems of mosses. Studies of soil stabilization by soil crust bryophytes have been conducted in two ecological zones, low latitude deserts and high latitude ecosystems, with the former claiming the most attention. Soil crust bryophytes in temperate regions are rarely studied. Bryophytes have distinct roles in each region they inhabit depending on the climatic characteristics that dominate.

Soil Stabilization by Low Latitude Bryophytes

Most work on soil crust bryophytes comes from arid regions such as the southwest United States, the Middle East or Australia (Evans and Johansen 1999) because this is where the functional importance of soil crusts was first realized (e.g. Booth 1941). The bryophytes of these areas include desiccation-tolerant mosses such as *Tortula* and *Bryum* (Scott 1982, Downing and Selkirk 1993). Sporadic but intense rainstorms that generate much erosive runoff often dominate the climate of deserts. Therefore, stems and rhizoids of desert mosses are important in reducing erosion by physically holding soil particles in place (Schofield 1985, Schulten 1985). Highly absorbent mosses such as *Tortula* also soak up the infrequent rainfall like sponges and thus reduce runoff (Brotherson and Rushforth 1983). This simultaneously curbs erosion and increases the availability of water at the soil surface, important to germinating seedlings. Also, the geometrically complex stems and leaves of bryophytes effectively reduce the flow of air or water passing over them (Proctor 2000), making moss crusts efficient traps for airborne and waterborne sediment (Danin and Ganor 1991). However, it also results in the accumulation of silt and clay near the surface of the soil (Brotherson and Rushforth 1983). Clay swells when moistened and impedes passage of water through it, increasing the potential for soil loss by runoff water.

Soil Stabilization by High Latitude Bryophytes

Despite their impressive tolerance to desiccation, bryophytes are comparatively infrequent in deserts. They increase in abundance with latitude, approaching or exceeding the productivity of vascular plants because of cooler summer temperatures (Alpert and Oechel 1984, Longton 1988). Here, soil stability is threatened by freeze-thaw cycles that cause frost heaving, killing vascular plants by uprooting them (Gold and Bliss 1995). Biological soil crusts composed partly of mosses such as *Tortula* and *Hypnum* help to stabilize soils against such cryoturbation (Bliss and Gold 1999). Unfortunately, high latitudes pose logistic problems to research, so knowledge about bryophyte soil crusts in these regions is limited.

We are therefore faced with a situation where, on the one hand, mosses are comparatively rare in the highly arid parts of the world where soil crust research is concentrated. On the other hand, the high latitudes in which mosses are abundant are only beginning to see soil crust research because of difficulty of access. Furthermore, temperate ecosystems between these two extremes are rarely studied from a biological soil crust standpoint because stressful soil conditions are comparatively rare, and a line distinguishing moss soil crusts from simply thick moss carpets in productive regions becomes difficult to draw.

Even in these mesic intermediate latitudes, however, there are isolated ecosystems that resemble one of the extremes and present a unique opportunity to study ecosystem engineering by bryophytes where it is otherwise rare. An example is Jasper National Park, which contains geomorphologically active valley ecosystems resembling arid southern deserts, complete with active sand dunes (Holland and Coen 1982). The loose soil is colonized by bryophytes such as *Ceratodon purpureus*.

Objectives

In this chapter I investigate the mechanical stability provided by the moss *Ceratodon purpureus* to Regosolic soil in an aeolian lakeside ecosystem in Jasper National Park, Alberta. Specifically, I evaluated (1) the ability of *C. purpureus* to generate greater shear strength against trampling than lichen crust or bare sediment, (2) protection from water erosion that *C. purpureus* provides to the soil and (3) the influence of *C. purpureus* on the infiltration rate of water into the soil. I hypothesized that the crust formed by *C. purpureus* significantly increases the soil's resistance to both erosion and mechanical disturbance by ungulate trampling. However, the stems of *C. purpureus* should also increase the bryophyte's ability to accumulate silt and clay and *C. purpureus* should therefore reduce the infiltration rate of water.

Methods

Study Site

My study was located along a 1 km long section of the northeast shore of Jasper Lake, Jasper National Park, Alberta, at 53°06'15"N latitude and 117°59'30"W longitude and an altitude of 1300 m. It is part of the unique Devona 1 Ecosite between Jasper Lake and Talbot Lake, characterized by a ridged landform composed of calcareous aeolian material deposited from material originating on the floor of Jasper Lake (Holland and Coen 1982). Jasper Lake is a widening of the Athabasca River that experiences annual cycles of flooding and exposure. During the winter and spring, winds funneled down the Athabasca River valley remove sediment from the exposed floodplain and deposit it along the northeastern shore of Jasper Lake, creating sand dunes (Holland and Coen 1982). Leeward of this geomorphologically active zone, finer material is deposited, generating the Orthic Regosolic soil of the Devona 1 Ecosite (Holland and Coen 1982). This soil is categorized as an extremely calcareous silt loam with a pH of 7 to 8 (Holland and Coen 1982).

The plant community is shrubby grassland dominated by creeping juniper (*Juniperus horizontalis*), wheatgrass (*Agropyron inerme*) and sedge (*Carex scirpoidea*) interspersed with stands of white spruce (*Picea glauca*) (Holland and Coen 1982). The open alkaline soil also bears an extensive cryptogamic community indicative of lime-rich soils (Belnap et al. 2001), including the lichens *Psora*, *Squamarina*, *Fulgensia* and *Toninia*. Bryophytes are also common, particularly the genera *Bryum*, *Barbula* and *Ceratodon*.

The locally abundant *Ceratodon purpureus* is commonly reported from recently disturbed sites (Vitt et al 1988). Its high tolerance of both desiccation (Robinson et al. 2000), and toxic soils (Jules and Shaw 1994) makes *C. purpureus* a successful a colonist of harsh environments. At Jasper Lake, *C. purpureus* typically forms crusts that range in thickness from less than 1 cm to more than 2 cm (Figure 2.1).

Because of the dry, windy climate, the Jasper Lake vicinity is comparatively snow-free during winter (Holland and Coen 1982). The resulting availability of winter forage attracts ungulates such as elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*). Their abundance and large mass threaten the mechanical stability of the soil.

Penetrability

In September 1999 I compared how well soil crusts composed of *C. purpureus*, the lichen *Toninia* and a physical rain crust protect the soil by resisting mechanical penetration. Physical crusts result from rearrangement of fine particles on the ground surface after dislodgment by rain (Bradford and Huang 1992). I measured the force required to break through to loose sediment beneath using a Humboldt H-4200 pocket soil penetrometer. I haphazardly selected 20 interspersed replicates of each surface type. For *C. purpureus*, I took care to select plots with uniformly dense cover. While I attempted to minimize the distance between treatments, guaranteeing uniformity in density meant sacrificing some proximity. For each measurement I pressed down on the penetrometer with even pressure until the soil surface broke and gave way to the easily penetrable soil below. Analysis consisted of a Kruskal-Wallis test followed by a Dunnett's T3 multiple comparison test.

Erosion

I compared the amount of surface sediment vulnerable to mobilization by flowing water on moss-crusted and physical-crusted soils in May 2001. Fresh aeolian sediment is most abundant at this time of the year as Jasper Lake nears the end of its winter/spring exposure to the wind. It is at this season therefore, that surface sediment is most vulnerable to mobilization by raindrops and subsequent entrainment by wind or water. Consequently, the stabilizing action of moss stems is most crucial at this time.

I measured erosion from 19 haphazardly selected pairs of moss-crusted and physical-crusted surfaces. Each replicate consisted of a pair of measurements on soil plots separated by no more than 2 m. I designed an apparatus to capture and channel runoff water away from a 5 x 5 cm plot of soil into a collection bag. It consisted of an aluminum plate bent into the shape of an open square tube with three sides. For each plot I drove this instrument into the soil to a depth of about 5 cm into the soil, taking care to minimize disturbance of the soil on entry. I then poured 120 mL of water onto the soil from a height of 20 cm. Just under half of the applied water was absorbed by the soil; the rest generated runoff. The aluminum barrier channeled this runoff water and its sediment load into a plastic water collection bag, with its open end placed flush with the edge of the soil in a pit excavated next to the soil plot. I double-bagged each sample to prevent leaks.

The advantages of this water pouring approach over a simulated rainfall technique, such as one used by Williams et al. (1995), are (1) minimal loss of water to infiltration, and therefore copious runoff for delivery of the loosened sediment into a collection chamber; (2) rapidity of execution; and (3) simplicity of the experimental apparatus. Because it also generates turbulent flowing water, this method allowed me to evaluate the protective capacity of the moss crust under the most severe weather conditions, when the need for protection is most crucial.

In the lab, I weighed, air-dried and reweighed samples to determine the mass of runoff water collected. After removing plant litter I measured the mass of remaining sediment. Using the volume of runoff water collected and the mass of sediment suspended in it, I calculated the sediment yield, or the concentration of sediment in runoff water from 25 cm^2 of substratum. Analysis consisted of a Wilcoxon signed ranks test on sediment yield.

Infiltration

To determine how moss crust influences the infiltration rate of water into the soil I measured the infiltration rates on moss-crusted and scalped soil in September 1999. To prepare scalped surfaces I removed existing moss crust from these treatments instead of selecting previously bare soil to avoid confounding the results with differences in soil characteristics induced by the presence or absence of moss crust over an extended period.

My methods were similar to those of Brotherson and Rushforth (1983). I created a ring infiltrometer by removing the ends of a 6.5 x 11.5 cm can and driving the lower 2 cm into the soil. For 25 pairs of moss-crusted and scalped replicates I poured 40 mL of water into the cylinder and timed the absorption of standing water. This allowed me to calculate the maximum infiltration rate:

$$\text{Maximum infiltration rate} = 40\ \text{mL} / (\text{Infiltration time})$$

I compared maximum infiltration rate of crusted versus uncrusted soil with a Wilcoxon signed ranks test.

Results

Penetrability

Crusts of *C. purpureus* provided three times as much protection against mechanical breakage as *Toninia* lichen crusts did (Figure 2.2). Physical soil crusts were only one-fourteenth as strong as moss crusts (Figure 2.2). Furthermore, when a dry lichen crust or physical soil crust broke, it did so without compressing first; it was brittle. Moss crust compressed before it broke, making exposure of sediment less likely.

Erosion

On physical soil crusts, water mobilized 15 times as much sediment as on moss-encrusted surfaces (Figure 2.3). The relationship between the volume of runoff produced and sediment yield was also different between moss-crusted and physical-crusted surfaces. While sediment yield did not depend on runoff volume for physical soil crusts (Figure 2.4a), it increased linearly for moss soil crusts (Figure 2.4b). Regression predicts that if less than 27 mL of runoff water is generated on 25 cm^2 of moss-covered soil, it will remove no sediment from the surface (Figure 2.4a).

Infiltration

Scalping soil decreased the time required for infiltration of 40 mL of water from 107 seconds to 40 seconds (Figure 2.5a). This increased the infiltration rate of water by a factor of 1.5 for scalped plots compared to moss-crusted plots (Figure 2.5b).

Discussion

In this chapter, I demonstrate three important ecosystem engineering roles of the moss *Ceratodon purpureus* in the mechanical stability of aeolian Regosolic soils of the Athabasca River Valley. First, the closely packed stems of *C. purpureus* significantly increased the surface strength of the soil over that of bare sediment or lichen soil crust, shielding the surface against trampling damage by ungulates. Second, crusts of *C. purpureus* reduced rates of erosion from that experienced by bare sediment with only physical crusts. Potentially stable sites are thus created on this geomorphologically dynamic landscape, possibly accelerating vascular plant establishment. Third, *C. purpureus* reduced the infiltration rate of water into the soil, which may lead to the generation of erosive runoff water and may influence the moisture status of other plants.

Penetrability

Populations of large ungulates such as elk (*Cervus elaphus*) are highest in the montane ecoregion of Jasper National Park, the smallest of the park's three ecoregions (Holroyd and Van Tighem 1983). Within the montane ecoregion, much winter ungulate traffic is concentrated into the small strip of aeolian landscape on which my study took place. Currently, two herds of 40 elk frequent the Jasper Lakeside ecosystem (Dekker and Bradford 2000), although up to 173 animals can occur at this location at any given time (W. Bradford, personal communication). Large ungulates disturb the soil surface as they walk because their weight is distributed over a very small area of hard, sharp hoof surface. In a region where removal of vegetation results in significant erosion (Holland and Coen 1982), some form of protection against exposure of the fragile sediments is crucial to the stability of the soil. As my results show, crusts of the moss *C. purpureus* provide the potential for such mechanical protection.

Ceratodon purpureus provided three times as much protection against penetration as crusts composed mainly of the lichen *Toninia*, and 14 times as much protection as bare sediment covered by a physical soil crust (Figure 2.2). Hoof prints at Jasper Lake have a surface area of 51.7 ± 1.6 cm^2. Since the maximum pressure exerted on the soil occurs when three feet are on the ground, an animal weighing only 33 ± 8 kg could break the physical crust on a bare sediment surface (ignoring allometric relationships of hoof area to body weight). A bull elk's weight is an order of magnitude greater then this, at 320 to 350 kg, while cow elk weigh 200 to 250 kg (Gadd 1995). Therefore, physical crusts do not provide sufficient protection against penetration by elk hooves. Even lichen crusts of *Toninia*, which can withstand the weight of a hypothetical animal weighing up to 112 ±

12 kg, would break under the strain. A dense growth of *Ceratodon purpureus*, on the other hand, should resist penetration by the hoof of an animal weighing 337 ± 26 kg, potentially protecting the soil from the trampling of even large individuals. Naturally, forces exerted during running are considerably greater, but elk are rarely seen running.

Erosion

The soil near the shore of Jasper Lake is also disturbed by the action of wind and water. Rain, possessing up to 25 times as much erosive energy per drop as overland flow (Wood et al. 1987), is probably the most important agent of particle detachment here. Detention of soil particles not only prevents sediment loss at the site of erosion, but probably also reduces erosion downwind from the impact of detached and saltating sediment grains (Briggs et al. 1993). Even under conditions resembling a torrential downpour, with generation of runoff, my results indicate that a mat of *C. purpureus* reduces the vulnerability of sediment to detachment and entrainment by a factor of 15. This agrees well with values of 15 and 20 reported for biological soil crusts in southwestern deserts with a large cyanobacterial component (Booth 1941, Harper and Marble 1988).

Mosses limit sediment availability to erosion in three ways. First, moss rhizoids and stems physically entangle particles (Schulten 1985), increasing their frictional resistance to motion. Second, the roughness of moss stems extending above the ground slow the flow of air within the moss canopy (Proctor 2000). Hence, wind does not even reach sediment particles. Third, the leaves of many mosses, closely appressed to the stem while dry to minimize water loss, quickly extend outward upon rehydration (Scott 1982).

This umbrella of foliage intercepts and absorbs the erosive energy of raindrops before they hit the sediment (Eldridge and Kinnell 1997, Eldridge and Tozer 1996, Scott 1982).

Although there was probably not enough time during water delivery for *C. purpureus* to reduce erosion by expansion of its leaves, my results suggest that its closely packed stems do entrap particles and slow the flow of water through the canopy. On moss crust, sediment concentration decreased with the volume, and therefore with the kinetic energy, of the runoff generated. Moreover, regression predicts that below a critical volume of runoff, no sediment is liberated at all (Figure 2.4b). Therefore, even if runoff occurs during rainstorms, significant erosion from moss-crusted soils should only occur during particularly intense storms. In contrast, unprotected surfaces liberated about ten times as much sediment. Although physical soil crusts may protect the surface by "armoring" it (Miller and Radcliffe 1992), physical soil crusts at my study site were weak. They easily disintegrated under the force of the water, allowing channels to form in which erosion occurred even more intensely (Miller and Gardiner 2001). Hence, prevention of channel formation may also be an important function of moss crusts at Jasper Lake, although this remains to be tested *per se*.

