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Dungpat Microenvironmental Effects on Germination and Establishment of Crested Wheatgrass

Ghulam Akbar
Utah State University

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DUNGPAT MICROENVIRONMENTAL EFFECTS ON GERMINATION AND ESTABLISHMENT OF CRESTED WHEATGRASS

by

Ghulam Akbar

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1994

DEDICATION

To the memories of my mother, the late Khadija Bibi,
who always had high aspirations for me.
May God rest her soul in peace.

ACKNOWLEDGMENTS

First of all, I wish to thank God Almighty who enabled me to achieve this destiny of my academic life. I am highly indebted to my major professor, Dr. Christopher A. Call, whose patience and untiring guidance were always with me during my stay at Utah State University. I found him not only an ideal teacher and scientist but an excellent human being. I am also thankful to my committee members, Drs. John C. Malechek, Eugene W. Schupp, Brien E. Norton, and Randall D. Wiedmeier, for their guidance and interest in my research project and for providing me a valuable learning experience during my stay at Utah State. Dr. Schupp was particularly helpful to me throughout my research, especially in analyzing data of seedling cohorts and also for his comments and guidance from time to time. Dr. Wiedmeier was extremely helpful for providing me facilities during the course of my research work. Drs. John Malechek and Ben Norton took a keen interest in my studies and encouraged me to fulfill this assignment successfully. Memory of Dr. Norton's thought-provoking lectures on grazing management and pastoral societies will go a long way with me.

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Ghulam Akbar

CONTENTS

CONTENTS (continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

ABSTRACT

Dungpat Microenvironmental Effects on Germination and Establishment of Crested Wheatgrass

by

Ghulam Akbar, Doctor of Philosophy

Utah State University, 1994

Major Professor: Dr. Christopher A. Call
Department: Range Science

Complementary greenhouse and field studies investigated the effects of ambient environmental conditions on cattle dungpat moisture, temperature, nutrient concentration, and crust formation dynamics, which in turn influence seed germination and seedling establishment in dungpats. 'Hycrest' crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) X *A. cristatum* (L.) Gaert.] was used as a representative revegetation species.

After collecting feces from Holstein steers that had been fed crested wheatgrass seeds, uniform dungpats were prepared and placed on two soil types (loam and coarse sand) in containers under three watering treatments (field capacity, ½ field capacity, and no water) in the greenhouse. Dungpat and underlying soil microenvironmental factors, and germination and seedling development, were monitored for 14 weeks. Moisture and temperature were favorable for germination during the first 4 weeks, but increasing crust thickness prevented most of the developing seedlings from emerging from dungpats. Seedling emergence, development, and survival were greatest at the peripheral region of dungpats on the loam soil at moisture contents of ½ field capacity or higher.

Uniform dungpats containing passed seeds and unpassed seeds were placed on a silt loam soil in the field in the spring (late April 1993) under natural and above-normal precipitation regimes and in the fall (late October 1993) under natural precipitation. Unpassed seeds were also broadcast and drill-seeded into soil seedbeds at the same times. Microenvironmental factors and germination and plant establishment were monitored for 49 weeks in the spring experiment and 17 weeks in the fall experiment. For dungpat treatments, seedling emergence and survival were greater for unpassed than passed seeds in both precipitation regimes; however, sufficient numbers of seedlings established from passed seeds, and these plants had greater biomass and similar or greater seed production than plants from unpassed seeds. Slight changes in nutrients in dungpats and underlying soil indicated that partial decomposition and mineralization of dungpats had occurred by the end of the spring experiment.

Both studies indicate that dungpat microenvironmental factors are greatly influenced by ambient moisture, temperature, and insolation, and by the nature of the underlying soil. These studies support the claim that plants established in dungpats could serve as nuclei of seed production for surrounding areas.

(154 pages)

CHAPTER 1

INTRODUCTION

Reseeding of rangelands by artificial means can be costly and risky. It typically involves the use of expensive equipment that may not be available in developing countries. An alternative method for reseeding rangelands is the use of domestic livestock (cattle and small ruminants) as seed disseminators. Although this approach is slower than large-scale mechanical approaches, it is inexpensive and environmentally benign (Dale 1992). Cattle not only disseminate the seeds, they may also provide a favorable microenvironment (dung) for seed germination and plant establishment in stressful environments.

Several studies have evaluated the potential of using domestic livestock, particularly cattle, to distribute seed onto rangelands. Some studies have shown that passage through the animal enhances germination while other studies have shown that it does not (Janzen 1984). Large seeds fed to cattle tend to be damaged more by mastication than smaller seeds (Ocumpaugh et al. 1992). However, if damage occurs, larger seeds retained a higher germination capability than did smaller seeds. There is evidence that small seeds of both herbaceous dicots and grasses consumed by livestock can survive passage through the animal gut and germinate directly in the dung or the soil where the dung is deposited (Janzen 1984).

Researchers have investigated the time of passage through, and the recovery of seeds from, the gut of different animals. When seeds of grass species were fed to dairy cows, it was found that although the bulk of the seed was passed in 72 hours, the time required for passage varied from 24 hours to 10 days, depending upon the plant species. During a 10-day collection period, recovery of ingested seed can vary from one-eighth to one-half of the amount fed (Lehrer and Tisdale 1956, Ozer 1979, Simao Neto et al. 1987, Gardener et al. 1993). Al-Mashikhi (1993) fed seeds of bluebunch wheatgrass (*Pseudoroegneria spicata*), crested wheatgrass (*Agropyron cristatum* x *A. desertorum*), tall wheatgrass (*Thinopyrum ponticum*), Russian wildrye (*Psathyrostachys juncea*), and a synthetic hybrid (*Pseudoroegneria spicata* x *Elytrigia repens*) to Holstein steers (300 kg) and found that the highest recovery of seeds for all species occurred 2 and 3 days after feeding, with about 20% of the ingested seeds being recovered within 6 days of feeding. Germination of undamaged, recovered seeds decreased with increased retention time in the digestive tract.

Seed size also plays an important role in seed retention time in the digestive tract of animals. For a number of animal species, the larger the seed, the longer the time it will remain in the gut, thus increasing the probability of digestion (Fenner 1985, Janzen 1984). Simao

Neto and Jones (1987) reported that viability of subtropical grass seeds decreased with increased time in the rumen. Viable seed recovery from the gut also depends on a number of factors such as the nature of the seed coats, the amount of seed in the diet, dietary quality, and animal type (Janzen 1984, Jones and Simao Neto 1987, Thomson et al. 1990, Schupp 1993).

Animal dung may provide better microenvironmental conditions for germination and establishment (Janzen 1984) than adjacent soil seedbeds. Animal dung not only enriches the soil for better seedling establishment, but freshly deposited dung may kill or suppress the resident vegetation and reduce competition for seedlings emerging from dung (Janzen 1984). Dung not only kills or suppresses the plants underneath, it also releases nutrients for those plants that emerge through it (Parish and Turkington 1989).

Although the potential role of livestock in range reseeding has been recognized, there is little information available on the influence of the dung microenvironment on seed germination and plant establishment. Jones et al. (1991), while investigating the levels of germinable seeds in topsoil and cattle dung in legume-grass and nitrogen-fertilized pastures in southeast Queensland, Australia, observed comparatively more emergence of grass and sedge seedlings (*Digitaria didactyla, Axonopus affinis, Eleusine indica and Cyperus* spp.) from dried rather than wet cattle feces during the first 3 months after excretion. Germination declined after 12 months. Seedling emergence was found to be higher in feces collected in summer and fall because most of the range species flower and seed during this period. More dicotyledons (*Desmodium triflorum* and *Zornia dyctiocarpa*) were found germinating in soil than in feces. However, no dung or soil microenvironmental factors were measured or related to germination and emergence in their study. To determine the effects of storage of seed in cattle dung on seed viability, Simao Neto and Jones (1986) mixed seeds of four pasture species [Signal grass (*Brachiaria decumbens*), Carpet grass (*Axonopis affinis*), Safari (*Trifolium semipilosum*), and Seca (*Stylosanthes scabra*)] with cattle feces, and then stored the feces for 0, 2, 7, and 21 days at three temperatures (constant temperatures of 10° C and 35° C, and 35/10° C with 8-hour day/16-hour night diurnal fluctuations). Seed viability decreased significantly with increased storage time at higher temperatures. All grass seeds and almost all of the soft seeds of legumes lost their viability when stored for 7-21 days, but there was little effect on hard legume seeds. The seeds used in this study were not passed through the animal gut.

Similarly, only limited information is available on decomposition of dungpats. Cattle dung is composed of water, residues of undigested herbage, a variety of microbial fauna and their metabolic products, and a significant amount of proteinaceous substances of animal origin (Marsh and Campling 1970, Matthiessen and Palmer 1988). Decomposition of these heterogenous substances is highly complex, and it begins as soon as dung is deposited. Microorganisms in the dungpat, insects, climate, and soil type are the factors that play an important role in decomposition and nutrient release from dung over time (Holter 1990, Madsen et al. 1990). While examining the effects of invermectin (a broad-spectrum antiparasitic drug) on the decomposition of dungpats, Madsen et al. (1990) collected as many as 20,000 invertebrates in 60 experimental pats over 2 years. Diptera insects comprised almost 80% of the total invertebrate population. Madsen et al. (1990) found that the composition of the fauna varied between years and seasons. Small invertebrates, animals, birds searching for insect larvae, and coprophagous beetles also facilitate the decomposition of dungpats (Ferrar 1975, Marsh and Campling 1970).

The rate of decomposition of dungpats is highly variable. Under optimal conditions in the tropics, only 24 hours may be required for dung beetles to degrade a dungpat, whereas under adverse conditions a dungpat may persist as long as 3 or 4 years (Madsen et al. 1990). The authors, however, did not define the optimal and adverse conditions. They further mentioned that under temperate conditions dungpats usually degrade and disappear within one grazing season, with maximum decomposition activity during autumn. Moreover, pats having a high fluid consistency disappeared at a faster rate in pasture studies (Weeda 1967, Marsh and Campling 1970). Holter and Hendriksen (1987) related disappearance and mineralization of dungpats to catabolism, and they measured respiration using chromium oxide and devised a mathematical model for disappearance.

The rate of drying of dungpats is governed by various factors such as temperature, precipitation, relative humidity, wind conditions, crust formation, soil moisture, and other properties of the soil where dung is deposited (Palmer and Bay 1982, Matthiessen and Palmer 1988). Due to hygroscopic properties of soils, water loss from sandy loam soils can occur more rapidly than from soils having more impervious conditions or from moist soils (Palmer and Bay 1982). The rate of drying of dungpats also depends on the consistency of the pat when dropped. Soft and wet pats excreted by dairy cattle dried to relatively thin crusts with a loosely fibrous texture that tended to break down easily (Ferrar 1975). Crust formation begins as dungpats are exposed to sunlight and the air. Shading reduces the rate of crust formation. The thickness of the crust typically increases with exposure time (Palmer and Bay 1982). Marsh and Campling (1970) described seven stages of ageing of dungpats, ranging from the wet, greenish-brown color of the freshly dropped pats to the light-brown chip of the well-dried dung. They noted that early formation of a crust in sunny, dry weather protected dungpats and delayed their disintegration. However, not much information is available on how crusting influences seedling emergence.

Moisture content of freshly voided cattle dungpats can range from 80 to 90%, depending upon diet quality (Palmer and Bay 1982). The innermost part (core) of the pat remains wetter than the periphery. The escape of moisture through the pat is either through evaporation or seepage into the ground. Palmer and Bay (1982) found that even under extreme summer conditions the moisture level in the core remained at 65-75% after 4 days. However, no details of the extreme summer conditions were given.

Dungpat temperature is also an important factor for the growth of micro-fauna and subsequent decomposition of the dung. Matthiessen and Palmer (1988) measured the temperature within dungpats using a thermistor probe. They measured the temperature in the center of one-liter and two-liter pats of fresh dung placed on the ground on an hourly basis for three weeks. After every third week the pats were replaced by fresh ones and the process of temperature recording was continued. Minimum dung temperature was found to be equal to the minimum air temperature, whereas maximum dung temperature was usually considerably higher than maximum air temperature. This difference was greater on sunny days and greater in the summer than in the winter. Dungpats 3 or 4 days old had a daily maximum temperature about 3.5° C greater than fresh dungpats. Greenham (1972) also measured the temperature within the dungpats using thermistors. He found a linear relationship between air and dung temperatures. He noted that dung temperature was affected by the sun's radiation and the angle of incidence. Due to evaporation, the temperature within fresh dung was lower, but once the surface crust started building up and evaporative cooling diminished, there was an increase in the temperature within the pat.

Cattle dung can have relatively high amounts of nutrients that are important for plant establishment (2.5 to 4% N, 0.8% K, 0.4% Na, 2.4% Ca, and 0.7% P) (Marsh and Campling 1970, Macqueen and Beirne 1975, Stevenson and Dindal 1987). Much of the N found in feces is in the form of live and dead bacteria. However, the number of bacteria in the dung varies between cows and between diets. Protozoa, parasitic nematodes, cestodes, and trematodes are also found in cattle feces (Marsh and Campling 1970). Total carbon content in dung dry matter has been estimated to be 36.7% (Murwira et al. 1990). In the same study, dung had a C/N ratio of 19, a pH (1:10 in water) of 7.6, and a water-holding capacity of 422%. A decrease in carbon content was reported at higher moisture contents in the dung (at >50% water holding capacity). Also, availability of carbon for decomposition was found to be lower under situations of water stress, i.e., at 12% and 24% water-holding capacity (Murwira et al. 1990).

Although some information is available on dungpat microenvironmental factors and decomposition, it has not been directly related to seed germination and plant establishment on rangelands. Most of the studies cited on dung dynamics have been carried out by the scientists in other disciplines, particularly entomology. Microenvironmental changes in animal feces over time may influence seed germination and subsequent plant establishment; therefore, it is important to investigate the impact of these changes on range forage species whose seeds retain their viability after passing through the animal digestive tract. This could be an important mechanism for introducing new species onto rangelands and maintaining or enhancing the spread of species already present. By having these aspects in mind, the broad objective of this research project is to investigate the influence of dung and soil microenvironmental factors, i.e., temperature, moisture, nutrients, and crusting, on the germination and establishment of 'Hycrest' crested wheatgrass [*Agropyron cristatum* (L.) Gaert. x *A. desertorum* (Fisch. ex Link) Schult.].

A series of related studies was designed to achieve this objective. The specific questions addressed in these studies are: (1) What is the ratio of damaged and undamaged seeds in the dungpats after passing through the cattle's digestive tract and is there any pattern of distribution of these seeds in dungpats? (2) Are passed seeds of crested wheatgrass superior to fresh seeds (not passed through digestive tract of cattle) in terms of viability, germinability, and seedling survival in dungpats under field conditions? (3) How long do crested wheatgrass seeds remain intact and germinable in dungpats and soil? (4) How do nutrients change in dungpats and underlying soil compared to soil without dungpats? (5) Is seedling vigor or dry matter yield per plant in dungpats comparable, superior, or inferior to that of plants in soil seedbeds? (6) What is the magnitude and intensity of different microenvironmental factors (temperature and moisture) inside dungpats and underlying soil and how do these factors influence seed germination and plant establishment? (7) Finally, how do different seasons of the year pose different stresses (drought and cold, freezing and thawing, etc.), and how do seeds and seedlings inside dungpats and soil respond to these stresses?

A preliminary experiment investigated the impacts of mastication and ruminant digestive processes on seed germinability. Passed seeds contained in feces were quantified and their locations were mapped in artificial (uniform) as well as naturally deposited dungpats. A greenhouse experiment determined how different soil types and soil moisture regimes affected dungpat moisture, temperature, nutrient, and crust formation dynamics, which, in turn, affected germination and seedling development of crested wheatgrass at different locations in a dungpat. The details of these studies are presented in Chapter 2. A field study compared microenvironmental factors (temperature, moisture, nutrients) of dungpats and soil seedbeds that influence germination and plant establishment at different planting times during the year. This study is discussed in Chapter 3. Chapter 4 provides a synthesis of research described in the earlier chapters and highlights the areas to be considered for future research.

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CHAPTER 2

CATTLE DUNGPAT MICROENVIRONMENTAL EFFECTS ON GERMINATION AND ESTABLISHMENT OF CRESTED WHEATGRASS: GREENHOUSE STUDY[1]

Abstract

A greenhouse study was conducted to determine the effects of ambient environmental conditions on cattle dungpat temperature, moisture, nutrients, and crust formation dynamics, which in turn influence ingested/passed seed germination and plant establishment at different locations in dungpats. 'Hycrest' crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult. X *A. cristatum* (L.) Gaert.] was used as a representative revegetation species. After collecting feces from Holstein steers (300 kg) that had each been fed 60,000 seeds of crested wheatgrass, uniform dungpats were prepared and placed on two soil types (loam and coarse sand) in containers under three initial watering treatments (field capacity, ½ field capacity, and no water). Dungpat and underlying soil microenvironmental factors were monitored over a 14-week period. Dungpat moisture and temperature conditions were favorable for germination during the first 4 weeks, but rapid crust formation prevented most of the

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[1] Coauthored by G. Akbar, C.A. Call, and R.D. Wiedmeier.

developing seedlings from emerging from the dungpats. Seedling emergence and development were greater at the periphery than at the interior of the dungpats, and greater on the underlying loam soil at ½ field capacity or higher than on the underlying sandy soil at similar moisture contents. Seedlings developing in dungpats on drier soils did not survive, but some remaining ungerminated seeds in dungpats might germinate at a later date if ambient environmental conditions became more favorable. These results indicate that cattle dungpats can serve as a favorable substrate for the germination and establishment of crested wheatgrass.

Introduction

Dispersal of seeds of desirable range plant species by domestic livestock has been recognized as a potential revegetation strategy for degraded rangelands (Archer and Pyke 1991). Several studies have characterized the survival of seeds passing through ruminant digestive systems (Lehrer and Tisdale 1956, Yamada and Kawaguchi 1971, 1972, Wilson and Hennessy 1977, Wicklow and Zak 1983, Simao Neto et al. 1987, Thomson et al. 1990, Barrow and Havstad 1992, Gardener et al. 1993, Peinetti et al. 1993). It is generally assumed that seeds surviving ingestion and digestion will be deposited in a moist, nutrient-rich medium that will facilitate germination and establishment (Archer and Pyke

1991), but little information is available concerning the effects of the dungpat microenvironment on these processes. Cattle dungpat microenvironmental conditions have been characterized primarily in relation to the development of insect pests that spend part of their life cycle in dung (Palmer and Bay 1982) or the role of coprophagous insects in dung decomposition (Ferrar 1975, Stevenson and Dindal 1987, Matthiessen and Palmer 1988).

A controlled environment study, using 'Hycrest' crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Schult. X A. cristatum (L.) Gaert.] as a representative range revegetation species, was conducted to determine: 1) the location of passed seeds in cattle dungpats, and 2) the effects of ambient environmental conditions on cattle dungpat temperature, moisture, nutrient, and crust formation dynamics, which in turn influence seed germination and plant establishment at different locations in dungpats.

Methods and Materials

Animal Feeding and Dungpat Preparation

Feeding and dung collection schedules were based upon results from a seed passage study (Al-Mashikhi 1993) conducted 2 months prior to this study. Al-Mashikhi (1993) fed approximately 60,000 seeds of 'Hycrest' crested wheatgrass to each of four Holstein steers (300 kg) and recovered 2, 8, 11, and 1% of ingested seeds, respectively, from their dung 1, 2, 3, and 4 days after feeding. The same four Holstein steers were fed the same grass hay diet (Bromus inermis, Dactylis glomerata, Festuca arundinacea, Phleum pratense, Juncus spp.; 69% *in vivo* dry matter digestibility, 7.8% crude protein, 63.6% neutral detergent fiber, and 39.2% acid detergent fiber) throughout the present study. A daily ration of 7.3 kg of grass hay per steer was equally divided between morning (0800 hours) and evening (1600 hours) feeding times. Steers were adapted to elevated metabolism crates indoors (14-hour light period/10-hour dark period, constant 10° C temperature) to facilitate dung collection.

During a preliminary 9-day feeding period, each steer was fed approximately 60,000 seeds of crested wheatgrass just prior to the morning feeding time on day 7. Dung containing passed seed was collected from the steers 48 hours later. Five naturally deposited dungpats were collected from two steers in a 7 X 7 m open pen. Dung collected beneath metabolism crates of the other two steers was mixed and poured into aluminum circular molds to form five uniform dungpats (20 cm diameter, 4 cm thickness, and weighing 2 kg). Uniform and naturally deposited dungpats were frozen at -20° C for 24 hours. Partially thawed (firm) dungpats were then cut into 5-cm-wide concentric circular bands, the outermost band being the peripheral region, the innermost circle being the core region, and the middle band(s) being the intermediate region (Fig. 1). Seeds in each band were recovered by passing the thawed dung slurry through a series of sieves (4 x 4 mm and 1 x 1 mm sizes). Recovered seeds were separated by hand (using a 10X magnifying lens) into two categories: undamaged [entire seeds (florets) with no visible damage to lemma and palea] and damaged [caryopsis only or entire seeds (florets) with visible damage to lemma and palea].

Dungpats used to study microenvironmental effects on seed germination and plant establishment were prepared during a subsequent 13-day feeding period. On days 7, 9, and 11, each steer was fed approximately 60,000 seeds of crested wheatgrass just prior to the morning feeding time. Dung containing passed seed was collected beneath metabolism crates 36-48 hours after each of the three seed-feeding events. At each of the three dung collection times (days 9, 11, and 13), dung was mixed and formed into 36 uniform dungpats (as previously described), resulting in a total of 108 uniform dungpats.

Soil Treatments and Controlled Environment Conditions

Fifty-four plastic containers (30 cm diameter, 50 cm deep, no drainage holes) were filled with air-dried loam soil and another 54 containers were filled with air-dried, coarse, washed sand. Within each soil type, 18 containers were watered to field capacity, 18 containers were watered

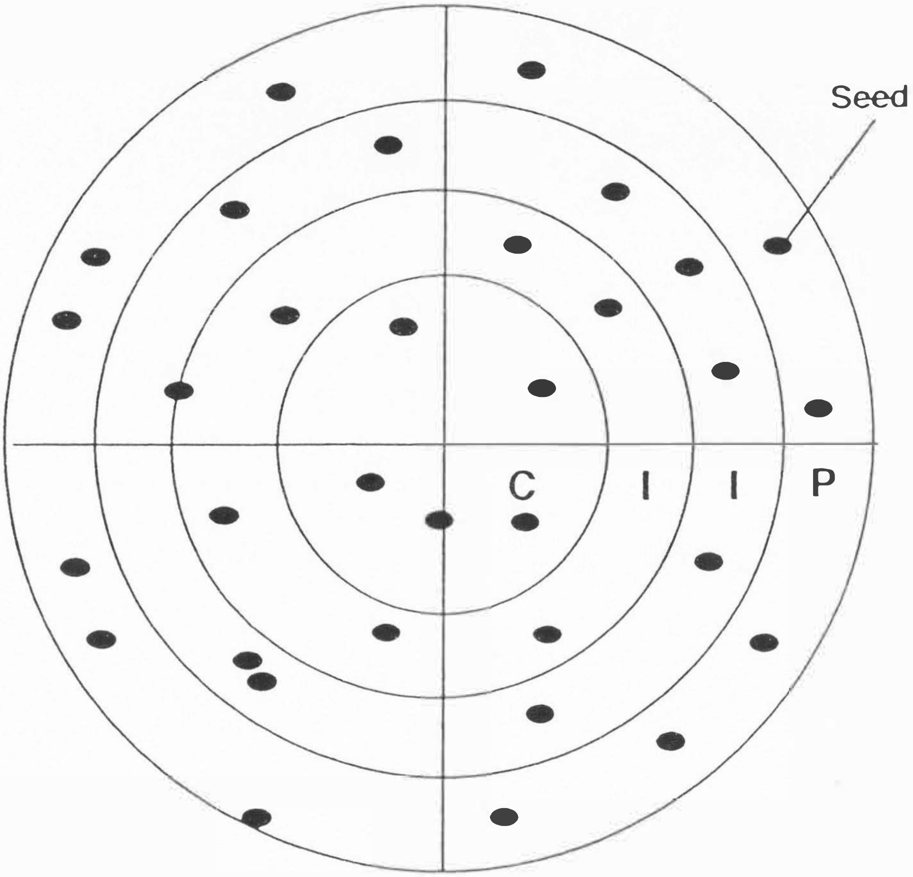

Figure 1. Uniform and natural dungpats were divided into 5-cm-wide concentric bands to determine the distribution of passed seeds. C = core region, I = intermediate region, and P = peripheral region.

to ½ field capacity, and 18 containers received no water. Watering treatments (based on soil moisture release curves developed from pressure plate analyses) were applied only once, just prior to placing a uniform dungpat on the soil in each container. Containers were then arranged in the greenhouse in a randomized complete block design with two replications of each of the six soil types by watering treatment combinations for each of nine sampling times (n = 108). Five days were required to set up the entire experiment due to previously described dungpat preparation constraints (36 dungpats prepared 48 hours after each of three seed-feeding events). To ensure uniform age of dungpats at the nine sampling times (weeks 1, 2, 3, 4, 6, 8, 10, 12, and 14) of the 14-week experiment, 36 dungpats were assigned to weeks 10, 12, and 14 on the first day, 36 dungpats to weeks 4, 6, and 8 on the third day, and 36 dungpats to weeks 1, 2, and 3 on the fifth day. The study was initiated on 22 March 1993 and terminated on 29 June 1993. During that period, ambient temperatures in the greenhouse ranged from 16-31° C and relative humidity ranged from 30-65%.

