

THESIS

EVALUATION OF TECHNIQUES FOR RESTORATION OF
DISTURBED SITES IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

Submitted by

Todd A. Ontl

Department of Forest, Rangeland, and Watershed Stewardship

In partial fulfillment of the requirements

for the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2006

COLORADO STATE UNIVERSITY

May 5, 2006

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR
SUPERVISION BY TODD A. ONTL ENTITLED EVALUATION OF TECHNIQUES
FOR RESTORATION OF DISTURBED SITES IN ROCKY MOUNTAIN NATIONAL
PARK, COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

Advisor

Department Head

ABSTRACT OF THESIS

EVALUATION OF TECHNIQUES FOR RESTORATION OF DISTURBED SITES IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

Restoration of areas disturbed by human activities to late-seral plant communities is a primary goal of the National Park Service. Modern anthropic disturbances in Rocky Mountain National Park include the installation of utilities, construction or improvement of facilities, and the construction or removal of roads, trails, and parking lots.

Approaches to restoring these disturbances include natural revegetation, seeding treatments, transplanting containerized material, or a combination thereof. The costs associated with these different approaches vary considerably, emphasizing the need for an evaluation of the cost effectiveness of these methods in the establishment of late-seral plant communities following disturbance.

Data were collected on 20 pairs of disturbed and undisturbed sites in 2004 on lands within and adjacent to Rocky Mountain National Park that had been treated with different restoration approaches. Treatments differed in effectiveness when evaluated with different criteria to judge restoration success. Plant cover data showed the highest cover values of native and perennial species on disturbed sites where containerized material was transplanted. Sites that were seeded and transplanted showed no differences compared to undisturbed sites in cover of native perennial grasses, while transplanted sites showed no differences in native perennial forb cover. No differences were detected

between treatments for richness of native, perennial, or annual species on disturbed sites. Community similarity between disturbed and undisturbed sites was highest for sites that included seeding based on species presence and species cover data, suggesting the importance of including seeding as a treatment for producing plant communities most similar to undisturbed communities.

Cost effectiveness analysis revealed large differences between treatments when using a ratio of cost to effectiveness, based on total and native species cover values. Sites treated with a combination of seeding and transplanting had the highest effectiveness, with transplanted sites showing the lowest effectiveness. Average costs of treatments varied greatly. Seeding treatment had the lowest costs while transplanted sites had the largest associated costs, resulting in the lowest cost effectiveness ratio for seeded sites and the highest ratio of costs to effectiveness for transplanted sites. These results suggest that when financial resources are not limited, the combination of seeding and transplanting is the most effective restoration approach. However, when financial resources are limited, seeding is the most cost-effective restoration approach.

Sites that were allowed to naturally revegetate were assessed to determine the long-term effects on seeding a nurse crop. Richness and cover of native and perennial species were not shown to be affected by the use of a nurse crop. However, richness and cover of exotic and annual species were higher on sites seeded with a nurse crop. These results may suggest long-term effects on plant community development from nurse crop seeding. However results may be influenced by the presence of populations of exotic species in the vicinity of disturbed sites.

Sites disturbed and revegetated by transplants in 2004 were sampled in 2005 to evaluate natural colonization of native species and survival rates of transplanted material. Disturbed sites were colonized by more native species than exotic species, suggesting that natural colonization by native species contributes to successional development following disturbances. Many native perennial species were frequently observed colonizing disturbed sites which may prove to be useful species for managers when actively restoring disturbances. Natural colonization of disturbed alpine tundra sites was low. However survival of transplants was high, suggesting that transplanting can be an effective approach for restoring disturbances on these more difficult to restore sites.

Todd A. Ontl
Colorado State University
Fort Collins, Colorado, 80523
Summer 2006

ACKNOWLEDGMENTS

There are many people who deserve recognition for their willingness to share their time, advice, and support throughout my graduate studies. I would like to thank my adviser, Dr. Edward Redente, for the opportunity to work on a challenging project, his confidence in me throughout the entire process of this project, as well as advice and support. Members of my committee, Drs. Mark Paschke and Ken Barbarick, were valuable assets to my graduate education and provided much support and advice as well.

Thanks also to the staff at Rocky Mountain National Park, especially to Jeff Connors, without whom this project would not have been possible. Thanks also to Karl Cordova, Michael Margo, and the many members of natural resources staff. My field assistants Jesse Dillon, Peter Landon, and Dayle Funka were invaluable to me during my summers of data collection both for their hard work as well as the distractions from work.

I am grateful to many fellow FRWS and GDPE graduate students for their assistance during my years in graduate school. Many graduate students shared their useful thoughts, discussed ideas, and gave important feedback. Thanks to members of the Restoration Ecology Lab including Élan Alford, Matt Schultz, Spencer Cronin, and post-doc Laura Perry. Seth Munson was not only a great help outside of classes, but also a great friend. A very special thanks goes to Melissa McHale for her many contributions to my graduate education, as well as my life. I am grateful for the numerous late-night science discussions, technical help, emotional support, and encouragement of my goals. You

have been an enormous influence on my development as a scientist, and my graduate school experience would not have been the same without your friendship and support.

Finally I'd like to thank and honor my family and friends for all of their support. My parents, Allan and Judy, brother Craig, many friends in Colorado and Iowa City, and of course my four-legged companion, Sego, who have provided love and support that has sustained me throughout all the ups and downs of the past few years. For all of you, I am tremendously grateful.

TABLE OF CONTENTS

INTRODUCTION.....	1
Problem Statement.....	1
Objectives.....	4
Hypotheses.....	5
LITERATURE REVIEW.....	6
Disturbance.....	6
Succession.....	7
Nudation.....	9
Migration.....	10
Establishment.....	10
Competition.....	11
Reaction.....	14
Development of climax communities.....	16
Restoration of Disturbances.....	18
System degradation and reversal.....	19
Goals of restoration.....	19
Restoration methods.....	20
Evaluation of restoration success.....	27
Restoration in RMNP.....	30
Goals of restoration.....	30
Preservation of genetic integrity.....	31
Sources of plant material for restoration.....	34
Cost effectiveness analysis.....	35
METHODS.....	37
Site Description.....	37
Experimental Design.....	41
Statistical Analysis.....	48
Cost Effectiveness Analysis.....	50
RESULTS AND DISCUSSION.....	54
Success of Restoration Treatments.....	54
Species richness.....	56
Plant cover.....	59
Community similarity.....	63
Cost effectiveness analysis.....	66

Effects of age on treatment averages.....	73
Effects of Nurse Crop Seeding.....	75
Plant cover.....	75
Species richness.....	79
Community similarity.....	83
Natural Colonization of Disturbances.....	85
Transplant Survival on Alpine Tundra Sites.....	88
Conclusions: Recommendations to NPS Manager.....	89
LITERATURE CITED.....	93
APPENDICES.....	109

LIST OF TABLES

Table

1. Description of 20 disturbance study sites, Rocky Mountain National Park, Colorado.....	39
2. Taxonomic classes of undisturbed soils adjacent to 20 experimental disturbed sites, Rocky Mountain National Park, Colorado.....	40
3. Description of one-year disturbed sites, Rocky Mountain National Park, Colorado.....	47
4. Hypothetical seed mixture approximating the relative cover values of undisturbed plant communities on reference sites in Rocky Mountain National Park, Colorado.....	51
5. Species richness data from undisturbed and disturbed sites treated by seeding, transplanting, and a combination of seeding and transplanting.....	58
6. Percent cover data of origin and life form from undisturbed and disturbed sites treated by seeding, transplanting, and a combination of seeding and transplanting.....	62
7. Determination of ratio of costs and <i>EI</i> for various disturbed sites, Rocky Mountain National Park, Colorado.....	69
8. Percent cover data of origin and life form from undisturbed sites and disturbed sites with no treatment or by seeding a nurse crop.....	77
9. Species richness data for reference and naturally revegetated disturbed sites with and without a nurse crop seeded.....	82

LIST OF FIGURES

Figure

1. Locations of disturbed and adjacent undisturbed reference sites, Rocky Mountain National Park, Colorado.....	38
2. Locations of sites disturbed summer 2004, Rocky Mountain National Park, Colorado.....	46
3. Comparison of methods used in restoration projects in Rocky Mountain National Park, Colorado.....	55
4. Average richness of annual, perennial, native, exotic, and total species for disturbed and undisturbed sites, Rocky Mountain National Park, Colorado.....	57
5. Comparison of cover values for disturbed and reference sites based on origin, life form, and class of species.....	60
6. Sorenson's quantitative and qualitative similarity index for disturbed/reference pairs, Rocky Mountain National Park, Colorado.....	64
7. Estimated costs of restoration treatments using locally collected plant material	67
8. Cost-effectiveness ratio of restoration treatments, Rocky Mountain National Park, Colorado.....	70
9. Linear regression of <i>EI</i> and cost estimations from 10 disturbed sites, Rocky Mountain National Park, Colorado.....	72
10. Comparison of cover values for reference and disturbed sites restored through passive revegetation based on origin, life form, and class of species.....	76
11. Soil N-NO ₃ on passively restored sites with and without a nurse crop seeded, Rocky Mountain National Park, Colorado.....	80
12. Average richness of annual, perennial, native, exotic, and total species for passively restored sites with and without a nurse crop seeded.....	81

13. Sorenson's quantitative and qualitative similarity index for disturbed/ reference pairs of passively restored sites with and without seeding a nurse crop.....	84
14. Total and colonizer species richness by origin on sites one year after disturbance.....	87

INTRODUCTION

“Land...is not merely soil; it is a fountain of energy flowing through a circuit of soils, plants, and animals.”

-Aldo Leopold, *A Sand County Almanac*, 1949

Problem Statement

As human populations grow, society's impacts on the natural environment have increasingly negative effects on our relationship with global ecosystems. Vitousek et al. (1997) estimated that between one-third and one-half of the earth's surface has been transformed by human activities. Increased rates of pollution, destruction of habitat, and invasion by exotic species are among many of the consequences of modern society that lead to the degradation of the ecosystem services that human populations depend upon for survival (Ehrlich and Ehrlich 1991, Daily 1997).

Ecological restoration is a collection of approaches aimed at reversing habitat degradation, destruction, or damage as a result of various types of disturbances (Baldwin et al. 1994, Hobbs and Norton 1996, SER 2004). Disturbances differ widely in terms of the spatial scale, severity, intensity, and frequency of occurrence. As the recognition of the need for ecological restoration increases and the science of restoration ecology matures, methodologies and concepts that are important for successful restoration have been increasingly developed. Among the concepts crucial to the success of the restoration process are 1) determining realistic goals, 2) developing practical methods for

implementing those goals, and 3) assessing the success of these strategies (Hobbs and Norton 1996).

Numerous anthropic disturbances have historically occurred within Rocky Mountain National Park (RMNP) prior to, and following its inception in 1915. Disturbances have included mines, sawmills, homesteads, camps, settlements, lodges, roads, ski slopes and lifts, a golf course, and an asphalt mixing plant. It has been the policy of the National Park Service (NPS) to acquire any in-holdings, remove structures not determined to be culturally significant, and restore these areas either through natural or artificial revegetation efforts to appropriate late-seral plant communities. In recent years, anthropic disturbances in RMNP have occurred mostly in areas of high human use, including the park utility areas, trails, trailheads, picnic areas, campgrounds, and parking lots. The characteristics of these disturbances vary greatly depending on the activities that took place, and thus the approaches to restoration in these areas cover a variety of natural and artificial restoration techniques.

In situations where the size and/or intensity of the disturbance is small and the risk of establishment of exotic species is low, managers may choose to allow for passive restoration of the site. This approach has the lowest costs associated with it and may only require initial site preparation, such as scarification to reduce soil compaction. Restoration of the vegetation occurs through natural recruitment from the seedbank and dispersal of seed from surrounding populations. In some situations where site stabilization may be desired due to a high risk of soil erosion, seeding of a nurse crop may be done. On sites where the disturbance size or intensity is more extensive, an active approach to restoring the site is often desirable. This generally entails the addition

of plant material to the site in order to decrease the establishment of exotic species and increase cover of native perennial species. Sites can be seeded with an appropriate mixture of native mid- to late-seral grass, forb, and shrub species. Alternatively, containerized plant material can be used to provide immediate cover for the purposes of aesthetics, site stabilization, as well as serving as a seed source for the site. Occasionally sites are treated with various combinations of seeding, transplanting, or the use of a nurse crop. Costs associated with active restoration approaches vary depending on the techniques used, but are significantly higher than passive approaches.

The goal of the National Park Service (NPS) system is to preserve the natural and cultural resources for both recreational and educational purposes. The Rocky Mountain National Park Act of 1915 states:

"...said area is dedicated and set apart as a public park for the benefit and enjoyment of the people of the United States...with regulations being primarily aimed at the freest use of the said park for recreation purposes by the public and for the preservation of the natural conditions and scenic beauties..." (38 Stat. 798)

In addition to this legislation, later laws such as the NPS Organic Act of 1916 (16 USC 1) and the Redwood Act amendment to the 1970 NPS General Authorities Act (16 USC 1a-1) provide provisions for managers to conserve the native flora and fauna in the nation's parks, and have been incorporated into NPS management policies for restoration of disturbances (NPS Management Policies 2001).

In October 1976, RMNP was named a UNESCO Biosphere Reserve. One of the three basic functions of the World Biosphere Reserve network is "to contribute to the conservation of landscapes, ecosystems, species and genetic variation" in natural areas representative of major biogeographical regions. Due in part to the goals of the NPS management policies as well as the Biosphere Reserve network objectives, the Park

Service made a management decision in 1985 to use local genotypes of native plants for restoration projects when possible in order to preserve the genetic integrity of the native plant communities. In order to meet these objectives, the park constructed a small greenhouse and nursery in 1995 to propagate locally collected plant material. However, using only local plant material in restoration projects has placed limitations on the park due to the increased costs associated with the collection and propagation of local genotypes. Large differences in costs associated with passive versus active approaches to restoration combined with the limitation in funding available for restoration projects in the park emphasize the need for evaluation of the effectiveness of the different approaches to restoring disturbances in RMNP. It is unknown if higher costs associated with more intensive restoration activities are justified by increased restoration success, or if less intensive approaches to restoration are the most cost-effective strategy.

Objectives

- 1) To assess the relative success of different restoration approaches in order to identify methods that accelerate plant succession and produce plant communities most similar to pre-disturbance communities.
- 2) To analyze the cost-effectiveness of treatments by comparing actual treatment costs to a measure of restoration effectiveness based on cover values of the species present on restoration sites.
- 3) To characterize the vegetation present on newly disturbed sites in a variety of settings in order to determine the frequency of native species colonizing disturbed sites that may

be potentially useful in stabilizing disturbed sites for the purpose of erosion control and limiting exotic species establishment.

Hypotheses

- H₁. Disturbed sites restored with containerized plant material have greater cover of native perennial forbs and shrubs compared to sites without transplanting.
- H₂. The greatest values for native species diversity occur on sites restored using a combination of seeding and transplanting material, as compared to sites that were only seeded or transplanted.
- H₃. The greatest values for cover of native perennial species occur on sites restored using a combination of seeding and transplanting material, as compared to sites that were only seeded or transplanted.
- H₄. The greatest values for community similarity occur on sites restored using a combination of seeding and transplanting material, as compared to sites that were only seeded or transplanted.
- H₅. Costs vary more than effectiveness among treatments, resulting in the treatment with the lowest costs as the most cost-effective approach among active restoration treatments.
- H₆. Disturbed sites seeded with a nurse crop have lower cover of native species resulting in lower similarity to undisturbed conditions, than sites not seeded with a cover crop.

LITERATURE REVIEW

“In the planting of the seeds of most trees, the best gardeners do no more than follow nature, though they may not know it...So, when we experiment in planting forests, we find ourselves at last doing as nature does. Would it not be well to consult with nature in the outset? For she is the most extensive and experienced planter of us all...”

-Henry David Thoreau, *The Succession of Forest Trees*, 1860

DISTURBANCE

White and Pickett (1985) define disturbance as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources or substrate availability or the physical environment”. A disturbance can alter the density, biomass, or spatial distribution of the biota of a system, affect resource availability, and change the physical environment (Walker and Willig 1999). Disturbances can be a consequence of either natural or anthropogenic forces. Natural disturbances are a result of either physical or biological processes (Sousa 1984). Physical disturbances include floods, drought, fire landslides, and high winds. Examples of biological disturbances include herbivory, pathogens, invasion of an exotic species, and activity of animals such as prairie dogs or ants that disturb the soil and result in the removal of one or more individuals of the plant community. Anthropogenic disturbances result from human activities that result in the removal of vegetation such as logging, agriculture, or mining; the construction of facilities such as roads and buildings; the installation of buried utilities such as water lines and communication cables; and soil compaction, erosion, and

vegetation removal associated with recreational activities. Disturbances are extremely dynamic, and can be characterized according to many different descriptors. A disturbance may originate outside (exogenous) of the system or within (endogenous) the system (Walker and del Moral 2003). Variables important in the characterization of any disturbance are spatial extent, temporal scale, severity, intensity, and frequency (White 1979, Bazzaz 1983). Spatial characteristics include patch size, shape and distribution (Chaneton and Facelli 1991, Turner et al. 1997). Temporal characteristics can indicate frequency or seasonality of a disturbance (White and Pickett 1985). Severity is a measure of the effect on the biota, such as the percentage of the biomass of an ecosystem affected. Intensity is an estimation of the physical force of the disturbance, such as wind speed or magnitude of an earth quake on the Richter scale. The disturbance regime is the cumulative effect of all the disturbances that operate at different spatial and temporal scales that affect a certain area. This cumulative effect of multiple disturbances occurring at varying scales is that one disturbance may act synergistically to enhance frequency, extent, severity, or intensity of another disturbance. For example, invasive plant species can alter the disturbance regime by increasing erosion, altering resistance to herbivory, or changing fire return intervals of a system (Ehrenfeld and Scott 2001).

SUCCESSION

Beginning with early ecologists such as Warming (1895) and Cowles (1899, 1901), who both studied changes in vegetation over time on sand dunes, succession has been a central theme of ecology (McIntosh 1985). These early studies on dune succession introduced the concepts of pioneer communities, species richness, biotic and abiotic

drivers of succession, and retrogression to earlier successional stages that are still a part of succession theory today. More than a century later, succession is still considered one of the most important themes in ecology (Cherrett 1989, McIntosh 1999), and has become increasingly relevant as a model for habitat restoration.

Clements (1916, 1928) was the first to give successional studies a conceptual framework. He proposed a highly directional and deterministic model of the processes that drive plant community change over time: nudation initiates succession through disturbance by creating bare soil; migration is the arrival of seeds or other propagules from outside the disturbance; ecesis is the process of establishment of propagules that have either dispersed onto the site or that remained on the site having survived the disturbance; competition between individuals on the site results from species interactions, followed by the modification of the site by the organisms in a process described as reaction. Clements viewed stabilization as the development of a climax phase that is the result of the preceding five stages.

Clements' ideas dominated successional theory for many decades (Glenn-Lewin et al. 1992). There has been a vast amount of research investigating the mechanisms involved in each of his six processes since Clements' initial conceptual model was published. Many different conceptual models have been proposed describing mechanisms driving species turnover during succession since Clements (Gleason 1927, Tansley 1935, Egler 1954, Odum 1969, Drury and Nisbet 1973, Connell and Slayter 1977, Peet and Christiansen 1984, Walker and Chapin 1987, Tilman 1994; and others). Although there has been much debate and discussion over Clements' original concepts, many of his original successional processes remain valid today (Glenn-Lewin et al.

1992). The mechanisms involved in these processes are essential to understanding the variables important for both natural recovery and successful restoration of disturbances.

Nudation

Due to the multitude of characteristics of a disturbance, the nudation process can leave a variable amount of pre-disturbance influence on the site. “Ecological legacy” (Swanson and Franklin 1992) describes the plants, plant propagules, microbes, invertebrates and other organisms, as well as litter, soil organic matter, and physical structures that remain after a disturbance occurs. Variability in the remaining functional capacity of these important ecosystem components on a site produces a range of successional potential. Drastic disturbances such as volcanoes, floods, and mining can leave little if any ecological legacy in a site, initiating primary succession. Secondary succession occurs on sites with soil, seeds, rhizomes, or other pre-disturbance biotic influence remaining.

Working in semi-arid sagebrush steppe in northwestern Colorado, McLendon and Redente (1990) showed disturbance type affects successional trajectories and the resulting plant community dominance after 12 years though effects on seed banks, perennial plant parts, and edaphic conditions. Sites with the lowest levels of disturbance resulted in less impact on the seed bank and vegetation structure were dominated by perennial grasses that recovered quickly and prevented the establishment of shrubs that dominated the site prior to disturbance. Plots where more extensive disturbance occurred leaving the seed bank and existing perennial vegetation buried were dominated by annuals for the first four seasons. Following the fourth season, these plots began to be

dominated by the early-seral shrub *Chrysothamnus nauseosus*, and eventually by the dominant predisturbance shrub, *Artemisia tridentata*, 12 years after disturbance.

Migration

The process of migration depends to a large extent on the mode of dispersal of a species. Most species fail to disperse beyond a short distance from the parent plant (Malanson and Cairns 1997). Thus the larger or more isolated a disturbance is from a natural seed source, the less input of seeds, spores, animals, and organic matter from adjacent habitats it will receive. Seed dispersal rates can influence the pace of successional change, resulting in slower development of late-seral plant communities on isolated sites (Ash et al. 1994). Initial colonists on disturbed sites are generally dispersed by wind, water, or animals. Because wind is a dominant feature of the environment in arid and semi-arid ecosystems, horizontal and vertical movement of propagules is especially important for the recovery of these systems following disturbance (Chambers 2000). Soil surface characteristics have been shown to be important for the entrapment of seeds: soil texture (Chambers et al. 1991), surface litter (Fowler 1986, Stamp 1989), and surface roughness (Reichman 1984, Eckert et al. 1986) all have been shown to contribute to trapping seeds.

Establishment

Species that initially establish on disturbed sites originate either from surrounding vegetation or from buried viable seeds in the soil (Thompson 2000). The seed bank of a site can affect successional rates by influencing the initial composition of vegetation

following disturbance (Bekker et al. 1997). The use of seed banks in reestablishing natural vegetation can be a highly cost-effective method when feasible (van der Valk and Peterson 1989). However, many studies have found significant differences in the composition of vegetation and the seed bank without disturbance, due partly to the differential survival of species in the soil. Smaller seeded, shorter-lived, and weedy species all tend to have higher persistence in the soil (Davy 2002).

The environmental characteristics of sites that seeds are in contact with determine to a large extent the likelihood of seedling establishment (Harper et al. 1965, White, 1979, Pickett et al. 1987, Stamp 1989, Chambers 1995, and many others). Physical structures on the soil surface such as logs, rocks, cracks, holes, and existing vegetation create micro-topography that can act as “safe-sites” for seeds and seedlings. These safe sites enhance germination and establishment by relieving stresses related to low water potential, temperature extremes, wind, and low nutrient levels (Harper 1977). Differences in adaptations to micro-site characteristics can allow competing species to germinate and establish within a common plant community supporting higher species richness (Grubb 1977).

Competition

Competition between individuals for limiting resources occurs in all plant communities (Huston and Smith 1987) and is a central paradigm in their organization and structure (Connell 1983, Aarsen and Epp 1990). Successional dynamics have been linked to changes in the availability of resources following disturbance and competition between species in a community (Whittaker 1965, Tilman 1982, Parish and Bazzaz 1982, Inouye

et al 1987, McLendon and Redente 1991). Site conditions often dictate which resources are limiting and the extent to which they are limiting. Competition for light is important in structuring of both forests and productive grasslands during later successional stages as plant densities increase (Tilman 1988). However, due to the climatic conditions in arid and semi-arid regions, competition for belowground resources such as water and nutrients is most important in community structure and successional dynamics (Laurenroth and Coffin 1992).

Disturbance characteristics such as intensity and frequency impact water availability and nutrient pools by affecting species composition and edaphic conditions. The availability of essential resources changes throughout succession, resulting in replacement of dominant plant species over time (Odum 1969, Tilman 1982, Tilman 1985, McLendon and Redente 1991). Limitations in resources required for germination, establishment, growth and reproduction create selective pressures that have resulted in the evolution of physiological and life-history characteristics of early- and late-successional species (Huston and Smith 1987). These traits are often inversely correlated, and are termed *r*-selection and *K*-selection characteristics (MacArthur and Wilson 1967). Pioneer species such as annuals are described as *r*-selected, and can generally be characterized by rapid growth, short life span, high resource-acquisition rate, and production of many small, widely dispersed seeds. Late-successional, or *K*-selected species, grow slowly, have long life spans, a lower resource-acquisition rate, and produce fewer large seeds dispersed over shorter distances (Pianka 1970).

Availability of soil nitrogen (N) often decreases during succession in old-fields (Foster et al. 1980, Vitousek 1983, Dormaar et al. 1990). Limitation in the availability of

soil N has been shown to be a driving factor in successional dynamics (Parish and Bazzaz 1982, Tilman 1984, Inouye et al. 1987, Carpenter et al. 1990, McLendon and Redente 1991). Studies involving experimental manipulation of soil N availability during different successional stages of old-fields in semi-arid shortgrass steppe revealed significant effects on plant community composition and biomass (Paschke et al. 2000a). Increased soil N from fertilization increased the abundance of annual grasses and forbs on early-, mid- and late-seral sites relative to plots without fertilization. Reduction of soil N availability through the addition of sucrose resulted in a relative increase of late-seral perennials on all sites. Thus rates of succession were faster when soil N availability was lower, emphasizing the importance of decreased N availability in the development of late-seral plant communities.