Infiltration

Channel formation depends on the generation of runoff in the first place, which is influenced by the infiltration rate of water into the soil. The silt and clay content of the soil may limit infiltration rate (Blackburn and Skau 1974, Brotherson and Rushforth 1983) because fine particles seal pores through which water would pass (Evenari et al. 1982). The silt loam soil adjacent to Jasper Lake is already high in silt, but moss crusts may further increase its silt content because their stems project into the air stream and create a calm boundary layer (Proctor 2000). Sediment drops out of the slowed air (Thomas 1989) and becomes deposited among the moss stems. Hence, *C. purpureus* crusts may actually increase the chances that erosive runoff will be generated.

However, my results indicate that runoff is unlikely to be generated in even the most severe rainstorms at Jasper Lake, either on moss crusts or on bare sediment. The infiltration rates of scalped and moss-encrusted soil are 1141 mm/hr and 785 mm/hr, respectively (Figure 2.5b), while the maximum rate of precipitation recorded in Jasper National Park was 108 mm in a 24-hour period (Janz and Storr 1977). This is only about one tenth of the maximum sustainable infiltration rate of water into bare soil and one eighth of the infiltration rate of water into moss crust.

Brotherson and Rushforth (1983) reported infiltration times 15.5 times greater for scalped soil than for moss-covered soil on sandy soils of the Navajo National Monument, Arizona. In contrast, at Jasper Lake, infiltration times of scalped soil were 0.37 times as great as those of moss covered soil. The 40-fold difference between the studies in the relative influence of moss is probably due to different moss species under investigation. Although Brotherson and Rushforth (1983) do not report the identity of their species, the xerophytic *Tortula ruralis* is a common soil crust species in that region (Flowers 1973). This species soaks up water particularly quickly. It illustrates that it is impossible to generalize about not only the influence of biological soil crusts on their habitats, but even about the influence of a single taxonomic group such as the bryophytes.

Conclusions and Implications for Succession

Ceratodon purpureus is an engineer of soil properties at the Devona 1 Ecosite in Jasper National Park by increasing the strength of its soil habitat. Furthermore, from the perspective of vascular plants, this moss is likely a *beneficial* engineer for two of the three properties of stability that I measured. By protecting the soil from erosion both directly and indirectly, it may facilitate the development of vascular plant cover in this successionally young landscape. *Ceratodon purpureus* limits the availability of sediment to erosive wind and water by locking it in place among its stems and rhizoids. This process also increases the stability of the soil surface habitat for young vascular plants and potentially reduces the sediment load of the sandblasting wind. The reduction of fine soil loss also benefits vascular plants because nutrients such as nitrogen are associated with fine particles (Pallis et al. 1990), and accumulation of fine particles is associated with increased vascular plant vigor (Williams et al. 1995). The moss also indirectly reduces erosion by increasing the soil's resistance to mechanical damage, thus reducing the chance of its exposure to wind and water in the first place. Plants may therefore establish on a more geomorphologically stable substratum than bare silt loam. Finally, although this silt-rich moss crust impedes water infiltration, it does not reduce infiltration enough on the rapidly draining soils of this ecosystem to make erosion likely. The reduction of water flow into the soil, however, probably stimulates the growth of moss by trapping water at the surface and maintaining a moist microhabitat for itself. Thus *C. purpureus* may engineer its environment to facilitate the development of both the vascular plant community and its own growth.

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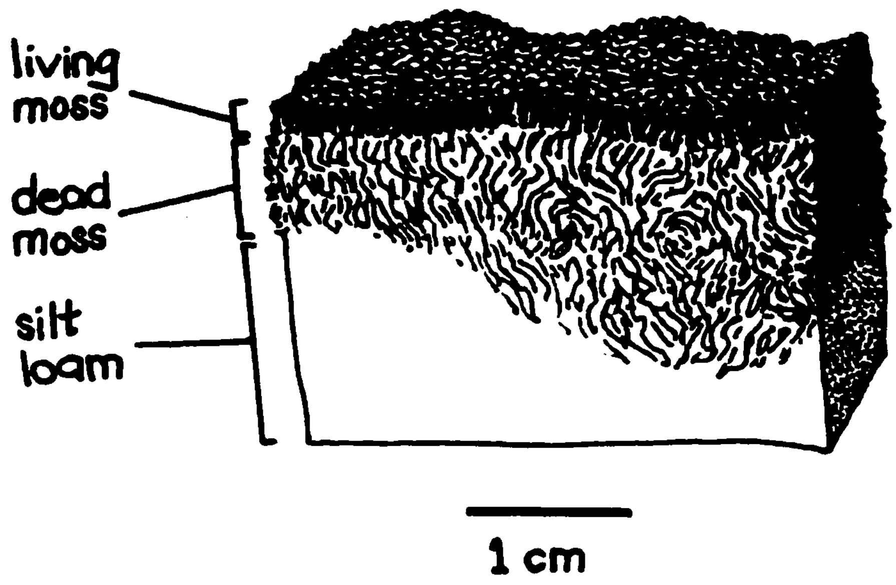

Figure 2.1. Profile of *Ceratodon purpureus* soil crust. Sitting atop the silt loam characteristic of soils near the Jasper Lakeshore, a soil crust of *C. purpureus* consists of a thin green to reddish layer of living moss (usually less than 1 cm thick) covering a thicker layer of brown dead stems (1 to 2 cm or more thick). These dead stems nonetheless provide structural stability. This profile illustrates a densely packed living moss layer; not all *C. purpureus* soil crusts have living stems as densely packed as this example. However, the dead moss layer is always heavily impregnated by fine soil particles.

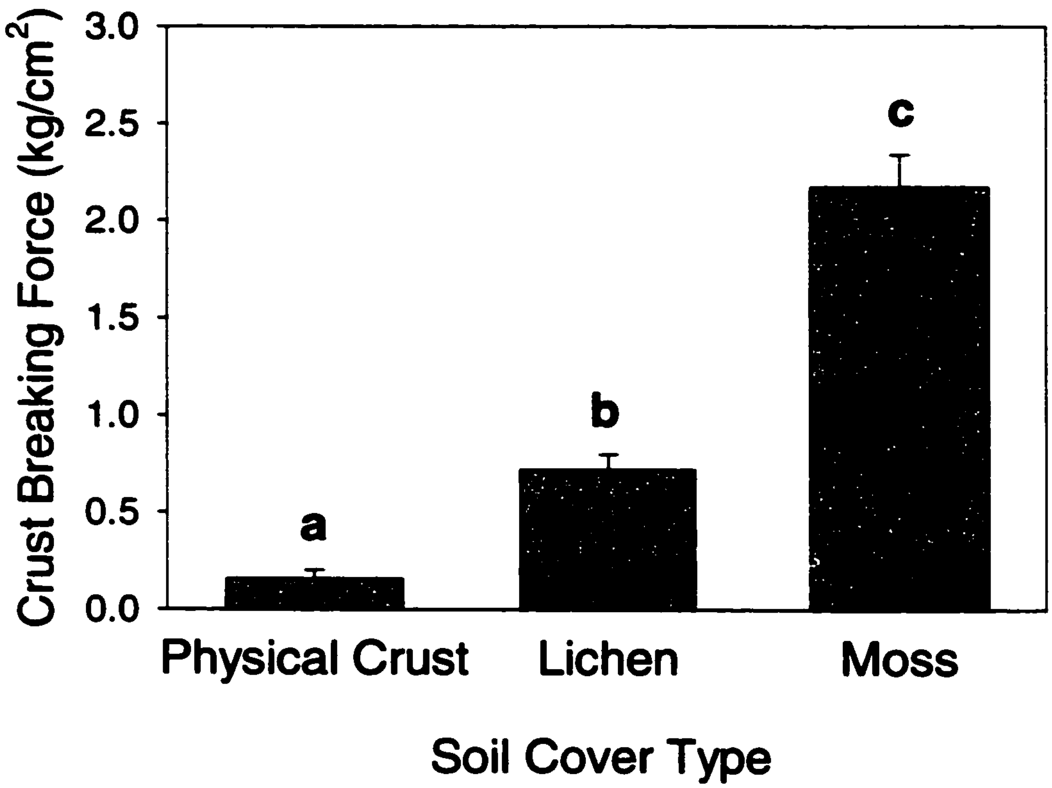

Figure 2.2. Penetrability of soil crusts. Force required to break through soil crust, with standard error (Kruskall Wallis $X^2 = 47.13$, $df = 2$, $p < 0.001$; Dunnett T3, $p < 0.001$ for all comparisons). Letters above bars represent statistically significant differences among treatments.

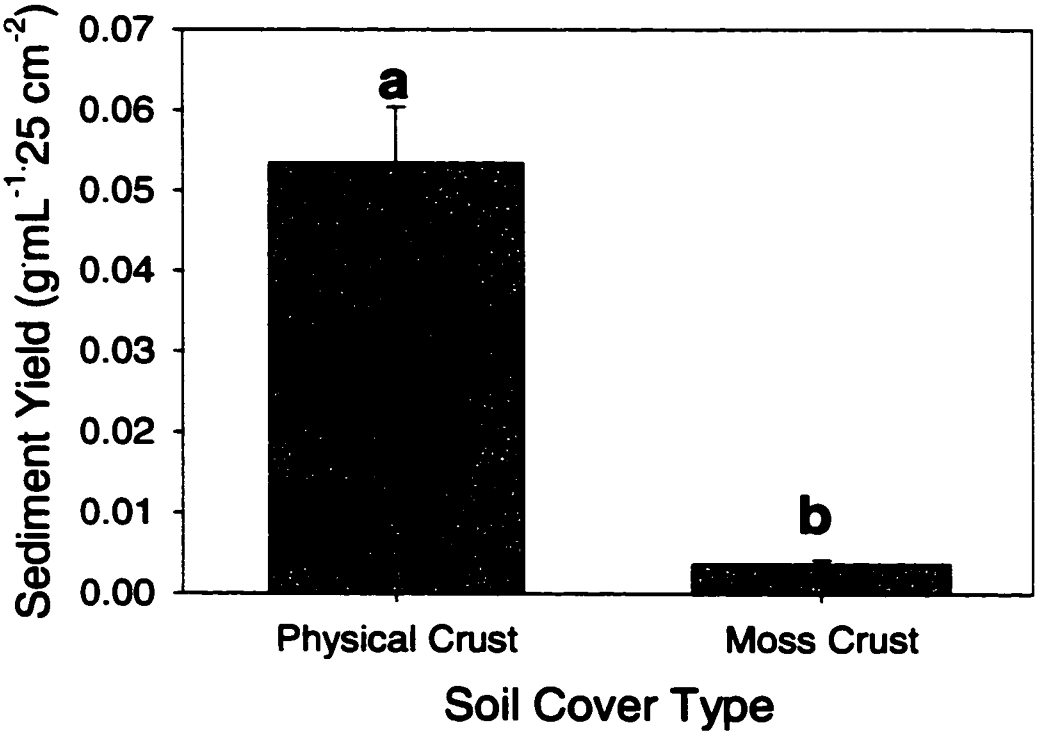

Figure 2.3. Erosion from moss versus physical soil crusts. Sediment yield (mass of sediment per unit volume runoff water from 25 cm^2 plot) from plots, with standard error (Wilcoxon signed ranks $T_+ = 0$, $N = 19$, $p < 0.001$). Letters above bars represent statistically significant differences between treatments. Erosion is greatest from physical crusted surfaces.

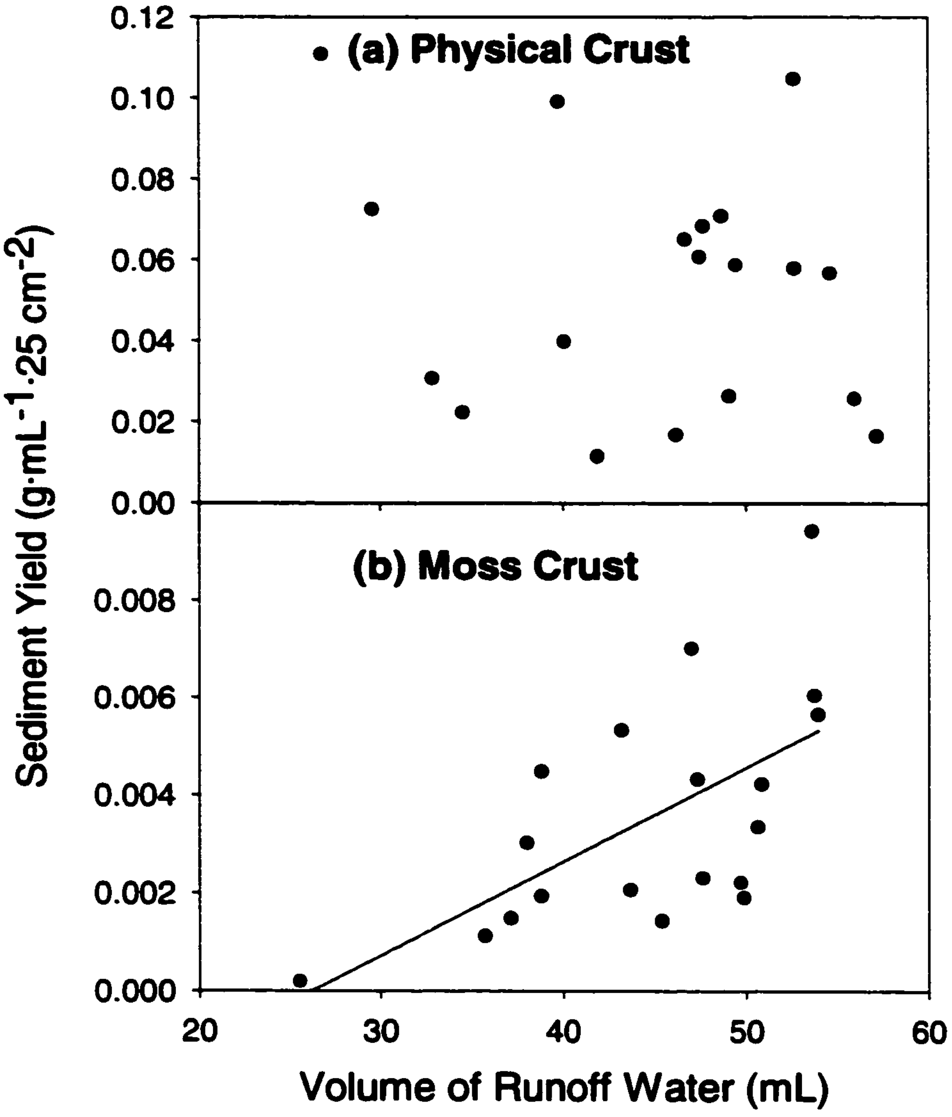

Figure 2.4. Erosion - dependence on runoff water volume. Relationship between the volume of runoff water generated and the concentration of sediment in it. Symbols represent observations; line represents relationship predicted by linear regression. **(a)** For physical soil crusts there is no significant relationship ($p = 0.373$). **(b)** For surfaces covered by a layer of Ceratodon purpureus the relationship is described by the regression: $y = -0.0051 + 0.00019x$, where y = sediment yield and x = runoff volume. ($p = 0.016$, $r^2 = 0.34$).