Dungpat and Underlying Soil Microenvironmental Parameters

Dungpat and underlying soil moisture content, and dungpat crust formation were determined at nine sampling times, and dungpat and underlying soil nutrient content and pH were determined at weeks 1, 5, and 14. At each sampling time, one dungpat in each replication of a soil type-watering treatment was cut into four equal pie-shaped sections while still on the soil surface. Two opposite sections were set aside for retrieval of ungerminated seeds (described below). Crust formation was measured in the other two opposite sections at the core, intermediate, and peripheral regions. Initially a handheld penetrometer was employed to measure crust hardness; however, penetration proved difficult after week 1. Crust formation (thickness) was subsequently measured with a vernier calliper on all remaining sampling dates. After measuring crust formation, samples were taken for moisture content at peripheral, intermediate, and core regions of the two dungpat sections, and soil samples were collected for moisture content at the same locations underneath the dungpat sections (Fig. 2).

Moisture content of dungpat and soil samples was determined gravimetrically by weighing samples, oven-drying at 60° C for 48 hours, and then reweighing. Additional samples were taken at core and peripheral regions of the dungpat sections and underlying soil for pH and nutrient analyses. Samples for nutrient analyses were dried at 40° C for 72 hours to avoid any loss of nitrogen from dungpats or soil. Dungpat pH was determined by the methods used by Christiansen and Webb (1990) while soil pH was determined by procedures described by McLean (1982). Total nitrogen (TN)

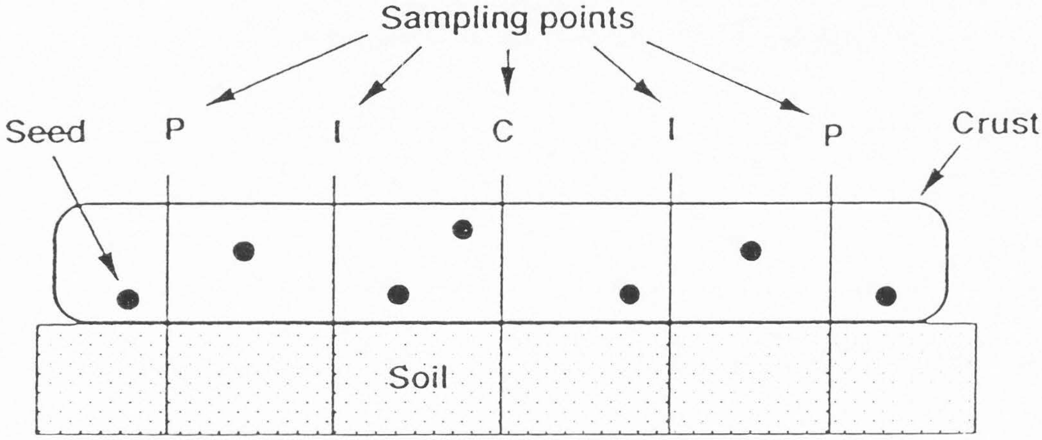

Figure 2. Cross-sectional diagram of uniform dungpat and underlying soil, showing sampling points for crust thickness, moisture content, and nutrient levels. C = core region, I = intermediate region, and P = peripheral region.

was measured by the Kjeldahl method (Bremner and Mulvaney 1982), ammonium (NH_4^+) and nitrate (NO_3^-) were determined using Lachet Quickchem AE following extraction with two molar KCl (Keeney and Nelson 1982), total phosphorus (P) was determined by Inductively Coupled Plasma Spectroscopy following digestion with nitric-perchloric acids (Jones et al. 1991), and organic matter (OM) was determined using the Walkley-Black method (Nelson and Sommers 1982).

Dungpat and underlying soil temperatures were monitored for two replications of each soil type-water treatment until the end of the study. Thermocouples were inserted in peripheral (2 cm from outer edge), upper core (1.5 cm from top), and lower core regions (3 cm from top) of dungpats, and in soil (2 cm depth) underlying peripheral and core regions of dungpats. These thermocouples were connected to a handheld digital thermometer, and temperatures were recorded daily at 0800 hours and 1300 hours.

Germination and Seedling Establishment

Seedlings were counted and harvested for aboveground biomass determination just prior to cutting dungpats into sections at each sampling time. Biomass was determined after oven-drying seedlings at 60° C for 48 hours. Seedling recruitment was monitored on a weekly basis over the 14-week study on two replications of each soil type-watering treatment that were harvested on weeks 10, 12, and 14.

Newly emerged seedlings were marked with a colored wire ring, and each cohort of seedlings was monitored until the time of sampling.

Fifty undamaged (no visible damage to lemma and palea under 10X lens), ungerminated seeds were extracted from the two remaining dungpat sections at each sampling time. Seeds were placed on moistened filter paper in petri dishes to determine germinability. Petri dishes were placed in a controlled environmental chamber with a night/day temperature regime of 10/20° C and a 12-hour photoperiod. A light intensity of 400 μmol m^{-2} s^{-1} was maintained during the daylight period. Filter paper in petri dishes was kept moist by adding distilled water as needed on a daily basis. Germinated seeds were counted daily over a 28-day period. Seeds were considered germinated when the coleoptile had emerged and the radicle had elongated to 5 mm (Copeland 1978).

Statistical Analysis

All data, except seedling survival data, were analyzed by analysis of variance using the Minitab Statistical Package (Minitab Inc. 1992). Moisture data were analyzed using a split-split plot design. At each sampling time, soil-water treatment combinations were treated as whole plots, substrates (dungpat or the underlying soil) were treated as split plots, and locations in substrates were treated as split-split plots. Seed germination, crust thickness, and seedling biomass data were analyzed using a randomized complete block design. The Least Significant Difference Test (*P*<0.05) (Steel and Torrie 1980) was used to separate mean values for germination and seedling biomass following a significant soil type x watering treatment interaction, and to separate means for dungpat and underlying soil moisture content and dungpat crust thickness following a significant soil type x watering treatment x dungpat location interaction. Survival of seedling cohorts was analyzed by a Mantel log-rank test (Mantel and Haenszel 1959) using the Systat-Survival Package (Steinberg and Colla 1988) and contingency tables (Wilkinson 1990).

Results and Discussion

Seed Location in Uniform and Natural Dungpats

Similar trends were noted for relative numbers of seeds at different locations in uniform and natural dungpats, even though uniform dungpats had 3.3 times the dung volume and 3.3 times the total number of passed seeds of natural dungpats (Table 1). Numbers of total seeds cm^{-3} and undamaged seeds cm^{-3} were highest in the core region and lowest in the peripheral region in both types of dungpats. The size and shape of natural dungpats (15.0 ± 0.6 cm diameter, 2.1 ± 0.2 cm thickness) and uniform dungpats (20.0 ± 0 cm diameter, 4.0 ± 0 cm thickness) differed, but the

Table 1. Number of seeds (± SE) at different locations in uniform dungpats (n=5) and natural dungpats (n=5)[1].

Location (band)	Volume (cm^3)	Average Number of Total Seeds	Average Number of Undamaged Seeds	Average Number of Damaged Seeds	Total Number Seeds/cm^3	Undamaged Seeds/cm^3	Damaged Seeds/^{3}
			Uniform dungpats				
Periphery	550	744 ± 33	660 ± 30	83 ± 7	1.4	1.2	0.2
Intermediate	392	582 ± 34	514 ± 28	68 ± 12	1.5	1.3	0.2
Intermediate	236	348 ± 30	314 ± 29	34 ± 5	1.5	1.3	0.1
Core	78	155 ± 11	137 ± 10	18 ± 2	2.0	1.8	0.2
Total	1256	1829 ± 61	1625 ± 57	203 ± 11	1.5	1.3	0.2
			Natural dungpats				
Periphery	211	243 ± 36	224 ± 31	19 ± 5	1.2	1.1	0.1
Intermediate	127	199 ± 29	185 ± 25	15 ± 4	1.6	1.5	0.1
Core	42	117 ± 18	111 ± 18	7 ± 1	2.8	2.6	0.2
Total	380	559 ± 75	520 ± 67	41 ± 9	1.5	1.4	0.1

[1] Uniform dungpats had a diameter of 20 cm and a thickness of 4 cm, and were divided into four concentric bands, each having a 5 cm width; band 1 = periphery, bands 2 and 3 = intermediate zone, and band 4 = core. Natural dungpats had an average diameter of 15 cm and an average thickness of 2.1 cm, and were divided into three concentric bands, each having a 5 cm width; band 1 = periphery, band 2 = intermediate zone, and band 3 = core.

distribution of seeds in uniform dungpats was representative of that in natural dungpats.

Moisture Content in Uniform Dungpats and Underlying Soils

Moisture content of dungpats on the various soil type/watering treatments decreased in a similar manner over the study period (Fig. 3). Moisture content was 78-79% within 24 hours after dungpat placement, and declined to about 70% at week 3. With the exception of dungpats on the loam/field capacity treatment (Fig. 3d), moisture content decreased to less than 10% by week 6. After that time, dungpat moisture content was not significantly different ($P<0.05$) from the moisture content of the surface soil underlying dungpats in all soil-type/watering treatments (Figs. 3). Moisture content in the core region of dungpats was not significantly higher ($P<0.05$) than in the intermediate and peripheral regions throughout the study period (data not shown).

Cattle dungpat moisture content is dependent on a number of factors, including water intake, quantity and quality (fiber content) of dry matter consumed (Lysyk et al. 1985), and environmental factors such as insolation, air temperature and relative humidity, and hygroscopic properties of underlying soils (Palmer and Bay 1982). Several studies have reported that freshly voided cattle dung has a moisture content ranging from 80-90% (Bornemissza

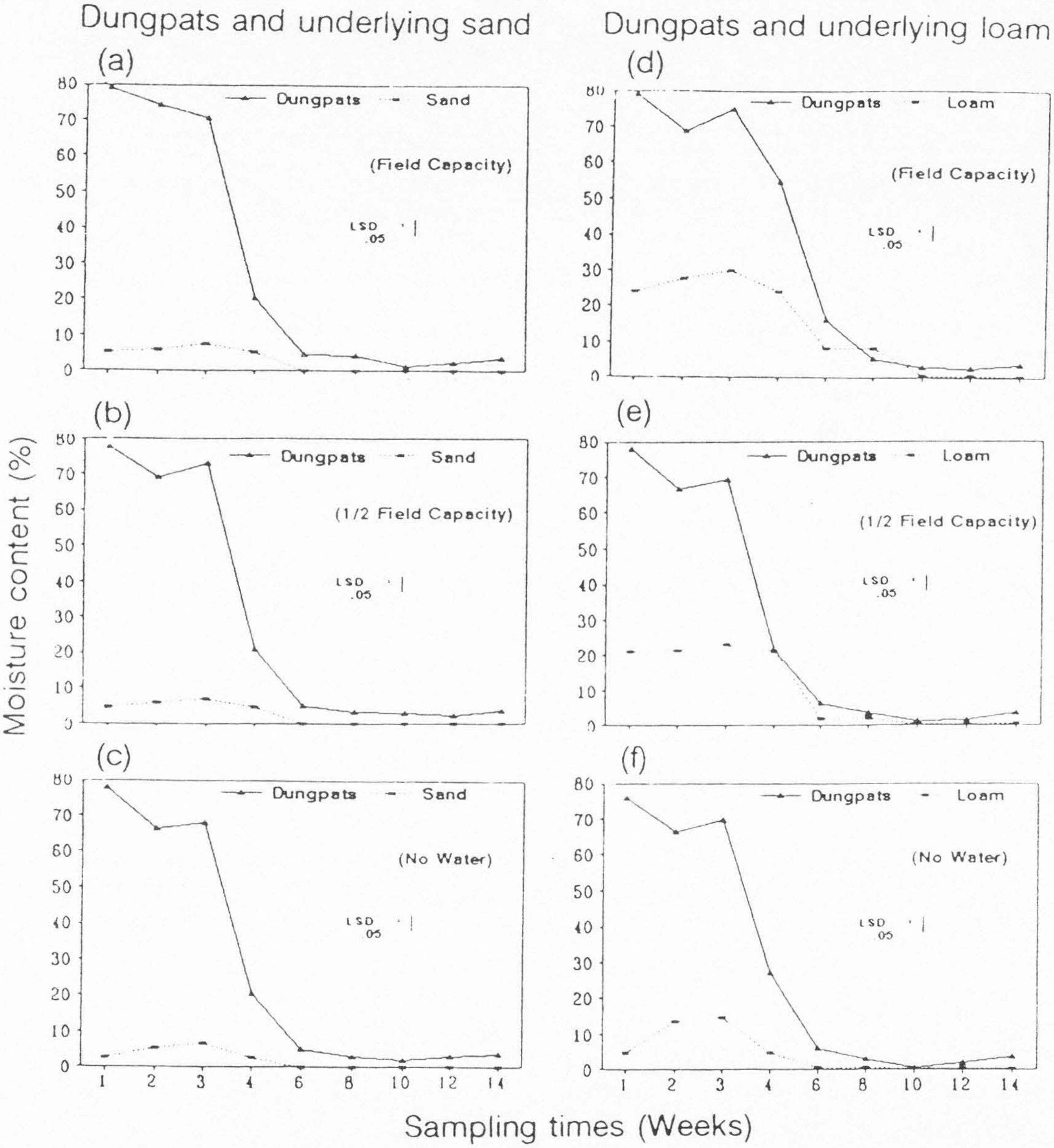

Figure 3. Moisture dynamics in uniform dungpats and underlying sand (a-c) and loam (d-f) soils at three initial watering regimes (field capacity, ½ field capacity, and no water).

and Williams 1970, Palmer and Bay 1982). Stevenson and Dindal (1987) reported that after 40 days, cattle dung was nearly dry except in the center of the pat where moisture was still available. Palmer and Bay (1982) investigated the effects of the dung deposition environment on moisture loss by placing cattle dungpats on dry sand and plastic sheeting, and in shade and direct sunlight. After 6 days, shaded pats retained more moisture than those exposed to direct sunlight, and pats placed on plastic sheeting retained more moisture than those placed on dry sand. Palmer and Bay (1982) concluded that loss of dungpat moisture to the underlying soil was the most important factor to be considered in the deposition environment.

Regardless of initial soil-watering treatment, moisture contents of sand (Fig. 3a-c) and loam (Fig. 3d-f) soils beneath dungpats increased during weeks 2 and 3 as moisture was withdrawn from dungpats. The loam/no-water treatment extracted the most water from dungpats during this period (Fig. 3f). Moisture contents of underlying surface soils decreased to near 0% at week 6 in all soil-type/watering treatments except the loam/field-capacity treatment (Fig. 3d), which decreased to near 0% at week 10. Moisture contents were not measured deeper in the soil profiles because of the disruption caused by gravimetric sampling; however, enough moisture was available over the 14-week period to support the growth of plants that emerged from dungpats in the loam soil initially watered to field capacity and ½ field capacity.

The three initial soil water levels (field capacity, ½ field capacity, and no water) were selected to represent field conditions that can exist in the Great Basin region, where soil moisture is recharged to varying degrees from spring snowmelt and decreases gradually over the growing season. Moisture content of dungpats and soil immediately beneath dungpats remains favorable for germination and initial seedling development during the first 3-4 weeks after dungpat placement. Roots of seedlings developing in dungpats should penetrate below the underlying surface soil layer and follow the moisture front as it moves deeper into the soil profile by week 6 (week 10 for loam soil initially at field capacity) to ensure survival. Thus, the initial high moisture content in dungpats may extend the normal period for germination and seedling development by only a few weeks.

Temperature in Uniform Dungpats and Underlying Soils

Maximum temperatures (measured at 1300 hours) in dungpats and underlying surface soils followed similar, fluctuating trends over the 14-week period, but dungpat temperatures generally remained higher than soil temperatures (Fig. 4). Increases in temperatures in both substrates were associated with sunny days and higher

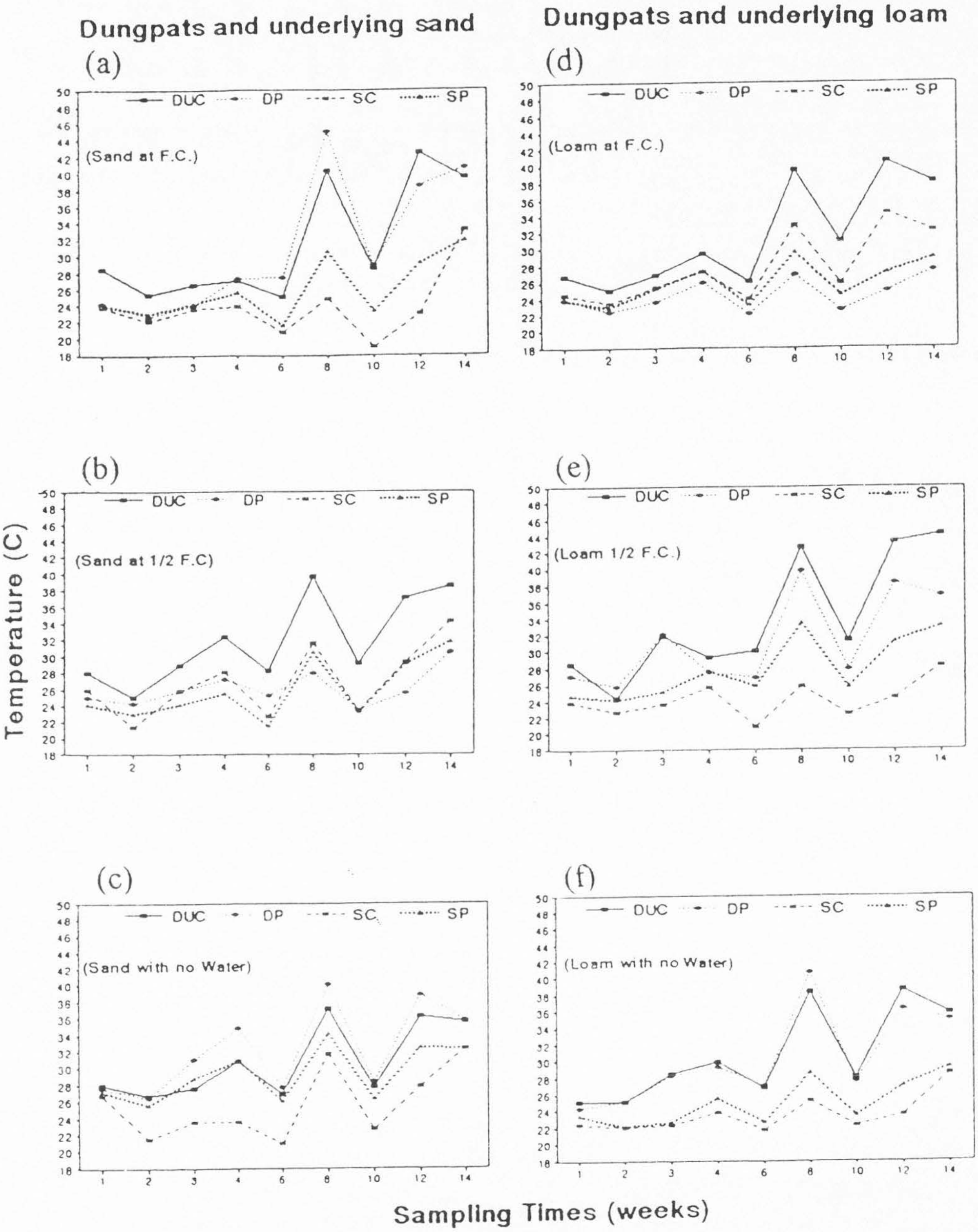

Figure 4. Maximum temperature taken at 1300 hours in uniform dungpats and underlying sand (a-c) and loam (d-f) soils at three initial watering regimes (field capacity, ½ field capacity, and no water). DUC = dungpat upper core, DP = dungpat periphery, SC = soil core (at 2 cm depth), and SP = soil periphery (at 2 cm depth).

greenhouse air temperatures, whereas decreases were associated with cool, rainy, and cloudy days. Temperatures in dungpats during the first few weeks were lower than during the latter weeks because of evaporative cooling and an initial lighter color. With the passage of time, dungpat crust development reduced evaporative moisture loss and an increasingly darker color absorbed more solar radiation, resulting in increased temperatures. Up to week 6, maximum temperatures at the core and peripheral regions of dungpats on all soil-type/watering treatments were near the maximum temperature (30° C) for crested wheatgrass seed germination (Young and Evans 1982). After week 6, dungpat temperatures were generally too high for effective germination. The lowest dungpat maximum temperatures were maintained in the peripheral region of dungpats on the loam/field-capacity treatment (Fig. 4d). The highest emergence and establishment of crested wheatgrass seedlings was also observed in the peripheral region of these dungpats. Maximum temperatures in the core and peripheral regions of the surface soils underlying dungpats were generally near or below 30° C, and thus favorable for the development of seedling roots extending down from dungpats. Dungpat peripheral temperatures may have been elevated above core temperatures in some soil-type/watering treatments because the container edges may have blocked air movement and reflected radiation.

Nutrient Dynamics in Uniform Dungpats and Underlying Soils

Nutrient data for dungpats and underlying soils (Tables 2 and 3) represent one composite sample from two replications. These data were collected for the purpose of identifying general trends only.

For dungpats (Table 2), total N increased slightly, total P did not change, and organic matter decreased slightly over the 14-week study period, regardless of underlying soil type and initial moisture level. The increase in the concentration of total N in dungpats reflects the simultaneous decrease in organic matter in dungpats, due to the leaching of organic acids into the underlying soil. Both NO_3^- and NH_4^+ increased from week 1 to week 5 and remained at these higher levels until week 14, indicating that ammonification and nitrification were taking place in dungpats.

Prior to dungpat placement on the two soil types, total N, NO_3^-, total P, and organic matter were lower in the sand than in the loam (Table 3). The sand, however, had a higher NH_4^+ content than the loam. After dungpat placement, total N increased slightly in the sand and loam over the 14-week period, regardless of initial moisture level. Nitrate increased in both soil types from week 1 to week 5 and then decreased slightly from week 5 to week 14. Ammonium increased slightly in the sand by week 1 and then decreased below the pretreatment level for the remainder of the study.

Table 2. Nutrient status of dungpats 1, 5, and 14 weeks after placement on sand and loam soils at three moisture levels.

Soil Type and Moisture[1]	Total N (%)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)	Total P (%)	O.M. (%)
		Week 1			
S1M1	1.81	<0.20	28.4	0.24	82.6
S1M2	1.71	<0.20	29.6	0.20	75.6
S1M3	1.86	<0.20	28.2	0.23	79.8
S2M1	1.81	<0.20	29.5	0.25	83.2
S2M2	1.93	<0.20	31.0	0.21	85.5
S2M3	1.80	3.60	31.3	0.22	80.1
		Week 5			
S1M1	2.11	3.67	36.4	0.23	84.9
S1M2	2.10	2.20	33.4	0.24	83.8
S1M3	2.10	0.74	37.2	0.23	82.9
S2M1	2.18	3.20	37.6	0.23	85.0
S2M2	2.18	2.23	35.9	0.24	85.5
S2M3	2.18	1.06	35.1	0.24	85.1
		Week 14			
S1M1	2.09	1.92	31.6	0.23	77.8
S1M2	1.97	2.05	29.9	0.21	77.4
S1M3	2.13	3.09	35.1	0.25	79.7
S2M1	2.29	4.44	39.0	0.26	84.3
S2M2	2.17	3.94	37.8	0.24	82.2
S2M3	2.01	3.66	36.0	0.24	79.7

[1] S1 = sand, S2 = loam, M1 = field capacity, M2 = ½ field capacity, M3 = no water.

Table 3. Nutrient status of sand and loam soils prior to placement of dungpats (pretreatment) and 1, 5, and 14 weeks after placement of dungpats.

Soil Type and Moisture[1]	Total N (%)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)	Total P (%)	O.M. (%)
		Week 1			
		Pretreatment			
Sand (S1)	<0.005	<0.5	3.83	0.01	0.05
Loam (S2)	0.020	4.5	2.23	0.06	0.22
		Week 1			
S1M1	0.01	<1.0	3.70	0.01	0.13
S1M2	<0.01	1.1	3.99	0.01	0.10
S1M3	<0.01	<1.0	4.75	0.01	0.05
S2M1	0.02	2.5	20.85	0.05	0.43
S2M2	0.02	3.3	20.95	0.05	0.50
S2M3	0.02	3.3	23.05	0.05	0.50
		Week 5			
S1M1	<0.01	2.5	2.26	0.01	0.07
S1M2	<0.01	1.1	3.05	0.01	0.09
S1M3	<0.01	1.5	2.89	0.01	0.06
S2M1	0.03	28.1	2.55	0.05	0.55
S2M2	0.03	57.1	3.22	0.05	0.46
S2M3	0.04	23.0	38.16	0.05	0.50
		Week 14			
S1M1	0.01	1.7	1.76	0.01	0.06
S1M2	0.01	<1.0	2.62	0.01	0.17
S1M3	0.01	<1.0	7.61	0.01	0.14
S2M1	0.04	12.6	13.21	0.06	0.87
S2M2	0.03	50.8	3.86	0.05	0.55
S2M3	0.03	6.0	22.05	0.05	0.44

[1] S1 = sand, S2 = loam, M1 = field capacity, M2 = 1/2 field capacity, and M3 = no water.

Ammonium increased about five-fold in the loam by week 1 and then decreased at later sampling times. Total P did not change in any of the soil-type/watering treatments. Percent organic matter doubled in the underlying loam by week 1 and remained near that level until week 14, while an increase in the underlying sand was not noted until week 14.