Many factors can influence the competitive interactions between and among species during succession. Herbivory can have important consequences for successional rates and trajectories by affecting the competitive balance between species (Edwards and Gillman 1987, Urbanek 1989). Species composition, primary productivity, vulnerability to disease or drought can all be influenced by herbivory from both vertebrates and invertebrates (Whelan 1989, Farrell 1991, Helm and Collins 1997). Depending on whether early- or late-seral species are impacted more significantly, herbivory may accelerate or arrest successional rates, or can alter successional trajectories (Davidson 1993). Preferential grazing or browsing of early-seral species has been shown to reduce biomass and release nutrients from pioneer species favoring late-seral species, thus accelerating succession (Kielland et al. 1997, Olff et al. 1997, Grootjans 1998). Likewise, succession has been shown to be delayed when 1) herbivores preferentially

graze on understory species of the next successional stage (Dalhskog 1982); or 2) graze on early-seral N-fixing species, when N accumulation is important for succession (Ramsey and Wilson 1997). Granivory can slow succession by preferential consumption of large seeded late-seral species (Davidson 1993). Selective seed predation by rodents was shown to more negatively affect plant establishment of large-seeded species compared to small-seeded species on disturbed sites on the Colorado shortgrass steppe (Hoffmann et al. 1995). However, herbivory, weed competition, and resource stress such as low soil moisture or nutrients, may constrain plant establishment more than seed predation (De Steven 1991a, b). Pathogens may affect rates and trajectories of succession by killing or damaging dominants favoring the growth of other species (Oremus and Otten 1981, Van Andel et al. 1993, van der Putten et al. 1993).

Reaction

Clements (1928) believed reaction to be the key to succession because he believed it explained the progression of stages observed following disturbance. Egler (1954) proposed an alternative to Clements' idea of change in species dominance due to alteration of the habitat by previous species, which he termed "relay floristics". Egler placed emphasis on the concept that plant community change is "inseparable from time". He introduced the idea of "initial floristic composition" (IFC), which hypothesized that all the species that occur throughout the different seres are present from the beginning of the successional process. Only those species adapted to the early successional environment will be successful in the early-seral stages, while other species are present as seeds or seedlings. Once these early successional species die off, the later seral species

predominate. Egler's hypothesis was part of a shift in thinking of succession towards a process driven more by traits of individual species that started with Gleason (1927).

Since Clements' time, our understanding of the mechanisms of organization of plant communities and species change over time have progressed to include both competition and reaction as co-occurring processes within the same community, producing complex and variable effects (Callaway and Walker 1997). Connell and Slayter (1977) presented three models of succession that emphasized interactions among species. Their facilitation model slightly expands on the "relay floristics" concept that emphasizes changes to the environment which make it more suitable for later colonists. Connell and Slayter's facilitation model includes the idea that earlier colonists are actively replaced by later species through competition for resources and germination sites.

The tolerance model presented by Connell and Slayter (1977) resembles a combination of Egler's (1954) IFC model and their own facilitation model. This model states that modification of the environment by early colonists does not effect the recruitment of later succession species, and species change is a consequence of arrival times and growth rates of later colonists. Their third model, the inhibition model, hypothesizes that changes in environmental conditions as a result of early colonists inhibit establishment of other species. As long as early-seral species occupy the site, they are able to suppress late-seral species from invading the site. This model incorporates life history attributes of species, such as arrival time and longevity, in addition to competition between species. Connell and Slayter (1977) found more evidence in the literature to support this model than the facilitation or tolerance models.

Numerous studies have tested the models proposed by Connell and Slayter, as well as other models published since. Many experiments have produced data that suggest support for one or more of these successional paradigms (Iverson and Wali 1982, Chapin et al. 1994, Walker 1995, and many others). Yet it has been recognized that there are many combinations of these positive, neutral, and negative interactions between species that occur during all stages of succession (Connell et al. 1987, Huston and Smith 1987, Pickett et al. 1987, and others).

The value in these models lies in the understanding of the variables and processes that influence successional rates and trajectories. Thus, species change over time is a result of the interplay of disturbance and the sum of all the biotic and abiotic conditions of a particular site (Walker and Willig 1999).

Development of climax communities

Clements (1916, 1936) viewed the endpoint of succession as the development of a stable, self-reproducing plant community no longer subject to change without further disturbance. He recognized that plant community development was a consequence of regional climate, and that heterogeneity of soils at finer spatial scales than climate could result in different endpoints, which he termed ‘edaphic climaxes’. Although it is widely recognized that climatic conditions at the regional scale determine vegetation type (Holdridge 1967, Bailey 1998), many ecologists have disagreed with Clements’ deterministic and directional views of succession. Gleason’s (1917, 1939) viewpoint was that species assemblages were spatially and temporally independent, and that individual species were dispersed independently across a variable landscape. Given this, he saw no

reason to expect predictable communities. Even before Clements, Cowles (1901) recognized the inherent variability of succession trajectories, describing succession as ‘a variable approaching a variable’.

Ecologists now generally recognize the abiotic factors of climate and disturbance act as broad-scale filters, with biotic interactions acting at finer scales. These filters can act to remove plants or animals with particular traits or functions, or prevent initial establishment (Díaz et al. 1999). Some amount of prediction of succession may be possible, however, by modeling local conditions of a site. Major inputs to such a model would include: colonization probabilities for all species in the vicinity; establishment probabilities under site conditions; rates of habitat amelioration; interactions among species; alteration of colonization and establishment probabilities over time as dispersal agents, facilitation, inhibition, and herbivory change; and changes in environmental conditions such as light, soil moisture, and fertility. Inherent to any such model must be the development of multiple stable states as end-points of succession (Walker and del Moral 2003).

Often systems do not respond predictably following disturbance, producing inconsistent and often unexpected plant communities. Sites that are dominated by early-seral or exotic species may persist in such a degraded state indefinitely (D’Antonio and Vitousek 1992). Recent studies suggest that unexpected outcomes are often due to changes in biotic factors and feedback between biotic and abiotic factors that developed following disturbance (Suding et al. 2004). Often degraded systems are occupied by species that have distinctive traits that change characteristics of the system, such as nutrient cycling and distribution and disturbance regimes (Gordon 1998, D’Antonio and

Meyerson 2002). Once system processes have changed, feedbacks can then make systems resistant to further change (Mack et al. 2001). Lack of landscape connectivity to sources of seed can limit the regenerative potential of native species on a site and often results in dominance by exotic species (Bakker and Berendse 1999, Smith et al. 2002). Patterns of herbivory may also change following disturbance, causing positive feedbacks between reduced plant cover and increased losses of biomass to grazing that maintain a degraded system (Van de Koppel 1997).

The process of returning of a degraded system to a more 'natural' state resembling site conditions prior to disturbance requires an understanding of the biotic and abiotic factors at work in shaping the system. Rather than allowing a system to reach a degraded state through invasion of exotic species or soil losses due to wind or water erosion, managers often turn to techniques based on the knowledge of the dynamics of species replacement. These methods are aimed at both minimizing degradative processes and accelerating succession in order to help them meet predefined goals of plant community structure and function.

RESTORATION OF DISTURBANCES

Hobbs and Norton (1996) identified several key processes in restoration ecology that they consider to be essential to successful restoration: 1) identification of processes leading to damage or degradation; 2) development of methods to reverse damage or degradation; 3) determination of realistic goals for restoration; 4) development of practical techniques for implementing goals appropriate to the project; 5) development of easily observable measures of success; 6) document and communicate these techniques

for inclusion in future strategies; 7) monitor the system in order to assess progress relative to goals.

System degradation and reversal

Degrading and damaging processes can lead to a variety of ecosystem responses depending on the characteristics of the disturbance. The impact of the disturbance and potential for reversal varies depending on which system components and processes are affected (Brown and Lugo 1994). Natural disturbances such as fire, flooding, and grazing may require management decisions in order to ameliorate the causes of system degradation or damage. Human-caused disturbances such as road construction that remove vegetation and disturb soils are often spatially and temporally distinct processes. Amelioration of further system degradation generally entails controlling soil loss from erosion until vegetation can be established and colonization of invasive species is controlled.

Goals of restoration

Society for Restoration Ecology (SER) defines restoration as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004). This definition implies a continuum from rebuilding totally destroyed sites, such as those associated with drastic disturbances like mining, to the management of relatively unmodified sites for the purposes of conservation of protected species or returning a site to sustainable levels of productivity (Hobbs and Norton 1996). Inherent

to the concept of a continuum of restoration is the importance of determining realistic goals for individual projects.

Determination of the desired end-point for a restoration project should be developed appropriate to the scope and reasons for the restoration effort (Ehrenfeld 2000). Goals for restoration of an area impacted by coal mining will not apply to the restoration of habitat for an endangered species. Realistic goals recognize both the ecological limitations and the socioeconomic and cultural barriers to successful implementation (Hobbs and Norton 1996). Specification of goals for restoration projects is important because it sets project expectations, drives project planning, and determines the kind and extent of post-implementation monitoring (Ehrenfeld 2000).

Endpoints of restoration may focus on several components of a system. Structural endpoints include the composition and diversity of species present on a site. Functional endpoints relate to system processes such as primary production or decomposition (Palmer et al. 1997). Considerable evidence suggests feedbacks between species composition and ecosystem processes, which both develop over time. Therefore it may be appropriate for restoration projects to include sequential, multi-step goals aimed at assessing the structure and function of systems as well as the linkages between them (Palmer et al. 1997).

Restoration Methods

The purpose of the application of methods in restoration is to accelerate the development of plant communities through the manipulation of the biotic and abiotic factors of a site following disturbance. Appropriate methods for restoring a site depend

on the site characteristics that limit project goals from being achieved. Characteristics of the disturbance such as size, shape, and severity can affect the existing vegetation and seed bank, colonization rates from surrounding vegetation, and erosion potential such that succession to late seral plant communities may take several decades. Presence of populations of exotic species on the site prior to disturbance or in the surrounding vegetation increases the risk of their establishment and can prevent the establishment of perennial native species indefinitely. Thus, the most effective approach in restoring a disturbance may be different for different sites.

Human disturbances are generally characterized by the removal of existing vegetation, disturbance of the soil profile to some depth, frequently followed by compaction of the soil. There are several general site manipulations that apply to these types of disturbances that accelerate succession: site preparation, addition of plant material to the site, and control of undesirable species. Studies on drastically disturbed lands show clear differences in vegetation cover, biomass production, and soil conditions with reshaping topography, replacement of subsoil and topsoil, and the addition of plant propagules (Iverson and Wali 1992)

Site preparation involves activities that create seedbed conditions conducive for effective germination, establishment, and persistence of the desired vegetation on the site. Disturbances that drastically disturb the soil and result in the mixing of soil profiles create conditions of low water holding potential and nutrient availability. The separation of topsoil from subsoil or additions of topsoil following disturbance greatly improve soil characteristics important for plant establishment and growth such as infiltration rates, water holding capacity, soil structure, organic matter and nutrient availability (Packer and

Aldon 1978). Topsoil can also contain organisms that accelerate plant community development such as plant propagules and soil microbes (Munshower 1994).

Compaction of soil often results from the use of heavy machinery during disturbance activities. Ripping or harrowing breaks up surface crusts, subsoil compaction, and lowers overall bulk density of soils to improve infiltration rates and water-holding capacity of soils (Luce 1997). Ripping has been shown to facilitate forest restoration following mining (Ward et al. 1996) and improve native plant establishment following road abandonment (Cotts et al. 1991). The creation of depressions in the soil surface can further improve infiltration and decrease erosion allowing for additional micro-sites that enhance plant germination and establishment in arid and semi-arid regions (Munshower 1994). The placement of rocks, logs, and plant litter can improve conditions for plant germination and establishment by the creation of safe sites (Winkel et al. 1991, Peterson et al. 2004).

Mulches are used to improve seedbed characteristics by reducing evaporation of soil moisture, moderating temperatures, reducing wind velocities at the soil surface, controlling erosion, increasing infiltration rates, and supplying nutrients through decomposition of organic material (Packer and Aldon 1978). Materials appropriate for use as mulch include wood fiber, straw and hay, excelsior, jute matting, and wood chips. Mulches such as straw and hay are subject to loss or redistribution by wind or overland flow of water. Crimping is an effective method of keeping straw or hay in place by pushing it partly into the seedbed. Organic tackifiers can be added to hydromulch, which are applied in a water slurry. This method is an economical way of mulching large areas such as mined lands or roadsides.

Seeding of a nurse crop, such as an annual or short-lived perennial species, can act to stabilize soil on sites where erosion potential is high. Nurse crops can act like mulches by reducing wind velocity and soil surface temperatures (Valentine 1989). The use of a nurse can also reduce annual grass establishment by competing for soil moisture during the first year (Munshower 1994). However, they compete with perennial plants for limiting soil resources as well, often resulting in altered patterns of vegetation cover and species diversity in the resulting plant community (Beyers et al. 1993, Regelbrugge and Conrad 1990). For this reason, nurse crops are not recommended in areas where annual precipitation is less than 30 cm (Munshower 1994). Studies on roadside restoration in Glacier National Park have shown that seeding of a nurse crop had no effect in establishment of native vegetation (Tyser et al.,1998). However, Densmore et al. (1990) showed that seeding of a nurse crop in Denali National Park reduced establishment and growth of the desired native species.

Restoration of disturbances often includes artificial modification of species availability by the addition of plant propagules to the site. Direct seeding is a common method of introducing species onto disturbed sites. Seed can be either drilled or broadcast onto the site. Good soil-seed contact is required for seeding to be effective. Seed planted in soil without large air pockets has a more constant supply of soil moisture resulting in more reliable germination and establishment (Whisenant 1999). The soil surface should be firmed prior to drilling or following broadcast seeding to reduce large air pockets.

The success of seeding is dependant on proper site preparation, appropriate seeding techniques, and correct timing. Depth of planting depends on seed size and germination

requirements. Drill seeding is preferred for larger seeded species and less diverse seed mixes. It has the advantage of placing seed at a specific depth in the soil guaranteeing proper seed placement. The accuracy in seed placement of this technique maximizes the probability of successful germination and plant establishment (Munshower 1994).

Broadcast seeding is any method of seed dispersal that drops seed on the soil surface. Seeding rates are normally doubled for broadcasting over drilling due less precision in proper seed placement. Seed should be lightly covered with soil by hand raking or through some mechanical process such as harrowing. Hydroseeding is a form of broadcast seeding where seed is mixed with water, emulsifier, and a carrier such as wood fiber and sprayed onto the site. Broadcast seeding has several advantages over drilling in restoring natural areas: 1) it results in a more natural looking plant community due to the random dispersal pattern of seed, 2) a more diverse seed mix can be used due to the variety of depths of soil spaces seed can come into contact with, 3) it can be accomplished on small areas and sites inaccessible to heavy equipment.

Proper timing is important to the success of seeding in restoration. In arid and semi-arid regions, the best time to seed is immediately prior to the period of most predictable precipitation (Moser and Newman 1988). In a study of grass seedings into wheat stubble in North Dakota, McWilliams (1955) reported better establishment of cool-season grasses when seeded September to October, while warm-season grasses established better when seeded between April and May. Reis and Hofmann (1996) showed significant variability in the number of seedlings m^{-2} for the same seeding date in different years for five grasses species in North Dakota. Spring seeding in semi-arid and arid areas where spring precipitation is abundant seems to be more advantageous than fall seeding on average

(Hart and Dean 1986). Seed sown in the fall is subject to loss from seed predation and desiccation. Weeds germinate in the spring when sown seeds germinate creating competition that can reduce establishment of desired species. Spring seedings can be advantageous due to required cultivation that can help control weed germination and reduce competition (Munshower 1994).

Effective germination and establishment of a seeding can depend on proper selection of species in a seed mix. Germination requirements vary for different species depending on the habitat type species are adapted to. Some small-seeded species that cannot emerge from burial have light requirements for germination, while germination of some large-seeded species is inhibited by light (Davy 2002). Species composition of the seeding mix depends on the goals of the restoration project. If the goal for a project is maximum forage production, the seed mix would be different than if the goals are for a species rich native grassland. Working in a semi-arid shrubland in northwest Colorado, Stevenson et al. (2000) showed that development of a community dominated by late-seral native perennial species is accelerated when late-seral species are seeded compared to seeding of early-seral species.

A second method of manipulating species availability at a site is transplanting of vegetation directly onto the site. This method is effective for clonally propagated species such as perennial grasses that produce adventitious roots (Ranwell and Boar 1986) or cuttings from certain trees and shrubs such as *Salix* spp. (Schiechl and Stern 1996). Alternatively, seed may be germinated and propagated in a greenhouse until sufficiently large enough for transplanting onto the site (Whisenant 1999).

Transplanting vegetation can achieve the desired restoration goals more rapidly than seeding or natural succession in certain systems. On unstable sites where erosion may result in seeding failure the addition of seedlings provides an immediate stabilizing effect (Whisenant 1999). Transplanting container-grown individuals is preferred for species with erratic germination or slow seedling growth (Packham et al. 1995). When restoring communities dominated by long-lived woody perennial species, transplanting may speed successional rates considerably. Restoration of alpine tundra sites pose unique challenges due to harsh conditions, such as desiccating winds, limited soil resources, and a short growing season. Natural succession on disturbed sites is often slow and unpredictable in these areas (Macyk 2000) and seeding often leads to high seedling mortality due to severe conditions (Roach and Marchand 1984). However, successful restoration of alpine tundra has been reported with the transplantation of turf (Buckner and Marr 1988, Urbanska 1997).

There are disadvantages to transplanting as a technique to introduce vegetation to a disturbed site. Planting failure can occur due to water stress or improper planting technique. Competition for water and nutrients from grasses and forbs is a common cause of tree and shrub death following transplanting. Salvage of existing vegetation, propagation under horticultural conditions, and planting out individuals on-site can all be labor-intensive and result in high costs. Individuals also require frequent maintenance such as watering during the first few years after transplanting to ensure survival, adding to these costs.

Evaluation of restoration success

What is meant by "recovery" of a system? The SER Primer (SER 2004) states a system has recovered "when it contains sufficient biotic and abiotic resources to continue its development without further assistance or subsidy". The stated attributes of a restored system include: 1) the presence of appropriate species, functional groups, and environmental conditions; 2) normal ecological functioning, including resilience to further disturbances within the natural range of variability; 3) integration into the landscape, including normal abiotic and biotic flows and exchanges; and 4) elimination of the processes leading to damage or degradation (SER 2004).

What is selected as the desired end-points of a restoration project directly affect the assessment of success. Thus the components of a site to be measured in determining success of a project should focus on the desired characteristic of the particular site, which may be different for each project. Ruiz-Jaen and Aide (2005) reviewed all articles published in the journal *Restoration Ecology* from 1993 through 2003 (Vols. 1[1] – 11[4]) to determine what attributes are most often measured in determining restoration success. Measures of success were most often based on: 1) species diversity; 2) vegetation characteristics (such as cover); or 3) ecosystem processes.

Plant and arthropod species diversity are the most common measures of diversity recovery. Diversity is measured by determining richness and abundance of organisms. These can be measures of diversity within functional groups (Peterson et al. 1998), or within different trophic levels (Nichols and Nichols 2003). Measures of diversity have been thought of as an indirect assessment of ecosystem resilience (Peterson et al. 1998). Studies on restoration success can include measures of diversity of several taxa. In

studies on coastal dune recovery in South Africa, van Aarde et al. (1996) measured seedlings, millipedes (Order: Diplopoda), beetles (Order: Coleoptera), birds (Class: Aves), rodents (Order: Rodentia) and shrews (Order: Insectivora).

Vegetation characteristics can include plant cover, density, biomass, and height. Vegetation structure is often included in assessment of restoration success because it is relatively rapid to measure resulting in lower costs. These measures can be important because they are often useful in predicting the direction and rate of succession. Ecologists often assume that the recovery of fauna and ecological processes follow the establishment of native vegetation subsequent to disturbance (Toth et al. 1995, Young 2000). Development of complexity in vegetation structure has been shown to enhance seed dispersal (Robinson and Handel 1993) and nutrient availability (Bradshaw 1997).

Measures of ecosystem processes can also provide information on ecosystem resilience as well as self-sustainability. Nutrient cycling is important for the establishment and persistence of organisms in a system because it determines the availability of organic and inorganic components to individuals (Davidson et al. 2004). Evaluation of nutrient cycling rates is often measured indirectly by estimating nutrient availability (Fuhlendorf et al. 2002). Rhoades et al. (2002) measured soil nitrogen, soil organic matter (SOM), organic carbon, and litter dynamics to measure the recovery of a tropical montane forest in Ecuador. Biological interactions crucial to species establishment and persistence that have been evaluated for restoration success include seed dispersal (Holl et al. 2000, Donath et al. 2003), mycorrhizal colonization (Greipsson and El-Mayas 2000), herbivory (Helm 1994), and pollination (Holl 1995).

Assessment processes can be expensive and complicated. Few studies have the financial resources to measure many variables or for long-term studies that are required for some attributes. Ecological processes are slower to recover in comparison to diversity and vegetation structure (Chambers et al. 1994, Kindscher and Tieszen 1998) and often require long-term monitoring or multiple measurements which increase the time and costs of a project (Herrick 2000). For these reasons ecological processes are utilized less frequently than diversity or vegetation structure in assessing restoration success (Ruiz-Jaen and Aide 2005).

A frequent goal of restoration projects is the re-creation of a system that approximates pre-disturbance conditions. This can create many questions for ecologists and practitioners when systems have been extensively degraded by a history of land management decisions such as overgrazing and fire suppression (Allen et al. 2002). For many anthropic disturbances where disturbance is spatially and temporally distinct such as road construction, the structure and function of a site can be assessed prior to disturbance. Alternatively, nearby undisturbed systems can serve as a model or reference for approximating site characteristics prior to disturbance. This allows a comparison of values for a similar site under current conditions such as climate and natural disturbance regime (White and Walker 1997).

Reference information is used to set restoration goals, to determine restoration potential and develop appropriate restoration methods, and evaluate the success of restoration efforts. Thus, the selection of appropriate reference sites is critical in the restoration process. Inherent to the proper selection of reference sites is the need to understand the spatial and temporal variability of natural systems (White and Walker

1997). Temporal variation includes seasonal and inter-annual variation, as well as the dynamics of disturbance and succession that all systems are subject to. Dominance of plant cover and production, nutrient cycling, and decomposition rates all shift according to many variables, such as precipitation levels, temperature, and biological interactions (Walker and Boyter 1993). Spatial variation exists because of variability in the physical environment and the mosaic of successional states created by natural and human disturbances. Physical variables include differences in soil, topography, relief, edge effects on microclimate, isolation from similar sites, and patch size (Walker and Boyter 1993). The spatial correlation among biotic and abiotic variables produces a “distance decay” of similarity between any two places that states that the similarity between two places will decrease with increasing distance between them (Tobler 1970). As a result of the spatial and temporal variation of natural systems, several authors have recommended reference sites be as close as possible to the disturbance when environmental conditions are similar, as well as sampling multiple reference sites in order to estimate the natural range of variability (Hobbs and Norton 1996, White and Walker 1997, SER 2004).

RESTORATION IN RMNP

Goals of restoration

National Park Service goals for restoration of anthropic disturbances are: 1) site stabilization, 2) control of exotic species, and 3) the creation of an appropriate plant community dominated by native late-seral species. Site stabilization is a short-term goal that can be achieved by the establishment of vegetation on disturbed sites. Vegetation acts to stabilize sites by reducing runoff and rates of soil loss (Gross et al. 1991). Many

exotic species in RMNP are early-seral invader species that rapidly establish following disturbance. They are typified by rapid rates of establishment and growth, but are not good competitors against perennial slower-growing species for limiting resources. Establishment of native late-seral perennial species on disturbed sites to compete with exotic species will control their establishment.

The long-term goal of the restoration of disturbed sites in RMNP is the creation of a plant community as similar as possible to the plant community that existed on the site prior to disturbance. The goal is for the disturbed area to "blend in" to the surrounding vegetation to the greatest extent possible. For this reason, adjacent areas of relatively undisturbed native vegetation and similar environmental conditions are often used to set restoration goals. Similarity to surrounding vegetation encompasses the factors commonly used to assess restoration success: 1) vegetation structure, 2) species diversity, and 3) ecological processes.

Preservation of genetic integrity

An additional goal of restoration is the preservation of the genetic integrity of the native plant communities to the greatest extent possible (NPS 2004). Preservation of genetic integrity involves the maintenance of the genetic diversity and structure of the native plant population characteristic of the site. Genetic structure of a population describes the non-random distribution of genetic diversity in space or time. Inter-specific genetic diversity is the diversity of species within and among populations in a given region. Intra-specific genetic diversity is a measure of the different genotypes and alleles found within and among populations of a given species. Genetic variation is necessary

for populations to undergo changes in response to changing environmental conditions. Therefore maintaining genetic variation in a population is believed by many to be important for its long-term survival (Lacy 1987).

Numerous studies have shown that plants evolve adaptations to local environmental conditions (Linhart and Grant 1996). This is reflected by the ability of a plant to adjust to a fluctuating environment by structural modification and physiological adjustment (Conrad 1983). Brown and Amacher (1999) state that adaptability is the physiological range of stress tolerance of a population to environmental conditions. These authors assert that populations adapted to particular conditions define a genotype of that species. Local genotypes of species are often called ecotypes, and have been shown to be more effective in establishment and persistence on a site following disturbance, perhaps due to adaptation to local edaphic and environmental conditions (Cotts et al. 1991, Lippitt et al. 1994).

