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An Ecological Analysis of Prairie Rehabilitation on Petroleum Wellsites in Southeast Alberta

By

Andrew Markus Hammermeister

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Doctor of Philosophy*

in

Water and Land Resources

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DEDICATION

In memory of our son Samuel Quinn Hammermeister.

ABSTRACT

Ongoing disturbance of native prairie in Alberta necessitates understanding rehabilitation practices and their effectiveness. Observations indicate that wheatgrass (*Agropyron* spp.) cultivars currently used in seed mixes may suppress other typically more dominant species. High diversity seed mixes and natural recovery have been suggested as alternatives. Various plant community and biogeochemical attributes were studied in four rehabilitation treatments: three seed mixes (Current - low diversity dominated by wheatgrass cultivars, Simple - low diversity dominated non-wheatgrass perennial grasses, Diverse - high diversity) and natural recovery. Treatments, at seven petroleum wellsites on Chernozemic and Solonetzic soils in Dry Mixed Grass prairie, were compared with an undisturbed control for three years following wellsite construction and abandonment. Surface soil was stripped, stored for less than six months, and replaced as part of standard reclamation practices. Soil disturbance resulted in a 16.5 and 19% reduction in organic carbon and total nitrogen, respectively; a reduction in nutrient supplying potential and long term implications for ecosystem development were postulated. Few significant differences were found among seeded treatments. Soil disturbance increased nitrate availability relative to the control; nitrate was highest in the Natural Recovery and lowest in the Current treatment. Native wheatgrass cultivars dominated plant community development and suppressed establishment of other species. Dominance was attributed to life history strategy and high establishment rate, growth rate, competition, and reproduction. The Diverse treatment did not increase community diversity and similarity to undisturbed prairie. Natural recovery was characterized by annual forb domination and increasing perennial species. Soil nitrate was positively correlated with annual forb biomass which was negatively correlated with grass biomass. After three years, the principal conclusions were that species attributes were more important than seed mix diversity for plant community development; with relatively high nitrogen availability, wheatgrass cultivars suppressed establishment of other species; seeded treatments accelerated recovery of biogeochemical cycling relative to natural recovery; natural recovery was most effective in initiating community development towards a predisturbance condition.

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CHAPTER 1. INTRODUCTION

It is one thing to use up oil and precious metals
to fly aircraft and drive cars and trucks,
to build an industrialized world.
It is quite another to squander four billion years'
worth of the planet's genetic endowment,
to tear great rents of ignorance in the potential learning of our descendants,
all for the sake of a fleeting profit in rosewood and ply.

(Timothy Ferris describing the potential tragedy in destruction of the rainforests.
From his book: "In The Mind's Sky: Human Intelligence In A Cosmic Context." (p. 200).

1.1 OVERVIEW

Applied ecology is defined as "a scientific discipline that attempts to predict the ecological consequences of human activities and recommend ways to limit damage to, and to restore, ecosystems" and includes restoration ecology among its subdisciplines (Kaufman and Franz, 1993, p. 112). Ecological restoration[1] has three goals: "a) to repair biotic communities after a disturbance, to re-establish them on the original site if the communities have been destroyed, or to establish them on other sites if the original sites can no longer be used; b) to maintain the present diversity of species and ecosystems by finding ways to preserve biotic communities or to protect them from human disturbances so that they can evolve naturally; and c) to increase knowledge of biotic communities and restoration techniques that can be applied to restore or manage other systems" (Kaufman and Franz, 1993, p.113).

Restoration involves management of numerous ecosystem components and interactions among them to achieve a specific goal. Due to the complexity of biological systems it is impossible to control all components and interactions. Therefore, successful rehabilitation requires an ability to predict ecosystem response to management practices. These predictions can only be made based on an understanding of the structure and function of ecosystems resulting from thorough scientific examination. This is what differentiates the science of restoration from the art of restoration (Bradshaw, 1993). Ecological principles must be integrated into restoration, and, the scientific study of restoration contributes to ecology by testing ecological theory. Each of the ecosystem components form disciplines and subdisciplines of study. The role of the ecologist is to find the relationship between these components. The role of the applied ecologist is to use an understanding of relationships among ecosystem components to measure and predict the ecological impacts of human activity and recommend ways to limit damage to, and to restore, ecosystems.

---

[1] The term 'restoration' is used here for discussion purposes; the term 'rehabilitation' will be used throughout the remainder of the thesis for reasons described in section 1.3.

The native prairie ecosystem is at great risk of being lost due to the combined frequency, duration, and extent of disturbance coincident with the introduction of exotic species with highly competitive, persistent, and invasive traits. Conservation of remaining blocks of native prairie is critical for this ecosystem to continue to exist. Anthropogenic disturbance continues to occur on native prairie in a variety of forms and for varying duration. In some cases small parcels of land are disturbed for periods of less than a year prior to abandonment. These disturbances offer a tremendous opportunity to study how this ecosystem recovers from disturbance, how our attempts to accelerate recovery may support or interfere with it, and how these processes relate to current ecological theory. This dissertation will describe research on the influence of selected rehabilitation practices on recovery from disturbance of the vegetative and soil components of the ecosystem, will link research results with the relevant literature, and outline practical implications for industry.

The dissertation consists of six chapters plus appendices. The purpose of this introductory chapter is threefold: to provide an overview of current ecological theory related to ecosystem succession and biodiversity, to introduce the reader to issues surrounding petroleum industry disturbance of native prairie and how this research came about, and to outline the objectives of this research. A more detailed review and discussion of relevant literature is included in the ensuing chapters.

Chapters two and three provide a detailed description and discussion of research results. While plant community development is the emphasis of chapter two, biogeochemical cycling is the focus in chapter three. Chapter four is intended to be an integrated discussion of the results presented in chapters two and three. Existing theory related to plant community succession is applied to the research results. Chapter five is intended to bring the results of this research together in an applied manner and includes a ranking of the relative success of each treatment that was studied. Chapter six provides a summary of future research needs based on this research. The dissertation is presented in paper format such that each chapter can be considered independently by the reader. Therefore, the contents of chapters two and three are summarized in chapters four and five.

1.2 PERSPECTIVES IN ECOLOGY

1.2.1 Plant Community Succession

The Dry Mixed Grass Natural Sub-region of Alberta has been disturbed in a variety of ways since European settlement. Some of these areas of prairie disturbance have been abandoned while others have been seeded to exotic species, or more recently, cultivars of native species. There are two questions that arise. What successional pathway will these seres follow? What mechanisms are causing succession to occur?

A comprehensive understanding of succession in these environments would allow researchers to predict the long-term influence of various disturbance and revegetation regimes and their ecological implications. Ultimately, it would be desirable to have a model that describes this process. A brief overview of successional theory to date follows.

Successional theory is relatively young. The first substantial contribution to this topic was by Clements (1916) who introduced the monoclimax theory of succession. Clements took an organismal approach to succession where community development was primarily determined by climate and would follow a predetermined sequence eventually reaching maturity (i.e., a climax community). Each seral stage would modify the environment, making it suitable for the next stage (i.e., early stages facilitated development of late stages). Clements suggested that succession was caused by nudation (i.e., disturbance), migration (i.e., species arrival onto the site), ecesis (i.e., species establishment), competition (species interactions on the site), reaction (alteration of the site), and stabilization (reaching dynamic equilibrium or climax). Many of the ideas continue to be used in successional theory today. However, the monoclimax theory did not account for multiple pathways and endpoints in succession. This led to the advent of the polyclimax theory (Tansley, 1920, 1935, 1941). The polyclimax theory suggested that factors such as soil, topography, fire, and grazing had an overriding influence on succession although the community may continue to slowly develop toward a climatic climax.

Both the monoclimax and polyclimax theories were based on communities replacing communities as succession progressed. However, individual species may occur in a variety of communities along an environmental gradient. In these communities, species realized niche in the presence of competition determines its presence or removal (i.e., the individualistic concept of species replacement as per Gleason, 1939 (presented in Kimmins, 1987). This led to development of the climax pattern hypothesis (Whittaker, 1953) that vegetation is a complex pattern of integrating communities rather than distinct entities. In conjunction with this theory, Egler (1954) presented the initial floristic model of succession where species prevalent throughout the successional process were present at the onset of succession, but their populations developed at different rates. Species dominant early in succession were displaced by later successional species through competition. This model contrasted the relay floristics model where early seral stages facilitated establishment of late stages (as per Clements' monoclimax theory). The initial floristics model and climax pattern hypothesis are especially useful in explaining seres where early seral stages inhibit, but don't prevent, establishment of late seral stages. These observations lead to the hypothesis that "succession occurs as a result of differential survival and growth of individual species that are adapted to grow best at different stages in the successional sequence." (Kimmins, 1987, p. 410).

Connell and Slatyer (1977) described three models of community succession and their role in community stability and organization. In the facilitation model, early successional species modify the environment making it suitable for the establishment of late successional species. In the tolerance model, the environment permits establishment of early and late successional species. The early successional species become displaced, however, as the late successional species modify the environment making it unsuitable for the early successional species. In the final model, inhibition, early and late successional species coexist until the environment is modified and dominated by a single species to such an extent that other species cannot establish. Pickett et al. (1987) reviewed these models (which they described as mechanisms) and suggested that they did not account for all successional pathways found in nature. They further suggested that complex successions often include combinations of the Connell and Slatyer mechanisms as well as others. Pickett et al. (1987) go on to discuss facilitation, tolerance, and inhibition as mechanisms in succession and ultimately arrive at five generalizations about mechanisms of species replacements in succession: succession may exhibit several mechanisms, different mechanisms of replacement may act in one sere at a given time, one species can participate in several mechanisms, the mechanisms can be discriminated only by determining the demographic and ecophysiological causes of turnover, and coordinated work is needed on environmental change and the demography and ecophysiology of successional turnover.

From these generalizations, Pickett et al. (1987) built a comprehensive hierarchy of successional causes. They identify three general causes of succession: site availability, differential species availability, and differential species performance. For each cause they identify contributing mechanisms or conditions (e.g., propagule pool, life history strategy, competition) for which they further identify modifying factors (e.g., topography, allocation patterns).

Pickett et al. (1987) presented a broad and general framework for causes of succession that may form the basis of determining which factors are most important. This all encompassing approach can become rather complex when attempting to develop a model for succession. A simpler approach was taken by Grime (1977) who suggested that all plants follow one of three strategies (i.e., competitors, ruderals, or stress tolerators) in response to constraints in the form of stress and disturbance. Ruderal plants are best suited to frequently-disturbed habitats, competitors are adapted to systems with high potential productivity and low stress or disturbance, and stress tolerators are predominant where environmental constraints are severely limiting. Plant community succession will progress based on frequency of disturbance and the changing inherent productivity of the ecosystem as it develops.

While Grime (1977) based his succession model on inherent productivity of the ecosystem, Tilman (1994, p. 328) stated "All theories of succession assume that there are one or more factors that constrain the growth and/or survival of organisms (i.e., their fitness) and that organisms have unavoidable trade-offs in their abilities to deal with these constraints. Given these assumptions, a change in the intensity of an environmental constraint unavoidably leads to a change in the composition of the community, i.e., to succession." For example, every species has a minimal requirement for soil resources to survive; the species that has the lowest requirement for that resource will competitively displace other species (Tilman, 1990). While Tilman acknowledged that there are numerous constraints within and among ecosystems, he indicates that in most cases there are only one or two constraints that are of primary influence. These constraints are ecosystem dependent and related to the environment. Tilman (1990) also reminded us that allocation of resources within plants typically results in tradeoffs in the plant's ability to address these constraints. In a nutrient impoverished soil, for example, high allocation of resources to roots as opposed to shoots would help the plant maintain its nutritional balance. Allocation to roots, however, will prevent this species from being an effective competitor for light in a nutrient rich environment.

With reference to the literature, Tilman (1990) described four primary constraints on plants in successional habitats: access to disturbed sites, availability of limiting soil resources, availability of light, and herbivores, pathogens, and other sources of loss and mortality. Tilman suggested that any combination of these four constraints may exist to cause and direct succession. Succession occurs because each species will have tradeoffs in dealing with these constraints. Each combination forms its own hypothesis for succession in the specific system of interest (e.g., the colonization-nutrient competition hypothesis).

The mechanisms of succession must be determined before we can proceed to assign a particular model of successional recovery from anthropogenic disturbance. These mechanisms may be related to ecosystem constraints and/or the physiological and life history strategy of individual species. Disturbances to Dry Mixed Grass prairie vary in size, duration, and impact on the plant community and soil. However, soil properties, topography, and site history will have influenced the nature of the plant community prior to disturbance and propagules that are available for recovery. In addition, anthropogenic introduction of propagules, mostly seed, alters the quantity, composition, and balance of species present at the end of disturbance and onset of succession. The variety of disturbance impacts and post-disturbance anthropogenic influence will alter the environmental constraints and species composition that direct succession. While there may be relatively few constraints in this system that regulate species performance and succession, other factors will determine what species will participate in succession and the pathway that is followed. This, combined with limited knowledge of the long-term influence of individual species on succession, will severely restrict development of a general model of succession.

1.2.2 Biodiversity And Stability

The widespread loss of natural ecosystems and resulting decline in diversity both globally and locally, has lead to considerable discussion and debate among academics, resource managers, and politicians. Policy makers and resource managers looked to academia to provide guidance related to the importance of diversity, how diversity should be managed, and if it should be attempted in ecosystem rehabilitation.

Functional arguments for conserving biodiversity include: greater ecosystem stability (i.e., tolerance to a disturbance such as grazing or a stress such as drought), more efficient utilization of resources by occupying a broader range of niches (Naeem et al., 1994; Tilman and Downing, 1994), and providing food and habitat for other species (Patrick, 1997).

Biodiversity has commonly been measured as species richness at the community and ecosystem levels (Takacs, 1996; Tilman, 1996). There are two opposing hypotheses proposed describing the relationship between species richness and function: the hypothesis that each species provides a unique functional role in the ecosystem, and the "redundant species hypothesis" (Lawton and Brown, 1994). In the first hypothesis, each species added to the ecosystem makes an equal and cumulative contribution to function as illustrated by the Type 1 curve in Figure 1.1. On the other extreme, the Type 3 curve represents the redundant species hypothesis in which a single species of plant maximizes some aspect of ecosystem function and subsequent addition of species has no further influence. The asymptotic Type 2 curve illustrates a declining marginal return with the consecutive addition of species. Vitousek and Hooper (1994, p. 6) suggested that the Type 2 curve "...will prove to be the most widespread in natural ecosystems".

Sala et al. (1996) recognized that the curves represented in Figure 1.1 did not account for species dominance nor that some species may have considerably greater influence on ecosystem function than other species. Sala et al. (1996) presented a conceptual model using rank-abundance curves to illustrate the influence of species deletion or addition on function. Removal of the most dominant or highest ranked species will have a large influence on function whereas removal of the least dominant species will have little or no influence on function. As such, a large number of species with low abundance contribute greatly to species richness but have little additive influence on ecosystem function. Conversely, a single species with high abundance makes little contribution to species richness, but has a large influence on ecosystem function. Based on this model, a small number of abundant species could maximize biogeochemical function.

Sala et al. (1996) also recognized that species dominance varies temporally due to phenology, climate, and or disturbance. The physiological adaptations of some species may make a unique contribution to ecosystem function. For example, some species may be better adapted to grow during hot/dry conditions while most other species become dormant. Removal of this species may have no effect on function during wet periods but may have great impact during drought. A group of species providing the same ecological function may be described as a functional group or 'guild'. Following the redundancy hypothesis, species providing the same functional role are redundant and only a single representative of the guild is necessary (Walker, 1992; Lawton and Brown 1994). Removal of a redundant species should, theoretically, not influence function of the community. Conversely, the absence of an entire guild (e.g., C_3 grasses, C_4 grasses, early season forbs, legumes) may have significant implications for function depending on the ecosystem specific importance of the guild (Hooper and Vitousek, 1997; Tilman et al., 1997; Sala et al., 1996). However, species composition of a guild may have greater influence on function than the number or kinds of guilds present (Hooper and Vitousek, 1997). To complicate things further, an individual species may fulfill more than one functional role (i.e., contribute to more than one guild), including roles that we may be unaware of (Walker, 1992).

Sala et al. (1996) recognized that the removal of the dominant species would not continue to influence function indefinitely since other species will respond in a compensatory manner. However, "Loss of some species may well lead to an increase in abundance of others (i.e., density compensation occurs), but because the diversity of response to environmental conditions has been reduced, net guild abundance may then fluctuate more in response to environmental fluctuations." (Walker, 1992, p. 21). This would suggest that ecosystem stability would decline under disturbance.

A more diverse community may have a broader range of functional attributes including tolerance to disturbance and should therefore have greater stability than a less diverse community (Tilman, 1996). As such, we should manage for greater species richness and/or functional group richness. Alternatively, we should improve our understanding of the functional biology and resource dynamics of key species within an ecosystem (Grime, 1997), and apply this knowledge to ecosystem management. In this case, species richness would become much less relevant to ecosystem function that may be regulated by a few key species.

1.2.3 Measuring Plant Community Succession And Ecosystem Function

O'Connor (1974) suggested that there were two approaches to the conservation and practical management of biological systems. The first approach would be to obtain sufficiently detailed knowledge of the nature, direction, and rates of the processes of energy flow and mineral cycling to enable researchers to predict the effects upon the whole system of changes imposed on any part. This approach inevitably leads to the development of predictive models. The second approach emphasizes the phenomenon of structural simplification and reduction in biodiversity in response to increasing severity of environmental condition or land use condition. In this second approach it is assumed that a high degree of diversity is associated with high internal stability, and that a structurally diverse system is more resilient than naturally less diverse systems. O'Connor (1974) concluded that the first, more detailed, approach was unlikely to provide solutions in the short term due to the vast amount of data which would need to be collected and analyzed. The second approach, however, was more likely to provide practical solutions in the shorter term.

Aronson et al. (1993) outlined a set of vital ecosystem attributes (VEA) related to ecosystem structure: perennial species richness, annual species richness, total plant cover, aboveground phytomass, beta diversity, life form spectrum, keystone species, microbial biomass, and soil biota diversity. They also provided a set of VEA related to ecosystem function: biomass productivity, soil organic matter, maximum available water reserves, coefficient of rainfall efficiency, rain use efficiency, length of water availability period, nitrogen use efficiency, microsymbiant effectiveness, and cycling indices. Naeem et al. (1994) measured five ecosystem processes to indicate the influence of reduced biodiversity on ecosystem function: community respiration, decomposition, nutrient retention, plant productivity, and water retention. Vitousek and Hooper (1994) suggested that primary plant productivity was the most obvious measure of the influence of biodiversity on biogeochemical function.

A number of functional properties of ecosystems outlined by Woodward (1994) were divided into universal functions and endogenous properties accruing from function. The universal functions included carbon dioxide, energy, nutrient, and water cycling. The endogenous properties included abiotic (e.g., fire) and biotic (herbivory) processes, ecosystem resistance to and resilience following change, microclimate, succession, and characteristic interactions among species (e.g., trophic levels such as plants, animals, and decomposers). In this case plant community succession would be directed by the universal functions.

Soil quality has been used as an indicator of the capability of an ecosystem to sustain biochemical function. The Soil Quality Criteria Working Group (SQCWG) (1993) and Doran and Parkin (1994) have each outlined a group of physical, chemical, and biological characteristics used to determine soil quality following disturbance. Soil characteristics used for wellsite certification on grasslands have also been developed (Alberta Environmental Protection (AEP), 1995). Another alternative is agricultural capability classification which provides a rating of a soil based on critical soil properties (Leskiw and Kutash, 1993).

Soil fauna are an intrinsic component of a functioning ecosystem because of their role in nutrient cycling. The dynamics and activity of microfauna are regulated by complex interactions among soil abiotic properties (Zak et al., 1994). Soil enzyme activity is sometimes used as an indicator of biological activity and microbiological populations (Dormaar et al., 1994, 1984; Zak et al., 1990; Ross et al., 1982). The dehydrogenase enzyme acts as a catalyst in the initial stages in the breakdown of organic matter (Ross, 1971) and is regarded as a good indicator of total microbial activity (Pancholy and Rice, 1973).

Soil fertility is another important characteristic influencing ecosystem processes and plant communities (Vitousek and Hooper, 1994; Palmer, 1990; Rice, 1984). Dormaar et al. (1994) used the relative contents of ammonium (NH_4^+) and nitrate (NO_3^-) nitrogen in the soil as indicators of successional status. The form of available N in the soil can be a useful indicator of the successional status and biogeochemical function in an ecosystem. The influence of prairie successional development on nitrification is not yet well understood (Rice, 1984).

1.3 RESEARCH BACKGROUND

Agricultural and petroleum industry development in the past century has resulted in considerable disturbance of native prairie ecosystems. Only 24 % of Mixed Grass and Dry Mixed Grass prairie remains undisturbed in Alberta (Alberta Environmental Protection, 1994). Current industry practices continue to raise concerns despite the development of guidelines and criteria for disturbance and reclamation of native prairie (Native Plant Working Group, 1998; Alberta Environmental Protection, 1995, 1996; Kerr et al., 1993). Some issues of concern include: sustainability, productivity, aesthetic value, integrity, diversity, ecosystem fragmentation, invasion of non-native species, wildlife habitat value, and soil quality and capability. A limited understanding of grassland ecosystem processes, their disturbance, and practices used to rehabilitate them has compounded problems associated with disturbance of native prairie.

Until the early 1990s, *Agropyron pectiniforme* R. & S. (crested wheatgrass) or *Elymus junceus* Fisch. (Russian wild rye) were used to revegetate pipelines and wellsites on native and tame grasslands in the Dry Mixed Grass Natural Subregion of Alberta. These revegetation practices have produced virtual monocultures of these bunch-grass species due to their competitive nature. Seeded stands of *A. pectiniforme* have been associated with lower soil quality than native stands (Dormaar et al., 1995).

More recently, industry has adopted the use of native plant cultivars and some wild collected species for revegetation on native prairie. Native cultivars of wheatgrasses are commonly used due to their high and rapid establishment rates and rapid provision of ground cover. Although regarded as a much better alternative than *A. pectiniforme*, some prairie conservationists are concerned that current practices may still reduce the integrity and sustainability of native grasslands. To meet current reclamation criteria and ensure rapid and successful certification, wellsites are often seeded at relatively high rates with the wheatgrass cultivars. The competition and litter production resulting from this practice may inhibit encroachment and establishment of other naturally occurring species onto the wellsite. Such domination of seeded species would result in a less diverse plant community than the surrounding native community and could threaten the integrity of a native grassland ecosystem. Crossbreeding of potentially genetically weakened cultivars of native species with those naturally occurring on surrounding undisturbed grassland is another potential problem. Furthermore, revegetation with native cultivars may reduce the aesthetic appeal of native grasslands by producing patches among the prairie species. However, the long-term influence of wheatgrass dominated seed mixes on native prairie recovery has not been studied scientifically.

Few practices have been suggested as alternatives to the use of low diversity seed mixes consisting of cultivars. Alternatives may include: the use of wild type seed, native hay mulch, natural recovery (i.e., no seeding), sod transplants, low seeding rates, and sprigging. These alternatives have met with limited success or in many cases scepticism due to: low commercial availability of seed, low rate of plant community establishment, need for specialized equipment, concerns regarding soil erosion potential, and the time frame required to meet the reclamation criteria. As with using wheatgrass cultivars, however, these practices have been subjected to little scientific investigation.

The success of any process is inherently dependent upon what goals were established at its onset. Depending upon perspective, such goals for repairing native prairie may include: conserving soil quality and land capability, conserving the integrity, diversity, and/or sustainability of the prairie, maintaining productivity of the prairie for grazing, expeditiously meeting the reclamation criteria to permit certification, maintaining the aesthetic quality of the prairie, and providing habitat for wildlife.

For the purposes of this research, the following goal for rehabilitating native grassland has been assigned: to leave a wellsite disturbance in a stable form that will allow it to return to a native prairie condition. I prefer the term rehabilitation because it assumes a goal extending beyond simply providing a vegetative cover (i.e., revegetation). Rehabilitation has been defined as the process in which "... the land will be returned to a form and productivity in conformity with a prior land use plan, including a stable ecological state that does not contribute substantially to environmental deterioration and is consistent with surrounding aesthetic values" (Powter, 1994). The definition of rehabilitation permits considerable flexibility in the ultimate outcome of rehabilitation related activities depending on land use objectives and aesthetic values such as native prairie conservation. This goal does not preclude the goal of 'equivalent land capability' as defined in the Alberta Environmental Protection and Enhancement Act (Powter, 1994).

To address the revegetation issues outlined above, a cooperative research effort, the Native Prairie Revegetation Research Project, was initiated involving individuals from government, industry, and research institutions. The objective of the industry-sponsored research was to determine the relative success of selected revegetation treatments in rehabilitating petroleum wellsite disturbance. From an academic perspective, this project provided an opportunity to improve our understanding of the response of native grassland ecosystems to disturbance and their recovery under different plant communities. Furthermore, it provided an opportunity to investigate the influence of wheatgrass cultivars on the establishment of other native species.

Fieldwork for the Native Prairie Revegetation Research project was initiated in 1996. The project consisted of two sub-projects: the Dry Mixed Grass prairie sub-project and the Fescue Grassland sub-project. The Alberta Research Council in Vegreville AB conducted the Fescue Grassland portion of the research. The research in this dissertation was conducted as the Dry Mixed Grass sub-project through the University of Alberta. A detailed description of the planning, design, site selection, and treatment application stages of project development were provided in Hammermeister and Naeth (1996). A summary of results and recommendations has also been prepared for industry (Hammermeister and Naeth, 1999).

1.4 SUMMARY OF RESEARCH NEEDS

Native prairie disturbance and subsequent abandonment continues to prompt secondary ecological succession in the Dry Mixed Grass region of Alberta. Abandoned agricultural and petroleum industry disturbances have been observed to return to a plant community composition similar to that prior to disturbance. In contrast, however, the use of exotic species to revegetate abandoned land suppressed native prairie recovery at least temporarily. The recently introduced practice of revegetation with cultivars of native wheatgrasses has produced considerable and varied speculation related to their influence on prairie rehabilitation. This speculation has led to a need for field research where the dynamics of community development in response to various rehabilitation practices is studied. Study of species interactions in seeded communities and their influence on communities will lead to a better understanding of the mechanisms directing succession and hence will facilitate improved resource management.

1.5 RESEARCH OBJECTIVES AND HYPOTHESES

1.5.1 Research Objectives

The overall objective of this research is to evaluate the effect of various anthropogenic rehabilitation practices on early ecosystem succession on Dry Mixed Grass prairie. Two specific research objectives have been identified.

a. To determine how ecosystem recovery proceeds through natural recovery (i.e., non-anthropogenically influenced succession) compared to seeding.
b. To determine how anthropogenic intervention in the form of seed mixes of differing diversity and/or composition may influence early succession. Seed mixes to be tested will include:
    i. A simple seed mix dominated by native wheatgrass cultivars,
    ii. A diverse seed mix dominated by species prevalent in the surrounding landscape and including others such as wheatgrass cultivars, and
    iii. A simple seed mix dominated by a few grass species prevalent in the surrounding landscape and including cultivars of native wheatgrasses.

1.5.2 Hypotheses

The following null hypotheses will be tested based on the objectives of this research:

a. Early plant community succession by natural recovery does not differ from seeding intervention in species composition, diversity, richness and similarity to the undisturbed plant community.
b. Early plant community succession of seeded treatments does not differ due to seed mix composition in species composition, diversity, richness, and similarity to the undisturbed plant community.
c. Biogeochemical cycling in early ecosystem succession by natural recovery does not differ from seeded treatments in plant biomass production (carbon and nitrogen capture), available soil nitrate, ammonium, and phosphorus, dehydrogenase enzyme activity, and microbial carbon use patterns.
d. Biogeochemical cycling in early ecosystem succession of seeded treatments does not differ due to seed mix composition in plant biomass production (carbon and nitrogen capture), available soil nitrate, ammonium, and phosphorus, dehydrogenase enzyme activity, and microbial carbon use patterns.

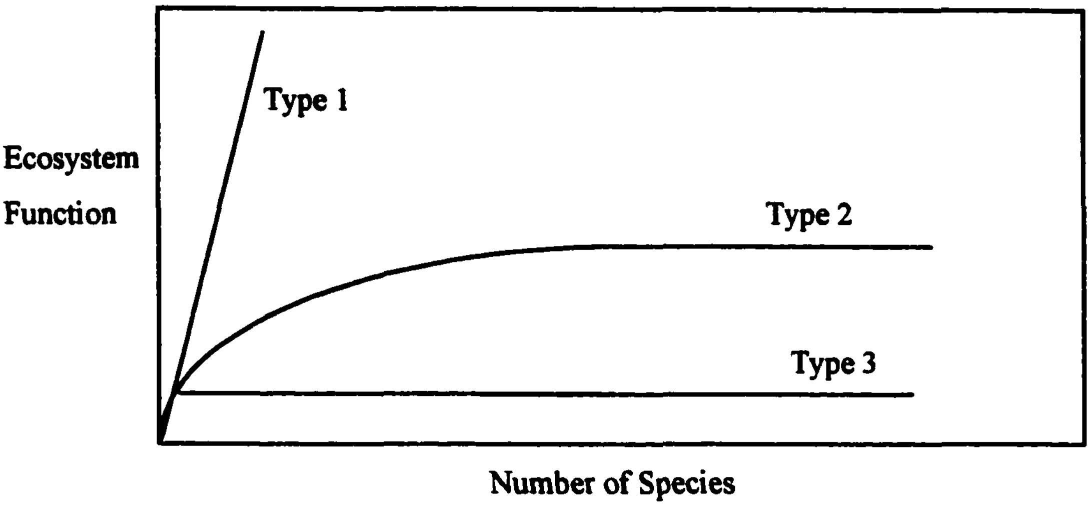

Figure 1.1 Three hypotheses related to the influence of species richness on some component of ecosystem function. Type 1 – each added species increases ecosystem function equally. Type 2 – the marginal increase in function declines with the addition of each species eventually reaching a point where no increase in function is observed with species addition. Type 3 – ecosystem function is maximized with the addition of a single or very few species. (Figure from Vitousek and Hooper (1994) with permission).

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CHAPTER 2. EARLY PLANT SUCCESSION FOLLOWING WELLSITE REHABILITATION BY NATURAL RECOVERY AND SEEDING IN SOUTHEASTERN ALBERTA

2.1 INTRODUCTION

Areas of native prairie are disturbed by agricultural cultivation or petroleum industry development for periods of varying duration. Upon cultivation abandonment or reclamation these disturbed lands have been reverted to forage production either by natural prairie recovery, revegetation with exotic species, or, more recently, rehabilitation with cultivars of native species.

The plant communities of cultivated and abandoned Dry Mixed Grass prairie returned to a predisturbance composition through natural secondary succession (Dormaar and Smoliak, 1985; Dormaar et al., 1994). In contrast, land seeded to exotic species, especially *Agropyron pectiniforme* R. & S. (crested wheatgrass), has not returned to native species composition. Succession seems to have been suppressed (Dormaar et al., 1978) and soil quality has declined (Dormaar et al., 1995; Christian and Wilson, 1999).

Coupland (1950) suggested that the rate at which abandoned cultivations in Dry Mixed Grass Prairie returned to equilibrium vegetation depended partly on the number of years of cultivation and the intensity of cultivation. In addition to Coupland's observations, Judd (1940) found that the rate of succession on abandoned fields in Montana was more rapid on fields enclosed by native prairie and on smaller fields rather than larger. Kotanen (1997) also found that gap size and shape influenced the rate of species invasion, however, groups of species responded differently depending on their reproductive biology. Vitousek et al. (1989) found differences in nutrient cycling in seres of abandoned cultivation and secondary succession resulting from a single, short-duration disturbance event. Because abandoned petroleum wellsite disturbances are intense but of short duration, of small scale, and surrounded by prairie, succession on these sites may differ from an abandoned cultivation in the same region.