Nutrient data from a 14-week greenhouse study such as this must be interpreted with caution. Increases in NH_4^+ and NO_3^- in dungpats over time indicate that mineralization and nitrification were taking place. However, it is more difficult to characterize the increases in NH_4^+ and NO_3^- in the underlying soils because they could be the result of nitrogen transformations occurring in the soil and/or NH_4^+ and NO_3^- additions from dungpat leachates, and they are influenced by soil pH and root absorption. Over the 14-week period, the pH of dungpats increased from 7.1 to 8.9, and the pH of underlying loam and sand soils increased from 7.8 to 9.0 and 8.2 to 9.5, respectively. In general, a higher pH favors the uptake of NH_4^+ over NO_3^- (Reisenauer 1978). In addition, important variables that influence nutrient transformations under field conditions, e.g., periodic precipitation, wide diurnal changes in temperature, and a diversity of invertebrate microfauna were absent or highly constrained under greenhouse conditions.

Crust Development on Uniform Dungpats

Crust development started as soon as dungpats were placed on the soils in the greenhouse. During week 1, crust development, as measured by a penetrometer, was greater on the peripheral regions (0.05 kg cm^{-2}) than on the core regions (0.03 kg cm^{-2}) of loam and sand soils. By week 2, it was not possible to use the penetrometer to measure crust development, so crust thickness was measured using a calliper.

Crust thickness increased by 4-6 mm from week 2 to week 3 at core and peripheral locations on dungpats on both soil types (Fig. 5). Crust thickness at the periphery was significantly greater ($P<0.05$) than at the core from week 4 to week 10 for both soil types. The core and peripheral regions were similar in terms of crust thickness by the last week of the study. Crusting also occurred on the underside of dungpats on dry loam and dry sand soils by week 2.

Crusting is an important factor in terms of creating a mechanical resistance for emerging coleoptiles and radicles of crested wheatgrass seedlings. Seeds germinated inside dungpats until week 4, but most seedlings, and especially those located deep in dungpats, could not emerge through the increasingly thick crust by this time. Crust development is strongly influenced by dungpat temperature and moisture content (Landin 1961, Palmer and Bay 1982), which were previously described. As crust development and maximum

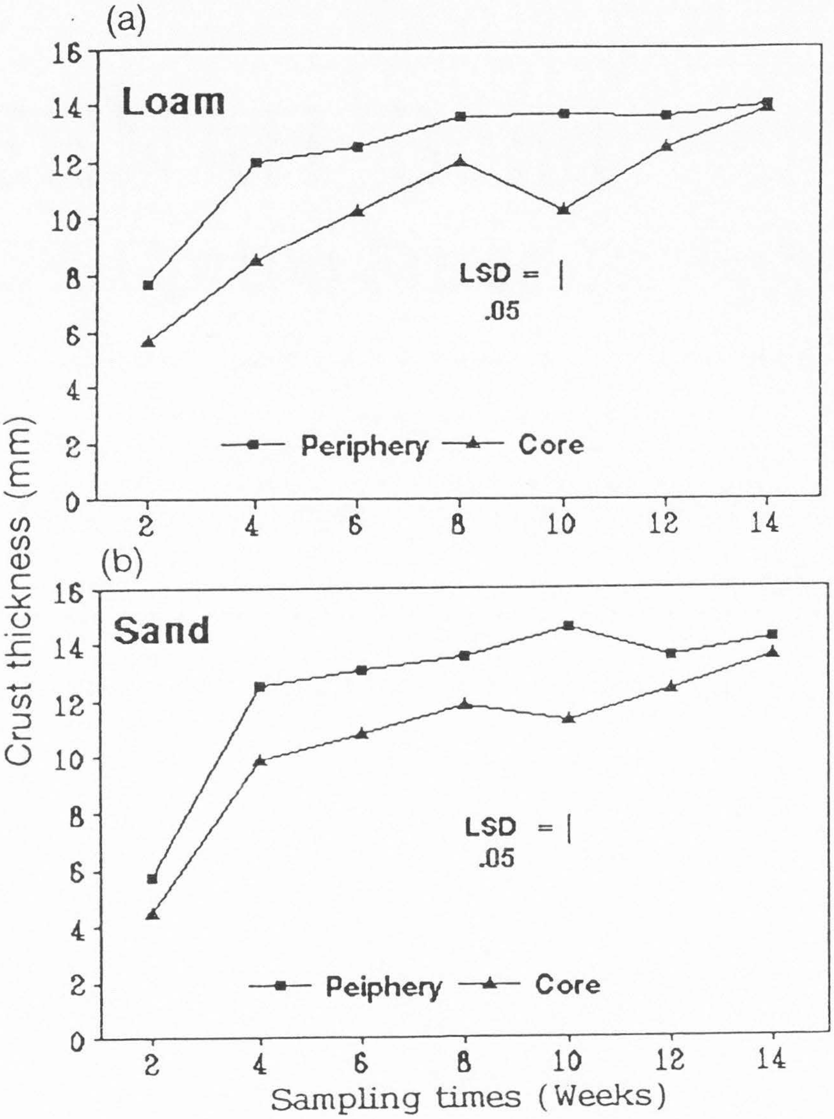

Figure 5. Crust thickness (mm) at core and peripheral regions of uniform dungpats placed on loam (a) and sand (b) soil.

temperature increase, and moisture content decreases with time, it becomes evident that conditions that favor germination and seedling development may only occur during the first 4 weeks after dungpat placement. Although crust development on natural dungpats was not measured, observations during the time of seed counting revealed that crusts were similar in thickness to those of uniform dungpats.

Germination and Seedling Development

Previously described dungpat moisture and temperature conditions promoted germination of passed seeds in all dungpats during the first 4 weeks of the study. However, most of the newly developing seedlings failed to penetrate through the rapidly forming crust and decomposed inside dungpats, primarily in the core region. The seedlings that did emerge were grouped into four cohorts based upon their week of emergence, i.e., cohort 1 emerged during week 1, cohort 2 emerged during week 2, etc.

A total of 82, 21, 8, and 7 seedlings emerged in cohorts 1, 2, 3, and 4, respectively. Thus seedling recruitment was highest in cohort 1, followed by cohorts 2, 3, and 4, respectively (Fig. 6a). Although a greater number of seedlings survived from the earlier cohorts (Fig. 6a), no significant difference (*P*=0.264) was observed when proportional survival of all the seedling cohorts was

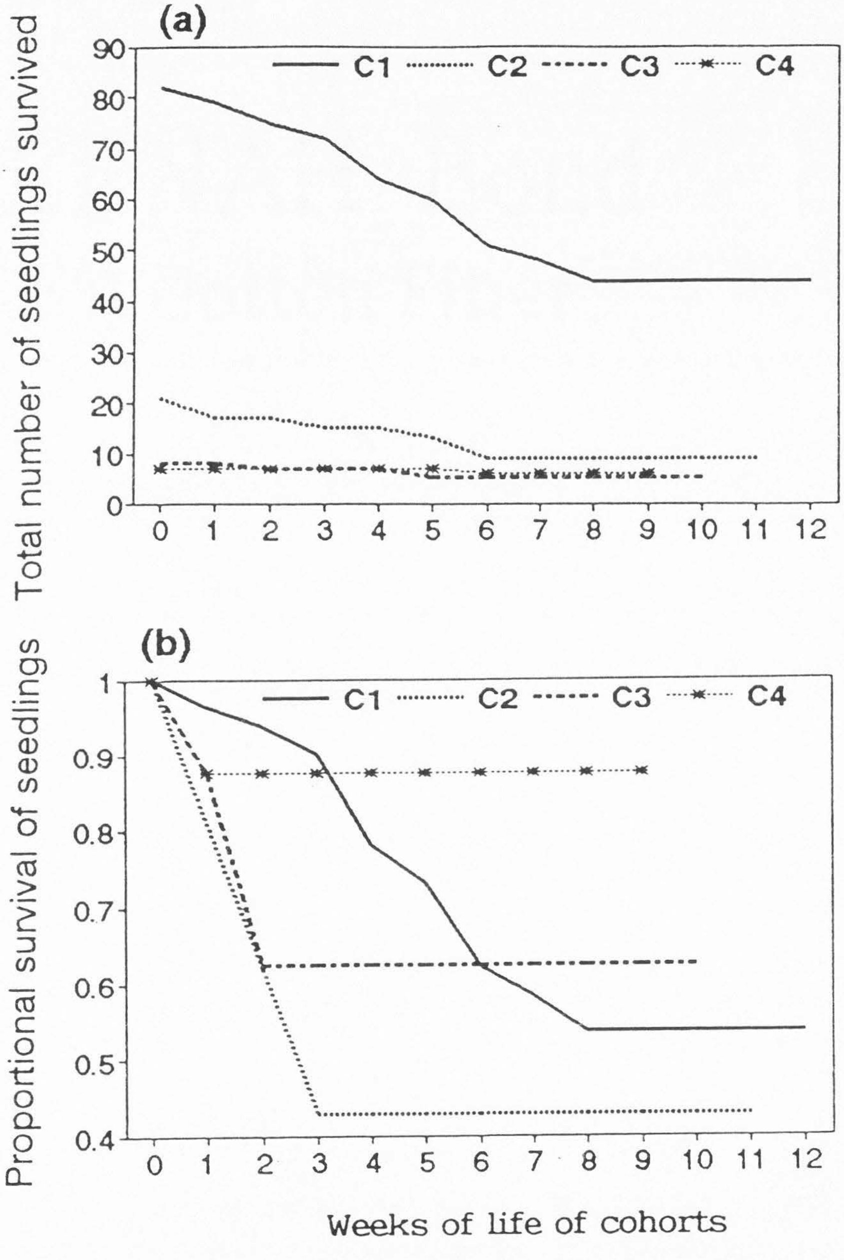

Figure 6. Survivorship curves for cohorts of seedlings emerging from uniform dungpats: (a) total number of seedlings that survived in each cohort, and (b) proportional survival of seedlings in each cohort.

analyzed (Fig 6b). Seedling survival was greatly influenced by the initial moisture content of the underlying soils and the location of germination and seedling emergence in the dungpat. Most of the seedlings in each cohort emerged from dungpats placed on the loam soil at field capacity and ½ field capacity. Some seedlings emerged from dungpats on the dry loam and from dungpats on the sand at all three moisture levels. However, no significant difference (*P*=0.797) was observed in terms of survival of seedlings at the field capacity or ½ field capacity moisture level. Regardless of soil-type/watering treatment, most of the seedlings in each cohort emerged at the peripheral region of dungpats, while some seedlings emerged through cracks in the crust at the core and intermediate regions. The periphery and cracks in the core region of dungpats proved to be safe sites for seedlings. These "safe sites" allowed the newly emerging seedlings to push their root system down into the soil to extract moisture and nutrients. The most hazardous event for the newly emerging seedlings is considered to be desiccation, particularly at the time when the root system is not fully developed (Johnson and Aguirre 1991, Harper 1977). Under greenhouse conditions, where moisture was applied only once, desiccation may have been one of the major causes of mortality. In spite of the beneficial role of the peripheral location for the newly emerging seedlings, no significant difference (*P*=0.574) was observed in seedling survival between core and the peripheral regions. Seedling survival was also analyzed using a contingency test (Wilkinson 1990), but no significant difference was observed for the above-mentioned locations (*P*=0.537).

Seedling mortality occurred in cohorts 1 and 2 the first week after emergence and continued until week 8 for cohort 1 and week 6 for cohort 2 (Fig. 6a). Seedlings that emerged from dungpats on dry sand and dry loam soils accounted for most of the early mortality in these two cohorts. All seedlings that emerged from dungpats on sand at field capacity and ½ field capacity died by the midpoint of the study. Seedlings emerging from the core and intermediate regions of dungpats on the loam soil at field capacity and ½ field capacity accounted for most of the later mortality in cohorts 1 and 2. Seedlings that emerged at the peripheral region near the soil surface were able to establish roots in the soil much faster than those emerging at higher locations in the intermediate and core regions. Peripheral seedlings were able to access water at deeper depths in the soil profile as gradual drying occurred over the course of the study. By the fourth week after emergence in cohort 1, peripheral seedlings had two to three tillers and were 22 cm tall, while seedlings at the intermediate and core regions had only one tiller and were only 13 cm tall. By the end of the study, most plants at the periphery produced inflorescences, while all plants at the intermediate and core regions remained vegetative.

Soil moisture not only played a significant role in early seedling establishment, but also in biomass production during the latter half of the study. Plants growing in the loam soil initially at field capacity had 12 times the biomass of plants growing at ½ field capacity by week 14 (Fig. 7).

Ungerminated seeds retrieved from dungpats over the course of the study had 10 to 35% germination after being placed in a controlled environment with optimum temperatures for germination (Fig. 8). The increase in germination at weeks 4 and 6 is probably due to the retrieval of more seeds from the crust rather than from inside the dungpats. Most seeds embedded in the crust did not germinate due to early evaporative moisture loss. Differences could also be due to variability in the separation of undamaged and damaged seeds, i.e., possibly more undamaged seeds were separated during those 2 weeks. Gardener et al. (1993) reported some variability when separating viable and nonviable seeds of several grass species after their exposure to rumen digestion in fistulated cattle. Simao Neto et al. (1987) and Barrow and Havstad (1992) investigated the effects of ruminant digestive systems on the germination of recovered seeds of several grass species; however, these studies did not examine the germination of seeds over an extended period

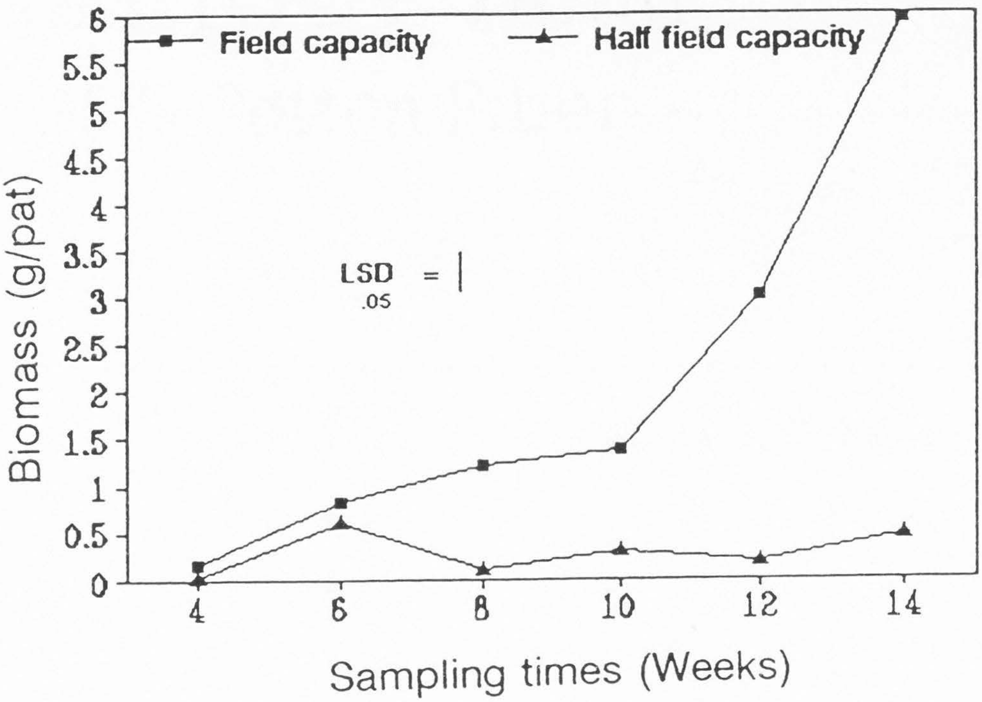

Figure 7. Biomass (g/dungpat) of seedlings in uniform dungpats on a loam soil initially at field capacity and ½ field capacity.

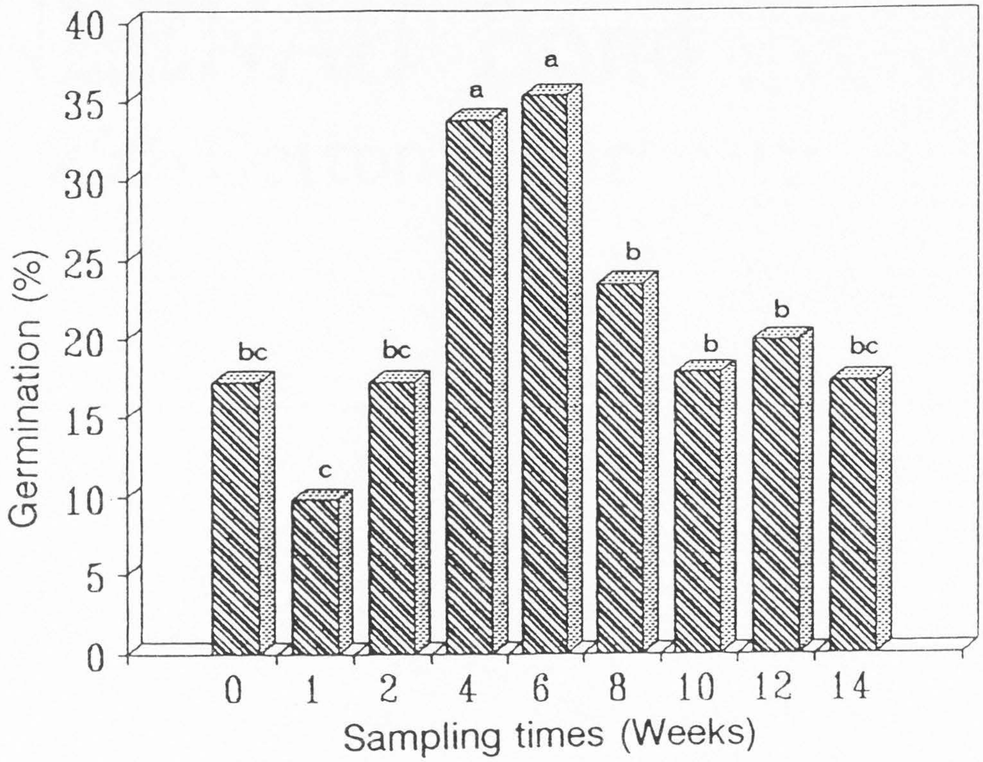

Figure 8. Percent germination of undamaged, ungerminated seeds retrieved from uniform dungpats. Means with the same letter are not significantly different (*P*<0.05).

of time such as in this study. Ozer (1979) fed seeds of several grass and legume species to sheep and stored the postingested seed in dung for 3 months. The germination of seeds declined from 100 to 52% among all species, but each species exhibited different germinability.

Conclusions

This 14-week greenhouse study characterized several cattle dungpat and soil factors that influence seed germination and initial seedling development in cattle dungpats, and subsequent seedling establishment in underlying soils. Dungpat moisture and temperature conditions were favorable for crested wheatgrass seed germination during the first 4 weeks, but rapid crust formation prevented most of the developing seedlings from emerging from the dungpats. Seedling recruitment and development were greater at the periphery than at the interior of the dungpat, and greater on an underlying, medium-textured (loam) soil at initial moisture levels of ½ field capacity or higher than on an underlying coarse-textured soil (sand) at similar initial moisture levels. Seedlings developing in dungpats on dry soils do not survive, but remaining ungerminated seeds in dungpats could germinate at a later date when soil moisture conditions were more favorable. These results must be interpreted with caution since important field variables such as periodic precipitation, widely fluctuating temperatures, and a diversity of invertebrate decomposers were absent or highly constrained in this greenhouse study. A longer term field study is necessary to better understand the role of these factors in germination and plant establishment in dungpats.

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CHAPTER 3

CATTLE DUNGPAT MICROENVIRONMENTAL EFFECTS ON GERMINATION AND ESTABLISHMENT OF CRESTED WHEATRGASS: FIELD STUDIES[2]

Abstract

A field study was conducted to determine the effects of ambient environmental conditions on cattle dungpat moisture, temperature, nutrients, and crust formation dynamics, which influence seed germination and plant establishment in dungpats. 'Hycrest' crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult. X *A. cristatum* (L.) Gaert.] was used as representative revegetation species. Uniform dungpats were prepared by collecting feces from Holstein steers (300 kg) that had been fed crested wheatgrass seeds (passed seeds) and by mixing undigested crested wheatgrass seeds (unpassed seeds) with feces from Holstein steers that had been fed a seed-free diet. Dungpats were placed on a silt loam soil in the field in the spring (late April 1993) under natural and above-normal precipitation regimes, and in the fall (late October 1993) under natural precipitation. Unpassed seeds were also broadcast and drill-seeded in soil seedbeds at the same times. Dungpat and soil microenvironmental factors, and

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[2] Coauthored by G. Akbar, C.A. Call, and R.D. Wiedmeier

crested wheatgrass germination and plant establishment, were monitored for 49 weeks in the spring experiment and 17 weeks in the fall experiment. In general, dungpats had higher moisture contents and a greater range between maximum and minimum temperatures than underlying soil and soil seedbeds. Crust thickness on dungpats varied with the frequency and intensity of precipitation events and changes in dungpat temperature. The crust was softened by precipitation, and most seedlings, except those developing at the deepest depths of dungpats, emerged at all locations on dungpats. Slight changes in total N, NH_4^+, NO_3^-, and organic matter in dungpats and underlying soil indicated that partial decomposition and mineralization occurred by the end of the 49-week spring experiment. Unpassed seeds had higher germination and seedling emergence in dungpats than passed seeds. Both passed and unpassed seeds in dungpats, and unpassed seeds in soil seedbeds, had higher germination and seedling emergence under above-normal than natural spring precipitation. Seedling emergence, development, and survival were greatest at the peripheral region of dungpats, regardless of seed type or precipitation regime. Successful seedling establishment occurred in dungpats placed in the field in the fall and spring seasons, indicating that plants established on dungpats could serve as nuclei of seed production for surrounding areas.

Introduction

Considerable information is available in the literature regarding seed germination, seedling establishment, and growth characteristics of crested wheatgrass (*Agropyron cristatum, A. desertorum*) and other range grasses in soil seedbeds in the Intermountain West (Plummer 1943, Mueggler and Blaisdell 1955, Maynard and Gates 1963, Hull 1964, Wilson 1971, Anderson and Marlette 1986, Johnson 1986, Young and Evans 1986, Vallentine 1989, and Johnson and Aguirre 1991). However, little information is available on the germination and establishment of these species in cattle dung or other animal feces.

Fragmented information is available relating the effects of some animal dung microenvironmental factors on the germination and establishment of plant species in a variety of settings outside of the Intermountain West (Yamada et al. 1972, Wilson and Hennessy 1977, Ozer 1979, Wicklow and Zak 1983, Janzen 1984, Welch 1985, Lewis 1987, Middletone and Mason 1992, and Gardener et al. 1993a). Entomologists and animal scientists have conducted the most thorough investigations of animal dung microenvironmental factors (moisture content, temperature and nutrient dynamics, decomposition, and/or crusting) as they relate to the life cycles of dung-inhabiting fauna (Mohr 1943, Greenham 1972, Ferrar 1975, Palmer and Bay 1982, Stevenson and Dindal 1987, Matthiessen and Palmer 1988, Madsen et al.

1990, Yokoyama et al. 1991a, 1991b, and Lumaret et al. 1992), dung decomposition and the "fouling" of pastures (MacLusky 1960, Weeda 1967, Marsh and Campling 1970), and animal waste management (Prigge and Bryan 1991, Sweeten 1991).

There is most likely a suite of biotic and abiotic factors influencing seed germination and the long-term survival of seedlings emerging in cattle dung (Archer and Pyke 1991, Gardener et al. 1993b). These factors include temperature, moisture, and nutrient fluctuations in dung and soil, dung crust development, postdispersal predation, and density-dependent competition for resources in a relatively small dung substrate. Examination of such factors, particularly under field conditions, can enhance our understanding of plant recruitment in rangeland environments, and the potential of using cattle as an economically viable and ecologically compatible method for revegetating rangelands (Gardener 1993). The objective of this study was to investigate the influence of these factors on the germination and establishment of 'Hycrest' crested wheatgrass [*Agropyron cristatum* (L.) Gaert. X *A. desertorum* (Fisch. ex Link) Schult.] in cattle dungpats under field conditions.

Study Area

Research was conducted at the Green Canyon Ecology Center Research Area, 4 km north of the Utah State University campus (41° 45′ N, 111° 48′ W, 1460 m elevation). The soil is a silt loam (coarse-silty, carbonatic, mesic Typic Haploxeroll) with a pH of 7.9. Mean annual precipitation is 468 mm. Most of the precipitation is snow that falls from October to April. Spring and fall rains also occur, while summers are mostly dry. Maximum temperatures exceed 30° C in the summer and minimum temperatures can occasionally drop below -18° C in the winter.

Methods and Materials

The research approach included two separate but complementary experiments to simulate dungpat deposition on, and conventional seeding in, soil at recommended spring and fall seeding times in the Intermountain West. Similar methods and materials were used for most aspects of the spring experiment (22 April 1993 to 1 April 1994) and the fall experiment (30 October 1993 to 1 April 1994).

Animal Feeding and Dungpat Preparation

The animals, feed ration, and methods used in feeding seeds of crested wheatgrass and preparing uniform dungpats were the same as described in Chapter 2. Two of the four

Holstein steers were fed approximately 60,000 seeds per animal per day on 14, 16, 18, and 20 April 1993, and their dung containing passed seeds was collected on 16, 18, 20, and 22 April. Approximately 18,000 unpassed seeds of crested wheatgrass (not fed to animals) were thoroughly mixed with the dung collected from the other two Holstein steers on the same dates. Unpassed seeds were mixed with dung as a check to better understand the influence of cattle digestive processes on the germinability of passed seeds. Dung containing either passed or unpassed seeds was poured into aluminum circular molds to form 24 uniform dungpats (20 cm diameter, 4 cm thickness, 2 kg mass) at each collection time. Dungpats contained approximately 1,800 passed seeds (damaged and undamaged) or 900 unpassed, undamaged seeds. A total of 96 dungpats, 48 containing passed seeds and 48 containing unpassed seeds, was prepared over the 6-day dung collection period. A total of 20 dungpats, 10 containing passed seeds and 10 containing unpassed seeds, was prepared in the same manner on October 30.