Introduction of non-local and possibly maladapted genotypes is a major concern because of the potential for failure of the restoration. Not only is restoration success potentially compromised by maladaptation, but the use of plant material collected from a limited number of sources may produce founder effects. Founder effects can occur when restored populations represent only a portion of the allelic diversity of the source populations. When genetic variation is low, inbreeding of a population may result in reduced fitness and ultimately impact the self-sustainability of the population. Founder effects have been identified in restored populations of the endangered Mauna Kea silversword *Argyroxiphium sandwicense* ssp. *sandwicense* (Robichaux et al. 1997)

Non-local genotypes may also negatively affect adjacent native plants populations adapted to local populations through gene flow. Consequences of gene flow are not well understood due to a lack of empirical studies (McKay et al. 2005). The use of non-local genotypes can have consequences for local indigenous populations through multiple mechanisms: 1) genetic swamping, 2) heterosis, 3) outbreeding depression (Hufford and Mazer 2003).

Genetic swamping is the rapid increase in the frequency of an introduced genotype (or allele) that might lead to the replacement of local genotypes (or alleles). A recent study of common reed *Phragmites australis* showed that the current expansion of this species native to North America is due to the introduction of a genetic variant from Eurasia in the early 1900's (Saltonstall 2002). Use of particularly aggressive cultivars of native species in a restoration project can possibly result in the displacement of locally adapted ecotypes adjacent to the site.

Use of genotypes with compatible mating systems can result in intra-specific hybridization between the two. Heterosis can result from intra-specific hybridization, producing first generation hybrids with increased vigor. Hybrid fitness is enhanced relative to the parent generation due to the masking of recessive deleterious alleles or by an overall fitness advantage produced by heterozygosity (Hufford and Mazer 2003). Intra-specific hybridization can result in a reduction of fitness of progeny as well, known as outbreeding depression. Outbreeding depression can be the result of one of several mechanisms. When local populations exhibit local adaptation, hybridization may cause a 'dilution' of locally adapted alleles creating hybrid progeny with reduced fitness. Hybrid breakdown can result from mating between genotypes with distinct combinations of

interacting groups of alleles, called co-adapted gene complexes. If recombination occurs between the corresponding co-adapted gene complexes of two different genotypes, a reduction in fitness can result (Hufford and Mazer 2003)

Sources of plant material for restoration

In order to preserve the genetic integrity of a restored population, collection of local material is only the beginning. Sampling from a sufficient number of individuals within a population is necessary to adequately represent the genetic variation and structure of a population. Information on the variation in genotypes and genetic structure of populations is rarely available, but general guidelines for the collection of plant material should be followed.

The number of plants from which material is collected depends not only on the genetic information of a population, but on its size. In order to decrease the probability of loss of genetic information, material should be collected from as many individuals as possible in a population. When collecting seed, Namkoong (1988) suggests that several hundred to a few thousand individuals may be necessary for adequate sampling of genetic diversity in a population such that there is a low probability of loss of infrequent alleles. If populations are relatively genetically homogenous or there is interest only in acquiring the most common alleles, fewer plants can be sampled. Lippitt et al. (1994) suggests collecting seed from a minimum of 50 individuals for most restoration projects.

Genetic variation can be captured by collection from individuals in different stands that have a range of environmental conditions. A range in environmental characteristics may greatly affect germination and growth traits of the seed (Hartmann and Kester 1983).

However, the structure of genetic variation among plants of different stands should determine sampling strategies. Genetic structure is related to several factors of a particular species: 1) the pollination mechanism of the species, 2) propagule and pollen dispersal, and 3) life form (Loveless and Hamrick 1984).

Self-pollinating species generally exhibit greater genetic variation between different populations. Outcrossing species usually have less genetic variation between different populations, but will have more diversity within the same population relative to a selfing species. Species with mixed mating systems frequently show genetic diversity and structure in between selfing and outcrossing species, the extent of which is dependant on the proportion of progeny produced by each method (Conner and Hartl 2004).

Dispersal mechanisms of pollen and seed (or progeny) can have an affect on genetic structure of populations. Animal dispersed seed creates genetic structure dependant on animal behavior. Wind dispersal of pollen or seed reduces diversity between populations, whereas gravity or explosive dispersal of seed creates more structure by increasing the among population diversity (Conner and Hartl 2004).

The longer lived a perennial species is, the less likely populations of that species will have diversity between populations. Annual species have more highly differentiated populations due to faster generation times resulting in more progeny and more chances for recombination (Loveless and Hamrick 1984). Species can have any combination of these three factors which all interact to form the genetic structure, and all should be considered when collecting material with the goal of maximizing genetic diversity in restored populations.

Cost-effectiveness analysis

Multiple goals for restoration and the use of several attributes for the assessment of restoration success can make the determination of Best Management Practices (BMPs) for restoration difficult. A single treatment may not be most effective in all aspects of success criteria, making a conclusion on the most effective approach ambiguous. Managers are regularly faced with limitations in the availability of financial resources for restoration projects. Given this monetary constraint, BMPs are often determined by the combination of costs and the ability to meet project objectives for a given treatment. Thus managers are in need of tools in order to determine optimum approaches for achieving restoration success with limited financial resources.

Cost-effectiveness is an analytic tool which can assist decision-makers with limited financial resources in choosing an optimum treatment among several different restoration approaches (Pinjuv et al. 2001). This analytic approach compares different courses of action by evaluating the costs and effectiveness in achieving some specified goal (Quade 1967, Gittinger 1982). Costs are based on labor, equipment, fuel, and other direct costs. Effectiveness is estimated by a treatment's ability to meet pre-defined project objectives. This technique is based on the selection of acceptable measures that quantify a treatment's effectiveness, which is determined by analyst assumptions of appropriate attributes of success.

Cost-effectiveness analysis has advantages over other economic decision-making approaches. The use of measures for estimating treatment effectiveness allows decision-makers to follow analytic assumptions of attributes that indicate restoration success. Other analytic approaches to decision-making can mask these assumptions of criteria for

effectiveness. For example, cost-benefit analysis can conceal assumptions of effectiveness measures by assigning dollar values to non-market benefits, such as cover or richness of native species (Quade 1967).

METHODS

SITE DESCRIPTION

All data collected for this study was gathered from lands within or directly adjacent to Rocky Mountain National Park (RMNP). Rocky Mountain National Park is located in north-central Colorado just west of Estes Park, CO, and covers 107,323 hectares ranging in elevation from approximately 2300 m to 4345 m. Data were collected from 20 disturbed and 20 adjacent undisturbed sites within the montane zone (Figure1) ranging in elevation from 2380 m to 2740 m (Tables 1 and 2).

Climate in RMNP is highly variable depending on elevation. Sites within the montane zone are described as temperate semi-arid steppe, with most precipitation occurring in the form of summer rain (Bailey 1998). Average annual precipitation in this region of the park is 382 mm for the period 1980 through 2004 (NADP 2006). Annual daily temperatures average 6 °C, with an average daily maximum temperature of 25 °C occurring in July and an average daily low temperature of -8 °C occurring December through February for the period of record 1948 through 1994 (NCDC 2006).

The formation and subsequent properties of soils in RMNP are strongly influenced by landform and climate. Upland soils in the lower elevations of the park, particularly on the east side of the park where most of the study sites were located, are deep, loamy-course textured, and have dark-colored surface horizons. Soil taxonomic classes were determined for all undisturbed soils adjacent to disturbed study sites (Table 2). Soils in these areas are somewhat excessively drained and were formed on structural benches, or

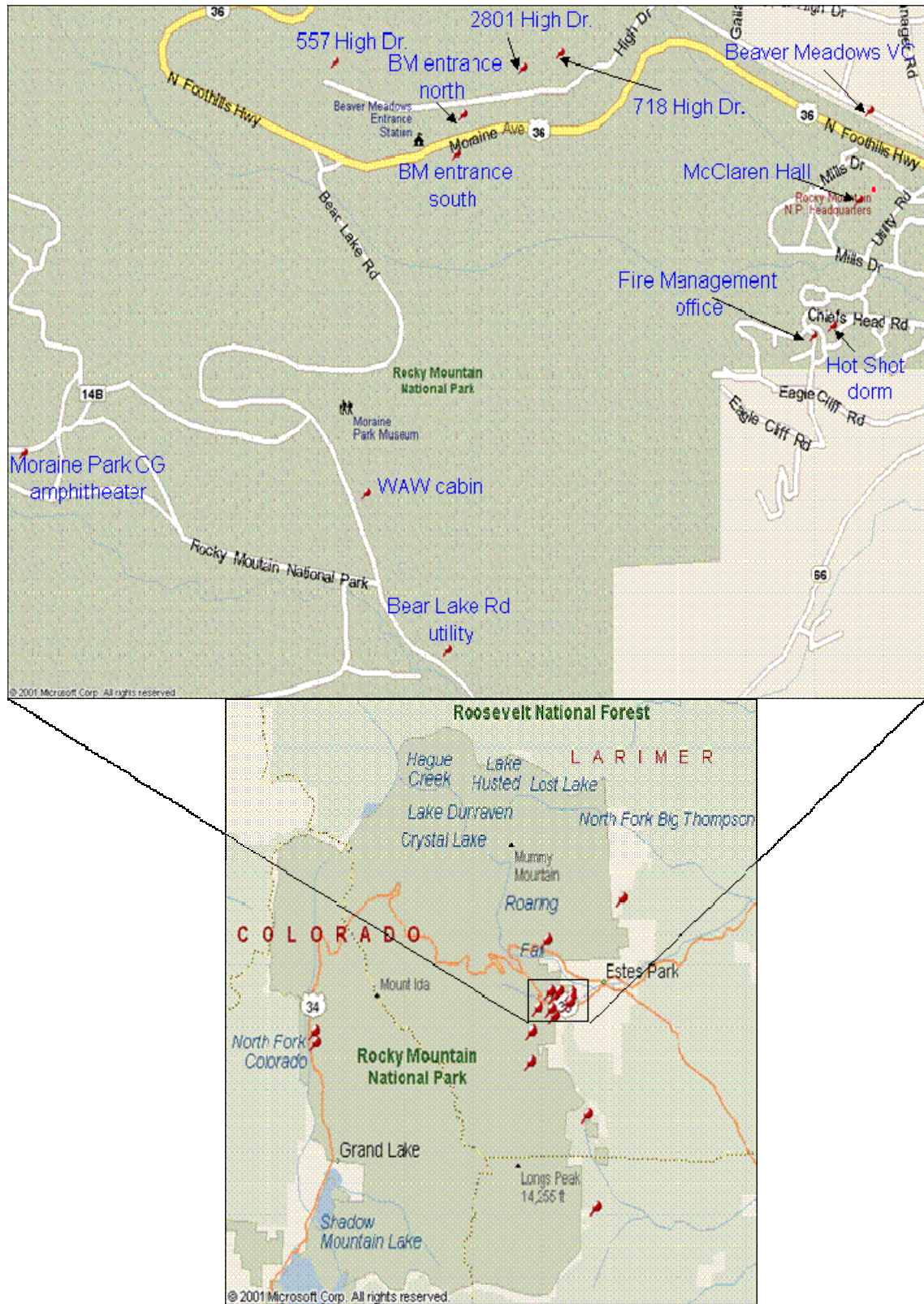


Figure 1. Locations of disturbed and adjacent undisturbed reference sites, Rocky Mountain National Park, Colorado.

Table 1. Description of 20 disturbance study sites, Rocky Mountain National Park, Colorado.

Site	Elevation (m)	Years Since Disturbance	Disturbance Size (m ²)	Restoration Treatment*	UTM coordinates (Datum WGS84/ NAD83)
Beaver Meadows	2380	3	7650	Seeded	13 452298E 4468660N
Fire Management Office	2380	3	790	Seeded + Transplanted	13 452127E 4468997N
McGraw Ranch	2440	3	1250	Transplanted	13 457322E 4475829N
MPCG Amphitheater	2490	3	615	Transplanted	13 448996E 4467777N
BM Entrance-North	2500	3	5050	Seeded	13 450557E 4468572N
BM Entrance -South	2500	3	3000	Seeded	13 450557E 4468526N
McClaren Hall	2380	5	1855	Seeded + Transplanted	13 452363E 4468336N
Sprague Lake	2650	5	1370	Transplanted	13 448290E 4463509N
Fisherman's Access	2680	5	750	Seeded	13 427520E 4463856N
Jenning's Bridge	2680	5	1500	Seeded + Transplanted	13 427186E 4459585N
Twin Sisters	2740	5	290	Transplanted	13 453938E 4459585N
Hot Shot Dorm	2380	8	230	Transplanted	13 452166E 4468031N
WAW cabin	2460	8	100	Seeded + Transplanted	13 450481E 4467434N
Wild Basin	2560	8	300	Transplanted	13 454478E 4452294N
Bear Lake Rd. Utility	2460	13	3220	NT	13 450559E 4467185N
718 High Dr.	2500	13	610	NC	13 451379E 4468945N
2801 High Dr.	2510	13	1900	NC	13 451230E 4468818N
Fall River Entrance	2510	13	150	NC	13 449866E 4472782N
557 High Dr.	2520	13	490	NT	13 450374E 4468796N
Hollowell Park	2560	13	125	NT	13 448217E 4465864N

*Restoration treatments:

NT = no treatment applied

NC = seeded nurse crop

Table 2. Taxonomic classes of undisturbed soils adjacent to 20 experimental disturbed sites, Rocky Mountain National Park, Colorado.

Site	Taxonomic class
Beaver Meadows VC	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
Fire Management Office	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
McGraw Ranch	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
MPCG Amphitheater	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
BME-North	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
BME-South	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
McClaren Hall	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
Sprague Lake	Sandy-skeletal, mixed, Lamellic Cryorthents
Fisherman's Access	Loamy-skeletal, mixed, superactive, Lamellic Haplocryalfs
Jenning's Bridge	Loamy-skeletal, mixed, superactive, Lamellic Haplocryalfs
Twin Sisters	Loamy-skeletal, paramicaceous Lamellic Eutrocrepts
Hot Shot Dorm	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
WAW cabin	Loamy-skeletal, mixed, superactive frigid, Alfic Argiustolls
Wild Basin	Sandy-skeletal, mixed, Lamellic Cryorthents
Bear Lake Rd. Utility	Loamy-skeletal, mixed, superactive frigid, Alfic Argiustolls
718 High Dr.	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
600 High Dr.	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
Fall River Entrance	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
557 High Dr.	Coarse-loamy, paramicaceous, frigid Pachic Haplustolls
Hollowell Park	Fine-loamy, paramicaceous, frigid, Typic Argiustolls

mountain slopes either in alluvium, colluvium, or residuum derived from schist, granite, or gneiss (NRCS 2005).

Composition of montane grasslands and shrublands can vary considerably according to site conditions (Peet 2000). Montane grasslands and shrublands of this region are a patchwork of *Pinus ponderosa* stands interspersed between openings dominated by bunchgrasses, with an abundant and diverse array of forbs. Depending on site conditions, shrubs may form a significant component of the vegetation as well. Dominant grasses on undisturbed montane sites include *Hesperostipa comata* (Trin. & Rupr.), *Bouteloua gracilis* (Willd. Ex. Kunth) Lag. Ex. Griff, and *Muhlenbergia montana* (Nutt.) A.S.Hitchc.; common forbs include *Heterotheca villosa* (Pursh) Shinnery, *Grindelia subalpina* Greene; common subshrubs include *Artemisia frigida* Willd. and several species of the genus *Potentilla*; shrubs are mainly *Artemisia tridentata* Nutt., *Chrysothamnus viscidiflorus* (Hook.) Nutt., and *Purshia tridentata* (Pursh.) DC.

EXPERIMENTAL DESIGN

The 20 experimental sites sampled in this study were initially disturbed through anthropogenic activities, such as construction/ improvement of park facilities, installation of utilities, and road, trail and parking lot construction/ removal. Experimental sites are areas where either some manipulative revegetation activity took place following a disturbance or where the disturbed area was left to revegetate naturally with no manipulation of the area. Sites were selected based on the time since restoration activities took place or time since disturbance, as well as the type of restoration treatment applied (Table 1).

Undisturbed areas adjacent to the disturbance were also sampled for comparison to disturbed areas and are referred to as reference areas. Due to the physical proximity of these reference areas to the disturbed area and the frequency of human activities in these areas of the park, reference areas cannot be considered truly 'undisturbed'. Rather they are areas of similar physical and ecological characteristics to the disturbed site, but have not been subjected to the same intensity or severity of disturbance.

Reference areas are commonly used as a standard to evaluate the level of restoration success (Chambers 1994, White and Walker 1997, Passell 2000, Purcell et al. 2002) as well as being representative of a desired end-point of the restoration process (SER 2004). Management guidelines for restoration in RMNP state that one of the goals of restoration is the creation of a plant community similar in characteristics such as cover, biomass production, and species composition as adjacent undisturbed plant communities, such that the disturbance 'blends in' with the surrounding landscape (Connor 2005). Thus, data from disturbed areas were compared to reference areas in order to determine the relative success of different restoration approaches.

Vegetative cover by species was determined during the 2004 and 2005 growing seasons on disturbed and reference sites. Cover was estimated by use of the line-point transect method (Bonham 1989), with points read every 0.5 m along a 50 m transect. A minimum of five transects were randomly sampled in disturbed sites within the boundaries of the disturbed area, as well as randomly within an equivalent area for adjacent reference sites. The total number of transects to be sampled was based on the

level of variation in cover according to the following equation for sample adequacy (Bonham 1989)

$$n = \frac{t^2 s^2}{\left(k \bar{X} \right)^2}$$

where n is the estimated number of observations needed to obtain an estimate of the difference between the sample mean ($\bar{X}$) and the true population average (μ) within a given probability (k). The value for t is taken from a table of the Student's t distribution. Its value is dependant on the number of observations used to estimate the sample mean ($\bar{X}$) and variance (s^2), as well as the confidence level desired for using $\bar{X}$ as an estimate of μ . The value used for k was 0.1, and the confidence level used was 90%. Using these values, the calculation of sample adequacy allows for a detection of a 10% change in total live cover 90% of the time under repeated sampling.

Soil samples were taken from each site at the time of vegetation sampling. Eight one-inch diameter cores were randomly taken to a depth of six inches using a standard 1" auger bit in a cordless drill. The samples were combined into one composite sample per site and analyzed at the Colorado State University Soil Testing Laboratory for pH, electrical conductivity (EC), percent organic matter, texture, $\text{NO}_3\text{-N}$, P, and K. Texture was also determined for each sample using the hydrometer method.

Several different restoration approaches were used at the various disturbed sites selected for this study (Table 1). Sites disturbed in 1991 had no restoration treatment beyond site preparation (passive restoration). Nurse crop sites were seeded with either Regreen (*Triticum aestivum* x *Elytrigia elongata*) or annual ryegrass (*Lolium multiflorum*) after site preparation, with no further restoration treatments applied. Seeded

sites were treated by broadcasting with a mixture of native perennial grasses and forbs, followed by hand raking to increase seed-soil contact. Seed used in restoration activities was hand collected in the park, after which it was cleaned and stored until needed. Some seed hand collected in the park was also sent to the Natural Resources Conservation Service (NRCS) Plant Materials Center in Meeker, Colorado where it was propagated for seed increase. Occasionally park staff are not able to collect enough seed and seed quantities are supplemented through commercial seed suppliers.

Transplanted sites are disturbed areas in which containerized plant material is used, either from salvaged vegetation recovered prior to disturbance or from another site, or from hand collected seed that is propagated in the park's greenhouse until it is ready for transplanting. Some sites were treated with a combination of seeding a nurse crop, seeding native perennial species, and transplanting.

Monitoring disturbed sites for species composition is an important management consideration for RMNP in order to determine the relative success of various restoration approaches and to provide managers with important information on the successional processes occurring on these sites. Five sites disturbed in the summer of 2004 were sampled in August 2005 to determine native and exotic species colonizing newly disturbed sites (Figure 2, Table 3). Native species present on newly disturbed sites are generally early-seral species that can act to stabilize the site and compete with exotics to minimize their establishment while allowing for mid- to late-seral species to establish over time. The presence of exotic species on newly disturbed sites is important to evaluate and track over time to identify sites where undesirable species may persist or invade other areas.

Five 2-m x 10-m belt transects were randomly sampled within sites disturbed the previous year and revegetated by transplanting native grasses, forbs, and shrubs raised in the park's greenhouse. All species with basal parts within the boundary of the belt transect were recorded. Transplants were counted to differentiate between individual plants naturally established and those manually added to sites.



Figure 2. Locations of sites disturbed summer 2004, Rocky Mountain National Park, Colorado.

Table 3. Description of sites disturbed summer 2004, Rocky Mountain National Park, Colorado.

Site	Elevation (m)	UTM coordinates (Datum WGS84/NAD83)
Hidden Valley	2725	13 444295E 4471638N
Lily Lake parking lot	2730	13 454302E 4461952N
McGraw Ranch	2400	13 457467E 4475757N
Park-N-Ride islands	2630	13 448817E 4464457N
Roessler Property	2730	13 454482E 4461945N

Sites located on the alpine tundra disturbed in 2005 were sampled in August 2005 to evaluate transplant survival and natural colonization. A total of 12, 5-m x 5-m, permanent plots were established at two sites on the alpine tundra. Nine plots are located at the old Alpine Visitor Center (AVC) sewage lagoon adjacent to Fall River Road, and three plots are located behind the Fall River vault toilets on the west site of the Alpine Visitor Center parking lot. Permanent plots were established to estimate survivability of transplanted plugs and savaged tundra sod.

Permanent plots on these sites will allow for managers to estimate the expansion of plant cover from transplanted vegetation and monitor the colonization of bare areas by species in future years. Both live and dead transplants were counted within each of the nine plots to determine transplant survivability after one year. Plant cover was determined by ocular estimation with the use of a 0.5-m x 1.0-m quadrat placed randomly within each plot. Three quadrats were sampled per plot to estimate the average cover within each plot.

STATISTICAL ANALYSIS

Vegetation data for all sites were analyzed using analysis of variance (ANOVA) with the general linear models procedure (PROC GLM) in SAS 9.1. Significant differences were estimated by the using the least significance difference method (LSMEANS) at a significance level of $p \leq 0.05$ (SAS Institute, Inc. 2002). Plant cover and species richness data were tested for homogeneity of variances by comparing studentized residuals versus predicted values. Data that did not satisfy the assumption of equal variances were

transformed by taking the square root divided by 100. The analyses were conducted on treatment means averaged across age groups.

The use of a single reference site may inadequately express the range of variation in plant communities under late-seral conditions. Reference conditions are best represented by multiple reference sites combined to form a composite description of an undisturbed plant community (Hobbs and Norton 1996, SER 2004). Therefore means for all reference sites within each age group were averaged in order to reduce site to site variations and typify a more realistic description of undisturbed conditions.

Floristic similarity of the vegetation was estimated in order to compare similarity of plant community composition between disturbed and associated undisturbed sites. Sorenson's qualitative index of similarity (Mueller-Dombois and Ellenberg 2002) estimates community similarity based on the presence of species common to both sites divided by the sum of the total number of species on both sites:

$$SI = \left(\frac{2c}{A + B} \right) * 100$$

Where c is the number of species common to both species, A is the total number of species on one site, and B is the number of species on the other site.

The similarity of communities is not only a function of the number of common and unique species on two sites, but also the amount of each species present. Sorenson's quantitative index of similarity (Mueller-Dombois and Ellenberg 2002) is estimated by cover values of species common to both sites:

$$SI = \left(\frac{2M_w}{MA + MB} \right) * 100$$

Where M_w is the sum of the smaller quantitative value of cover of species common to both sites, MA is the sum of the quantitative value of cover of all species on one site, and MB is the sum of the quantitative value of cover of all species on the other site.

Similarity indices were calculated for sites based on treatment method averaged across age groups and were compared using analysis of variance (ANOVA) with the general linear models procedure (PROC GLM) in SAS 9.1. Significant differences were estimated by the using the least significant difference method (LSMEANS) at a significance level of $p \leq 0.05$ (SAS Institute, Inc. 2002).

COST-EFFECTIVENESS ANALYSIS

Estimated costs of native hand collected seed were based on a seeding rate of 400 seeds/m² of a hypothetical seed mixture containing 5 common grasses and forbs at rates approximating the relative cover values on reference sites and estimated from wildland seed collection rates (Table 4) multiplied by the GS-5 pay rate of \$12.75/ hr. Based on these estimates, the cost of producing this seed mix by hand collection is approximately \$545 per pound. Labor required for site preparation varied widely, therefore estimates were based on an average of several sites rather than on an individual basis. Seeding required on average 160 hours of labor per acre based on RMNP records of the number of hours of labor per acre averaged from several seeded sites. This resulted in average costs of approximately \$2040 per acre. Total estimated costs of seeding one acre of land were approximately \$6040. These costs include seed collection, site preparation, broadcast seeding, and hand raking of the soil surface to incorporate seed and increase seed-soil contact.

Table 4. Hypothetical seed mixture approximating the relative cover values of undisturbed plant communities on reference sites in RMNP. Seed amounts based on seeding rate of 400 seeds/m².