Use of cultivars of native wheatgrasses instead of exotic grasses has become more common in conserving native prairie and preventing ecological degradation. However, the long-term influence that revegetation with these cultivars will have on ecological succession is not well understood. The wheatgrasses most commonly used include *Agropyron trachycaulum* Link. (slender wheatgrass), *A. dasystachyum* Hook. (northern wheatgrass), and *A. smithii* Rydb (western wheatgrass). They are used for their high germination, rapid establishment, and rapid ground cover production. While these species are effective in rapidly providing ground cover and forage for grazing, their aggressive nature may suppress establishment of other species. *Bouteloua gracilis* (HBK) Lag. (blue grama grass) establishment decreased with increased competition from *A. smithii* (Samuel and Hart, 1992). In research in Colorado, Redente et al. (1984) found that wheatgrasses dominated seeded treatments regardless of seed mix richness. Gill Environmental Consulting (1996) verified competitive exclusion of other species by wheatgrasses in a study of disturbances with varying revegetation practices and age in southeast Alberta. Rhizomatous grasses (primarily seeded wheatgrasses) increased in density with time from revegetation, and prevented the establishment of other native species. Currently, industry seeding rates for wheatgrass dominated seed mixes on Dry Mixed Grass prairie range from 15 to 25 kg ha^{-1}. DePuit and Coenenberg (1979) found that plant community diversity was lower at higher seeding rates. After seeding abandoned farmland in Great Britain to native grassland species, Stevenson et al. (1995) found that ruderal species were initially dominant but their composition decreased with increasing seeding rate. Species richness was initially higher with higher seeding rates, however, no difference was found after two years and low seeding rates were equally as successful in producing the desired vegetation as high seeding rates.

Soil nutrient supply rate may determine plant community composition (Tilman, 1987; Wilson and Tilman, 1991a). Johnston et al. (1967) found that basal area of *A. smithii* and *A. dasystachyum* increased under moderate and high fertilizer application while non-wheatgrass species such as *Stipa comata* Trin. & Rupr. (needle and thread grass), *B. gracilis*, and *Koeleria macrantha* (Ledeb.) J.A. Schultes f. (June grass) decreased. Wight (1976) also indicated that aggressively responding *A. smithii* often accounted for a large proportion of yield increase under native prairie fertilization while some species, such as *B. gracilis* declined. Samuel and Hart (1998) recently presented similar species responses to nitrogen fertilization. Hence, an increase in nitrogen availability, as is commonly found in recently disturbed grassland, may favour wheatgrasses over other native grasses. Nitrogen cycling in secondary seres following destructive disturbance and immediate growth may differ from seres beginning from an abandoned cultivation and primary seres (Vitousek et al., 1989). The wellsite disturbances in this research increased availability of mineral nitrogen and influenced plant community composition (Chapter 3).

Thus there is reason to hypothesize that revegetation with native wheatgrass cultivars may suppress succession toward an equilibrium predisturbance plant community. Wheatgrass domination is not consistent with the rehabilitation goal of eventually having these wellsites return to a predisturbance community composition. Vegetation on medium textured soils in Dry Mixed Grass prairie typically consist of the *Stipa-Bouteloua* faciation of which *A. dasystachyum* and *A. smithii* comprise <10 % (Coupland, 1950). Clay-loam textured Solonetzic soils are dominated by the *Bouteloua-Agropyron* faciation where *A. smithii* comprises <15 % of species composition (Coupland, 1950). Seeding typically dominant native species with the wheatgrass cultivars may direct and accelerate succession towards the predisturbance community while maintaining the benefits of the wheatgrasses. The direction, rate, and mechanisms of succession in each of these cases require further investigation on Dry Mixed Grass prairie.

Species rich seed mixes are being promoted to increase diversity of rehabilitated plant communities based on the perception that diversity increases ecosystem stability and increases as succession progresses. However, both of these issues have been debated in the ecological literature with contradictory evidence being provided (Ghilarov, 2000; Wali, 1999). The effectiveness of species rich seed mixes in increasing diversity of the rehabilitated plant community is also not well documented.

The objective of this research was to measure the effect of selected rehabilitation practices on plant community composition, ground cover, and diversity in the first three years of succession on Dry Mixed Grass prairie. Specific treatment comparisons include: natural recovery versus use of native seed mixes, a native wheatgrass cultivar dominated seed mix versus non-wheatgrass dominated seed mixes, and a diverse native seed mix versus low diversity seed mixes. Mechanisms of plant community development are discussed.

2.2 MATERIALS AND METHODS

2.2.1 Experimental Design, Study Area, Site Preparation, And Treatments

The research was conducted on loam textured Orthic Brown Chernozemic and loam textured Brown Solodized Solonetzic soil with a loam to clay loam subsoil in the Dry Mixed Grass natural subregion of Alberta (Alberta Environmental Protection, 1994). Vascular plant cover in this region is dominated by *S. comata*, *B. gracilis*, *K. macrantha*, *A. dasystachyum* and/or *A. smithii* depending on soil texture, topography, and grazing (Gerling et al. 1996). Seven drilled and abandoned, non-producing petroleum wellsites were selected based on soil properties, topography, state of wellsite, absence of contamination, and site availability (Hammermeister and Naeth, 1996) in the Brooks-Bow Island-Medicine Hat area (Figure 2.1, see Appendix A for research site coordinates). The disturbance area of the wellsites ranged in size from 0.9 to 1.2 ha. Participating companies reclaimed their wellsite(s) using standard practices up to the point of seeding. These practices varied slightly among sites but included: surface soil salvage to approximately 10 cm using a crawler tractor, subsoil salvage to varying depths as required to produce a level drilling pad, soil stockpiled for less than 6 months, drilling, subsoil and surface soil replacement using a crawler tractor (sometimes with straw added to stabilize soil), and seed bed preparation (Hammermeister and Naeth, 1996). Some sites were paratilled to a 40-cm depth to reduce soil compaction. Paratilling is a tillage technique that alleviates compaction at depth but results in minimal surface soil disturbance.

A randomized complete block design was employed on each soil consisting of four replicate blocks (i.e., wellsites) on Chernozemic soil and three on Solonetzic soil. Five treatments were applied at each wellsite consisting of three seed mixes (Current, Diverse, and Simple treatments), a non-seeded natural recovery treatment (Natural Recovery), and an undisturbed Control (Figure 2.1). The study area was the same for each rehabilitation treatment on a wellsite but varied from 0.068 ha to 0.240 ha not including buffer zones between treatments. Species compositions of seed mixes (Table 2.1) were selected based on the treatment strategy, typical composition of Dry Mixed Grass prairie (Gerling et al., 1996; Nernberg, 1995), and seed availability. All wellsites and Control areas were fenced to exclude grazing by cattle.

Seeding rates were calculated based on a desired number of pure live seeds (PLS) per unit area (300 PLS/m^2). The seeding rate was approximately 50 % of that typically used by industry to improve colonization from the surrounding native plant community and reduce competition with perennial species potentially establishing from the seed bank. The seed mix composition was adjusted for seed weight and percent viability and purity. Because purity and viability data were not available for the forbs, they were estimated as 66 % (based on Smreciu et al., 1988; Sorenson and Holden, 1974). Legume seed was rubbed with sandpaper until visibly scarified. Chick starter (pelleted food for newly hatched chickens) was used as a carrier to ensure even seed distribution and improve flow through the seed drill. Most species were seeded with two perpendicular passes of a calibrated Truax native seed drill. *K. macrantha* and forbs were broadcast with chick starter as a carrier. A thin straw mulch (wheat and/or oats) was applied to each rehabilitation treatment (i.e., Current, Diverse, Simple, and Natural Recovery) and crimped (i.e., pressed into the soil with discs) to prevent soil erosion. Seeding was completed June 21, 1996.

2.2.2 Climate

Mean monthly and long term average precipitation and temperature for summer months were obtained from Medicine Hat, Brooks, and Bow Island (Table 2.2). Growing season conditions were generally warmer and drier throughout the study period than long-term averages. Of particular importance is the prevalence of these conditions in the first few months following seeding.

2.2.3 Vegetation Assessments

Plant species were identified as per Moss (1983). Plant community characteristics were determined from three systematically located transects of ten evenly spaced assessment points in each treatment (Figure 2.1). Spacing of the observations varied from 3.5 to 5 m depending on size of wellsite disturbance. A 10-m buffer zone was left between treatments comprising 5 m of each adjacent treatment. Species canopy cover, ground cover, and density were determined from 0.1-m^2 quadrats placed at each of the 30 aforementioned observation points. Offshoots of rhizomatous plants were counted as individual plants and stems arising from the same bunch were recorded as one plant. In 1996, seedling emergence did not begin until August/September and individual species were difficult to identify. Therefore, 1996 data are not presented. Species composition of each treatment was supplemented by a visual reconnaissance of the treatment area between and around observation points and transects for less frequent species.

2.2.4 Plant Community Analyses

Plant species were split into nine groups based on physiology (C_3, C_4, or crassulacean acid metabolism), morphology (grasses, sedges, shrubs, forbs, bryophytes), life history strategy (annual forbs versus perennial forbs), and special interest (wheatgrass cultivars). The groups were: annual forbs, perennial forbs, wheatgrasses (WG) including both seeded and non-seeded species and varieties, other C_3 grasses (C_3G), C_4 grasses (C_4G), sedges, ground cover species (i.e., moss and moss-like species), shrubs, and cacti. A complete list of species and their vegetation groups is provided in Table A.2.

When described by only ground cover, canopy cover, or density, some species tended to be overrated due to high canopy cover but low density, ground cover, or frequency. Other species with a very high density and/or frequency but low cover were also overrated. To account for these differences in stature, importance values of individual species were calculated as an average of their relative abundance by density, canopy cover, ground cover, and frequency (Table 2.3) as modified from McCune and Mefford (1995).

Establishment rates were calculated as the number of plants of a species established divided by seeding rate and is presented as a percentage. Diversity (Shannon-Weiner index (H')) and evenness were calculated as per Poole (1974) using species importance values. Spatz similarity index of rehabilitation treatments to the Control was calculated as per Mueller-Dombois and Ellenberg (1974) from the average importance value of each species in 30 quadrats. Mean species richness (SR) was calculated for each experimental unit by quadrat (SR_Q) and by whole treatment area (SR_T). A single quadrat, for example, may contain only five species due to its small area. However, over 20 species may be encountered when considering the entire study area of an experimental unit or a wellsite. For each treatment, SR_Q was calculated by first averaging the 30 quadrats in each treatment on a wellsite and then calculating the overall treatment mean from the wellsites. SR_T was used to calculate evenness; species not recorded in the 30 observation points but found in SR_T were assigned an importance value of 0.01 %.

Pearson correlation coefficient between vegetation groups and the wheatgrasses was determined using canopy cover estimates from the total of 120 quadrats within the four experimental units of a treatment on Chernozemic sites. Analyses are only presented for the Simple and Diverse treatments of the Chernozemic sites because wheatgrasses were seeded in equal amount in these treatments and other species were included that increased their abundance and allowed a measure of correlation (i.e., without seeding non-wheatgrasses, their abundance was so low that no correlation with wheatgrasses could be measured in the Current treatment). Each wheatgrass species was seeded at the same rate within a treatment and these treatments also included other seeded perennial grasses and forbs.

2.2.5 Statistical Analyses

The results were analyzed as a randomized block design independently for Chernozemic and Solonetzic sites. The mean of the 30 subsamples in each experimental unit was used to calculate treatment means (i.e., the 30 subsamples were not regarded as replicates). Tests for significant differences among treatments were conducted using Fisher's Protected Least Significant Difference (FPLSD) where significance was first required by using analysis of variance (ANOVA) before testing for treatment differences by LSD (Steel and Torrie, 1980). SPSS® (Norusis, 1993) was used to conduct these analyses. The time component of community development was analyzed as the change in a variable from 1997 to 1998 (e.g., 1998 canopy cover minus 1997 canopy cover equals the change in canopy cover). The change in variables with time was subsequently analyzed in the same manner as all other variables. Similarity among plant communities of treatments was further assessed using PC-ORD's Detrended Correspondence Analysis (DCA) (McCune and Mefford, 1995). These results are not presented since they were consistent with the results provided by the Spatz similarity index. Pearson correlation was calculated using SPSS™ (Norusis, 1993).

All data were checked for violations of assumptions with emphasis placed on homogeneity of variance. Most variables met the homogeneity of variance assumption; transformations were attempted to address those that did not. However, all analyses were conducted on non-transformed because: negative values from change with time could not be transformed, in most cases data transformation did not alter interpretation of results, and presentation of both transformed and non-transformed data would have complicated interpretation by the reader (Finney, 1989).

2.3 RESULTS

2.3.1 Species Establishment

The emergence and establishment of seeded and non-seeded species was delayed by dry conditions (Table 2.2). Thus, establishment rates (Table 2.1) are based on 1997 density data. Detailed density (1997 and 1998) and establishment rates for seeded species are presented in Table A.1. Of the 21 species seeded, eight were commonly found in the undisturbed Control: *S. comata*, *B. gracilis*, *K. macrantha*, *A. smithii*, *A. dasystachyum*, *Achillea millefolium* L. (yarrow), *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (broomweed), and *Vicia americana* Muhl (American vetch) (Table A.1). Seeded grasses not common in the Control included *Elymus canadensis* L. (Canada wild rye), *S. viridula* Trin. (green needle grass), *Oryzopsis hymenoides* (R. & S.) Ricker (Indian rice grass), and *Agropyron trachycaulum*. Several seeded grasses and forbs also established in the unseeded Natural Recovery treatment (Table A.1). Although not seeded, *S. comata*, *B. gracilis*, and *K. macrantha* established in the Current treatment (Table A.1).

Where seeded *S. comata*, *B. gracilis*, and *K. macrantha* establishment rarely exceeded 10 %; establishment of *E. canadensis*, *O. hymenoides*, and *S. viridula* was less than 3 % (Table 2.1). Wheatgrass establishment rates varied by species, treatment, and site from 3.3 to 63.5 % (Table 2.1).

2.3.2 Community Composition: Species And Vegetation Group Importance Values

Species importance value was found to be highly correlated (P<0.02) with ground and canopy cover, density, and frequency. Therefore, importance value was accepted as a reasonable representation of species abundance.

The Control at each site was generally dominated by *Selaginella densa* Rydb. (little club moss), *Carex* spp., *B. gracilis*, *Stipa comata*, and/or *A. smithii* on Chernozemic sites as well as *A. dasystachyum* on Solonetzic sites (Table A.2). Several species were notably absent or of much lower importance value among the rehabilitation treatments than the Control including: *Selaginella densa*, *Carex* spp. L., *Stipa comata*, *B. gracilis*, and *Sphaeralcea coccinea* (Pursh) Rydb (scarlet mallow). Annuals dominated the forb component of the rehabilitation treatments although the species and their importance values varied by treatment and site.

The seeded rehabilitation treatments were dominated by the WG group on both soils with either *A. trachycaulum* (Current and Diverse treatments only) or *A. dasystachyum* dominant and on most sites with *A. smithii* also relatively important (Table A.2). These species were of notably low abundance in the Control and Natural Recovery treatments. The WG group was significantly more important in the Current treatment than in the Diverse and Simple treatments (Figure 2.2). WG group importance increased from 1997 to 1998 in all seeded treatments on Chernozemic sites, but decreased in the Simple and Diverse treatments on Solonetzic sites. Change in importance value from 1997 to 1998 was not significantly different among treatments.

Importance value of annual forbs in 1998 was significantly higher in the Natural Recovery than all other treatments and the seeded treatments were significantly higher than the Control (Figure 2.2). The most common annual forbs were: *Descurainia* spp. (L.) Webb (flixweed), *Lappula occidentalis* (S. Wats.) Greene (bluebur), *Kochia scoparia* (L.) Schrad. (kochia), and *Salsola kali* L. (Russian thistle) (Table A.2).

Importance values of the C_3G and C_4G groups were significantly lower in the rehabilitation treatments than the Control (Figure 2.2), however, there were no significant differences among the rehabilitation treatments. There also were no significant differences among treatments between 1997 and 1998. *Stipa comata* and *B. gracilis* were present, although of low importance, in the Diverse, Simple and Natural Recovery treatments on sites of both soils (Table A.2).

Perennial forb importance was significantly higher in Natural Recovery than Simple and Current treatments on Chernozemic sites (Figure 2.2). No significant differences occurred among treatments on Solonetzic sites or in the change from 1997 to 1998 on either soil. The perennial forbs group was heavily dominated by *Artemisia frigida* Willd (pasture sage) in all rehabilitation treatments.

Importance values for the ground cover (35 to 40 %) and sedge (4 to 7 %) groups were significantly higher in the Control than in any rehabilitation treatment among which there were no significant differences (data not presented). Low importance values for the shrub group were found in the Control on Solonetzic sites and for the cactus group in the Control of Chernozemic sites (data not presented).

2.3.3 Species Correlations And Abundance Per Seed Planted

A significant negative correlation was found between annual forbs and wheatgrass groups in the Simple and Diverse treatments (Table 2.4). The wheatgrass group was not correlated with the C_3G, C_4G, and perennial forb groups except for a positive correlation with the C_3G group in 1997. Aside from a negative correlation between annual forbs and *Agropyron dasystachyum*, no significant relationships were found between the remaining vegetation groups and *A. dasystachyum* and *A. smithii* in the Simple treatment. In the Diverse treatment, no significant correlation was found between wheatgrass species and the perennial forb group. In most cases no significant correlation was found between wheatgrass species and non-wheatgrasses. *A. trachycaulum* was negatively correlated with *A. dasystachyum* and *A. smithii* in 1998.

Plant density of vegetation groups increased with time in most treatments with exceptions of C_3G and C_4G density in some treatments (Table 2.5). Canopy cover per plant decreased from 1997 to 1998 in most vegetation groups and treatments. An increase was observed for C_3G and C_4G groups in the Simple and Natural Recovery treatments where wheatgrasses were least abundant. No significant differences were found among rehabilitation treatments for change in canopy cover, density, and cover per plant for most vegetation groups (Table 2.5). The only exceptions were cover per plant for the perennial forb group on Chernozemic sites and C_4G group on Solonetzic sites and change in density in the wheatgrass group on both soils.

Per seed planted, importance value and density were higher for the wheatgrasses than other grasses in all treatments (Table 2.6) (statistical significance not determined due to size of difference and resulting violation of the homogeneity of variance assumption). *A. dasystachyum*, *A. smithii*, and *A. trachycaulum* did not differ ($P<0.10$) in density or importance value per seed planted in the Diverse treatment, where all three were seeded at the same rate. However, importance values for wheatgrass species were in most cases significantly lower in the Current treatment than in the Diverse and Simple treatments (Table 2.6). *A. smithii* density was significantly lower for the Current treatment than the Diverse and Simple treatments on Chernozemic and Solonetzic sites; *A dasystachyum* density was significantly lower in the Current treatment on Solonetzic sites only.

2.3.4 Community Similarity

Similarity of the Simple treatment to the Control was significantly higher than other treatments on Chernozemic sites (Table 2.7); no other significant differences were found. The amount of change in similarity from 1997 to 1998 was not significantly different among treatments on either soil. However, all treatments on Chernozemic soil and the Current treatment on Solonetzic soil became less similar to the Control over one year (Table 2.7).

2.3.5 Richness, Diversity, And Evenness

Species richness of an entire treatment area at a wellsite (SR_T) ranged from approximately 17 to 31 species. However, only 3 to 7 species typically occurred within a quadrat (SR_Q) (Table 2.7). There were no statistically significant differences among rehabilitation treatments in SR_Q or SR_T on either soil (Table 2.7). Control SR_Q was significantly higher than most rehabilitation treatments on both soils. The increase in SR_Q of the Natural Recovery treatment with time on Solonetzic soils was significantly greater than that for the Current treatment. No statistically significant differences in change in SR_T from 1997 to 1998 were measured.

There were no statistically significant differences among rehabilitation treatments in diversity, evenness, or their change from 1997 to 1998 on either soil. Diversity changed little with time for any treatment. Diversity and evenness were slightly lower in 1998 than 1997 (Table 2.7) except in the Natural Recovery treatment where they increased.

No correlation or a significant positive correlation was found between SR_Q and wheatgrasses (group and individual species) in both the Simple and Diverse treatments in 1997 (Table 2.4). In 1998, however, a significant negative correlation was found between SR_Q and the wheatgrass group and *A. dasystachyum* in the Simple and Diverse treatments, and with *A. trachycaulum* in the Diverse treatment. SR_Q and *A. smithii* were positively correlated in the Diverse treatment in 1998 and but were negatively correlated in the Simple treatment.

2.3.6 Ground Cover

Bare ground on the rehabilitation treatments decreased in most treatments from 1997 to 1998 but there were no significant differences among treatments in the amount of change with time (Table 2.8). On Chernozemic sites, bare ground was significantly lower in the Control than the rehabilitation treatments, among which there were no significant differences. Only the Natural Recovery treatment had significantly more bare ground than the Control on Solonetzic sites.

The straw mulch provided 40 to 50 % ground cover across all rehabilitation treatments in 1997. Straw cover dropped substantially from 1997 to 1998, however, amounts were difficult to separate from litter cover produced in 1997 (data not presented). Thus, straw cover was included as a component of litter cover in 1998. Litter cover increased on the rehabilitation treatments from <6 % in 1997 to levels comparable to or greater than the Control in 1998 (Table 2.8). Litter did not differ significantly among treatments in 1998, but the increase from 1997 to 1998 was significantly higher in the rehabilitation treatments than in the Control for both soils with the exception of the Natural Recovery treatment on Solonetzic soil. Total ground cover of live vegetation (i.e., basal cover) in the rehabilitation treatments was significantly lower than the Control for each soil in 1998 (Table 2.8).

2.4 DISCUSSION

2.4.1 Plant Community Development

The dominance of wheatgrasses in the rehabilitation treatments may have implications for long term plant community development. The influence of the wheatgrasses was most evident from the vegetation group importance value data and correlations with species richness and apparent in other parameters related to diversity and ground cover. Non-wheatgrass species were not seeded in either the Current or Natural Recovery treatments and therefore the abundance of propagules of these vegetation groups were presumed to have been of equal initial abundance. However, differences in abundance of non-wheatgrass species existed between these two treatments. Importance of C_3G, C_4G, and perennial forb vegetation groups were clearly lower and decreasing with time in the Current treatment compared with an increase with time the Natural Recovery treatment. These patterns were apparent even though annual forbs were more dominant in the Natural Recovery treatment than wheatgrasses were in the Current treatment. This indicates that annual forbs were less competitive than wheatgrasses and less likely to suppress establishment of other perennial species. While the lack of significant differences among seeded treatments can be attributed to wheatgrass domination, some trends are still apparent due to differences in wheatgrass abundance. Both the Current and Natural Recovery treatments were dominated by two or three species from one vegetation group and were lower in diversity and species richness than the Diverse and Simple treatments. Based on the trends described above, one can speculate that these similarities will not persist as perennial non-wheatgrass species are expected to progress toward dominance in the Natural Recovery treatment.

The lack of statistically significant differences in diversity and evenness between the Control and rehabilitation treatments does not indicate that the treatments are becoming more similar. Their composition remains quite different as indicated by the similarity index. Where low diversity is largely a function of a few wheatgrass species and/or annual forbs in the rehabilitation treatments, it is a function of a few other species in the Control. Species richness and diversity were increasing more rapidly in the Natural Recovery than in the Current treatment (although differences were not significant) due to a larger variety of annual species and a shift in dominance from one annual species to two or three. Therefore, diversity in itself cannot be used as an indicator of successional development in this system. The lack of statistically significant difference in evenness indicates that despite very different community composition, diversity is reaching the same potential based on the number of species present. If we consider the Natural Recovery to be early successional, the seeded treatments as mid-successional, and the Control as late successional, we are seeing similar evenness at different stages of prairie succession. This may suggest that plant community evenness reaches a maximum at around 0.5 to 0.6 in this ecosystem. Further research is required to test this hypothesis.

2.4.2 Mechanisms Of Succession Leading To Wheatgrass Domination

Early plant community development in each treatment was determined initially by differential species availability and then by differential species performance as per Pickett et al.'s (1987) causes of succession. Initially, each treatment was assumed equal in the nature and severity of disturbance, subsequent site availability, and availability of species propagules. Based on community composition in the Natural Recovery treatment, few vegetative propagules survived the disturbance, and the active seed bank was dominated by annual species with few perennial species except *Artemisia frigida*. Seeding influenced community development by adding viable propagules of perennial grass species to the seed bank. It also increased perennial forb availability and variety in the Diverse treatment. The availability of each perennial species was not equal in each seed mix, hence a treatment effect was expected. Community development beyond this point was primarily a function of differential species performance (Pickett et al., 1987).

The relatively high establishment rates of the wheatgrass cultivars compared with the non-wheatgrasses provided an advantage in initial plant density despite their relatively low seeding rate in the Diverse and Simple treatments. The low establishment of non-wheatgrass species may be related to germination rate, dormancy, viability, competition, predation, or decomposition (Harper, 1977).

Importance value and density per seed planted were used as an overall assessment of performance and spread of each species. After three field seasons the wheatgrasses outperformed the other principle grasses in the seed mixes. Density per seed planted integrates establishment and reproductive rates. In comparing establishment rates with the density per seed planted, a rapid increase in the population of wheatgrass species is evident compared with a decline in the population of other seeded species. The rhizomatous reproductive mode of *Agropyron dasystachyum* and *A. smithii*, and seed production of *A. trachycaulum* account for the rapid spread of these species. A more competitive environment can be interpreted from the lower wheatgrass performance in the Current treatment than the Diverse and Simple treatments. Preliminary results did not indicate significant differences in performance among wheatgrass species. However, *A. smithii* importance per seed planted was often less than half of that for the other two species despite comparable population growth. The smaller stature of *A. smithii*, as was observed in the field, explains this relationship.

Redente et al. (1984) tested a variety of seed mixes, including a wheatgrass dominated native grass and forb mix, on reclaimed land in Colorado. The native grass and forb seed mix was dominated by three wheatgrasses, *A. dasystachyum*, another rhizomatous wheatgrass, and a bunchgrass. They also found that the rhizomatous wheatgrasses dominated community composition through the first five years. Although not calculated, the combined composition of wheatgrasses in the native grass and forb mix was greater than 5 % per seed planted at the 0.1 m^2 scale through the first five years as compared with a <1 % per seed planted for other species. Their results and explanations for wheatgrass domination are consistent with those for our research. *A. pectiniforme* rapidly became dominant when seeded in mixtures with *A. dasystachyum*, *A. smithii*, *A. trachycaulum*, and *Stipa viridula* even though it was seeded at only 25 % of the rate of other species (Schuman et al. 1982). *A. trachycaulum* was least competitive and was removed from the stand within three years; other species declined to a low but stable composition under *A. pectiniforme* domination. Schuman et al. (1982) suggested that native species should not be seeded with *A. pectiniforme* if a native stand was desired. Under the conditions of this research, similar recommendations could be made related to seeding non-wheatgrass species with *A. dasystachyum* and possibly other wheatgrass species.

Grime (1973) listed four competitive attributes of herbaceous plants: tall stature, growth form (large tussocks or strongly rhizomatous), high maximum potential growth rate, and a tendency to deposit thick litter. *A. dasystachyum* and *A. trachycaulum* have exhibited these competitive traits based on biomass (see Chapter 3) and litter production, density increases, and importance values relative to other species. The more competitive wheatgrasses also are expected to have taken advantage of higher availability in nutrients and possibly water (see Chapter 3). The aggressive establishment, spread, and domination of the wheatgrasses in an early successional environment of relatively high availability of nutrients, light, and water (immediately following disturbance) may indicate support for Grime's theory of competition. Grime (1977) predicted that species with the highest growth rate of vegetative tissues will have a competitive advantage in acquiring resources over species with lower vegetative growth rates. In contrast, Tilman (1982) predicted that species with the lowest resource requirements will competitively displace all other species at equilibrium. None of the rehabilitation treatments have approached equilibrium since sites for plant establishment still exist (i.e., bare ground) and nutrient availability is still higher than in the Control (Chapter 3). As the treatments approach equilibrium, the limiting resource may change resulting in a shift in species composition (if establishment sites are available).

In summary, differential species availability was an important factor determining potential community composition and succession. However, differential species performance in germination and establishment, reproductive mode, and competition were the primary mechanisms influencing early succession following colonization.

2.4.3 Natural Recovery vs. Seeded Treatments

Overall, establishment of perennial grasses in the Natural Recovery treatment progressed slowly relative to the seeded treatments. From this perspective, seeding accelerated succession. Compared with the Natural Recovery treatment, however, seeding did not generally increase plant community similarity to the Control.

There are several possible explanations for the decline in treatment similarity to the Control from 1997 to 1998: species establishing in the rehabilitation treatments were not present in the Control, species present in the Control were not establishing in the rehabilitation treatments, and the relative importance of established species were not consistent with those in the Control. The high importance of *Selaginella densa* and *Carex* spp. in the Control and absence of these species in the rehabilitation treatments was a major factor influencing similarity to the Control. Low similarity also resulted from rehabilitation treatment domination by a few species that were not abundant or present in the Control. Annual forbs dominated the Natural Recovery treatment and wheatgrasses dominated the seeded treatments. This difference in composition between the seeded treatments and Natural Recovery may produce quite different successional trajectories. The early successional status of annual forbs is well recognized (Coupland, 1950; Grime, 1977; Iverson and Wali, 1982; Wilson and Tilman, 1991b; Stevenson et al., 1995). Although these species may initially shade and reduce tillering of grasses they also may improve environmental conditions that facilitate establishment of other species (Iverson and Wali, 1982). Despite dominance early in succession, annual forbs are typically replaced by perennial grasses (Grime, 1977; Iverson and Wali, 1982; Stevenson et al., 1995; Wali, 1999) due to differential species performance (Pickett et al., 1987). However, a change in composition of an established perennial grass community would require the 'advancing' species to have superior 'performance' under the prevailing conditions than the existing group of species. The wheatgrass cultivars will be much harder to replace considering their competitive growth characteristics and longevity compared with annual forbs. Hence, the Natural Recovery treatment would be expected to return to a predisturbance community composition more rapidly than the seeded treatments assuming the established density and availability of non-wheatgrass perennials are comparable among the rehabilitation treatments.

2.4.4 Wheatgrass Dominated Versus Non-Wheatgrass Dominated Seed Mixes

Wheatgrass inclusion in relatively small amounts in the Diverse and Simple treatments was intended to provide a low to moderate vegetative cover for erosion control but still allow space for other species to establish. Provision of gaps seemed to have been accomplished based on the relatively high bare ground observed. However, decline in importance and/or density of non-wheatgrass vegetation groups in the seeded treatments indicates that the wheatgrasses suppressed the establishment of other species, was observed by Gill Environmental Consulting (1996) and Samuel and Hart (1992, 1998). After seeding native species into established stands of exotic species, Wilson and Gerry (1995) found that spraying and disturbance were necessary to provide space for native species establishment. Biondini and Redente (1986) found that species diversity was inversely related to high biomass production and suggested that both may not be attainable at the same time. Tilman (1993) suggested that species richness and diversity in productive grasslands were lower because accumulated litter inhibited germination and/or survival of seedlings and therefore decreased rates of establishment of new species. Based on the high litter cover generated by wheatgrasses, recruitment of non-wheatgrass species is expected to be inhibited in the seeded treatments. The Native Plant Working Group (1999) suggested that the composition of rhizomatous wheatgrasses should be limited to 20 % in seed mixes seeded at a rate of 6 to 8 kg ha^{-1} to reduce competition with non-seeded native species (as recommended by Gill Environmental Consulting, 1996). In this research the rhizomatous wheatgrasses became dominant even when seeded at much lower rates. The mechanisms of wheatgrass domination were related to establishment rates, reproductive capacity, and resource use efficiency as discussed above and in Chapter 3.