Seeding and Watering Treatments

Six days were required to set up the spring field experiment (96 dungpats) due to previously described dungpat preparation constraints (24 dungpats prepared 48 hours after each of four seed-feeding events). Each set of 24 dungpats was assigned to a specific set of subsequent sampling times to ensure uniformity in dungpat age at the time of sampling.

Only one day was required to set up the fall field experiment (20 dungpats prepared 48 hours after one seed-feeding event). In both experiments, dungpats were placed on bare soil in a grid design with 1-meter spacing between dungpats. Each dungpat/seed-type treatment (passed or unpassed seeds) was replicated four times for each sampling date.

Seeds of crested wheatgrass were also sown in the soil at a rate of 250 live seeds/m^2 using simulated broadcast and drill seeding methods. Seeds were broadcast by hand on bare soil in 0.5 m^2 plots and partially covered by hand-raking the surface. Drill seeding was simulated by placing seeds in hand-dug furrows (1 meter long X 2 cm deep, 50 cm between furrows) and covering them with soil. The number of broadcast seeded plots and drill seeded furrows was equal to the number of dungpat-seed type treatments at each sampling date.

Two replicates of each dungpat/seed-type treatment and each soil seeding treatment were subjected to natural precipitation, and two replicates of the same treatments were subjected to a supplemental watering regime that simulated above-normal precipitation in the spring (spring 1993) in the Intermountain West (Ashcroft et al. 1992). Above-normal precipitation for April (147 mm), May (128 mm), and June (114 mm) was divided into four equal weekly amounts for each month. Each week from 22 April to 30 June 1993, the amount of supplemental water applied through a sprinkler system was determined by subtracting the current precipitation from the above-normal precipitation. In the fall experiment, two replicates of each dungpat/seed-type treatment and each soil seeding treatment were subjected to natural precipitation only.

Dungpat and Soil Microenvironmental Parameters

Dungpat and underlying moisture content, and dungpat crust formation were determined at 12 sampling times for the spring experiment (23 and 28 April, 3, 10, 17, 24, and 31 May, 15 June, 15 July, 15 September, 15 November 1993, 1 April 1994) and at 5 sampling times for the fall experiment (2 and 16 November, 1 December 1993, 1 March, 1 April 1994). Dungpat and underlying soil nutrient content (total N, NO_3^-, NH_4^+, total P, and organic matter) and pH were determined at three sampling times (April 28, September 15 1993, April 1 1994) for the spring experiment. The sampling procedures used in this study were the same as those described in Chapter 2.

Dungpat and underlying soil temperatures were continuously monitored for two replications of each dungpat/seed-type treatment, and soil seedbed temperatures were continuously monitored near two replications of broadcast and drill seeding treatments that were not destructively sampled until the end of the spring experiment. Thermocouples were inserted in peripheral (2 cm from outer edge), upper core (1.5 cm from top), and lower core (3 cm from top) regions of dungpats, in soil underlying peripheral (2 cm depth) and core (interface between dungpat and soil, and 2 and 8 cm depths) regions of dungpats, and at three depths in soil seedbeds (1.5, 3, and 8 cm). All thermocouples were attached to a datalogger that was programmed to record readings at each 10-minute interval and average them every 2 hours. One datalogger was placed in the natural precipitation regime and the other was placed in the above-normal precipitation regime. Rainfall, relative humidity, and wind velocity were also measured throughout the study period using the datalogger in the natural precipitation regime.

Germination and Plant Development

Emerged seedlings were counted and harvested for aboveground biomass just prior to measuring previously described microenvironmental factors. Seedlings were harvested for each of the dungpat/seed-type/precipitation treatments and soil-seeding/precipitation treatments at each sampling time in the spring and fall experiments. Newly emerged seedlings on dungpat/seed-type/precipitation treatments to be sampled at the end of the study were grouped into cohorts each week and marked with colored wires. Locations of seedling emergence on dungpats, i.e., peripheral or core region, were noted for each cohort.

Seedlings emerging in soil seedbeds were not grouped into cohorts. Biomass was determined after oven-drying plant material at 60° C for 48 hours, and expressed in two ways: 1) total biomass per dungpat, and 2) biomass per plant in each seeding treatment.

Undamaged, ungerminated seeds were excavated from dungpats and from drill and broadcast seedbeds at each sampling time in spring and fall experiments and tested for germinability using the same procedures as described in Chapter 2.

When plants in the spring experiment reached reproductive maturity, five inflorescences were randomly selected from the randomly selected plants in the different dungpat/seed-type/precipitation treatments and soil-seeding/precipitation treatments and measured for spike length and weight of 10 randomly selected seeds. Fifty seeds per spike from each treatment were tested for germinability as described in Chapter 2.

Statistical Analysis

All data, except seedling survival data, were analyzed by analysis of variance using the Minitab Statistical Package (Minitab Inc. 1992). Moisture data for dungpats and underlying soil were analyzed using a split-split plot design. At each sampling time, seed-type/precipitation regime combinations were treated as whole plots, substrates (dungpat or the underlying soil) were treated as split plots, and locations in substrates were treated as split-split plots. Dungpat crust thickness, seed germination, plant biomass, seed production, and soil seedbed moisture content data were analyzed using a randomized complete block design. The Least Significant Difference Test ($P<0.05$) was used to separate mean values for moisture content and dungpat crust thickness, and Duncan's Multiple Range Test ($P<0.05$) was used to separate mean values for plant-related data (Steel and Torrie 1980). Survival of seedling cohorts was analyzed by a Mantel log-rank test (Mantel and Haenszel 1959) using the Systat-Survival Package (Steinberg and Colla 1988) and contingency tables (Wilkinson 1990).

Results and Discussion

Moisture Content in Dungpats and Underlying Soil and Soil Seedbeds

Due to frequent precipitation events during late April, May, and June 1993, no significant differences ($P<0.05$) were found in moisture contents of dungpats and underlying soil in natural and above-normal precipitation regimes in the spring experiment; thus, data were pooled across the two precipitation regimes. The initial dungpat moisture content of 84%, similar to that of freshly voided cattle dung in other studies (Bornemissza and Williams 1970, Palmer and Bay 1982, Lysyk et al. 1985), decreased gradually to about 50% in the core region and more rapidly to about 10% in the peripheral region by late May 1993 (Fig. 9a). Palmer and

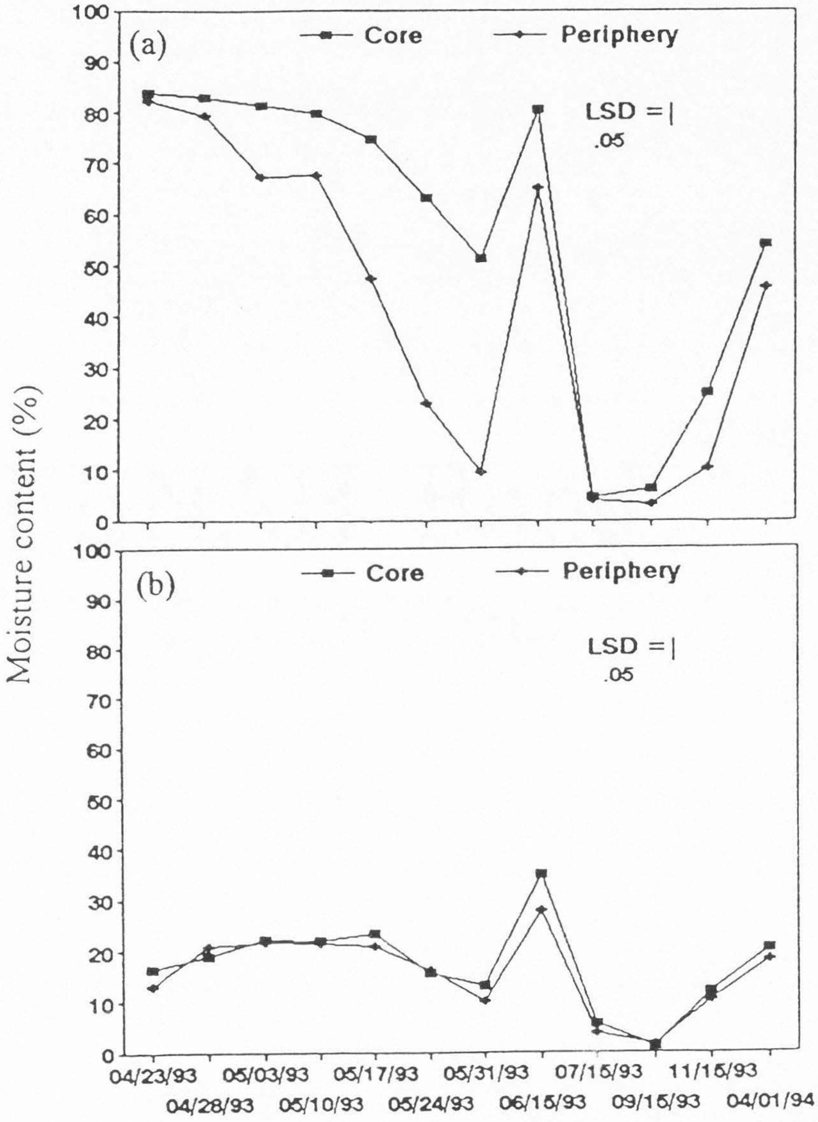

Figure 9. Moisture content in (a) periphery and core regions of dungpats and (b) underlying soil at the same locations. Moisture content is averaged over natural and above-normal precipitation regimes in the spring experiment.

Bay (1982) and Janzen (1984) also noted that moisture content remained highest in the core region relative to other regions of dungpats as they dried over time. Core and peripheral regions of dungpats absorbed considerable moisture from numerous, heavy precipitation events in June 1993 (Fig. 10), and then moisture content rapidly decreased to less than 10% during the drier period from mid-July to mid-September 1993. October 1993 rains, winter snow cover, and March 1994 rains increased the moisture content in both regions of dungpats (Fig. 9a).

Moisture contents in core and peripheral regions of surface soil underlying dungpats were almost identical in the spring experiment (Fig. 9b). Soil moisture increased slightly from late-April to mid-May, indicating a withdrawal of moisture from dungpats. Numerous, heavy rainfall events in June 1993 doubled underlying soil moisture content to about 30%, which then decreased to near 0% by mid-September 1993. Subsequent rains and snow cover increased soil moisture content to a level in April 1994 that was slightly greater than the initial moisture content at the beginning of the study in April 1993.

When averaged across both precipitation regimes in the spring experiment, moisture content in the surface soil of drill and broadcast seeding treatments decreased rapidly from 33% one day after planting (23 April 1993) to 17% one week after planting (28 April 1993) (Fig. 11a). Moisture

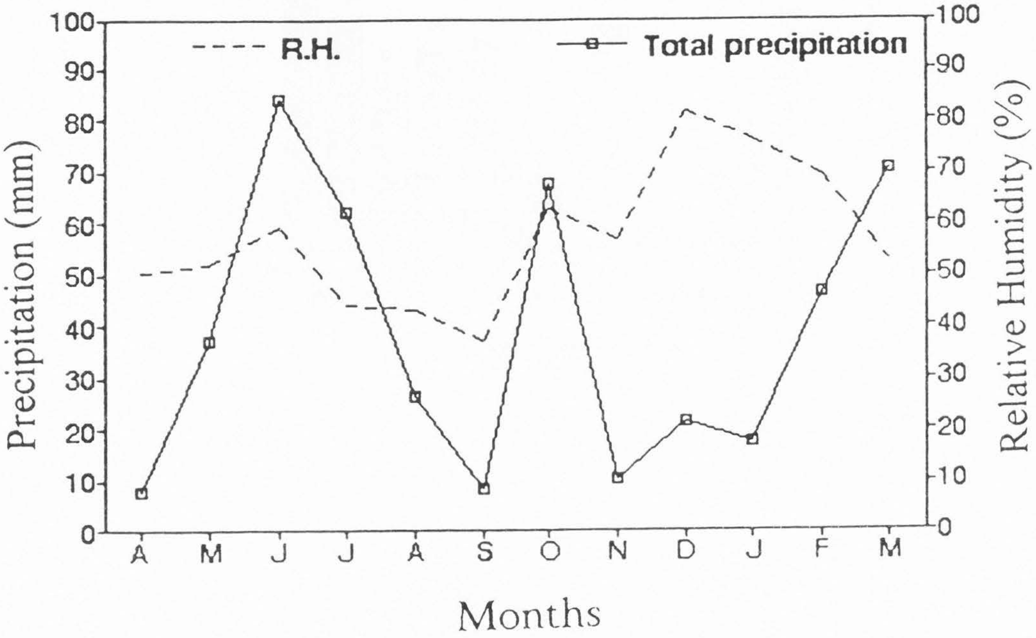

Figure 10. Mean monthly relative humidity and total monthly precipitation during the study period (April 1993 to March 1994).

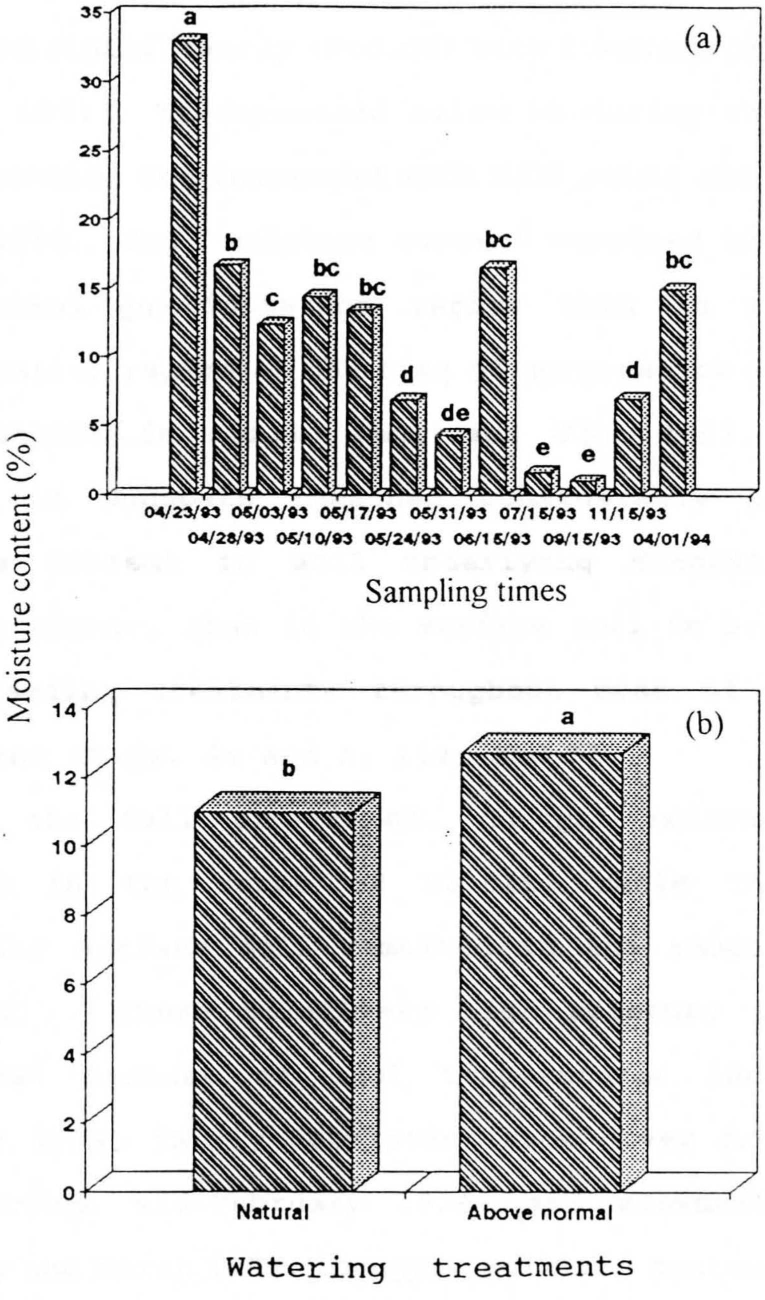

Figure 11. Moisture content at 2 cm deep in soil seedbeds (a) at different sampling times and (b) under natural and above-normal precipitation regimes in the spring experiment averaged over sampling times.

content decreased to near 5% by the end of May 1993, but increased significantly (*P*<0.05) with frequent precipitation in June 1993. It decreased below 5% during the remaining summer months, and increased with fall rains and snowmelt in spring 1994. Soil moisture content remained higher in the above-normal precipitation regime than in the natural precipitation regime at the time of germination and seedling establishment in April, May, and June 1993. Moisture content in dungpats remained considerably higher, and moisture content in soil underlying dungpats remained slightly higher, than in the surface soil in broadcast and drill seeding treatments throughout most of the spring experiment (Figs. 9a and b, 11a, and b).

In the fall experiment, dungpat moisture content remained in the range of 62-82%, while that of the underlying surface soil remained in the range of 15-21% (Fig. 12). These relatively high moisture levels were maintained because of cool temperatures and rains in November 1993, fairly persistent snow cover from December 1993 through mid-February 1994, and snowmelt in late-February and March 1994. Dungpat moisture content decreased in April 1994 with increasing air and dungpat temperatures and increasing evaporational losses; however, ample moisture was available for germination and seedling establishment in March and April 1994.

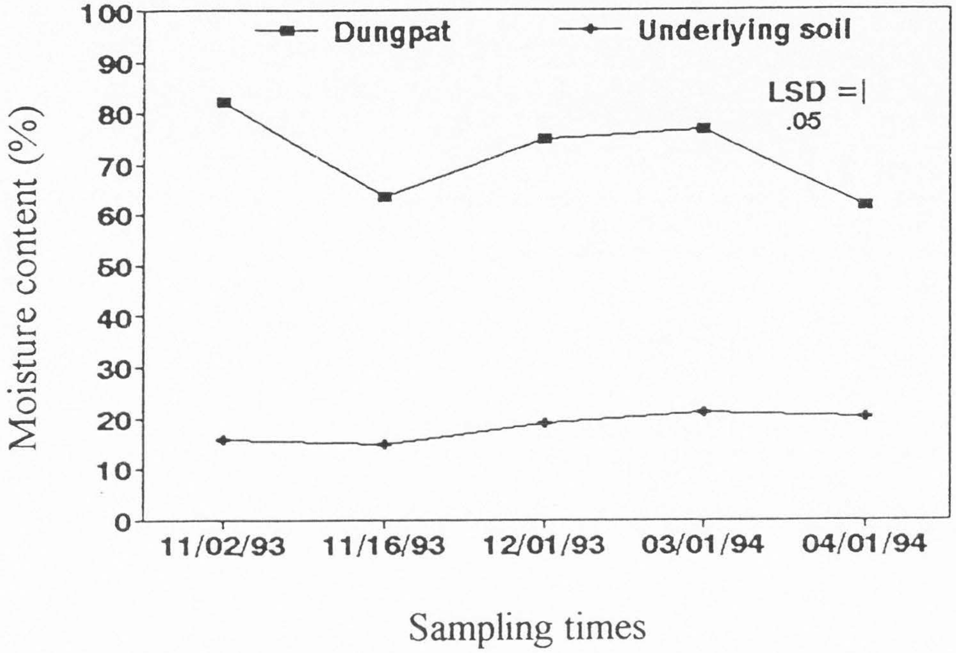

Figure 12. Moisture content in dungpats and underlying soil (averaged across locations) in the fall experiment.

Surface soil moisture content in drill and broadcast seedbeds remained at or above 10% throughout the fall experiment (Fig. 13). The highest moisture level occurred after snowmelt in March 1994 and provided favorable conditions for germination and seedling establishment in both soil seeding treatments.

Temperature in Dungpats and Underlying Soil and Soil Seedbeds

Similar trends in mean monthly maximum and minimum temperatures were noted for different regions of dungpats placed in the two precipitation regimes in the spring experiment. From April through November 1993, mean monthly maximum temperatures in dungpats were slightly higher in the upper core (1.5 cm from top) than in the lower core (3 cm from top) and peripheral (2 cm from outer edge) regions, while mean monthly minimum temperatures in dungpats were slightly lower in the upper core than in the lower core and peripheral regions (Figs. 14 and 15). During August 1993, the warmest month of the study period, maximum temperatures reached 30-40° C and minimum temperatures reached near 10-15° C. The absolute maximum temperature (averaged across all dungpat regions, data not shown) during August 1993 was 58.8° C. With cooler air temperatures and a fairly persistent snow cover, dungpat maximum and minimum temperatures in each region approached 0° C in December 1993, and remained at or near 0° C during January and

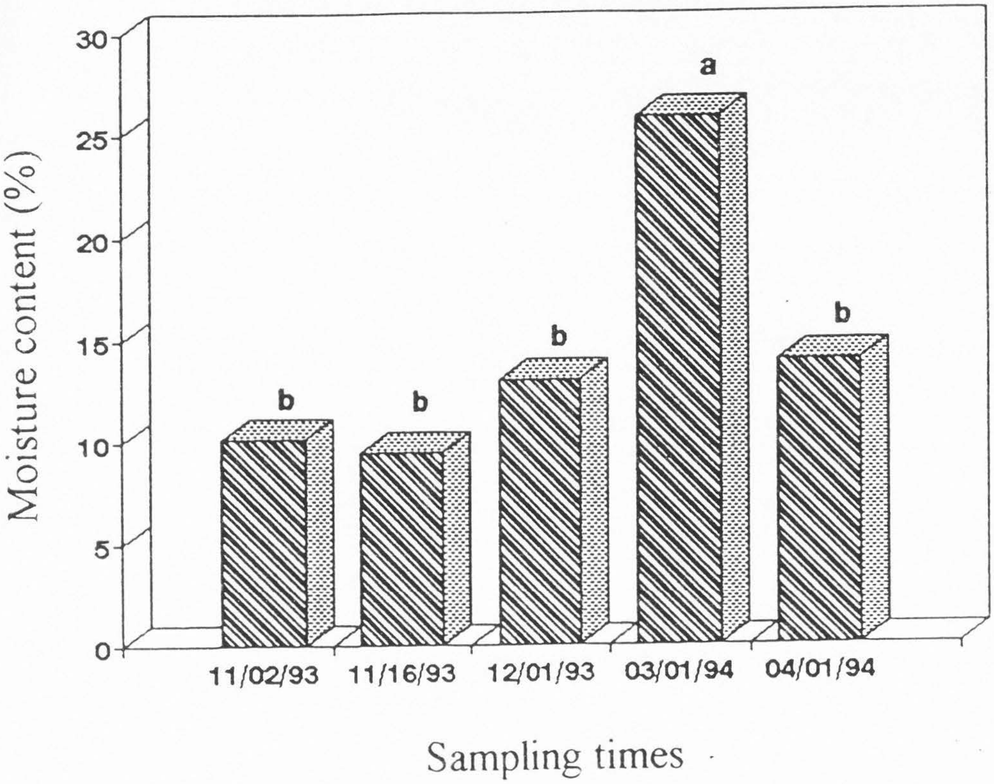

Figure 13. Moisture content at 2 cm deep in soil seedbeds in the fall experiment. Means with the same letters are not significantly different ($P<0.05$).

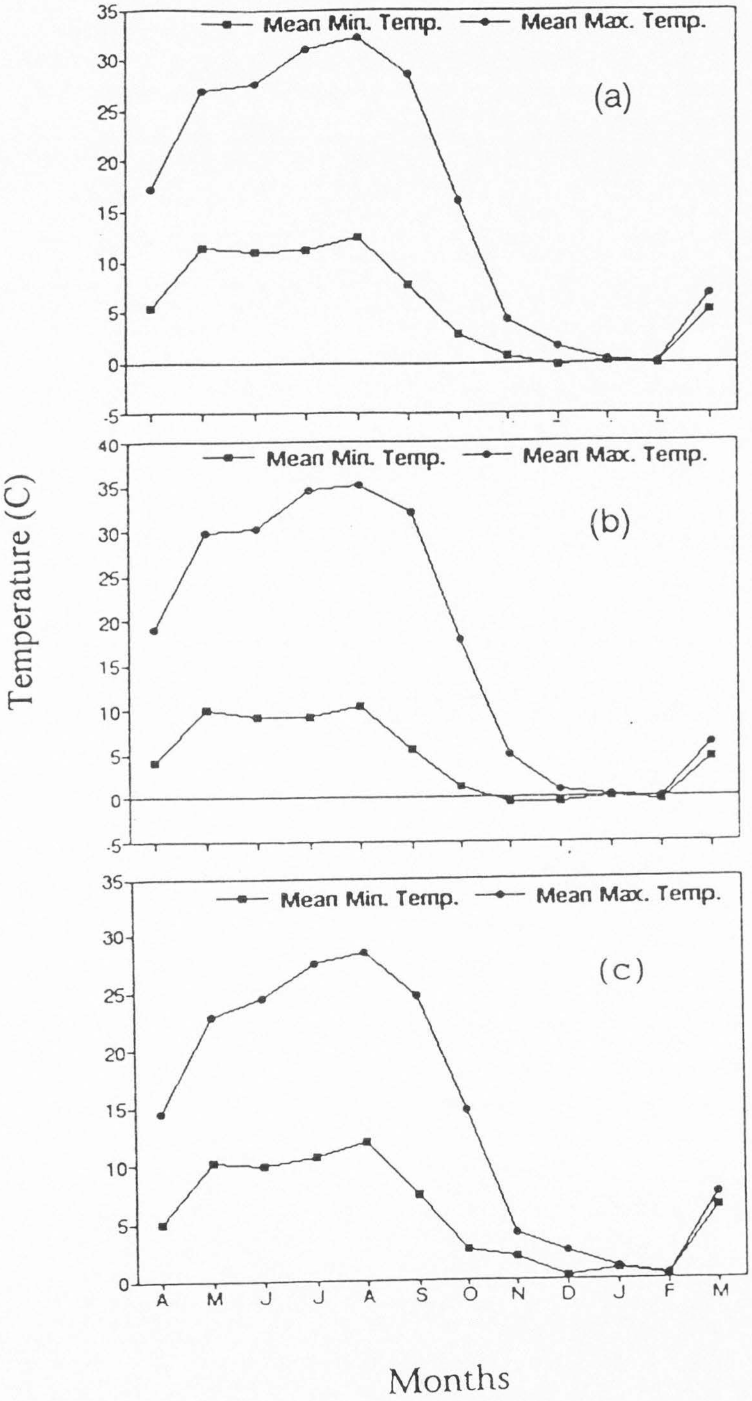

Figure 14. Mean minimum and maximum monthly temperatures in (a) dungpat lower core at 3 cm (b) dungpat upper core at 1.5 cm depth and (c) dungpat periphery at 2 cm depth under the natural precipitation regime in the spring experiment.