Species	% seed mix	Amount seed needed (grams/ac)	Collection rate (grams/hr)*	Collection time (hr/ac)
<i>Hesperostipa comata</i>	25	2700	100	27
<i>Bouteloua gracilis</i>	20	180	10**	18
<i>Koeleria macrantha</i>	20	775	3	258
<i>Pascopyron smithii</i>	10	400	400	1
<i>Pseudoroegneria spicata</i>	10	456	150	3
<i>Heterotheca villosa</i>	5	48	20	2.5
<i>Potentilla hippiana</i>	3	130	40	3
<i>Penstemon unilateralis</i>	3	8	50	<1
<i>Achillea millifolium</i>	3	7	40	<1
<i>Gaillardia aristata</i>	1	2	150	<1

* Winslow and Majerus 2005.

** Phan and Smith 2000.

Estimated transplanting costs were determined from RMNP records from the years 2001 to 2004 and are based on the number of employee hours required for the total number of containerized plants produced multiplied by the GS-5 pay rate of \$12.75/ hr. Cost of containerized plant production averaged \$3.80 per plant. Costs include site preparation and labor involved in planting out material on site.

Sites restored with seeding, transplanting, or a combination of the two can have differing application rates of these treatments. Sites are transplanted at different densities or seeded at variable rates. Application rates affect both the estimates of total restoration cost for a site as well as the effectiveness of the treatment. Costs of a restoration project are dependant on the size of the disturbed area as well as the application rates of the treatments. Transplanting or seeding at higher densities will increase costs. Criteria used for estimation of restoration effectiveness, such as vegetative cover, are most likely dependant on application rates as well. Transplanting or seeding at higher densities will potentially result in higher total and native species cover.

Data on application rates of treatments were not available for all sites sampled on this study. Cost-effectiveness analysis was performed on 10 of the 14 sites with active site manipulation that had data available on application rates of various treatments. Project costs were estimated by determining the size of the disturbance in addition to seeding and/or transplanting rates, then multiplying by the estimated costs associated for treatments at the given application rate for that site. Effectiveness of restoration treatments was estimated by the calculation of an Effectiveness Index (*EI*) based on the absolute cover of native species (*N*) multiplied by the relative cover of native species ($N/N+I$, where *I* is the absolute cover of invasive species):

$$EI = \left[N * \left(\frac{N}{N + I} \right) \right] * 100$$

The calculation of *EI* allows for a comparison of costs of treatments to an estimation of the efficacy of treatments in restoring native perennial plant communities. Therefore, treatments are analyzed on a site-specific basis, with costs estimations normalized to dollars per acre for all sites. Thus, this approach allows for a comparison of sites with different sizes of disturbance and application rates of treatments.

RESULTS AND DISCUSSION

Restoration projects in RMNP have used natural revegetation, transplanting containerized material, seeding, and a combination transplanting and seeding activities. Treatments used in restoration projects between 1991 and 2004 were evaluated from RMNP records (Figure 3). Of the 124 projects evaluated, 85 (69%) used transplanting, 20 (16%) used a combination of seeding and transplanting, 10 (8%) utilized natural revegetation, and 9 (7%) projects used seeding of native species. In a study evaluating articles using seeding or transplanting to assist restoration following disturbances resulting from human activities such as agricultural abandonment and mining, Ruiz-Jaen and Aide (2005) found that transplanting was the most frequently used restoration technique (56%) followed by seeding (36%) and a combination of seeding and transplanting (13%).

SUCCESS OF RESTORATION TREATMENTS

Active treatments that add plant material to a site are commonly used to assist in the recovery from anthropic disturbances. The relative success of different restoration approaches were assessed based on several criteria of the plant communities present on disturbed and reference sites. Characteristics of vegetation evaluated included 1) species richness, 2) plant cover values, and 3) a community similarity index.

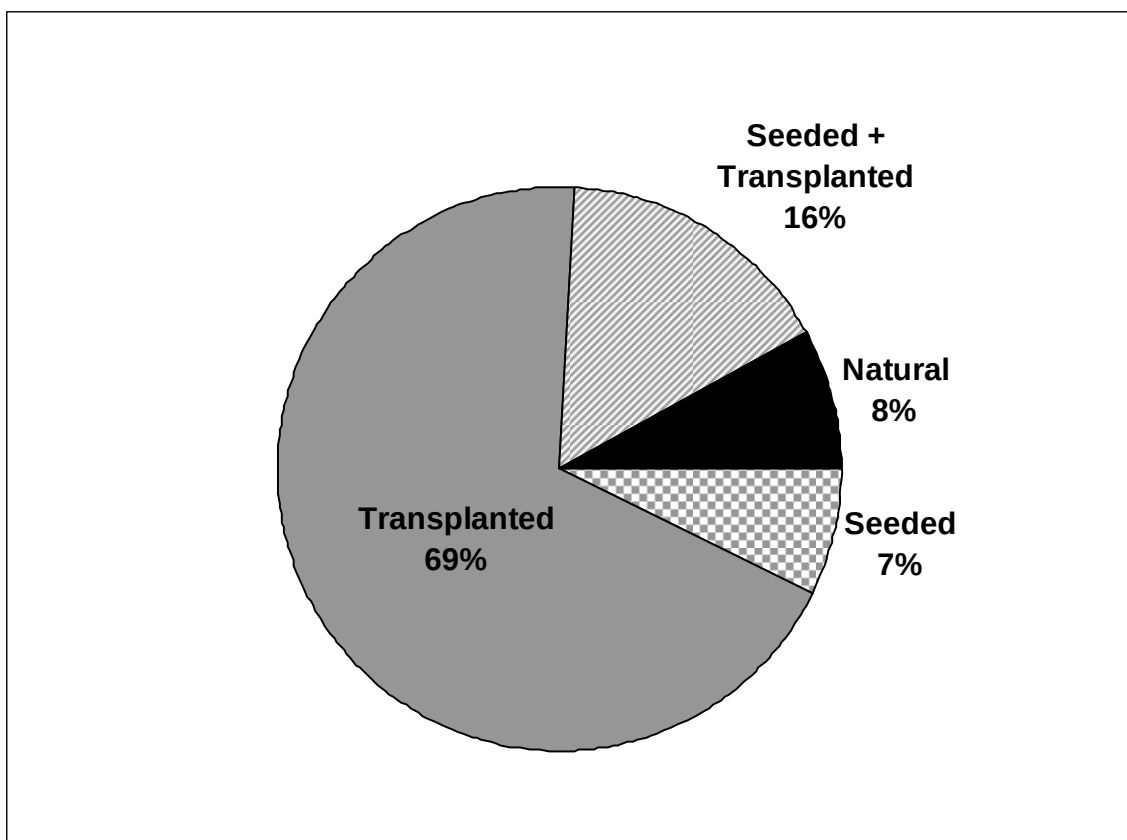


Figure 3. Comparison of methods used in restoration projects at Rocky Mountain National Park. 124 restoration projects were evaluated from park records from 1991 to 2004.

Species Richness

Treatments showed few differences in effects on species richness (i.e. number of species) (Figure 4, Table 5). Average richness of native species was lower for all disturbed sites compared to reference sites. Treatments did not differ in their average number of native species. The average number of exotic species on disturbed sites was greater than on reference sites. Seeded sites had significantly fewer exotic species than sites treated with a combination of transplanting and seeding ($p \leq 0.05$). However, this difference is an average of less than one species. Average richness of annual species was higher for all disturbed sites compared to undisturbed conditions. Treatments did not differ in average annual species richness. Average perennial species richness was lower on disturbed sites relative to reference sites. Treatments had no effect on average perennial species richness. Total species richness was not different among disturbed sites. Seeded sites had significantly lower average total species richness compared to reference sites. However, average total species richness on seeded sites was lower than on sites transplanted or treated with a combination of transplanting and seeding by only 1.2 and 1.0 species, respectively.

A combination of seeding and transplanting allows for management strategies that can result in greater species richness on disturbed sites. Initial seeding with perennial grasses permits the use of broadleaf-specific herbicides during the establishment phase of grasses. Introduction of native herbaceous dicots following seeding of grasses to increase species richness of a site is most effective when forbs are transplanted rather than seeded (Brown and Bugg 2001). Paschke et al. (2000b) recommended a combination of seeding

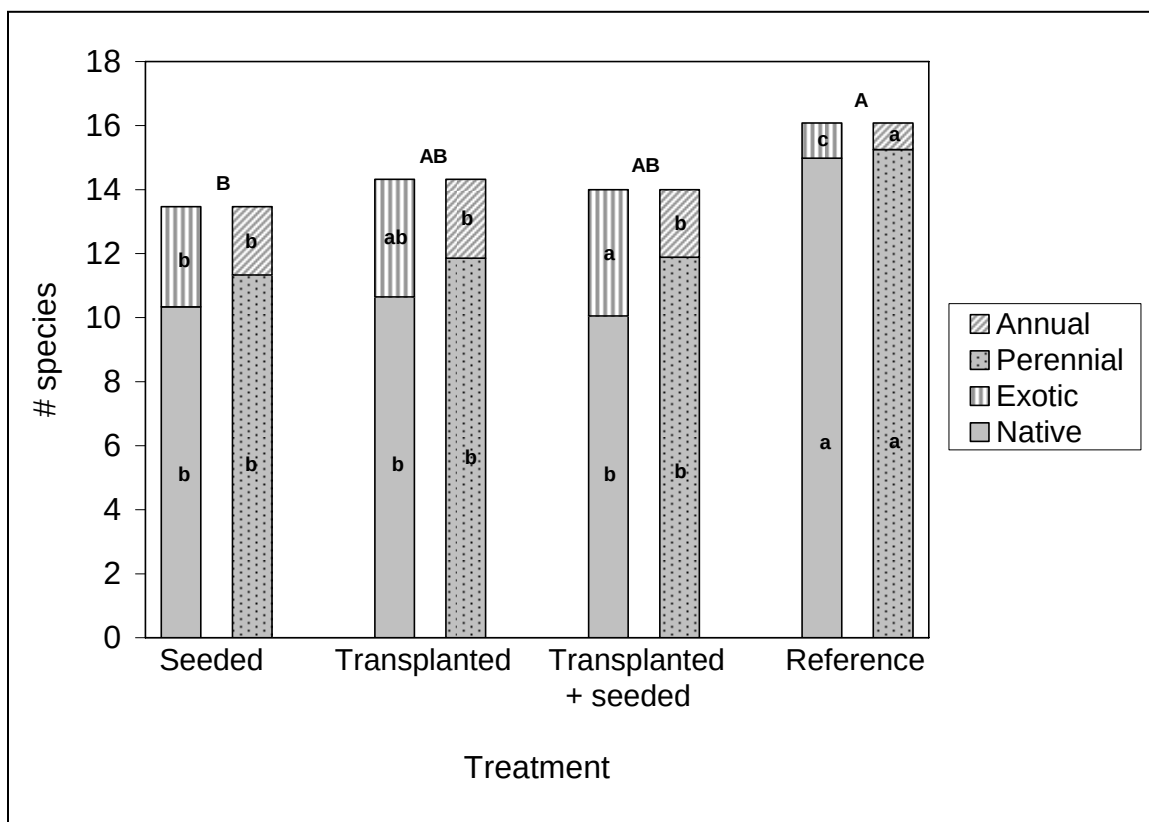


Figure 4. Average richness of annual, perennial, native, exotic, and total species for disturbed and undisturbed sites, Rocky Mountain National Park. Different letters across treatments represent significance at $p \leq 0.05$. Lower-case letters show significance within life-form categories; upper-case letters show significance for total species richness.

Table 5. Species richness data of undisturbed and disturbed sites, Rocky Mountain National Park. Disturbed sites were treated by seeding, transplanting, and a combination of seeding and transplanting. Different letters within treatments for each category represent significance at $p \leq 0.05$.

<i>Treatment</i>	Life-form category				
	Native	Exotic	Annual	Perennial	Total
<i>Seeded</i>	10.3b	3.1b	2.1a	11.3b	12.9b
<i>Transplanted</i>	10.6b	3.7ab	2.5a	11.9b	14.1ab
<i>Transplanted + seeded</i>	10.1b	3.9a	2.1a	11.9b	13.9ab
<i>Reference</i>	15.0a	1.1c	0.8b	15.3a	15.3a

grasses and transplanting forbs and shrubs as an effective approach to maintaining species diversity on disturbed road-cut slopes in Mesa Verde National Park.

Plant cover

Treatments differed in their effect on cover values of life-form categories, such as exotic annual forbs (Figure 5, Table 6). Total live cover was significantly different between disturbed and reference sites, with the lowest total live cover observed on seeded sites. Cover of exotic species was greater for all disturbed sites relative to reference sites, and did not differ among treatments. Native species cover was lower for all disturbed sites compared to reference sites. Seeded sites had significantly less native species cover than transplanted sites or sites seeded and transplanted. All treatments had less native perennial grass cover than reference sites. However, seeded and transplanted sites had the highest cover of perennial grasses of the three treatments. No significant difference in cover was observed between transplanted sites and reference sites for species of both shrub and native perennial forbs. Sites treated with seeding and seeding in addition to transplanting had significantly less shrub and native perennial grass cover compared to reference areas. There was no difference in native annual forb cover among the three treatments and reference sites. Native annual grasses were not observed on any of the sites. These results suggest that using containerized material will result in cover values of native perennial forb and grass species most similar to reference conditions.

Various studies have assessed the relative effectiveness of seeding versus transplanting for restoring disturbances based on estimates of plant cover. Seeding native species has been found to be a more effective method of restoring native plant

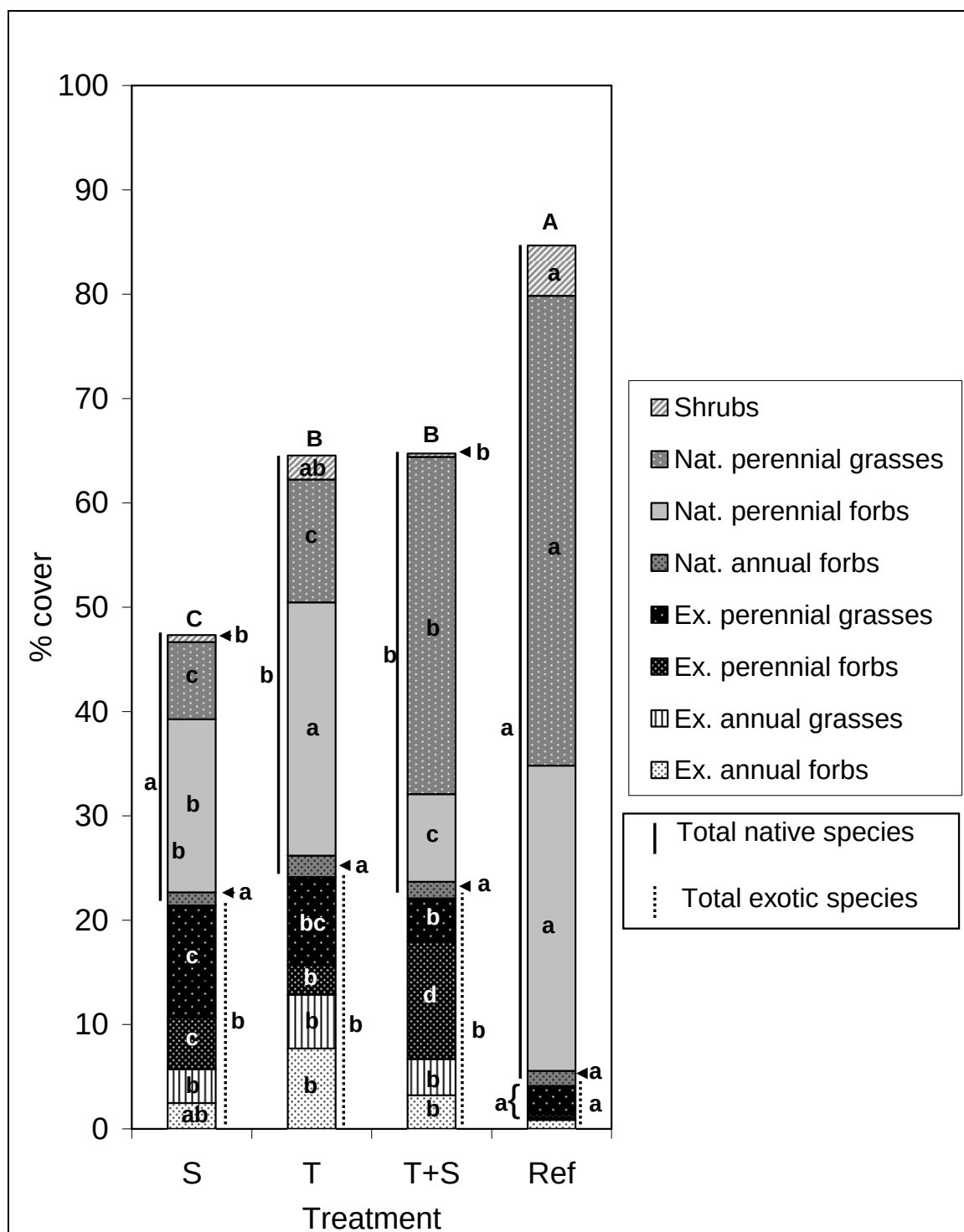


Figure 5. Comparison of cover values for disturbed and reference sites, Rocky Mountain National Park. Treatments: S - seeded; T – transplanted; T+S - transplanted and seeded; Ref – reference. Nat. - native; Ex.-exotic. Different letters represent significance at $p \leq 0.05$. Lower-case letters show significance within life-form categories; upper-case letters show significance for total cover values.

Table 6. Percent cover data of origin and life form from undisturbed and disturbed sites treated by seeding, transplanting, and a combination of seeding and transplanting, Rocky Mountain National Park.. Different letters across treatments represent significance at $p \leq 0.05$ within each category.

<i>Treatment</i>	Life-form category*													
	EAF	EAG	EPF	EPG	NAF	NAG	S	NPF	NPG	TA	TP	TE	TN	TLC
<i>Seeded</i>	2.5ab	3.3b	4.9c	10.7c	1.3a	0.0a	0.7b	16.6b	7.4c	7.0b	39.7c	20.2b	28.8c	49.0c
<i>Transplanted</i>	7.7b	5.2b	2.8b	8.4bc	2.1a	0.0a	2.3ab	24.3a	11.8c	14.9a	47.3c	26.9b	38.3b	64.1b
<i>Transplanted + seeded</i>	3.2b	3.5b	11.3d	4.1b	1.6a	0.0a	0.3b	8.4c	33.3b	8.0ab	56.1b	21.1b	43.5b	64.6b
<i>Reference</i>	0.9a	0.2a	0.4a	2.7a	1.5a	0.0a	4.8a	29.3a	45.0a	2.5c	77.4a	5.3a	82.8a	88.1a

*Life-form categories: EAF=exotic annual forbs; EAG=exotic annual grasses; EPF=exotic perennial forbs; EPG=exotic perennial grasses; NAF=native annual forbs; NAG=native annual grasses; S=shrubs; NPF=native perennial forbs; NPG=native perennial grasses; TA=total annual species; TP=total perennial species; TE=total exotic species; TN=total native species; TLC=total live cover.

communities than transplanting in areas that receive adequate precipitation (Shearer et al. 1996, Cole and Spildie 2000). Transplanting is often the most effective method of restoration in arid climates where seed germination is highly variable because of the infrequent occurrence of conditions favorable for seed germination and seedling establishment (Bainbridge et al. 1995, Grantz et al. 1998)

Competition from undesirable vegetation such as exotic species can reduce the effectiveness of seeding treatments relative to transplanting in restoration projects. In a study in grasslands in southeastern Australia, O'Dwyer and Attiwill (2000) found that transplanting seedlings was more effective than seeding in increasing cover of the dominant native perennial grass. The poor establishment of native grasses on seeded sites was attributed to competition from exotic grasses, which can reduce available soil moisture, light, and nutrients. Depletion of soil moisture by exotic annual grasses has been shown to reduce the germination and establishment of native shrubs seeded in disturbed areas in southern California coastal sage scrub (Eliason and Allen 1997). The authors recommend transplanting shrubs in order to bypass the seedling stage where individuals are more susceptible to competition for soil moisture from annual grasses. Increases in basal diameter of seedlings of the native perennial grass *Nassella pulchra* in California grasslands was shown to be reduced by intraspecific competition as well as competition from exotic annual grasses (Dyer and Rice 1997). These results emphasize the importance of modification of the biotic environment by removal of undesirable vegetation in order to reduce competition and increase the chances of successful seedling establishment.

The use of transplanted material in arid and semi-arid areas may increase the chances of plant establishment by avoiding the critical stages of seed germination and seedling survival thus facilitating restoration success. Environmental conditions of the disturbed site may not be conducive for seed germination for many seasons depending on abiotic factors such as edaphic and climatic conditions. Seed germination and seedling establishment are often reduced by conditions of low soil moisture that are normally found under climatic conditions typical of arid and semi-arid regions (Barbour 1968). Transplanting may also increase the chances of establishment and survival of desired vegetation in arid regions due an increase in competitive ability of larger individuals (Eliason and Allen 1997), especially when techniques are used to reduce environmental stresses (Bainbridge et al. 1995).

Community Similarity

Community similarity (*SI*) did not differ between treatments based on either species presence or cover values ($p \leq 0.05$) (Figure 6). Transplanted sites had significantly lower similarity to undisturbed reference sites compared to seeded and seeded + transplanted sites ($p \leq 0.1$) ($p = 0.095$, quantitative *SI*; $p = 0.059$, qualitative *SI*). Sorenson's quantitative *SI* was highest for seeded sites and lowest for transplanted sites, suggesting that seeding disturbed sites produced plant communities with species cover most similar to undisturbed conditions. Species presence data show sites treated with a combination of seeding and transplanting have the highest similarity, while transplanted sites have the lowest similarity. These data indicate that including seeding as a treatment for restoration

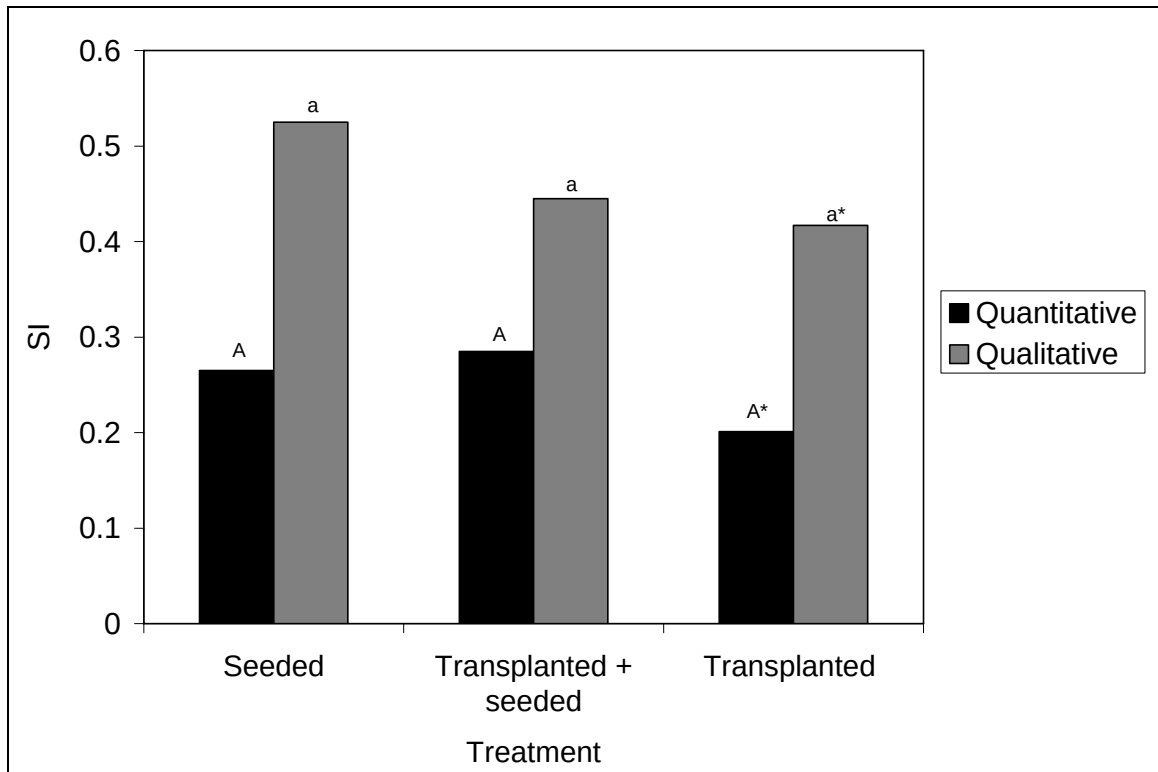


Figure 6. Sorenson's quantitative and qualitative similarity index for disturbed/ reference pairs, Rocky Mountain National Park. Different letters across treatments represent significance at $p \leq 0.05$ (* shows significance at $p \leq 0.1$). Upper-case letters show significance across treatments for quantitative similarity. Lower-case letter show significance across treatments for qualitative similarity.

of disturbed areas is important for maximizing the similarity of plant community structure between disturbed and undisturbed conditions.

Cover and community similarity may be influenced by the species chosen for addition as seed or transplant material on a site. Data on species seeded or transplanted were not available for all sites included in the study (Appendix A). Species lists for transplanted sites show that most containerized material used on these sites were perennial forbs. Most sites that included seeding incorporated several grass species in the seed mixture. Differences in species selection may account for the differences in both cover values of perennial grasses and forbs as well as similarity.

Cover of undisturbed reference areas was dominated by several native perennial grass species, including *Hesperostipa comata* (Trin. & Rupr.), *Bouteloua gracilis* (Willd. ex. Kunth) Lag. ex. Griff, and *Muhlenbergia montana* (Nutt.) A.S.Hitchc. Transplanted sites without significant addition of grasses resulted in lower cover of native perennial grasses and thus lower similarity to undisturbed conditions. Treatments that included seeding of grasses in addition to transplanting forbs and shrubs had the highest cover of perennial grasses resulting in the highest quantitative *SI*.