The results of this research may have been different if wild harvested wheatgrass seed had been used instead of native cultivars that are often selected for their high performance characteristics. These characteristics would provide a competitive advantage over species for which these traits have not been selected. It is unlikely that simply reducing the wheatgrass component of the Diverse and Simple seed mixes would do more than temporarily delay the wheatgrass domination. The wheatgrasses may have been less dominant in a community where populations of individual established species were equal and where total plant density was similar to that in Control areas. The competitiveness of the wheatgrass cultivars may decline as gaps close and resources become less available. However, a decline in wheatgrass competitiveness in early succession was not observed by Gill Environmental Consulting (1996).

2.4.5 High Diversity Versus Low Diversity Seed Mixes

The success of the Diverse seed mix was limited by the lower performance of non-wheatgrass species relative to the wheatgrasses in conjunction with low relative composition of some species in the seed mix. Wheatgrass domination resulted in low diversity in all three seeded treatments. The non-significant difference in evenness among all treatments indicates that the proportional abundance of species in the rehabilitation treatments is similar to the Control. This means that the Control was dominated by relatively few species just as the rehabilitation treatments were.

Species richness of both the Simple and Current seed mixes was designed to be identical. Despite this, differences in plant community species richness between the Diverse and Current treatments were generally higher than between the Diverse and Simple treatments. Hence, seed mix composition greatly influenced plant community richness in addition to seed mix richness. As described above, wheatgrass domination may have suppressed establishment of other species more in the Current treatment than in the Simple and Diverse treatments. This, in turn, is attributed to the higher composition of wheatgrasses in the Current seed mix than in the Diverse and Simple treatment seed mixes. Thus, further discussion related to seed mix diversity will be limited to the Diverse and Simple treatments where the initial compositions of wheatgrasses were similar.

In the Diverse and Simple treatments a significant negative correlation was found between wheatgrasses and SR_Q in 1998 even though a positive correlation was found in 1997. In 1997 the plant communities were still establishing and higher SR_Q would be expected. A negative correlation with SR_Q in 1998 indicates more species were present in a quadrat when wheatgrasses, especially *A. dasystachyum*, were less abundant. It appears that the wheatgrasses displaced species from quadrats where they were dominant even though SR_Q increased in all the treatments from 1997 to 1998. However, the question of how these species were displaced still remains. Stevens and Carson (1999) described two hypotheses that may answer this question. The first is the interspecific competitive exclusion hypothesis. It is assumed in this hypothesis that mortality is not equal among species and that some species displace others due to better adaptation to the environment and hence competition. The second possible explanation, the assemblage-level thinning hypothesis, suggests that mortality is equal among species and that replacement is a result of differing performance among individual plants and not species. Therefore, density of plants is expected to decline as individual plant biomass increases in a unit area. Even though there is equal likelihood of mortality among species, species that were initially uncommon will become even less common or displaced due to density reduction. In this research, overall density increased with time due to increased density of annual forbs and to a lesser extent the wheatgrasses and canopy cover per plant decreased. The assemblage-level thinning hypothesis did not apply on a 0.1-m^2 scale at this early stage of succession and species displacement was more likely a result of interspecific competitive exclusion. However, assemblage level thinning may become more important as succession progresses, plants reproduce and spread, and bare ground decreases.

Community composition of the Diverse treatment was less similar to the Control than the Simple treatment on Chernozemic sites. This is partially explained by the composition of species in the Diverse seed mix not reflecting the composition of the Control plant community. The effectiveness of a diverse seed mix in increasing plant community similarity to the Control could be improved by site specific planning of the seed mix. The higher importance value of wheatgrasses in the Diverse treatment will also have influenced the relative similarity of the Diverse and Simple treatments to the Control.

Using seed mixes including wheatgrasses on mined land in Colorado, Redente et al. (1984) also found that increasing seed mix richness did not increase stand diversity.

Rapidly growing and competitive species, mostly grasses, were the primary species that persisted in seeded stands after five growing seasons. To the contrary, DePuit and Coenenberg (1979) found that increasing seed mix diversity, also including wheatgrasses, resulted in higher community diversity. They also found that diversity decreased with increasing seeding rate.

After 2 years, the highest treatment diversity (Shannon-Weiner Index) of native seed mixes including wheatgrass species was 1.0 in the DePuit and Coenenberg (1979) and 0.58 in the Redente et al. (1984) work, compared with a diversity of 2.0 in this research. Evenness of the most diverse treatment in the DePuit and Coenenberg study was 0.32 compared with 0.62 in our research. Seeding rates in our research (6 to 10 kg ha^{-1}, 300 PLS m^{-2}) were lower than that used by Redente et al. (1984) in their native grass and forb mix (15.5 kg ha^{-1}, 537 PLS m^{-2}) and much lower than those used by DePuit and Coenenberg study (28 to 56 kg ha^{-1}). Higher diversity in our research may be related to differences from other studies in seeding rate, environment, and/or seeded species composition.

Pärtel et al. (2000) found that species richness was related to the size of the regional species pool (i.e., richness of the region) in nutrient poor plant communities, but there was no significant relationship between productive plant communities and the richness of the regional pool. These differences were attributed to higher competition for light in the productive plant communities where biomass and litter production are higher. Nutrient availability was increased by disturbance on the wellsites resulting in higher biomass (Chapter 3) and litter production. Nutrient availability is expected to decline as the plant communities develop, therefore, wheatgrass productivity is also expected to decline. Thus, species richness should eventually reflect the regional species pool, providing colonization sites are available for species establishment as was described above.

Seed mixes need to be designed considering relative performance of species in the field. Hooper and Vitousek (1998) found that nutrient cycling processes were influenced more by plant composition than richness. Mixing of non-compatible species should be avoided or carefully planned to meet conservation objectives. Although the Simple and Diverse treatments have initially been successful in establishing perennial non-wheatgrass species relative to the Current treatment, the magnitude of this success was small and its duration questionable.

2.4.6 A Wheatgrass Forecast

Ultimately, the trajectory and rate of plant community succession in the seeded treatments will be determined by the duration and intensity of wheatgrass domination. Wheatgrass domination will, in turn, depend on four factors. First, they must have a competitive advantage during the early periods of high resource availability. Second, they must be at least equally as competitive as other species while availability of nutrients, light, and water decline. Third, they must have equal or greater longevity and reproductive potential as other species (i.e., they must be capable of self-sustained presence). Fourth, they must be equally as tolerant as other species to forms of stress such as drought or disturbance such as grazing.

Agropyron dasystachyum has high germination and establishment rates, is well adapted to the climate of the study area, prefers medium to coarse textured soils, prefers dry conditions, is highly drought tolerant, is considered tolerant of low nutrient regimes, is long lived, has an aggressive rhizomatous sod forming root system, and high seed production (Hardy BBT Limited, 1989). *A. dasystachyum* can withstand heavy grazing and is expected to increase in a stand if conservatively grazed (Alberta Agriculture, 1981). The Critana cultivar of *A. dasystachyum* used in this research was developed from a simple collection along road ditches in Montana without further selection (Stroh et al, 1972). Because its traits have not been specifically selected for, Critana would be expected to respond in a manner more typical of its occurrence in native communities and may be less competitive than other cultivars as a result. However, its rapid contribution to wheatgrass domination of the seeded treatments in this study indicates that it is well adapted to the sites where it was seeded. Based on these traits and its observed response in the treatments, the abundance of *A. dasystachyum* is expected to increase during the next few years and continue to dominate the seeded treatments for an unknown duration.

A. smithii is well adapted to the climate of the study area, has high drought tolerance, is highly capable of spreading vegetatively, but establishes slowly and is susceptible to drought and grazing during the establishment period (Hardy BBT Limited, 1989). The reported slow establishment rate of *A. smithii* relative to *A. dasystachyum* and *A. trachycaulum* is consistent with that observed in this study and may allow the establishment of other species. If conditions are favourable, however, this species may spread rapidly and competitively exclude other species with its sod-forming habit. Although it is a decreaser under grazing, grazing preference for bunch grass species allows *A. smithii* some reprieve. Its removal by grazing would most likely be accompanied or prefaced by removal of other decreasers such as *S. comata* (Smoliak, 1965). The Walsh cultivar of *A. smithii* was developed from 20 of 468 ecotypes in southern Alberta and Saskatchewan for regrassing clay and clay loam soils (Smoliak and Johnston, 1983) although the species in general is also suited to lighter textured soils (Hardy BBT Limited, 1989). Considering these traits and the results of this research, *A. smithii* abundance is expected to continue increasing and to retain, if not increase its importance in the plant community for at least the next few years. In doing so, *A. smithii* will probably contribute to the continued delay in plant community development in the seeded treatments. The extent of this delay will be site specific.

A. trachycaulum is regarded as a relatively competitive species in the first two or three years due to its high germination rate, high seedling vigour, rapid establishment, high biomass production, and high seed production (Hardy BBT Limited, 1989). These traits in conjunction with abundant litter production in the absence of grazing may repress establishment and growth of other species. From this perspective, *A. trachycaulum* may still contribute to a delay in plant community development toward the undisturbed condition. However, it is also known to be short-lived, have moderate to low drought tolerance, prefer areas with higher precipitation than the study area (Hardy BBT Limited, 1989), have low resistance to close and/or heavy grazing (Alberta Agriculture, 1981), and decline quickly under competition with other wheatgrasses (Schuman et al., 1982).

Considering these traits and its composition in the seed mixes, *A. trachycaulum* is not expected to remain a dominant component of the community for more than four to eight years.

2.5 CONCLUSIONS

The cultivars of *Agropyron dasystachyum*, *A. smithii*, and *A. trachycaulum* outperformed other grass species commonly dominant or present on Dry Mixed Grass prairie. Higher performance of the wheatgrass cultivars was associated with high rates of establishment, growth and reproductive spread relative to the other species. These traits led to domination of all seeded treatments by wheatgrasses after three years.

Seeded treatments were more effective than Natural Recovery in establishing perennial species and therefore in accelerating early succession. However, an observed trend of increasing abundance of non-wheatgrass species in the Natural Recovery treatment compared to a decline in treatments with a wheatgrass dominated seed mix has led to speculation that Natural Recovery may become more similar to the undisturbed prairie more quickly than by seeding to wheatgrasses. Diversity and evenness of seeded treatments were not different from the Natural Recovery treatment or undisturbed prairie suggesting that these variables were not good indicators of succession status in this research. Preliminary results from research also indicate that species richness may be lower in wheatgrass dominated communities on a 0.1 m^2 scale.

This research clearly indicated that seed mix composition (i.e., what species were included and their relative performance potential) was more important than species richness and relative abundance in determining composition of an early successional plant community. As a result, use of a diverse seed mix generally did not increase plant community diversity, species richness, or similarity to undisturbed prairie compared with low diversity seed mixes. Performance traits of seed mix species must be considered in seed mix formulation. Results from this research indicate that *Agropyron dasystachyum* may be more competitive in this environment than *A. smithii* and *A. trachycaulum*.

The extent of wheatgrass domination in the seeded treatments was not expected. In retrospect, inclusion of a seeded treatment that excluded wheatgrasses would have permitted a better assessment of the performance of other species in early secondary succession.

Table 2.1 Species composition of seed mixes and mean establishment for seeded rehabilitation treatments.

					Establishment (%)					
		Seed Mixes (% PLS)[1]			Chernozemic			Solonetzic		
Sceintific name (Authority)	**Common Name**	**Current**	**Diverse**	**Simple**	**Current**	**Diverse**	**Simple**	**Current**	**Diverse**	**Simple**
Agropyron smithii (Rybd.)	Western wheatgrass	50	7	10	5.8	17.9	27.8	8.3	17.5	33.7
A. dasystachyum ((Hook.) Scribn.)	Northern wheatgrass	30	7	10	26.4	44.4	47.8	19.0	27.0	37.8
A. trachycaulum ((Link) Malte)	Slender wheatgrass	15	7	-	31.7	39.3	-	36.3	52.4	-
Stipa viridula (Trin.)	Green needle grass	5	7	-	1.3	1.6	-	0.0	2.1	-
Bouteloua gracilis ((HBK) Lag.)	Blue grama grass	-	22	30	-	6.6	6.4	-	4.5	3.8
Stipa comata (Trin. & Rupr.)	Needle and thread grass	-	22	30	-	7.7	5.6	-	3.4	3.1
Koeleria macrantha ((Ledeb.) J.A. Schultes f.)	June grass	-	7	20	-	1.5	2.5	-	0.3	0.2
Oryzopsis hymenoides ((R. & S.) Ricker)	Indian rice grass	-	7	-	-	0.2	-	-	0.2	-
Elymus canadensis (L.)	Canada wild rye	-	3	-	-	0.0	-	-	0.0	-
Vicia americana (Muhl.)	American vetch	-	1.85	-	-	12.5	-	-	1.1	-
Ratibida colmunifera ((Nutt.) Wooton & Standl)	Prairie coneflower	-	1.33	-	-	1.9	-	-	5.6	-
Achillea millefolium (L.)	Common yarrow	-	1.25	-	-	3.3	-	-	1.7	-
Gutierrezia sarothrae ((Pursh) Dunal)	Broom weed	-	1.17	-	-	13.9	-	-	11.1	-
Petalostemon purpureum ((Vent.) Rybd)	Purple prairie clover	-	1.17	-	-	6.4	-	-	0.0	-
Aster ericoides (L.)	Tufted white prairie aster	-	1.08	-	-	0.0	-	-	1.1	-
Solidago missouriensis (Nutt.)	Missouri goldenrod	-	1.08	-	-	1.7	-	-	3.3	-
Astragalus striatus (Nutt.)	Ascending purple milk vetch	-	1.00	-	-	0.8	-	-	1.1	-
Gaillardia aristata (Pursh)	Gaillardia	-	0.33	-	-	2.5	-	-	0.0	-
Geum triflorum (Pursh)	Three-flowered avens	-	0.33	-	-	0.0	-	-	0.0	-
Petalostemon candidum ((Willd.) Michx.)	White prairie clover	-	0.33	-	-	0.0	-	-	0.0	-
Hedysarum spp. (L.)	Northern sweetvetch	-	0.03	-	-	31.7	-	-	22.2	-
Thermopsis rhombifolia ((Nutt.) Richards)	Golden bean	-	0.03	-	-	16.7	-	-	0.0	-

[1] PLS – Pure live seed; seeding rate 300 PLS m^{-2}.

Table 2.2 Total precipitation (mm) and mean air temperature at locations near the research sites. (May to September).

	1996	1997	1998	LTA[1]
		Precipitation		
Brooks	192	141	176	218
Bow Island	174	133	195	211
Medicine Hat	172	141	279	207
		Temperature		
Brooks	15.2	16.3	17.1	15.0
Bow Island	16.1	17.1	18.3	16.4
Medicine Hat	15.0	16.7	18.1	16.3

[1] LTA - Long term average (Brooks, 1961-1988; Bow Island and Medicine Hat, 1961-1997).

Table 2.3 Equations for plant community analyses.

$$\text{Frequency } (F_j) = \text{number of quadrats containing species j}$$

$$\%\text{ Frequency } (\%\text{Freq.}_j) = \frac{F_j}{\text{total number of observation units}} \text{x}100$$

$$\text{Density } (D_j) = \frac{\text{number of individuals of species j}}{\text{unit area}}$$

$$\%\text{ Ground } (GC_j) \text{ or Canopy } (CC_j) \text{ Cover} = \frac{\text{portion of observation area covered by species j}}{\text{total observation area}}$$

$$\text{Relative Frequency } (RF_j) = \frac{F_j}{\sum_j F_j} \text{x}100$$

$$\text{Relative Density } (RD_j) = \frac{D_j}{\sum_j D_j} \text{x}100$$

$$\text{Relative Canopy Cover } (RCC_j) = \frac{CC_j}{\sum_j CC_j} \text{x}100$$

$$\text{Relative Ground Cover } (RGC_j) = \frac{GC_j}{\sum_j GC_j} \text{x}100$$

$$\%\text{ Importance Value } (IVj) = \frac{(RFj + RDj + RCCj + RGCj)}{4}$$

$$\text{Species Richness } (SR) = \frac{\text{number of species}}{\text{unit area}}$$

$$\text{Shannon – Weiner Diversity } (H') = -\sum_{j=1}^{s} p_j \ln p_j \left(\text{where } p = \frac{\text{abundance of species j}}{\Sigma \text{ abundance of all species}}\right)$$

$$\text{Maximum } H' \ (H'\max) = \ln(SR)$$

$$\text{Evenness } (J) = \frac{H'}{H'\max}$$

$$\text{Spatz Similarity Index (Spatz)} = R \text{x} \frac{Mc}{Ma + Mb + Mc} \text{x}100$$

(Ma = sum of species abundance values restricted to community 'a')

(Mb = sum of species abundance values restricted to community 'b')

(Mc = sum of abundance values of species common to both community 'a' and 'b')

$$\left(R = \frac{\Sigma \left(\dfrac{\text{smaller quantitative value of species j common to 'a' and 'b'}}{\text{larger quantitative value of species j common to 'a' and 'b'}} \right)}{\text{total number of species in 'a' and 'b'}} \right)$$

Table 2.4 Pearson correlation coefficients for species richness per 0.1 m^2 (SR$_Q$) and canopy cover of selected vegetation groups and wheatgrasses on the Simple and Diverse treatments on Chernozemic sites (n=120).

Simple Treatment	Wheatgrasses (C$_3$W)		*Agropyron dasystachyum*		*Agropyron smithii*	
	1997	1998	1997	1998	1997	199
SR$_Q$	-0.08	-0.28	0.18	-0.23	0.21	-0.1
P>F	0.40	0.00	0.05	0.01	0.02	0.0
Annual forbs	-0.21	-0.48	-0.27	-0.43	0.08	-0.1
P>F	0.02	0.00	0.00	0.00	0.38	0.1
C$_3$G grasses	-0.08	-0.16	0.03	-0.12	-0.04	-0.0
P>F	0.39	0.08	0.76	0.18	0.63	0.3
C$_4$G grasses	-0.11	0.09	0.08	0.04	0.00	0.1
P>F	0.23	0.35	0.36	0.63	0.99	0.2
Perennial forbs	-0.11	-0.07	-0.07	-0.03	0.04	-0.0
P>F	0.23	0.67	0.48	0.78	0.66	0.7

Diverse Treatment	Wheatgrasses (C$_3$W)		*Agropyron dasystachyum*		*Agropyron smithii*		*Agropyron trachycaulum*	
	1997	1998	1997	1998	1997	199	1997	1998
SR$_Q$	-0.08	-0.28	0.35	-0.23	0.11	0.2	0.24	-0.18
P>F	0.36	0.00	0.00	0.01	0.22	0.0	0.00	0.05
Annual forbs	-0.19	-0.38	-0.25	-0.20	-0.23	-0.0	-0.15	-0.22
P>F	0.03	0.00	0.01	0.03	0.01	0.3	0.11	0.02
C$_3$G grasses	0.20	-0.12	0.16	-0.04	0.18	-0.0	0.11	-0.08
P>F	0.03	0.21	0.08	0.65	0.05	0.6	0.24	0.40
C$_4$G grasses	0.05	-0.14	0.41	-0.03	-0.09	0.2	0.12	-0.18
P>F	0.56	0.13	0.00	0.78	0.31	0.0	0.20	0.05
Perennial forbs	0.00	-0.01	0.03	-0.07	0.10	-0.0	-0.05	0.05
P>F	0.97	0.88	0.74	0.46	0.29	0.3	0.57	0.57
Agropyron dasystachyu	.	.	.	.	0.21	-0.0	0.17	-0.29
P>F			.	.	0.02	0.6	0.07	0.00
Agropyron smithii	.	.	.		.		-0.06	-0.22
P>F			.				0.49	0.01

Table 2.5 Mean change in canopy cover, density, and cover per plant from 1997 to 1998.

	Wheatgrasses	Annual Forbs	C_3 grasses	C_4 grasses	Perennial Forbs	Overall
			Canopy cover per plant			
Chernozemic						
Control	-0.3	-0.1	-1.7	0.3	-0.2a	0.2
Current	-3.0	-7.9	-3.0	2.0	0.4a	-4.2
Diverse	-5.7	-7.5	-2.2	-0.7	1.1a	-5.4
Simple	-4.2	-5.5	1.6	0.2	-5.4b	-3.4
NR[1]	-2.7	-4.2	5.1	4.7	-0.8a	-3.5
P>F	*0.15*	*0.52*	*0.11*	*0.58*	*0.01*	*0.22*
SE[2]	*1.4*	*3.2*	*2.1*	*1.7*	*1.1*	*1.6*
Solonetzic						
Control	0.1ab	-0.3a	-1.0	-0.3b	0.0	-0.3
Current	-4.4ab	-3.7ab	-1.3	0.0b	-3.6	-4.9
Diverse	-7.3b	-7.1b	2.5	-0.6b	-1.8	-6.8
Simple	-3.5ab	-6.0ab	-0.8	0.3b	-1.5	-4.9
NR	-2.7ab	-9.2b	4.4	18.5a	5.0	-8.5
P>F	*0.03*	*0.03*	*0.15*	*0.01*	*0.23*	*0.08*
SE	*1.2*	*1.6*	*1.6*	*0.8*	*2.4*	*1.7*
			Canopy Cover			
Chernozemic						
Control	-1.2	-3.5a	-8.8b	-3.1	-1.0b	-17.6b
Current	9.3	-11.4a	-0.6a	-0.2	-0.2b	-3.0ab
Diverse	7.3	-15.5a	-1.6a	-0.5	0.7ab	-9.6ab
Simple	7.6	-6.6a	0.4a	0.1	-0.6b	0.9ab
NR	-0.2	22.0a	2.3a	0.4	2.2ab	26.7a
P>F	*0.19*	*0.04*	*0.03*	*0.89*	*0.03*	*0.00*
SE	*3.6*	*7.7*	*2.1*	*2.6*	*0.7*	*6.4*
Solonetzic						
Control	4.9	-0.2	-7.5b	-0.6	-3.0	-6.4
Current	9.1	-2.9	-0.3a	-0.5	-1.4	4.0
Diverse	9.1	1.6	2.0a	0.0	4.7	17.4
Simple	11.3	-4.4	1.0a	0.3	1.7	9.9
NR	0.0	18.4	2.0a	1.0	7.7	29.0
P>F	*0.18*	*0.22*	*0.02*	*0.86*	*0.06*	*0.10*
SE	*3.1*	*6.8*	*1.6*	*1.1*	*2.3*	*7.9*
			Density			
Chernozemic						
Control	-0.3b	-5.0	-3.6	-2.7b	-1.9	-13.4
Current	6.9a	11.2	-0.1	0.0a	0.0	17.9
Diverse	5.6a	27.1	-0.1	-0.2a	0.1	32.5
Simple	4.5a	9.3	-0.2	-0.1a	0.1	13.6
Nat. Rec.	0.1b	47.9	0.2	0.0a	0.5	48.7
P>F	*0.00*	*0.23*	*0.49*	*0.05*	*0.10*	*0.21*
SE	*0.9*	*15.7*	*1.6*	*0.6*	*0.6*	*17.6*
Solonetzic						
Control	5.4a	0.4	3.4	-0.8	-3.9	4.6
Current	8.7a	13.7	-0.1	-0.1	-0.2	22.0
Diverse	6.1a	78.6	0.1	0.0	1.9	86.8
Simple	5.6a	100.8	0.4	0.1	0.5	107.5
NR	0.3b	190.0	0.3	0.2	0.3	191.2
P>F	*0.03*	*0.18*	*0.18*	*0.83*	*0.13*	*0.18*
SE	*1.4*	*52.9*	*0.87*	*0.7*	*1.4*	*51.7*

[1] NR - Natural Recovery

[2] SE - Standard error

Table 2.6 Importance value and density per seed planted in 1998.

	Agropyron dasystachyum	*Agropyron smithii*	*Agropyron trachycaulum*	*Bouteloua gracilis*	*Koeleria macrantha*	*Stipa comata*
			Importance value (%) per seed planted			
Chernozemic						
Current[1]	4.0	0.8 b	4.5	-	-	-
Diverse	8.5	4.3 a	9.5	0.41	0.03	0.48
Simple	10.4	4.4 a	-	0.55	0.18	0.44
P>F	*0.07*	*0.00*	*0.05*	*0.55*	*0.29*	*0.78*
SE[2]	*1.6*	*0.4*	*1.1*	*0.15*	*0.08*	*0.09*
Solonetzic						
Current	2.7 b	1.1	6.3	-	-	-
Diverse	6.0 ab	4.7	7.3	0.36	0.14	0.40
Simple	9.4 a	3.5	-	0.40	0.18	0.40
P>F	*0.03*	*0.07*	*0.82*	*0.82*	*0.61*	*0.91*
SE	*1.1*	*0.8*	*4.5*	*0.11*	*0.04*	*0.04*
			Density per seed planted			
Chernozemic						
Current	0.7	0.2 b	0.6	-	-	-
Diverse	1.2	1.1 a	1.4	0.04	0.00	0.05
Simple	1.1	1.2 a	-	0.06	0.03	0.03
P>F	*0.2*	*0.0*	*0.1*	*0.41*	*0.21*	*0.39*
SE[3]	*0.4*	*0.3*	*0.5*	*	*	*
Solonetzic						
Current	0.4	0.3 b	1.1	-	-	-
Diverse	1.1	1.5 a	1.2	0.05	0.02	0.04
Simple	1.4	1.3 a	-	0.05	0.03	0.05
P>F	*0.01*	*0.04*	*0.90*	*0.99*	*0.51*	*0.64*
SE	*0.2*	*0.4*	*0.6*	*	*	*

[1] SE - standard error.

[2] - Species not seeded in treatment where indicated by "-"

[3] * Indicates values too small to report.

Table 2.7 Mean similarity to the Control (%), richness by whole treatment area (SR_T) or quadrat (SR_Q, plants/0.1m^2), and diversity and evenness calculated from importance values on Chernozemic and Solonetzic sites in 1998 and change from 1997 to 1998.[1]

	Chernozemic			Solonetzic	
	1998	1998-1997		1998	1998-1997
			Similarity		
Current	1.6b	-0.69		4.3	-0.19
Diverse	2.8b	-0.51		5.7	0.16
Simple	5.7a	-0.43		10.5	0.47
NR	2.6b	-0.12		6.8	0.48
P>F	*0.00*	*0.17*		*0.10*	*0.48*
SE	*0.53*	*0.17*		*1.40*	*0.33*
			SR_Q		
Control	6.0a	-0.95b		7.0a	-1.58c
Current	3.5b	0.23ab		3.8b	0.40b
Diverse	4.2b	0.37ab		4.7b	1.41ab
Simple	4.3b	0.70a		4.3b	1.25ab
NR	3.3b	1.45a		3.8b	2.11a
P>F	*0.01*	*0.02*		*0.01*	*0.01*
SE	*0.34*	*0.35*		*0.38*	*0.32*
			SR_T		
Control	28.8	1.75		30.3	4.00
Current	18.8	-3.25		16.7	0.00
Diverse	31.0	2.00		26.0	-0.33
Simple	24.5	0.50		20.0	-1.33
NR	27.0	5.00		23.3	2.00
P>F	*0.14*	*0.36*		*0.10*	*0.64*
SE	*2.59*	*2.44*		*2.92*	*4.08*
			Diversity		
Control	1.92	-0.20		2.31	0.00
Current	1.59	-0.20		1.63	-0.17
Diverse	1.88	-0.19		2.01	-0.08
Simple	1.66	-0.29		1.84	-0.07
NR	1.54	0.14		1.58	0.11
P>F	*0.42*	*0.80*		*0.07*	*0.85*
SE	*0.06*	*0.11*		*0.07*	*0.08*
			Evenness		
Control	0.57	-0.09		0.68	-0.03
Current	0.55	-0.09		0.59	-0.07
Diverse	0.55	-0.08		0.62	-0.03
Simple	0.52	-0.13		0.62	0.00
NR	0.51	0.06		0.50	0.02
P>F	*0.86*	*0.90*		*0.13*	*0.85*
SE	*0.04*	*0.09*		*0.04*	*0.06*

---

[1] Treatment means followed by the same letter are not significantly different using Fisher's Protected LSD (P≤0.05).

[2] NR – Natural Recovery.

[3] SE – Standard error.

Table 2.8 Mean ground cover components (%) on Chernozemic and Solonetzic sites in 1998 and relative change (%) from 1997 to 1998.[1]

	Chernozemic		Solonetzic	
	1998	1998-1997	1998	1998-199
		Bare Ground		
Control	3b	-9	7b	-
Current	35a	-13	34ab	-1
Diverse	33a	-10	44ab	-
Simple	44a	-7	44ab	
NR[2]	49a	-1	49a	-
P>F	*0.01*	*0.63*	*0.11*	*0.2*
SE[3]	*6.1*	*9.4*	*9.4*	*6.*
		Litter Cover		
Control	43	-6b	19	- b
Current	53	51a	52	1 a
Diverse	57	54a	43	1 a
Simple	41	36a	42	1 a
NR	35	34a	28	ab
P>F	*0.17*	*0.02*	*0.27*	*0.1*
SE	*6.8*	*8.8*	*9.3*	*12.*
		Live Vegetation		
Control	65a	-17b	78a	
Current	13b	3a	16b	
Diverse	11b	1a	13b	
Simple	16b	8a	15b	
NR	16b	12a	24b	2
P>F	*0.00*	*0.01*	*0.00*	*0.4*
SE	*4.3*	*2.6*	*5.0*	*4.*

[1] Treatment means followed by the same letter are not significantly different using Fisher's Protected LSD (P≤0.05).

[2] NR – Natural Recovery.

[3] SE – Standard error.

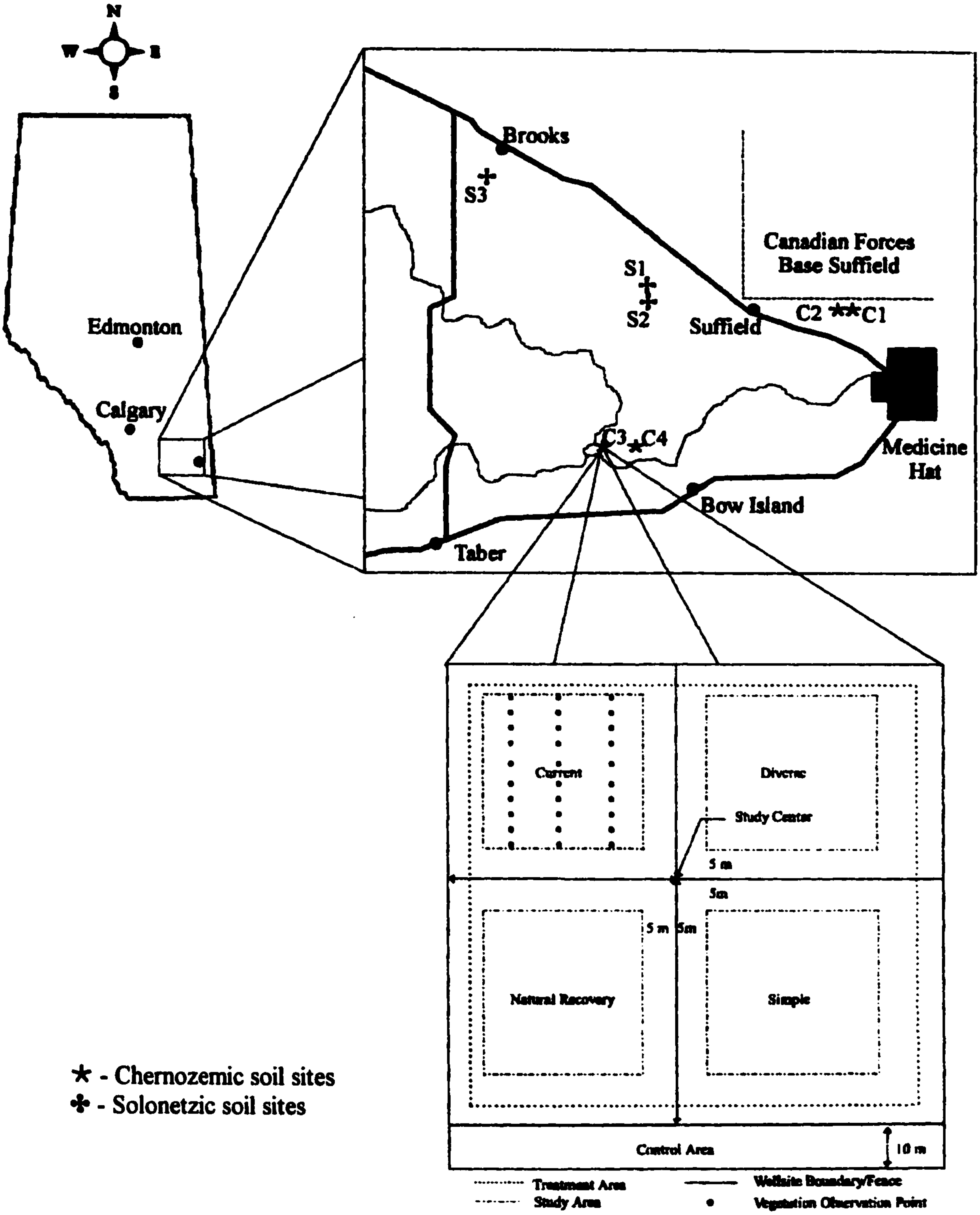

Figure 2.1 Sketch map of study area and an example of treatment layout on study sites.