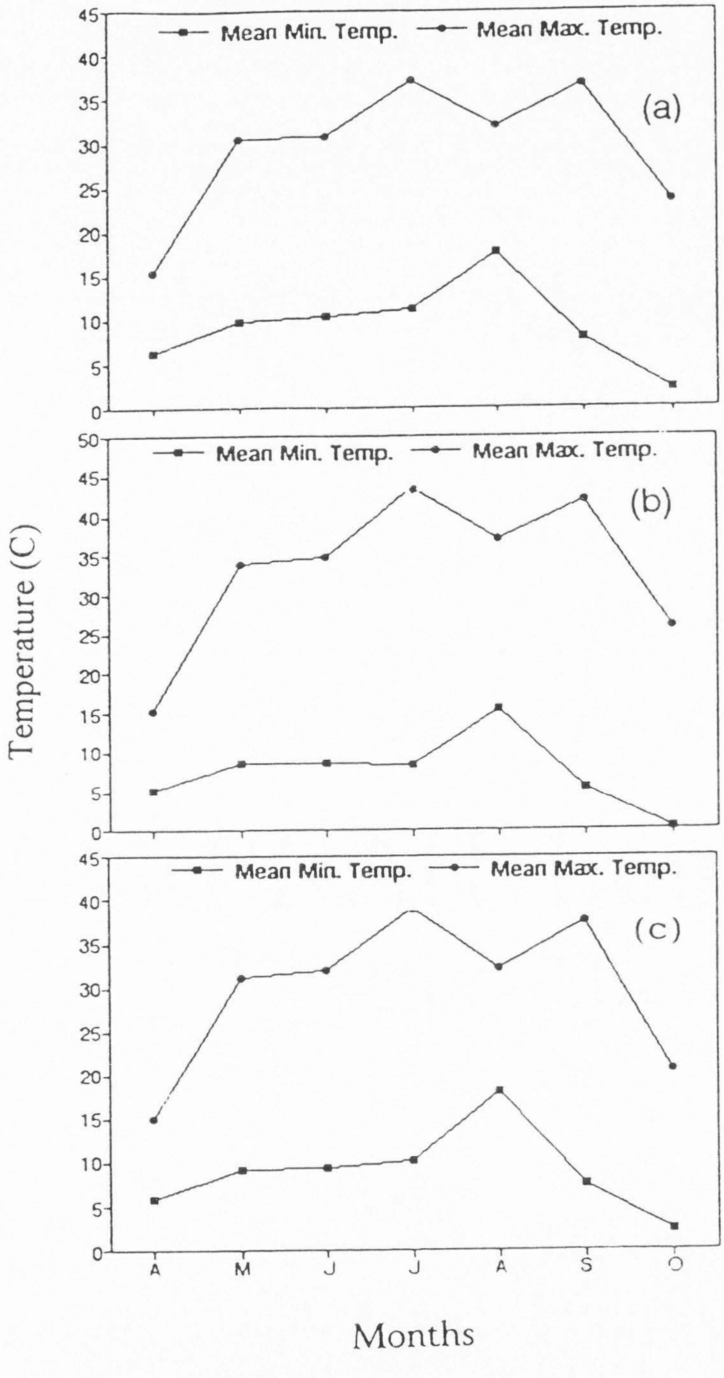

Figure 15. Mean minimum and maximum monthly temperatures in (a) dungpat lower core at 3 cm depth (b) dungpat upper core at 1.5 cm depth and (c) dungpat periphery at 2 cm depth under the above-normal precipitation regime in the spring experiment.

February 1994. The absolute minimum temperature (averaged across all dungpat regions, data not shown) during December 1993 was -12.8° C. After snowmelt and an increase in air temperature in March 1994, dungpat maximum and minimum temperatures began to diverge near 5° C. Dungpat maximum temperatures were slightly higher in the above-normal precipitation regime from May through July 1993 because the more frequently moistened dungpats were darker in color and absorbed more solar radiation than dungpats in the natural precipitation regime.

Mean monthly maximum and minimum temperatures at different depths in soil underlying dungpats and in drill and broadcast seedbeds were very similar in natural and above-normal precipitation regimes in the spring experiment. In general, maximum temperatures were highest and minimum temperatures were lowest at the interface between dungpats and underlying soil (Figs. 16a and 17a) and near the surface (1.5 cm depth) in soil seedbeds (Figs. 18a and 19a). The opposite generally occurred at the deepest depth (8 cm below surface) in soil beneath dungpats (Figs. 16c and 17c) and in soil seedbeds (Figs. 18c and 19c). Maximum and minimum temperatures in soil 2 cm below dungpats (Figs. 16b and 17b) and 3 cm deep in soil seedbeds (Figs. 18b and 19b) were generally intermediate between those at previously mentioned upper and lower sampling depths.

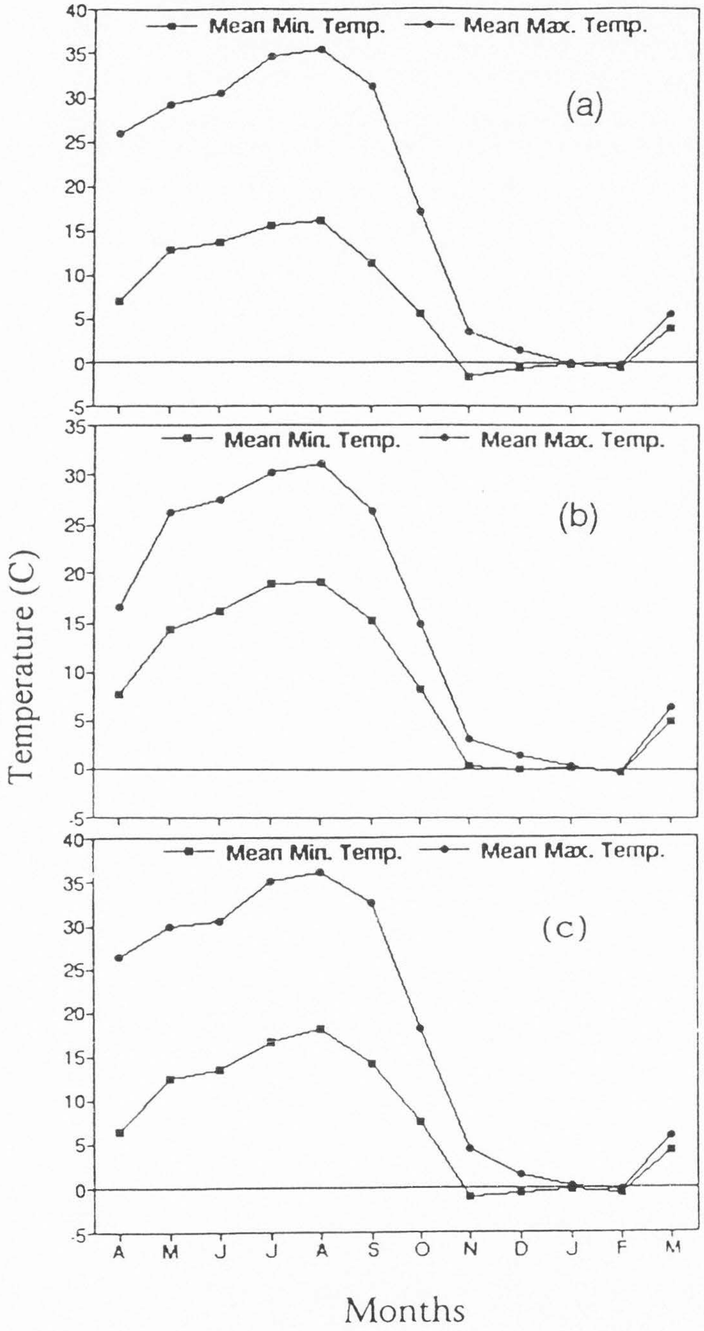

Figure 16. Mean minimum and maximum monthly temperatures in underlying soil at (a) the interface between the dungpat and the soil; (b) 2 cm below the dungpats; and (c) 8 cm below the dungpat under the natural precipitation regime in the spring experiment.

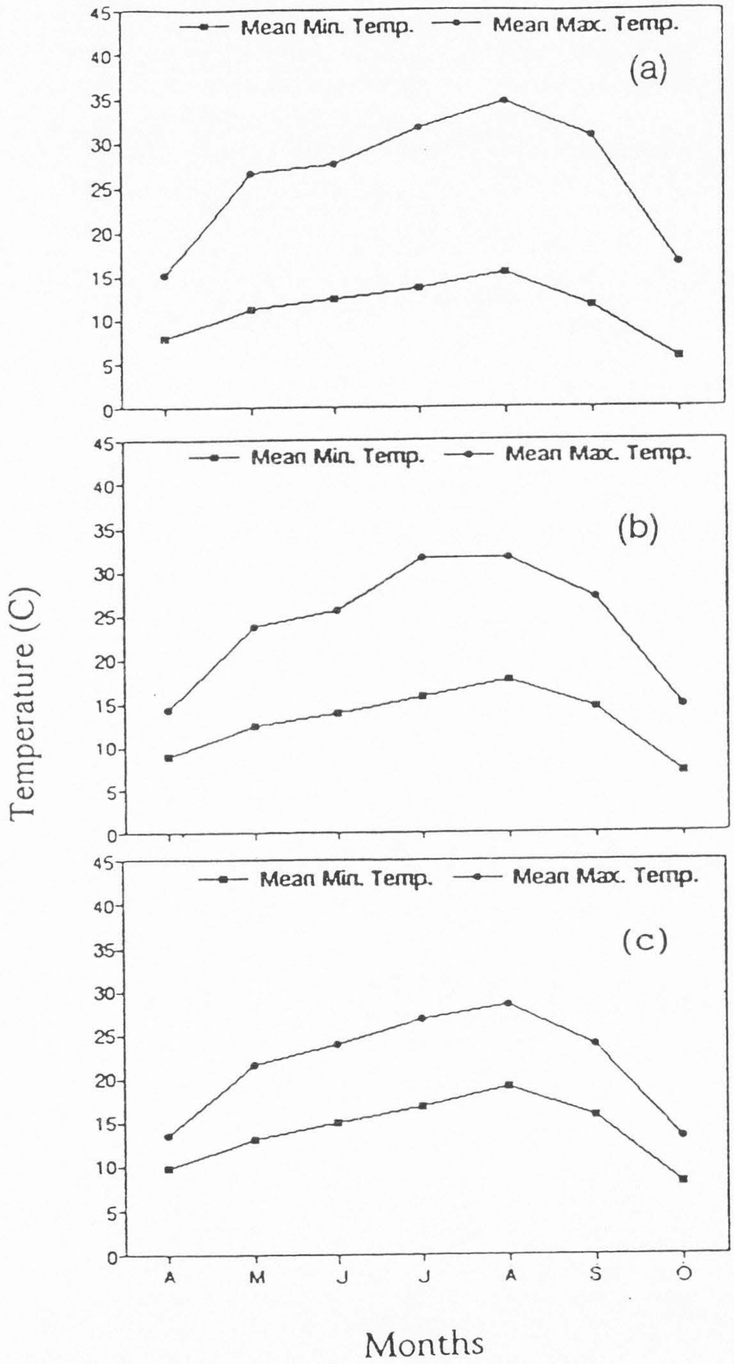

Figure 17. Mean minimum and maximum monthly temperatures in underlying soil at (a) the interface between the dungpat and soil; (b) 2 cm below the dungpat; and (c) 8 cm below the dungpat under the above-normal precipitation regime in the spring experiment.

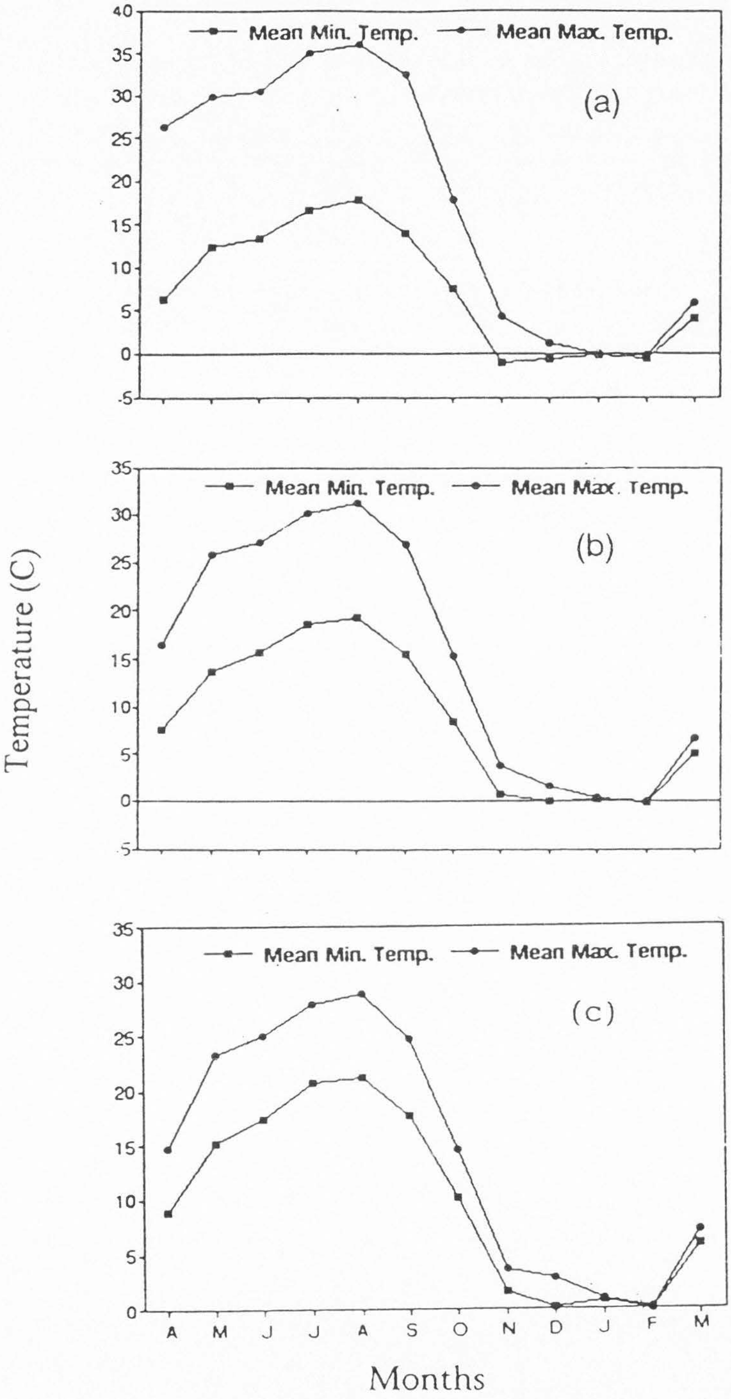

Figure 18. Mean minimum and maximum monthly temperatures in soil seedbeds at (a) 1.5 cm depth; (b) 3 cm depth; and (c) 8 cm depth under natural precipitation regime in the spring experiment.
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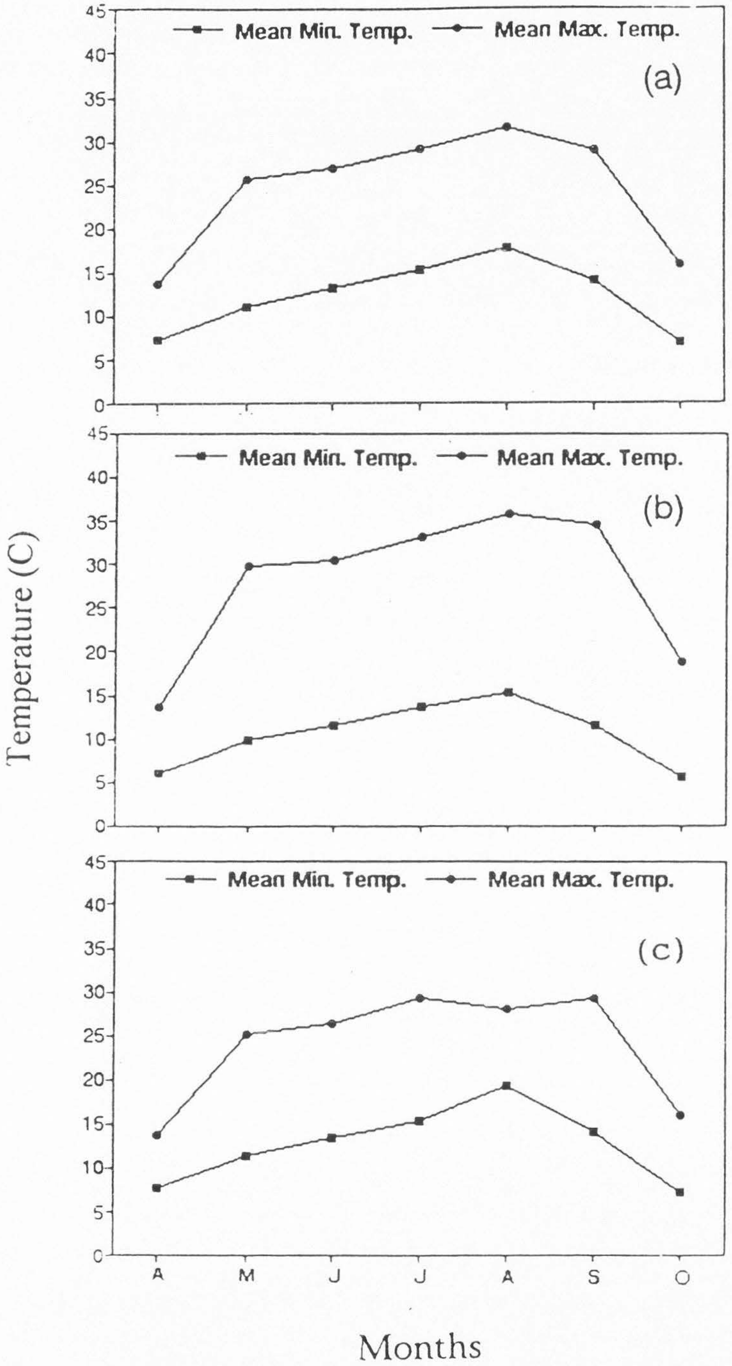

Figure 19. Mean minimum and maximum monthly temperatures in soil seedbeds at (a) 1.5 cm depth; (b) 3 cm depth; and (c) 8 cm depth under the above-normal precipitation regime in the spring experiment.

Trends for mean monthly maximum and minimum temperatures were also quite similar for different locations in dungpats, underlying soil, and soil seedbeds in the fall experiment (Figs. 20, 21, and 22). Mean maximum temperatures ranged between 2 and 10° C and mean minimum temperatures were slightly below or near 0° C in the three substrates in November 1993. However, absolute maximum and minimum temperatures of 30.3° C and -23.4° C, respectively, indicate the range of temperatures to which seeds in dungpats were exposed in November 1993. Mean monthly maximum and minimum temperatures remained near 0° C under fairly persistent snow cover from December 1993 to February 1994, and increased 3-14° C after snowmelt in late February and March 1994, depending on depth of sampling. Within 24 hours after placement in the field, moist dungpats became frozen, and underwent alternate freezing and thawing with changes in ambient temperatures and snow cover until March 1994. Broadcast seeds lying on the soil surface were exposed to more frequent freezing and thawing than seeds buried at 2 cm in drill rows.

Crust Development on Dungpats

Crust development started as soon as dungpats were placed in the field. Crust thickness increased rapidly as dungpat temperatures and evaporation rates increased throughout May 1993 in natural and above-normal precipitation regimes in the spring experiment (Figs. 23a

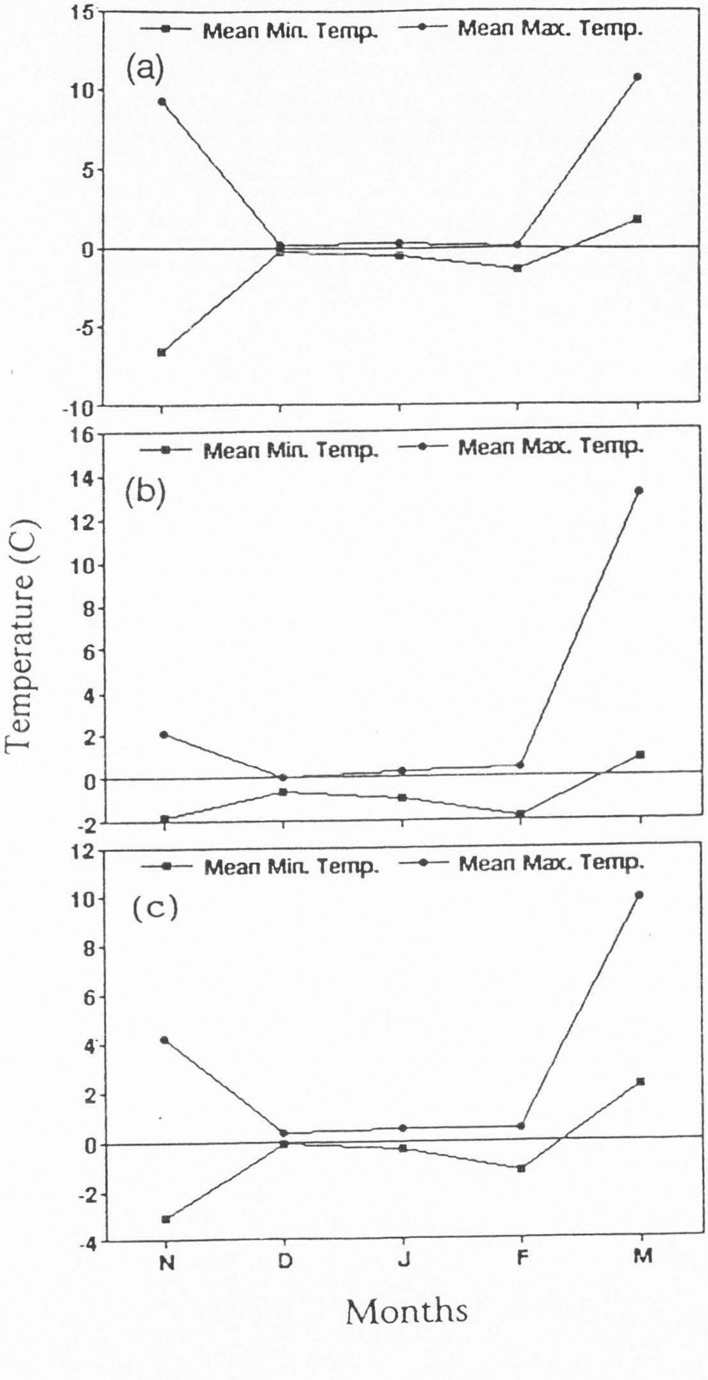

Figure 20. Mean minimum and maximum monthly temperatures in (a) dungpat core at 3 cm depth (b) dungpat upper core at 1.5 cm depth and (c) dungpat periphery at 2 cm depth in the fall experiment.