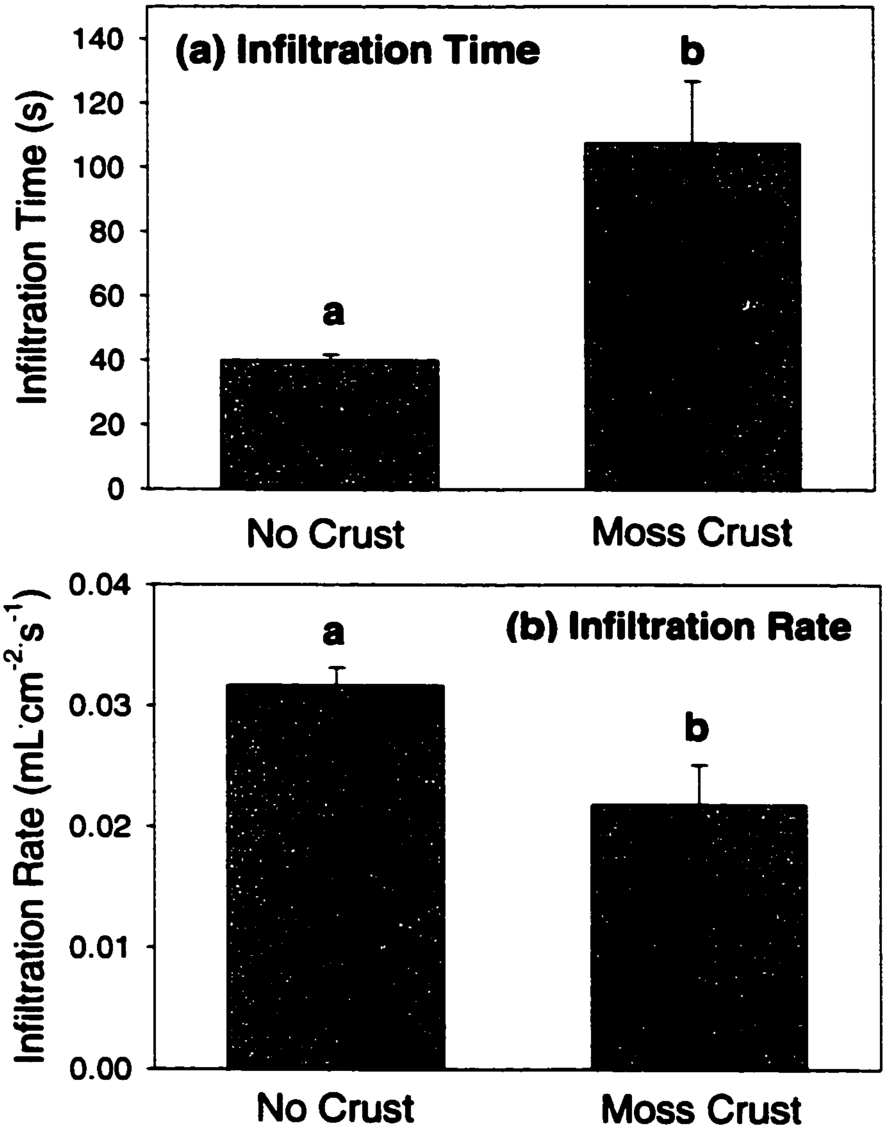

Figure 2.5. Permeability of soil crust. In each case, letters above bars represent statistically significant differences between treatments. (**a**) Time taken by water to enter soil for moss-crusted and scalped surfaces, with standard error (Wilcoxon signed ranks $T_- = 59$, N = 25, p = 0.005). (**b**) Infiltration rate of soil on moss-crusted and scalped surfaces, with standard error (Wilcoxon signed ranks $T_+ = 76$, N = 25, p = 0.005).

Chapter 3

Response of Moss to Microtopography Created by Trampling

Abstract

I studied the response of the moss *Ceratodon purpureus* (Hedw.) Brid. to microtopography created by ungulate trampling in Jasper National Park. Ungulates such as elk (*Cervus elaphus*) are ubiquitous habitat modifiers on the northeast shore of Jasper Lake, Jasper National Park, Alberta. Trampling increases the microtopographic heterogeneity of the soil by creating pits (hoof prints), raised barriers (tip-ups) and sloping soil. To determine how *C. purpureus* responds to this microtopography, I generated artificial microrelief and compared the growth rate of moss on north versus south exposures. *Ceratodon purpureus* grew taller (1) in the pits of artificial hoof prints, (2) in the shade of tip-ups and plastic barriers and (3) on north-sloping soil. This response is due to the shelter provided by terrain from desiccation, and possibly to moisture concentration in pits. I also related the height of moss plants to naturally occurring relief at two scales: hoof prints and microrelief within hoof prints. The response of moss height to natural microtopography was scale-dependent: moss height responded to fine scale microrelief more than to hoof print scale microrelief. Finally, I related trampling intensity/frequency to the percent of ground covered by moss. Moss cover does not decline with hoof print density until 25 percent of the ground is covered by hoof prints. Microhabitat creation by trampling seems to buffer *C. purpureus* from the otherwise exclusively negative effects of trampling by ungulates.

Introduction

Ecological interactions generally become more positive as abiotic stress increases (Bertness and Leonard 1997). This may occur because competition is weak in poorly populated harsh environments (Callaway and Walker 1997). However, it also occurs because the positive effects of organisms relative to their negative effects are greater when conditions stand to be improved greatly (Bertness and Leonard 1997). Hence, normally disruptive activity such as trampling may have positive effects in stressful environments. Disturbance may also have more positive effects when it creates structure, i.e. when it engineers the environment. In this chapter I ask how microtopography created by trampling in a marginal environment influences soil crusts composed of the moss *Ceratodon purpureus.*

Trampling as a Form of Ecosystem Engineering

Ecosystem engineering is the creation and modification of habitat by organisms (Jones et al. 1994), such as the incidental trampling of the soil by large animals. The engineering effects of trampling are numerous from the point of view of soil organisms, and the effects are scale-dependent.

At the regional scale, the impact of hooves enhances the rate at which sediment and water are removed from the soil. Trampling compacts the soil, increasing its bulk density, which reduces infiltration and increases erosive runoff (Butler 1995 and references therein). Nutrients such as nitrate and phosphate are then carried away by sheet erosion (Ladyman and Muldavin 1996, Pallis et al. 1990). Trampling also enhances erosion by physically breaking the soil surface and dislodging pieces of it (Butler 1995). Finally, removal of the thermally insulating layer of litter at the surface of the soil increases the depth to which needle ice penetrates into soil, further increasing erosion rates (Perez 1992, in Butler 1995).

However, trampling may also modulate resources on a small-scale by generating microtopography. Ungulates compress the soil immediately beneath their rigid hooves and leave behind well-defined hoof prints a few centimeters in depth. Trampling by ungulates may convert smooth soil with a relatively homogeneous microclimate into a patchwork of varying moisture, light and temperature conditions. Depressions such as hoof prints influence the local microclimate in at least two ways. First, runoff water may collect in hoof prints after rain (West 1990). Second, the walls of hoof prints may provide shelter from desiccating wind as well as from solar radiation, which further increases water content.

The effects of trampling are therefore complex. On the one hand, trampling may damage or kill soil organisms. On the other hand, trampling may alter the environment favourably for soil crust organisms via the microtopography that it creates. The outcome depends on (1) how the physical environment responds to the disturbance (i.e. how amenable the soil is to hoof print creation), (2) how soil crust organisms respond to the altered conditions and (3) the intensity of trampling. Interaction of these factors may have impacts on soil crust organisms that range from strongly negative to unexpectedly positive.

Response of Soil Crust Organisms to Microtopography

Several recent studies focus on the responses of organisms to gradients occurring along distances of only centimeters or millimeters. For example, soil crust cyanobacteria in Spanish badlands migrate only 2 mm below the surface of the soil to escape desiccation as the surface begins to dry after rain (Garcia-Pichel and Pringault 2001). On the Colorado Plateau, the abundances of the cyanobacterium *Microcoleus vaginatus* and of the lichen *Collema* are significantly higher on shaded than exposed aspects of soil mounds that measure only 5-15 cm wide and 7 cm tall (George et al. 2000). In fact, there may be as much patchiness in the distribution of algae (Grondin and Johansen 1993) and bacteria (Wheeler et al. 1993) at a scale of 0.013 m as there is at a scale of 24 m.

Mosses, like other biological soil crust organisms, are poikilohydric, meaning that their water content varies with that of their environment (Vitt 1989). Therefore, small variations in surface microclimate are more likely to affect the moisture status of mosses than that of endohydric vascular plants, which can tap into the soil for additional moisture. Although the crowded growth form of cushion-forming mosses maintains higher humidity for longer than in species with more open growth (Alpert 1991, Birse 1958, Schofield 1985), they still dry out quickly as their habitat dries. This terminates metabolic activity and growth (Tuba et al. 1996). High temperatures and radiation levels can also directly inhibit metabolic activity (Lewis Smith 1999, Seel et al. 1992). It is therefore advantageous for bryophytes to inhabit sheltered microhabitats.

Objectives

In this chapter I document the growth of the moss *Ceratodon purpureus* in response to microtopography induced by ungulate trampling near the shores of Jasper Lake in Jasper National Park, Alberta. The high ungulate traffic and fine texture of the soil at Jasper Lake generate a surface with high microtopographic heterogeneity. In windy, dry environments such as this, the microtopography generated by hoof prints should benefit *C. purpureus* by providing shelter from strong winds and intense solar radiation in the pits of hoof prints. Since both wind and sun are incident from the south, moss should grow more quickly on north-facing aspects of small mounds and pits than in southern exposures. To investigate this, I created artificial microtopography and measured the growth rate of moss occurring on or adjacent to it. I also quantified existing microtopography and related it to the size of naturally occurring *C. purpureus*, hypothesizing that moss plants would be taller in protected locations within hoof prints. Finally, because of the positive effects of microtopography, I predicted that negative impacts of trampling should only appear at high trampling intensity, when microtopography is obliterated rather than created.

Methods

Study Site

My study took place on the northeast shore of Jasper Lake, in a section of the Devona 1 Ecosite in Jasper National Park. For a more complete description of this location, refer to Chapter 2. *Ceratodon purpureus* colonizes much of the ground near the lakeshore, where it stabilizes the silt-loam soil. Ungulates such as elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) heavily utilize the shores of Jasper Lake because of the availability of winter forage (Holland and Coen 1982, Holroyd and Van Tighem 1983). As a result, the same soil that is colonized by extensive *C. purpureus* crusts is crisscrossed by ungulate trails. Soil between the trails is also heavily marked by clearly discernible hoof prints, which persist for a long time in the fine-textured soil.

Trampling creates microtopography of at least three types: pits, tilted soil and tip-ups. I evaluated the effect of each of these three forms of microtopography on the growth of *C. purpureus* in separate experiments. Pits are formed when ungulates step into the soil and compress its surface. Tilted soil results when the animal pushes off against the soil to gain forward momentum while walking. The soil is pushed backwards and tilted forward. Finally, a "tip-up" is a detached clod of soil that has been thrown from its original location, presumably by a running ungulate.

Pits

To create pits similar to those produced by walking ungulates, I constructed a device to generate artificial hoof prints. The artificial hoof consisted of a spruce post 10 cm across and 1 m tall, cut flat on one end, with a raised ring of wire glued to the rim to emulate the extended rim of real ungulate hooves. To create prints, I placed my whole weight onto a crosspiece of wood nailed to the post as a footrest. Before stepping off, I leaned the post in the direction of travel to create the inclined hoof print floors that ungulates generate. The maximum force exerted by an elk hoof during walking should be one third of the animal's total weight, since three feet are the minimum number that are in contact with the ground at any time. Each limb of an elk cow weighing 200 to 250 kg would therefore contribute 67 to 83 kg, while a bull weighing 320 to 350 kg would contribute 107 to 117 kg per limb (Gadd 1995). Given my mass of 70 kg and the post's mass of 10 kg, for a total of 80 kg, I could simulate the walking of a heavy cow elk with the experimental apparatus.

In mid June 1999 I generated 200 artificial hoof prints on patches of *C. purpureus*, 100 pointing north and 100 pointing south. The deepest point in south-facing prints, adjacent to the anterior rim, experiences greater shade than the same point in north-facing prints. I also included 50 control plots that received no compaction. For this and all subsequent experiments I avoided plots of ground containing ungulate dung pellets to avoid confusing the effects of nutrient input with the effects of shelter from desiccation. Dung pellets remain visible for several years, making avoidance possible.

To calculate moss growth rate for this and all subsequent experiments, I measured the height of moss plants at the beginning and end of a 44-day period, from July 14 to August 27, 1999. To measure the height of moss plants I constructed a high-precision ruler using the image of a ruler from a photographic slide made with a Pentax K-1000 camera. I analyzed the results using a single factor analysis of variance and a Tukey multiple comparison test.

Tip-ups

Ungulate traffic also extracts clods of dirt from the ground and deposits them upside-down next to hoof prints. Enhanced moss growth is often observed at the bases of these 'tip-ups'. To test the response of moss to shelter offered by tip-ups, I created 100 artificial square tip-ups. Using a pocketknife, I removed 4 x 4 x 2 cm blocks of moss-capped soil and laid them upside-down on undisturbed plots of soil, orienting them along a north-south axis. I compared moss growth rate immediately to the south of each tip-up with that immediately to the north (Figure 3.1). I used a paired t-test to compare moss growth on north and south sides of tip-ups.

Tilted Soil

To determine how the direction of slope of the soil affects moss growth, I measured the growth rate of moss for 100 paired plots of north-sloping and south-sloping soil. Each replicate consisted of a pair of adjacent 4 x 4 cm blocks of soil crust excised from the ground using a pocketknife and then returned to the ground so that one sloped northward and the other southward at about 30 degrees to the horizontal (Figure 3.2).

Control plots consisted of 100 pairs of excised soil crust squares that were replaced without inclination. I compared growth on north- and south-facing slopes using a paired t-test. I used the same analysis to compare the performance of control plot pairs.

Effects of Sun Versus Wind

Since both wind and sun are mainly incident from the south at Jasper Lake I designed an experiment to determine the relative importance of each factor in inhibiting moss growth. The experiment consisted of four complementary treatments in which I systematically blocked out one, both or neither factor from 200 moss patches divided equally among the treatments.

To block out both sun and wind I shaded moss patches with plastic cups cut in half, spray painted with neutral gray primer and secured to the soil due south of each moss plot by a nail glued to their bases (Figure 3.3a). I repeated this setup for an equal number of clear, unpainted cups that admitted sunlight but blocked out the wind (Figure 3.3b). To block out the sun but not the wind I used sheets of cardboard mounted horizontally on bamboo poles placed 70 cm above the ground, immediately to the south of moss plots (Figure 3.3c). This arrangement also allowed rain through. Because each plots was not associated with a plastic barrier, I marked plots with galvanized nails placed at one corner of each plot. Finally, a fully exposed treatment consisted of plots marked by galvanized nails, but not associated with any protective structure (Figure 3.3d). I compared growth rates in the four treatments using a two-factor analysis of variance, with presence/absence of wind and presence/absence of sun as the factors.

Natural Patterns: Hoof Print Microtopography

Because moss plants are generally slower growing than vascular plants, these manipulative experiments could only measure the initial response of moss to disturbance. Therefore, to investigate long-term response, I related natural patterns of moss canopy height to the microrelief on which they grew in naturally occurring hoof prints, under the assumption that natural patterns reflect long-term patterns of growth.

For 120 hoof prints I measured both the height of moss plants and the local elevation of the ground at 1 cm intervals along north-south transects passing through the center of each hoof print. For each print I measured elevation relative to a reference level established using a 'microaltimeter' device that I constructed. It consisted of a frame-mounted pin that could slide in three dimensions, allowing the tip to occupy any position within a 20 x 20 x 15 cm space. I used a level to ensure that the device was inserted into the ground horizontally along both the x and y axes. At each sampled point, I first lined up the probe tip with the surface of the moss canopy to record canopy position, and then I lowered it to the soil below to obtain ground position. Moss height was the difference between these values. This method of measuring microtopography, similar to that described by Armstrong (1974), allowed me to generate a number of microtopographic variables (such as depth, height of adjacent terrain and concavity) from a single dataset.