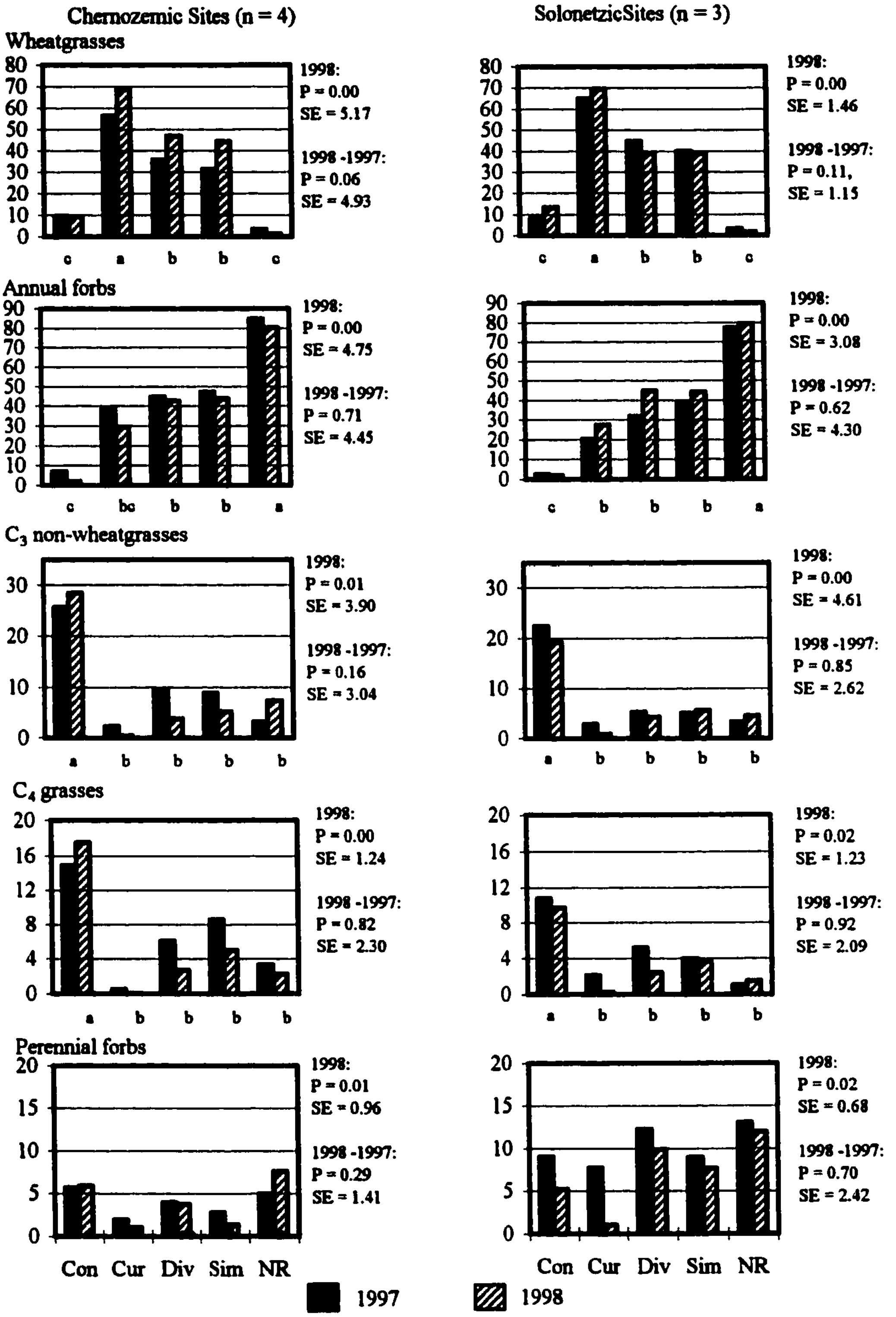

Figure 2.2 Mean importance value (%) of vegetation groups for 1998 and 1997. Although data for 1997 is presented, statistical analyses were only conducted for the 1998 data and the difference between 1997 and 1998 (1998-1997). Probability values (P) from ANOVA and pooled standard error (SE) are provided for each vegetation group. Treatments with different lowercase letters have different mean importance values in 1998 (LSD P<0.05). There were no significant differences among treatments in the amount of change from 1997 to 1998 for any group. Con - Control, Cur - Current, Div - Diverse, Sim - Simple, NR - Natural Recovery.

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CHAPTER 3. SOIL AND PLANT RESPONSE TO WELLSITE REHABILITATION ON CHERNOZEMIC AND SOLONETZIC SOILS IN SOUTHEASTERN ALBERTA

3.1 INTRODUCTION

Petroleum industry exploration and development has resulted in continued disturbance of native Dry Mixed Grass prairie ecosystems in southeastern Alberta. Current reclamation and revegetation policy in Alberta requires that these disturbances are returned to a predisturbance equivalent capability and that native species must be used in revegetation (Alberta Environmental Protection, 1995). Cultivars of native wheatgrasses are typically used in revegetation because of their performance, availability, and price. However, these cultivars have become viewed as highly competitive and may inhibit the recovery of the predisturbance plant community (Gill Environmental Consulting, 1996). Wheatgrass domination of early plant community succession following revegetation was confirmed in this research (Chapter 2). However, the effect of this plant community on biogeochemical cycling in early succession also needed to be investigated.

Both the form and quantity of available soil nitrogen changes with disturbance and subsequent secondary succession. Prairie disturbance typically results in a period of increased nitrogen availability (Campbell et al. 1976; Dormaar and Willms, 1990) due to increased mineralization of soil organic matter and low nitrogen uptake by the reduced or absent plant community (Campbell et al., 1975; Vitousek et al., 1989; Redmann, 1995). Vitousek et al. (1989) indicated that patterns in nitrogen availability vary depending on the sere. They also indicated that nitrogen availability in old-field succession, where continuous disturbance and cropping reduces total soil N, may differ from other secondary succession where only the plant community is destroyed and soil fertility does not decline. Therefore, the overall effect of disturbance on nitrogen availability will depend on the nature of the disturbance and its duration; old-field succession may differ from a petroleum wellsite disturbance.

Soil mineral nitrogen primarily occurs in the form of nitrate in early secondary succession and as ammonium in late succession (Rice, 1984; Dormaar et al., 1994; Dormaar and Smoliak, 1985). As a result, the ratio of ammonium to nitrate (NH_4^+:$N0_3^-$) increases with succession but decreases with disturbance. Rice (1984) attributes the increasing NH_4^+:NO_3^- to allelopathic inhibition of nitrification. An alternative explanation is that under a highly competitive environment, uptake capabilities of microorganisms and plants together exceed mineralization potential (Woodmansee et al., 1981; Paul and Clark, 1989). In such systems NH_4^+ is immobilized before nitrification can occur. Regardless of the cause, decline in availability of mineral nitrogen and increase in the NH_4^+:NO_3^- ratio may be a good indicator of the rate of successional development and equilibration of biogeochemical processes following disturbance.

Cultivation or construction of petroleum wellsites often results in some mixing of the A and B horizons. This mixing of horizons is expected to influence soil properties such as pH, organic carbon, total nitrogen, and cation exchange capacity, and ultimately soil productivity as found on cultivated lands (Anderson and Coleman, 1985). Reclamation

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criteria have been adopted to limit the extent of such impacts (Alberta Environmental Protection, 1995). Alteration of these properties may affect biogeochemical cycling of nutrients. Rowell and Florence (1993) evaluated 23 conventional and biological soil assays as indicators of disturbance and influence of rehabilitation practices. Variables deemed to be most effective in distinguishing disturbed and undisturbed soil included the biological variables aralsulfatase activity, dehydrogenase activity, extractable organic carbon, and basal respiration and the conventional variables sulphate, pH, organic carbon, and cation exchange capacity. High dehydrogenase enzyme activity was typically associated with undisturbed soils. Dehydrogenase enzyme activity has been regarded as a useful indicator of soil biological activity for some time (as opposed to populations of soil microorganisms) (Casida et al., 1964) and has been used in evaluating industrial disturbance and the influence of rehabilitation practices (Rowell and Florence, 1993; Biondini et al. 1984/85; Fresquez et al. 1987).

Carbon and nitrogen losses through root exudation vary among species and ecosystems (Biondini et al., 1988). Grayston et al. (1998) found a clear difference in carbon utilization patterns of miroorganisms from the rhizospheres of different plants. Grayston et al. (1998) suggested that these differences resulted from different microbial species associating with different exudates from each plant species. Vinton and Burke (1995) found differences in biogeochemical cycling attributes between perennial bunchgrasses and rhizomatous grasses, and between perennial species and annual species. Therefore seeding versus not seeding and the composition of seed mixes may influence biogeochemical function of the rehabilitated ecosystem.

Increased vegetation productivity and shifts in community composition in response to nitrogen fertilization have been commonly observed on rangeland (e.g., Johnston et al. 1967); however, responses to increased nitrogen availability vary among species and with time as secondary succession occurs. Annual forbs are typically expected to dominate early secondary succession following a disturbance event but will eventually be overcome by perennial species (see Chapter 2; Odum, 1969; Grime, 1977; Vitousek et al, 1989). Tilman (1987) attributed early domination of annual species under highly fertile conditions to higher relative growth rates compared with perennial species. He found that by the second or third year in high nitrogen treatments, artificial maintenance of high nitrogen may have allowed perennials to increase stores of energy and nutrients in their rhizomes, and they subsequently grew taller early in the season and displaced the annuals. Light then became the primary limiting factor as taller growing species shaded others.

Tilman (1990) indicated that succession was influenced by environmental constraints and tradeoffs in each species' ability to deal with these constraints. He included availability of limiting soil resources among these constraints. He also indicates that every species has a minimal requirement for soil resources to survive; the species that has the lowest requirement for that resource will competitively displace other species. The primary soil constraints vary among ecosystems; however, nitrogen is most often limiting (Tilman, 1994). Therefore, the nature of secondary succession will be strongly influenced by how the availability of soil resources, especially mineral nitrogen, is altered by disturbance. A disturbance that lowers soil quality may reduce nitrogen supply and therefore influence plant community composition. McLendon and Redente (1992) suggested that the availability of available soil nitrogen, and therefore the dynamics of nitrogen incorporation in perennial plant tissue, was a primary mechanism in controlling the rate of secondary succession. They found that tissue nitrogen of early successional dominants increased with soil nitrogen availability but mid-successional species displayed the opposite pattern. They determined that the shift in abundance from annual forbs to perennials resulted from inadequate nitrogen availability for the annuals not competitive displacement by perennials.

Perennial species vary in their response to increased nutrient availability. *Agropyron smithii* (Rybd.) has commonly increased in abundance under fertilization while *Stipa comata* (Trin. & Rupr.), *Bouteloua gracilis* ((HBK) Lag.), and *Koeleria macrantha* ((Lebed.) J.A. Schultes f.) have declined in composition (Samuel and Hart, 1998; Wight, 1976; Johnston et al., 1967). Based on these observations, plant community response to revegetation of disturbed fertile sites may vary depending on the initial species composition and species response to nutrient availability. Seeded wheatgrasses rapidly dominated the plant communities of recent wellsite disturbances while other seeded species such as *B. gracilis*, *S. comata*, and *K. macrantha* and non-seeded annual forbs appeared to be in decline (Chapter 2). At the same time, the non-seeded Natural Recovery treatment was dominated by annual forbs while species such as *B. gracilis*, *S. comata*, and *K. macrantha* were increasing in abundance.

The purpose of this research was to examine the relative influence of selected rehabilitation practices on selected biogeochemical processes (i.e., nitrogen availability, plant uptake of nitrogen, biomass production, carbon allocation, and soil biological activity) in early secondary succession. More specifically, the following rehabilitation comparisons were of interest: a) natural recovery versus use of native seed mixes, b) a wheatgrass dominated seed mix versus non-wheatgrass dominated seed mixes, and c) a diverse seed mix versus low diversity seed mixes.

3.2 MATERIALS AND METHODS

3.2.1 Experimental Design, Study Area, Site Preparation, And Treatments

The study area is located in the Dry Mixed Grass Natural Subregion (Alberta Environmental Protection, 1994) of southeastern Alberta (Figure 3.1). Vascular plant cover in this region is dominated by *S. comata*, *B. gracilis*, *K. macrantha*, *A. smithii*, and/or *A. dasystachyum* ((Hook.) Scribn.) depending on soil texture, topography, and grazing. Seven drilled and abandoned, non-producing petroleum wellsites were selected (Hammermeister and Naeth, 1996) in the Brooks-Bow Island-Medicine Hat area (Figure 3.1, see Appendix A for research site coordinates). A randomized block design was employed consisting of four blocks (i.e., wellsites) on Orthic Brown Chernozemic soil and three on Brown Solodized Solonetzic soil (Hammermeister and Naeth, 1996). All wellsites were constructed on native prairie, abandoned without petroleum production, and were reclaimed to the point of revegetation. The wellsite disturbances areas ranged in size from 0.9 to 1.2 ha. Participating companies reclaimed their wellsite(s) using standard practices which included: surface soil salvage to approximately 10 cm, subsoil salvage to varying depth as required, soil stockpiled typically for less than 6 months, drilling, subsoil replacement, and surface soil replacement (sometimes with straw added to stabilize soil) (Hammermeister and Naeth, 1996). The Solonetzic soil sites and the Chernozemic C4 site (Figure 3.1) were paratilled to alleviate soil compaction. The sites were not contaminated by petroleum products.

Five treatments were studied at each wellsite: a non-disturbed Control, a non-seeded Natural Recovery, and three seed mixes: Current – wheatgrass dominated mix; Diverse – nine grasses and 13 forbs, and Simple – five grasses, not wheatgrass dominated (Figure 3.1, Table 3.1). Species composition of seed mixes (Table 3.1) was selected based on treatment strategy, typical composition of Dry Mixed Grass prairie (Gerling et al., 1996; Nernberg, 1995), and seed availability. All grasses except *K. macrantha* were drill seeded at a depth of 2.5 cm. *K. macrantha* and the forbs were broadcast seeded. All wellsites and Control areas were fenced to exclude grazing. Seeding was completed June 21st, 1996. The study area was the same for each rehabilitation treatment on a wellsite but varied from 0.068 ha to 0.240 ha not including buffer zones between treatments.

3.2.2 Climate

Mean monthly and long term average precipitation and temperature for summer months were obtained from Medicine Hat, Brooks, and Bow Island (Table 3.2). Growing season conditions were generally warmer and drier throughout the study period than long-term averages. Of particular importance was the prevalence of these conditions in the first few months following seeding.

3.2.3 Soil Analyses

Three soil subsamples were collected in each treatment from the 0 to 10-cm depth increment in July 1997. Soil pH and electrical conductivity (EC) were determined by 1:1 soil:water suspension (McKeague, 1978) on each subsample. Particle size analysis was conducted by the hydrometer method (McKeague, 1978). Sodium adsorption ratio (SAR) was determined by saturation paste extract (McKeague, 1978) on samples collected at 0 to 10-cm, 10 to 20-cm, and 20-40-cm depth increments. Soil volumetric bulk density (Db) measurements to a 7.5-cm depth were taken with a Campbell Pacific Nuclear MC1 Surface Water/Density Gauge in July 1997.

Soil nitrate (NO_3^-), ammonium (NH_4^+), and phosphorus supply rates were measured using ion exchange membranes (IEM) following the method described by Qian and Schoenau (1995). The membranes, manufactured by BDH Ltd., Poole, England (55164-2S), were used in the form of Plant Root Simulator probes (Western Ag. Innovations, Saskatoon, Saskatchewan, Canada) where a membrane is attached to a plastic frame for insertion into the soil. The cation (CEM) and anion (AEM) exchange membranes were saturated with Na^+ and HCO_3^-, respectively, by washing in 1 N $NaHCO_3$ solution for several hours before field use. The IEMs were inserted to a 7.5-cm depth and left in the field for two weeks. In 1997, four CEM/AEM probe pairs were inserted 30 cm apart, 5 m from the inner corner of each rehabilitation treatment. The IEMs were located randomly along transect(s) in the Control. Two consecutive two-week sampling periods were conducted beginning May 26 and ending June 23. For the 1998 sampling, eight CEM/AEM probe pairs per treatment were planted along three transects in each rehabilitation treatment, and along the Control transect(s). Three two-week sampling periods were conducted: May 6 to 20, June 9 to 23, and July 6 to 20. The sample points along each transect were randomly chosen in May, and the same points were used in June and July. On retrieval, the IEMs were rinsed with deionized water to remove soil, sealed in a ziploc bag, and kept cool until elution. The probes were eluted for 1 hr in 20 ml/probe of 0.5 N HCl. NO_3^-, NH_4^+, and HPO_4^- were colorimetrically determined from the elutant using a Technicon Autoanalyzer II, Industrial Method No. 100-70W, 325-74W, and 94-70W respectively (Technicon Industrial Systems, 1973). Results were standardized to a 10 cm^2 IEM. Similar patterns among treatments in IEM uptake of NO_3^- were observed on both soils and over time. Therefore, mean NO_3^- uptake by IEMs over the five sample dates was calculated for each treatment on each soil.

At the beginning of each sampling period in 1997 and 1998, a composite soil sample was collected from adjacent to the PRS sampling points in each treatment. These samples were used for determination of 2 *M* KCl extractable NO_3^- and NH_4^+ (Bremner, 1965). KCl extractable NO_3^- and NH_4^+ were also determined in 0 to 10 cm samples collected in September of 1996, 1997, and 1998. All samples were dried immediately following sampling and passed through a 2 mm sieve prior to analysis.

Total carbon (C_{Tot}) and nitrogen (N_{Tot}) content of ground soil samples were determined by combustion at 1100 °C (Leco® Corporation, 1994) for samples collected in the fall of 1996. Soil inorganic carbon (C_{Inorg}) was determined by acid digestion (Tiessen et al., 1983). Organic carbon (C_{Org}) was calculated as the difference between C_{Tot} and C_{Inorg} (i.e., $C_{Org} = C_{Tot} - C_{Inorg}$). The mean of all samples from the rehabilitation treatments on each site were used for statistical analyses when comparing with the Control.

Soil dehydrogenase enzyme activity was determined by triphenyl formazan evolution, a slightly modified method of Casida et al. (1964) and was conducted under the supervision of Dr. Bix Biederbeck, Semiarid Prairie Agriculture Research Station, Agriculture and Agri-Food Canada, Swift Current. Composite soil samples were collected for each treatment on each wellsite in September 1996, 1997, and 1998. Soil samples were refrigerated until analysis. Samples from 1996 were accidentally saturated in 1996 and therefore results are not presented.

Preliminary measurements of microbial carbon utilization patterns were conducted on soil samples collected in August of 1998. These results are not presented in this paper due to the single sampling date, however, a summary can be found in Appendix B.

3.2.4 Vegetation Assessments

In 1997, nine plant subsamples were clipped from three 0.1 m^2 quadrats randomly located along the three transects in each treatment. Subsamples were clipped at a height of 2.5 cm. In 1998, subsamples were collected at each IEM sampling point totalling eight subsamples of 0.1 m^2 per treatment. Grasses, forbs, and shrubs were separated, oven dried at 55 °C, and weighed to determine aboveground biomass. Samples were not collected in 1996 because of delayed establishment.

Root samples were collected from eight 7.5-cm diameter by 30-cm deep cores. The cores were collected in August 1998 from near the IEM sample points in each treatment. Each core was separated into 0 to 10-cm and 10 to 30-cm depth increments. Samples were washed through a sieve (<1 mm) to remove soil, litter, stones, and other debris. The remaining root material was dried at 40 °C and weighed for biomass determination. Data for the two depth increments were later combined because patterns among treatments were similar for each depth.

Subsamples of plant materials collected in 1998 were combined for each treatment on each site and were ground. Total carbon (% C) and nitrogen (% N) content of ground plant material were determined by combustion at 1000 °C (Leco® Corporation, 1994). Total biomass C ($C_{Biomass}$) and N ($N_{Biomass}$) were calculated on an area and depth basis from biomass samples and plant % C and % N analyses.

3.2.5 Statistical Analyses

Data were analyzed as a randomized block design separately for Chernozemic and Solonetzic sites. SPSS® software (Norusis, 1993) was used to test for significant differences among treatments using Fisher's Protected Least Significant Difference (Steel and Torrie, 1980) and relationships among selected variables were assessed by Pearson correlation.

All data were checked for violations of assumptions with emphasis placed on homogeneity of variance. Most variables met the homogeneity of variance assumption; transformations were attempted to address those that did not. However, all analyses were conducted on non-transformed because: negative values from change with time could not be transformed, in most cases data transformation did not alter interpretation of results, and presentation of both transformed and non-transformed data would have complicated interpretation by the reader (Finney, 1989).

3.3 RESULTS

3.3.1 Soil Analyses

3.3.1.1 Reclamation Impact On Soil Properties

Surface soil salvage and replacement on the disturbed portion of the wellsites altered several soil properties relative to the Control at each site. Soil pH, inorganic carbon, and bulk density were higher on the wellsites than for the Controls on both soils (Table 3.3). Organic carbon and total nitrogen were significantly lower on the wellsites than the Controls on Chernozemic sites. SAR on the Solonetzic wellsites was lower than on the Controls. Electrical conductivity of all sites was less than 1 dS m^{-1}, and was not altered by disturbance (data not presented).

The disturbance had little effect on mean composition of soil separates of the rehabilitation treatments compared with the Control on either soil (data not presented). On Solonetzic sites, surface soil texture varied from loam to clay loam among sites, and among cores within the Control of each site. On Chernozemic sites, every soil sample collected from every site had a loam texture.

3.3.1.2 Soil N And P Uptake By Ion Exchange Membranes (IEM)

IEM uptake of NO_3^- on both soils was significantly higher in the Natural Recovery treatment and lowest in the Control (Figure 3.2). It did not differ among seeded treatments on either soil. The seeded treatments were not significantly different from the Control or the Natural Recovery treatment on Chernozemic soil. On Solonetzic soil, however, it was significantly higher in the Diverse and Simple treatments than the Control, and was significantly lower in all seeded treatments than the Natural Recovery. Differences in IEM uptake of NH_4^+ and phosphorus among treatments were not statistically significant (data not presented). However, NH_4^+ uptake was numerically lower for the Natural Recovery treatment than for other rehabilitation treatments on both soils during the 1998 measurement periods.

3.3.1.3 Soil Ammonium To Nitrate Ratio By KCl Extraction

Although KCl extractable NO_3^- followed the same pattern among treatments as that observed using the IEM technique, differences among rehabilitation treatments were not significant. NO_3^- was significantly lower in the Control than all rehabilitation treatments on Solonetzic sites but only lower than the Diverse and Natural Recovery treatments on Chernozemic sites. Mean values for NO_3^- in the Control were 4.0 and 2.8 $\mu g\ g^{-1}$ soil for Chernozemic and Solonetzic sites, respectively, compared with 6.9 and 6.4 $\mu g\ g^{-1}$ soil, respectively, in the Natural Recovery treatment. No statistically significant differences in NH_4^+ were measured for either soil with values ranging from 3.7 to 5.0 $\mu g\ g^{-1}$ soil on Chernozemic sites and 3.8 to 4.3 $\mu g\ g^{-1}$ soil on Solonetzic sites. On Chernozemic sites NH_4^+:NO_3^- ratio was significantly higher in the Control than the rehabilitation treatments (Figure 3.2) and higher in the Current treatment than the Natural Recovery treatment. There were no statistically significant differences among the treatments in NH_4:NO_3^- ratio on Solonetzic soil.

3.3.1.4 Soil Dehydrogenase Enzyme Activity

Mean dehydrogenase enzyme activity was higher in the Control than the rehabilitation treatments in both 1997 and 1998 although differences were only significantly different on Chernozemic sites in 1997 (Table 3.4). Dehydrogenase activity did not differ significantly among rehabilitation treatments in either year but varied by soil and year of measurement. Dehydrogenase activity was lower in 1997 than in 1998 for both soil types.

3.3.2 Plant Community Characteristics

A detailed analysis of plant community characteristics is provided in Chapter 2 but is briefly summarized here. Grasses dominated canopy cover, density, and frequency, in the seeded treatments after three growing seasons. Annual forbs were dominant in the Natural Recovery treatment throughout the study period. In all seeded treatments, the grass component of the plant community was dominated by wheatgrasses; other grasses were present but of low importance. The Control treatment was dominated by *Selaginella densa* (Beauv.), *Carex* spp, *Stipa comata*, *Bouteloua gracilis*, and *Koeleria macrantha* on most wellsites. *Selaginella densa* occupied virtually all ground space not occupied by grasses or forbs.

3.3.2.1 Plant C And N In 1998

Few significant differences in plant C or N were observed among treatments for grasses or forbs on either soil (Table 3.5). N was higher in forbs (average 2.09 %) than in grasses (average 1.58 %). No statistically significant differences in C:N ratio were measured among treatments for grasses or forbs. Grasses in the seeded treatments and forbs in the Natural Recovery treatment dominated biomass production. No significant differences in forb, grass, root, total $C_{Biomass}$, or $N_{Biomass}$ were measured among seeded rehabilitation treatments on either soil in 1998 (Figure 3.2). $C_{Biomass}$ and $N_{Biomass}$ for the Natural Recovery treatment, however, were significantly higher for forbs and lower for grasses than for the seeded rehabilitation treatments. Grass $C_{Biomass}$ and $N_{Biomass}$ were significantly lower in the Control than in the seeded treatments. Most Control $C_{Biomass}$ and $N_{Biomass}$ in was found in the roots and was significantly higher than in the roots of plants from the rehabilitation treatments.

3.3.2.2 Change In Biomass From 1997 To 1998

As expected, grass and forb biomass in 1998 (Table 3.6) followed the same patterns as $C_{Biomass}$ (Figure 3.2). The Simple and Diverse treatments, however, were dominated by annual forbs in 1997 before grasses became dominant in 1998 (Table 3.6). Annual forbs remained dominant in the Natural Recovery treatment throughout 1997 and 1998. No significant differences in grass, forb, or aboveground biomass were measured among the seeded treatments in 1998. The seeded treatments were, however, significantly higher in grass biomass and lower in forb biomass than the Natural Recovery treatment. Aboveground biomass of the Control was significantly lower than that for the rehabilitation treatments among which there were no significant differences in 1997 or 1998. Root biomass, however, was significantly higher in the Control than in the rehabilitation treatments, among which there were no statistically significant differences.

3.3.3 Soil And Plant Correlations

On Chernozemic sites, a significant negative correlation was found between forb C:N ratio and available NO_3^- while a significant positive correlation was found between forb N and available NO_3^-. No significant correlation of NO_3^- with grass C or N variables was observed (Table 3.7). Root $C_{Biomass}$, however, was negatively correlated with available NO_3^-. On Solonetzic sites, forb $C_{Biomass}$ and $N_{Biomass}$ were positively correlated with available NO_3^- (Table 3.7). Grass $C_{Biomass}$ and $N_{Biomass}$ variables were all strongly negatively correlated to available NO_3^-. Root $C_{Biomass}$ and $N_{Biomass}$ were also negatively correlated with available NO_3^-. Forb and grass $C_{Biomass}$ were significantly and negatively correlated with each other on both soils ($P \leq 0.05$, data not shown). Grass $C_{Biomass}$ was also significantly and positively correlated with total biomass C. This means that grass biomass was the primary contributor to high biomass production.

3.4 DISCUSSION

3.4.1 Disturbance Impact On Soil

Mixing of subsoil with surface soil was evident by increased inorganic carbon and related increase in soil pH. Considering that the optimum pH for nitrification ranges from 6.6 to 8.0 (Paul and Clark, 1989), the slightly higher soil pH is not expected to have had a major influence on nitrification. Increased soil bulk density is commonly observed on petroleum industry disturbances that have been reclaimed (Thacker et al., 1994; Naeth et al., 1987). Based on suggested threshold values (Naeth et al., 1991), surface bulk density was not expected to limit plant growth on any of the rehabilitated wellsites.

On a gravimetric basis, the lower surface soil organic carbon and total soil nitrogen on disturbed treatments versus the Control on Chernozemic sites would be a direct result of dilution from admixing surface soil with subsoil. A 16 % loss in organic carbon and 19 % loss in total nitrogen would roughly equate to the loss associated with 10 years of cultivation (Campbell et al., 1976). The differences in organic carbon and total soil nitrogen between the Control and wellsite were smaller on a quantitative basis (mass/volume) due to soil compaction on the wellsite. The lack of change with disturbance on Solonetzic sites in organic carbon and total nitrogen resulted from blowout portions of the landscape (where topsoil had been eroded away) being sampled with the rest of the landscape. The blowouts, having very low organic carbon, lowered the average organic carbon content of the Control. Surface soil salvage practices, however, would have removed little surface soil from the blowouts and the surface soil with now higher mean organic carbon was spread evenly across the wellsite.

Soil organic matter content (i.e., organic carbon) is considered one of the most important attributes of soil quality and its inherent productivity (Gregorich et al. 1994). On Chernozemic sites the lower soil organic carbon and total nitrogen following disturbance are expected to result in lower productivity due to lower nutrient availability (Campbell and Souster, 1982) resulting from lower microbial biomass, organic substrate availability, and nitrogen mineralization (Burke et al., 1997; Anderson and Coleman, 1985). Under perennial species cover, active soil nitrogen pools, and hence nitrogen availability, may recover much more quickly than total nitrogen but may be species dependent (Vinton and Burke, 1995; Burke et al., 1995). Therefore, wheatgrass domination may alter the rate of recovery on nutrient availability relative to Natural Recovery or by plant communities dominated by *Stipa comata* and *Bouteloua gracilis*. A fundamental difference between cultivation and a wellsite disturbance is that organic carbon under cultivation is a result of carbon mineralization whereas organic carbon is primarily lost by surface soil dilution in the wellsite disturbances, providing the disturbance is of short duration. Long term changes in soil biological function may occur under frequent cultivation that may not be as prevalent on a wellsite disturbance. The resulting soil properties (lower organic carbon and higher soil pH) grade toward those found for shallower calcareous soils in upper slope positions that are pedogenically younger than those in mid and lower slopes. The plant community on these upper slopes differs from mid- and lower slopes, although differences have primarily been attributed to water relations (Coupland, 1950). However, soil quality, especially organic matter content increases the magnitude of differences in productivity between upper and lower slopes (Verity and Anderson, 1990).

A lower SAR was expected on the rehabilitation treatments of the Solonetzic sites compared with the Control. Deep ripping has been used extensively to lower SAR and break up the impermeable Bnt horizon by mixing it with the calcareous Cca horizon. This procedure has improved productivity on agricultural land for up to five years by reducing the negative influences of a Solonetzic B horizon on productivity (Boehm, 1988).