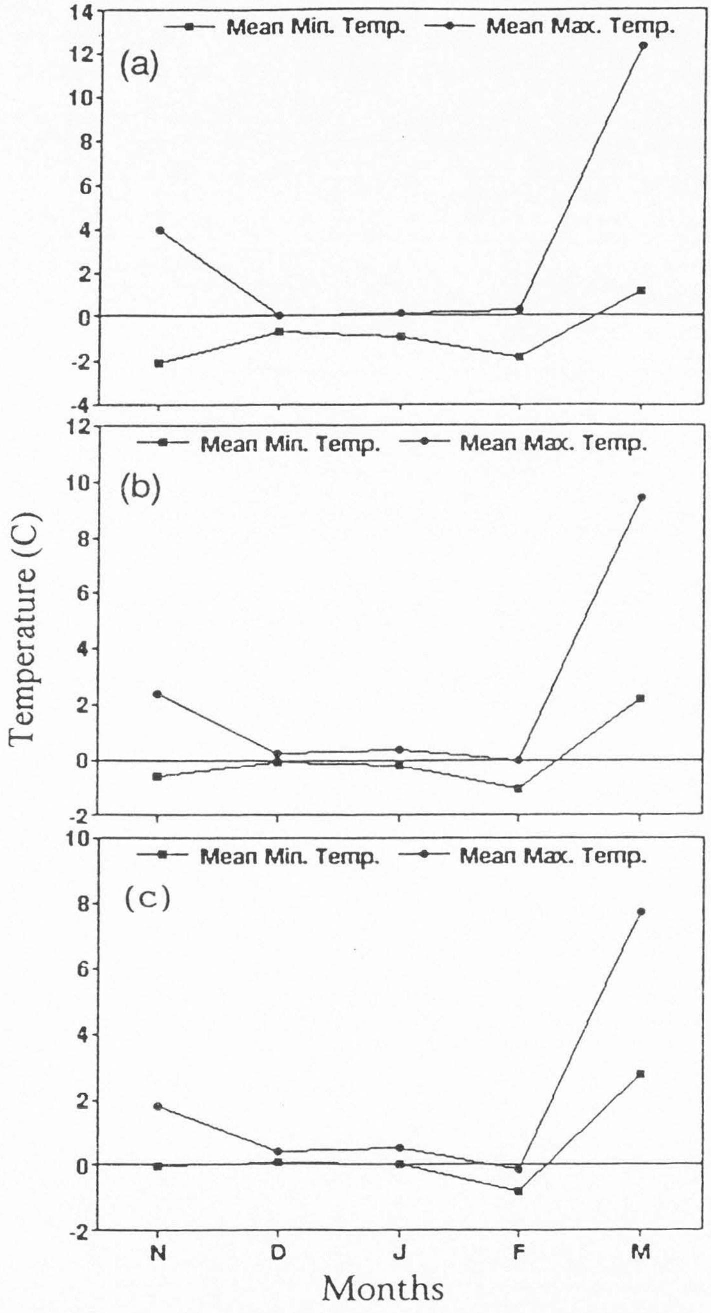

Figure 21. Mean minimum and maximum monthly temperatures in underlying soil at (a) the interface between the dungpat and soil; (b) 2 cm below the dungpat; and (c) at 8 cm below the dungpat in the fall experiment.

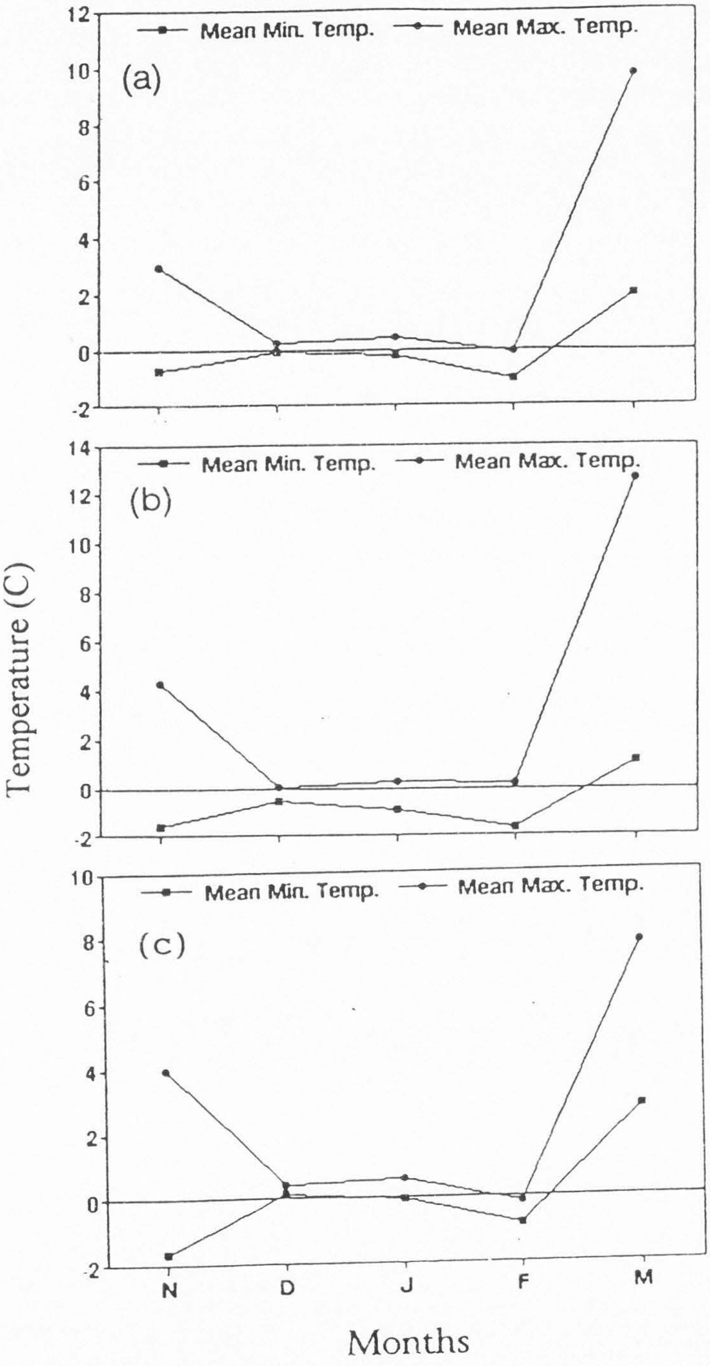

Figure 22. Mean minimum and maximum monthly temperatures in soil seedbeds at (a) the 1.5 cm depth; (b) 3 cm depth; and (c) 8 cm depth in the fall experiment.

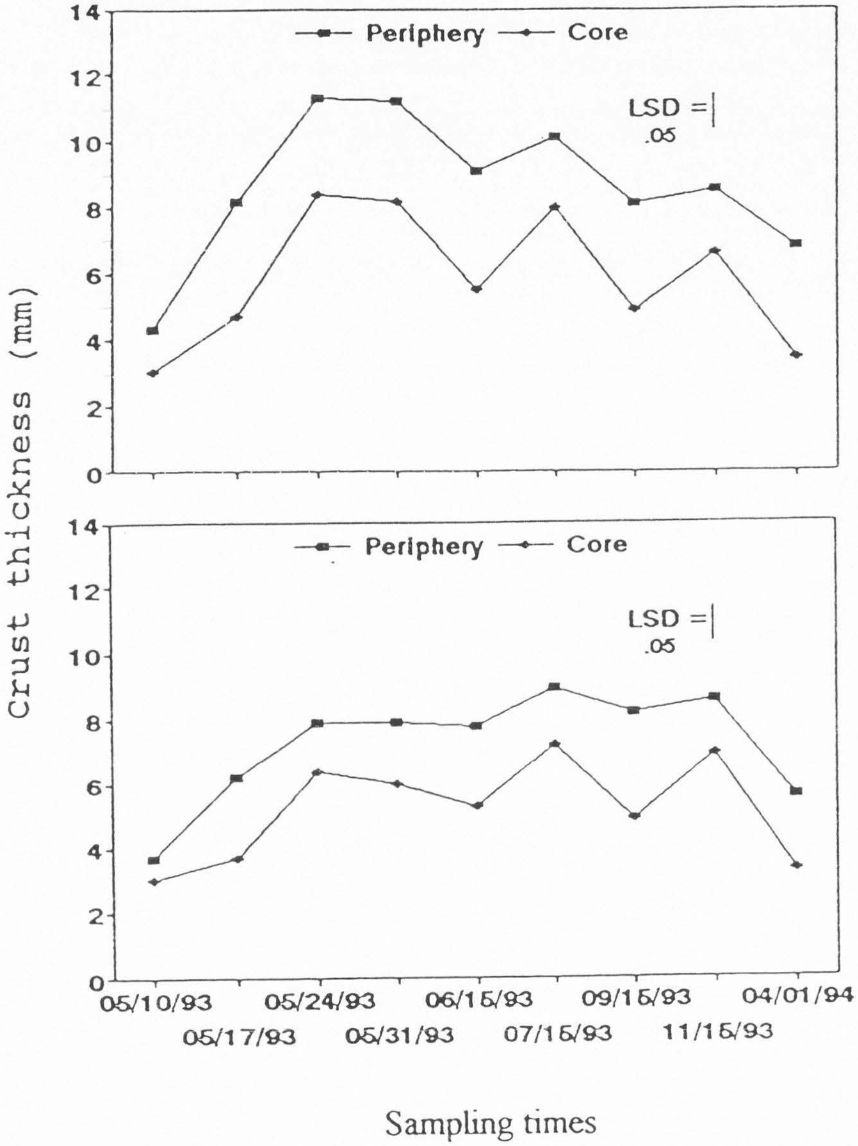

Figure 23. Crust thickness at core and peripheral regions of dungpats under (a) the natural precipitation regime and (b) the above-normal precipitation regime in the spring experiment.

and b). The majority of crested wheatgrass seedlings that emerged from dungpats did so before maximum crust thickness was reached. After May 1993, crust thickness fluctuated with changes in precipitation, relative humidity, and temperature. Regardless of thickness, dungpat crusts absorbed moisture and softened for a few days after each natural or artificial precipitation event. With the exception of the first sampling period (10 May 1993), crust thickness at the peripheral region was significantly greater ($P<0.05$) than at the core region in natural and above-normal precipitation regimes (Figs. 23a and b). Crust thickness increased more rapidly and remained higher in both dungpat regions under natural precipitation than under above-normal precipitation. The greatest decrease in crust thickness occurred with the absorption of snowmelt in spring 1994.

Crust thickness was significantly greater ($P<0.05$) at the peripheral region than at the core region of dungpats for all sampling times in the fall experiment (Fig. 24). Maximum thickness was reached during the first month after dungpat placement (November 1993), and decreased with snow cover, freezing and thawing, and absorption of snowmelt over the course of the study. Crested wheatgrass seedlings readily emerged through the thinner, softer crust at core and peripheral regions of dungpats in early March 1994.

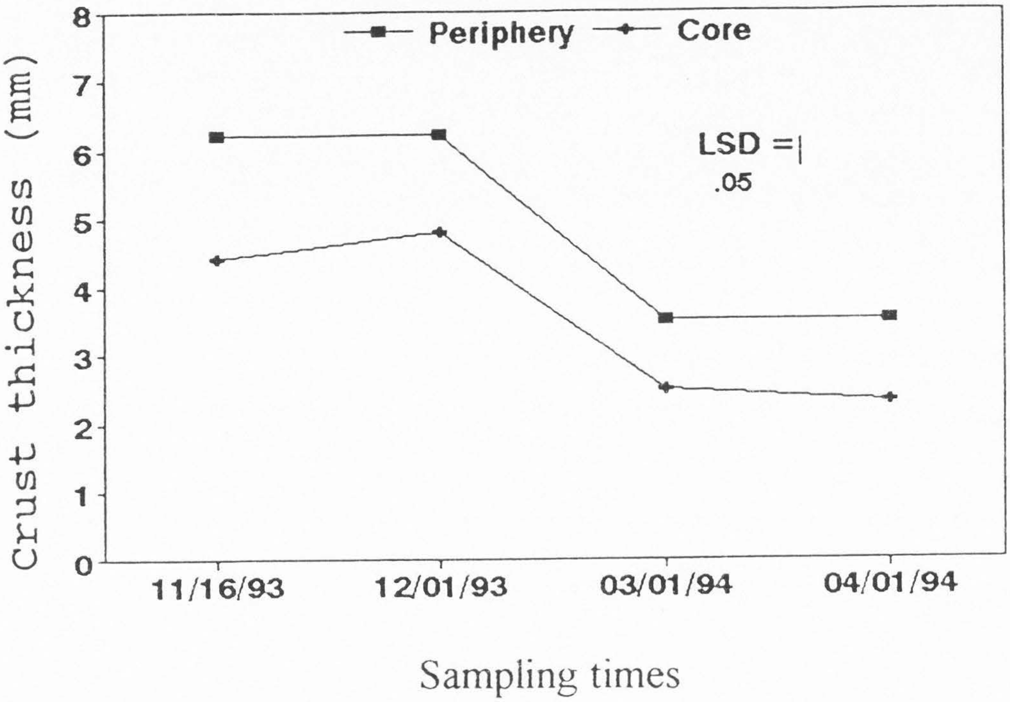

Figure 24. Crust thickness at core and peripheral regions of dungpats in the fall experiment.

Nutrients in Dungpats and Underlying Soil

As mentioned in Chapter 2, nutrient data of dungpats and underlying soils represent one composite sample from two replications. These data were collected for the purpose of identifying general trends in the spring experiment.

Dungpat total N, NH_4^+, and total P did not change by the middle of the study, but levels of the three nutrients increased by the end of the study (Table 4). As explained earlier in Chapter 2, the concentration of total N in dungpats might have increased due to a simultaneous decrease in organic matter in the dungpats. Nitrate decreased midway through the study and generally remained at lower levels until the end of the study (Table 4). Only organic matter showed a greater change (decrease) with supplemental watering in the above-normal precipitation regime. This decrease was probably due to the leaching of organic acids.

Total N values in dungpats were within the range of 1.81-4.0% for cattle dung reported by other investigators (Lysyk et al. 1985, Stevenson and Dindal 1987). About 30% of the total N ingested by cattle is excreted in dung (Prigge and Bryan 1991), but the majority of this N is in an organic form that must be mineralized before it can be taken up by plants (Stewart 1991). The rate of mineralization depends upon several factors, including dungpat moisture content, temperature, and crust formation, precipitation, relative humidity, microbial and invertebrate activities,

Table 4. Nutrient status of dungpats under natural and above-normal precipitation regimes at three time intervals in the Spring experiment.

Dungpat Placement	Total N (%)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)	Total P (%)	O.M. (%)
		Beginning of Study (23 April 1993)			
M1 (P)	1.91	6.50	28.86	0.22	81.65
M2 (P)	1.89	6.35	28.18	0.23	79.12
M1 (UP)	1.94	6.40	28.00	0.22	81.90
M2 (UP)	1.92	7.60	27.10	0.24	82.65
		Middle of Study (15 September 1993)			
M1 (P)	1.99	2.50	25.88	0.26	83.93
M2 (P)	1.90	4.95	34.79	0.24	68.00
M1 (UP)	2.03	3.05	24.89	0.29	84.15
M2 (UP)	1.87	5.15	24.93	0.24	74.10
		End of Study (1 April 1994)			
M1 (P)	2.66	8.75	48.57	0.31	80.70
M2 (P)	2.18	3.50	48.97	0.24	68.05
M1 (UP)	2.48	4.70	47.90	0.33	80.95
M2 (UP)	2.45	5.25	50.02	0.28	75.40

M1 - natural precipitation, M2 - above-normal precipitation during spring season, P - seeds passed through cattle's digestive tract, UP - unpassed seeds mixed in the dungpat.

properties of underlying soils, and season of deposition (Landin 1961, Weeda 1967, Castle and MacDaid 1972, Ferrar 1975, Macqueen and Beirne 1975, Underhay and Dickinson 1978, Putman 1983, Lumaret et al. 1992). Dungpat disappearance (mineralization) has been shown to vary from 35 days under tropical conditions to almost 3 years under arid conditions (Putman 1983). Dungpats did not disintegrate during the one-year period of this study, even though they were exposed to alternate wetting and drying and freezing and thawing. Only limited insect activity was noted on moist dungpats in May 1993, and birds made small holes in a few dungpats in search of seeds and insects. Roots of crested wheatgrass plants did create cracks in many of the dungpats. Increases in NH_4^+ by the end of the study indicate that some limited mineralization had taken place. Volatilization and leaching losses can also reduce the availability of dungpat N (MacDiarmid and Watkin 1972b, Yokoyama et al. 1991a, 1991b).

Total N in the surface soil underlying dungpats increased slightly by the middle of the study and remained higher than the pretreatment level until the end of the study (Table 5). Soil organic matter and NO_3^- increased midway through the study, but their levels decreased considerably by the end of the study (Table 5). Ammonium levels in underlying soil did not increase until the end of the study (Table 5). Total P levels in underlying soil remained essentially unchanged throughout the study (Table

Table 5. Nutrient status of underlying soil prior to placement of dungpats (pretreatment) and at three time intervals after placement of dungpats in the Spring experiment.

Dungpat Placement	Total N (%)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)	Total P (%)	O.M. (%)
		Pretreatment			
Drill (M1)	0.21	7.2	3.05	0.08	8.2
Drill (M2)	0.17	0.2	10.06	0.08	5.8
B.C. (M1)	0.25	17.6	20.50	0.07	7.9
B.C. (M2)	0.16	1.9	1.96	0.07	4.7
		Beginning of Study (23 April 1993)			
M1 (P)	0.22	14.82	5.60	0.07	6.78
M2 (P)	0.20	18.23	3.25	0.07	6.82
M1 (UP)	0.19	11.30	9.57	0.07	5.42
M2 (UP)	0.22	20.37	6.12	0.08	7.37
		Middle of Study (15 September 1993)			
M1 (P)	0.25	44.27	3.45	0.07	7.02
M2 (P)	0.26	44.50	9.50	0.07	8.43
M1 (UP)	0.24	29.50	5.50	0.07	7.05
M2 (UP)	0.27	7.98	5.65	0.07	9.03
		End of Study (1 April 1994)			
M1 (P)	0.23	9.55	18.20	0.08	4.65
M2 (P)	0.19	7.42	32.65	0.08	4.95
M1 (UP)	0.23	5.80	12.98	0.08	3.65
M2 (UP)	0.23	5.75	31.65	0.07	4.65

M1 - natural precipitation, M2 - above-normal precipitation during spring season, B.C.- Broadcast seeding, P - seeds passed through cattle's digestive tract, UP - unpassed seeds mixed in the dungpat.

5). Phosphorus levels generally do not increase until dungpats thoroughly disintegrate and mix with the underlying soil (During and Weeda 1973).

Increases in total N in soils underlying dungpats have been reported by other investigators (MacDiarmid and Watkin 1972a, During et al. 1973). Their studies showed that the effect of increased N was most pronounced in the upper 7.5 cm soil layer, and it was noticed up to 15 cm from the edge of dungpats (MacDiarmid and Watkin 1972a). In this study, slight increases in NH_4^+ and NO_3^- indicate that mineralized N may have been transferred from dungpats to the top 2-3 cm (sampling depth) of underlying soil. However, NH_4^+ is subject to leaching losses under high precipitation, and NH_3^- can be volatilized when soil pH exceeds 7.0 (Schlesinger and Peterjohn 1991). Dungpat pH and underlying soil pH ranged from 7.4-9.2 and 7.5-8.5, respectively, over the course of this study. Increases in the pH of soils underlying dungpats have been reported to persist for up to 3.5 years after dungpat deposition (During and Weeda 1973, Weeda 1977). Other factors, such as nitrification and microbial immobilization of N, were not accounted for in this study.

Changes in organic matter content in the underlying soil may also be related to an increase in pH. Humic and fulvic acids are soluble in alkaline solutions, and may have been leached from dungpats through the surface layer into a deeper layer of underlying soil (Stark, pers. comm.).

Germination and Seedling Development

Crested wheatgrass seeds germinated inside dungpats and in soil seedbeds in both precipitation regimes from the first to the sixth week (early May to early June 1993) after the initiation of the spring experiment. Previously described moisture and temperature conditions were favorable for germination in both substrates at this time (Figs. 9, 11, 14-19). Even though crust thickness was increasing rapidly during this time, it remained relatively soft due to frequent precipitation events, and did not impose as much of a mechanical barrier to seedling emergence as it did in the greenhouse study. Seedlings emerged at all locations on dungpats; however, those seedlings growing from deeper depths were not able to penetrate through the crust. These trapped seedlings died and decomposed inside dungpats as in the greenhouse study. The seedlings that did emerge from dungpats in the different seed-type/precipitation treatment combinations were grouped into cohorts based upon their week of emergence. Seedlings that emerged from broadcast and drill seeding treatments in soil seedbeds were not grouped into cohorts.

When averaged across cohorts, total emergence and survival were greater for seedlings from unpassed seeds than from passed seeds in dungpats under both natural and above-normal precipitation regimes (Fig. 25). Data revealed no significant difference (*P*=0.074) when survival of seedlings

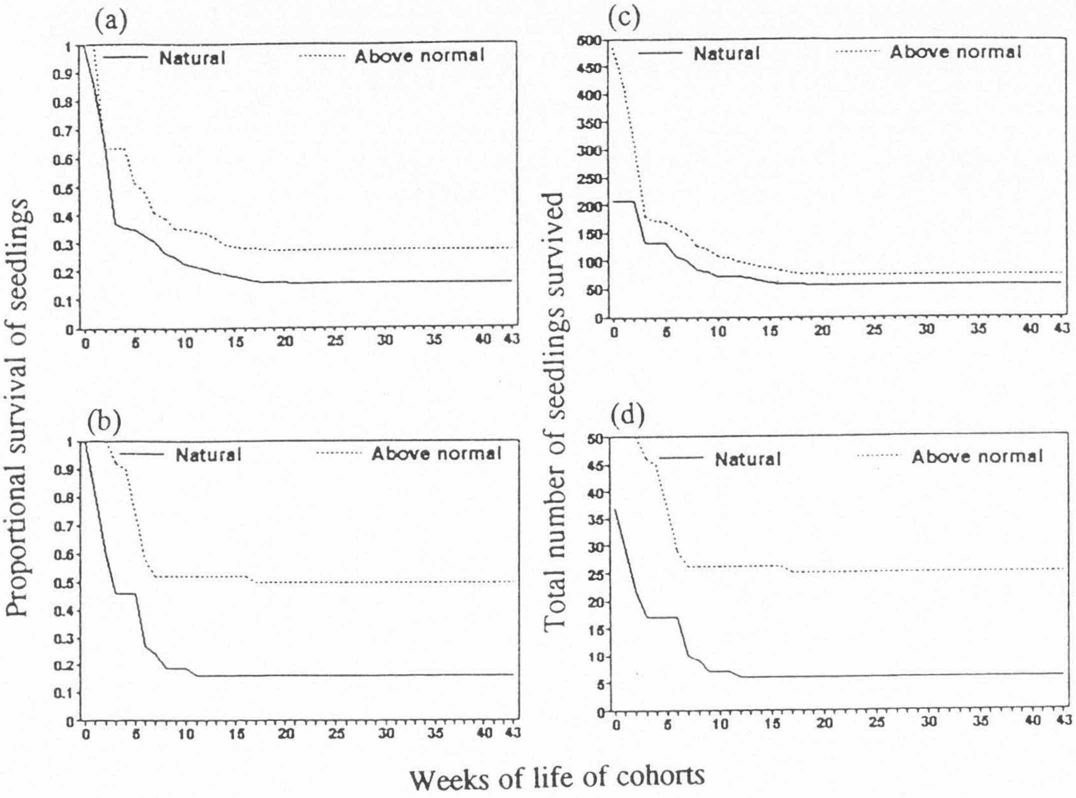

Figure 25. Proportional and total survival of seedlings in dungpats over two precipitation regimes emerged from (a and c) unpassed seeds and (b and d) passed seeds in dungpats over the 43-week spring experiment.

either from passed or unpassed seeds under natural precipitation regime was analyzed using a Mantel log rank test and a contingency test ($P=0.487$). However, lower seedling numbers in the passed seed treatment resulted in lower competition for dungpat and underlying soil resources and seedlings from passed seeds were more vigorous and phenologically advanced than seedlings from unpassed seeds. Proportional and total survival of seedlings from passed and unpassed seeds were greater under above normal precipitation than under natural precipitation (Fig. 25). Significantly higher ($P=0.006$) proportional survival was noted for seedlings that emerged from passed and unpassed seeds in dungpats and placed in the above-normal precipitation regime. However, a contingency test did not reveal any significant difference ($P=0.505$) for the seedlings emerging from the above mentioned seed treatments under the above-normal precipitation regime.