I analyzed the relationship between microtopography and moss canopy height at two scales: (1) hoof prints, and (2) microrelief within hoof prints. For the latter, the units of observation were individual moss stems at horizontal intervals of 1 to 2 cm. Measurements of zero-moss-height were a large source of variation in both analyses. I removed these observations on the assumption that the process determining the presence or absence of *C. purpureus* at any given point (probably dispersal success) is likely independent of the process determining the height of moss plants once they are established (physiological response to microtopography).

To analyze patterns of moss height at the scale of hoof prints, I calculated the mean moss canopy height for each hoof print and regressed it on four hoof print scale variables: (1) mean hoof print depth, (2) maximum hoof print depth, (3) hoof print age and (4) hoof print direction. I estimated age of prints visually and assigned each a score from 0 (fresh) to 4 (old). While mean and maximum hoof print depth are straightforward microtopographic variables, the effect of age is more complex. As hoof prints age, they fill in; while moss plants should respond less favourably to shallow hoof prints (with less shelter), those in old hoof prints have had more time to grow and may therefore be taller than plants in deep but recent hoof prints. Since hoof print floors are sometimes inclined, the compass direction of hoof prints may influence their radiation budget. For hoof print direction, I calculated the cosine of the compass direction in which hoof prints faced. This allowed me to distinguish north-facing hoof prints (for which the cosine of direction approaches 1) from south-facing prints (for which the cosine of direction approaches -1), the orientation along which I expected the radiation budget to differ most strongly.

Second, I analyzed the relationship between moss height and microrelief at the smallest spatial scale. I pooled the measurements of moss height and of relative hoof print elevation for all hoof prints and regressed moss height onto eight indices of microtopography calculated as explained in Table 3.1.

Natural Patterns: Frequency/Intensity of Trampling

In quadrats placed along three transects I recorded the percent of ground covered by *C. purpureus* and the percent of ground covered by hoof prints. I estimated cover by counting the number of squares occupied by each subject in a 30 x 30 cm grid divided into 100 squares. Because I did not record the age of hoof prints, it was impossible to distinguish between disturbance frequency and intensity. However, an overall estimate of the impact of trampling was still possible. For analysis I performed a regression of the relative cover of moss on the relative cover of hoof prints.

Results

Pits

Except for a subtle increase in growth in shaded locations, moss growth rate showed no difference between north and south facing artificial prints (Figure 3.4). However, presence or absence of a pit influenced growth three times as strongly as the exposure direction did (Figure 3.4).

Moss growth in this experiment occurred during a snapshot of time spanning merely 44 days. However, regressing net growth on initial height allowed me to predict the height to which moss plants would equilibrate assuming constancy of growing conditions. In this experiment, net growth depended on the initial height of the moss canopy: tall canopies decreased in height while short ones increased. This is probably due to death of emergent individuals that are subject to more severe desiccation than plants fully contained within the moss canopy (Okland 2000). In this experiment there was no appreciable difference in the equilibrium height of north and south facing hoof prints; moss stems for both orientations equilibrated to about 3 mm (Figure 3.5). However, the moss within hoof prints equilibrated to a height about twice as great as that of exposed populations (Figure 3.5).

Tip-ups

Moss growth on the shaded north sides of artificial tip-ups was significantly greater than moss growth immediately to the south (Figure 3.6). The shaded moss grew 0.40 mm taller than fully exposed moss. In the shade, the moss canopy equilibrated to a height about 1.5 times as great as on south exposures (Figure 3.7).

Tilted Soil

The net moss growth over the season was greater for north-tilted than for south-tilted moss crust (Figure 3.8). Adjacent pairs of control blocks that were not inclined, in contrast, showed no significant difference in growth (Figure 3.8). It was not possible to calculate equilibrium moss canopy heights for the north facing treatment. However, the moss canopy on south facing soil blocks equilibrated to a height of only about two-thirds of that of the paired controls (Figure 3.9).

Effects of Sun Versus Wind

In the sun- and wind-exclusion experiment, both solar radiation and wind had significant inhibitive effects on the growth of moss (Figure 3.10). However, solar radiation had nearly 1.5 times stronger an effect than wind, with both factors together having a further 1.5-fold greater effect than sun alone (Figure 3.10). There was no interaction between the factors. Initial canopy height was a weak predictor of growth rate in the sun- and wind-exclusion experiment (Figure 3.11). It was only possible to reliably predict an equilibrium height for the control treatment, which equilibrated to a height of 1.43 mm.

Naturally Occurring Hoof Prints

The relationship between moss height and microtopography was scale-dependent. At the scale of hoof prints, maximum and mean hoof print depth were significant predictors of mean moss height (Figure 3.12). Mean moss height increased with maximum hoof print depth but decreased with mean hoof print depth.

However, patterns were stronger at the scale of microtopography within prints. Out of the five microtopographic indices and four interactions that I tested (Table 3.1), concavity of the ground was the strongest predictor of moss height, followed by the vertical position of moss in hoof prints (Figure 3.13). Moss height increased with both variables. Concavity is the average difference in ground elevation between the point of interest and the two points immediately surrounding it, 1 cm to the south and 1 cm to the north. (Table 3.1). Positive values represent dips in the ground while negative values represent mounds. Vertical position in hoof prints is the vertical distance between the point of interest and the rim of the hoof print.

Natural Patterns: Frequency/Intensity of Trampling

Percent of ground covered by moss decreased as hoof print density increased, but not monotonically. Instead, commencement of this decline was displaced toward higher hoof print densities. There was no appreciable decrease in relative moss cover until about 30 percent of the ground was altered by disturbance (Figure 3.14). This corresponds to a density of about 50 hoof prints per square meter.

Discussion

Most work on recovery of biological soil crusts from trampling concludes that trampling sets soil crusts back successionally. Moss-rich soil crusts revert to a cyanobacteria- and algae- dominated community. Apparently, the decimated moss populations may take up to 250 years to return to predisturbance levels (Belnap 1993). However, these estimates are largely based on studies from arid lands of the American Southwest, on loose soils of such high sand content, up to 92.8% (Jeffries and Klopatek 1987), that they cannot preserve a hoof print for long. The forces of erosion quickly erase any microtopography that trampling generates. In fact, on these coarse soils, trampling itself reduces microtopography created by soil crust organisms (Cole 1990).

My study demonstrates that on fine soils, the microtopography created by trampling may actually stimulate moss growth. Agents of disturbance may become agents of beneficial ecosystem engineering in soils capable of preserving the shape of hoof prints. Long-lasting hoof prints shelter soil crust bryophytes from the desiccating effects of the sun and wind. Shelter comes in three forms: (1) raised barriers to sun and wind, (2) soil tilted away from radiation or wind and (3) pits.

Barriers to Sun and Wind

Bryophytes are highly sensitive to the moisture level of the atmosphere because they must take up water directly through their aerial stems and leaves. They must take advantage of dew and precipitation that briefly replenish soil surface moisture and raise the humidity of the boundary layer above the soil. Any factors that extend the duration of moist conditions will prolong the effective growing season of mosses (Vitt 1989).

My work indicates that even small barriers, such as 2-cm tall clods of soil kicked up by ungulates while walking, can shelter *C. purpureus* from desiccation sufficiently to extend its growing period. Over 44 days, sheltered plants grew 0.4 mm taller plants exposed to full sun and wind (Figure 3.6), equilibrating, under constant growing conditions, to a height 1.5 times as great as an unprotected canopy. By systematically blocking out wind, sun or both, I found that the beneficial effects of microtopography stem from its ability to shelter moss from the desiccating influence of these agents (Figure 3.10).

Studies relating microtopography to moss growth support my findings regarding the benefits of refuge from wind and sun. In Antarctica *Bryum pseudotriquetrum* colonizes only the 5-cm deep troughs between ridges of *C. purpureus*, where it is protected from the drying and scouring action of wind (Lewis Smith 1999). In California, the distributions of five desiccation tolerant mosses reflected the distribution of low evaporation microhabitats a few centimeters in size that were shaded from direct sun, such as small concavities (Alpert 1985).

Tilted Soil

In addition to shadow, slope and aspect of the ground can also influence the intensity of sunlight that the soil receives. A surface perpendicular to the incident angle of light presents the smallest cross sectional area to incident rays and therefore experiences the maximum intensity of radiation per unit area. Rotation away from this angle reduces the energy absorbed by the surface and the subsequent rate of evaporation from that surface.

At high northern latitudes, the effects of slope on microclimate are more complicated than the effects of raised barriers. While moss growing on a northerly slope experiences similar protection to moss growing in a shadow, plants on a south slope must contend with the increased radiation caused by inclination of the land toward the sun. Exposed plants on flat ground do not suffer this enhanced radiation. Runoff patterns also depend on the direction and steepness of the slope, and even barely perceptible changes in slope result in distinct soil moisture distribution patterns (Scott 1982).

It is therefore not surprising that at Jasper Lake, *C. purpureus* grew better on north-facing slopes than on south-facing slopes, tilted at about 30 degrees to the horizontal. Moss on north-facing exposures grew 0.4 mm more than moss on south-facing slopes and 0.17 mm more than plants on flat ground (Figure 3.8). At equinox at 53°N latitude, a soil inclined at 30 degrees to the south receives 92% of the photon flux of normally incident sunlight, while an equivalent north incline intercepts only 12% of the maximum value. Evaporation should therefore proceed 7.6 times as quickly on south-facing treatments as on north-facing ones. Wind, which at Jasper Lake is also predominantly southerly, may be relatively more important in years of high cloud cover, when incident light is scattered, reducing north-south thermal and evaporative gradients (Young et al. 1997).

While the effects of slope on bryophytes are relatively well studied at regional scales (Alpert 1985, O'Keefe van der Linden and Farrar 1983) few researchers investigate these effects at very fine-scale. Significant slope-induced microclimatic heterogeneity may exist at fine scales. Alpert (1982 in Alpert 1991) found that potential evaporation on boulders was lowest on near-vertical, north facing aspects, which remained moist significantly longer than exposed south aspects.

Pits

The final and most abundant form of microtopography generated by ungulate trampling is the pit that we recognize as a hoof print. Pits may serve three hydrologic functions: (1) reduction of distance to the water table, (2) shielding from sun and wind, like barriers and (3) gravitational concentration of water. In wetlands, the water table may reside near ground level. As a result, pits and mounds of vegetation exhibit large moisture gradients over short vertical distances (Vivian-Smith 1997). Despite the proximity to Jasper Lake, these conditions are absent at my study site, because the lake level is still several meters below sampling locations.

The artificial hoof print experiment weakly supported the second hypothesis that hoof prints provide shade from wind and sun. Southern exposures showed no significant difference in moss growth from northern exposures (Figure 3.4). This was unexpected in light of results from the manipulative experiments, but perhaps both north and south facing prints provided adequate protection from wind while receiving the same amount of sun. Further investigation is required to resolve this problem.

Ungulate hoof prints at Jasper Lake appear to concentrate water gravitationally, especially at a very fine scale. While runoff may accumulate in pits (West 1990), most work demonstrates this process at a larger scale (e.g. Boeken and Shachak 1994) than is probably important at Jasper Lake. Water accumulation from the surrounding soil depends on the generation of runoff, but the rapidly draining soil of my study site inhibits runoff (Chapter 2). Instead, the sloping soil *within* hoof prints may channel water to the lowest point, created by the sharp points of cloven hooves. Mosses growing in these foci could obtain water that is channeled here both over sloping soil and through the interconnected bryophyte canopy itself. Even though the rapidly draining soil does not normally generate runoff, compression by hooves may increase bulk density enough to create runoff *within* hoof prints. These low points would also remain moist for longer as water drains into the soil profile following precipitation.

Evidence from both experimental manipulation and analysis of natural moss populations supports this water concentration hypothesis. The artificial hoof print experiment demonstrated a strong beneficial effect of growing in hoof prints, where moss equilibrated to a height twice as great as when growing on exposed ground (Figure 3.5). I took care to measure moss height at the lowest point in each print. The rarity of such low points within any hoof print may explain why maximum hoof print depth was a stronger predictor of mean moss height than mean hoof print depth in naturally occurring hoof prints. Although mean moss height decreased with increasing mean hoof print depth (Figure 3.12), contrary to expectation, the significance of this variable is not great ($p = 0.032$). Fine-scale concavity contributed significantly to explaining moss height because extreme low points generated by pointed hoof tips are associated with intense concavity. Hence, the ecosystem engineering influence of hoof prints on moss growth is scale-dependent because their water-modulating effects depend on their fine-scale morphology.

Trampling Intensity

The merit of my study is that it addresses the influence of *individual* hoof prints, whereas existing soil crust studies typically consider only the cumulative large-scale effects of disturbance. However, it is equally insufficient to consider only the individual level effects, because the impact of trampling depends on its intensity and frequency. Often, the abundance of plants declines rapidly with increasing intensity or frequency of trampling (Cole 1993). In contrast, the percent cover of *C. purpureus* at Jasper Lake does not begin to decline until 25 percent of the soil is covered by hoof prints. At low to moderate trampling intensity, the positive effects of trampling-induced microrelief buffer moss from the negative impacts of crushing. At high trampling intensity, such as on game trails, disturbance is great enough to eliminate microrelief. This resulting pattern that described by the intermediate disturbance hypothesis (Connell 1978), in which richness peaks at intermediate intensities or frequencies of disturbance. At Jasper Lake, however, the beneficial effects of disturbance are not strictly a function of the interval between disturbance events; spatial structure created by the disturbance itself is responsible. The creation of microtopography by disturbance distinguishes this system from biological soil crusts typically studied on sandy desert soils. Studies of the latter report only negative influences of trampling because on these soils, *any* trampling immediately obliterates microtopography (Cole 1990).

Conclusions

Ungulates are important ecosystem engineers in the Devona 1 Ecosite on the shores of Jasper Lake in Jasper National Park, Alberta. Trampling creates microrelief that modulates the action of sun and wind, and alters the availability of water to mosses. In this chapter I show by experimental manipulation and by analysis of natural pattern that the shelter provided to *Ceratodon purpureus* by this microtopography enhances the moss' growth. As a likely result, increasing hoof print density does not cause a decline in the percent of ground covered by moss until 25 percent of the ground is covered by prints. In this system, the very elk that disturb *C. purpureus* may also promote its recovery, and hence lessen their net negative impact on the moss.

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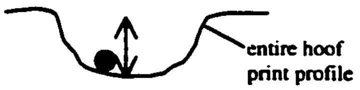
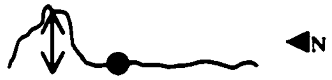
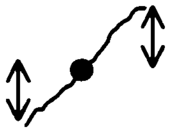
Table 3.1. Microtopographic indices and interaction terms entered as independent variables in forward stepwise multiple regression to predict height of moss in naturally occurring hoof prints (Figure 3.13). Y_x represents the local elevation at the point where moss height was measured. Y_N and Y_S represent local elevation 1 cm to the north and 1 cm to the south of the point of measurement, respectively. Y_0 represents the elevation of the hoof print rim. In the diagrammatic explanations, the curves represents the profile of the local microtopography, the heavy dots represents the points of measurement of moss height and the double-headed arrows refer to the quantities that the index in question quantifies. Asterisks indicate significance at the $\alpha = 0.05$ level.