3.4.2 Dehydrogenase Enzyme Activity

Lack of statistically significant differences in dehydrogenase enzyme activity is primarily attributed to high variance among wellsites and inconsistent results within treatments. The numerically higher dehydrogenase activity in the Control than the rehabilitation treatments supports Rowell and Florence (1993) who found that low dehydrogenase activity was an indicator of disturbance. In a study of the effects of topsoil thickness and fertilization on the secondary succession of reclaimed areas, Biondini et al. (1984/85) found dehydrogenase activity increased with succession and was positively correlated with perennial grass production. However, Dormaar and Smoliak (1985) found higher dehydrogenase activity on younger abandoned farmland than on older abandoned land, and higher activity on abandoned land than on native range in Alberta. More recently, however, Dormaar and Willms (2000) found lower dehydrogenase activity on disturbed soils than in undisturbed prairie in Alberta. Moore and Russell (1972) found a number of factors could influence dehydrogenase activity including soil pH, water content, texture, grinding, and NO_3^- levels. Dehydrogenase activity decreased with increasing NO_3^-; denitrification of nitrate under anaerobic conditions influenced reduction of TTC (2,3,5-triphenyltetrazolium chloride). Higher NO_3^- availability in the rehabilitation treatments may partly explain the difference from the Control. These treatments may not have had sufficient time to equilibrate following disturbance. Soil samples among treatments from each site varied in texture and had to be adjusted for water holding capacity potentially affecting results. The large difference in dehydrogenase activity between 1997 and 1998 may be a result of decline in activity from storage of the 1997 samples (Ross, 1970). Further and more detailed study is required to determine if there are differences among treatments.

3.4.3 Mineral Nitrogen Availability

Ion exchange resins have been used extensively in a variety of forms for measuring soil ion exchange (see Skogley and Dobermann, 1996 for a review). Exchange membranes can act as a sink if the exchange is not filled or a dynamic indicator of the relative contribution of ions on the soil exchange if the membrane is filled. In this case membranes acted as an ion sink since ion exchange was relatively low. In the absence of competition with plants, differences in ion uptake, in this case NO_3^-, can thus be associated with differences in plant available nitrogen and organic nitrogen mineralization (Qian and Schoenau, 1995).

In the presence of plant competition, the membranes indicate the combined effects of mineralization and plant uptake on availability of the measured nutrients. In retrospect, measurement of NO_3^- uptake by probes in root exclusion cores and in the presence of plant uptake would have provided a more clear indication of both plant uptake and mineralization rates. Despite this, results from the ion exchange membranes were very similar to those measured by KCl extraction and were generally less variable. The ion exchange membranes also provided a measure of nutrient availability over a two week period for each sample compared with a measurement at a single moment in time using the KCl technique. Therefore the ion exchange membrane method using probes was a useful and convenient tool for measuring relative nitrogen availability among treatments. They are less useful, however, in dry soil conditions when low soil moisture limits exchange with the membrane.

Higher soil mineral nitrogen as a result of disturbance was expected (Dormaar et al., 1994; Dormaar and Willms, 1990; Campbell et al., 1975). The duration and magnitude of high N availability will largely depend on the severity of disturbance and the rate of plant community development. Jowkin and Schoenau (1998) found NO_3^- uptake by IEM ranged from roughly 25- to less than 5 ug cm^{-2} 2 $weeks^{-1}$ (i.e., from 250 to 50 ug 10 cm^{-2} 2 $weeks^{-1}$) between May and July on Brown Chernozemic soil. The decline in NO_3^- availability was primarily attributed to increased N uptake by the developing crop. The NO_3^- uptake measurements from Jowkin and Schoenau (1998) are generally higher than that of the rehabilitation treatments or native prairie in this research. The difference was most likely associated with higher mineralization rates resulting from frequent cultivation in conjunction with lower immobilization rates by microorganisms and plants on cropland.

3.4.4 Biogeochemical Nitrogen Cycling As An Indicator Of Succession

Soil NH_4^+:NO_3^- ratio was expected to increase with time from disturbance indicating that the seeded treatments were more advanced in succession than the Natural Recovery treatment. Since there were no significant differences in soil NH_4^+ among the rehabilitation treatments, the change in NH_4^+:NO_3^- can be attributed to the differences in soil NO_3^-. There are three possible explanations for lower soil NO_3^- and therefore a higher NH_4^+:NO_3^- ratio in the seeded treatments compared with Natural Recovery. Rapid plant uptake of NO_3^- in the more competitive seeded treatments and undisturbed prairie may have resulted in lower extractable levels of NO_3^- than found in the Natural Recovery treatment. High plant uptake of NH_4^+ prior to nitrification in the seeded treatments may have resulted in lower extractable levels of NO_3^- than in the Natural Recovery. Alternatively, allelopathic inhibition of nitrification may have reduced NO_3^- availability in conjunction with increased NH_4^+ uptake by plants. A highly competitive environment for N exists in the Control treatment where root biomass was relatively high (Figure 3.2). Very little nitrification would be expected to occur here since high demand combined with higher root density would result in rapid uptake of NH_4^+ before nitrification could occur. Plants would rapidly use any NO_3^- that did form. In the less competitive below ground environment in the rehabilitation treatments with lower root biomass, plant density, and ground cover, nitrification is more likely to occur where interference by plants is lower. This combined with lower plant uptake and suspected higher mineralization rates following disturbance would largely explain the difference between the Control, the seeded treatments, and the Natural Recovery treatment.

Excess availability of NO_3^- may result in undesirable losses of nitrogen from the system by leaching and/or denitrification. Campbell et al. (1975) found that a wheat-fallow crop rotation did not provide sufficient plant uptake potential to prevent substantial loss of nitrate by leaching. They further point out that NO_3^- loss by leaching in the Brown soil zone would be quite possible in fallow years but unlikely in crop years. These results have implications for disturbance management. Potential losses in NO_3^- will increase with the duration that the site remains, or is maintained, in a disturbed state. Due to higher total biomass production, the seeded treatments in this study were clearly more effective in immobilizing mineral nitrogen and reducing potential losses than the Natural Recovery treatment. However, the presence of annual forbs would be expected to provide at least some benefit in preventing leaching losses of NO_3^- from the Natural Recovery treatment as compared with nonvegetated soil.

This research was not designed to determine the presence of allelopathy. However, the increasing NH_4^+:NO_3^- ratio is consistent with patterns in succession attributed to allelopathy. Rice (1984) has summarized considerable literature evidence supporting allelopathic inhibition of nitrification as succession progresses. However, Robertson and Vitousek (1981) did not support the hypothesis that nitrification is inhibited as succession progresses. More detailed study is required of in-situ mineralization and nitrification rates, biochemical interactions between plants and microorganisms, N immobilization by plants and microorganisms, and populations of nitrifying bacteria (Robertson and Vitousek, 1981).

With the increase in nitrogen availability resulting from disturbance, the wellsites could be regarded as temporarily more fertile than the undisturbed prairie. Habitats of high and moderate fertility are most effectively exploited by ruderal and competitive species which have high relative growth rates (Chapin, 1980). A positive correlation between forb biomass and NO_3^- availability was measured supporting this relationship. The abundance of ruderal species (eg. annual forbs) on fertile soils in early secondary succession has been well established (Wilson and Tilman, 1991; Grime, 1977; Odum, 1969; Coupland, 1950; Judd and Jackson, 1939; Chapter 2). Annual forbs typically dominate early secondary succession following disturbance due to their seed longevity in the soil, rapid growth rates, and high and rapid seed production. These characteristics allow the plants to establish quickly following disturbance, and take advantage of low competition for resources (Odum, 1969; Grime, 1977). Ruderal species are expected to have higher N assimilation rates than late successional species due to their life history strategies (McLendon and Redente, 1992; Grime,1977) and associated higher activity of nitrate reductase enzyme (Gebauer et al., 1988; Mengel and Kirkby, 1987). The forb component of the Natural Recovery treatment primarily consisted of annual forbs with few perennials (Chapter 2). The decrease in tissue nitrogen concentration of annual forbs with time was expected because of decreasing nitrogen availability in the presence of grasses (McLendon and Redente, 1992). This was further supported by a positive correlation between forb tissue nitrogen and soil NO_3^- and a negative correlation between grass and forb biomass. These findings are consistent with those of Tilman and Wedin (1991) who found that species capable of reducing soil mineral N the lowest levels in monoculture displaced species that could not reduce N to similarly low levels when grown together.

Tissue nitrogen concentrations of wheatgrasses and non-wheatgrasses were not determined separately. This would have provided an interesting insight into the relative competitiveness of these two groups of species and to further determine if wheatgrass cultivars were exhibiting traits more typical of species adapted to fertile habitats (Chapin, 1980). The wheatgrasses were more competitive than other perennial species (Chapter 2) and probably responded to the relatively high nutrient availability. Wilson and Gerry (1995) found that neighbour-free establishment sites were needed to establish native species in stands of exotic grasses. Under fertilized conditions, low establishment rates of native species were attributed to high cover produced by exotic grasses and annual forbs resulting low light penetration. A positive correlation between grass biomass and NO_3^- availability would typically be expected as demonstrated by extensive rangeland fertilization research. In this research, however, a negative correlation without a decline in biomass indicates that the grasses are reducing an excess supply of nitrogen in the soil. However, the rapid growth and high colonization rates of the wheatgrasses may limit their competitiveness when available nitrogen declines. If this is the case, and the other perennial forbs and grasses can reduce available nitrogen to lower levels than the wheatgrasses, then the other perennial species may replace the wheatgrasses as nitrogen levels decline (Tilman and Wedin, 1991).

This research provides an example of how two or three species can regulate biogeochemical cycling as discussed by Sala et al. (1996). The wheatgrasses clearly dominated plant community composition of the seeded treatments (Chapter 2) and were therefore considered to be the primary species influencing biomass production and available nitrogen. Hooper and Vitousek (1998) also concluded that plant composition explained more about nutrient cycling than did functional group richness even though they found that relative resource use increased with diversity. However, conclusions associated with the relationship between plant diversity and function cannot be drawn due to lack of significant differences between the Diverse treatment and the Current and Simple treatments.

3.4.5 Root Biomass Versus Aboveground Biomass

The difference in root biomass between the Control, the seeded treatments, and the Natural Recovery treatment could be attributed to nitrogen availability. Wilson and Tilman (1995) found that root:shoot ratio of selected annual and perennial species decreased significantly with added nitrogen. Dormaar and Smoliak (1985) suggested that increased aboveground productivity, i.e., lower root:shoot ratio, could be attributed to both the effect of $NH_4^+:NO_3^-$ and increased mineralization due to disturbance. The shift in the plant community from annual forbs (lower root:shoot) to perennial grasses (higher root:shoot) (Chapter 2) may also be partly attributed to competition for nutrients and other resources belowground. Wilson and Tilman (1991) found that plant competition shifted from primarily belowground under low nutrient regimes to both above- and belowground in fertilized plots. Perennial species, with their higher root:shoot ratio than annual species, would be better adapted to lower nutrient regimes and further reduce N levels to below that required by annuals (Wilson and Tilman, 1991; McLendon and Redente 1992).

Root biomass of the Natural Recovery treatment reached approximately 30 % of that in the Control in three growing seasons. These results are comparable to those published by Judd and Weldon (1939). In a study of natural succession following cultivation in western Nebraska, they found that root biomass recovered to 27 % of that on native prairie in three years and to 47 % in 7 years. The accelerated recovery in the seeded rehabilitation treatments in this research (50 % of the Control in three growing seasons) can be attributed to the wheatgrasses (Chapter 2).

Nutrient uptake rate by plants from infertile habitats is generally lower than nutrient uptake rate by plants from fertile habitats (Chapin, 1980). Further, when nutrient availability increases, plants from infertile habitats only slightly increase uptake of nutrients and retain their root:shoot ratio as compared with a large increase in uptake and decrease in root:shoot ratio by species from fertile habitats. Under high nitrogen availability, *A. dasystachyum* increased allocation of biomass and nitrogen to aboveground parts of the plants at the expense of decreasing root biomass and nitrogen (Li et al., 1992). Although the wheatgrass species in this research are native and have originated from prairie ecosystems, they have undergone a process of selection and cultivation. Based on the observed domination of the wheatgrasses (see Chapter 2), one may hypothesize that the wheatgrass cultivars may have acquired some traits more typical of species from fertile habitats. This hypothesis could be tested by comparing plants from cultivars with those grown from wild-type seed.

While there are considerable soil benefits to the rapid root development under the wheatgrasses, continued belowground domination by these species may have a long-term influence on soil properties. A dramatic reduction in soil quality, such as that associated with *Agropyron pectiniforme* (R. & S.) and *Elymus junceus* (Fisch.) (Dormaar et al., 1995), is not expected due to inclusion of the rhizomatous *Agropyron dasystachyum* and *A. smithii* in addition to the bunch grass *A. trachycaulum*. However, differences in chemical properties have previously been attributed to differences in plant community composition (Dormaar and Wilms, 1990). Plant community domination by two or three grasses may alter the composition of the microbial community (Grayston et al., 1991).

3.4.6 Other Environmental Constraints

While nitrogen is an important factor influencing and responding to succession, Dry Mixed Grass prairie is limited by water availability throughout the growing season (Coupland, 1950), and possibly light as seedlings establish. Based on cursory soil water measurements in 1997 (results not presented), water use in the Natural Recovery treatment may be lower than in the seeded treatments. Competition among species for water may have contributed to the shift from annuals to perennials as was also suggested by Judd and Jackson (1939). It is possible that perennial species establishment contributed to the displacement of the annual forbs by producing a combination of environmental constraints. In this research a strong correlation with nitrogen availability was found, however, competition for other resources can also contribute.

3.5 CONCLUSIONS

Wellsite construction on Chernozemic sites lowered soil organic carbon and total nitrogen, and increased soil pH, inorganic carbon, and bulk density. On Solonetzic soils, however, differences were less prominent due to the patches of very poor quality surface soil typically found in blowouts of undisturbed Solonetzic soils. Disturbance of the Solonetzic soils also increased the sodium adsorption ratio of the upper subsoil which should temporarily alleviate some restrictions to plant growth. The reduction in soil quality of Chernozemic sites is expected to eventually result in lower nutrient availability. In the short term, however, high mineralization rates and low plant uptake associated with disturbance resulted in higher soil fertility as measured by increased NO_3^- availability during at least the first three years following disturbance. These conditions supported domination of treatments by annual forbs and competitive species. Differences in NO_3^- availability among treatments were attributed to differences in plant uptake.

The wheatgrasses as a group demonstrated traits typical of competitive species. The seeded treatments, all dominated by wheatgrasses, increased root production, total biomass production, and plant uptake of nitrogen relative to the Natural Recovery treatment. More efficient utilization of resources associated with these attributes was deemed to be an indication of improved biogeochemical cycling and accelerated plant community succession in the seeded treatments as compared with the Natural Recovery treatment.

It was speculated that long-term wheatgrass domination of the plant community would lead to different soil biochemical properties than that for the Natural Recovery treatment and undisturbed prairie. However, competitiveness of the wheatgrasses may also decline as nitrogen supply rates equilibrate to levels below that of undisturbed soils.

Ion exchange membranes were a useful tool for measuring the relative in-situ availability of mineral nitrogen under different disturbance regimes and plant communities in early succession.

The principal contribution of this research was to find a positive interaction between increased nutrient availability resulting from disturbance and performance of wheatgrasses that led to domination of this group over other native species. This domination indicated that under conditions of high fertility, species attributes such as rapid growth rate and colonization were more important than richness and diversity of seed mixes at this early stage of succession on Dry Mixed Grass prairie.

Further research is required for species proposed to be used in seed mixes on Dry Mixed Grass prairie to a) determine their relative response (e.g., establishment rate, growth rate, biomass allocation, competitiveness) under varying environmental conditions, especially

nutrient availability, and b) predict their relative response in seed mixes including other species.

Table 3.1 Species composition of seed mixes used in the rehabilitation treatments.

		Seed Mixes (% PLS)[1]		
Latin name (Authority)	Common Name	Current	Simple	Diverse
Agropyron smithii (Rybd.)	Western wheatgrass	50	10	7
Agropyron dasystachyum ((Hook.) Scribn.)	Northern wheatgrass	30	10	7
Agropyron trachycaulum ((Link) Malte)	Slender wheatgrass	15		7
Stipa viridula (Trin.)	Green needle grass	5		7
Bouteloua gracilis ((HBK) Lag.)	Blue grama grass		30	22
Stipa comata (Trin. & Rupr.)	Needle and thread grass		30	22
Koeleria macrantha ((Ledeb.) J.A. Schultes f.)	June grass		20	7
Oryzopsis hymenoides ((R. & S.) Ricker)	Indian rice grass			7
Elymus canadensis (L.)	Canada wild rye			3
Vicia americana (Muhl.)	American vetch			1.85
Ratibida columnifera ((Nutt.) Wooton & Standl)	prairie coneflower			1.33
Achillea millefolium (L.)	Common yarrow			1.25
Gutierrezia sarothrae ((Pursh) Dunal)	Broom weed			1.17
Petalostemon purpureum ((Vent.) Rybd)	Purple prairie clover			1.17
Aster ericoides (L.)	Tufted white prairie aster			1.08
Solidago missouriensis (Nutt.)	Missouri goldenrod			1.08
Astragalus striatus (Nutt.)	Ascending purple milk vetch			1.00
Gaillardia aristata (Pursh)	Gaillardia			0.33
Petalostemon candidum ((Willd.) Michx.)	White prairie clover			0.33
Geum triflorum (Pursh)	Three-flowered avens			0.33
Hedysarum spp. (L.)	Northern sweetvetch			0.03
Thermopsis rhombifolia ((Nutt.) Richards)	Golden bean			0.03

[1] PLS – Pure live seed.

Table 3.2 Total precipitation (mm) and air temperature at locations near the research sites, (May to September).

	1996	1997	1998	LTA[1]
		Precipitation		
Brooks	192	141	176	218
Bow Island	174	133	195	211
Medicine Hat	172	141	279	207
		Temperature		
Brooks	15.2	16.3	17.1	15.0
Bow Island	16.1	17.1	18.3	16.4
Medicine Hat	15.0	16.7	18.1	16.3

[1] LTA - Long term average (Brooks, 1961-1988; Bow Island and Medicine Hat, 1961-1997).

Table 3.3 Summary of wellsite disturbance impact on soil inorganic C, pH, organic C, total N, bulk density, and sodium adsorption ratio (SAR) for 0 to 10-cm depth increment unless otherwise noted.

	Chernozemic				Solonetzic			
	Control	Wellsite	P>F	SE[1]	Contro	Wellsite	P>F	SE
Reaction (pH)	6.9	7.5	0.00	0.03	6.	7.5	0.15	0.17
Inorganic Carbon (% $CaCO_3^-$ equivalent)								
gravimetric (mass/mass)	0.06	0.33	0.05	0.01	0.1	0.42	0.42	0.02
quantitative (mass/volume)	0.07	0.42	0.05	0.07	0.2	0.55	0.38	0.19
Organic Carbon (%)								
gravimetric (mass/mass)	2.18	1.82	0.06	0.09	1.7	1.79	0.48	0.02
quantitative (mass/volume)	2.43	2.29	0.20	0.06	2.0	2.30	0.02	0.02
Total N (%)								
gravimetric (mass/mass)	0.21	0.17	0.02	0.01	0.1	0.16	0.79	0.00
quantitative (mass/volume)	0.23	0.22	0.02	0.00	0.2	0.21	0.07	0.00
Bulk Density								
Mean	1.12	1.26	0.01	0.02	1.1	1.29	0.01	0.01
Maximum	1.22	1.40	0.03	0.03	1.3	1.37	0.21	0.01
Minimum	1.01	1.15	0.00	0.01	1.0	1.17	0.00	0.00
Sodium Adsorption Ratio								
0 to 10 cm	.	.	.	.	3.4	2.62	0.48	0.59
10 to 20 cm	.	.	.	.	4.5	3.18	0.05	0.19
20 to 40 cm	.	.	.	.	6.5	4.21	0.18	0.70

[1] SE - Standard error.

Table 3.4 Mean dehydrogenase enzyme activity (μg triphenyl formazan g $soil^{-1}$ hr^{-1}).

	Chernozemic		Solonetzic	
Treatment	**1997[1]**	**1998**	**1997**	**1998**
Control	24	116	27	107
Current	17	92	17	81
Diverse	19	104	22	85
Simple	17	113	18	81
Natural Recovery	15	102	20	95
P>F	*0.07*	*0.33*	*0.49*	*0.50*
SE	*2.0*	*8.5*	*3.8*	*11.8*

[1] Treatment means followed by the same letter are not significantly different (LSD, P≤0.05).

Table 3.5 Percent C and N and C:N ratio of grasses and forbs in 1998.[1]

	Chernozemic		Solonetzic	
		Grasses		
	%C	%N	%C	%N
Control	43.8	1.2	43.6	1.6
Current	43.3	1.5	43.4	1.4
Diverse	42.7	1.7	43.8	1.5
Simple	43.4	1.6	43.5	1.3
NR[2]	42.6	1.6	43.2	1.9
P>F	*0.37*	*0.51*	*0.66*	*0.22*
SE[3]	*0.44*	*0.20*	*0.11*	*0.11*
		Forbs		
	%C	%N	%C	%N
Control	42.4	2.0	43.7	2.3
Current	41.5	1.9	44.2	2.0
Diverse	39.2	1.9	43.	2.2
Simple	38.8	2.5	44.57	1.8
NR	38.5	2.1	43.6	2.0
P>F	*0.15*	*0.43*	*0.96*	*0.52*
SE	*1.21*	*0.24*	*0.85*	*0.18*
		C:N		
	Grasses	Forbs	Grasses	Forbs
Control	34.6	21.5	26.6	18.9
Current	29.0	22.2	31.6	22.6
Diverse	27.6	20.1	27.7	20.2
Simple	25.7	16.5	32.9	25.3
NR	27.1	19.3	22.9	23.6
P>F	*0.34*	*0.48*	*0.22*	*0.50*
SE	*3.07*	*2.32*	*2.57*	*2.33*

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[1] No statistically significant differences were measured.

[2] NR – Natural Recovery.

[3] SE – Standard error.

Table 3.6 Mean grass and forb biomass (g 0.1 m^{-2}) in 1998 and change from 1997 to 1998.[1]

	Chernozemic		Solonetzic	
	Grass	Forb	Grass	Forb
		1998		
Control	5.30b	0.95b	2.47b	3.00b
Current	17.61a	4.39b	16.00a	2.89b
Diverse	18.80a	4.22b	18.09a	4.34b
Simple	15.67a	4.82b	14.82a	4.03b
NR[2]	1.56b	17.18a	0.78b	15.15a
P>F	*0.00*	*0.00*	*0.00*	*0.03*
SE[3]	*2.60*	*1.67*	*1.69*	*2.07*
		Change from 1997		
Control	-1.89b	0.26	-0.82	2.79
Current	3.00ab	-1.98	-3.32	2.10
Diverse	7.78ab	-11.89	3.93	-1.47
Simple	11.95a	-11.30	10.59	-0.09
NR	0.97b	0.65	0.61	-4.98
P>F	*0.05*	*0.07*	*0.06*	*0.36*
SE	*2.43*	*3.24*	*2.0*	*2.20*

[1] Treatment means for a variable are not significantly different ($P \leq 0.05$) if followed by the same letter. Absence of letter indicates no significant difference was found.

[2] NR – Natural Recovery.

[3] SE – Standard error.

Table 3.7 Correlation of selected plant C and N variables with mean IEM available NO_3^- of rehabilitation treatments in 1998.

	Chernozemic		Solonetzic	
Parameter	Pearson Correlation	Significance (P, N=16)	Pearson Correlation	Significance (P, N=12)
Forb C:N	-0.62	0.01*	0.00	0.99
Forb N%	0.45	0.08	0.06	0.86
Forb $C_{Biomass}$	0.43	0.09	0.71	0.01*
Forb $N_{Biomass}$	0.66	0.01*	0.73	0.01*
Grass C:N	-0.02	0.93	-0.60	0.04*
Grass N%	-0.02	0.94	0.64	0.03*
Grass $C_{Biomass}$	-0.23	0.39	-0.74	0.01*
Grass $N_{Biomass}$	-0.18	0.52	-0.66	0.02*
Root C:N	-0.17	0.52	-0.15	0.64
Root N %	0.57	0.02*	0.40	0.20
Root $C_{Biomass}$	-0.45	0.08	-0.56	0.06
Root $N_{Biomass}$	-0.38	0.14	-0.52	0.08
Total $C_{Biomass}$	-0.36	0.18	-0.61	0.04*
Total $N_{Biomass}$	-0.08	0.77	-0.47	0.12

* Significant at $P \leq 0.05$.

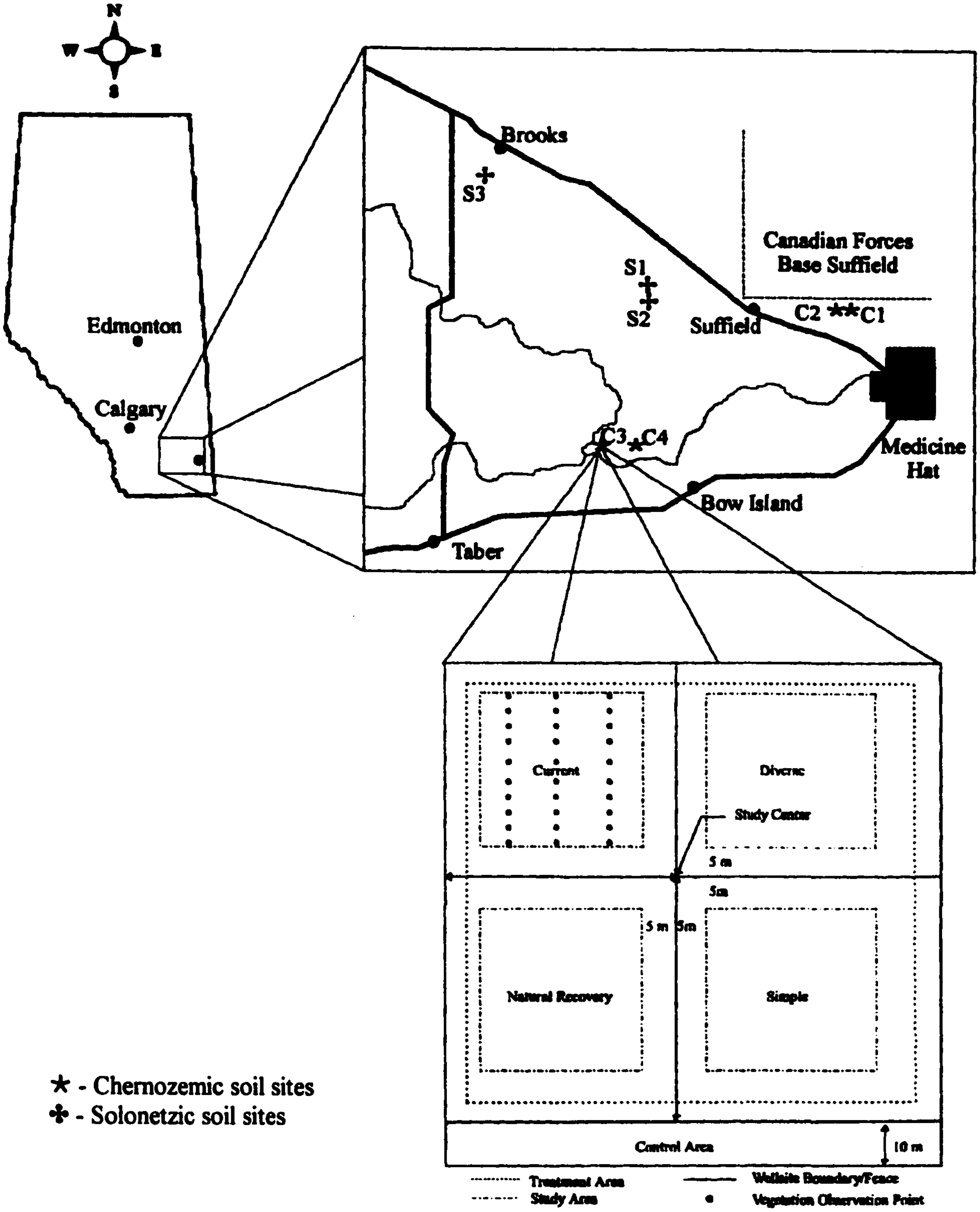

Figure 3.1 Sketch map of study area and an example of treatment layout on study sites.

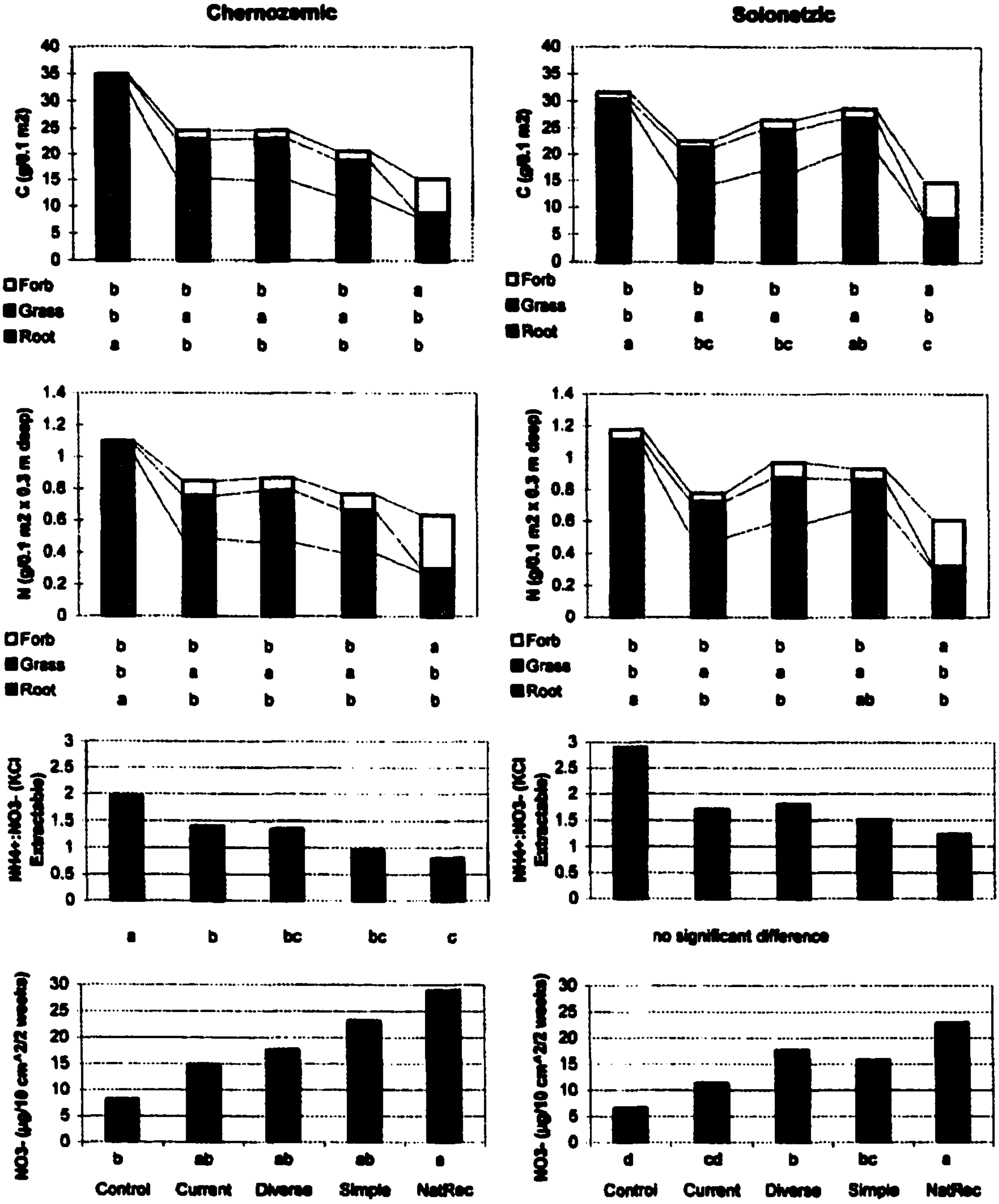

Figure 3.2 Biomass C and N for forbs, grasses and roots (to 0.3 m) (1998); mean NO_3^- for five sample periods by ion exchange membranes in (May and June 1997; May, June, and July 1998); and mean NH_4^+:NO_3^- ratio by KCl extraction over seven sample times (fall 1996; May and fall 1997; May, June, July, and fall 1998); Chernozemic and Solonetzic soil. NatRec – Natural Recovery. Treatments with the same letter are not significantly different ($P \leq 0.05$).