Three cohorts of seedlings from passed seeds (Figs. 26a and d) and six cohorts of seedlings from unpassed seeds (Figs. 27a and d) were monitored on dungpats under the natural precipitation regime. Seedling emergence was probably restricted by crust development after cohorts 1 and 2 emerged from passed seeds. Frequent, heavy precipitation events in early June reduced and softened the crust, and allowed cohort 6 to emerge from both seed types. Many of these seedlings emerged from passed and unpassed seeds

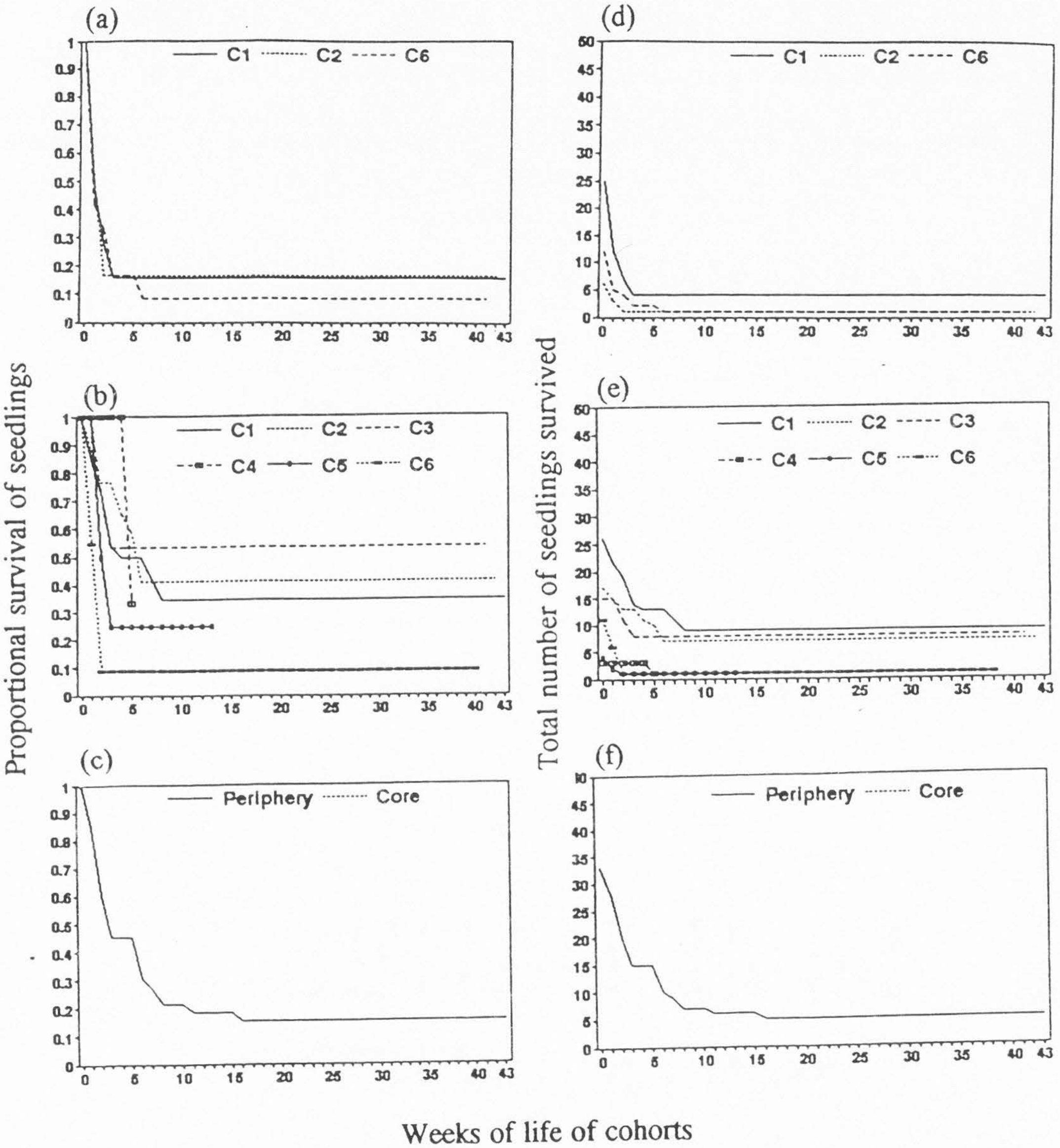

Figure 26. Proportional and total survival of cohorts of seedlings from passed seeds in dungpats over the 43-week spring experiment: (a and d) cohorts under natural precipitation regime; (b and e) cohorts under above-normal precipitation regime and (c and f) survival of all cohorts at periphery and core regions of dungpats averaged over the two precipitation regimes.

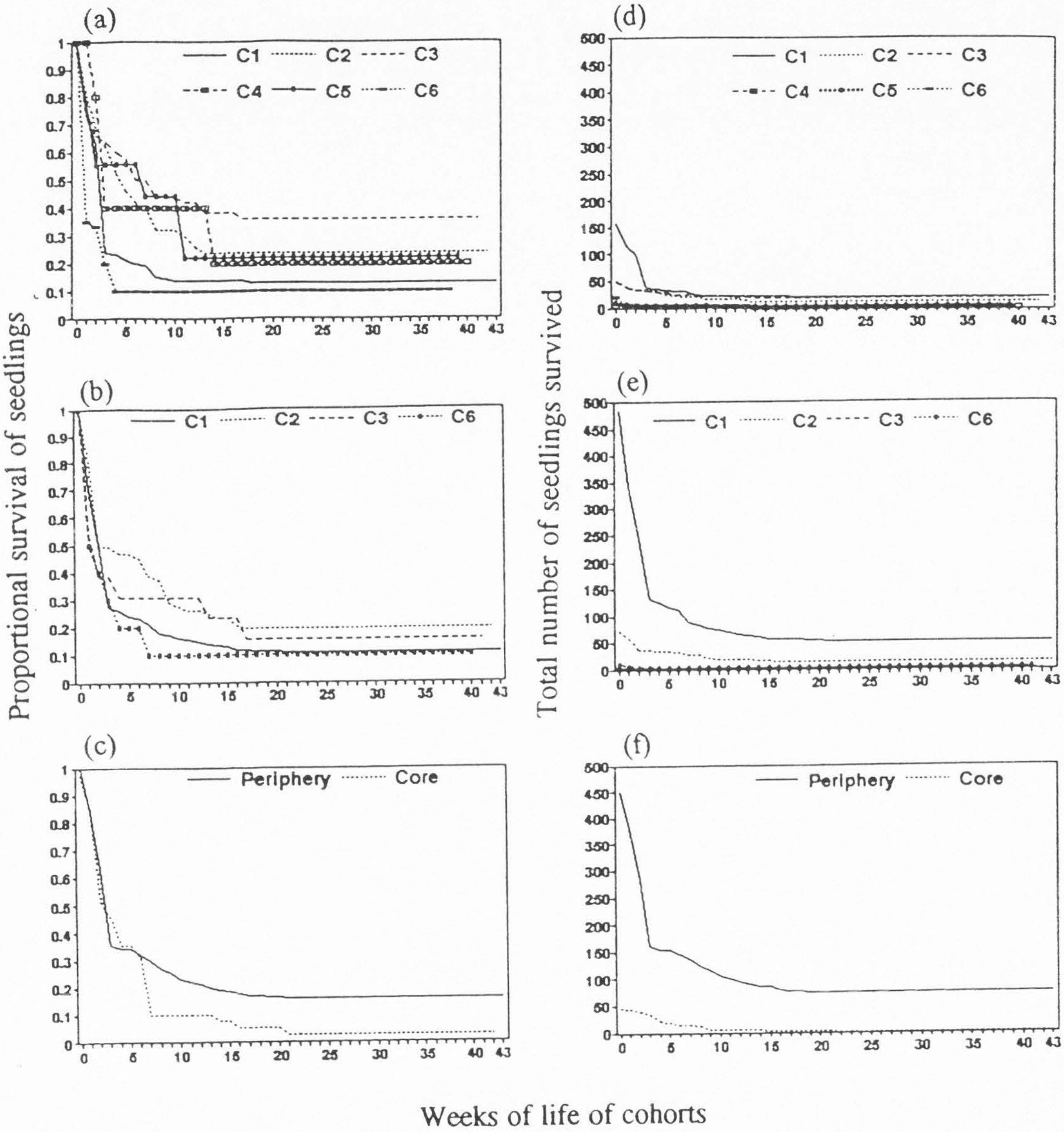

Figure 27. Proportional and total survival of cohorts of seedlings from unpassed seeds in dungpats over 43-week spring experiment: (a and d) cohorts under natural precipitation regime; (b and e) cohorts under above-normal precipitation regime; and (c and f) survival of all cohorts at periphery and core regions of dungpats averaged across the two precipitation regimes.

located in the crust. The total number of surviving seedlings from passed seeds was highest in cohort 1, followed by cohorts 2 and 6, respectively (Fig. 26d), and proportional survival was highest for cohorts 1 and 2 compared to cohort 6 (Fig. 26a). No significant difference (*P*=0.107) was noted in terms of survival of seedlings in all three cohorts of seedlings from passed seeds. A contingency test also did not reveal any significant difference (*P*=0.608) in the survival of these cohorts. The total number of surviving seedlings from unpassed seeds was highest in cohort 1, followed by rest of the cohorts (Fig. 27d), and proportional survival was highest for cohort 3, followed by cohorts 2, 5, 4, 1, and 6, respectively (Fig. 27a). Most seedlings in later cohorts (3 and 6) could not compete effectively with older, better established seedlings from cohorts 1 and 2 for limited resources in dungpats and underlying soil and remained smaller and weak. When survival of seedling cohorts from unpassed seeds was analyzed using a Mantel log-rank test, a highly significant difference (*P*=0.00) was noted. Similarly, a contingency test also identified highly significant survival (*P*=0.003) among these cohorts.

Six cohorts of seedlings from passed seeds (Fig. 26b and e) and four cohorts from unpassed seeds (Fig. 27b and e) were monitored on dungpats under the above-normal precipitation regime. Supplemental water maintained a thinner, softer crust and higher dungpat moisture content promoted more continuous seedling emergence than in the natural precipitation regime. However, as in the natural precipitation regime, the earlier cohorts (1-3) had a greater number of seedlings surviving than the later cohorts (Figs. 26e and 27e). Proportional survival of seedlings tended to be greater for earlier cohorts (1-3) of seedlings emerged from passed seeds (Fig. 26b). A Mantel log-rank test showed highly significant (P=0.003) survival for seedlings among all the cohorts that emerged from passed seeds under above-normal precipitation regime; however, a contingency test did not reveal any significant differences (P=0.596), due to a small sample size. For unpassed seeds, cohorts 3, 2, and 1 had significantly higher survival than cohort 6 (P=0.009). A contingency test also revealed a significant difference in the comparative survival of these seedling cohorts (Fig. 27b).

The location of seedling emergence in dungpats played an important role in proportional and total survival of seedlings from passed and unpassed seeds. When averaged across cohorts and precipitation regimes, seedling emergence and survival was significantly greater (P=0.004) at the peripheral region of dungpats than at the core region (Figs. 26c and f, 27c and f). Seedlings that emerged at the peripheral region near the soil surface were able to establish roots in the soil much faster than seedlings emerging in the core region. Early and rapid root penetration of grass seedlings is a prerequisite for subsequent establishment (McWilliam et al. 1970, Aguirre and Johnson 1991a, 1991b, Call and Roundy 1991, Ries and Svejcar 1991). Most of the seedlings that emerged at the core region remained in a weakened vegetative stage, while most of the seedlings that emerged from the peripheral region were more vigorous in the vegetative stage and were able to set seed by the end of the growing season. In addition, the crowns of most seedlings that emerged in the core region were located in the upper layer of dungpats, well above the dungpat/soil-surface interface. After dungpat disintegration, plants with elevated crowns and exposed roots may not be well anchored in the soil and they may be more susceptible to desiccation.

Total aboveground biomass per dungpat, harvested at the end of the growing season, was not significantly higher ($P<0.05$) for crested wheatgrass plants established from unpassed seeds (8.1 g/dungpat) than from passed seeds (6.0 g/dungpat), when averaged across the two precipitation regimes. Plants from both passed and unpassed seeds had significantly ($P<0.05$) greater total aboveground biomass per dungpat when they established under above-normal spring precipitation (12.1 g/dungpat) than under natural spring precipitation (2.0 g/dungpat).

When expressed on an aboveground biomass per plant basis across the two precipitation regimes, the mean weight of the plants established from passed seeds was numerically at least two times greater than the mean biomass of plants established from unpassed seeds in dungpats and in broadcast and drill seedbeds (Fig. 28), but the differences were nonsignificant ($P>0.05$). Fewer plants established from passed seeds in dungpats, but they were widely spaced along the periphery of dungpats, apparently allowing access to more resources for greater individual plant growth.

The importance of spring precipitation was evident later in the growing season as crested wheatgrass plants in all seeding treatments set seed. Plants established from passed and unpassed seeds in dung and from seeds in broadcast and drill seedbeds under above-normal precipitation had significantly ($P<0.05$) greater numbers of seeds per inflorescence (Fig. 29a) and significantly ($P<0.05$) greater mean weight of seeds (Fig. 29b) than plants established under natural precipitation. Also, plants established in dungpats had comparable or greater numbers of seeds per inflorescence and seed weight than plants established in soil seedbeds under both precipitation regimes. This supports the claim of Archer and Pyke (1991) that dungpats have the potential to serve as nuclei of seed production for the surrounding area. Seedling development was not quantified in the fall experiment because of time

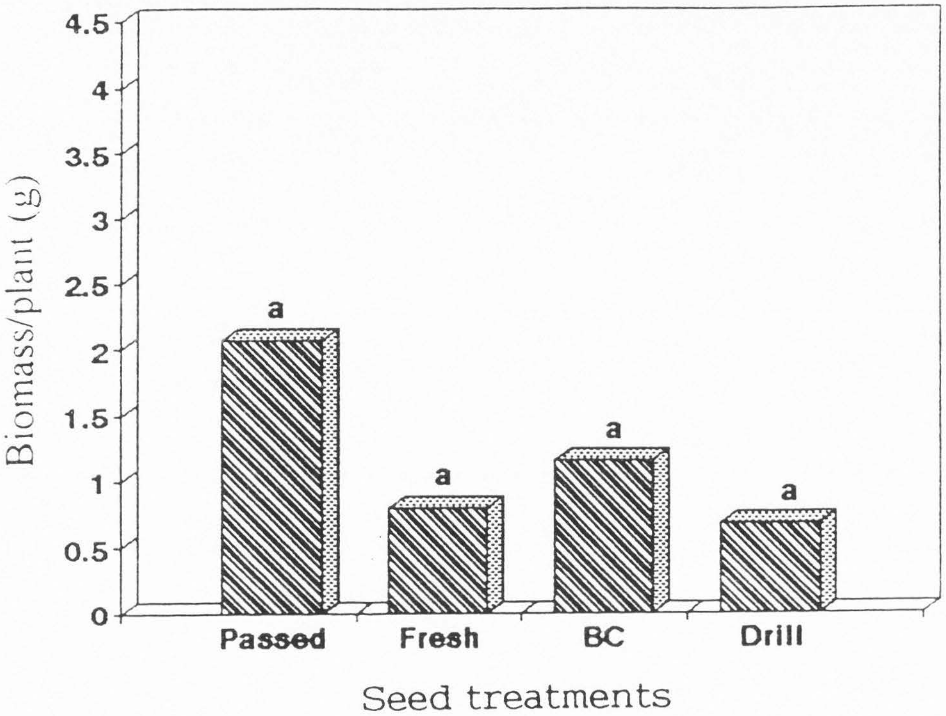

Figure 28. Aboveground biomass/plant of plants emerged from passed and unpassed (fresh) seeds in dungpats and seeds in broadcast and drill seedbeds averaged over natural and above-normal precipitation regimes.

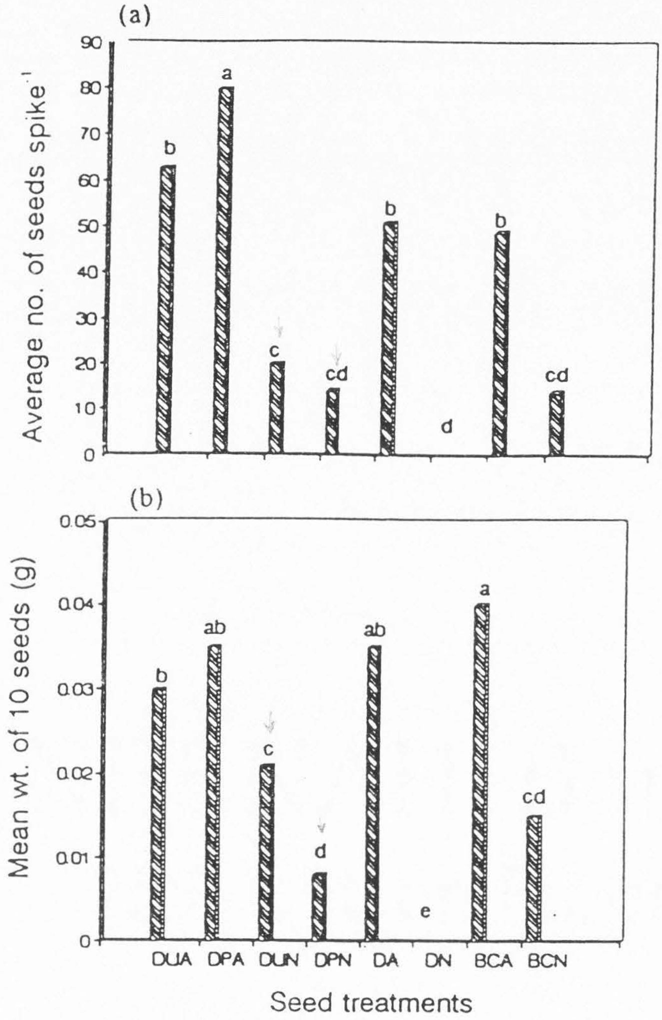

Figure 29. (a) Mean number of seeds per spike (inflorescence) of plants emerging from different seeding treatments and (b) mean weight of 10 randomly selected seeds per spike from the same plants emerging from the same seed treatments in the spring experiment. Means with the same letter are not significantly different ($P<0.05$). DUA, dungpats containing unpassed seeds under above-normal precipitation; DPA, dungpats containing passed seeds under above-normal precipitation; DUN, dungpats containing unpassed seeds under natural precipitation; DPN, dungpats containing passed seeds under natural precipitation; DA, drill seeding under above-normal precipitation; DN, drill seeding under natural precipitation; BCA, broadcast seeding under above-normal precipitation; and BCN, broadcast seeding under natural precipitation.

constraints in relation to the preparation of this dissertation; however, it will be briefly discussed in a descriptive manner. Low ambient temperatures at and after the time of dungpat placement, and broadcast and drill seeding in soil seedbeds (30 October 1993), delayed seed germination until late February 1994. By 1 March 1994, seedlings were emerging from all locations on dungpats and in the broadcast and drill seedbeds. Most seedlings that emerged from dungpats did so through cracks created by frequent freezing and thawing. The lowest relative seedling emergence was observed in dungpats containing passed seeds. Low seedling emergence was also noted for passed seeds in the spring experiment, but much lower ambient temperatures in the fall may have increased cold injury to seeds that were imbibed and softened in the digestive tract. Frischknecht (1959) noticed that crested wheatgrass seed germinability did not decrease when initially dry seeds were stored under snow; however, presoaking seeds resulted in cold damage and reduced germinability.

Ungerminated seeds were retrieved from dungpats during the first 6 weeks following dungpat placement in the spring experiment. After the 6th week (24 May 1993), seeds had completely germinated, and seedlings had either emerged from or remained trapped inside dungpats. After placing retrieved seeds in a controlled environment with optimum germination temperatures, germination was significantly greater ($P<0.05$) for unpassed seeds (66%) than for passed seeds (28%). When averaged across seed types, germinability ranged from 29 to 57% over the sampling period (Fig. 30). Differences in germinability are probably due to variability in retrieval location (crust vs. interior of dungpat) and in separation of damaged and undamaged passed seeds. Seeds retrieved from drill and broadcast seedbeds over the course of the spring experiment had mean germination percentages of 80 ± 0.8 and 78 ± 1.2, respectively.

Germinability of seeds retrieved from dungpats and soil seedbeds declined over the course of the fall experiment (Fig. 31a). Most of this decrease in germinability was related to the significantly lower ($P<0.05$) germinability of seeds in dungpats compared to soil seedbeds (Fig. 31b). Moist dungpats (elevated on the soil surface) experienced greater variability in freezing and thawing (and possibly cold injury to seeds) than soil seedbeds.

Conclusions

Microenvironmental factors in dungpats, underlying soil, and soil seedbeds vary considerably, depending upon weather conditions in the field. Moisture content and temperature fluctuated with the season of the year, but also from day to day within the season, depending on cloud cover and insolation. Dungpats, however, tended to have higher moisture contents and a greater range between maximum and

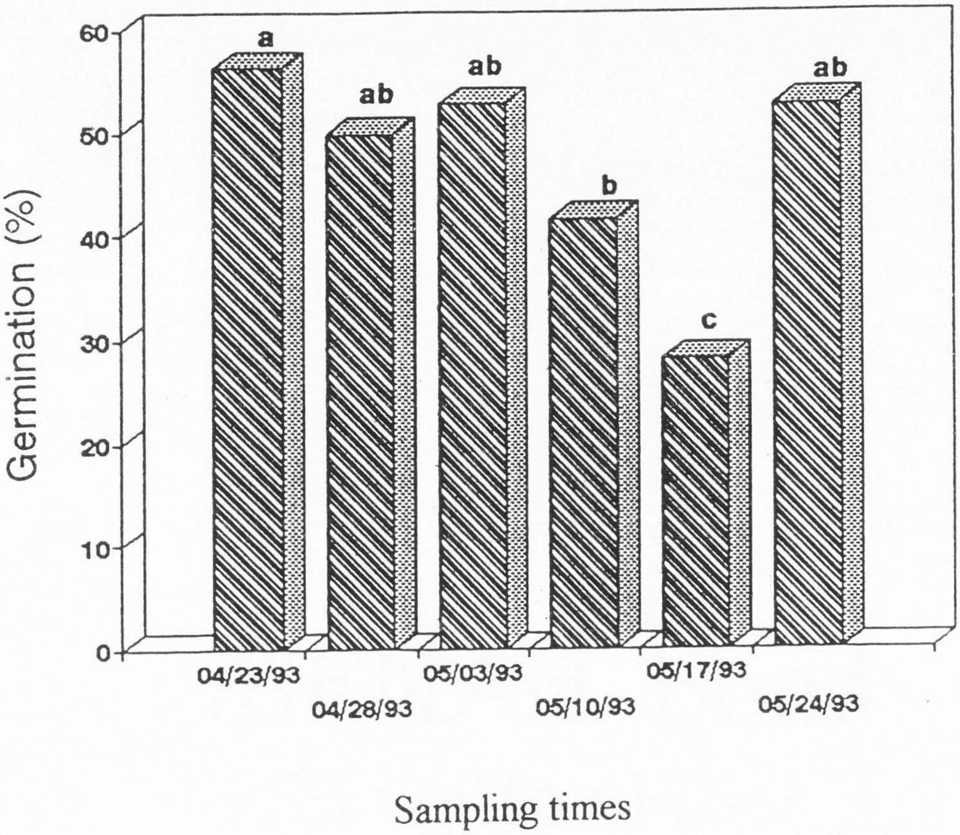

Figure 30. Percent germination of undamaged, ungerminated seeds retrieved from dungpats containing passed and unpassed seeds in the spring experiment. Means with the same letters are not significantly different ($P<0.05$).

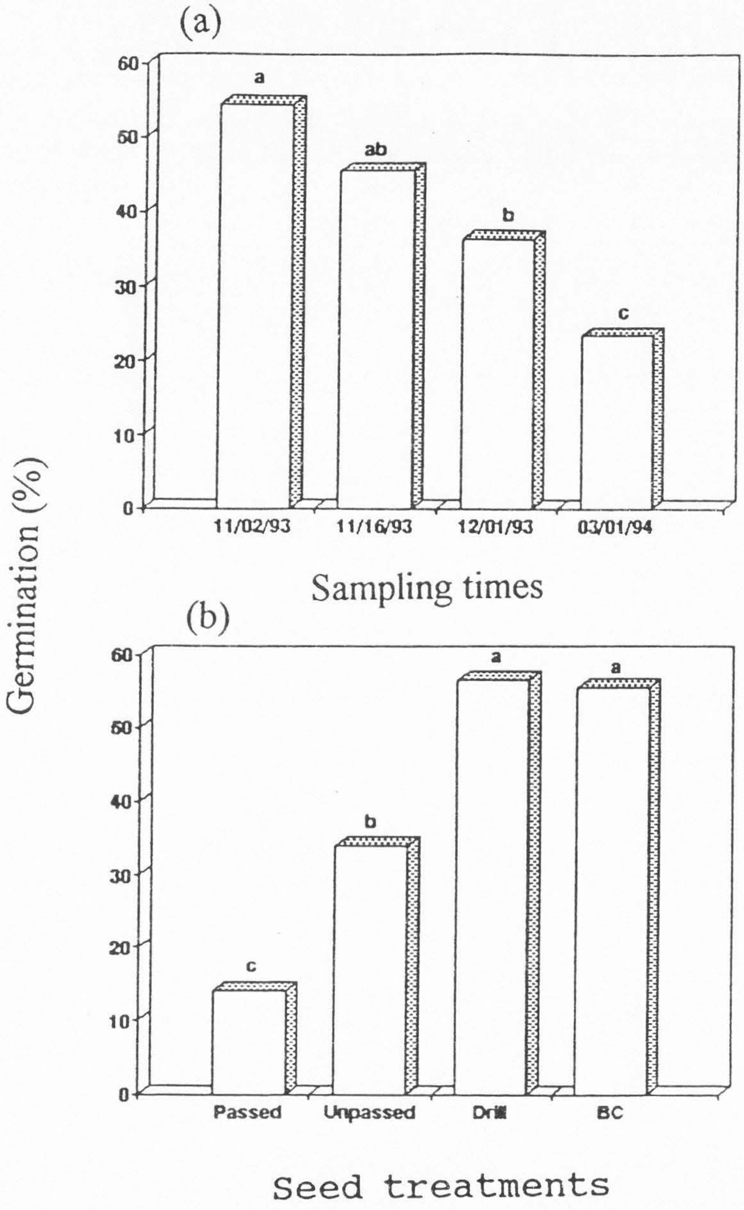

Figure 31. Germination of undamaged, ungerminated seeds (a) retrieved from dungpats at different sampling times in the fall experiment and (b) passed and unpassed seeds retrieved from dungpats and seeds retrieved from drill and broadcast seedbeds. Means with the same letter are not significantly different (*P*<0.05).

minimum temperatures than underlying soil and soil seedbeds. Crust thickness on dungpats varied with the frequency and intensity of precipitation events and changes in ambient and dungpat temperatures. Most crested wheatgrass seedlings, except those growing from deeper depths in dungpats, emerged through the developing crust during the spring, particularly when the crust was softened by precipitation. Slight changes in total N, NH_4^+, NO_3^-, and organic matter in dungpats and underlying soil indicated that only partial decomposition and mineralization occurred over the entire study period of one year.

Unpassed seeds had higher germination and seedling emergence in dungpats than passed seeds. Both seed types had higher germination and seedling emergence in dungpats placed under above-normal than natural spring-time precipitation. Seedling recruitment and development were greatest at the peripheral region of dungpats, regardless of seed type and precipitation regime. Seedlings from passed seeds established in sufficient numbers and reached reproductive maturity by the end of the growing season, indicating that dungpats can serve as nuclei of seed production for surrounding areas. Successful seedling establishment occurred in dungpats placed in the field in the spring and fall seasons.