Microtopographic Index	Calculation (and graphical explanation)	p (significance)
Vertical position in hoof print (VP)	$Y_x - Y_0$ 	0.002*
Southern Terrain Height (STH)	$Y_S - Y_x$ 	0.053
Northern Terrain Height (NTH)	$Y_N - Y_x$ 	0.053
Slope (S)	$(Y_S - Y_x) - (Y_N - Y_x)$ 	0.053
Concavity (C)	$(Y_S - Y_x) + (Y_N - Y_x)$ 	< 0.001*
Interactions		
VP x STH		0.344
VP x NTH		0.187
VP x S		0.184
VP x C		0.748

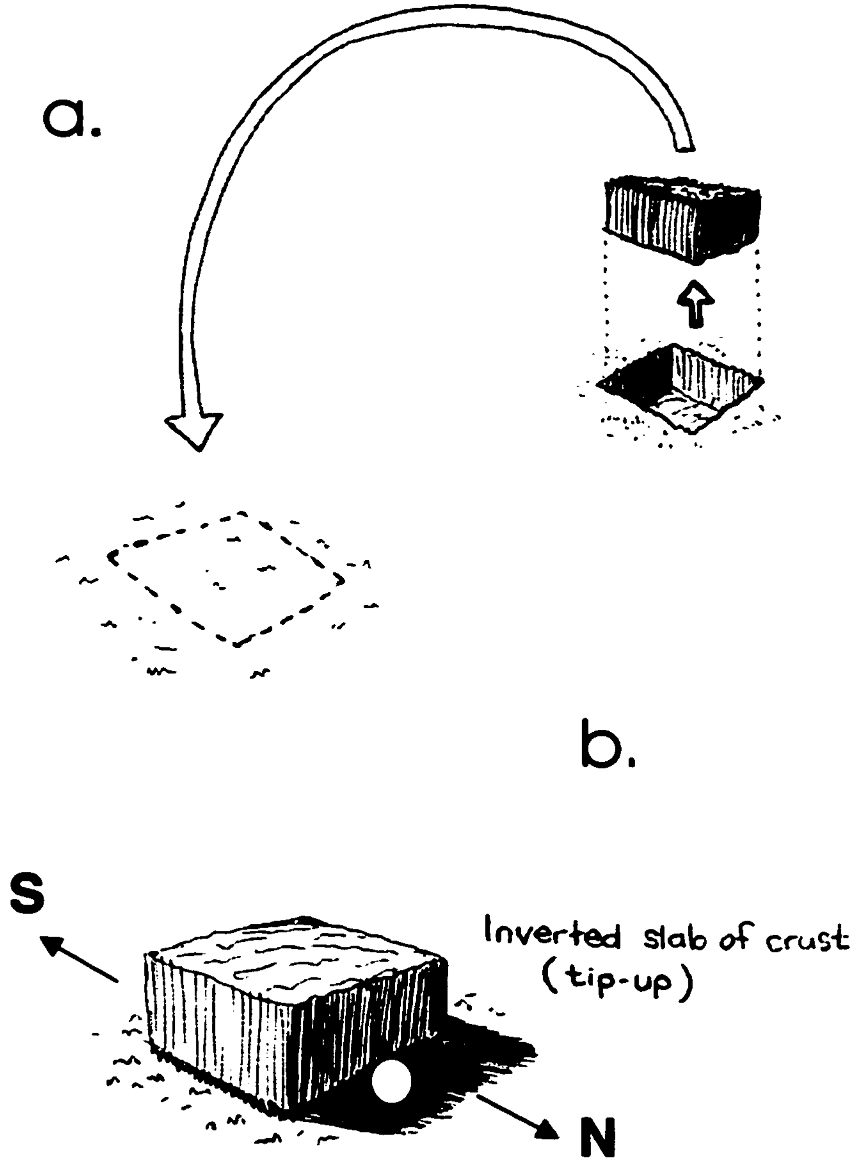


Figure 3.1. Tip-up experimental setup. Experimental setup for testing the effects of 'tip-ups' on the growth of *C. purpureus* immediately adjacent to the exposed south side of the tip-up and the shaded north side. (**a**) A slab of moss soil crust measuring 4 x 4 x 2 cm in size was excised from the soil and (**b**) was laid upside down onto undisturbed soil. The heavy white dot immediately adjacent to the shaded north wall of the tip-up indicates where moss height was measured for north exposures.

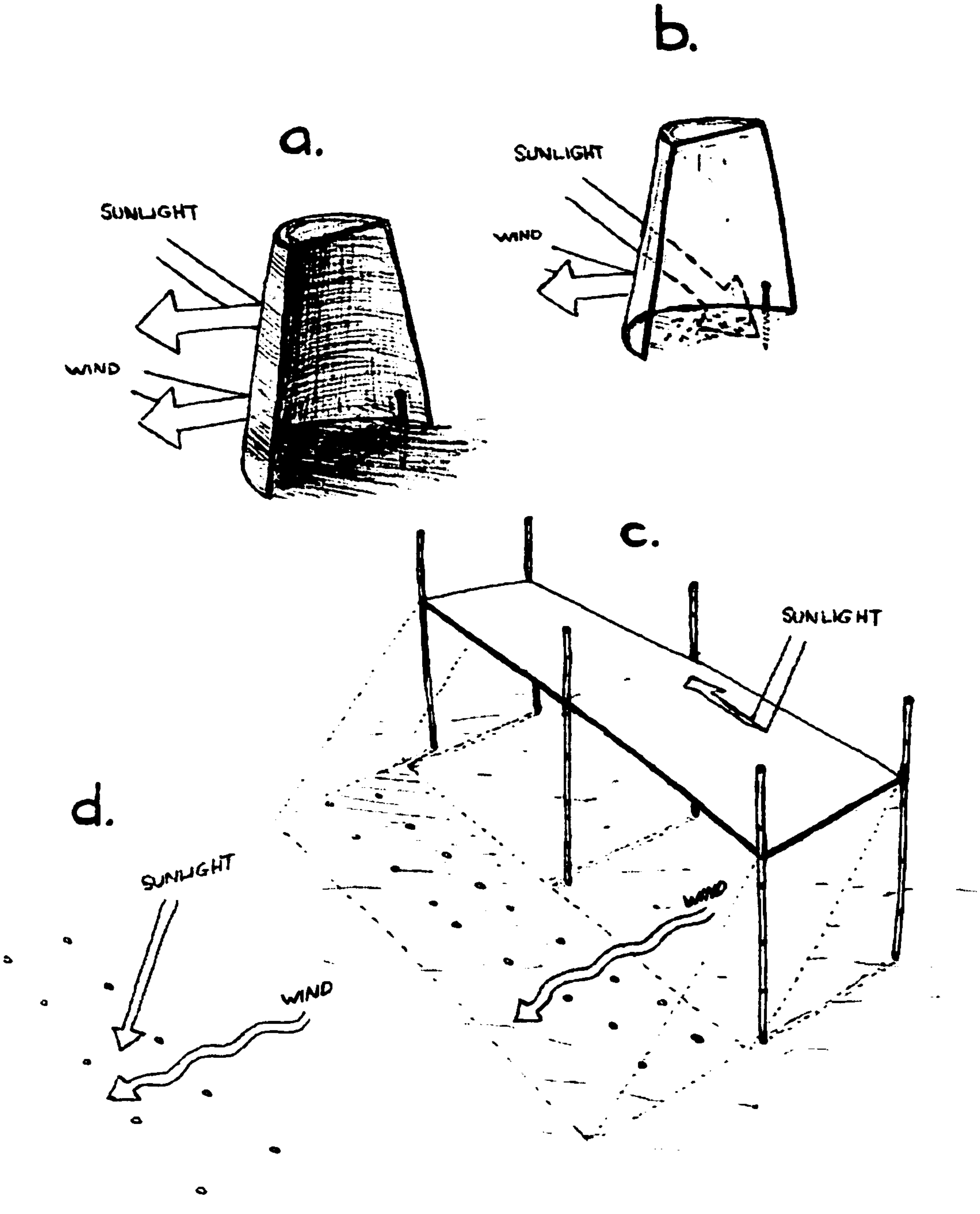


Figure 3.2. Sun-and-wind-exclusion experimental setup. Experiment to determine the relative effects of wind and sun on the growth of *C. purpureus*. **(a)** An opaque guard constructed from a spray-painted, split plastic cup blocked out both wind and sun, **(b)** a transparent guard blocked out wind but allowed sun, through, **(c)** a raised cardboard shade on bamboo poles blocked out sun but allowed wind through and **(d)** controls were exposed to both wind and sun. The small circles on the ground in (c) and (d) are the galvanized nails inserted into the ground to mark plots.

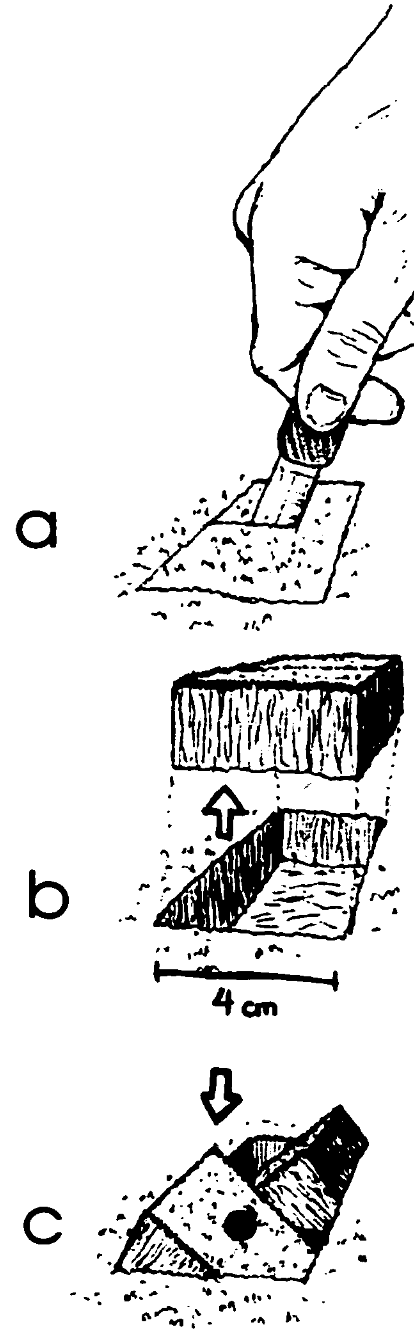


Figure 3.3. Tilted soil experimental setup. Experiment to test the effect of aspect of exposure on the growth of *C. purpureus*. **(a)** For each experimental replicate, crust was cut with a pocketknife into two equal squares and **(b)** removed from the ground. **(c)** One square was replaced so that it slanted northward at an angle of about 30 degrees while the other slanted southward. Heavy black dot in (c) represents location where moss height measurement was taken for that slab.

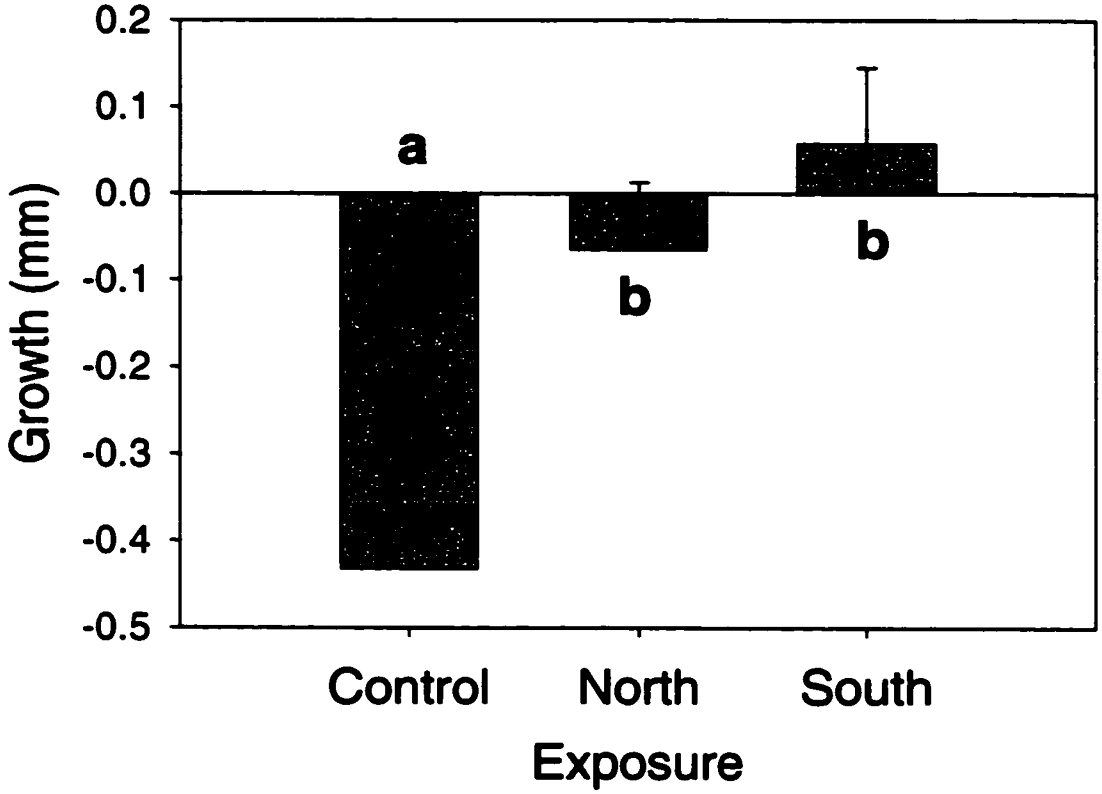


Figure 3.4. Artificial hoof print experiment. Mean net moss growth on north- and south-facing artificial hoof print, with standard error (ANOVA F = 4.77, df = 2, p = 0.009). Letters represent statistically different treatments (Tukey, p = 0.063, 0.007, 0.558 for Control vs North, Control vs South and North vs South, respectively).