Assessment of the success of restoration treatments based on multiple plant community attributes for disturbed and undisturbed sites makes the determination of optimum approaches unclear. Treatments had no significant effects on total, native, annual, or perennial species richness. Exotic species richness of seeded sites was significantly lower than sites treated with transplanting and seeding. Analysis of vegetation cover showed treatments that include transplanting result in the highest total cover as well as cover of native perennial species on disturbed sites. Community

similarity indices suggest the importance of including seeding for the creation of plant communities similar in cover values and species presence. However, these indicators of restoration success may be sensitive to the species chosen for addition to the site as well as the restoration approach used.

Cost-effectiveness Analysis

Using only local plant material in restoration projects has placed limitations on the park due to the increased costs associated with the collection and propagation of local plant material. Large differences in estimated costs associated with the various active approaches to restoration (Figure 7) combined with the limitation in funding emphasize the need for evaluation of the cost-effectiveness of the different approaches to restoring disturbances in RMNP. Comparison of costs to relative effectiveness for alternate treatments can provide important information for managers during the restoration planning process. The calculation of an Effectiveness Index (*EI*) allows for a comparison of costs of treatments to an estimation of the efficacy of different treatments in restoring native perennial plant communities.

Sites restored with seeding, transplanting, or a combination of the two have differing application rates of these treatments. Sites are transplanted at different densities or seeded at variable rates. Criteria used for estimation of restoration effectiveness discussed in the previous sections are most likely sensitive to application rates of treatments. Total costs of a project are also dependant on the application rates of the treatments as well as the size of the disturbed area. Transplanting or seeding at higher densities will increase costs while potentially resulting in higher total and native species

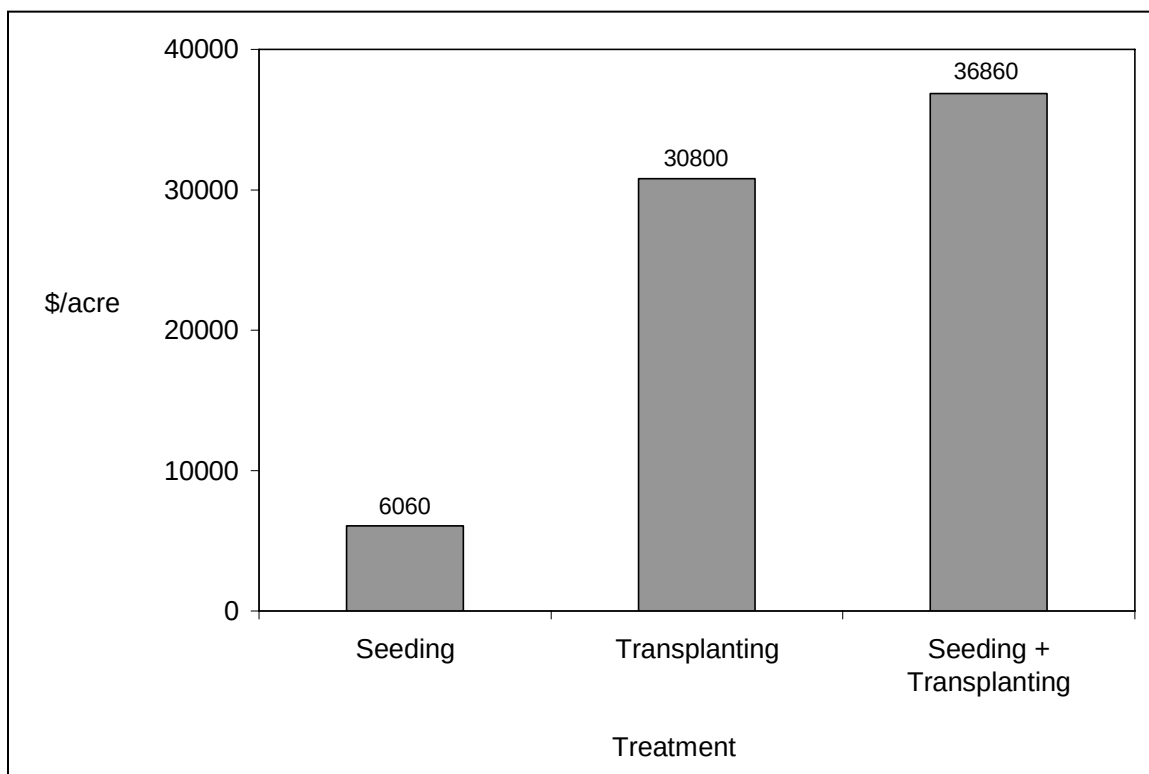


Figure 7. Estimated costs of restoration treatments using locally collected plant material, Rocky Mountain National Park.

* Costs based on a seeding a hand collected seed mixture at a rate of 400 seeds/m².

** Costs based on a transplanting density 2 plants/m².

*** Costs based on the addition of seeding and transplanting costs.

cover. Therefore, treatments are analyzed on a site specific basis with cost estimations based on applications rates normalized to dollars per acre for all sites (Table 7). This approach allows for a comparison of sites with different sizes of disturbance and application rates of treatments

Calculation of *EI* is an attempt to quantify effectiveness by the cover of vegetation on each site. *Effectiveness Index* not only factors in native species cover, but also total and invasive species cover in order to weight competition from undesirable species. The greater the relative cover of native species, the less competition from exotic species there will be. Thus, *EI* will be low for plant communities with low total cover or on sites where the relative cover of native species is low due to greater cover of exotic species. *EI* will be high for sites with high total cover in addition to high relative cover of native species. A lower ratio of cost to *EI* is desirable, indicating a lower cost per unit effectiveness.

Cost-effectiveness analysis of restoration treatments in RMNP shows large relative differences between treatments (Figure 8). Seeded sites had absolute and relative cover of native species similar to transplanted sites resulting in a similar estimated *EI*. Costs associated with seeding were considerably lower than transplanting. Seeded sites had an average estimated cost 93% lower than transplanted sites, with an estimated *EI* 4% higher than transplanted sites. Average *EI* was 27% lower on seeded sites compared to sites where seeding and transplanting took place resulting in lower *EI*. However, the costs of seeding were significantly lower relative to sites treated with a combination of seeding and transplanting resulting in a lower cost per unit effectiveness.

Table 7. Determination of ratio of costs and Effectiveness Index (*EI*) for various disturbed sites, Rocky Mountain National Park.

I. Cost

Site	Size (acre)	Treatment	Application rate (per acre)	Total cost (per acre)	Treatment average
BME-S	0.74	seed	1.93 lb	\$3,090	\$3,090
BME-N	1.25	seed	1.93 lb	\$3,090	
MPC amphitheater	0.15	transplants	19,000 plants	\$72,200	\$45,210
Twin sisters	0.07	transplants	17,140 plants	\$65,130	
Sprague Lake	0.34	transplants	2780 plants	\$10,560	
Hot Shot Dorm	0.06	transplants	15,800 plants	\$60,040	
McGraw Ranch	0.31	transplants	4770 plants	\$18,130	
WAW cabin	0.03	transplants	6275 plants	\$25,890	\$27,050
		seed	N/A		
FMO	0.20	transplants	2420 plants	\$35,740	
		seed	45.1 lb		
McClaren Hall	0.46	transplants	4600 plants	\$19,520	
		seed	N/A		

II. Effectiveness

Site	cover native sp.	cover invasive sp.	relative cover native sp.	<i>EI</i>	Treatment average
BME-S	38.6	16.6	0.70	27.0	27.2
BME-N	31.0	4.4	0.88	27.3	
MPC amphitheater	38.6	27.6	0.58	22.5	26.1
Twin sisters	51.4	19.6	0.72	37.2	
Sprague Lake	23.0	14.0	0.62	14.3	
Hot Shot Dorm	59.7	18.0	0.77	45.8	
McGraw Ranch	27.0	40.0	0.40	10.9	
WAW cabin	52.3	13.7	0.79	41.5	37.7
FMO	47.8	14.0	0.77	37.0	
McClaren Hall	48.2	19.0	0.72	34.6	

III. Cost-effectiveness ratio

Site	C/E Ratio*	Treatment average
BME-S	113.7	113.8
BME-N	113.9	
MPC amphitheater	3207.9	1734.6
Twin sisters	1750.4	
Sprague Lake	738.9	
Hot Shot Dorm	1309.8	
McGraw Ranch	1665.9	
WAW cabin	623.8	717.8
FMO	966.7	
McClaren Hall	564.6	

* total cost (per acre)/*EI*

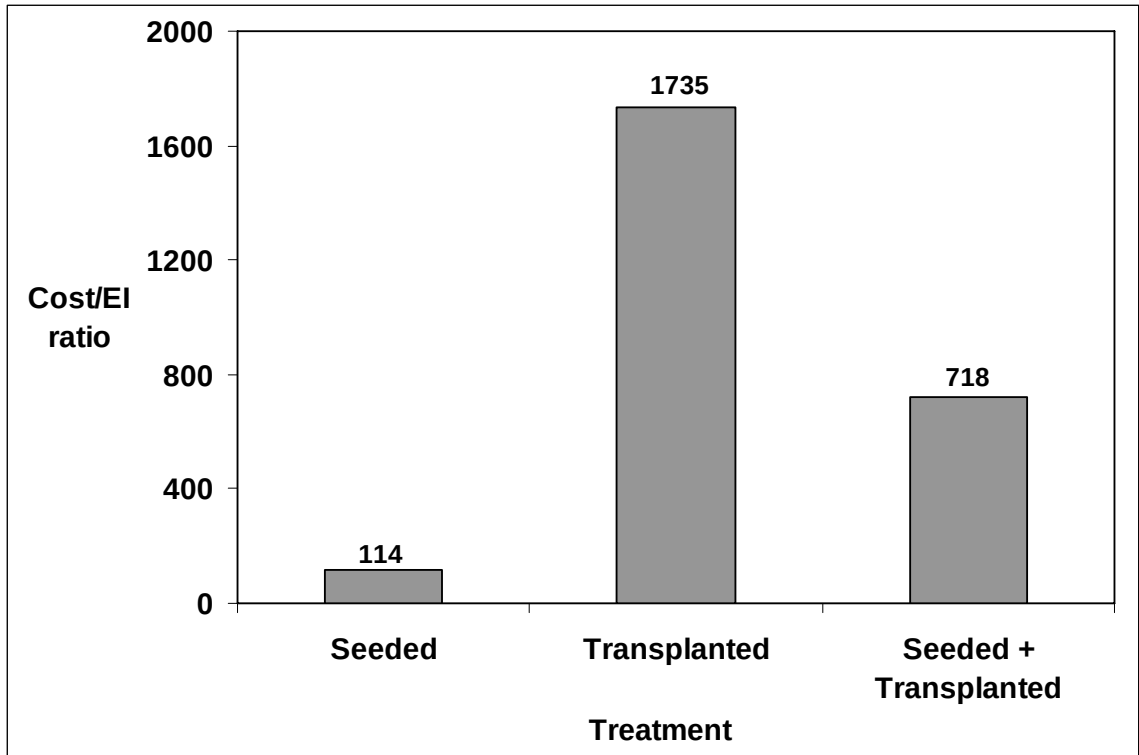


Figure 8. Ratio of average treatment costs to average Effectiveness Index scores for restoration treatments, Rocky Mountain National Park.

Data on seeding rates was not available for two out of the three sites where a combination of seeding and transplanting took place resulting in cost estimates for these sites lower than actual costs. This should be kept in mind when comparing cost-effectiveness ratios of transplanted sites to sites seeded and transplanted. Sites that used transplanting produced lower absolute and relative cover of native species compared to sites seeded and transplanted despite higher planting densities, resulting in a lower average *EI*. The increased planting density resulted in higher costs for transplanted sites compared to seeded and transplanted sites. Given the low relative costs of seeding, actual costs of sites seeded and transplanted were most likely comparable if not lower than transplanted sites. However, average *EI* of sites treated with seeding and transplanting were 44% higher than transplanted sites, most likely resulting in a lower cost effectiveness ratio. Seeded sites had an estimated *EI* 28% lower than sites transplanted and seeded, however costs of seeding were 88% lower than the combination of seeding and transplanting.

Of the 10 sites included in the cost-effectiveness analysis, transplanted sites had the lowest average absolute and relative cover of native species coupled with the highest costs, making this treatment the least cost effective treatment of the three. Sites treated with a combination of seeding and transplanting had the highest average *EI* compared to all other sites. However, the significantly lower costs associated with seeding resulted in the lowest cost-effectiveness ratio of the three treatments.

Linear regression analysis of *EI* and costs of individual disturbed sites (Figure 9) did not show a significant relationship between increased effectiveness on sites with higher costs, suggesting that treatment type was more important than absolute costs in increasing

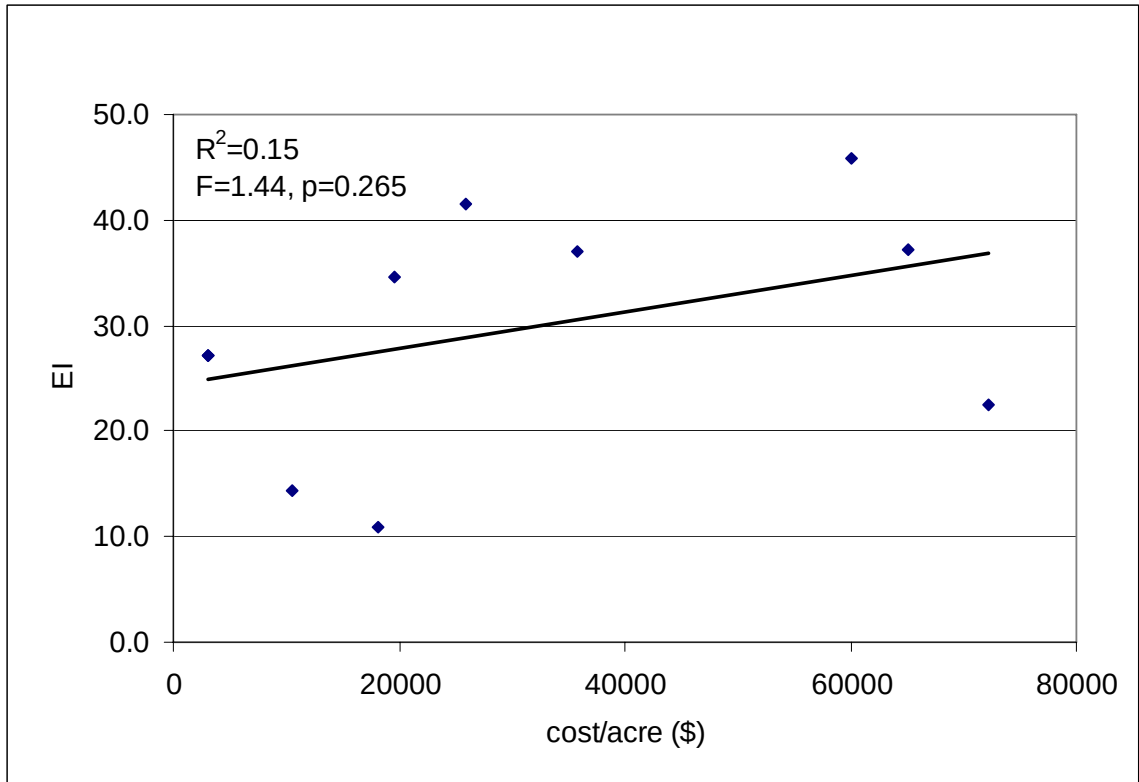


Figure 9. Linear regression of Effectiveness Index (*EI*) and cost estimations from 10 disturbed sites, Rocky Mountain National Park.

effectiveness of restoration projects. Thus, cost-effectiveness analysis of treatments for restoring disturbances in RMNP shows seeding disturbed areas is the most effective method per unit cost.

Effects of elapsed time since disturbance

There were differences in the sample sizes of treatment as well as the distribution of treatments among age groups representing the elapsed time between disturbance and sampling that may affect the interpretation of the results (Table 1). Seeded sites were disturbed an average of 3.5 years prior to sampling. Sites treated with transplanting or a combination of seeding and transplanting were disturbed an average of 5.3 years prior to sampling, a difference of 1.8 years longer than seeded sites. This difference in average age between seeded sites and sites treated with transplanting and a combination of seeding and transplanting may account for some of the differences between treatments in values of cover, community similarity, and *EI*.

The lower total, native, and perennial species cover values observed in seeded sites relative to the other treatments may be influenced by less time since the disturbance occurred on these sites. In a study comparing seeding and transplanting to restore closed wilderness campsites, total cover in the initial years following restoration activities was found to be higher on transplanted sites due to the immediate canopy provided by planted seedlings. However, by the third year seeded sites had higher total cover values due to germination and establishment of seeded species (Cole and Spildie 2000).

Composition and cover of vegetation have been shown to change significantly during the first 5 years following disturbance in semi-arid systems. Working in a sagebrush

community in northwestern Colorado, McLendon and Redente (1991) showed that plots were dominated by annuals for the initial three years after disturbance, after which herbaceous perennials became major components. By the fifth year, shrubs and perennial grasses dominated disturbed sites. Results from these authors suggest the difference in the average age of sites with different treatments in this study can affect relative cover of the various life-form categories. Younger sites would be expected to have greater cover of annuals while older sites would be expected to have greater cover of perennials and shrubs.

Reference sites were dominated by native and perennial species. Sites treated with transplanting and a combination of seeding and transplanting had greater cover values of both native and perennial species relative to seeded sites. Thus, the effects of time since disturbance on cover values for these categories could alter the estimation of similarity to reference sites for different treatment types. Increased cover of native and perennial species on disturbed sites in sagebrush communities in Wyoming resulted in increased similarity to undisturbed communities with increasing time since disturbance (Smith et al. 1988).

Numerous restoration goals may require a variety of criteria for determining the effectiveness of treatments, which can lead to uncertainty in decisions of optimal restoration approaches. Decisions regarding the most effective approaches to restoring disturbances are often based on plant community characteristics such as cover, diversity, and similarity to surrounding vegetation. Based on these assumptions, the results of this study suggest that the most effective restoration techniques should include seeding perennial grasses for increased cover, higher similarity to undisturbed conditions, soil

stabilization, and competition with exotic species. In addition to seeding, transplanting material can increase establishment of forbs and shrubs resulting in increased community similarity and absolute and relative cover of native species on these sites.

EFFECTS OF NURSE CROP SEEDING

Six sites disturbed in 1991 were sampled to study the long-term effects of seeding of a nurse crop on natural establishment of native perennial species. These sites had no active restoration treatments beyond initial site preparation. Three sites were seeded with a nurse crop of either Regreen (*Triticum aestivum* x *Elytrigia elongata*) or annual ryegrass (*Lolium multiflorum* Lam.) to stabilize soil, while three sites were left to naturally revegetate.

Plant cover

No individuals of Regreen or annual ryegrass could be found on any of the sites seeded with these nurse crops, suggesting that neither of these species has persisted on these sites in the 13 years since they were seeded. Plant cover showed significant differences 13 years following disturbance when seeded with a nurse crop but allowed to revegetate through natural colonization (Figure 10, Table 8). Disturbed sites restored through passive revegetation had significantly lower total live cover, cover of both total perennial and native species including perennial native grasses, and significantly higher cover of both total exotic and annual species, including exotic annual grasses and exotic perennial grasses compared to reference sites. Seeding of a nurse crop when sites were

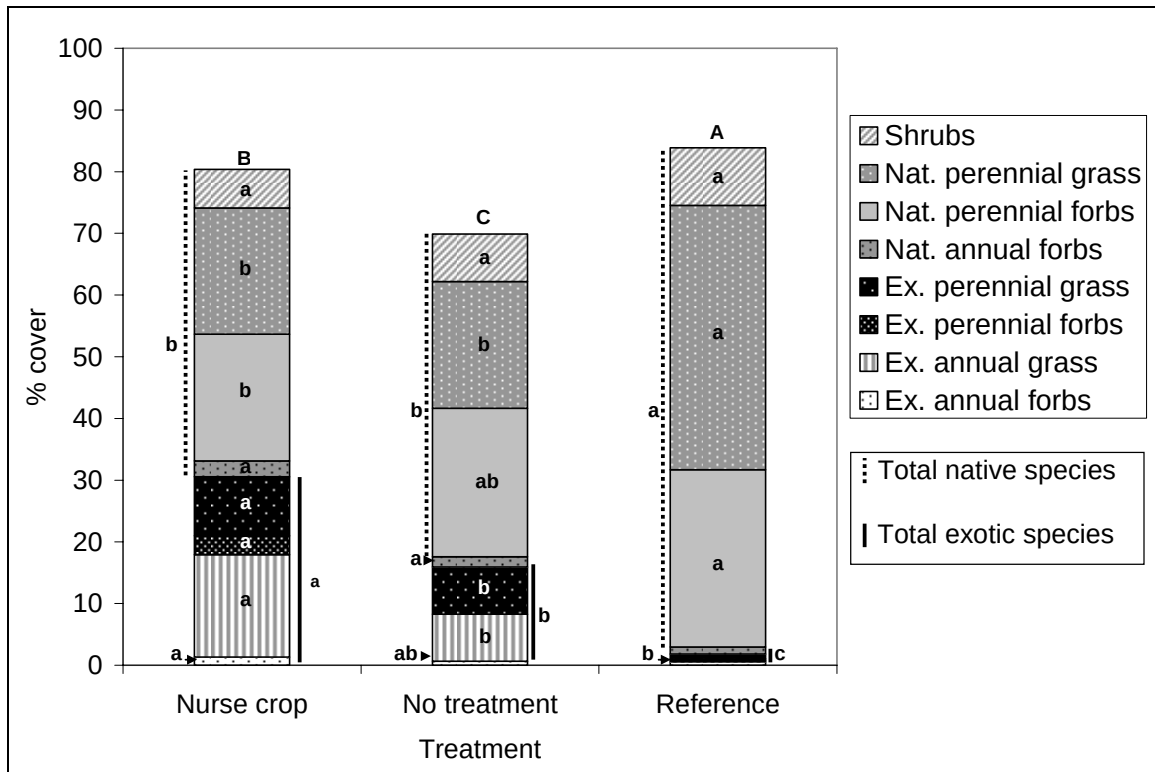


Figure 10. Comparison of cover values for reference and disturbed sites restored through passive revegetation, Rocky Mountain National Park. Nat.-native; Ex.-exotic. Different letters across treatments represent significance at $p \leq 0.05$ within each category. Lower-case letters show significance within life-form categories; upper-case letters show significance for total cover values.

Table 8. Percent cover data of origin and life form from undisturbed sites and disturbed sites with no treatment or by seeding a nurse crop in Rocky Mountain National Park. Different letters across treatments represent significance at $p \leq 0.05$ within each category*.

<i>Treatment</i>	Life-form Category*													
	EAF	EAG	EPF	EPG	NAF	NAG	S	NPF	NPG	TA	TP	TE	TN	TLC
<i>Nurse crop</i>	1.3a	16.6a	3.1a	9.5a	2.6a	0.0a	6.2a	20.5b	20.5b	20.5a	53.6b	30.5a	49.0b	79.5b
<i>No treatment</i>	0.7ab	7.6b	0.0b	7.7a	1.7a	0.0a	7.7a	24.1ab	20.5b	9.9a	52.3b	15.9b	54.0b	69.9c
<i>Reference</i>	0.6b	0.3c	0.2b	0.8b	1.1a	0.0a	9.4a	29.3a	42.8a	2.0c	72.6a	1.8c	82.1a	83.9a

*Life-form categories: EAF=exotic annual forbs; EAG=exotic annual grasses; EPF=exotic perennial forbs; EPG=exotic perennial grasses; NAF=native annual forbs; NAG=native annual grasses; S=shrubs; NPF=native perennial forbs; NPG=native perennial grasses; TA=total annual species; TP=total perennial species; TE=total exotic species; TN=total native species; TLC=total live cover.

passively restored resulted in significantly higher total cover and cover of exotic and annual species, including exotic annual grasses and exotic perennial forbs, compared to sites not seeded with a nurse crop. However, nurse crop sites did not show significant differences in total native or perennial species cover, including native perennial forbs and grasses as was predicted. These results suggest that seeding of a nurse crop may allow exotic species to become established and persist on disturbed sites without affecting establishment of native perennial species.

Seeding of nurse crops following disturbances has been shown to reduce establishment and cover of desired species in the initial years following seeding (Densmore et al. 1990, Pywell et al. 2002). However, results from Tyser et al. (1998) show no difference in seeded species cover in sites seeded with a nurse crop. These authors reported poor germination of the nurse crop that possibly resulted in little competition between seeded species and the nurse crop. Because these sites were seeded with a nurse crop 13 years prior to sampling, no data are available on germination rates of the nurse crop on these sites. However, the lack of effect on native and perennial species cover shown from these data could be due to either recovery of native and perennial species populations following senescence of the nurse crop, or poor germination of the nurse crop following seeding.

The largest difference in cover between sites seeded with a nurse crop was in exotic species cover, especially cover of exotic annual grasses. This is a result of the high cover values of *Anisantha tectorum* (L.) Nevski present on nurse crop sites. *A. tectorum* has been shown to respond to elevated levels of total soil nitrogen by increasing biomass and cover following disturbance (McLendon and Redente 1991, Paschke et al. 2000b). Soil

cores from nurse crop and no treatment sites were analyzed to determine levels of soil N-NO₃. ANOVA results show N-NO₃ levels were not significantly different between sites (Figure 11). The significantly increased cover of *A. tectorum* might be the result of established populations near the disturbed area that were able to establish on the site and persist. However, data on distance to established populations of *A. tectorum* for these sites were not collected. Undisturbed reference areas directly adjacent to the disturbance sampled for comparison did not have established populations of *A. tectorum*.