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CHAPTER 4

SYNTHESIS

Livestock can be used as a tool for reseeding rangelands if the seeds of the desired species can withstand the hazards of mastication, rumination, and digestion by animals (Gardener et al. 1993a, 1993b, Ocumpaugh and Swakon 1993). After passage through the digestive tract, seeds and developing seedlings in animal dung are exposed to variable moisture and temperature conditions, restrictive surface crusts, aerobic and anaerobic decomposition processes, and depredation by a variety of predators. Even after successful germination and emergence, seedling survival is affected by the density-dependent competition among a crowded population of conspecifics on a relatively small dungpat substrate (Silvertown 1987). Successfully established seedlings, however, can benefit from a fairly moist, nutrient-rich environment, and contribute to future generations that will ultimately occupy the areas surrounding dungpat satellite populations.

The objective of this project was to determine the effects of microenvironmental factors of dungpats and underlying soil (temperature, moisture, nutrients, and dungpat crust formation) on the germination and establishment of 'Hycrest' crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult X *A. cristatum* (L.) Gaert.]. The rationale for selecting 'Hycrest' crested wheatgrass was based on several considerations: 1) It is a persistent, drought- and grazing-tolerant species that is well adapted to the Intermountain region (Dwyer 1986, Johnson 1986, Young and Evans 1986); 2) It had one of the highest recovery rates and germination rates for seeds of range grass species fed to cattle in an earlier, related study (Al-Mashikhi 1993); and 3) It has a long coleoptile, which enables seedlings to not only emerge from deeper depths but also to keep their roots deeper in the germination medium (dungpat or soil) and reach the autotrophic stage earlier (Johnson 1986, Newman and Moser 1988).

Complementary greenhouse and field studies were implemented to measure the effects of microenvironmental factors on the germination and establishment of crested wheatgrass in dungpats. The greenhouse study (Chapter 2) was designed to determine the location of ingested/passed seeds in dungpats and simulate the deposition of cattle dungpats on two different soils (loam and coarse sand) at several water levels (field capacity, ½ field capacity, and no water) that can exist following spring snowmelt in the Intermountain region. The field study (Chapter 3) was designed to determine how germination and establishment were influenced by season of dungpat deposition (conventional spring and fall seeding times), spring precipitation regime (natural and above-normal), and passage of seeds through the digestive tract (passed and unpassed seeds), and to provide a general comparison of dungpats and soil seedbeds as substrates for germination and seedling establishment.

Results from the greenhouse study indicated that uniform, artificially prepared dungpats had greater volume and more passed seeds than natural dungpats, but that passed seeds were similarly distributed in both types of dungpats. The high initial moisture content and favorable temperatures in dungpats promoted germination of passed seeds, but many of the emerging seedlings were restricted by a rapidly forming crust. Even though dungpat moisture content remained relatively high for several weeks, emerging seedlings did not survive as their roots penetrated into the dry loam or the coarse sand at any initial moisture level. The majority of seedlings that survived in the loam at ½ field capacity or higher emerged at the peripheral region of dungpats near the soil surface. Very few seedlings survived after emerging in the interior (core) region of dungpats.

Results from the field study indicate that seedlings will establish in dungpats deposited at conventional spring and fall seeding times. Cold minimum temperatures in late fall delayed the germination of imbibed seeds in moist dungpats until the following spring, as they did for seeds in soil seedbeds. At the spring seeding time, the greatest seedling emergence and survival occurred with unpassed seeds in dungpats and soil seedbeds under the above-normal precipitation regime. Seedlings established from passed seeds in dungpats, in spite of their relatively low density, were comparable or superior to unpassed seeds in dungpats and soil seedbeds in terms of individual plant fitness attributes such as aboveground biomass, phenological development, number of seeds per inflorescence, and weight of seeds. Thus, if adequate underlying soil moisture is available, crested wheatgrass can be successfully established using cattle as seed dispersal agents.

One of the major findings of the field and greenhouse studies was the importance of location of seedling emergence in dungpats in relation to plant survival and development. Although seedlings emerged in all regions of dungpats in both studies, those that emerged at the periphery near the soil surface had the greatest survival and development. The fate of seedlings emerging at different locations in dungpats can be illustrated in three possible scenarios (Fig. 32): 1) Seeds germinate near the bottom in the interior of the dungpat and developing seedlings exhaust their stored reserves and/or do not have enough force to penetrate through the crust on the upper surface of the dungpat. These seedlings remain trapped inside dungpats and eventually die and decompose. 2) Seeds germinate near the top in the interior of the dungpat and the developing seedlings push their coleoptile through the upper crust and their primary root system into the underlying soil, but

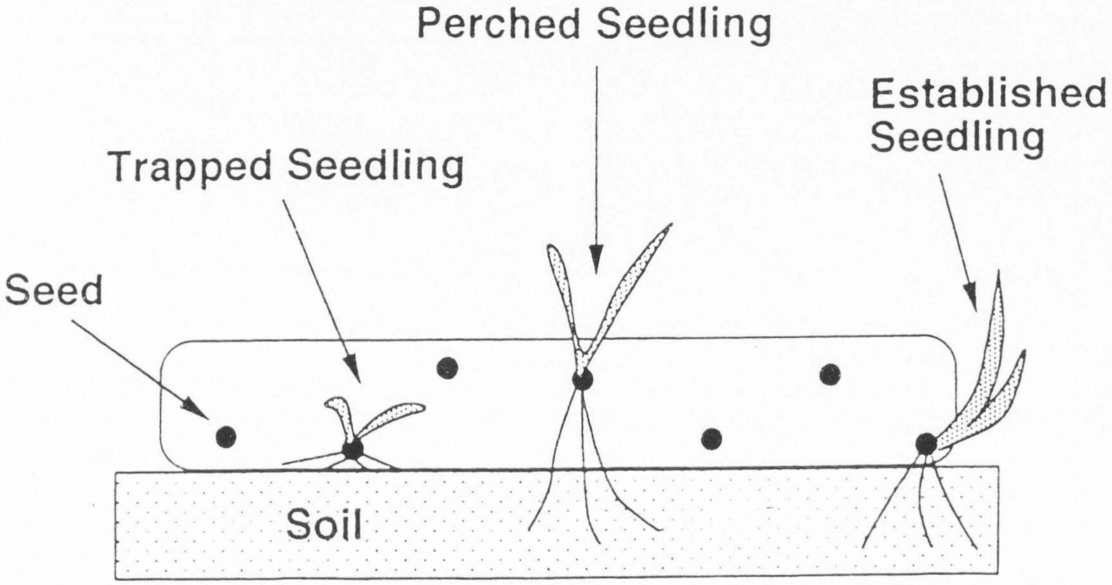

Figure 32. Location plays a highly important role in seedling establishment. Seedlings may be trapped, perched, or established depending upon the seed location in dungpats. See text for details.

their crown remains elevated in the upper portion of the dungpat. These perched seedlings may not survive after dungpat disintegration because of poor soil anchorage or root desiccation. 3) Seeds germinate at the dungpat periphery near the soil surface, and developing seedlings rapidly extend their coleoptile out along the periphery and their primary roots into the soil. These established seedlings become autotrophic at an early stage and have more rapid phenological development than conspecifics emerging from the interior region of dungpats.

Dungpats have been viewed not only as favorable substrates for germination and plant establishment soon after deposition, but also as transient seedbanks where viable seeds can exist for considerable time until conditions become favorable for germination and establishment (Karl et al. 1994a, 1994b). Dungpats generally did not act as transient seedbanks in the spring field study. Due to favorable temperature and moisture conditions, almost all seeds germinated inside dungpats during the first 6 weeks after deposition. In the fall field study, a portion of seeds retained their viability in dungpats over the winter months and germinated the following spring.

Areas for Future Research

Although these results indicate that cattle dungpats provide a favorable environment for the germination and establishment of crested wheatgrass, there are several aspects of this type of research that require further investigation:

1) Cattle were maintained on one grass hay diet during the greenhouse and field studies, and it is important to understand how different quality diets influence the rate of passage and thus the germinability of seeds of desirable range plant species adapted to the Intermountain region.
2) Similar germination and establishment studies should be performed with other types of animals (e.g., sheep, goats, horses) that have different digestive systems, diets, land use patterns, and dung types. It is important to find the proper combination(s) of animal type and revegetation species to match the terrain and vegetation type of the rangeland to be revegetated.
3) Only crested wheatgrass was used in these greenhouse and field studies. It is important to explore the potential of several grass, forb, and shrub species for this type of revegetation system.

4) Due to limited dungpat disintegration over the course of the spring field study, the impact of dungpats on the nutrient status of the underlying soil could not be assessed. Longer time frames should be allowed for dungpat decomposition and more complete nutrient transfer in semiarid environments in the Intermountain region.

5) Only dungpats and underlying soil were analyzed to determine the availability of nutrients for plants established in dungpats. Plants emerging from dungpats and nearby soil should be analyzed for nutrient content in order to make a more complete determination.

6) Uniform dungpats used in this study were prepared by thoroughly mixing cattle dung and pouring it into aluminum molds. Even though seeds are distributed in a similar manner in uniform and natural dungpats, uniform dungpats do not have the same size, shape, and consistency of natural dungpats. These differences could have significant effects on microenvironmental factors (particularly crust development) that influence germination and establishment.

7) Dungpats were only placed on bare ground in the field study. It is important to consider the impact of cattle dungpats and other animal dung

on the existing vegetation that might compete with plants establishing in dung.

8) Since plants establishing in dungpats readily produced seeds by the end of the first growing season, it is important to monitor seed dispersal and seedling recruitment in the area surrounding dungpats.

Management Implications

Cattle can be dosed with crested wheatgrass seeds and moved to a target area for seed dispersal about 36-48 hours later. An amount of 60,000 seeds fed to each steer in this research project seems to be quite optimum based on the subsequent number of seedlings that emerged and survived in the dungpats. Seeds of crested wheatgrass will have to be fed to the cattle before the animals are allowed to defecate on the target area. Herding will be required to ensure good cattle dungpat distribution in the target area. When dungpats are deposited in a foothill rangeland setting in the Intermountain region in mid to late spring, dungpat temperature and moisture conditions may promote germination of passed seeds during the first few weeks. When dungpats are deposited in late fall, cold minimum temperatures will delay germination of passed seeds until the following spring. Even though high dungpat moisture content promotes germination, late spring and early summer precipitation and underlying soil moisture are critical for seedling development and survival. The moist dungpat microenvironment may not compensate for poor seedling root growth in dry or coarse soils. Land managers should be aware that even under favorable moisture conditions, only a few seedlings will ultimately survive after emergence on the dungpat substrate. However, these seedlings will benefit from the gradual release of nutrients as the dungpat disintegrates over time. Established plants will serve as nuclei of seed production for the surrounding area. This revegetation method will require a long time frame (most likely years to decades), and it will depend on the number of dosed animals, their pattern of land use, and ambient environmental conditions.

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APPENDIX

Table A.1. Analysis of variance of moisture content in dungpats and the underlying soil (Greenhouse Experiment).

Sources of Variation	df	SS	MS	F	P
Replications	1	50.1	50.1		
Soil (S)	1	5451.8	5451.8	136.99	<0.001
Water (W)	2	3486.3	1743.1	43.55	<0.001
Time (T)	8	367207.5	45900.9	1146.71	<0.001
S x W	2	2050.7	1025.4	25.62	<0.001
S x T	8	4730.7	591.3	14.77	<0.001
W x T	16	2995.6	187.2	4.68	<0.001
S x W x T	16	2301.6	143.9	3.59	<0.001
Error (a)	53	2121.5	40.0		
Location (L)	4	2972.2	743.0	41.05	0.002
S x L	4	126.8	31.7	3.96	0.003
W x L	8	132.0	16.5	2.06	0.036
T x L	32	3416.7	106.8	13.35	<0.001
S x W x L	8	4.7	0.6	<1	0.999
S x T x L	32	252.0	7.9	<1	0.457
W x T x L	64	438.1	6.8	<1	0.740
S x W x T x L	64	570.2	8.9	1.11	0.246
Error (b)	216	1728.5	8.0		
Position (P)	1	147385.3	147385.3	4912.84	0.009
S x P	1	1941.7	1941.7	150.51	<0.001
W x P	2	348.1	174.0	13.50	<0.001
T x P	8	185942.3	23242.8	1801.77	<0.001
S x W x P	2	480.6	240.3	18.63	<0.001
S x T x P	8	3346.9	418.4	32.43	<0.001
W x T x P	16	1475.6	92.2	7.15	<0.001
S x W x T x P	16	1934.6	120.9	9.37	<0.001
L x P	4	1118.1	279.5	21.67	<0.001
S x L x P	4	62.8	15.7	1.22	0.300
W x L x P	8	119.4	14.9	1.16	0.321
T x L x P	32	1992.4	62.3	4.83	<0.001
S x W x L x P	8	48.0	6.0	<1	0.877
S x T x L x P	32	233.3	7.3	<1	0.971
W x T x L x P	64	312.1	4.9	<1	0.999
S x W x T x L x P	64	438.9	6.9	<1	0.998
Error (c)	270	3472.3	12.9		
Total		1079	150689.4		

Table A.2. Analysis of variance of crust thickness on dungpats (Greenhouse Experiment).

Sources of Variation	df	SS	MS	F	P
Replication	1	3.137	3.137		
Time (T)	6	2459.006	409.834	331.58	0.0000
Soil (S)	1	1.383	1.383	1.12	0.2963
Water (W)	2	113.968	56.984	46.10	0.0000
T x S	6	34.003	5.667	4.58	0.0012
T x W	12	25.741	2.145	1.73	0.0942
S x W	2	3.896	1.948	1.58	0.2190
T x S x W	12	23.498	1.958	1.58	0.1347
Error (a)	41	50.676	1.236		
Location (L)	4	243.016	60.754	314.11	0.0000
T x L	24	78.233	3.260	16.85	0.0000
S x L	4	1.249	0.312	1.61	0.1740
W x L	8	2.430	0.304	1.57	0.1372
T x S x L	24	11.350	0.473	2.45	0.0004
T x W x L	48	13.021	0.271	1.40	0.0622
S x W x L	8	2.639	0.330	1.71	0.0993
T x S x W x L	48	11.860	0.247	1.28	0.1291
Error (b)	168	32.494	0.193		
Total	419	3111.597			

Table A.3. Analysis of variance of germination of seeds retrieved from dungpats (Greenhouse Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	296.67	296.67	4.14	0.468
Time (T)	8	6616.07	827.01	11.55	0.000
Soil (S)	1	10.08	10.08	0.14	0.709
Water (W)	2	143.46	71.73	1.00	0.374
T x S	8	378.67	47.33	0.66	0.723
T x W	16	887.03	55.44	0.77	0.706
W x S	2	78.50	39.25	0.55	0.581
T x W x S	16	1080.00	67.50	0.94	0.538
Error	53	3795.82	71.62		
Total	107	13286.32			

Table A.4. Analysis of variance of seedling biomass (Greenhouse Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	0.086	0.086	1.34	0.252
Time (T)	8	11.776	11.472	22.96	0.000
Soil (S)	1	7.406	7.406	115.55	0.000
Water (W)	2	10.245	5.122	79.91	0.000
T x S	8	11.776	1.472	22.96	0.000
T x W	16	19.499	1.218	19.01	0.000
S x W	2	10.245	5.122	79.92	0.000
T x S x W	16	19.499	1.218	19.01	0.000
Error	53	3.397	0.064		
Total	107	93.932			

Table A.5. Analysis of variance of moisture content in dungpats and underlying soil in field study (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Replications	1	22.2	22.2		
Seed (S)	1	7.7	7.7	0.138	0.7119
Water (W)	1	3007.9	3007.9	53.983	0.0000
Time (T)	11	294106.9	26737.0	479.853	0.0000
S x W	1	96.1	96.1	1.725	0.1954
S x T	11	462.6	42.1	0.756	0.6803
W x T	11	5796.0	526.9	9.456	0.0000
S x W x T	11	493.4	44.9	0.806	0.6337
Error (a)	47	2618.8	55.7		
Location (L)	4	9755.5	2438.9	126.368	0.0000
S x L	4	184.8	46.2	2.394	0.0519
W x L	4	159.2	39.8	2.062	0.0873
T x L	44	6814.5	154.9	8.062	0.0000
S x W x L	4	47.9	12.0	0.622	0.6473
S x T x L	44	767.8	17.5	0.907	0.6398
W x T x L	44	1189.0	27.0	1.399	0.0648
S x W x T x L	44	621.0	14.1	0.731	0.8905
Error (b)	192	3704.0	19.3		
Position (P)	1	262155.9	262155.9	11703.390	0.0000
S x P	1	8.6	8.6	0.384	0.5360
W x P	1	3.1	3.1	0.138	0.7106
T x P	11	122069.2	11097.2	495.410	0.0000
S x W x P	1	33.3	33.3	1.487	0.2238
S x T x P	11	153.2	13.9	0.620	0.8110
W x T x P	11	989.7	90.0	4.018	0.0000
S x W x T x P	11	425.6	38.7	1.728	0.0680
L x P	4	7049.1	1762.3	78.674	0.0000
S x L x P	4	254.1	63.5	2.834	0.0252
W x L x P	4	108.2	27.0	1.205	0.3093
T x L x P	44	6791.2	154.3	6.888	0.0000
S x W x L x P	4	85.6	21.4	0.955	0.4329
S x T x L x P	44	911.6	20.7	0.924	0.6115
W x T x L x P	44	1297.7	29.5	1.317	0.1010
S x W x T x L x P	44	769.1	17.5	0.781	0.8363
Error (c)	240	5383.5	22.4		
Total	959	738344.4			

Table A.6. Analysis of variance of moisture content in soil seedbeds (drill and broadcast) under two watering treatments in field (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	10.935	10.935	0.794	0.3773
Seed (S)	1	1.500	1.500	0.109	0.7428
Water (W)	1	72.454	72.454	5.263	0.0263
Time (T)	11	6718.929	610.811	44.370	0.0000
S x W	1	2.160	2.160	0.157	0.6938
S x T	11	91.620	8.329	0.605	0.8149
W x T	11	162.631	14.784	1.073	0.4018
S x W x T	11	99.315	9.028	0.656	0.7715
Error	47	647.015	13.766		
Total	95	7806.559			

Table A.7. Analysis of variance of moisture content in dungpats and underlying soil in field (Fall Experiment).

Sources of Variation	df	SS	MS	F	P
Replications	1	164.5	164.5		
Seed (S)	1	21.0	21.0	0.231	0.6422
Time (T)	4	3432.9	858.2	9.446	0.0027
S x T	4	394.7	98.7	1.086	0.4188
Error (a)	9	817.7	90.9		
Location (L)	4	797.4	199.3	9.090	0.0000
S x L	4	144.1	36.0	1.642	0.1826
T x L	16	739.4	46.2	2.107	0.0284
S x T x L	16	476.7	29.8	1.359	0.2115
Error (b)	40	877.0	21.9		
Position (P)	1	144614.4	144614.4	7858.478	0.0000
S x P	1	77.6	77.6	4.217	0.0452
T x P	4	3492.6	873.2	47.457	0.0000
S x T x P	4	441.0	110.3	5.995	0.0005
L x P	4	201.9	50.5	2.745	0.0384
S x L x P	4	33.2	8.3	0.451	0.7711
T x L x P	16	254.9	15.9	0.864	0.6110
S x T x L x P	16	244.6	15.3	0.832	0.6448
Error (c)	50	919.3	18.4		
Total	199	158145.0			

Table A.8. Analysis of variance of moisture content in soil seedbeds (drill and broadcast) in field (Fall Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	9.248	9.248	1.305	0.2828
Seed (S)	1	18.050	18.050	2.546	0.1450
Time (T)	4	700.600	175.150	24.711	0.0001
S x T	4	8.380	2.095	0.295	0.8737
Error	9	63.792	7.088		
Total	19	800.070			

Table A.9. Analysis of variance of crust thickness on dungpats in field (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Replication	1	0.140	0.140		
Seed (S)	1	0.347	0.347	0.208	0.6511
Water (W)	1	97.126	97.126	58.264	0.0000
Time (T)	8	1057.108	132.138	79.267	0.0000
S x W	1	0.121	0.121	0.073	0.7886
S x T	8	7.295	0.912	0.547	0.8128
W x T	8	113.011	14.126	8.474	0.0000
S x W x T	8	3.065	0.383	0.230	0.9827
Error (a)	35	58.334	1.667		
Location (L)	4	289.645	72.411	309.449	0.0000
S x L	4	0.121	0.030	0.128	0.9720
W x L	4	6.245	1.561	6.671	0.0000
T x L	32	28.069	0.877	3.748	0.0000
S x W x L	4	0.512	0.128	0.547	0.7014
S x T x L	32	6.209	0.194	0.829	0.7270
W x T x L	32	14.101	0.441	1.885	0.0063
S x W x T x L	32	7.198	0.225	0.962	0.5320
Error (b)	144	33.722	0.234		
Total	359	1722.370			

Table A.10. Analysis of variance of crust thickness on dungpats in field (Fall Experiment).

Sources of Variation	df	SS	MS	F	P
Replication	1	2.964	2.964		
Seed (S)	1	0.000	0.000	0.000	1.0000
Time (T)	3	123.669	41.223	20.953	0.0007
S x T	3	1.990	0.663	0.663	0.6006
Error (a)	7	13.771	1.967		
Location (L)	4	23.112	5.778	60.566	0.0000
S x L	4	0.292	0.073	0.766	0.5552
T x L	12	3.653	0.304	3.191	0.0043
S x T x L	12	0.452	0.037	0.395	0.9552
Error (b)	32	3.054	0.095		
Total	79	1722.370			

Table A.11. Analysis of variance of number of seeds per spike of plants emerged from different seed treatments in dungpats and soil in field (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	9	10618.56	1179.84	3.86	0.000
Seed	7	55800.69	7971.53	26.05	0.000
Error	63	19272.94	305.97		
Total	79	85695.19			

Table A.12. Analysis of variance of weight of ten seeds per spike of plants emerged from different seed treatments in dungpats and soil in field (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	9	0.0004	4.17	5.91	0.000
Seed	7	0.0145	2.07	29.32	0.000
Error	63	0.0004	305.97		
Total	79	0.0153			

Table A.13. Analysis of variance of total (aboveground) biomass/plant of plants emerged from four seed types under two watering treatments in dungpat and soil seedbeds in field (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	0.106	0.106	0.011	0.9180
Time (T)	8	355.546	44.443	4.449	0.0002
Water (W)	1	33.850	33.850	3.389	0.0698
Seed (S)	3	42.805	14.268	1.429	0.2416
T x W	8	191.507	23.938	2.397	0.0239
T x S	24	130.368	5.432	0.544	0.9518
W x S	3	11.800	3.933	0.394	0.7578
T x W x S	24	244.085	10.170	1.018	0.4565
Error	71	709.112	9.987		
Total	143	1719.179			

Table A.14. Analysis of variance of germination of seeds retrieved from dungpats in field (Spring Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	157.687	157.687	1.242	0.2765
Water (W)	1	1598.521	1598.521	12.596	0.0017
Seed (S)	1	18291.021	18291.021	144.132	0.0000
Time (T)	5	4390.937	878.187	6.920	0.0004
W x S	1	609.187	609.187	4.800	0.0388
W x T	5	1794.104	358.820	2.827	0.0392
S x T	5	4458.604	891.720	7.026	0.0004
W x S x T	5	846.437	169.287	1.334	0.2853
Error	23	2918.812	126.904		
Total	47	35065.310			

Table A.15. Analysis of variance of germination of seeds retrieved from dungpats and soil seedbeds in field (Fall Experiment).

Sources of Variation	df	SS	MS	F	P
Blocks	1	536.28	536.28	4.005	0.0638
Time (T)	3	4181.59	1393.86	10.410	0.0006
Seed (S)	3	9765.09	3255.03	24.310	0.0000
T x S	9	2571.78	285.75	2.130	0.0934
Error	15	2008.21			
Total	31	19062.96			

VITA

Ghulam Akbar

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Dungpat microenvironmental effects on germination and establishment of crested wheatgrass

Major Field: Range Science

Biographical Information:

Personal Data:

Born at Dullah, Chakwal (Pakistan), September 13, 1955, son of Ghulam Haider and Khadija Bibi; married Ghulam Sakina April 9, 1974; three children, Naveed Akbar, Saeed Akbar and Rabia Akbar.

Education:

Graduated from Board of Intermediate and Secondary Education, Quetta, Balochistan (Pakistan) in 1972; received Bachelor of Science degree (Forestry) from University of Peshawar in 1975; received Master of Science degree (Forestry) from University of Peshawar in 1986; completed the requirements for a Doctor of Philosophy in Range Science at Utah State University in 1994.

Professional Experience:

1975-80 Range Forest Officer, Balochistan Forest Department; 1981-82 Horticulture Officer, Capital Development Authority, Islamabad; 1982-84 Assistant Director Research (Forestry & Environment), Pakistan Agricultural Research Council; 1984-86 Graduate student, Pakistan Forest Institute, University of Peshawar; 1986-88 Scientific Officer, Agroforestry Project, National Agricultural Research Center; 1988-89 Deputy Director Research (Forestry & Environment), Pakistan Agricultural Research Council, 1989-90 Senior Scientific Officer, Arid Zone Research Institute, Quetta; 1990-91 Deputy Director, Arid Zone Research Station Bahawalpur; 1991-94 Graduate fellow, Department of Range Science, Utah State University.