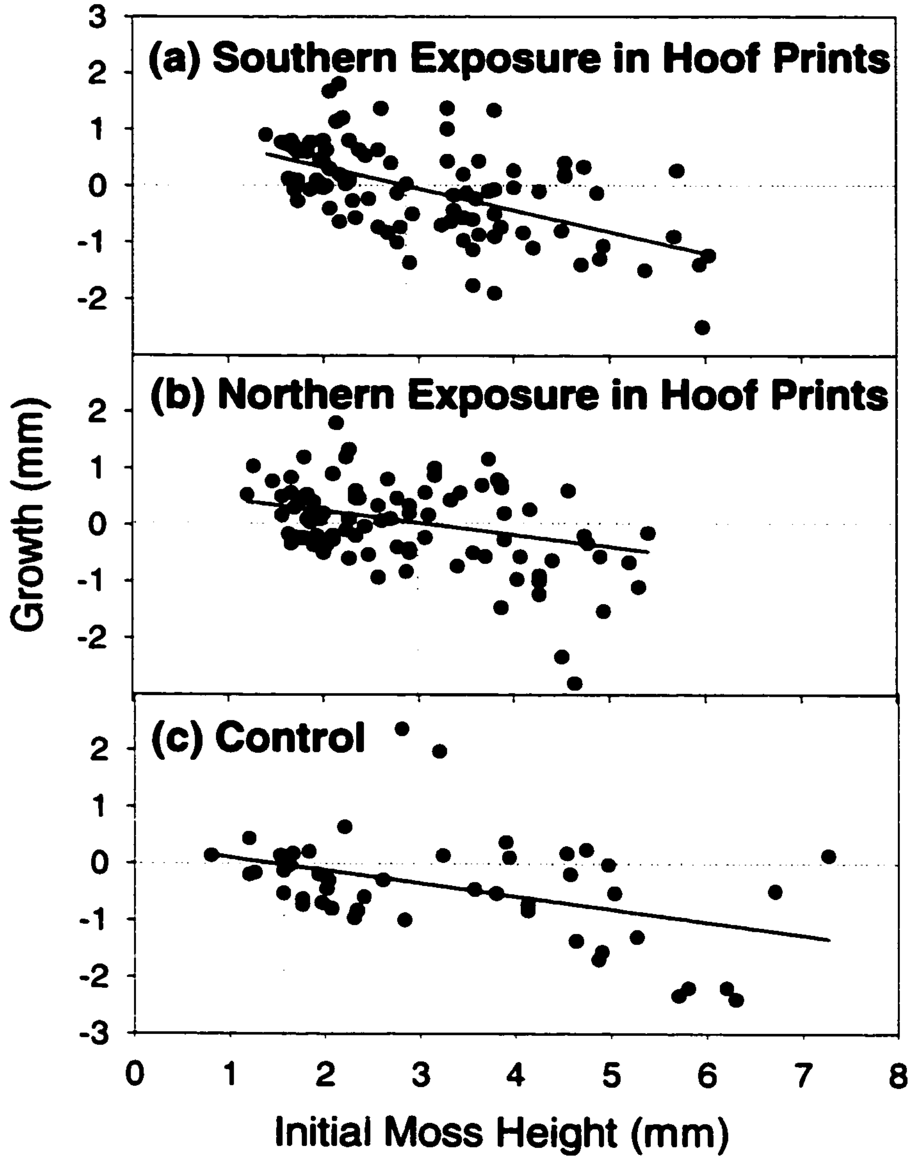


Figure 3.5. Equilibrium moss height (H_E) projected for all plots in artificial hoof print experiment. (a) Southern exposure in hoof print $H_E = 2.89$ mm; model: $y = 1.10 - 0.38x$; $p < 0.001$; $r^2 = 0.30$. (b) Northern exposure $H_E = 3.00$ mm; model: $y = 0.78 - 0.26x$; $p = 0.0018$; $r^2 = 0.093$. (c) Control on flat ground $H_E = 1.43$ mm; model: $y = 0.33 - 0.23x$; $p = 0.0032$; $r^2 = 0.159$. Vertical dotted line indicates H_E for each treatment.

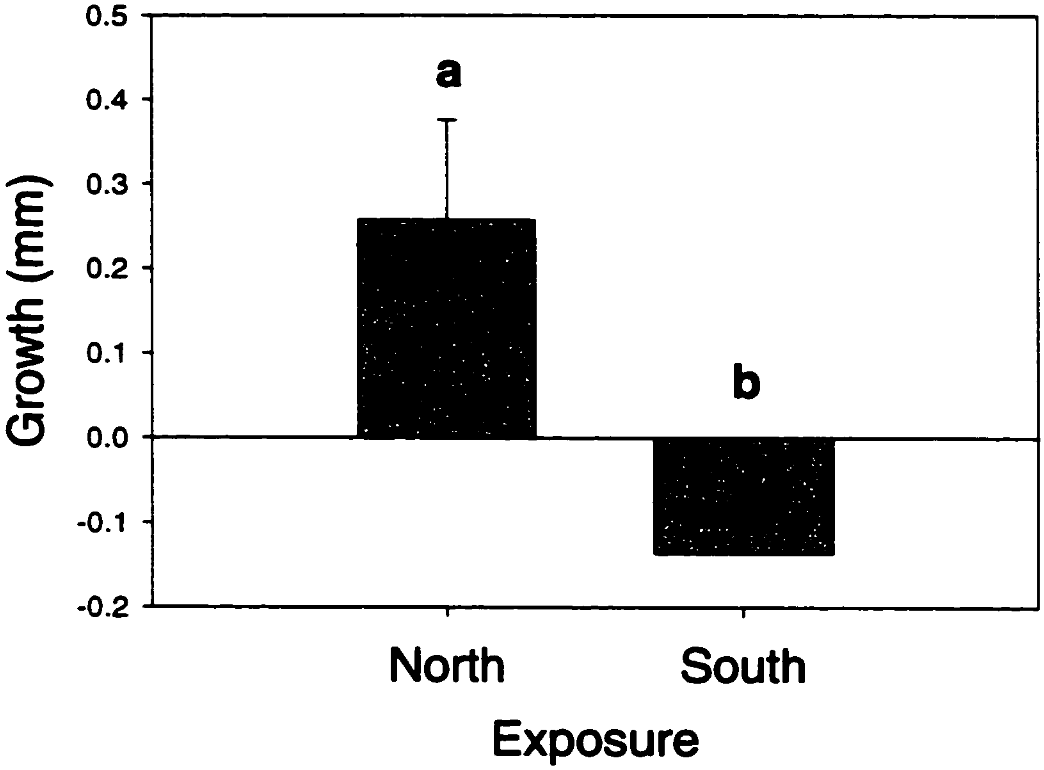


Figure 3.6. Tip-up experiment. Mean net moss growth on north and south exposures of tip-up experiment, with standard error (paired t = 3.22, df = 91, p = 0.002). Letters above bars represent statistically significant differences among treatments.

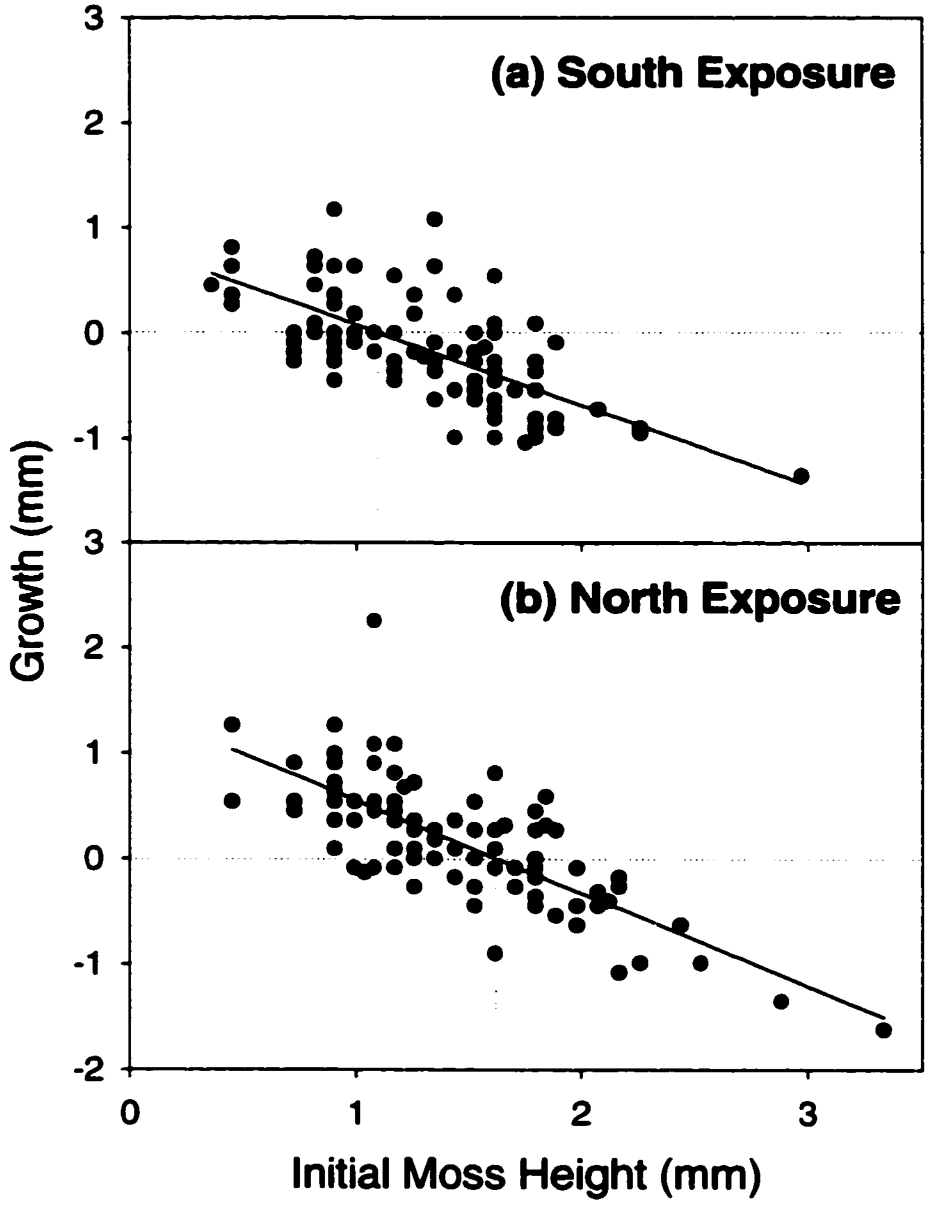


Figure 3.7. Equilibrium moss height (H_E) projected for all plots in tip-up experiment. (**a**) Southern exposure $H_E = 1.09$ mm; model: $y = 0.83 - 0.76x$; $p<0.0001$; $r^2 = 0.45$. (**b**) Northern exposure $H_E = 1.63$ mm; model: $f(x) = 1.43 - 0.88x$; $p<0.0001$; $r^2 = 0.56$. Vertical dotted lines indicate H_E for each treatment.

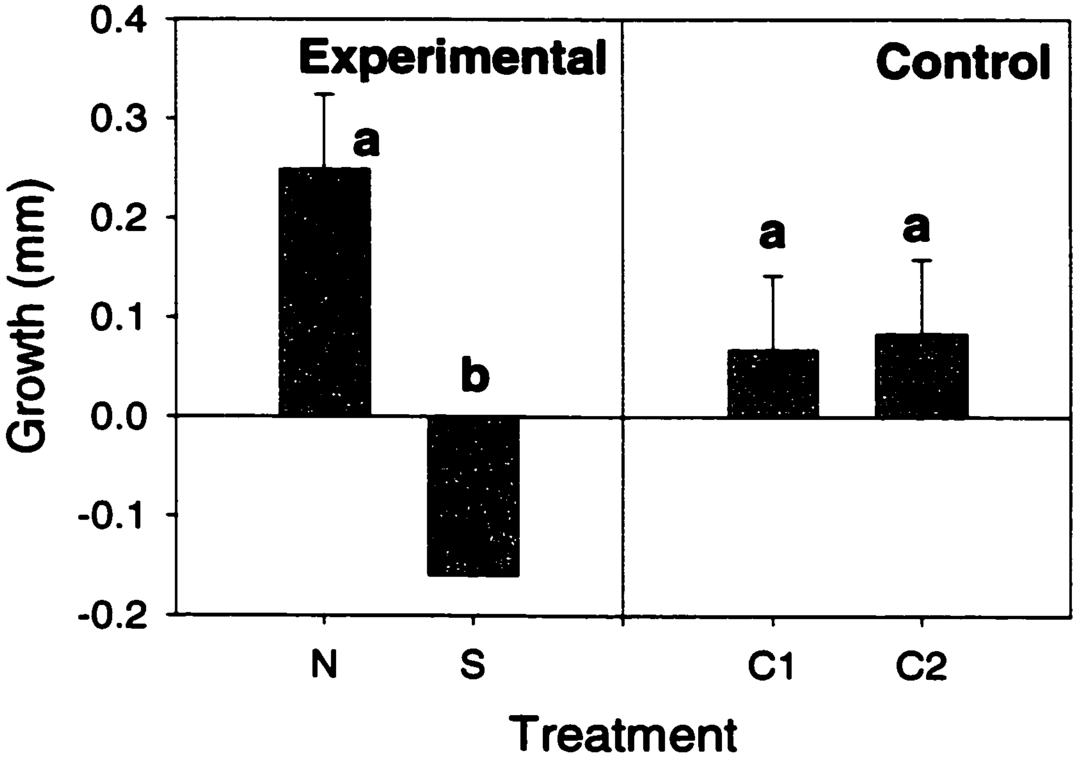


Figure 3.8. Tilted soil experiment. Mean net moss growth on north and south slopes, with standard error. (Experimental treatments: paired t = 4.28, df = 93, p < 0.001; Paired control treatments: paired t = 0.20, df = 94, p = 0.846). Letters above bars represent statistically different treatments. N = North, S = South, C1 = Control 1, C2 = Control 2.

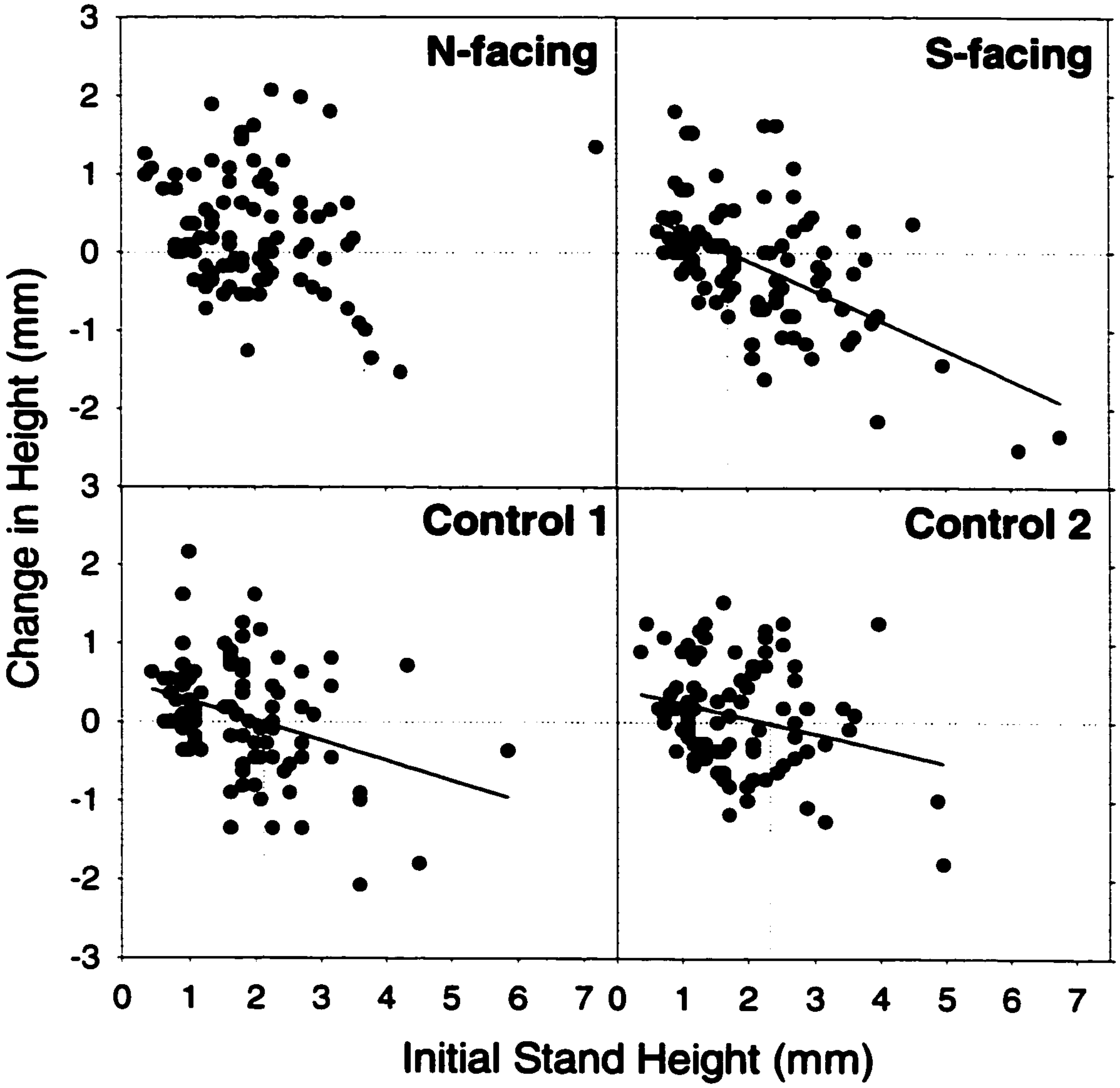


Figure 3.9. Equilibrium moss height (H_E) projected for all plots in tilted soil experiment. **(a)** North slope - No model (p = 0.299). **(b)** South slope H_E = 1.71 mm; model: y = 0.65 - 0.38x; p<0.0001; r^2 = 0.30. **(c)** Control 1 H_E = 2.12 mm; model: y = 0.53 - 0.25x; p = 0.0008; r^2 = 0.11. **(d)** Control 2 H_E = 2.26 mm; model: y = 0.43 - 0.19x; p = 0.013; r^2 = 0.055. Vertical dotted lines indicate H_E for each treatment.