The number of sites sampled were low ($n=3$) for both nurse crop and no treatment sites, which resulted in a single site with high exotic annual species cover and richness producing significant differences between treatments. One site in particular, 718 High Drive, was seeded with a nurse crop of Regreen and was dominated by *A. tectorum*. This site had an average of 41% cover of *A. tectorum*, compared to an average cover of 1% and 7.8% observed on the other sites seeded with a nurse crop. Sites not seeded with a nurse crop had cover values for *A. tectorum* of 0%, 3.4%, and 19.4%.

Species richness

Passively restored sites had significantly less richness of native and perennial species compared to reference sites (Figure 12; Table 9). Disturbed sites did not differ in cover of perennial or native species richness. Sites seeded with a nurse crop had significantly more exotic and annual species than sites not seeded with a nurse crop and reference sites. These results, as with the cover data, suggest that seeding of a nurse crop results in more exotic and annual species establishment following disturbance, while not affecting establishment of native or perennial species. However, species richness data suggest that

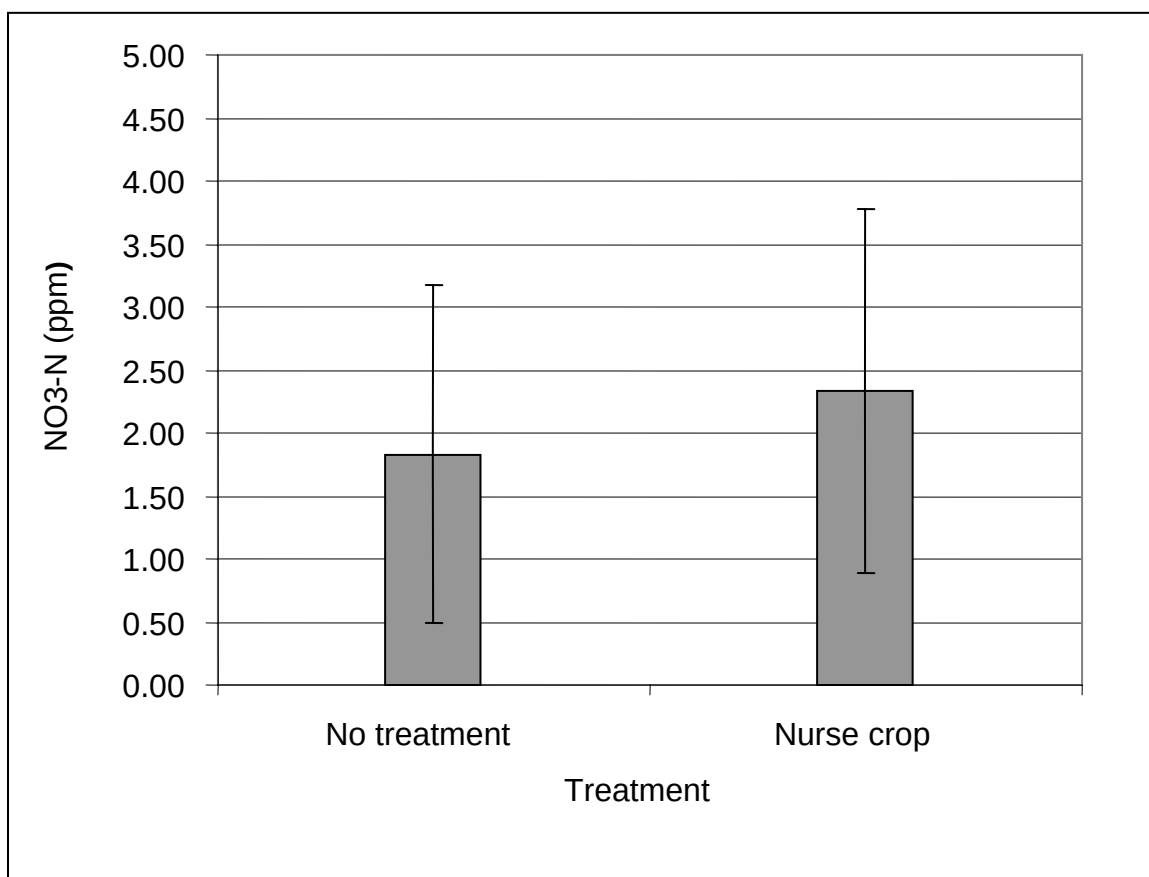


Figure 11. Soil NO₃-N on sites disturbed 13 years prior to sampling, Rocky Mountain National Park. Sites were passively restored with and without a nurse crop seeded. Error bars show 1 standard deviation.

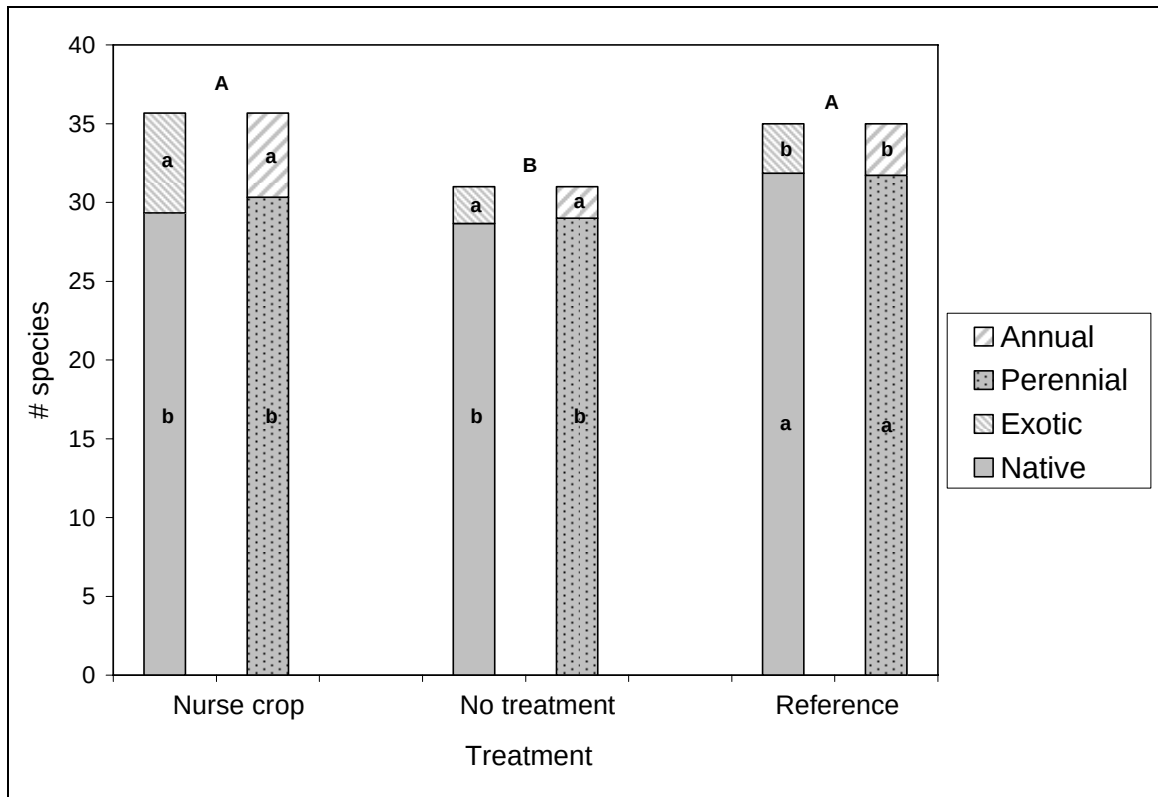


Figure 12. Average richness of annual, perennial, native, exotic, and total species for passively restored sites with and without a nurse crop seeded, Rocky Mountain National Park. Different letters represent significance at $p \leq 0.05$. Lower-case letters show significance within life-form categories; upper-case letters show significance for total cover values.

Table 9. Species richness data for reference and naturally revegetated disturbed sites with and without a nurse crop seeded. Different letters across treatments represent significance at $p \leq 0.05$ within each life-form category.

<u>Treatment</u>	Life-form category				
	Native	Exotic	Annual	Perennial	Total
<i>Nurse crop</i>	29.3b	6.3a	5.3a	30.3b	35.7a
<i>No treatment</i>	28.7b	2.3b	2.0b	29.0b	31.0b
<i>Reference</i>	31.9a	3.1b	3.3b	31.7b	35.4a

differences between nurse crop and non-seeded sites are due to several exotic or annual species instead of a single species such as *A. tectorum*.

Studies on species rich grasslands in England found that seeding of a nurse crop significantly reduced the total species richness by reducing the number of seeded forbs and unseeded grass species establishing on disturbed sites. However, richness of seeded grass species was not affected by the presence of a nurse crop (Pywell et al. 2002). Results from these authors suggest that competition from a nurse crop can reduce the number of species establishing following disturbance. Results from my study suggest competition from the seeded nurse crop was not significant enough to reduce native and perennial species establishment. As mentioned previously, these results could be a consequence of poor germination of the nurse crop or a result of established populations of exotic or annual species near the disturbance may result in nurse crop sites with higher numbers of exotic species establishing following disturbance.

Community similarity

Seeding of a nurse crop following disturbances appeared to have a significant effect on community similarity to undisturbed conditions (Figure 13). Both qualitative and quantitative similarity were lower for sites that were seeded with a nurse crop.

Community similarity is estimated by cover values or presence of species common to both sites. Differences in plant cover values and species presence most likely caused by the increase in cover and richness of exotic annual species on these sites resulted in fewer species and lower cover of species common to both disturbed and reference sites, causing lower *SI* values for nurse crop sites.

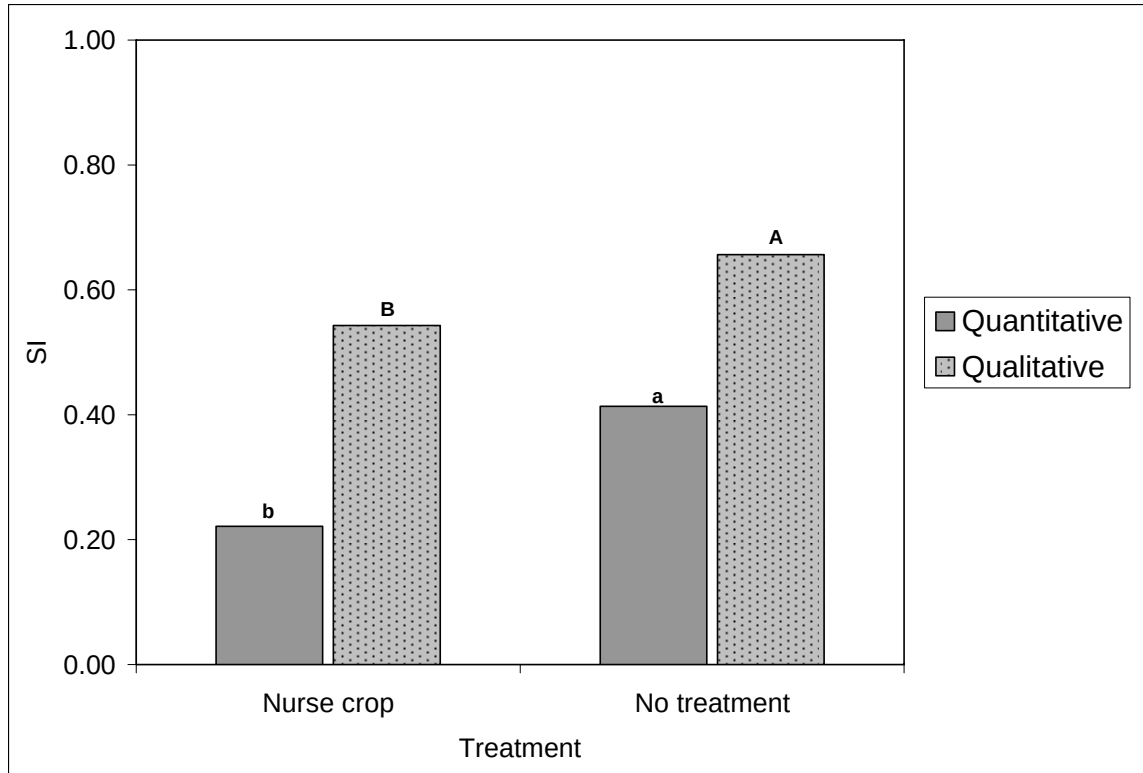


Figure 13. Sorenson's quantitative and qualitative similarity index for disturbed/reference pairs of passively restored sites with and without seeding a nurse crop, Rocky Mountain National Park. Different letters represent significance at $p \leq 0.05$. Upper-case letters show significance across treatments for qualitative similarity. Lower-case letter show significance across treatments for quantitative similarity.

Natural restoration of disturbed grassland and shrubland sites has been evaluated in RMNP (McLendon et al. 1995, Zadeh 2001). Similarity between disturbed and reference sites based on mean canopy cover was determined and used to estimate recovery rates of natural secondary succession following human disturbance. Grassland and shrubland recovery rates were estimated at approximately 120 to 160 years in these studies. Results from my study suggest that there may be long-term effects on natural recovery following disturbance when nurse crops are seeded. The establishment and persistence of exotic and annual species on sites seeded with nurse crops may delay the recovery of these systems further.

NATURAL COLONIZATION OF DISTURBANCES

The availability of plant propagules often limits plant community change following disturbance (Ash et al. 1994). Richness of native species has been shown to be a driver of early succession in grasslands following disturbance (van der Putten et al. 2000). Sites restored with transplanting often have a limited number of species and propagules added, potentially constraining succession on these sites. Five sites disturbed in the summer of 2004 were sampled to determine the frequency of species naturally colonizing sites in the first year following disturbance in order to determine if transplanted sites appear to be constrained by propagule availability. Transplanted material was added to these sites was distinguished from individuals naturally establishing from seed.

Native species that readily establish in the initial year after disturbance can act much like nurse crops in stabilizing soil and competing with exotic species. Presence of early-seral native species may facilitate the development of plant communities dominated by

native perennial species. Exotic species establishing on newly disturbed sites may persist on these sites reducing establishment of the desired native late-seral species.

Sites had greater average total richness of native species compared to exotic species one year following disturbance (Figure 14). Richness of native species was highest when transplanted individuals were included in the analysis. Richness of native species naturally colonizing disturbed sites was also significantly greater relative to richness of exotic species. These results show that in the initial year following disturbance, more native species are able to colonize sites compared to exotic species. These data suggest that transplanted sites one year after disturbance show potential for development of plant communities dominated by native late-seral species.

Native species naturally colonizing disturbed sites were most frequently perennial forbs (Appendix B). The most frequent species was the annual forb *Polygonum douglasii* Greene, which was present in 76% of the transects. The perennial grasses *Poa palustris* L. and *Agrostis scabra* Willd. were observed in 68% and 60% of transects, respectively. The most frequently occurring perennial forbs were *Oenothera villosa* Thunb. ssp. *villosa*, *Achillea millefolium* L. var. *occidentalis* DC., and *Virgulus falcatus* (Lindl.) Reveal & Keener, all of which were observed in 52% of transects. Many perennial forbs common in undisturbed plant communities were observed with appreciable frequency in transects as well: *Grindelia subalpina* Greene (32%), *Solidago missouriensis* Nutt. (32%), *Penstemon unilateralis* Rydb. (20%), *Heterotheca villosa* (Pursh) Shinn. (20%),

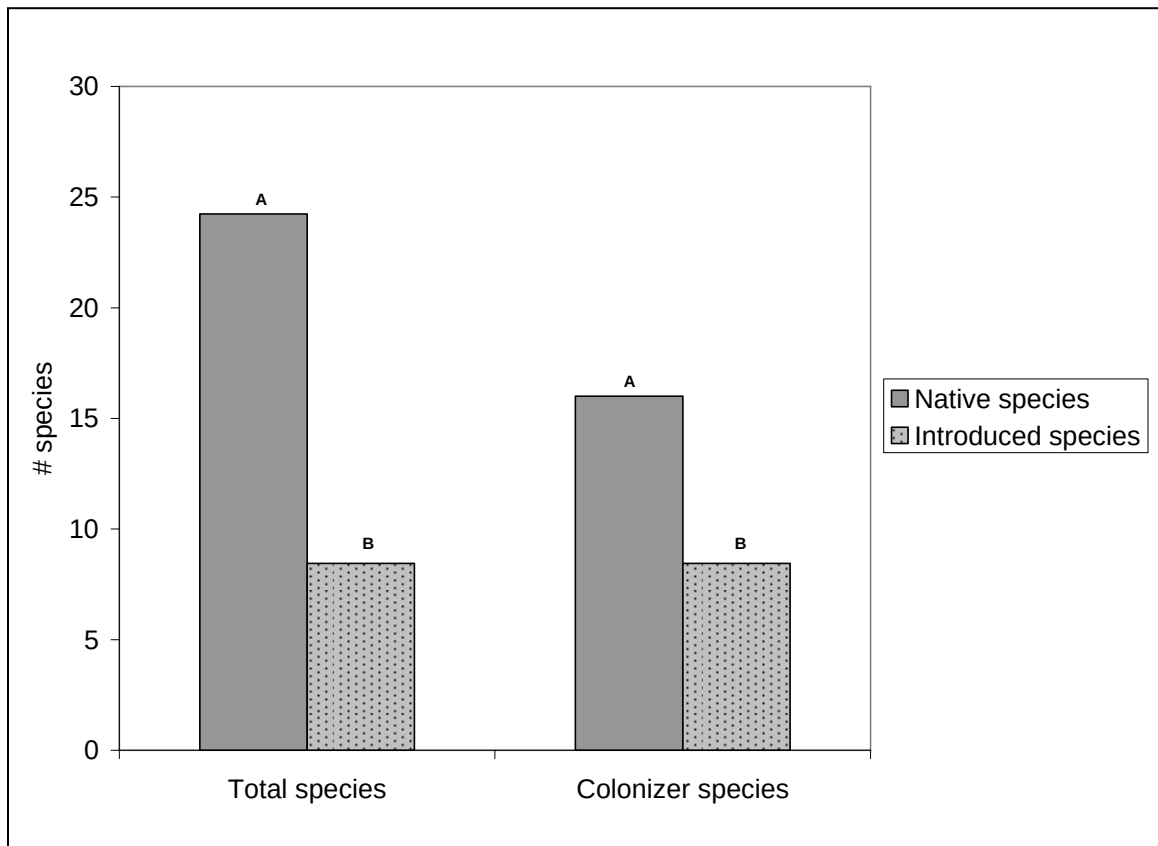


Figure 14. Total and colonizer species richness by origin on sites one year after disturbance, Rocky Mountain National Park. Different letters represent significance at $p \leq 0.05$.

and *Thermopsis divaricarpa* Nels. (20%). Common subshrubs include *Artemisia frigida* Willd. (44%) and *A. ludoviciana* Nutt.(36%). The shrub *Rosa woodsii* Lindl. was also common in disturbed transects (20%).

Exotic species most commonly observed in transects were perennial grasses (Appendix C). Both *Poa compressa* L. and *Bromus inermis* (Leyss) Holub occurred in 64% of transects. Other common exotic perennial grasses observed in transects include *Phleum pretense* L. (56%) and *Poa pratensis* L., *Elymus repens* (L.) Gould, and *Agrostis gigantea* Roth, which were all observed in 44% of transects. Several perennial forbs were also recorded frequently in transects. These include *Taraxacum officinale* Wiggers (64%), *Cirsium arvense* (L.) Scop. (52%), *Melilotus officianalis* L. (Lam.) (32%), and *Trifolium repens* L. (28%). Several of these species are of concern for park managers, including *Cirsium arvense*, *Melilotus officianalis*, and *Verbascum thapsus* L., and *Rumex crispus* L.. Their presence on disturbed sites should be monitored and control efforts implemented in order that these populations do not spread to adjacent areas of the park.

TRANSPLANT SURVIVAL ON ALPINE TUNDRA SITES

Restoration of alpine tundra sites pose unique challenges due to harsh conditions, such as desiccating winds, limited soil resources, and a short growing season. Natural succession on disturbed sites is often slow and unpredictable in alpine areas (Macyk 2000). Seeding can be successful, but may be expensive due to lack of commercially available native seed, and hand collection may be difficult due to variation in seed production for different species from year to year (Chambers 1989). Roach and Marchand (1984) reported seeding often leads to high seedling mortality due to severe

conditions of the alpine tundra. Successful restoration of alpine tundra has been reported by transplanting material (Buckner and Marr 1988, Urbanska 1997).

The establishment of permanent plots will allow for long-term monitoring of disturbed sites in the alpine tundra. Transplant survival rates at both the AVC sewage lagoon and Fall River vault toilets were high one year after planting (Appendix D). Survival rates were similar despite variable transplanting densities between the two sites. These results suggest that survivorship of transplanted material on alpine tundra sites is not dependant on transplant density for this range in planting densities. Estimated cover also differed between the two sites as a consequence of the difference in plant densities. Plant cover was estimated at 5.2% on the AVC plots and 12.8% on the Fall River vault toilet plots.

Natural colonization of the disturbance was very low (data not shown). The only species naturally colonizing the site one year following disturbance was the native forb *Androsace septentrionalis* L. This observation suggests that natural colonization of disturbances in the alpine tundra is a slow process that may not be an affective approach to restoration. However, transplanting both savaged sod and greenhouse plugs appear to be an effective method of increasing cover and plant densities on disturbed alpine tundra sites.

CONCLUSIONS: RECOMMENDATIONS FOR NPS MANAGERS

The vegetation of Rocky Mountain National Park consists of many late-seral plant community types. Vegetation type is dependant on many different factors, including elevation, aspect, soils, and hydrology. Successional processes and rates will likely differ between these plant community types potentially resulting in different Best Management Practices for restoration following disturbance in each community type. Thus, it should

be emphasized that application of results from this work should be applied to the specific vegetation types in which studies were conducted.

Various approaches for the restoration of human disturbances in montane grasslands and shrublands in the lower elevations of RMNP (approximately 2700 m and below) were assessed. Passive restoration through natural colonization by native species was shown to occur within the first year following disturbance. Passive restoration was shown to be an effective method of restoring disturbances in situations where populations of exotic species are not in close proximity to the disturbed site. Populations of exotic species in adjacent plant communities increase the chances of their establishment which may result in significant delays in successional development of these disturbed sites. The presence of nearby roads, trails, buildings, or other park facilities that receive use by park staff or visitors may increase the chances of introduction of propagules of exotic species onto disturbed sites. Therefore, passive restoration on disturbed sites near areas of human use may not be an acceptable alternative.

The seeding of a nurse crop (Regreen *Triticum aestivum* x *Elytrigia elongata*; or annual ryegrass *Lolium multiflorum*) on passively restored sites was assessed to determine effects on plant community development. No individuals of Regreen or annual ryegrass were found on any of the sites seeded with these nurse crops, suggesting that neither species had persisted in the 13 years since they were seeded. Seeding a nurse crop did not have an effect on native species cover or richness. However, sites seeded with a nurse crop had significantly higher cover and richness of exotic species compared to passively restored sites that were not seeded to a nurse crop. Nurse crop sites had significantly lower community similarity indices due to the increased cover and richness

of exotic species. These results suggest seeding of a nurse crop may promote the establishment of exotic species following disturbance.

Treatments consisting of seeding, transplanting containerized material, and a combination of seeding and transplanting in disturbed montane grassland and shrubland communities were compared to assess the relative affects of restoration techniques. Seeding treatments produced lower cover of native species compared to transplanting and a combination of seeding and transplanting. Treatments showed minor effects on species richness of disturbed sites. Community similarity indices were significantly lower for transplanted sites relative to seeded sites and seeded and transplanted sites. These results suggest a combination of seeding grasses and transplanting forbs and shrubs may be the best approach to restoring disturbances in montane grasslands and shrublands in RMNP.

A cost-effectiveness analysis of restoration treatments based on the calculation of *Effectiveness Index* (EI) scores and actual treatment costs on individual sites suggest that despite lower cover of native species on seeded sites, seeding is the most cost-effective treatment in restoring disturbances in the lower elevations of RMNP. Sites treated with a combination of seeding and transplanting had the highest *EI* scores, however the increased costs associated with transplanting resulted in lower cost-effectiveness compared to seeding. Overall recommendations to park managers are that when financial resources are not limiting, restoring disturbed sites using a combination of seeding grasses and transplanting forbs and shrubs may result in the greatest chance of restoration success based on high cover of native species and low cover of exotic species. However, when financial resources available for restoration projects are limited, seeding a

combination of native grasses, forbs, and shrubs is the most cost-effective approach to restoring native plant communities in montane grasslands and shrublands in RMNP.

All sites sampled in this study had slopes of less than 2%. It should be noted that sites with steep slopes may benefit from the seeding of a nurse crop or transplanting containerized material. These treatments may help to stabilize the soil and lessen soil loss through erosion resulting in increased establishment of native species that are present either from the seed bank or introduced through natural dispersion.