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CHAPTER 4. APPLYING SUCCESSIONAL THEORY TO PETROLEUM WELLSITE REHABILITATION ON DRY MIXED GRASS PRAIRIE IN ALBERTA

4.1 INTRODUCTION

Numerous forms of disturbance threaten the remaining native prairie on the Great Plains. Among these disturbances is the construction and eventual abandonment of petroleum wellsites. From a prairie conservation standpoint, these sites should be returned to a predisturbance community composition. Rehabilitation of these wellsites currently typically includes revegetation with cultivars of native plant species. However, the effect of current disturbance and rehabilitation practices on long-term plant community composition has not been studied. The mechanisms of succession must be identified and placed in the context of successional theory to provide a comprehensive understanding of how the plant community will respond to disturbance and rehabilitation.

Theories, models, and mechanisms of succession are discussed throughout the ecological literature and are often applied to specific ecosystems. Pickett et al. (1987) provided a comprehensive framework of succession focussing on site availability, differential species availability, and differential species performance as the general causes of succession. Contributing mechanisms and factors modifying these mechanisms are also identified. This approach is useful for providing an outline of factors and processes influencing succession following wellsite rehabilitation. It provides a full range of factors that may contribute to succession and allows the applied ecologist to determine which factors are most important.

To aid in understanding successional processes following wellsite rehabilitation, research was conducted on early successional response to three seed mixes and a natural recovery treatment in southeast Alberta (Chapters 2 and 3). The seeded treatments included a wheatgrass (*Agropyron* spp. Gaertn.) cultivar dominated seed mix (Current), a diverse mix consisting of 22 native species (Diverse), and a 5 species mix dominated by perennial non-wheatgrasses (Simple). Wheatgrass cultivars were present in varying amounts in each seeded treatment. The Natural Recovery treatment was characterized by annual forbs dominating the plant community and relatively high soil mineral N (Chapter 3). The seeded wheatgrasses became dominant in all of the seeded treatments despite large differences in seed mix composition (Chapter 2). Lower mineral N levels and a general decline in abundance of non-wheatgrass species in the seeded treatments were attributed to wheatgrass domination (Chapter 2 and 3). Differences between the Natural Recovery and seeded treatments were attributed to differential species availability between the treatments. However, differences in community composition and species response among the seeded treatments were attributed to differential species performance (Chapters 2 and 3).

The objectives of this paper are first to discuss the range of factors influencing succession in the wellsite rehabilitation treatments described in Chapters 2 and 3 and their possible implications for succession, and second to place this discussion in the context of current successional theory. The framework provided by Pickett et al. (1987) will be used to facilitate discussion of factors influencing succession.

4.2 MODELS AND MECHANISMS

Numerous factors may influence the direction of plant community succession following a wellsite disturbance. The predisturbance plant community is a product of centuries of development under varying environmental conditions and exposure to disturbance events such as fire and grazing. Plant communities that establish on the wellsites will be highly dependent on the propagules that survive the disturbance and the nature and proximity of neighbouring propagule sources. However, the plant community is also intricately linked to soil and topography that influence water redistribution and retention, nutrient supply, and other substrate properties. Therefore, the nature of wellsite disturbance impact on soil properties and the landscape will also be important factors directing succession.

4.2.1 Modeling Succession On Rehabilitated Wellsites

A general model illustrating causes and modifying factors of succession in the wellsite rehabilitation treatments is shown in Figure 4.1. The predisturbance plant community (stage S_o, Figure 4.1) was a function of environment and site history. Climate (including topographic influence), grazing, and fire were the primary factors directing plant community development prior to European settlement; however, parent material was the primary factor differentiating the Solonetzic sites from the Chernozemic sites. While many species remained common for both soils, the relative abundance of species differed as a response to soil development from differing parent materials. After European settlement, grazing management and fire suppression strongly influenced community composition. Wellsite construction and rehabilitation were the initial cause of secondary succession on the research sites due to removal of late successional species. Further details of disturbance impact on the soil, plants, and succession are discussed below and are shown in Figure 4.1.

4.2.2 Site Availability

The process of wellsite construction and rehabilitation produces an almost entirely bare soil surface with few if any plants surviving the reconstruction and seedbed preparation process. The size and shape of disturbance can be an important factor influencing migration of propagules, rate of succession, and species composition (Kotanen, 1997). These factors will be most important for succession in this research after the wellsites have been seeded (Figure 4.1). Malanson (1984) suggested that disturbance intensity must also be considered in conjunction with frequency and size. For the wellsites in question, however, the disturbance can be described as a single severe disturbance (from a plant perspective) of moderate size (1 ha). The disturbance is large enough for species relying on vegetative propagules and seeds not dispersed by wind to take a number of years to move to the disturbance centre.

4.2.3 Soil Disturbance Impact

Wellsite construction and rehabilitation had considerable impact on soil properties (Chapter 3). However, were these impacts severe enough to alter ecosystem function, environmental constraints and succession? The resulting soil provides the substrate for community development as indicated in stage S_1 (Figure 4.1). The prevalent soil impacts are related to loss and/or dilution of surface soil by admixing or by altering soil structure. Admixing of surface soil with subsoil may result in lower soil organic matter content, a change in soil texture, and an increase in soil pH depending on subsoil properties and amount of admixing. Approximately 16 % of soil organic carbon in the surface soil was lost as a result of the disturbance (Chapter 3). Losses in soil organic carbon and total nitrogen are expected to result in a reduction in potentially mineralizable N and vegetative productivity (Verity and Anderson, 1990). Dormaar and Smoliak (1985) found that organic C lost in short periods of cultivation of native prairie required several decades to restore soil quality and return to a predisturbance plant community.

Nitrogen availability increased early in succession following disturbance due to increased mineralization and lower plant uptake (Chapter 3). Aboveground biomass production increased as a result, however, lower belowground biomass was expected (Dormaar and Smoliak, 1985). Increased N availability also favours establishment of annual forbs (Chapter 3).

On Solonetzic sites the wellsite construction and rehabilitation process removed the patchiness created by blowouts where subsoil is exposed at the surface. These blowouts have very different soil and hydrologic properties from other parts of the Solonetzic landscape and therefore support a different plant community. The variability typical of the Solonetzic landscape was not present on the rehabilitated sites due to even surface soil replacement. Therefore, organic C levels were higher on average on the wellsite than off (see Chapter 3). In addition, breaking up the impermeable Bnt horizon of this soil and mixing with calcium carbonate from the C horizon may improve soil structure and therefore water infiltration (Chapter 3).

The impact of disturbance on soil physical properties may have severe implications for plant growth. Depending on its severity, soil compaction from construction activities may greatly impede plant rooting, water infiltration and percolation, and soil aeration (Naeth et al., 1991). Community composition, reproductive potential, and productivity may be altered as a result.

4.2.4 Differential Species Availability

In the initial floristics model of succession Egler (1954) suggested that plant community composition during succession will primarily be determined by what species or their propagules are present at the onset of succession. Most species establishing immediately following disturbance originate from seed and to a lesser extent propagules present in the seed bank. Therefore disturbance impact on the seed bank must be considered. Soil salvage on wellsites in this research typically resulted in mixing the entire soil A horizon or a minimum surface soil depth of 10 cm. Since the largest proportion of seeds in the seed bank occurs near the soil surface (Williams, 1984), admixing dilutes or buries the seed bank or portions thereof. On average, less than 20 % admixing occurred on the wellsites in this research (based on organic carbon loss, Chapter 3). This would suggest that less than one fifth of the seeds were lost from the top 10 cm of soil. However, most seed occurs in the top 2.5 cm of the soil (Williams, 1984); mixing of the upper 10 cm would have diluted this seed bank. The survival of seeds and other propagules will also be influenced by the season of disturbance and soil replacement (Froud-Williams et al., 1984), how soil is stored, and how long it is stored. Soil salvage and replacement in the dormant period (winter) may prevent propagules from germinating while in stockpiles. The impact of disturbance on species establishment from the seed bank will be highly species dependent (Froud-Williams et al., 1984; Bazzaz, 1979), however, the loss of seed will delay succession.

Approximately 30 to 35 species were present in the Chernozemic and Solonetzic Natural Recovery treatments in 1997. This amounts to approximately 60 to 70 % of the species richness observed in the Control treatments. This is a good indication of the role of the seed bank. In 1998, however, 10 to 15 species were present in the Natural Recovery treatment that were not present in 1997 (Table 4.1). This may indicate migration to the disturbance and/or establishment of propagules from the seedbank that remained dormant in 1997. On natural recovery wellsites of similar size and shape, Gill Environmental Consulting (1996) found that plant density generally declined with distance inward from the edge of the disturbance. This suggests that migration was an important factor in repopulation of the wellsites in question. However, the relationship between plant density and distance was species dependent and presumably related to reproductive mode as was also suggested by Kotanen (1997).

In the Natural Recovery treatment, community development was greatly influenced by differential species availability in the soil seed bank resulting in annual forb domination immediately following disturbance (Figure 4.1). This can be credited to the life history and reproductive strategies of the annual forbs. Perennial species were not abundant initially, however, their populations were increasing and growth was expected to continue (Chapter 2). While soil disturbance may have affected the rate of succession, the overall impact of the disturbance on species availability and subsequent community composition is not expected to be of primary importance.

Seeding may be considered a form of enhanced migration and therefore accelerates succession, particularly if the seeded species are present in the surrounding landscape. Johnston et al. (1969) found approximately 900 to 1200 viable seeds m^{-2} in the upper 2.5 cm of soil from pastures within the same natural subregion. Seeding 300 pure live seeds m^{-2} of any species adapted to the study region would be expected to have considerable influence on community composition and early succession. In some cases the seed mixes introduced species to the site that were not present in the immediate vicinity but that commonly occur in the region. Such seeding practices may increase the distribution of these species. Seeding would also have had considerable influence on the proportion of viable seed from late successional species, especially grasses, in the seed bank. Once the seed mixes have been planted, the individual and relative performance of each species will ultimately determine the efficacy of this practice and its influence on the outcome of succession. The composition of the seed mix will set the stage for plant community development; however, differential species performance will provide the platform ultimately determining community composition.

4.2.5 Differential Species Performance

The species present in the rehabilitation treatments can be separated into three groups with differing performance, annual forbs and grasses, seeded wheatgrasses, and other perennial forbs and grasses. The traits of these species and their performance in the Natural Recovery and seeded treatments are summarized in Table 4.2 and have been described in Chapters 2 and 3.

In the Natural Recovery treatment, differential availability of species propagules resulted in a high population of annual forbs and few late successional species (Figure 4.1, 1996 to 1997). Therefore, there is little interaction between the annual forbs and perennial species at this early stage of succession. However, gradual increase in the population of late successional species will result in a decline in water and nutrient availability (Chapter 3; Figure 4.1, 1997 to 1998). The annual forbs will not be able to compete and will decline under these conditions. Therefore differential species performance in ecophysiology, life history strategy, and competition will result in succession in the Natural Recovery treatment.

The addition of late successional species in the seeded treatments was expected to accelerate succession simply by increasing the population of these species. Differential species availability in the seed mix favoured the non-wheatgrasses in the Diverse and Simple treatments. However, differential species performance in 1997 and 1998 (Figure 4.1) in establishment rate, growth rate, reproductive strategy, and competition led to rapid suppression of early successional species, and domination of other late successional species by wheatgrass cultivars (Chapters 2 and 3). The ability of the wheatgrasses to compete as gaps fill, resource availability declines, and grazing is introduced remains to be seen. However, at least two of the wheatgrasses are not expected to decline early in succession (Chapter 2).

4.2.6 Nitrogen As An Indicator Of Succession

Resource availability is an important factor contributing to community development. Low competition for light, nutrients, and water is advantageous to species with rapid growth rates such as annual forbs. There was a significant nitrogen response to the rehabilitation treatments with available N declining more rapidly in the seeded treatments. The perceived effect of disturbance, seeding, and succession on N availability is illustrated in Figure 4.2. Disturbance increased N mineralization and reduced plant uptake resulting in an excess supply of N at the initiation of secondary succession. The amount of excess available N declined as N supply (i.e., excess mineralization over microbial immobilization) equilibrated and plant uptake increased. The quickly establishing annual forbs took advantage of high nitrogen availability immediately following disturbance. Rapid increase in grass uptake of N following seeding resulted in a decline in excess N available to annual forbs and presumably a decline in annual forb biomass due to competition (Figure 4.2). The duration of annual forb domination varied among treatments depending on the rate of grass establishment and domination (Figure 4.2).

Whether N availability was a mechanism that directed succession or a reactionary factor responding to it is difficult to ascertain. Pickett et al. (1987, p. 338) define a mechanism of succession as "an interaction that contributes to successional change". Nitrogen availability appeared to be a reactionary environmental factor from the perspective that it responded to soil disturbance and varying plant uptake. Grass biomass was negatively correlated with NO_3^- (Chapter 3) while a positive response would typically be expected. In this case, mineral N was available in excess of demand and increased grass biomass was reducing the surplus. Available N reacted to plant community development and therefore relative N availability among treatments was a good indicator of early succession. Alternatively, wheatgrass regulated decline in N availability and other resources restricted the growth and development of other species. The interaction between the wheatgrasses and other species through competition for N would be described as a mechanism of succession. Annual forb biomass was positively correlated with N availability (Chapter 3). From this perspective, N availability caused succession. Overall, however, mineral N availability reacted to other mechanisms in succession and was not an important mechanism in itself. Significant changes in community composition may occur as N demand begins to exceed supply.

4.3 SUCCESSIONAL THEORY

Numerous theories and hypotheses of succession have been proposed in the last century. Several of these concepts can be used to describe succession on the wellsites.

4.3.1 Tolerance And Inhibition

Connell and Slatyer (1977) presented three models of succession: facilitation, tolerance, and inhibition, which Pickett et al. (1987) later identified as mechanisms of succession. The tolerance mechanism can be viewed as endurance to low resource levels and/or successional turnover due to organisms having contrasting life history strategies (Pickett et al., 1987). The tolerance mechanism appears to be most applicable to this research because perennial grasses were principally responsible for reducing resource availability to levels that were not tolerated by annual forbs (i.e., reaction between stages S_1 and 1998 in Figure 4.1). The life history strategy, whereby the perennial species allocate more resources to root production rather than seed production, provides the perennials with an advantage as resources decline. The tolerance mechanism was observed in all seeded treatments and is expected in the Natural Recovery treatment.

The inhibition mechanism, whereby structural or competitive dominants prevent establishment of later successional species (Pickett et al., 1987), may apply in the wheatgrass dominated seeded treatments. In these treatments it appears that establishment and survival of non-wheatgrass perennial species were in decline. This would indicate that wheatgrasses might remain dominant until some disturbance and/or stress allows the establishment and eventual domination of other species. Both the tolerance and inhibition mechanisms may apply to interactions among different groups of species. However, this conclusion cannot be drawn at this early stage of succession while nutrient supply rates equilibrate and the plant community develops. It is still possible that the wheatgrasses will be displaced as resource availability declines and/or grazing is introduced.

The facilitation mechanism was least applicable because the disturbance impact was not so severe as to leave an environment where most late successional species could not immediately colonize, establish, and survive.

The apparent confusion between the tolerance and inhibition models in the seeded treatments exemplifies the problems with the approach taken by Connell and Slatyer (1977) as described by Pickett et al. (1987). In this case more than one model, as described by Connell and Slatyer (1977), can be applied to the same sere at different stages or in interactions among different species. These results are consistent with generalizations regarding succession made by Pickett et al. (1987) including that: succession may exhibit several mechanisms, different mechanisms of replacement may act in one sere at a given time, one species can participate in several mechanisms, the mechanisms can be discriminated only by determining the demographic and ecophysiological causes of turnover, coordinated work is needed on environmental change and the demography and ecophysiology of successional turnover.

4.3.2 Stable States

In the state and transition model of succession, Laycock (1991) suggested that a plant community may remain in a stable state under a given range of environmental and management conditions. The community will only move out of that stable state and into another if a drastic event alters the environment such that a new community develops and forms another stable state. Such a shift may be a product of changes in climate, drainage, grazing regime, fire frequency, anthropogenic disturbances such as wellsites, or introduction of exotic species. Community composition is expected to shift from season to season with changes in grazing and/or annual precipitation. However, a new stable state has been reached when changes in community composition are not reversed when the source of disturbance is removed. Such shifts in community composition to a new stable state have been observed to occur in overgrazed pastures where *Bouteloua gracilis* (HBK) Lag. (blue grama grass) becomes dominant in a *Stipa-Bouteloua* prairie (Dormaar et al. 1994). Cultivation was necessary to allow the community to return to a more productive *Stipa comata* Trin. & Rupr. (needle and thread grass) dominated community. Seeded stands of exotic *Agropyron pectiniforme* R. & S. (crested wheatgrass) remained in monocultures for decades (Dormaar et al. 1978). Mechanical or chemical disturbance is necessary to displace the exotic species and allow the native species to re-establish (Wilson and Gerry, 1995; Bakker et al. 1997). The process of achieving this new stable state must be a product of the inhibition mechanism described above (Connell and Slatyer, 1977; Pickett et al., 1987).

The wellsite disturbance at each site destroyed all the vegetation and will certainly impact short-term community composition. However, was the disturbance significant enough to move the ecosystem into another stable state, or, will the plant community return to its original composition and state? The possibility of wheatgrass inhibition that would result in a new stable state has already been discussed above. However, the wellsite disturbance may have moved even the Natural Recovery treatment on a trajectory to a new stable state. This will largely depend on the site history that directed the plant community to its predisturbance state. Was the plant community and soil at each site a product of specific historical conditions, and will these conditions be present, if required, to allow the community to return to its predisturbance state? For example, the predisturbance plant community at most wellsites included a large component of *Selaginella densa* Beauv. (little club moss) that is considered to be an indicator of historical heavy grazing pressure. A recovering plant community may not return to its predisturbance *S. densa* composition if it is not subjected to the same grazing pressure. Similarly, the use of seed mixes dominated by competitive cultivars of native species on the wellsite may inhibit establishment of other perennial species and result in a new stable state. A change in plant community composition will also be reflected by a change in the soil microbial community and nutrient cycling. So, the wellsite disturbance and rehabilitation processes may have had sufficient influence on the system at each wellsite to push it across a threshold into a new stable state. Whether or not a new stable state will be achieved for each treatment is difficult to determine at this early stage.

4.3.3 Competition, Stress, and Disturbance

Grime (1977) described three primary strategies of plants: ruderal (R), competitive (C), and stress tolerant (S). Combinations of these strategies may also be used to describe particular species. As previously mentioned, the native prairie was formed under conditions of disturbance in the form of fire and grazing, stress due to climate and limited nutrient availability. Therefore, the plant community would be described as having a C-S-R strategy prior to the wellsite disturbance. Upon wellsite construction and rehabilitation, the site is in a disturbed state suitable for the R-strategists. However, in the absence of continued disturbance the C-S-R strategists that typically dominate the prairie become dominant. The wheatgrass cultivars, however, tend toward a C strategy. They have relatively high aboveground biomass production and seem to have taken advantage of the relatively high availability of resources in the absence of disturbance. Whether the wheatgrass cultivars have sufficient and inherent ability to tolerate stress as resource availability declines will be determined as succession progresses.

4.3.4 Constraints And Tradeoffs

Tilman (1990) suggested that environmental constraints and tradeoffs in species' abilities to deal with these constraints ultimately direct succession. He listed four constraints on plants in successional habitats: access to disturbed sites (colonization), availability of limiting soil resources, availability of light, and sources of loss and mortality (e.g., herbivory, pathogens).

The initial abundance and subsequent replacement of annual forbs by perennial species is consistent with the colonization-nutrient competition hypothesis. The perennial species are better adapted for nutrient competition than the annual forbs but are less well adapted for colonization. Seeding, however, compensated for the lower colonization ability of perennial species, including the wheatgrasses, and accelerated succession from annual forb to perennial species domination. Once the colonization advantage of the annual forbs was lost, competition for nutrients, and possibly other resources, severely inhibited the annual forbs. The vegetative reproductive mode of *Agropyron dasystachyum* (Hook.) Scribn. (northern wheatgrass) was of considerable importance in its spread and high abundance relative to *Stipa comata*, *Koeleria macrantha* (Lebed) J.A. Schultes f. (June grass), and *Bouteloua gracilis*. The advantage of rapid growth rate through vegetative reproduction may decline, however, as nutrient competition increases. Therefore, the colonization-nutrient competition may also apply to this interaction.

Although emphasis was placed on nitrogen in this research, factors such as light, water, grazing, and other sources of mortality may also influence succession (Tilman, 1990). On Dry Mixed grass prairie, light is less important as a limiting factor because the plants are generally shorter growing and also restricted in height by grazing. However some taller annual forbs and grasses may produce a closed canopy if they dominate the site. In addition, litter production will shade the soil surface and may prevent seeds of some species from germinating and/or establishing. Water availability is another limiting factor in this ecosystem and competition for this resource may also have resulted in exclusion of annual forbs. Livestock grazing was excluded from the wellsites in the first three growing seasons. A three-way hypothesis of succession could be formulated (colonization-nutrient competition-herbivory hypothesis) if grazing was permitted in the research.

Tilman (1990) also discusses tradeoffs in maximal growth rate and nutrient competition. The rapid establishment of annual forbs and wheatgrasses is representative of this tradeoff since these species will decline with resource availability. *Agropyron trachycaulum* (Link) Malte (slender wheatgrass) is similar in this respect because it establishes quickly and but is expected to decline with increased competition for resources.

4.4 SUMMARY

The framework of the general causes of succession presented by Pickett et al. (1987) was a useful tool for identifying the broad range of factors contributing to succession following a wellsite disturbance. A number of these factors may have had little or no modifying influence on early succession; however, they may influence biogeochemical cycling and therefore community composition and development in the long-term. The prevalent mechanisms in early succession were differential species availability (in the seed bank or seeded) and differential species performance in terms of establishment, growth rate, resource allocation, life history strategy, competition, and reproductive mode.

The concept of succession is very complex and numerous approaches can be taken to describe community development. There is increasing recognition of the complexity of succession in the literature and single hypotheses are unlikely to completely explain succession at any one site. A number of successional hypotheses and models could be applied to this research. Each approach explained at least some part of early succession or could be used to develop hypotheses related to the eventual outcomes of the various rehabilitation treatments.

Table 4.1 Total species richness in the Natural Recovery and Control treatments in 1997 and 1998.

Total Number Species	Chernozemic	Solonetzic
Control	56	50
Natural Recovery 1997	35	34
Natural Recovery 1998	43	37
Natural Recovery only in 1998[1]	15	12

[1] Number of species present in 1998 that were not present in 1997.

Table 4.2 Traits and early successional role of annual forbs, seeded wheatgrasses, and other perennial species in wellsite rehabilitation treatments on Dry Mixed Grass prairie.

Plant Group	Traits	Natural Recovery	Seeded Treatments
Annual forbs	• Short lifespan, one growing season • Abundant in seed bank • Rapid establishment • High seed production • Low root biomass • High tissue N content • Low tolerance to competition	• Dominant immediately following disturbance • Gradual decline anticipated as perennial species establish and resources become limiting	• Initially abundant especially in the Diverse and Simple treatments • Low abundance in Current treatment • Biomass negatively correlated with grass biomass
Seeded wheatgrasses	• Perennial species with life expectance >4 years • Rapid establishment • Moderate to low seed production • Some species with vegetative reproduction • Moderate allocation to roots when resources abundant • Moderate allocation aboveground	• Not applicable	• Rapid establishment and spread • *Agropyron trachycaulum* reproduced by seed but expected to decline within 10 years • *Agropyron dasystachyum* spread very rapidly by rhizomes • *Agropyron smithii* established more slowly but spreading by rhizomes • Appear to inhibit establishment of other perennial species
Other perennial species	• Perennial species with long life expectancy • Slow establishment • Low seed production • High resource allocation to roots • Vegetative reproductive capacity minimal or absent • Low resource allocation aboveground	• Initially not abundant • Tolerate early competition with annual forbs • Slow population growth by seed production and migration • Expected to displace annual forbs	• Seeded but dominated by wheatgrasses due to low establishment rate and slow population growth • Wheatgrass competition appear to inhibit their survival

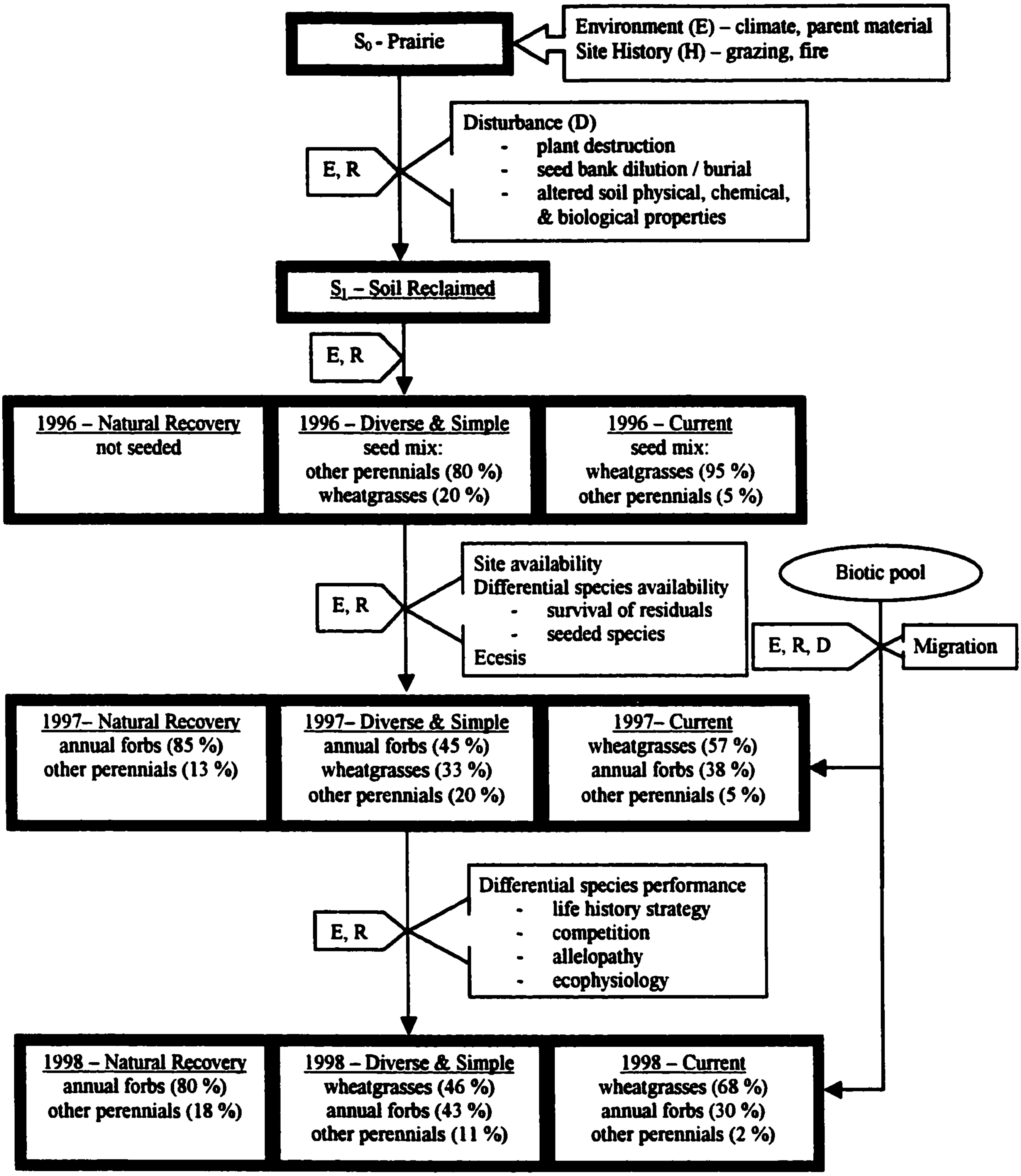

Figure 4.1 Early successional model of wellsite rehabilitation treatments. Seed mix composition (1996) and importance values (1997 and 1998) presented for each plant group are approximated (see Chapter 2). Causes of succession include disturbance, site availability, differential species availability, and differential species performance. Modifying factors include environment (E), reaction (R), and disturbance (D). (Model modified from MacMahon (1980) as presented by Pickett et al. (1987).)

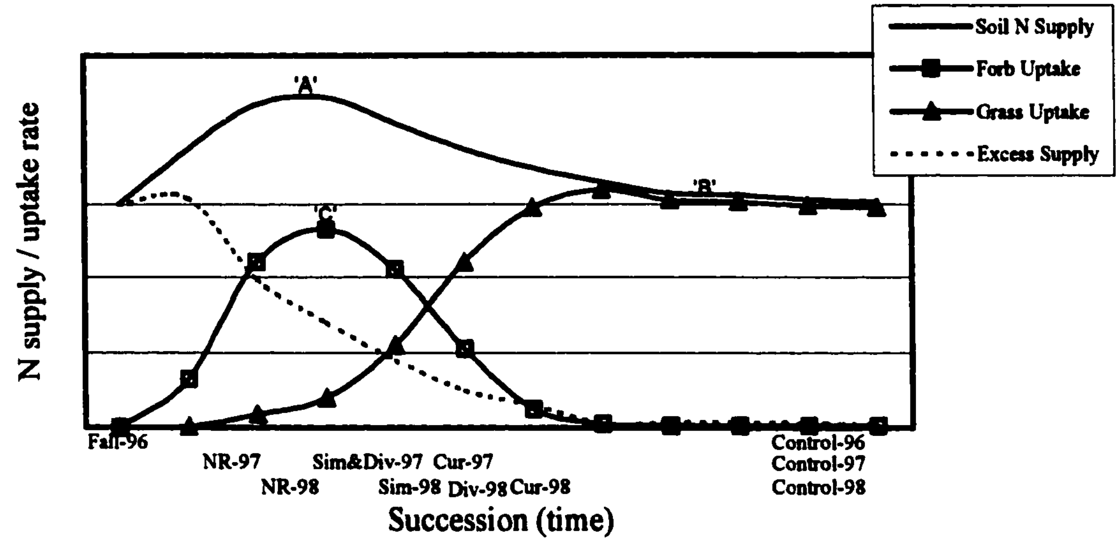

Figure 4.2 Suggested pattern of nitrogen supply, availability, and uptake with time for wellsite rehabilitation treatments on Dry Mixed Grass prairie. Fall-96 represents the approximate starting point for all treatments where plant uptake is negligible but where disturbance resulted in increased availability of N. Subsequent years of the research and relative position of the treatments along the successional coninuum are presented on the second and third rows of the x-axis. 'A' is the point of maximum N supply (i.e., excess mineralization over microbial immobilization) beyond which N supply begins to decline as it equilibrates to predisturbance levels 'B'. In the absence of competition with grasses, the annual forbs achieve maximum N uptake at 'C'. With grass establishment, however, competition gradually reduces excess N supply to levels below that required by annual forbs. Annual forb biomass and therefore N uptake declines at this point. Treatments and year designated by NR-Natural Recovery, Cur-Current, Div-Diverse, Sim-Simple. Note: figure for illustration purposes only, not based on actual data.