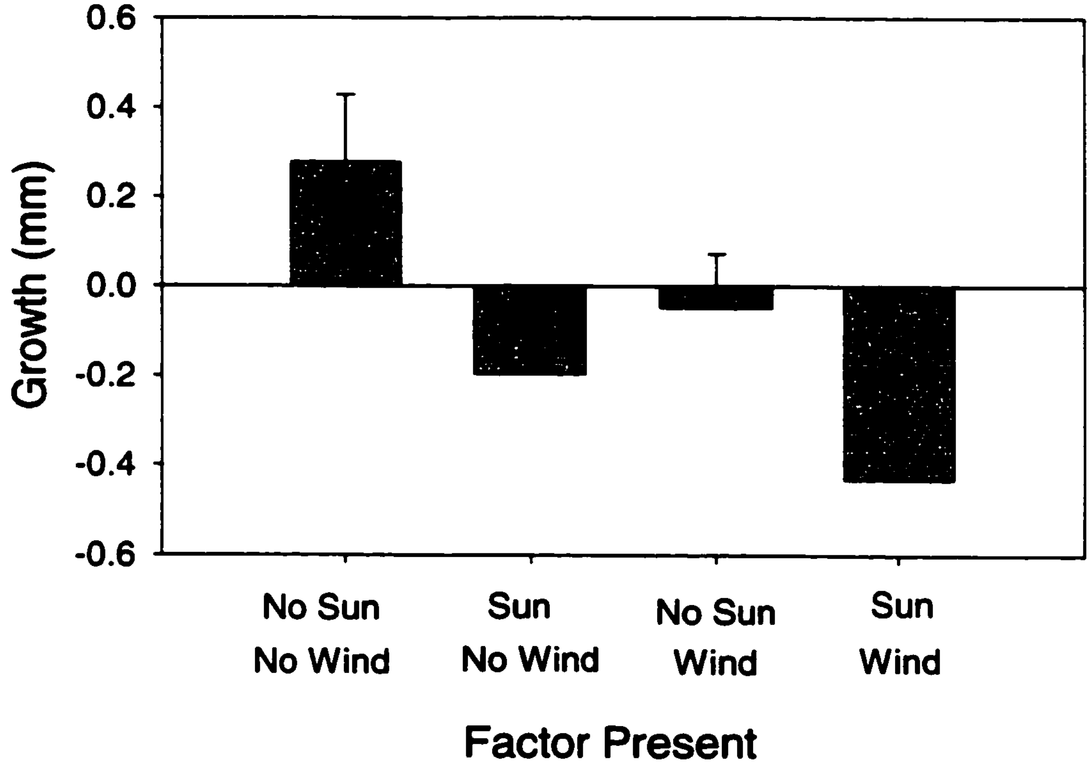


Figure 3.10. Sun-and-Wind-Exclusion Experiment. Mean net moss growth behind barriers that block out combinations of wind and sun, with standard error (2-way ANOVA, Model: F = 5.17, df = 3, p = 0.002; Sun: F = 10.40, df = 1, p = 0.001; Wind: F = 4.96, df = 1, p = 0.027).

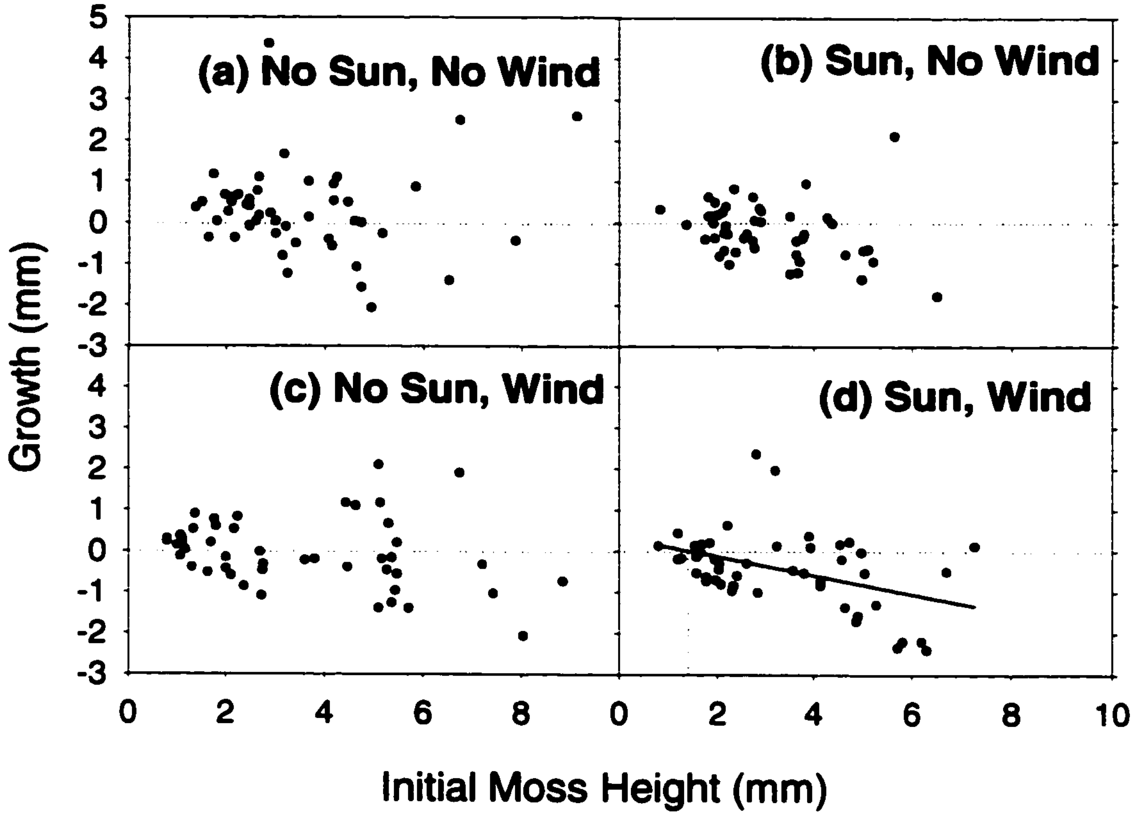


Figure 3.11. Equilibrium moss height (H_E) projected for all plots in sun-and-wind-exclusion experiment. (a) No sun + No wind: No model (p = 0.912). **(b)** Sun + No Wind: No model (p = 0.068) **(c)** No Sun + Wind: No model: (p = 0.096). **(d)** Sun + Wind: H_E = 1.43 mm; Model: y = 0.33 - 0.23x; p = 0.0032; r^2 = 0.159. Vertical dotted line indicates H_E for Sun + Wind treatment.

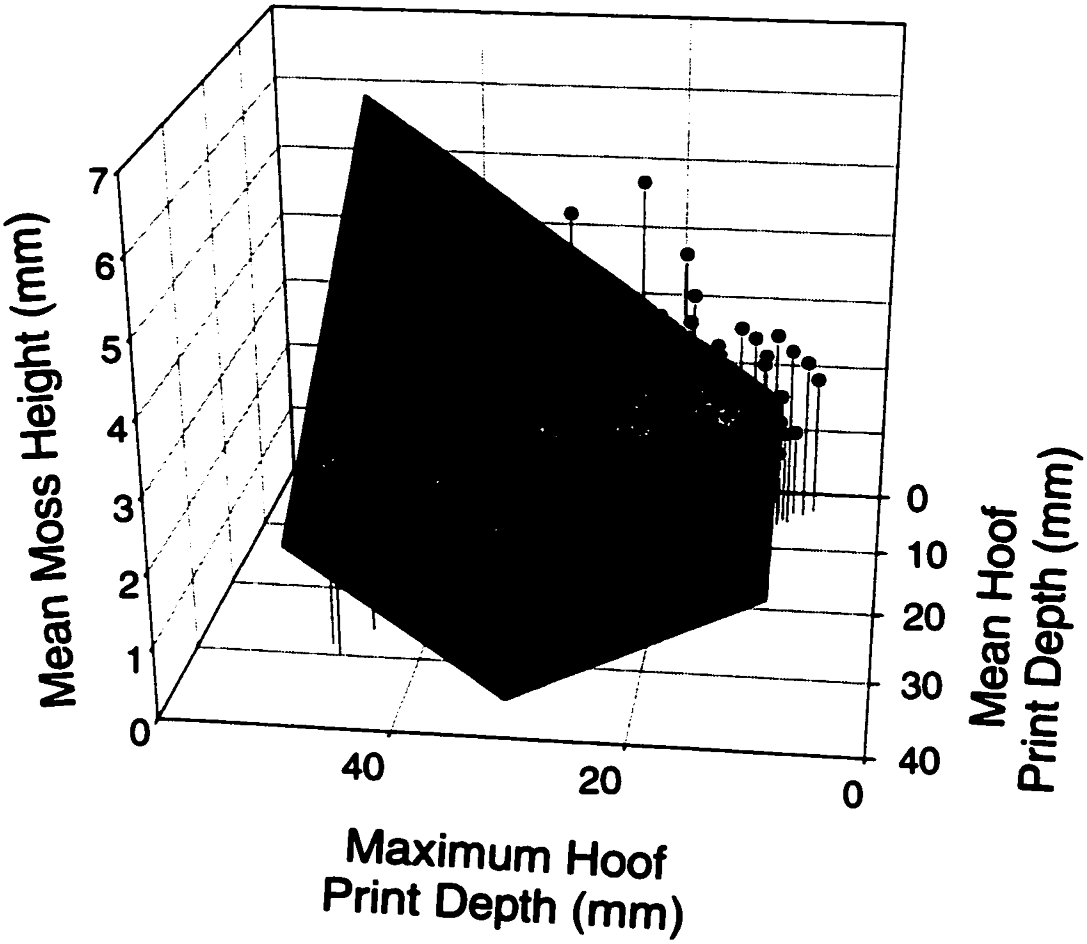


Figure 3.12. Natural patterns of moss growth in hoof prints (hoof print scale). Mean height of moss canopy as a function of maximum and mean hoof print depth. Symbols represent observed mean moss height for each hoof print. Surface plot represents the moss height predicted by the regression equation: $z = 1.487 + 0.105x - 0.136y$, where x = maximum hoof print depth, y = mean hoof print depth and z = mean moss height (Model: $p = 0.007$; $r^2 = 0.107$; Maximum hoof print depth: $p = 0.006$; Mean hoof print depth: $p = 0.032$).

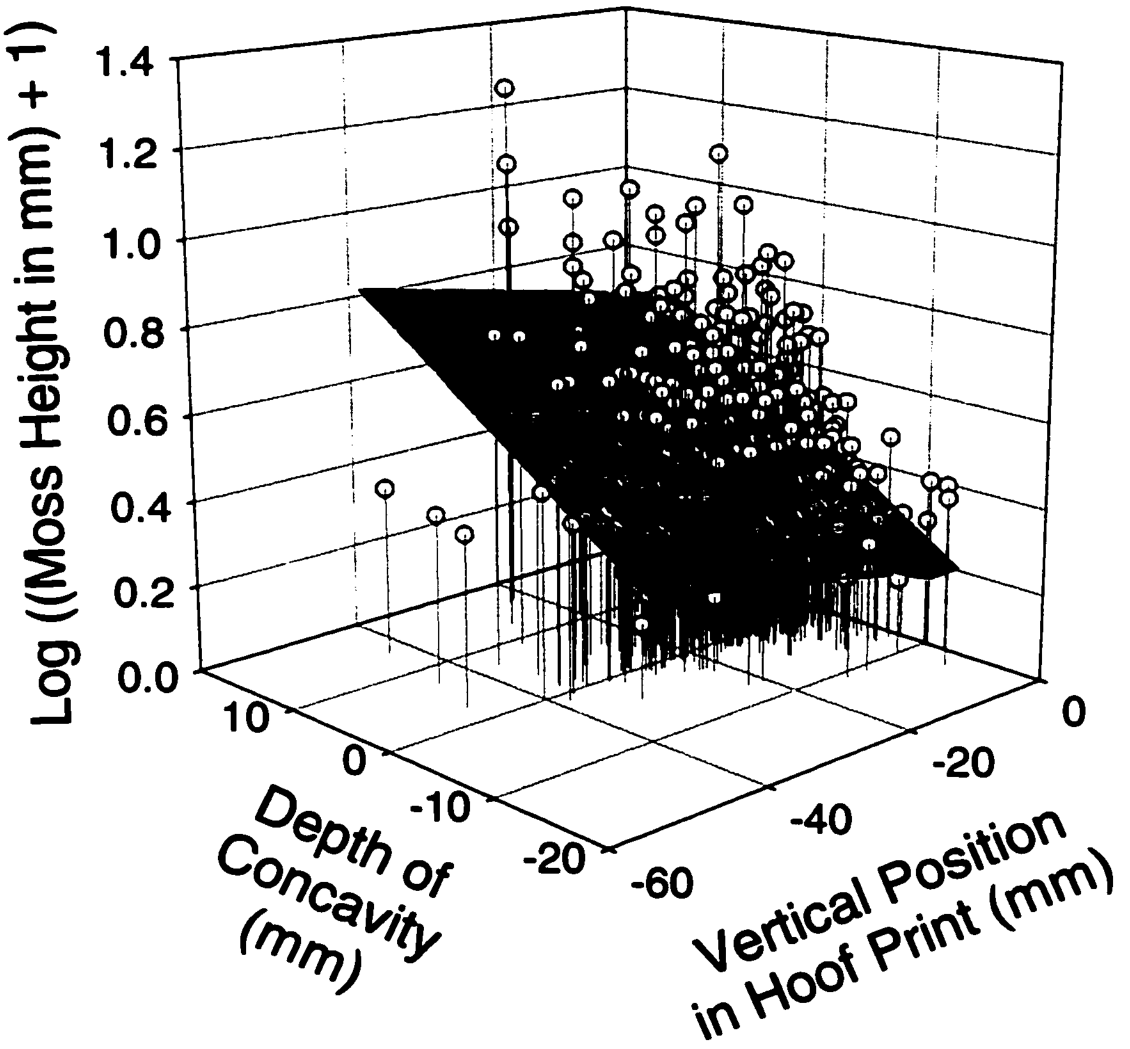


Figure 3.13. Natural patterns of moss growth in hoof prints (moss plant scale). Local height of moss canopy as a function of vertical position of moss within a hoof print and degree of concavity at measured point calculated for 1 cm on either side of measured point. Symbols represent observed moss height at a given depth and concavity. Surface plot represents the moss height predicted by the regression equation: Log (z + 1) = 0.438 - 0.00359x + 0.01786y, where x = vertical position, y = concavity and z = moss height ($p < 0.001$; $r^2 = 0.153$). For vertical position in hoof prints, increasing size of negative numbers represents increasing depth. For concavity, negative numbers represent mounds, zero represents flat surfaces and positive numbers represent dips.