Restoring disturbances on high elevation sites on the alpine tundra can be a challenge due to harsh environmental conditions and limited natural dispersion of plant propagules. Transplanting has been shown to be an effective method of increasing plant cover on disturbed alpine sites (Buckner and Marr 1988, Urbanska 1997). Sampling at the old Alpine Visitor Center sewage lagoon site was conducted in August 2005. Natural colonization was observed to be very low. Transplanting of greenhouse grown plugs and salvaged sod was shown to result in high survivability of plant material one year after planting activities occurred. These results suggest that planting either greenhouse grown material or salvaged sod may be an effective approach to restoring disturbances in the alpine tundra. Plots have been left in place for long-term monitoring of plant cover at this site. It is critical that these sites be monitored in the future for information on rates of natural colonization and increased cover from expansion of transplanted material on the alpine tundra.

LITERATURE CITED

- Aarson, L. W. and G. A. Epp. 1990. Neighbor manipulations in natural vegetation: A review. *Journal of Vegetation Science* 1:13-30.
- Allen, C., D. M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern Ponderosa pine ecosystems: A broad perspective. *Ecological Applications* 12:1418-1433.
- Ash, H. J., R. P. Gemmel, and A. D. Bradshaw. 1994. The introduction of native plant species on industrial waste heaps: a test of immigration and other factors affecting primary succession. *Journal of Applied Ecology* 31:74-84.
- Bailey, R. G. 1998. *Ecoregions: the ecosystem geography of the oceans and continents*. Springer. New York.
- Bainbridge, D., A. M. Fidelibus, and R. MacAller. 1995. Techniques for plant establishment in arid ecosystems. *Restoration and Management Notes* 13:190-197.
- Bakker, J. P. and F. Berendse. 1999. Constraints on the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* 14:63-68.
- Baldwin, A. D., J. J. De Luce, and C. Pletsch. 1994. *Beyond Preservation: Restoring and Inventing Landscapes*. University of Minneapolis Press. Minneapolis, MN.
- Barbour, M. G. 1968. Germination requirements for the desert shrub *Larrea divaricata*. *Ecology* 50:679-685.
- Bekker, R. M., G. L. Verweij, R. E. N. Smith, R. Reine, J. P. Bakker, and S. Schneider. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology* 34:1293-1310.
- Beyers, J. L., C. Wakeman, and S. G. Conrad. 1993. Effects of seeding chaparral burns with annual ryegrass on herbaceous plant cover and species diversity. *Bulletin of the Ecological Society of America* 74:163.
- Bonham, C. D. 1989. *Measurements for Terrestrial Vegetation*. John Wiley & Sons. New York.

- Bradshaw, A. D. 1997. The importance of soil ecology in restoration science. pp. 33-64. *In*: K. M. Urbanska, N. R. Webb P. J. Edwards. Restoration Ecology and Sustainable Development. Cambridge University Press. Cambridge, UK.
- Brown, C. S. and R. L. Bugg. 2001. Effects of established perennial grasses on introduction of native forbs in California. Restoration Ecology 9:38-48.
- Brown, R. W. and M. C. Amancher. 1999. Selecting plant species for ecological restoration: A perspective for land managers. pp. 1-16. *In*: L. K. Holzworth and R. W. Brown, editors. Revegetation with native species. Proceedings, 1997 Society for Ecological Restoration annual meeting, Ft. Lauderdale, FL 12-15 November 1997. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station. Ogden, UT.
- Brown, S. and A. E. Lugo. 1994. Rehabilitation of tropical lands: A key to sustaining development. Restoration Ecology 2:97-111.
- Buckner, D. L. and J. W. Marr. 1988. Alpine revegetation on Rollins Pass after 18 years. pp. 273-990. *In*: W.R. Keammerer and L.F. Brown, editors. Proceedings of the High Altitude Revegetation Workshop no. 8. Water Resources Research Institute, Colorado State University. Fort Collins, CO.
- Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958-1965.
- Carpenter, A. T., J. C. Moore, E. F. Redente, and J. M. Stark. 1990. Plant community dynamics in relation to addition following a major disturbance. Plant and Soil 126:91-100.
- Chambers, J. C. 1989. Seed viability of alpine species: variability within and among years. Journal of Range Management 42:304-308.
- Chambers, J. C. 1995. Relationships between seed fates and seedling establishment in an alpine ecosystem. Ecology 76:2124-2133.
- Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecological Applications 10:1400-1413.
- Chambers, J. C., R. W. Brown, B. D. Williams. 1994. An evaluation of reclamation success on Idaho's phosphate mines. Restoration Ecology 2:4-16.
- Chambers, J. C., J. A. MacMahon, and J. H. Haefner. 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. Ecology 72:1668-1677.

- Chaneton, E. J. and J. M. Facelli. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* 93:143-155.
- Chao, F. S., III L. R. Walker, C. L. Fastie, and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64:149-175.
- Cherrett, J. M. 1989. Key Concepts: the results of a survey of our members' opinions. pp 1-16. *In*: M. Cherrett, editor. *The Contribution of Ecology to the Understanding of the Natural World*. Blackwell. Oxford, UK.
- Clements, F. E. 1916. *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington Publication 242. Washington D. C.
- Clements, F. E. 1936. Nature and structure of the Climax. *Journal of Ecology* 24:252-84.
- Cole, D. N. and D. R. Spildie. 2000. Soil amendments and planting techniques: Campsite restoration in the Eagle Cap Wilderness, Oregon. pp. 181-187. *In*: D. N. Cole, S. F. McCool W. T. Borrie and J. O'Loughlin, compilers. *Wilderness Science in a Time of Change- Volume 5: Wilderness Ecosystems, threats, and Management*. May 23-27, 1999. Missoula, MT. Proceedings RMRS-P-15-VOL-5. Department of Agriculture, United States Forest Service, Rocky Mountain Research Station. Ogden, UT.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist* 122:661-696.
- Connell, J. H., I. R. Noble and R. O. Slayter. 1987. On the mechanisms producing successional change. *Oikos* 50:136-137.
- Connell, J. H. and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their roles in community stability and organization. *The American Naturalist* 111:1119-1144.
- Conner, J. 2005. United States Department of the Interior, Rocky Mountain National Park, Estes Park, Colorado. Personal communication.
- Conner, J. K. and D. L. Hartl. 2004. *A Primer on Ecological Genetics*. Sinauer Associates, Inc. Sunderland, MA.
- Cotts, N. R., E. F. Redente, and R. Schiller. 1991. Restoration methods for abandoned roads at lower elevation in Grand Teton National Park. *Arid Soil Research and Rehabilitation* 5:235-249.

- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27:95-117, 167-202, 281-308, 361-391.
- Cowles, H. C. 1901. The physiographic ecology of Chicago and vicinity: A study of the origin, development, and classification of plant societies. *Botanical Gazette* 31:73-109, 145-182.
- Crabbé, P, L. Ryszkowski and L. Westra. 2000. Introduction. pp. 1-22. *In*: Crabbé, P, A. Holland L. Ryszkowski and L. Westra, editors. *Implementing Ecological Integrity: Restoring Regional and Global Environmental and Human Health*. Kluwer Academic Publishers. Dordrecht, The Netherlands.
- D'Antonio, C. M. and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in restoration ecology: A synthesis. *Restoration Ecology* 10:703-713.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Dahlskog, S. 1982. Successions in a Lapland mountain delta. *Meddelanden fran Växtbiologiska Institutionen* 3:54-62.
- Daily, G. C. 1997. *Nature's services: societal dependence on natural ecosystems*. Island Press. Washington, D.C.
- Davidson, D. W. 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68:23-35.
- Davidson, E. A., C. J. R. de Carvalho, I. C. G. Vieira, R. D. Figueiredo, P. Moutinho, F. Y. Ishida, M. T. P. dos Santos, J. B. Guerrero, K. Kalif and R. T. Saba. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecological Applications* 14:S150-S163.
- Davy, A. J. 2002. Establishment and manipulation of plant populations and communities in terrestrial systems. pp. 223-241. *In*: M. R. Perrow and A. J. Davy, editors. *Handbook of Ecological Restoration. Volume 1: Principles of Restoration*. Cambridge University Press. Cambridge, UK.
- De Steven, D. 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* 72:1066-1075.
- De Steven, D. 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72:1078-1088.

- Densmore, R., V. L. Dalle-Molle, and K. E. Holmes. 1990. Restoration of alpine and subalpine plant communities in Denali National Park and Preserve, Alaska, USA. pp. 509-519. *In*: H. G. Hughes and T. M. Bonnicksen, compilers. First annual meeting of the Society for Restoration Ecology. University of Wisconsin Arboretum. Madison, WI.
- Díaz, S., M. Cabido, and F. Casanoves. 1999. Functional implications of trait-environmental linkages in plant communities. pp. 338-362. *In*: E. Weiher and P. Keddy, editors. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press. Cambridge, UK.
- Donath, T. W., N. Holzel, and A. Otte. 2003. The impact of site conditions and seed dispersal on restoration success of alluvial meadows. *Applied Vegetation Science* 6:13-22.
- Dormarr, J. F., S. Smoliak, and W. D. Wilms. 1990. Soil chemical properties during succession from abandoned cropland to native range. *Journal of Range Management* 43:260-265.
- Dyer, A. R. and K. J. Rice. 1997. Intraspecific and diffuse competition: The response of *Nassella puchra* in a California grassland. *Ecological Applications* 7:484-492.
- Echert, R. E., F. F. Peterson, M. S. Meurissee, and J. L. Stephens. 1986. Effects of soil surface morphology on emergence and survival of seedlings in big sagebrush communities. *Journal of Range Management* 39:414-421.
- Edwards, P. J. and M. P. Gillamn. 1993. Herbivores and plant succession. pp. 482-501. *In*: A. J. Gray, J. J. Crawley and J. P. Edwards, editors. *Colonization, Succession, and Stability*. Symposium of the British Ecological Society, vol. 26. Blackwell. Oxford, UK.
- Egler, F. E. 1954. Vegetation science concepts I. Initial floristics composition, a factor in old-field vegetation development. *Vegetatio* 4:412-417.
- Ehrenfeld, J. G. 2000. Defining the limits of restoration: The need for realistic goals. *Restoration Ecology* 8:2-9.
- Ehrenfeld, J. G. and N. Scott. 2001. Invasive species and the soil: effects on organisms and ecosystem processes. *Ecological Applications* 11:1259-1260.
- Ehrlich, P. R. and A. H. Ehrlich. 1991. *Healing the Planet*. Addison-Wesley Publishing. New York.
- Eliason, S. A. and E. B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology* 5:245-255.

- Farrell, T. M. 1991. Models and mechanisms of succession: An example from a rocky intertidal community. *Ecological Monographs* 61:95-113.
- Foster, M. M., P. M. Vitousek, and P. A. Randolph. 1980. The effect of ragweed (*Ambrosia artimisiifolia* L.) on nutrient cycling in a 1st yr old-field. *American Midland Naturalist* 106:106-113.
- Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. *American Midland Naturalist* 115:131-145.
- Fuhlendorf, S. D., H. Zhang, T. R. Tunnell, D. M. Engle, and A. F. Cross. 2002. Effects of grazing on restoration of southern mixed prairie soils. *Restoration Ecology* 10:401-407.
- Gleason, H. A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* 44:463-481.
- Gleason, H. A. 1927. Further views on the succession-concept. *Ecology* 8:299-326.
- Gleason, H. A. 1939. The individualistic concept of the plant association. *American Midland Naturalist* 21:92-110.
- Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Monographs* 68:975-989.
- Grantz, D. A., D. L. Vaughn, R. Faber, B. Kim, M. Zeldin, T. VanCuren, and R. Campbell. 1998. Seeding native plants to restore desert farmland and mitigate fugitive dust and PM10. *Journal of Environmental Quality* 27:1209-1218.
- Greipsson, S. and H. El-Mayas. 2000. Arbuscular mycorrhizae of *Leymus arenarius* on coastal sands and reclamation sites in Iceland and response to inoculation. *Restoration Ecology* 8:144-150.
- Grootjans, A. P., W. H. O. Ernst, and P. J. Stuyfzand. 1998. European dune slacks: Strong interactions of biology, pedogenesis, and hydrology. *Trends in Ecology and Evolution* 13:96-100.
- Gross, C. M., J. S. Angle, R. L. Hill, and M. S. Welterlen. 1991. Runoff and sediment loss from tall fescue under simulated rainfall. *Journal of Environmental Quality* 20:604-607.
- Grubb, J. P. 1977. The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Reviews* 52:107-152.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press. New York.

- Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology* 53:273-286.
- Hart, R. H. and J. G. Dean. 1986. Forage establishment: Weather effects on stubble vs. fallow and fall vs. spring seeding. *Journal of Range Management* 39:228-230.
- Hartmann, H. E. and D. E. Kester. 1983. *Plant Propagation: Principles and Practices*. Prentice Hall. Engelwood Cliffs, NJ.
- Helm, D. J. 1994. Establishment of moose browse on four growth media on a proposed mine site in south central Alaska. *Restoration Ecology* 2:164-179.
- Helm, D. J. and W. B. Collins. 1997. Vegetation succession and disturbance on a boreal forest floodplain, Susitna River, Alaska. *Canadian Field-Naturalist* 111:553-566.
- Herrick, J. E. 2000. Soil quality: indicator of sustainable land management? *Applied Soil Ecology* 15:75-83.
- Hoffmann, L. A., E. F. Redente, and L. C. McEwen. 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecological Applications* 5:200-208.
- Hobbs, R. J. and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4:93-110.
- Holdrige, I. R. 1967. *Life Zone Ecology*. Tropical Science Center. San Jose, Costa Rica.
- Holl, K. D. 1995. Nectar resources and their influence on butterfly communities on reclaimed coal surface mines. *Restoration Ecology* 3:76-85.
- Holl, K. D., M. E. Loik, E. H. V. Lin, and I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* 8:339-349.
- Hufford, K. M. and S. J. Mazer. 2003. Plant ecotypes: Genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* 18:147-155.
- Huston, M. and T. Smith. 1987. Plant succession: Life history and competition. *The American Naturalist* 130:168-198.
- Inouye, R. S., N. J. Huntley, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987. Old-field succession in a Minnesota sand plain. *Ecology* 68:12-26.

- Iverson, L. R. and M. K. Wali. 1982. The role of *Kochia scoparia* and other pioneers in the revegetation process of surface mined lands. *Reclamation and Restoration Research* 1:123-160.
- Iverson, L. R. and M. K. Wali. 1992. Grassland rehabilitation after coal and mineral extraction in the western United States and Canada. pp. 85-129. *In*: M. K. Wali, editor. *Ecosystem Rehabilitation. Volume 2: Ecosystem Analysis and Synthesis*. SPB Academic. The Hague, The Netherlands.
- Kielland, K., J. P. Bryant, and R. W. Ruess. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos* 80:25-30.
- Kindscher, K. and L. L. Tieszen. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. *Restoration Ecology* 6:181-196.
- Lacy, R. C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology* 1:143-158.
- Lauenroth, W. K. and D. P. Coffin. 1992. Belowground processes and the recovery of semiarid grasslands from disturbance. pp. 131-150. *In*: M. K. Wali, editor. *Ecosystem Rehabilitation. Volume 2: Ecosystem Analysis and Synthesis*. SBP Academic. . The Hague, The Netherlands.
- Lemons, J. and L. Westra. 1995. Introduction to perspectives on ecological integrity. *In*: L. Westra and J. Lemons, editors. *Perspectives on Ecological Integrity*. Kluwer Academic Publishers. Dordrecht, The Netherlands.
- Linhart, Y. B. and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27:237-277.
- Lippitt, L., M. W. Fidelibus, and D. A. Bainbridge. 1994. Native seed collection, processing, and storage for revegetation projects in the western United States. *Restoration Ecology* 2:120-131.
- Loveless, M. D. and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics* 15:65-95.
- Luce, C. H. 1997. Effectiveness of road ripping in restoring infiltration capacity of forest roads. *Restoration Ecology* 5:265-270.
- MacArthur, R. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press. Princeton, NJ.

- Mack, M. C., C. M. D'Antonio, and R. E. Ley. 2001. Alterations of ecosystem nitrogen dynamics by exotic plants: A case study of C₄ grasses in Hawaii. *Ecological Applications* 11:1323-1335.
- Macyk, T. M. 2000. Reclamation of alpine and subalpine lands. pp. 371-398. *In*: R.I. Barnhisel, R. G. Darmody and W. L. Daniels, editors. *Reclamation of Drastically Disturbed Lands*. American Society of Agronomy. Madison, WI.
- Malanson, G. P. and D. M. Cairns. 1997. Effects of dispersal, population delays, and forest fragmentation on tree migration rates. *Plant Ecology* 131:67-79.
- McIntosh, R. P. 1985. *The Background of Ecology*. Cambridge University Press. Cambridge, UK.
- McIntosh, R. P. 1999. The succession of succession: a lexical chronology. *Bulletin of the Ecological Society of America* 80:256-265.
- McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. "How local is local?" - A review of practical and conceptual issues in the Genetics of Restoration. *Restoration Ecology* 13:432-440.
- McLendon, T. and E. F. Redente. 1990. Successional patterns following soil disturbance in a sagebrush steppe community. *Oecologia* 85:293-300.
- McLendon, T. and E. F. Redente. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. *Ecology* 72:2016-2024.
- McLendon, T., M. W. Paschke, and E. F. Redente. 1995. Vegetation Restoration Research, Rocky Mountain National Park: Patterns of Secondary Succession Following Anthropogenic Disturbances. pp. 27-40. *In*: W. R. Keammerer and W. G. Hassell, editors. *Proceedings: High Altitude Revegetation Workshopp No. 11, March 16-18, 1994*. Colorado Resources Research Institute, Colorado State University. Fort Collins, CO.
- McWilliams, J. L. 1955. Effect of some cultural practices on grass production at Mandan, North Dakota. United States Department of Agriculture. Washington, D. C.
- Moser, L. E. and P. R. Newman. 1988. Grass seedling development. *Proceedings: Northern Plains Grass Seed Symposium, January 7-8, 1988*. Pierre, SD.
- Mueller-Dombois, D. and H. Ellenberg. 2002. *Aims and Methods in Vegetation Ecology*. Blackburn Press. Caldwell, NJ.
- Munshower, F. F. 1994. *Practical Handbook of Disturbed Land Revegetation*. CRC Press. Boca Raton, FL.

- NADP (National Atmospheric Deposition Program). NADP/NTN Monitoring Location CO19, Rocky Mountain National Park-Beaver Meadows, Larimer County, Colorado. 2006. January 2006. (<http://nadp.sws.uiuc.edu/sites/siteinfo.asp?net=NTN&id=CO19>).
- Namkoong, G. 1988. Sampling for germplasm collection. *HortScience* 23:79-81.
- NCDC (National Climatic Data Center). Station 052761, Estes Park, Colorado. 2006. January 2006. (<http://www.ncdc.noaa.gov/oa/ncdc.html>).
- Nichols, O. G. and F. M. Nichols. 2003. Long-term trends in faunal recolonization after bauxite mining in the jarrah forest of southwestern Australia. *Restoration Ecology* 11:261-272.
- NPS (National Park Service). 2004. Management Policies. United States Department of the Interior. Washington, D. C.
- NRCS (Natural Resources Conservation Service). Soil survey of Rocky Mountain National Park, Colorado, parts of Boulder, Grand, and Larimer counties. 2005.
- O'Dwyer, C. and P. M. Attiwill. 2000. Restoration of native grassland as habitat for the golden sun moth *Synemon plana* Walker (Lepidoptera: Castniidae) at Mount Piper, Australia. *Restoration Ecology* 8:170-174.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164:262-270.
- Oloff, H., J. De Leeuw, J. P. Bakker, R. J. Platerink, H. J. Van Wijnen, and W. De Munck. 1997. Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology* 85:799-814.
- Oremus, P. A. I. and H. Otten. 1981. Factors affecting growth and nodulation of *Hippophaë rhamnoides* L. ssp. *rhamnoides* in soils from two successional stages of dune formation. *Plant and Soil* 63:317-331.
- Packer, P. E. and E. F. Aldon. 1978. Revegetation techniques for dry regions. pp. 425-450. *In*: F. W. Schaller and P. Sutton, editors. *Reclamation of Drastically Disturbed Lands*. American Society of Agronomy. Madison, WI.
- Pachham, J. R., E. V. J. Cohn, P. Millett, and I. C. Trueman. 1995. Introduction of plants and manipulation of field layer vegetation. pp. 129-148. *In*: R. Ferris-Kaan, editor. *The Ecology of Woodland Creation*. John Wiley. Chichester, UK.
- Palmer, M. A., R. F. Ambrose, N. L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5:291-300.

- Parish, J. A. D. and F. A. Bazzaz. 1982. Competitive interactions in plant communities of different successional ages. *Ecology* 63:314-320.
- Paschke, M. W., C. DeLeo, and E. F. Redente. 2000a. Revegetation of roadcut slopes in Mesa Verde National Park, U.S.A. *Restoration Ecology* 8:276-282.
- Paschke, M. W., T. McLendon, and E. F. Redente. 2000b. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144-158.
- Passell, H. D. 2000. Recovery of bird species in minimally restored Indonesian thin strip mines. *Restoration Ecology* 8:122-118.
- Peet, R. K. 2000. Forests and Meadows of the Rocky Mountains. pp. 75-122. *In*: M. G. Barbour and W. D. Billings, editors. *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, UK.
- Peterson, G., C. R. Allen and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Peterson, S. L., B. A. Roundy, and R. M. Bryant. 2004. Revegetation methods for high elevation roadsides at Bryce Canyon National Park, Utah. *Restoration Ecology* 12:248-257.
- Phan, A. T. and S. R. Smith. 2000. Seed yield variation in Blue grama and Little Bluestem plant collections in southern Manitoba, Canada. *Crop Science* 40:555-560.
- Pianka, E. R. 1970. On *r* and *K* selection. *The American Naturalist* 104:592-597.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *Biological Reviews* 53:335-371.
- Pinjuv, G., P. J. Daugherty, and B. E. Fox. 2001. Cost / effectiveness analysis of ponderosa pine ecosystem restoration in Flagstaff Arizona's wildland-urban interface. pp. 149-153. *In*: R. K. Vance, C. B. Edminster W. W. Covington J. A. Blake, compilers. *Ponderosa pine ecosystems restoration and conservation: steps toward stewardship*. 2000, April 25-27, Flagstaff, AZ. Proceedings RMRS-P-22. USDA Forest Service, Rocky Mountain Research Station. Ogden, UT.
- Purcell, A. H., C. Freidrich, and V. H. Resh. 2002. An assessment of a small urban stream restoration project in northern California. *Restoration Ecology* 10:685-694.
- Pywell, R. F., J. M. Bullock, A. Hopkins, K. J. Walker, T. H. Sparks, M. J. W. Burke, and S. Peel. 2002. Restoration of species-rich grassland on arable land: Assessing the limiting process using a multi-site experiment. *Journal of Applied Ecology* 39:294-309.

- Quade, E. S. 1967. Cost Effectiveness Analysis: New Approaches in Decision-making. Preager Publishers. New York.
- Ramsey, D. S. L. and J. C. Wilson. 1997. The impact of grazing by macropods on coastal foredune vegetation in southwest Queensland. *Australian Journal of Ecology* 22:288-297.
- Ranwell, D. S. and R. Boar. 1986. Coast Dune Management Guide. Institute for Terrestrial Ecology. Abbots Ripton, UK.
- Regelbrugge, J. C. and S. G. Conrad. 1990. Effects of fire intensity, rock type, and seeding on vegetation recovery following the 1987 Stanislas complex fires in California, USA. *Bulletin of the Ecological Society of America* 71:297.
- Reichman, O. J. 1984. Spatial and temporal variation in seed distributions of Sonoran desert soils. *Journal of Biogeography* 11:1-11.
- Rhoades, C. C., G. E. Eckert, and D. C. Coleman. 1998. Effect of pasture trees on soil organic nitrogen and organic matter: implications for tropical montane forest restoration. *Restoration Ecology* 6:262-270.
- Ries, R. E. and L. Hofmann. 1996. Perennial grass establishment in relationship to seeding dates in the Northern Great Plains. *Journal of Range Management* 49:504-508.
- Roach, D. A. and P. J. Marchand. 1984. Recovery of alpine disturbances: Early growth and survival in populations of the native species *Arenaria groenlandica*, *Juncus trifidus*, and *Potentilla tridentata*. *Arctic and Alpine Research* 16:37-43.
- Robichaux, R. H., E. A. Friar, and D. W. Mount. 1997. Molecular Genetic Consequences of a Population Bottleneck Associated with Reintroduction of the Mauna Kea Silversword (*Argyroxiphium sandwicense* ssp. *sandwicense* [Asteraceae]). *Conservation Biology* 11:1140-1146.
- Robinson, G. R. and S. N. Handel. 1993. Forest restoration on a closed landfill: Rapid addition of new species by bird dispersal. *Conservation Biology* 7:271-278.
- Ruiz-Jaen, M. C. and T. M. Aide. 2005. Restoration success: How is it being measured? *Restoration Ecology* 13:569-577.
- Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Science U.S.A.* 99:2445-2449.
- Schiechtl, H. M. and R. Stern. 1996. Ground Bioengineering Techniques for Slope Stabilization. Blackwell. Oxford, UK.