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CHAPTER 5. REHABILITATION PLANNING AND SUCCESS ON ABANDONED PETROLEUM WELLSITES IN SOUTHEASTERN ALBERTA

5.1 INTRODUCTION

Currently, there is considerable interest in the rehabilitation of natural ecosystems due to their continued disturbance or loss to industrial and urban development. Seed mix design is one of the most challenging aspects of rehabilitation planning. Rehabilitation planners must determine seed mix composition considering whether exotic or native species should be used, species richness, if forbs should be included, if cultivars, ecological varieties, or wild type native seed should be used, and the proportion of each species. Many of these decisions relate to the management objectives and/or goals of rehabilitation. Successful seed mix design must link value based management objectives with functional attributes of ecosystems. Functional attributes of ecosystems will, in turn, be regulated by the structural and compositional attributes of the plant community.

Alberta Environmental Protection (1995, p.33) developed reclamation criteria for oil and gas wellsites on grasslands that indicated, "Revegetation species and species composition should be compatible with original or control vegetation or meet reasonable land management objectives". On Crown Land, this has generally meant that native plant species must be used to revegetate sites on native prairie. Most petroleum companies began to use cultivars of native wheatgrasses (*Agropyron trachycaulum* Link., *Agropyron dasystachyum* Hook., and *Agropyron smithii* Rydb.) and green needle grass (*Stipa viridula* Trin.) in combination with other species to revegetate their wellsites. These native cultivars, had been selected for high and rapid establishment rates, and high biomass production. The compatibility of these cultivars with wild varieties has been questioned as they appeared to dominate the revegetated wellsites. Concern related to whether the original or predisturbance community composition would return following revegetation with cultivars.

This is an applied discussion paper with its first objective to introduce a four-step process for identifying ecosystem attributes that will fulfill management objectives, assist in seed mix design and ultimately promote rehabilitation success. Secondly, results from the prairie rehabilitation research described in Chapters 2 and 3 will be used as an example to discuss the relative effectiveness of different seeding treatments in fulfilling management objectives.

5.2 FUNCTIONAL GOALS AND ATTRIBUTES OF DRY MIXED GRASS NATIVE PRAIRIE

Connecting management objectives with functional attributes of ecosystems can be accomplished in a four step process that involves describing environmental limitations, identifying management objectives, determining what functional attributes of ecosystems are needed, and determining what structural/compositional attributes of the ecosystem will produce the desired functional attributes. The results of such a process for uplands in Dry Mixed Grass prairie are discussed below and listed in Table 5.1.

5.2.1 Step 1 - Understanding Environmental Limitations

The first step in ecosystem rehabilitation is to identify critical processes that regulate or determine the nature of the ecosystem in question. For Dry Mixed Grass prairie, these have been divided into primary processes, those that ultimately determined the nature of the ecosystem present, and secondary processes, that limit resource availability or community characteristics (Step 1, Table 1). Climate, fire, and grazing are considered to be the primary factors producing the inherent characteristics of grassland ecosystems (Sala et al., 1996).

Secondary factors such as nutrient cycling may influence the overall ability of the system to fulfill management objectives within the limitations of the primary factors. For example, organic matter decomposition progresses at a relatively slow rate under dry and seasonally cool conditions. Availability of nutrients, especially N, would then be limited for plant growth. Invasion and dominance of exotic species may result in less diverse ecosystems, impair species conservation efforts, and/or alter ecosystem function (Romo and Grilz, 1990). Inherent soil properties may also influence the nature of the plant community and resource capture (Reynolds et al., 1997).

5.2.2 Step 2 - Defining Management Objectives

Management objectives for Dry Mixed Grass prairie rehabilitation can be divided into the categories of ecological and 'others' (Step 2, Table 1) (see also Walker, 1992). The ecological objectives of management have been sub-divided into functional and structural/compositional groups. The 'others' category has been sub-divided into commodity/services, amenity, and moral groups. These objectives will vary with the nature of disturbance and the ecosystem, and societal values.

The functional management objectives emphasize efficient use of resources and a self-sustaining ecosystem. An ecosystem that efficiently captures energy, nutrients, and water will be more productive and stable in the event of disturbance or stress. The structural/compositional objectives emphasize returning the plant community to a native prairie condition similar to that surrounding the disturbance.

Some management objectives may be complimentary while others may not be fully compatible. For example, exotic species may be highly productive, however, they may not be self-sustaining. Therefore either priority must be set or a compromise must be reached. In this case, a self-sustaining ecosystem that is inherently productive within the limitations of the ecosystem is desired. Objectives that are mutually exclusive should not be assigned to the same land area.

5.2.3 Step 3 - Identifying Desirable Functional Attributes - Assigning Values

A rehabilitation planner's vision of a properly functioning ecosystem varies depending on how understanding of ecosystem function is integrated with societal values. An example would be questioning whether a highly productive system with rapid biogeochemical cycling functions more effectively than a less productive system that cycles slowly. The answer to this question greatly depends on predetermined land management objectives. Highly productive ecosystems are typically associated with rapid biogeochemical cycling (Odum, 1969). Conversely, ecosystems with a high capacity to entrap and hold nutrients for internal cycling are more likely to be self-sustaining and stable although less productive. Based on the limitations of Dry Mixed Grass prairie (Step 1, Table 5.1), it would be unlikely that high productivity could be sustained without additional inputs of water and nutrients. As such, a self-sustaining, stable ecosystem becomes a priority over maximizing productivity.

Functional properties of ecosystems can be divided into universal functions and endogenous properties accruing from function (Woodward, 1994). The functional management objectives identified in Step 2 (Table 5.1) include both universal functions and endogenous properties. These objectives emphasize efficient use of resources, self-sustainability, stability, and productivity (Step 1, Table 1). Since stability, productivity, and self-sustainability are endogenous properties accruing from universal functions, it becomes apparent that we should be managing the universal functions (i.e., energy flow and biogeochemical cycling) to fulfill functional management objectives (Step 3, Table 1).

5.2.4 Step 4 - Linking Function with Structure And Composition

The next step in rehabilitation planning is to identify the compositional and structural attributes of the plant community that provide the desired universal functions and endogenous properties (Step 4, Table 5.1). A seed mix must be designed from these structural and compositional attributes. Herein lies the question of whether or not the wheatgrass dominated seed mixes discussed above will provide the universal functions and fulfill the management objectives. Many of the structural and compositional attributes are associated with diversity in plant community composition. Alternatively, perhaps low diversity seed mixes will initially stabilize a site but eventually allow a more diverse plant community to develop. The research described in Chapters 2 to 4 was conducted to address these questions and is summarized below. In addition, the rehabilitation treatments that were studied are ranked in terms of their overall effectiveness in fulfilling various management objectives.

5.3 TESTING THE ECOLOGICAL DESIGN OF SEED MIXES – AN EXAMPLE

5.3.1 Description Of Research

Field research was initiated to test the effectiveness of three seed mixes and natural recovery in meeting management objectives. Detailed methods, results, and conclusions are presented in Chapters 2 and 3 but are summarized below. A total of seven drilled and abandoned wellsites were selected on Orthic Brown Chernozemic and Brown Solodized Solonetzic soil in the Dry Mixed Grass region of southeast Alberta. Topsoil and subsoil were removed prior to drilling and replaced upon site abandonment. Four rehabilitation treatments were applied to each wellsite including three seeded treatments and a nonseeded Natural Recovery treatment. The seeded treatments included a seed mix heavily dominated by three wheatgrasses (Current), a diverse mix consisting of 21 species (Diverse), and a five species mix dominated by perennial non-wheatgrasses (Simple) (Table 5.2). Approximately 20 % of the Diverse and Simple seed mixes consisted of wheatgrasses. All treatments were seeded at a rate of 300 pure live seeds per m^2. Overall seeding rates were reduced to approximately 50 % (i.e., to 300 pure live seeds per m^2)of that typically used by industry at the time the research was initiated. Seeding rates were lowered to reduce the perceived competitiveness of the wheatgrass cultivars and allow other perennial species to establish hence increasing diversity and similarity. As measures of plant community composition, species richness, diversity, and similarity to a non-disturbed Control area adjacent to each wellsite were calculated from species density, canopy cover, frequency, and ground cover estimates (Chapter 2). In addition, soil available nitrogen (N), above and below ground plant biomass, and nitrogen uptake by plants were measured as indicators of biogeochemical cycling (Chapter 3). From a practical perspective, cost and availability of species in the seed mixes were noted.

5.3.2 Summary Of Results And Conclusions

Rehabilitation success depended on the effectiveness of the plant community and its attributes in providing the universal functions needed to fulfill the management objectives. Based on Table 5.1, the key plant community traits that would fulfill these objectives related to diversity and the ability to capture resources efficiently. Return of the plant community to a predisturbance composition was considered desirable with the assumption that the undisturbed system was stable.

After three years, few statistically significant differences were found among treatments that were seeded. Lowering the seeding rate of wheatgrasses was, in itself, not effective in increasing diversity and similarity through establishment of non-wheatgrass perennials in the seeded treatments. To the contrary, the wheatgrass cultivars dominated plant community development and suppressed establishment of other species. Dominance was attributed to higher wheatgrass performance in terms of establishment rate, growth rate, life history strategy, competition, and reproduction. The Diverse treatment did not significantly increase community diversity and similarity to undisturbed prairie. However, species richness of an entire treatment area was higher in the Diverse treatment than in the Current treatment on Chernozemic sites; species richness was significantly lower in the Current treatment than the Control on both soils. In 0.1 m^2 quadrats, however, there were no differences in species richness among any treatments. This difference is important because it is diversity at this smaller scale where interactions among plants and the environment take place. In contrast to the seeded treatments, the plant community of the Natural recovery treatment was characterized by annual forb domination and slow but increasing perennial species establishment. From this perspective the seeded treatments were more effective establishing perennial species cover. However, the perennial species establishing in the Natural Recovery treatment were typically not wheatgrasses, rather, species more representative of the undisturbed Control. These species were decreasing in abundance in most of the seeded treatments. If this trend continues, the Natural Recovery treatment may reach a plant community composition similar to the Control more rapidly than the seeded treatments.

Soil disturbance during wellsite construction and rehabilitation increased nitrate availability relative to the undisturbed Control. Among the rehabilitation treatments soil nitrate was highest in Natural Recovery and lowest in the Current treatment. Soil nitrate was positively correlated with annual forb biomass which was negatively correlated with grass biomass. Total nitrogen uptake by plants was 18 to 37 % lower in the Natural Recovery treatment than in the seeded treatments and total carbon was up to 50 % lower in the Natural Recovery. From this perspective, seeding was more effective in sequestering energy and nutrients. However, there were no statistically significant differences among the seeded treatments.

After three years, the principal conclusions were: a) species attributes were more important than seed mix diversity for plant community development, b) with relatively high nitrogen availability, wheatgrass cultivars suppressed establishment of other species, c) seeded treatments accelerated recovery of biogeochemical cycling relative to natural recovery, d) natural recovery was most effective in initiating community development towards a predisturbance condition. Further research is required that predicts the relative performance attributes of seed mix species.

The importance and magnitude of species establishment and reproduction rates were underestimated in this research and seed mix design based only on viability or germination rates may not be effective. Alternatively, seed mixes may need to be designed considering in-field establishment rates, competitiveness relative to other species in the seed mix, and reproductive spread. However, these traits may be difficult to predict. Mixing of non-compatible species should be avoided or carefully planned to meet rehabilitation objectives. Although the Simple and Diverse treatments have initially been successful in establishing perennial non-wheatgrass species relative to the Current treatment, the magnitude of this success was small and its duration is questionable. The effectiveness of a diverse seed mix in increasing plant community similarity to the Control could be improved by site specific planning of seed mixes.

5.3.2.1 Cost Analysis Of Treatments

Seed cost is an important factor influencing seed mix design. Seed cost varies considerably by species (Table 5.3) and is greatly influenced by availability. Cost effectiveness of individual species depends on revegetation goals, characteristics of each species, and success of seedling establishment under varying seedbed conditions. The cost per unit area of each seed mix (Table 5.4) was calculated based on seeding rates used in this research and 1996 prices (Table 5.2). The Current mix was least expensive on both a weight basis and unit area basis. The cost of the Simple and Diverse mixes were similar on a weight basis, however, the Diverse mix was much more expensive on a unit area basis because of the high percentage of large seeded grasses and forbs. Based on the price of seed used in this research (Table 5.4) the Current treatment may meet the reclamation criteria at a lower cost than the Diverse or Simple. While seed cost may be prohibitive at this time, this should not preclude the use of diverse seed mixes in the future. If demand is sustained then supplies will increase, production practices will improve and cost will decline.

5.3.2.2 Treatment Ranking

The ranking of the rehabilitation treatments was based on their effectiveness in meeting four objectives: reclamation criteria (see Appendix C), efficiency in using resources (based on the four-step process outlined in Table 5.1), plant community similarity to surrounding un-disturbed Control areas, and practical considerations (Table 5.5). The treatments were qualitatively ranked in each factor based on several different variables, many of which were measurements of plant community or soil properties. Statistically significant differences were not found among treatments for many of the variables measured (see Chapters 2 and 3). However, lack of statistically significant differences do not necessarily imply that differences were not biologically significant as was discussed in early chapters. Therefore, the qualitative rankings were based on observed trends among treatments which in most cases were consistent with measured differences (but that were not necessarily statistically significant). For comparison purposes, rankings for each variable were also calculated using statistical significance to differentiate between treatments. The overall rankings for each objective based on statistical analyses are provided in parentheses in Table 5.5.

The Diverse treatment received the highest ranking among the rehabilitation treatments for all objectives except practicality (Table 5.5). On a subjective basis, the Diverse treatment was differentiated from the Current treatment by higher diversity, richness, and similarity to the Control and from the Simple treatment biomass production. However, benefits of high seed mix diversity and richness were not clearly demonstrated. High biomass production and resource capture were primarily a result of the wheatgrasses; these attributes could have been achieved equally as well with a low diversity seed mix. The higher diversity and richness of the Diverse treatment was related to seed mix diversity, however, lack of statistically significant differences and a trend toward decreasing diversity and similarity to the Control indicate that these benefits may not continue to exist as the treatments develop. Based on three years of plant community development, the diverse treatment would have been better served by a much lower composition or removal of aggressive wheatgrass cultivars. However, long-term trends and the response of this treatment to grazing pressure have not been investigated. Although it received the highest ranking, the feasibility of using a high diversity seed mix is presently restricted by seed cost and availability.

The Natural Recovery treatment had a low ranking for each objective (Table 5.5). This was a result of a low rate of perennial species increase in abundance and related low biomass production, nutrient capture, similarity to the Control, and compatibility with surrounding land uses. This low ranking, however, should not be regarded as an indication of a low long-term potential of this treatment returning to a predisturbance condition. In contrast with the seeded treatments, abundance of perennial non-wheatgrass species was increasing. These trends are consistent with those observed for natural revegetation of abandoned cultivated lands in Alberta (Dormaar et al. 1994). The Native Plant Working Group (1999) has indicated that natural recovery could be used where there is low risk of erosion and invasion of weedy species, on good or excellent condition rangeland, where the disturbance is less than 300 m wide, and when appropriate seed mixes were not available. The Current and Simple treatments were of intermediate ranking with differences primarily related to plant community similarity to the Control and biomass production (Table 5.5).

From the perspective of statistically significant differences, the seeded treatments were equally and of higher rank than the Natural Recovery treatment for the reclamation and nutrient and energy capture objectives (Table 5.5). The lack of difference among the seeded treatments is attributed to the influence of wheatgrass domination in each treatment. From a plant community perspective, however, the Natural Recovery treatment received the highest ranking and the Current the lowest. Natural Recovery was ranked higher than the Diverse and Simple treatments primarily because of observed trends in abundance of perennial non-wheatgrass species. The low ranking for the Current treatment was related to species richness and plant community similarity to the Control.

The Current treatment received the highest ranking from a practical perspective due to low cost, high seed availability, and short time frame for certification.

5.4 SUMMARY

A four-step process can be used to identify the structural/compositional attributes of an ecosystem that fulfill management objectives. However, determining the species composition of seed mixes that will provide the desired structural and compositional attributes can be complicated. When planning seed mixes for a specific community composition, differential species performance following seeding must be adjusted for. However, information related to the relative performance of species in mixes and under different environmental conditions is not readily available.

On wellsites in Dry Mixed Grass prairie, the performance of wheatgrass cultivars was underestimated when in mixes with other native species from wild sources. As a result, a diverse seed mix provided little additional benefit toward fulfilling ecological management objectives compared with less diverse seed mixes. Natural recovery was least successful primarily due to slow plant community development but showed highest potential for returning the plant community to a predisturbance composition.

Based on this discussion, seed mix design requires an integration of management objectives, desired attributes of the ecosystem, relative performance and attributes of species, and environmental conditions when seeding.

Table 5.1 Four step process for determining desirable plant community characteristics for Dry Mixed Grass prairie rehabilitation.

Step 1. Factors Regulating the Dry Mixed Grass Prairie Ecosystem

Primary[1]	Secondary
1. Low precipitation:evaporation ratio → periodic drought	1. Slow soil development related to climate → biogeochemical cycling restricted
2. Seasonally cold temperatures	2. Geology → relatively young glacial deposits (~10, 000 yrs old), some areas saline
3. Fire	3. Recent agricultural & industrial disturbance
4. Grazing	4. Recent invasion of exotic species

Step 2. Management Objectives for Dry Mixed Grass Native Prairie

1. Ecological Objectives[2]
    - a. Function
        - Efficient capture, use, and conservation of resources; carbon sink
        - Prevention of ecological degradation (erosion, organic matter loss, nutrient loss)
        - Stable ecosystem, in dynamic equilibrium with the environment; self-sustaining
    - b. Structure/Composition
        - Similar community composition, structure, and diversity as prior to disturbance
        - Conservation of genetic pool to permit adaptation to changing environment
2. Other Objectives
    - a. Commodity/Services
        - Conserve genetic pool for use by future generations
        - Multiple land use (grazing, wildlife, tourism)
    - b. Amenity
        - Should consist of native species and blend with surrounding landscape
        - Should have similar diversity and habitat for wildlife as prior to disturbance
    - c. Moral
        - Obligation to rehabilitate land to a pre-disturbance condition and conserve rare species

Steps 3 and 4. Ecosystem Attributes Fulfilling Management Objectives

3. Universal Functions[3]	4. Associated Structural/Compositional Attributes
a. Efficient energy capture and use (photosynthesis, respiration ≅ 1:1) b. Efficient water capture, use, & conservation c. Efficient nutrient capture, use, & conservation	a. Structural and physiological diversity b. High ground cover, low shoot:root ratio c. Diverse phenology d. Functional group diversity
Endogenous Properties Resulting From Function	
a. Stability, dynamic equilibrium	a. Species diversity, functional group diversity b. Diverse rooting and resource capture strategies c. Diverse reproductive strategies, d. Presence of disturbance/stress tolerant species
b. Occasional fire	a. Litter build-up
c. Exclusion of invading species	a. Minimize bare ground b. Broad range and efficient resource niche utilization
d. High forage supply	a. Diverse supply in terms of quality and quantity b. Diverse phenology c. Drought and grazing tolerance

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[1] Primary factors identified by Sala et al. (1996).

[2] Modified from Walker (1992).

[3] Modified from Woodward (1994).

Table 5.2 Species composition of seed mixes used in the rehabilitation treatments.

		Seed Mixes (% PLS)[1]		
Latin name (Authority)	**Common Name**	**Current**	**Simple**	**Diverse**
Agropyron smithii (Rybd.)	Western wheatgrass	50	10	7
Agropyron dasystachyum ((Hook.) Scribn.)	Northern wheatgrass	30	10	7
Agropyron trachycaulum ((Link) Malte)	Slender wheatgrass	15		7
Stipa viridula (Trin.)	Green needle grass	5		7
Bouteloua gracilis ((HBK) Lag.)	Blue grama grass		30	22
Stipa comata (Trin. & Rupr.)	Needle and thread grass		30	22
Koeleria macrantha ((Ledeb.) J.A. Schultes f.)	June grass		20	7
Oryzopsis hymenoides ((R. & S.) Ricker)	Indian rice grass			7
Elymus canadensis (L.)	Canada wild rye			3
Vicia americana (Muhl.)	American vetch			1.85
Ratibida colmunifera ((Nutt.) Wooton & Standl)	Prairie coneflower			1.33
Achillea millefolium (L.)	Common yarrow			1.25
Gutierrezia sarothrae ((Pursh) Dunal)	Broom weed			1.17
Petalostemon purpureum ((Vent.) Rybd)	Purple prairie clover			1.17
Aster ericoides (L.)	Tufted white prairie aster			1.08
Solidago missouriensis (Nutt.)	Missouri goldenrod			1.08
Astragalus striatus (Nutt.)	Ascending purple milk vetch			1.00
Gaillardia aristata (Pursh)	Gaillardia			0.33
Petalostemon candidum ((Willd.) Michx.)	White prairie clover			0.33
Geum triflorum (Pursh)	Three-flowered avens			0.33
Hedysarum spp. (L.)	Northern sweetvetch			0.03
Thermopsis rhombifolia ((Nutt.) Richards)	Golden bean			0.03

[1] PLS – Pure live seed.

Table 5.3 Price of seed mix species in 1996.

	$/kg	Seeds/kg	$/100,000 Seeds
Grasses			
Slender wheatgrass (Adanac)[1]	5.95	350,000	1.70
Indian rice grass	13.23	310,000	4.27
Green needle grass	21.72	400,000	5.43
Western wheatgrass (Walsh)[1]	22.80	240,000	9.50
Blue grama grass	26.57	1,820,000	1.46
Northern wheatgrass (Critana)[1]	28.95	340,000	8.51
June Grass	44.10	5,100,000	0.86
Canada wild rye[1]	62.00	200,000	31.00
Needle and thread grass	136.71	250,000	54.68
Forbs			
American vetch[2]	132.00	60,000	220.00
White prairie clover	132.00	312,000	42.31
Purple prairie clover	132.00	312,000	42.31
Prairie coneflower	178.00	1,250,000	14.24
Broomweed	178.00	2,000,000	8.90
Missouri goldenrod	178.00	500,000	35.60
Three-flowered avens	178.00	555,000	32.07
Golden bean	178.00	65,000	273.85
Ascending purple milk vetch	178.00	1,000,000	17.80
Sweet vetch	200.00	70,000	285.71
Yarrow	220.00	6,100,000	3.61
Blanket flower	220.00	250,000	88.00
Tufted white prairie aster	330.00	555,000	59.46

[1] This seed donated, prices estimated.

[2] Assumed price of American Vetch = $132.00/kg. Actual cost not available.

Table 5.4 Cost of seed mixes.

Seed Mix[1]	\$/kg	\$/ha
Current	22.21	239.83
Simple	80.07	598.12
Diverse	83.63	805.35

[1] All seed mix costs based on mixes and seed prices described in Table 5.3.

Table 5.5 Qualitative ranking[1] of wellsite rehabilitation treatments on Dry Mixed Grass Prairie.

Objective / variable	Current[2]	Diverse[3]	Simple	NR	Comments
1. Reclamation Criteria (overall)	2 (1)	1 (1)	3 (1)	4 (2)	Diverse and Current were most effective in meeting the criteria primarily due to the high productivity of wheatgrasses (especially northern and slender wheatgrass).
species compatibility with Control composition	4	2	2	2	Emphasis placed on presence of perennial non-wheatgrass species that were least abundant in the Current treatment, Low but increasing in the Natural Recovery treatment, and declining in the Diverse and Simple treatments.
species compatibility with land management objectives	2	1	3	4	Emphasis placed on potential as a grazing end land use and therefore grass biomass production.
density (perennial species)	1	2	3	4	Annual forb species density excluded due to their temporary influence. Total density, including annual forbs, would be highest in the Natural Recovery treatment.
height and health	-	-	-	-	Height not determined, however, growth not restricted by contaminants and generally not by compaction.
cover (bare ground)	1	2	3	4	Heavy litter production contributed significantly to ground cover in 1998.
2. Nutrient & Energy Capture (overall)	2 (1)	1 (1)	2 (1)	4 (2)	Seeded treatments were most effective in resource capture primarily due to the high productivity of wheatgrasses (especially northern and slender wheatgrass). Open spaces not occupied by grasses were filled by annual forbs in the Diverse and Simple treatments.
aboveground biomass	2	1	2	4	Combined grass and annual forb production was highest in the Diverse treatment by 1998.
root biomass	1	1	1	4	Root biomass increased by presence of seeded perennials.
soil nitrogen availability	1	2	3	4	Aggressive uptake and storage of mineral nitrogen by perennial species is returning nitrogen cycling back to normal more quickly than Natural Recovery.
species richness in a quadrat	3	1	1	3	Efficiency of resource use is generally higher with more species present within a quadrat.

Table 5.5. Ranking of wellsite rehabilitation treatments on Dry Mixed Grass Prairie (Continued).

Parameter	Current	Diverse	Simple	NR	Comments
3. Plant Community (overall)	**4** (3)	**1** (1)	**2** (1)	**3** (2)	Higher diversity and richness helped the Diverse treatment reach top ranking.
similarity index	4	2	1	3	Decline in similarity of seeded treatments to the Control expected to continue or stabilize, while similarity of Natural Recovery is expected to increase.
richness	4	1	3	2	Diverse seed mix and gaps in the community promoted species richness.
diversity index (by importance value)	3	1	2	3	Diversity of rehabilitation treatments similar to Control primarily because Control is also dominated by relatively few species but has high species richness.
perennial non-wheatgrass species density	4	2	1	2	Wheatgrass suppression of other perennial species was cause of low ranking in Current treatment. Duration of higher ranking in Simple and Diverse treatments may be limited as these species are in decline. These species are increasing presence in the Natural Recovery treatment.
long term potential for achieving original composition	4	2	2	1	This ranking primarily associated with the observed trends in density and importance of perennial non-wheatgrass species.
4. Practical Considerations (overall)	**1**	**3**	**3**	**2**	Current treatment was most effective in meeting practical obj.
treatment cost	2	4	3	1	Cost of seed, seed treatment, and carrier is especially prohibitive in the Diverse treatment.
seed availability	2	4	3	1	Seed availability especially prohibitive for Diverse and Simple treatments at this time.
weed problems	2	2	2	1	Seed mixes may introduce undesirable species. However, the lower competition under NR may allow naturally occurring perennial weeds such as green foxtail to become dominant.
time frame for certification	1	1	1	4	

[1] Rankings are qualitatively based on research results (see text). Overall rankings in () are based on statistically sig. dif. among treatments for each parameter.

[2] Current – 4 grasses mix dominated by wheatgrasses; Diverse – seed mix of 22 grasses and forbs; Simple – 5 grasses mix dominated by needle and thread and blue grama grass but including northern and western wheatgrass; NR - Natural Recovery, not seeded

[3] Note: due to wheatgrass domination, plant community diversity in the Diverse treatment was not significantly different from that found in the other treatments. Therefore, these relative rankings are not necessarily a reflection of diversity, rather the performance of the treatment as observed. See Chapters 2 and 3 for more detailed discussion.

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CHAPTER 6. THE NATIVE PRAIRIE REHABILITATION RESEARCH PROJECT: FUTURE RESEARCH

While this research has contributed to our understanding of ecosystem response to prairie rehabilitation, it has left several questions unanswered and generated a variety of new questions. A summary of these questions for future research follows.

6.1 RATE AND DIRECTION OF PLANT COMMUNITY SUCCESSION

This project has established seven sites as benchmarks for future research. The research to date has only investigated early successional response of the ecosystem to the rehabilitation treatments. Long term monitoring of these sites is recommended to evaluate: the rate of succession in the natural recovery treatment, the resilience of wheatgrasses as the plant community develops, competition increases, and resources become less available, the establishment rate of non-wheatgrass species in the seeded treatments, and the degree to which these treatments will return the wellsite to plant community composition similar to that prior to disturbance.

6.2 TREATMENT REPLICATION IN TIME

Numerous factors may influence early plant community succession including climate. In this research, plant community establishment was delayed by extremely dry conditions following seeding in June. Seeding earlier in the spring or during a year with average to above average precipitation could have altered the results in the first growing season considerably. Ideally, the study should be repeated in time to determine community response under different climatic conditions. In addition, fall seeding versus spring seeding should be assessed.

6.3 RELATIVE COMPETITIVENESS OF WHEATGRASSES

Considerable emphasis has been placed on wheatgrass domination in the rehabilitation treatments. The question of whether this is a typical wheatgrass response or a function of cultivar development has arisen several times. To facilitate improved seed mix design, the relative intraspecific competitiveness of wheatgrass cultivars, ecological varieties, and wild type seed must be determined. These wheatgrass types must also be tested against the same forms of other native species. This may involve competition studies in the field, or, greenhouse investigations where minimal resource requirements are measured.

6.4 TREATMENTS WITHOUT WHEATGRASSES

The wheatgrasses were included in all of the seeded treatments due to erosion concerns in the absence of rapidly establishing species. In retrospect, wheatgrasses should have been excluded from at least one seeded treatment. The Simple treatment was intended to fulfill this role to some extent by excluding *Agropyron trachycaulum* which was known to have high and rapid establishment and biomass production rates. However, the compensatory growth of *Agropyron dasystachyum* in the absence of *A. trachycaulum* was not anticipated. As such, a treatment consisting of only *Stipa comata*, *Koeleria macrantha*, and *Bouteloua gracilis* should have been included. A comparison of this mix with the Simple treatment seed mix would have been very useful and is recommended.

6.5 IMPACT OF GRAZING

Grazing was excluded from the rehabilitation treatments throughout the first three growing seasons following seeding. It was standard industry practice to exclude grazing from wellsites to maximize biomass production, prevent site destabilization, and alleviate industry concern related to potential site instability due to the nature of the seeding treatments. Controlled grazing could have been introduced at the end of the second growing season once it was apparent that site stability was no longer a concern. Grazing may have influenced the relative competitiveness of the wheatgrasses and altered community development. The impact of grazing on plant community composition should be investigated on the existing sites. (Note: Etienne Soulodre and Dr. Anne Naeth have already initiated this work.)

6.6 AVAILABLE SOIL NITROGEN

This research showed promising results in using ion exchange membranes (IEM) to measure available soil nitrate and ammonium as indicators of succession. If resources were available, it would have been even more useful if IEMs were used to monitor mineral nitrogen availability beginning in early spring accompanied mineral nitrogen supply rates as determined by using root exclusion cores. This would have provided a better indication of the impact of disturbance on nitrogen mineralization and nitrification rates in addition to N uptake rates.

The NH_4^+:NO_3^- ratio in soil has been used by other researchers as an indicator of successional state and potentially allelopathy. Monitoring of this ratio should be continued. In addition, the reason for its change on Dry Mixed Grass prairie should be investigated by determining if nitrification is regulated by allelopathy or plant uptake. In-situ monitoring of NH_4^+ and NO_3^- supply rates in the rhizosphere of different species and in communities of different successional stages should be conducted. In addition, populations of nitrifying bacteria could be monitored.

The process of soil salvage and replacement diluted the topsoil with subsoil resulting in loss of organic matter. This loss should be further quantified in conjunction with its influence on capacity to supply soil mineral N.

6.7 SOIL WATER CONTENT.

The primary plant resource investigated in this research was plant available N. However, plant community productivity and development is also water limited. The water use efficiency in various rehabilitation treatments would also be of interest from the perspective of competition and from influence on biogeochemical cycling.

6.8 SOIL MICROBIAL ACTIVITY AND COMPOSITION.

Preliminary investigations into the functional diversity of the soil microbial population were conducted using Biolog GN MicroPlates™. Microbial populations are expected to differ under different plant communities. Therefore, differences were expected among the rehabilitation treatments and similarity to the microbial population in the Control could be an indicator of succession. Although the investigations that were conducted did not indicate a difference among treatments, differences among sites were apparent. Further investigations into the functional diversity of soil microbial populations may provide a unique insight into plant community succession. Observations made from samples collected during periods when soil is moist and warm are recommended.

Dehydrogenase enzyme activity in the rehabilitation treatments was tested in the fall of each year. No significant difference was found among the treatments or when compared to the Control. The effectiveness of using dehydrogenase enzyme activity as an indicator of succession should not be discounted yet. Further investigations should be conducted including immediate analysis of samples collected during the spring and summer when soils are moist. The usefulness of dehydrogenase may be limited, however, by the soil variability resulting from salvage and disturbance. Representative sampling and analysis becomes more difficult.