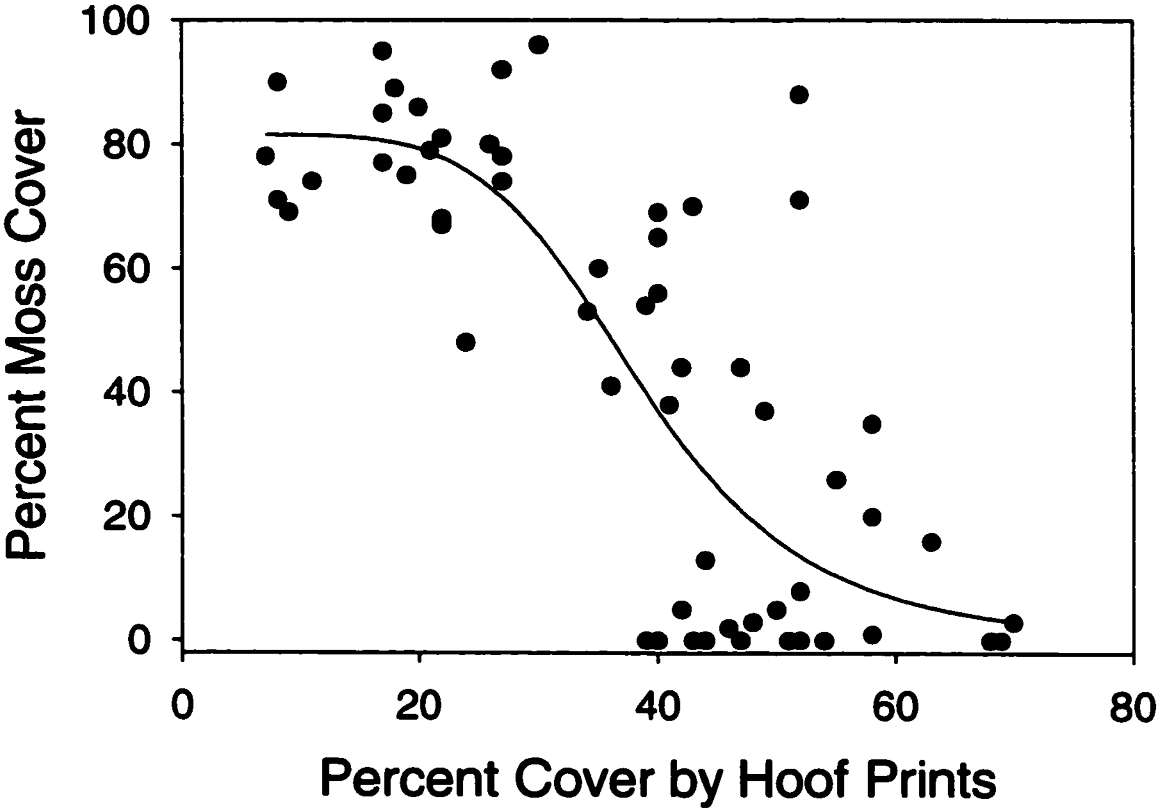


Figure 3.14. Effect of trampling intensity/frequency on moss abundance. Percent of ground covered by moss as a function of percent of ground covered by hoof prints of all ages. Symbols represent observed moss cover at a given print cover, which is a proxy for level of trampling intensity/frequency. Curve represents moss cover predicted by the regression equation: $y = 81.56/(1+(x/38.70)^{5.43})$, where x = percent cover by hoof prints and y = percent cover by moss ($p < 0.001$; $r^2 = 0.599$). The logistic model was a significantly better fit than a linear model for $0.01 < p < 0.02$.

Chapter 4

Summary

Overview

Ecosystem engineering is the process of habitat creation and modification by organisms, and the resulting modulation of resource flows to other species. It is as widespread as more familiar trophic interactions (Jones et al. 1994, 1997). Biological soil crust organisms are important autogenic ecosystem engineers. By mechanically fixing the soil surface (Eldridge and Kinnell 1997, Schulten 1985, Williams et al. 1995a, 1995b) they create a stable habitat for vascular plants and soil microflora and microfauna to colonize (Bliss and Gold 1999, Harper and Marble 1988, Watt 1938). However, disturbance may alter their distribution and the effectiveness of their engineering roles (Anderson et al. 1982a, Ladyman and Muldavin 1996, Marble and Harper 1989, Rogers and Lange 1971). Disturbance may itself be a type of ecosystem engineering. Trampling by ungulates creates physical structure at the air/soil interface (Butler 1995, Gifford et al. 1983) by generating microtopography. This microrelief influences the distribution of water by modulating desiccation caused by wind and radiation (Boeken and Shachak 1994). Poikilohydric soil crust organisms respond to the hydrological gradients generated by such microtopography (Alpert 1991, George et al. 2000, Scott 1982).

I investigated both the soil stabilizing ecosystem engineering roles of a soil crust bryophyte and the response of this moss in turn to ungulate trampling. Bryophytes are better suited to protect the soil from mechanical disturbance than algae, fungi or lichens because they often form thicker crusts (Belnap et al. 2001) and because they reduce erosion more effectively than bare soil, algae or lichens (Williams et al. 1995a, and references therein). This is because their complex stems and leaves slow air and water passing over them (Proctor 2000). As a result, however, they also effectively accumulate airborne sediment (Danin and Ganor 1991) that impedes the entrance of water into the soil (Blackburn and Skau 1974).

However, mosses may also be *recipients* of ecosystem engineering. They respond positively to microtopography that protects them from desiccation (Alpert 1991). Shaded microhabitats provide mosses with extended photosynthetic activity. While most research demonstrates that soil crust mosses are more sensitive to trampling than lichens or algae (Anderson et al. 1982b, Belnap 1993, Johansen and St. Clair 1986), these studies typically come from sandy desert environments, where trampling may not produce long-lasting microtopography in which mosses can reestablish.

On the Jasper Lakeshore in Jasper National Park, mechanical stabilization, inhibition of erosion and the influence on infiltration by the moss *Ceratodon purpureus* are important properties to evaluate. First, this is widespread on the otherwise sparsely vegetated soil, making its influence on the soil environment potentially important. Second, wind and rain are powerful agents of erosion in this ecosystem; therefore a stabilizing barrier at the soil/air interface is important to minimize soil loss. Third, the abundance of aeolian silt and clay captured by the moss may impede infiltration and lead to erosive runoff during particularly heavy rainstorms. Finally, the high intensity of trampling by ungulates (Dekker and Bradford 2000) requires a durable soil surface covering to prevent exposure of sediment to agents of erosion. This high intensity of trampling also necessitates evaluation of the response of *C. purpureus* to trampling, because the soil-stabilizing role of this moss obviously depends on its abundance.

Major Findings and Future Research

Ecosystem Engineering by the Moss

Stabilization Against Mechanical Damage

In this system, *C. purpureus* stabilizes the soil against two important agents of erosion: animals and weather. It forms a durable physical barrier on the soil surface that both resists penetration by the hooves of adult ungulates and reduces the access of flowing water to sediment particles (Chapter 2).

Well-developed crusts of *Ceratodon purpureus* resisted breakage 14 times as effectively as the weak physical crust that is formed on bare sediment abiotically (Chapter 2). Furthermore, these moss crusts supported three times as much mechanical pressure before breaking as did lichen soil crusts composed of the co-dominant *Toninia caeruleonigricans*. Most importantly, I calculate that well developed crusts of *C. purpureus* can support the weight of a typical adult elk, the largest species of ungulate encountered, without breaking. In reality, the sharp anterior edges of elk hooves often do penetrate moss crust, but sediment is exposed over only a small area. Future studies may investigate how this partial penetration of the crust influences the rate of germination of seeds captured from the wind by hoof prints, since particularly dense moss crusts may also impede penetration by seedling roots.

Prevention of Erosion

Undisturbed moss crust reduced sediment removal by falling and flowing water 15 times more than bare sediment did (Chapter 2). The erosive force generated per drop of water was comparable to that experienced during a light rain (Briggs et al. 1993), but turbulent water flow was also generated, likely causing rill erosion. Rainstorms often cause erosive runoff in deserts (Williams et al. 1995a). While rainstorms of similar proportions are rare in Jasper National Park, intense rainfall that causes rockslides and washes out railroad tracks is recorded every few decades (Holland and Coen 1982). The relationship between the volume of turbulent runoff water and the amount of sediment liberated suggests that the tightly packed moss stems slow the flow of water and reduce the access of this water to the sediment. Further work is required to confirm the exact mechanism by which the moss prevents erosion.

Reduction of Infiltration Rate

Unless record volumes of precipitation measured for 24-hour periods in Jasper fall within *one* hour, runoff is not likely to be generated at the Jasper Lakeshore because of the high infiltration rate of the soil, which can absorb up to 1141 mm/hr (Chapter 2). Moss reduced this rate to 785 mm/hr, probably both by its tightly packed stems and by the wind-captured silt and clay among its stems. Both moss tissue and clay swell when moist, potentially slowing infiltration (Blackburn and Skau 1974). Although runoff is unlikely to be generated, real-time rainfall intensity should be related to the volume of runoff water generated, if any, on moss-covered surfaces versus exposed sediment.

Facilitation of pedogenesis by sediment accretion in this aeolian environment may be an important function of *C. purpureus* that remains to be examined. Fine sediments are added to the Jasper Lakeshore in the winter when the Jasper Lakebed is exposed (Holland and Coen 1982). *Ceratodon purpureus* is particularly well suited to facilitate sediment accretion because it can emerge from under 7 cm of sand, its growth actually being *stimulated* by burial (Martinez and Maun 1999). This accelerated growth, coupled with enhanced growth inside sheltered microhabitats within hoof prints (Chapter 3), may explain the gradual infilling of hoof prints that occurs over time. The influence of this moss on natural rates of sediment accumulation merits further study.

Response of Moss to Ecosystem Engineering by Ungulates

Experimental Manipulation

The compressibility and structural integrity of the moss crust and of the sandy loam soil allows for the creation and persistence of microtopography that provides shelter from the desiccating agents of wind and solar radiation. The growth of *Ceratodon purpureus* responds positively to this ecosystem engineering (Chapter 3). Ungulate walking creates several types of microrelief. Trampled moss plants may therefore end up either in hoof prints, next to kicked up soil clods of soil called tip-ups or on the inclined floors of hoof prints.

In the deepest points in artificial hoof prints, moss plants equilibrated to a height twice as great as the height of undisturbed plants. This increase in height probably reflects a response to the concentration of water toward the lowest point in the hoof print by gravity and to shelter from wind.

When growing on undisturbed ground adjacent to simulated tip-ups, the moss equilibrated to a height 1.5 times as great on shaded northern exposures as on southern ones, demonstrating a strong response to shade. Second, an experiment designed to measure the relative influence of wind and sun on moss growth showed that solar radiation is the dominant desiccating agent, but that wind is also important. Moss plants in a fully exposed microhabitat equilibrated to a height four fifths as great as plants exposed to sun, but only one half as great as plants exposed to wind. Plants protected from both factors showed the greatest growth. Finally, moss plants equilibrated to a height three times as great on north-sloping soil as on south-sloping soil and about twice as great as on flat control plots.

The shoot growth dynamics of *C. purpureus* present an interesting topic for further research. When exposed to sun and wind, the moss population displays a net negative growth. Because most aeolian sediment delivery occurs in the winter, this pattern is probably not an illusion caused by burial, but an actual decrease in plant height. Instead of a decrease in height of individual shoots, however, it may be the disproportionate loss of taller segments due to death of these emergent shoots from moisture stress (Okland 2000) as the season progresses and the duration of daily solar radiation increases. This suggests that moss stems in dense crusts may exhibit inverse density-dependence of survival by protecting one another from desiccation (Bertness and Leonard 1997), a pattern sometimes observed in other bryophytes of xeric habitats (Pedersen et al. 2001). Because I did not track the heights of individual shoots, this hypothesis remains to be tested.

Another important field for experimentation is comparing the impact of ungulate trampling with that of human hiker trampling. Unlike the loose, sandy soils of the American Southwest, the silt-rich soil of the Jasper Lakeshore preserves impressions and boots probably create microrelief with a different geometry than elk hooves do. Boots may provide sufficient pressure to damage moss plants but because weight is distributed over a large area, there may not be enough pressure to create beneficial microrelief. Elk hooves, on the other hand, should ultimately do less damage to the moss crust by creating more shaded microhabitat relative to the area of soil that they disturb. As hiker populations increase in the mountain parks, this question will increase in importance.

Natural Patterns

Natural patterns of moss height and microtopography (Chapter 3) support the results of the experimental manipulations. They also reinforce the idea that moss plants respond most strongly to surface roughness at the smallest scale that I measured. Maximum hoof print depth, determined by measurements from a single point in a hoof print, predicted mean moss height better than did mean hoof print depth. Furthermore, when individual moss plants were used as units of observation, the depth of concavity at a horizontal scale of 2 cm was a better predictor of moss height than vertical position of the plants within hoof prints. Both results, however, suggest that water accumulation in small depressions influences the moisture budget of these poikilohydric plants.

Superimposed onto these patterns, however, was much unexplained variation in moss plant height, suggesting that an additional process may also influence moss growth and distribution. Colonization appears not to have occurred at many points within hoof prints, suggesting either differential survival of moss propagules in sheltered versus unsheltered locations or differential dispersal success. While I have addressed the effect of shelter on established moss crusts, dispersal remains to be investigated and may be an important determinant of pattern.

Two mechanisms of differential colonization may operate. First, by lowering air speed leeward of their walls (Lancaster 1994) hoof prints may act like traps for airborne moss propagules (Buck and Goffinet 2000), much as depressions do for seeds in deserts (Reichman 1984). This would increase the relative abundance of moss plants on the leeward sides of hoof print ledges. Second, ungulates may disperse moss propagules directly on their hooves. While little studied, dispersal of mosses by animal vectors is known from studies of both invertebrates (Koponen 1990) and vertebrates (Kimmerer and Young 1996). If either of these processes occurs at Jasper Lake, then ungulates may assist the recovery of the soil that they disturb by directly or indirectly "reseeding" it with moss. This hypothesis awaits controlled experimentation.

Conclusions

The Devona 1 Ecosite adjacent to Jasper Lake is characterized by active geomorphology, its surface constantly aggrading and eroding by the action of wind, water and mechanical disturbance (Holland and Coen 1982). This is especially true near the successionally young shore of the lake, where soil-stabilizing vascular plants are relatively sparse. To make matters worse, the area is heavily used by ungulates for winter forage (Holland and Coen 1982). To promote succession on this challenging site, a soil stabilizing agent is required that can resist the erosive action of weather and ungulate hooves alike. The moss *Ceratodon purpureus* fills this role particularly well. This autogenic engineer of the ecosystem minimizes exposure of erodible sediment by forming a biological soil crust that reduces ungulate hoof penetration 15-fold compared to bare sediment. Its tightly packed stems also impede water erosion by a factor of 15. While the moss also lowers the infiltration rate of water into the soil, generation of erosive runoff is unlikely because of the rapidly draining soil on which the moss grows.

However, not only does *C. purpureus* tolerate ungulate trampling, but also at low trampling intensity its growth is actually *stimulated* by the allogenic ecosystem engineering via trampling by ungulates. Experimental manipulation and study of natural moss growth patterns both demonstrate that *C. purpureus* responds positively to the hydrologically improved microhabitat created in the shade of hoof prints and tip-ups. The peculiar picture that emerges of this unique environment in the Canadian Rockies is one of interacting ecosystem engineers: the recovery of a crucial soil-stabilizing engineer is actually facilitated by the very organism that disturbs it in the first place.

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