APPENDIX A – VEGETATION DATA AND RESEARCH SITE LOCATIONS

Table A.0.1 Seeded species density. [1]

Treatment		*Elca*	*Koma*	*Orhy*	*Stco*	*Stvi*	*Agda*	*Agsm*	*Agtr*	*Bogr*	*Acmi*	*Aser*	*Asst*	*Gaar*	*Getr*	*Gusa*	*Hebo*	*Peca*	*Pepu*	*Raco*	*Somi*	*Thrh*	*Viam*
Seeding Rate (Plants/0.1m²)																							
	Cur					1.5	9	15	4.5														
	Div	0.9	2.1	2.1	6.6	2.1	2.1	2.1	2.1	6.6	0.4	0.3	0.3	0.1	0.1	0.3	0.5	0.1	0.3	0.4	0.3	0.5	0.6
	Sim		6		9		3	3		9													
Mean establishment (%) of plants seeded based on 1997 density																							
Cher	Cur					1.3	26.4	5.8	31.7														
Cher	Div	0.0	1.2	0.2	7.7	1.6	44.4	17.9	39.3	6.6	3.3	0.0	0.8	2.5	0.0	13.9	31.7	0.0	6.4	1.9	1.7	16.7	12.5
Cher	Sim		2.5		5.6		47.8	27.8		6.4													
Solon	Cur					0.0	19.0	8.3	36.3														
Solon	Div	0.0	0.3	0.2	3.4	2.1	27.0	17.5	52.4	4.5	1.7	1.1	1.1	0.0	0.0	11.1	22.2	0.0	0.0	5.6	3.3	0.0	1.1
Solon	Sim		0.2		3.1		37.8	33.7		3.8													
Mean density in late June, 1997 (plants/0.1 m²)																							
Cher	Cur		*0.05*		*0.09*	0.02	2.38	0.88	1.43	*0.05*	*0.00*		*0.00*								*0.00*		*0.03*
Cher	Div		0.03	0.01	0.51	0.03	0.93	0.38	0.83	0.43	0.01		0.00	0.00		0.04	0.02		0.02	0.01	0.01	0.01	0.08
Cher	Sim		0.15		0.51	*0.01*	1.43	0.83	*0.04*	0.58													*0.04*
Cher	NR		*0.02*		*0.08*		*0.12*	*0.03*		*0.08*							*0.00*						*0.03*
Solon	Cur		*0.04*		*0.10*		1.71	1.24	1.63	*0.09*	*0.02*												
Solon	Div		0.01	0.00	0.22	0.04	0.57	0.37	1.10	0.30	0.01	0.00	0.00			0.03	0.01			0.02	0.01		0.01
Solon	Sim		0.01	*0.00*	0.28		1.13	1.01	0.17	0.34	*0.04*												
Solon	NR				*0.11*		*0.03*	*0.05*	*0.01*	*0.03*	*0.01*	*0.00*	*0.00*			*0.01*				*0.00*			
Mean density in early July,1998 (plants/0.1 m²)																							
Cher	Cur		0.01		0.02		6.39	2.53	2.62	0.01													0.03
Cher	Div		0.01	0.01	0.36	0.04	2.62	2.21	2.88	0.28		0.03	0.02			0.03				0.01	0.01		0.08
Cher	Sim		0.15		0.31		3.29	3.52		0.53													0.04
Cher	NR		0.02		0.15		0.09	0.14	0.01	0.05		0.01									0.01		0.05
Solon	Cur		0.00		0.03	0.02	3.76	4.40	5.11	0.02	0.01												
Solon	Div		0.04		0.28	0.03	2.41	3.10	2.61	0.34	0.02	0.01	0.11			0.06							
Solon	Sim		0.16		0.43	0.01	4.20	3.77		0.47													
Solon	NR		0.03		0.16	0.01	0.06	0.33		0.10	0.01					0.01							
Cher	Con		0.85		8.78	0.05		6.15		3.98							0.01						0.23
Solon	Con		3.91	2.22	4.13	0.46	6.93	5.58		2.84	0.24					0.02						0.03	

[1] Italicized species density values in 1997 indicate species that are present but were not seeded. *Agsm - Agropyron smithii, Agda - Agropyron dasystachyum, Agtr - Agropyron trachycaulum, Stvi - Stipa viridula, Bogr - Bouteloua gracilis, Stco - Stipa comata, Koma - Koeleria macrantha, Orhy - Oryzopsis hymenoides, Elca - Elymus canadensis, Viam - Vicia americana, Raco - Ratibida colmunifera, Acmi - Achillea millefolium, Gusa - Gutierrezia sarothrae, Pepu - Petalostemon purpureum, Aser - Aster ericoides, Somi - Solidago missouriensis, Asst - Astragalus striatus, Gaar - Gaillardia aristata, Pepu - Petalostemon candidum, Getr - Geum triflorum, Hebo - Hedysarum boreale, Thrh - Thermopsis rhombifolia.* Cher – Chernozemic sites, Solon - Solonetzic sites, Con - Control, Cur – Current, Div – Diverse, Sim – Simple, NR – Natural Recovery

Table A.0.2 Mean species importance values (%) for Chernozemic and Solonetzic sites in 1997 and 1998.

		Chernozemic Sites										Solonetzic Sites									
		Control		Current		Diverse		Simple		NR^3		Control		Current		Diverse		Simple		NR	
Grp^1	Species^2	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98
C_3G	*Agrohordeum macounii*	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	0.3	-	-	-	-
C_3G	*Hordeum jubatum*	-	-	-	0.1	-	-	-	-	-	1.3	-	-	-	0.1	-	0.7	-	0.3	-	1.6
C_3G	*Koeleria macrantha*	6.9	2.4	0.2	0.1	0.4	0.1	2.0	1.1	0.5	0.3	9.0	5.7	0.3	-	-	0.3	0.5	1.1	-	0.3
C_3G	*Oryzopsis hymenoides*	-	-	-	-	-	0.1	-	-	-	-	0.2	1.0	-	-	-	-	-	-	-	-
C_3G	*Poa compressa*	-	-	-	-	-	-	-	-	-	-	-	1.2	-	-	-	-	-	-	-	-
C_3G	*Poa sandbergii*	1.4	0.8	-	-	-	0.2	-	0.1	-	-	5.3	2.3	-	-	-	-	-	0.6	-	0.5
C_3G	*Setaria viridis*	-	-	-	-	-	-	-	-	-	0.8	-	-	0.3	-	0.2	-	-	-	-	-
C_3G	*Sitanion hystrix*	-	-	-	-	-	-	-	0.0	-	0.4	-	-	-	-	-	-	-	-	-	0.4
C_3G	*Stipa comata*	18.5	25.0	1.3	0.2	7.8	3.2	6.3	4.0	2.2	4.5	8.4	7.7	2.0	0.5	3.9	2.6	4.1	3.6	2.9	1.5
C_3G	*Stipa viridula*	-	0.2	0.2	-	0.6	0.2	0.1	-	-	-	0.7	0.6	-	0.3	0.9	0.4	-	0.1	-	0.2
WG	*Agropyron dasystachyum*	1.5	-	28.3	36.4	14.9	17.9	21.3	31.1	2.7	0.5	4.4	7.1	21.9	24.2	11.8	12.5	22.8	28.3	0.8	0.5
WG	*Agropyron pectiniforme*	0.4	0.4	-	-	-	-	-	-	-	-	-	-	0.1	-	0.6	1.1	0.7	-	-	-
WG	*Agropyron smithii*	7.6	8.9	10.7	12.0	5.4	9.1	7.3	13.3	0.4	0.7	4.4	6.2	13.7	16.9	7.7	10.0	14.8	10.6	1.5	1.2
WG	*Agropyron trachycaulum*	-	-	19.6	20.4	17.0	19.9	2.6	-	-	0.1	-	-	32.7	28.4	26.1	15.3	3.1	-	0.5	-
C_4G	*Bouteloua gracilis*	14.1	17.5	0.4	0.1	5.3	2.7	7.7	5.0	2.8	0.7	9.8	9.6	1.8	0.2	4.7	2.4	3.7	3.6	0.9	1.4
C_4G	*Sporobolus cryptandrus*	-	-	-	-	-	-	-	-	-	1.5	-	0.0	-	-	-	-	-	-	-	0.1
AF	*Amaranthus retroflexus*	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AF	*Androsace occidentalis*	3.6	0.0	1.3	-	0.4	-	0.3	-	1.1	-	0.4	-	0.6	-	0.2	-	-	-	0.7	-
AF	*Chenopodium pratericola*	-	0.5	2.3	2.3	4.3	2.9	4.3	2.2	11.3	8.1	0.4	-	2.1	0.4	3.6	0.3	2.2	0.3	6.7	0.6
AF	*Crepis tectorum*	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	0.1
AF	*Descurainia* spp	1.2	0.6	17.6	6.7	26.5	13.2	30.0	14.5	44.4	16.1	0.1	0.3	2.8	8.4	3.6	8.9	1.0	7.1	7.7	27.2
AF	*Draba nemorosa*	1.1	0.4	0.8	0.3	3.1	-	1.9	-	-	-	-	0.1	-	-	0.2	-	0.3	-	-	-
AF	*Erucastrum gallicum*	-	-	0.3	-	0.8	-	1.0	-	0.6	-	-	-	-	-	-	-	-	-	-	-
AF	*Erysimum cheiranthoides*	0.6	-	-	-	-	-	-	0.1	1.7	0.9	-	-	-	-	-	-	-	-	-	-
AF	*Kochia scoparia*	-	-	0.0	7.0	1.7	14.7	0.9	12.6	1.7	18.1	-	0.1	0.4	8.4	6.7	18.8	13.6	19.9	16.4	24.2
AF	*Lappula occidentalis*	1.1	0.5	5.2	5.9	4.1	6.4	4.7	6.3	11.4	12.1	0.6	0.7	11.9	9.1	14.8	12.8	19.2	10.6	40.8	17.7
AF	*Lepidium densiflorum*	0.4	-	3.2	0.1	2.1	-	1.6	-	4.0	0.1	0.2	-	0.3	0.2	1.0	0.6	-	0.8	1.6	1.2
AF	*Linum rigidum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1
AF	*Monolepsis nuttalliana*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	0.3	-	2.1
AF	*Neslia paniculata*	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	0.1	-	0.0	-	0.5
AF	*Plantago elongata*	0.2	0.0	0.1	-	0.2	-	0.2	0.1	0.9	0.1	-	-	-	-	0.2	-	0.2	-	-	-
AF	*Plantago patagonica*	-	-	0.2	-	0.1	-	0.2	0.3	-	-	0.4	0.3	0.1	-	-	-	0.9	-	0.9	0.1
AF	*Polygonum* spp.	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	0.1	-	0.1
AF	*Salsola kali*	-	-	6.1	7.0	1.8	5.1	3.6	7.6	9.3	24.2	-	0.5	0.4	1.0	1.1	2.7	0.8	5.0	2.9	5.5
AF	*Thlaspi arvense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	0.2

Table A.2 Mean species importance values (%) for Chernozemic and Solonetzic sites in 1997 and 1998 (Continued).

		Chernozemic Sites										Solonetzic Sites									
		Control		Current		Diverse		Simple		NR		Control		Current		Diverse		Simple		NR	
Grp	Species	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98	'97	'98
PF	*Achillea millefolium*	-	-	-	-	0.1	-	-	-	-	-	0.5	0.5	0.5	0.2	-	0.2	0.6	-	0.3	0.2
PF	*Antennaria parvifolia*	0.5	0.4	-	-	-	-	-	-	-	-	1.5	0.1	-	-	-	-	-	-	-	-
PF	*Arabis holboellii*	-	-	-	-	0.1	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
PF	*Arnica fulgens*	-	0.1	-	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-
PF	*Artemisia frigida*	0.1	0.0	-	0.4	-	0.4	0.3	0.4	1.1	1.3	2.2	1.9	5.8	0.6	9.8	7.6	7.0	6.1	10.5	10.4
PF	*Artemisia ludoviciana*	-	-	-	-	-	-	-	-	-	-	0.2	0.2	-	-	-	-	-	-	-	-
PF	*Aster ericoides*	-	-	-	-	-	0.3	-	-	-	0.1	-	-	-	-	-	0.1	-	-	-	-
PF	*Astragalus crassicarpus*	-	0.0	-	-	-	0.1	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-
PF	*Astragalus dasyglotis*	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PF	*Astragalus striatus*	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-
PF	*Glycyrrhiza lepidota*	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-
PF	*Grindelia squarrosa*	-	-	-	-	-	-	-	-	-	-	0.0	0.1	-	-	-	0.0	-	0.2	-	-
PF	*Gutierrezia sarothrae*	-	-	-	-	0.7	0.4	-	-	-	-	0.1	0.1	-	-	0.6	0.5	-	-	0.4	0.1
PF	*Haplopappus spinulosus*	-	0.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PF	*Hedysarum boreale*	-	0.0	-	-	0.1	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-
PF	*Heterotheca villosa*	-	0.1	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-
PF	*Lygodesmia juncea*	0.1	0.2	-	-	0.2	0.1	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-
PF	*Medicago sativa*	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-
PF	*Penstemon albidus*	-	0.2	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-
PF	*Petalostemon purpureum*	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PF	*Potentilla pensylvanica*	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PF	*Ratibida columnifera*	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-
PF	*Solidago missouriensis*	-	-	-	-	-	0.1	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-
PF	*Sonchus arvensis*	-	0.2	-	-	0.2	0.1	-	0.1	0.4	1.4	-	-	-	-	-	0.1	-	0.1	-	0.3
PF	*Sphaeralcea coccinea*	3.8	3.7	0.1	-	-	-	0.3	0.6	1.3	0.4	3.1	2.0	0.4	0.2	0.2	0.2	0.8	1.0	1.4	0.9
PF	*Taraxacum officinale*	-	0.1	0.4	0.2	0.3	0.6	0.4	-	0.5	1.3	0.1	-	-	-	0.2	0.1	0.4	0.2	-	-
PF	*Thermopsis rhombifolia*	-	-	-	-	0.1	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-
PF	*Tragopagon dubius*	0.2	0.4	0.5	0.2	0.5	0.2	0.6	0.1	0.7	1.9	-	-	-	-	-	-	-	-	-	-
PF	*Vicia americana*	0.6	0.5	0.5	0.3	1.1	0.7	0.7	0.2	0.4	0.6	-	-	-	-	-	-	-	-	-	-
C	*Corypantha vivipara*	0.1	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GC	*Cladina mitis*	1.3	2.3	-	-	-	-	-	-	-	-	4.3	2.9	-	-	-	-	-	-	-	0.4
GC	*Phlox hoodii*	0.3	-	-	-	-	-	-	-	-	-	1.2	1.0	-	-	-	-	-	-	0.6	-
GC	*Selaginella densa*	13.3	13.6	-	-	-	-	-	0.1	-	-	17.1	18.6	0.1	-	0.8	-	3.2	-	0.6	0.1
S	*Artemisia cana*	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-
S	*Atriplex nuttallii*	-	-	-	-	-	-	-	-	-	-	-	0.5	0.1	-	-	-	-	-	0.9	-
SE	*Carex spp.*	21.1	20.7	0.4	0.1	-	0.3	1.4	0.2	0.6	1.2	24.5	26.9	1.7	0.8	-	-	0.2	0.1	-	0.6

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[1] Grp = plant groups: annual forbs (AF), perennial forbs (PF), wheatgrasses including both seeded and non-seeded varieties WG – wheatgrasses, C_3G - other C_3 grasses, C_4G - C_4 grasses, AF – annual forbs, PF – perennial forbs, SE - sedges, GC - ground cover species, S - shrubs, C – cacti.

[2] See Moss (1983) for species authorities.

[3] NR – Natural Recovery.

Table A. 0.3 Research site locations (UTM Zone 12U).

Site/position	UTM Easting	UTM Northing
C1 – IntE – LS3-S29-T14-R7 W4		
CONTROL - OM	0505263	5560441
NE CORNER	0505226	5560522
NW CORNER	0505170	5560526
SE CORNER	0505228	5560448
STUDY CENTER	0505198	5560488
SW CORNER	0505170	5560447
C2 – IntW – LS3-S29-T14-R7		
CONTROL - 0M	0504902	5560424
NE CORNER	0504975	5560525
NW CORNER	0504906	5560526
SE CORNER	0504973	5560443
STUDY CENTER	0504938	5560484
SW CORNER	0504905	5560448
C3 – Sceptre – LS1-S35-T11-R12 W4		
CONTROL - 0M	0453986	5529186
NE CORNER	0454081	5529298
NW CORNER	0453990	5529296
SE CORNER	0454079	5529203
STUDY CENTER	0454036	5529251
SW CORNER	0453988	5529205
C4 – StarTech – LS13-S18-T11-R12 W4		
CONTROL - 0M	1461811	5533091
NE CORNER	1461889	5533174
NW CORNER	1461807	5533179
SE CORNER	0461901	5533123
STUDY CENTER	0461844	5533150
SW CORNER	0461809	5533128
S1 – PCPN – LS7-S32-T15-R11 W4		
CONTROL - 0M	0465604	5572246
NE CORNER	0465755	5572242
NW CORNER	0465679	5572319
SE CORNER	0465684	5572174
STUDY CENTER	0465685	5572249
SW CORNER	0465615	5572255

S2 – PCPS – LS7-S20-T15-R11 W4		
CONTROL - 0M, TRAN-1	0465832	5569151
NE CORNER	0465790	5569203
NW CORNER	NO DATA	NO DATA
SE CORNER	0465851	5569110
STUDY CENTER	0465781	5569120
SW CORNER	0465763	5569053
S3 – PCPW – LS15-S3-T18-R15 W4		
CONTROL - 0M, TRAN-1	0430176	5594305
NE CORNER	0430157	5594416
NW CORNER	0430072	5594420
SE CORNER	0430154	5594307
STUDY CENTER	0430116	5594362
SW CORNER	0430075	5594306

Universal Transverse Mercator coordinates for research sites. Coordinates for corners are coordinates for the corners of the study area. The wellsite disturbance area extends beyond the boundaries of the study area on all sites. Study center coordinates indicate the middle of the wellsite study area. Coordinates taken in July, 1998.

APPENDIX B - SOIL DEHYDROGENASE ENZYME ACTIVITY AND MICROBIAL CARBON UTILIZATION PATTERNS

INTRODUCTION

Carbon and nitrogen losses through root exudation varies among species and ecosystems (Biondini et al., 1988). Therefore the nature of the seeded plant community on reclaimed land may influence biogeochemical function of the rehabilitated ecosystem. Under various reclamation treatments, Biondini et al. (1985, p.323) found that "Dehydrogenase enzymatic activity levels increased with succession and were positively correlated to ...perennial grass composition in the native seed mixture.".

Biogeochemical cycling of nutrients is considered to be an important indicator of ecosystem succession following rehabilitation. A number of parameters were measured to account for this and results were described in Chapter 3. Aside from dehydrogenase enzyme activity, these parameters did not measure changes in the microbial community and their response to the rehabilitation treatments. Therefore microbial carbon utilization patterns were measured as possible indicators of successional development. The results from these analyses were inconclusive with respect to the rehabilitation treatments and therefore were not included in an earlier chapter. These results are presented here for the reference of future interested parties.

METHOD

Carbon Utilization Patterns

Functional diversity of the soil microbial population was determined using Biolog GN MicroPlates™ (Biolog, 1993). Each Biolog plate consists of 95 wells containing different carbon sources and a blank well (Biolog, 1993). Each well on the microplate also contains a tetrazolium violet dye which, in the presence of microbial respiration, reduces and turns purple.

A composite soil sample was collected in early September 1998 consisting of 16, 0 to 10 cm cores collected in a stratified random design within each treatment. The field moist samples were passed through a 2 mm sieve and stored at 4 °C until analysis. The oven dried (105 °C) moisture content (w/w) of the soil samples ranged from 3.5 to 7.0 % with the exception of the Sceptre site where soil moisture ranged from 10.7 to 12.0 %. A 5 g subsample of each field moist composite samples was used to prepare a standard dilution with 150 µL aliquots of the final dilution (10^{-4}) added to each of the 96 wells on a Biolog microplate. Positive carbon use as indicated by purple colour development was visually determined at 24 hr intervals to 96 hrs. A very low positive response resulted in all treatments of this trial except for those on the Sceptre site (results not presented). The low response was a result of low soil moisture conditions and presumably very low microbial activity as determined by a series of small trials. As such a second trial was conducted in which 5 g of soil (oven dry basis) was brought to and maintained at 70 % field capacity for a six day incubation period at room temperature (22 °C). Field capacity was approximately 20 % (w/w). After incubation the samples were diluted and plated as described above. For the second major trial, colour formation in the microplate wells was analyzed using an EAR 400 FW (SLT-Labinstruments, Austria) microplate reader equipped with a 540 nm filter. A 590 nm (peak absorbance for tetrazolium dye) filter was not available. A lower wavelength filter should be acceptable, and possibly more conservative as suggested by Zak (1994) who used a 405 nm filter. Average well colour development (AWCD) was determined to account for potential variability in inoculum cell density and associated variability in the rate of well colour development (Grayston et al., 1998; Garland, 1996). AWCD was calculated for each microplate as the mean absorbance value for all 95 wells minus the blank well.

Average well colour development (AWCD) curves were used to determine the rate at which colour development, and hence, carbon substrate utilization occurred in each treatment. Treatments with a more rapid rate of AWCD may be responding to a higher population of microorganisms even though their carbon utilization pattern may not be different from other treatments. To compensate for this problem, the carbon utilization patterns of treatments are compared at similar stages of AWCD. In many cases, this means comparing carbon utilization patterns at different observation times. For example, Diverse and Simple treatment results from 72 hrs. may be compared with Current and Natural Recovery treatment results from 96 hrs, and Control results from 120 hrs. Average well colour absorbance values at which comparisons were made varied among sites from approximately 100 to 300. Results were analyzed by principle components analysis using PC-ORD multivariate software (McCune and Mefford, 1995).

RESULTS AND DISCUSSION

Soil Carbon Utilization Patterns

Carbon utilization patterns among treatments varied among sites and differed between the soils. Using principle components analysis (PCA), the mean carbon utilization patterns for treatments across all Chernozemic sites indicated that the Diverse treatment was most similar to the Control followed by the Simple treatment and then distantly by the Natural Recovery and Current treatments (Figure 7.1). PCA of means of Solonetzic sites indicated the Natural Recovery treatment was most similar to the Control followed by the Simple, Current and then Diverse treatments (data not presented).

PCA of treatment results for each wellsite independently generally produced clustering of treatments from a common wellsite (Figure 7.2). However, the carbon utilization patterns of rehabilitation treatments relative to the Control were not always consistent with the patterns produced by PCA of treatment means (Figure 7.1). For example, the Chernozemic Natural Recovery and Current treatments tended to be more similar to the Control than the Diverse and Simple treatments in direct contrast to the results obtained from PCA of means. Due to the treatment clustering for common wellsites and inconsistent patterns among sites, it becomes evident that site effects may be greater than treatment effects. Further investigation would only explain differences among sites and is therefore not warranted at this time.

SUMMARY

Microbial carbon utilization patterns showed interesting potential for use in differentiating sites with differences in historical management, plant community, and/or soil. However, a consistent pattern among treatments was not apparent in these preliminary investigations and therefore was ineffective in acting as an indicator of successional development.

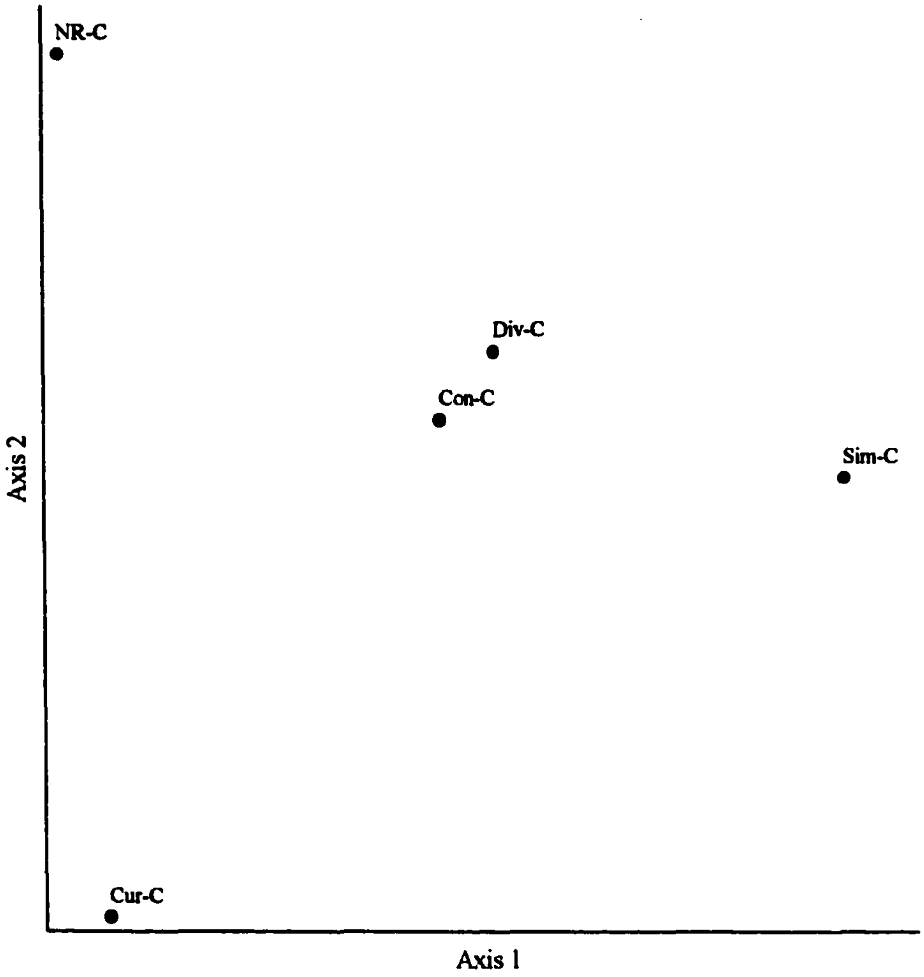

Figure B.1 Principle components analysis of mean results for each treatment from Biolog™ analysis on Chernozemic sites. Note: Con-Control, Cur-Current, Div-Diverse, Sim-Simple, NR-Natural Recovery.

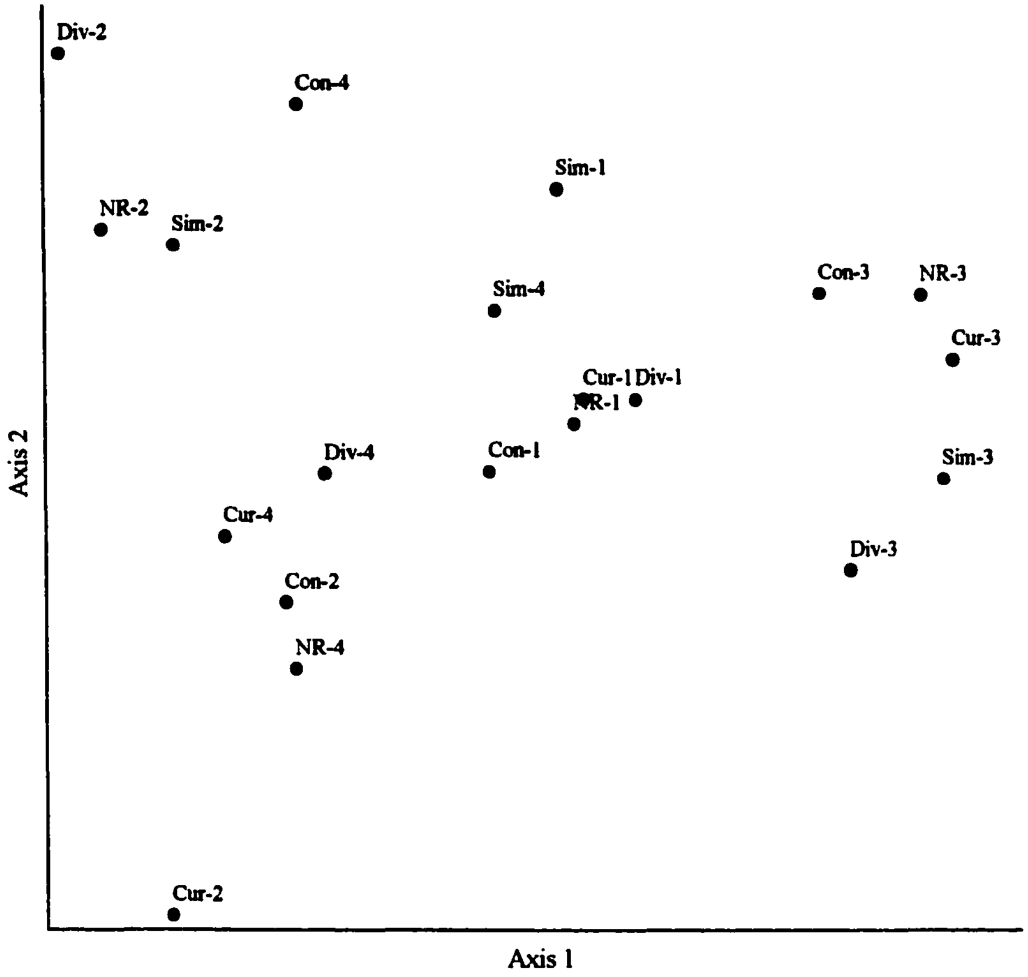

Figure B.2 Principle components analysis of results of Biolog™ analysis of rehabilitation treatments on each Chernozemic wellsite. Note: Con-Control, Cur-Current, Div-Diverse, Sim-Simple, NR-Natural Recovery. Wellsites numbered 1 to 4.

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APPENDIX C – CRITERIA FOR WELLSITE RECLAMATION

This section provides a brief excerpt of wellsite reclamation criteria especially pertinent to this research. Please refer to the complete wellsite criteria for details:

Alberta Environmental Protection. 1995. Reclamation criteria for wellsites and associated facilities - 1995 update. Land Reclamation Division. Edmonton AB. C&R/IL/95-3. 62 pp.

(This criteria document may be found on the internet at: www.gov.ab.ca/env/info/infocentre/publications/landrec.html.)

2.4 Surface Soil Quantity, Distribution, and Quality

2.4.1 Quantity of Replaced Surface Soil

The required replacement depth (RRD) is:

For sites constructed after April 30, 1994; 80% of control if the control surface soil is ≥15 cm.

If the control surface soil is <15 cm, salvage and replace as evenly as possible all available surface soil. Provide soil depth data.

2.4.4 Loss of Organic Matter Content

The loss of organic matter is to be measured by the % admixing of non-surface soil in the replaced surface soil. This parameter is used as a flag of potential problem soils, not as a criteria.

Report the control class and the % admixing class at each assessment location. Note that the control may be admixed (i.e., a mixture of soil layers).

Targets for % admizing of non-surface soil component:

Sites constructed after April 30, 1994: Less than 30% difference in non-surface soil in the sample (i.e., sample minus control).

2.6 Vegetation

Section 2.6.2 Criteria

Species Composition	Revegetation species and species composition should be compativle with original or control vegetation or meet reasonable land management objectives.
Density	≥80% of contol.
Height	≥80% of control.

Health	**Plants should be healthy. Characteristics to look for are vigour, height, colour, disease, and vegetation quality.**
Cover	**Where the control vegetation is similar, ≥80% of control.** **If the control vegetation has <40% cover, the site should be 100% of control.** **Where there is no control vegetation, or the control vegetation is different, ≥80% cover unless otherwise authorized by the Conservation Reclamation Inspector in writing.** **Litter can be included in the cover assessment, however cannot contribute more than the amount on the control.** **Amendment materials (e.g., straw) are not included as litter in the calculation for cover. The required cover must be evenly distributed on the site or be similar to the distribution on the control.**