- SER (Society for Ecological Restoration International Science & Policy Working Group). The SER International Primer on Ecological Restoration. 2004. January 2006. (http://www.ser.org/content/ecological_restoration_primer.asp)
- Shearer, R. C., R. W. Potter, L. L. Kurth, and J. M. Asebrook. 1996. Cooperation enhances revegetation efforts in Glacier National Park. *Park Science* 16:20-21.
- Smith, R. S., R. S. Shiel, D. Millward, P. Corkhill, and R. A. Sanderson. 2002. Soil seed banks and the effects of meadow management on vegetation change in a 10-year meadow field trial. *Journal of Applied Ecology* 39:279-293.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Stamp, N. E. 1989. Efficacy of explosive vs. hygroscopic seed dispersal by an annual grassland species. *American Journal of Botany* 76:555-561.
- Stevenson, B. A., T. McLendon, and E. F. Redente. 2000. Effects of soil fumigation and seeding regimes on secondary succession in a semiarid shrubland. *Arid Soil Research and Rehabilitation* 14:87-99.
- Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19:46-53.
- Swanson, F. J. and J. F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* 2:262-274.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284-307.
- Thompson, K. 2000. The functional ecology of soil seed banks. pp. 215-236. *In*: M. Fenner, editor. *Seeds: the Ecology of Regeneration in Plant Communities*. CAB International. Wallingford, UK.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press. Princeton, NJ.
- Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. *Ecology* 65:1445-1453.
- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist* 125:827-852.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press. Princeton, NJ.

- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16.
- Tobler, W. R. 1970. A computer movie simulating urban growth in the Detroit area. *Economic Geography* 46:234-240.
- Toth, L. A., D. A. Arrington, M. A. Brady, and D. A. Muszick. 1995. Conceptual evaluation of factors potentially affecting restoration of habitat structure within the channelized Kissimmee River ecosystem. *Restoration Ecology* 3:160-180.
- Turner, M. G., V. D. Dale, and E. H. Everham III. 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. *BioScience* 47:758-767.
- Urbanek, R. P. The influence of fauna on plant productivity. pp. 71-106. *In*: J. D. Majer, editor. *Animals in Primary Succession: The Role of Fauna in Reclaimed Land*. 1989. Cambridge University Press. Cambridge, UK.
- Urbanska, K. M. 1997. Restoration ecology of alpine and arctic areas: are the classical concepts of niche and succession directly applicable? *Opera Botanica* 132:189-200.
- Vallentine, J. F. 1989. *Range Development and Improvements*. Academic Press. San Diego, CA.
- van Aarde, R. J., S. M. Ferreira, J. J. Kritzing, P. J. Van Dyk, M. Vogt, T. D. Wassenaar. 1996. An evaluation of habitat rehabilitation on coastal dune forests in northern KwaZulu-Natal, South Africa. *Restoration Ecology* 4:334-345.
- Van Andel, J., J. P. Bakker, A. P. Grootjans. 1993. Mechanisms of vegetation succession: A review of concepts and perspectives. *Acta Botanica Neerlandica* 42:413-433.
- Van de Koppel, J., R. Rietkirk, and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution* 12:352-356.
- van der Putten, W. H., C. van Dijk, and B. A. M. Peters. 1993. Plant-specific soil-born diseases contribute to succession in foredune vegetation. *Nature* 362:53-56.
- van der Putten, W. H., S. R. Mortimer, K. Hedlund, C. Van Dijk, V. K. Brown, J. Leps, C. Rodriguez-Barrueco, J. Roy, T. A. Diaz Len, D. Gormsen, G. W. Korthals, S. Lavorel, I. Santa Regina, and P. Smilauer. 2000. Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. *Oecologia* 124:91-99.

- van der Valk, A. G. and R. L. Peterson. 1989. Seed banks and the management and restoration of natural vegetation. pp. *In*: M. A. Leck, V. T. Parker and R. L. Simpson, editors. Ecology of Soil Seed Banks. Academic Press. San Diego, CA.
- Vitousek, P. M. 1983. Nitrogen turnover in a ragweed-dominated 1st yr old-field in southern Indiana. *American Midland Naturalist* 110:46-53.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of the earth's ecosystems. *Science* 277:494-499.
- Wali, M. K. 1999. Ecological succession and the rehabilitation of disturbed terrestrial ecosystems. *Plant and Soil* 213:195-220.
- Walker, L. R. 1995. How unique is primary plant succession at Glacier Bay? *In*: D. R. Engstrom, editor. *Proceeding of the Third Glacier Bay Science Symposium, 1993*. National Park Service. Anchorage, AK.
- Walker, J. L. and W. D. Boyter. 1993. An ecological model and information needs assessment for longleaf pine ecosystem restoration. pp. 138-147. *In*: L. H. Foley, editor. *Silviculture: From the Cradle of Forestry to Ecosystem Management*. General Technical Report SE-88. USDA Forest Service. Southeastern Forest Experiment Station. Asheville, NC.
- Walker, L. R. and R. del Moral. 2003. *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press. Cambridge, UK.
- Walker, L. R. and M. R. Willig. 1999. An introduction to terrestrial disturbances. *In*: L. R. Walker, editor. *Ecosystems of Disturbed Ground, Ecosystems of the World* 16. Elsevier. Amsterdam.
- Ward, S. C., J. M. Koch, and G. L. Ainsworth. 1996. The effect of timing of rehabilitation procedures on the establishment of a jarrah forest after bauxite mining. *Restoration Ecology* 4:19-24.
- Warming, E. 1895. *Plantesamfund: Grundtræk af den Ökologiska Plantegeografi*. Philipsen. Copenhagen.
- Whelan, R. J. 1989. Influence of fauna on plant species composition. pp. 107-142. *In*: J. D. Majer, editor. *Animals in Primary Succession: The Role of Fauna in Reclaimed Land*. Cambridge University Press. Cambridge, UK.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Biological Reviews* 45:229-299.
- White, P. S. and S. T. A. Pickett. 1985. The Ecology of Patch Dynamics and Natural Disturbance. pp. 3-16. *In*: White, P. S. and S. T. A. Pickett, editors. *Patch dynamics: a synthesis*. Academic Press. Orlando, FL.

- White, P. S. and J. L. Walker. 1997. Approximating nature's variation: Selecting and using reference sites and reference information in restoration ecology. *Restoration Ecology* 5:338-349.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147:250-260.
- Winkel, V. K., B. A. Roundy, and J. R. Cox. 1991. Influence of seedbed microsite characteristics on grass seedling emergence. *Journal of Range Management* 44:210-214.
- Winslow, S. R. and M. E. Majerus. 2005. United States Department of Agriculture, Natural Resources Conservation Service, Bridger Plant Materials Center, Bridger, MT. Personal communication.
- Young, T. P. 2000. Restoration ecology and conservation biology. *Restoration Ecology* 92:73-83.
- Zadeh, H. 2001. Successional Patterns and Rates of Recovery of Disturbed Sites in Rocky Mountain National Park, Colorado. Thesis. Colorado State University. Fort Collins, CO.

APPENDIX A

Rocky Mountain National Park Disturbed Site Treatment Data

1. Beaver Meadows Visitor Center.

Highway 36 was widened in 2002 as part of improvements to the Beaver Meadows Visitor Center. In 2002 a contractor was hired to hydroseed roadsides with a combination of native species and Regreen followed by application of hydromulch.

Disturbance size: 7650 m²

Seeding rate: 26.4 lb./ acre

Species	weight
Native species mixture	0.25 lbs.
<i>Stipa robusta</i>	50 lbs.
Regreen	350 lbs.

Labor: N/A

2. Fire Management Office

The Fire Management Office was constructed in 2002. This site was revegetated in 2002 with a combination of seeding and transplanting.

Disturbance size: 790 m²

Seeding rate: 8.8 lbs; (45.1 lbs./acre)

Species	Weight
<i>Bouteloua gracilis</i>	2.5 lbs.
<i>Koeleria macrantha</i>	6 lbs.
<i>Hesperostipa comata</i>	0.3 lbs

Transplanting rate: 472 plants total (2420 plants / acre)

Species	Number planted
<i>Achillea millifolium</i>	24
<i>Artemisia ludoviciana</i>	5
<i>Aster porteri</i>	24
<i>Bouteloua gracilis</i>	12
<i>Chrysothamnus vicidiflorus</i>	12
<i>Erigeron flagellaris</i>	208
<i>Gaillardia aristata</i>	24
<i>Heterotheca villosa</i>	11
<i>Koeleria macrantha</i>	24
<i>Penstemon unilateralis</i>	3
<i>Potentilla pennsylvannica</i>	3
Misc. salvage	98
<i>Potentilla</i> species	24

Labor: 87 hours

Duties	Hours
Harrowing	14.5
Raking	31
Planting	23.5
Seeding	18

3. McGraw Ranch.

The park installed a water tank approximately 80 meters northwest of the cabins in 2002. The site was revegetated in 2002 by transplanting.

Disturbance size: 1250 m²

Transplanting rate: 1474 plants total (4770 plants/acre)

Species	Number planted
<i>Artemisia frgida</i>	430
<i>Aster porteri</i>	160
<i>Danthonia parryi</i>	56
<i>Potentilla fissa</i>	16
<i>Erigeron</i> spp.	22
<i>Gaillardia aristata</i>	19
<i>Koeleria macrantha</i>	140
<i>Muhlenbergia montana</i>	166
<i>Oenothera</i> spp.	24
<i>Eriogonum alatum</i>	177
<i>Rosa woodsii</i>	3
<i>Rudbeckia hirta</i>	115
<i>Solidago</i> spp.	76
<i>Hesperostipa comata</i>	72
Total	1476

Labor: 147 hours

4. Moraine Park Campground amphitheater.

The park built a new amphitheater in 2001 in the Moraine Park Campground. The site was restored with transplanting in 2002.

Disturbance size: 615 m²

Transplanting rate: 751 plants total (4940 plants/acre)

Species	Number planted
<i>Allium cernuum</i>	41
<i>Antennaria</i> spp.	24
<i>Aquilegia caerulea</i>	13
<i>Artemisia</i> spp.	12
<i>Artemisia frgida</i>	430
<i>Bouteloua gracilis</i>	129
<i>Campanula rotundifolia</i>	4
<i>Potentilla fissa</i>	140
<i>Erysimum capitatum</i>	29
<i>Gaillardia aristata</i>	12
<i>Heterotheca villosa</i>	126
<i>Muhlenbergia montana</i>	24
<i>Penstemon unilateralis</i>	11
<i>Potentilla gracilis</i>	23
<i>Eriogonum alatum</i>	49
<i>Rudbeckia hirta</i>	24
<i>Solidago</i> spp.	24
<i>Hesperostipa comata</i>	33
Total	751

Labor: 104 hours

5. Beaver Meadows entrance station roadside - north side

The Beaver Meadows entrance station was widened and more kiosks added resulting in disturbance of the roadsides in 2002. The disturbance was revegetated by seeding in 2002.

Disturbance size: 5050 m²

Seeding rate: 1.93 lb./ acre

Labor: N/A

6. Beaver Meadows entrance station roadside - south side

The Beaver Meadows entrance station was widened and more kiosks added resulting in disturbance of the roadsides in 2002. The disturbance was revegetated by seeding in 2002.

Disturbance size: 5050 m²

Seeding rate: 1.93 lbs./acre

Species	Weight
Native species mixture	0.03 lbs
<i>Stipa robusta</i>	1.4 lbs
Regreen	5 lbs.

Labor: 155 hours.

7. McLaren Hall

McLaren Hall was renovated in 1998 resulting in disturbance surrounding the main building and post office. The site was revegetated in 1998 and 1999 by seeding and transplanting.

Disturbance size: 1855 m²

Seeding rate: N/A

Transplanting rate: 2110 plants total (4600 plants/acre)

8. Sprague Lake picnic area

Renovation of the Sprague Lake picnic area in 1999 resulted in disturbance that was revegetated by transplanting.

Disturbance size: 1370 m²

Transplanting rate: 940 plants (2780 plants/acre)

9. Fisherman's access

Disturbed in 1998, revegetated with seeding.

Disturbance size: 750 m²

Seeding rate: N/A

Labor: N/A

10. Jennings Bridge

Disturbed in 1998, revegetated with seeding and transplanting.

Disturbance size: 1500 m²

Seeding rate: N/A

Transplanting rate: N/A

Labor: N/A

11. Old Twin Sisters parking lot.

The former Twin Sisters parking lot was closed and revegetated by transplanting in 1999.

Disturbance size: 290 m²

Transplanting rate: 1200 plants (17,140 plants/acre)

Labor: N/A

12. Hot Shot Dorm

Hot Shot Dormitory was constructed in 1996. The south and east sides of the building were restored by transplanting in 1997.

Disturbance size: 230 m²

Transplanting rate: 898 plants (15,800 plants/acre)

Labor: N/A

13. William Allen White Cabin

Restoration of the east side of the cabin and along the footpath leading up from Bear Lake Rd. by transplanting in 1996.

Disturbance size: 100 m²

Seeding rate: N/A

Transplanting rate: 155 plants (6275 plants/acre)

Species	Number
<i>Vicea</i> spp.	18
<i>Aquilegia</i> spp.	18
<i>Rudbeckia hirta</i>	7
<i>Monarda fistulosa</i>	10
<i>Antennaria parviflora</i>	1
<i>Juniperus communis</i>	2
<i>Holodiscus dumosus</i>	36
<i>Amelanchier alnifolia</i>	1
<i>Ribes cereum</i>	3
<i>Rosa woodsii</i>	1
<i>Ribes inerme</i>	14
<i>Anaphalis margaritacea</i>	3
<i>Adenolinum lewisii</i>	1
Misc. species	39

Labor: N/A

14. Wild Basin Kiosk

Renovation of the Wild Basin Kiosk in 1998. Revegetation in 1998 and 1999 with transplanting.

Disturbance size: ~300 m²

Transplanting rate: 678 plants (9162 plants/acre)

Labor: N/A

15. 718 High Drive

Installation of new septic system in 1991 on south side of residence. Site seeded with sterile wheatgrass hybrid (Regreen: *Triticum aestivum* x *Elytrigia elongata*).

Disturbance size: 610 m²

Labor: N/A

16. Fall River Entrance Station

Installation of utility lines in 1991, starting at roadside continuing northwest up hillside. Disturbed area marked with PVC pipe. Site seeded with sterile wheatgrass hybrid (Regreen: *Triticum aestivum* x *Elytrigia elongata*).

Disturbance size: 150 m²

Labor: N/A

17. 2801 High Drive

Removal of an old foundation in 1990 on north side of a private residence. Site seeded with annual ryegrass (*Lolium multiflorum*).

Disturbance size: 1900 m²

Labor: N/A

18. Bear Lake Road Utility Line

Installation of a new utility line on east side of Bear Lake Road in Moraine Park in 1991. No treatment applied to this site.

Disturbance size: 3220 m²

Labor: N/A

19. 557 High Drive

Installation of new septic system in 1991 on the south side of residence. No treatment was applied.

Disturbance size: 490 m²

Labor: N/A

20. Hollowell Park

Site of Dr. Terry McLendon's scarification experiment. Site disturbed in 1991 by removal of vegetation and scraping off the top 5 cm of soil. No treatment applied.

Disturbance size: 5 x 25 m²

Labor: N/A

APPENDIX B

Frequency of Native Plant Species Naturally Colonizing Undisturbed Sites, Rocky Mountain National Park

Table 1. Frequency of native species observed in belt transects colonizing disturbed sites one year following disturbance, RMNP. Percent frequency is estimated by dividing the number of belt transects containing a species by the total number of belt transects sampled (n=25).

Species	% frequency
<i>Polygonum douglasii</i> Greene	76
<i>Poa palustris</i> L.	68
<i>Chenopodium fremontii</i> S. Wats.	60
<i>Agrostis scabra</i> Willd.	60
<i>Oenothera villosa</i> Thunb. ssp. <i>villosa</i>	52
<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC.	52
<i>Virgulus falcatus</i> (Lindl.) Reveal & Keener	52
<i>Potentilla norvegica</i> L.	48
<i>Fragaria virginiana</i> Duchesne	44
<i>Artemisia frigida</i> Willd.	44
<i>Potentilla gracilis</i> Dougl. ex Hook. var. <i>pulcherrima</i> (Lehm.) Fern.	44
<i>Plantago major</i> L.	40
<i>Androsace septentrionalis</i> L.	36
<i>Artemisia ludoviciana</i> Nutt.	36
<i>Descurainia incana</i> (Bernh. ex Fisch. & C.A. Mey.) Dorn	32
<i>Potentilla pensylvanica</i> L.	32
<i>Solidago missouriensis</i> Nutt.	32
<i>Grindelia subalpina</i> Greene	32
<i>Lepidium virginicum</i> L.	28
<i>Veronica peregrina</i> L.	28
<i>Rudbeckia hirta</i> var. <i>pulcherrima</i>	28
<i>Rumex salicifolius</i> Weinm. ssp. <i>triangulivalvis</i> Danser	28
<i>Chamerion angustifolium</i> (L.) Holub	28
<i>Barbarea orthoceras</i> Ledeb.	24
<i>Verbena bracteata</i> Lag. & Rodr.	24
<i>Bromus anomalus</i> Rupr. ex Fourn.	24
<i>Epilobium brachycarpum</i> K. Presl	24
<i>Arabis drummondii</i> Gray	24
<i>Eriogonum alatum</i> Torr.	20
<i>Penstemon unilateralis</i> Rydb.	20
<i>Heterotheca villosa</i> (Pursh) Shinners	20
<i>Carex</i> sp.	20
<i>Thermopsis divaricarpa</i> Nels.	20
<i>Rosa woodsii</i> Lindl.	20
<i>Machaeranthera pattersonii</i> (Gray) Greene	16
<i>Dracocephalum parviflorum</i> Nutt.	16
<i>Erigeron flagellaris</i> Gray	16
<i>Poa secunda</i> J. Presl	16
<i>Koeleria macrantha</i> (Ledeb.) Schult.	16
<i>Ranunculus</i> sp.	16
<i>Rubus deliciosus</i> James	12

Species	% frequency
<i>Thalictrum fendleri</i> Engelm. ex Gray	12
<i>Lupinus bakeri</i> Greene	12
<i>Gaillardia aristata</i> Pursh	12
<i>Antennaria parvifolia</i> Nutt.	12
<i>Hordeum jubatum</i> L.	12
<i>Drymocallis fissa</i> (Nutt.) Rydb.	12
<i>Chenopodium berlandieri</i> Moq.	8
<i>Potentilla fruticosa</i> auct. non L.	8
<i>Cerastium brachypodum</i> (Engelm. ex Gray) B.L. Robins.	8
<i>Salix</i> sp.	8
<i>Eriogonum umbellatum</i> Torr.	8
<i>Calamagrostis purpurascens</i> R. Br.	8
<i>Chenopodium leptophyllum</i> (Moq.) Nutt. ex S. Wats	8
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	8
<i>Helianthus pumilus</i> Nutt.	8
<i>Astragalus paryii</i> Gray	8
<i>Anaphalis margaritacea</i> (L.) Benth.	4
<i>Ambrosia artemisiifolia</i> L.	4
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	4
<i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex. Griff	4
<i>Artemisia campestris</i> L. ssp. <i>borealis</i> (Pallas) Hall & Clements var. <i>scouleriana</i> (Hook.) Cronq.	4
<i>Arabis glabra</i> (L.) Bernh.	4
<i>Hesperostipa comata</i> (Trin. & Rupr.)	4
<i>Symphyotrichum spathulatum</i> (Lindl.) Nesom	4
<i>Shepherdia canadensis</i> (L.) Nutt.	4
<i>Ribes cereum</i> Dougl.	4
<i>Pseudoroegneria spicata</i> (Pursh) A. Löve ssp. <i>spicata</i>	4
<i>Potentilla hippiana</i> Lehm.	4
<i>Populus tremuloides</i> Michx.	4
<i>Phacelia neomexicana</i> Thurb. ex Torr. var. <i>alba</i> (Rydb.) Brand	4
<i>Phacelia heterophylla</i> Pursh ssp. <i>virgata</i> (Greene) Heckard	4
<i>Penstemon virens</i> Pennell ex Rydb.	4
<i>Galium boreale</i> L.	4
<i>Linum lewisii</i> Pursh	4
<i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.	4
<i>Geranium richardsonii</i> Fisch. & Trautv.	4
<i>Festuca idahoensis</i> Elmer.	4
<i>Erigeron peregrinus</i> (Banks ex Pursh) Greene ssp. <i>callianthemus</i> (Greene)	4
<i>Erigeron formosissimus</i> Greene	4
<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	4
<i>Elymus elymoides</i> (Raf.) Swezey	4
<i>Elymus canadensis</i> L.	4
<i>Deschampsia caespitosa</i> (L.) Beauv.	4

<i>Species</i>	<i>% frequency</i>
<i>Conyza canadensis</i> (L.) Cronq.	4
<i>Collomia linearis</i> Nutt.	4
<i>Oenothera coronopifolia</i> Torr. & Gray	4

Nomenclature follows:

USDA, NRCS. 2006. The PLANTS Database, 10 January 2005. National Plant Data Center, Baton Rouge, LA. (<http://plants.usda.gov>).

APPENDIX C

Frequency of Exotic Plant Species Naturally Colonizing Undisturbed Sites, Rocky Mountain National Park

Table 1. Frequency of exotic species observed in belt transects colonizing disturbed sites one year following disturbance, RMNP. Percent frequency is estimated by dividing the number of belt transects containing a species by the total number of belt transects sampled (n=25).

Species	% frequency
<i>Poa compressa</i> L.	64
<i>Bromus inermis</i> (Leyss) Holub	64
<i>Taraxacum officinale</i> Wiggers	64
<i>Phleum pratense</i> L.	56
<i>Cirsium arvense</i> (L.) Scop.	52
<i>Matricaria discoidea</i> DC.	48
<i>Poa pratensis</i> L.	44
<i>Elymus repens</i> (L.) Gould	44
<i>Agrostis gigantea</i> Roth	44
<i>Acetosella vulgaris</i> (Koch) Fourr.	36
<i>Thlaspi arvense</i> L.	32
<i>Melilotus officianalis</i> L. (Lam.)	32
<i>Trifolium repens</i> L.	28
<i>Alopecurus pratensis</i> L.	20
<i>Alyssum alyssoides</i> (L.) L.	16
<i>Silene latifolia</i> Poir. ssp. <i>alba</i> (P. Mill.) Greuter & Burdet	16
<i>Verbascum thapsus</i> L.	16
<i>Chenopodium foliosum</i> (Moench) Aschers.	16
<i>Anisantha tectorum</i> (L.) Nevski	16
<i>Dactylis glomerata</i> L.	12
<i>Erodium cicutarium</i> (L.) L'Hér. ex Ait.	12
<i>Sisymbrium altissimum</i> L.	12
<i>Tragopogon dubius</i> Scop.	12
<i>Convolvulus arvensis</i> L.	8
<i>Chenopodium glaucum</i> L.	8
<i>Cerastium fontanum</i> Baumg.	8
<i>Capsella bursa-pastoris</i> (L.) Medik.	8
<i>Medicago lupulina</i> L.	8
<i>Salsola tragus</i> L.	8
<i>Berteroa incana</i> (L.) DC.	4
<i>Arctium minus</i> Bernh.	4
<i>Rumex crispus</i> L.	4
<i>Kochia scoparia</i> (L.) Schrad.	4

Nomenclature follows:

USDA, NRCS. 2006. The PLANTS Database, 10 January 2005. National Plant Data Center, Baton Rouge, LA. (<http://plants.usda.gov>).

APPENDIX D

Transplant survival and Cover On disturbed Alpine Tundra Sites, Rocky Mountain National Park

Table 1. Survival of transplanted material in plots on disturbed alpine tundra sites one year following disturbance, RMNP.

Alpine Visitor Center sewage lagoon

Plot	0-1 m	1-2 m	2-3 m	3-4 m	4-5 m	Total live	Total dead	% survival
Plot 1	14.0	15.0	14.0	15.0	16.0	74.0	1.0	98.7
Plot 2	18.0	11.0	16.0	16.0	14.0	75.0	4.0	94.9
Plot 3	16.0	13.0	16.0	18.0	19.0	82.0	0.0	100.0
Plot 4	18.0	15.0	20.0	13.0	16.0	82.0	1.0	98.8
Plot 5	15.0	20.0	15.0	16.0	15.0	81.0	0.0	100.0
Plot 6	17.0	7.0	17.0	15.0	20.0	76.0	1.0	98.7
Plot 7	13.0	15.0	12.0	12.0	11.0	63.0	1.0	98.4
Plot 8	12.0	16.0	14.0	18.0	14.0	74.0	0.0	100.0
Plot 9	17.0	12.0	19.0	17.0	12.0	77.0	2.0	97.5
Ave	15.6	13.8	15.9	15.6	15.2	76.0	1.1	98.6

Fall River Road vault toilets

Plot	0-2.5 m	2.5-5 m	total live	total dead	% survival
plot 1	24	31	55	1	98.21
plot 2	33	22	55	0	100.00
plot 3	25	27	52	3	94.55
Ave	27.3	26.7	54.0	1.3	97.6

Total survival: 98.31 %

Table 2. Plant cover in plots on disturbed alpine tundra sites one year following disturbance, RMNP.

Alpine Visitor Center sewage lagoon

Plot	1	2	3	Plot ave
Plot 1	9	3	2	4.7
Plot 2	3	8	1	4.0
Plot 3	7	4	4	5.0
Plot 4	8	5	10	7.7
Plot 5	5	17	9	10.3
Plot 6	4	6	8	6.0
Plot 7	3	2	2	2.3
Plot 8	2	3	6	3.7
Plot 9	4	5	1	3.3
Ave % cover				5.2

Fall River Road vault toilets

Plot	1	2	3	Plot ave
plot 1	11	9	14	11.3
plot 2	16	18	9	14.3
plot 3	15	13	10	12.7
Ave % cover				12.8

Total average % cover: 7.1

APPENDIX E

Summary of climate data from Estes Park, Colorado

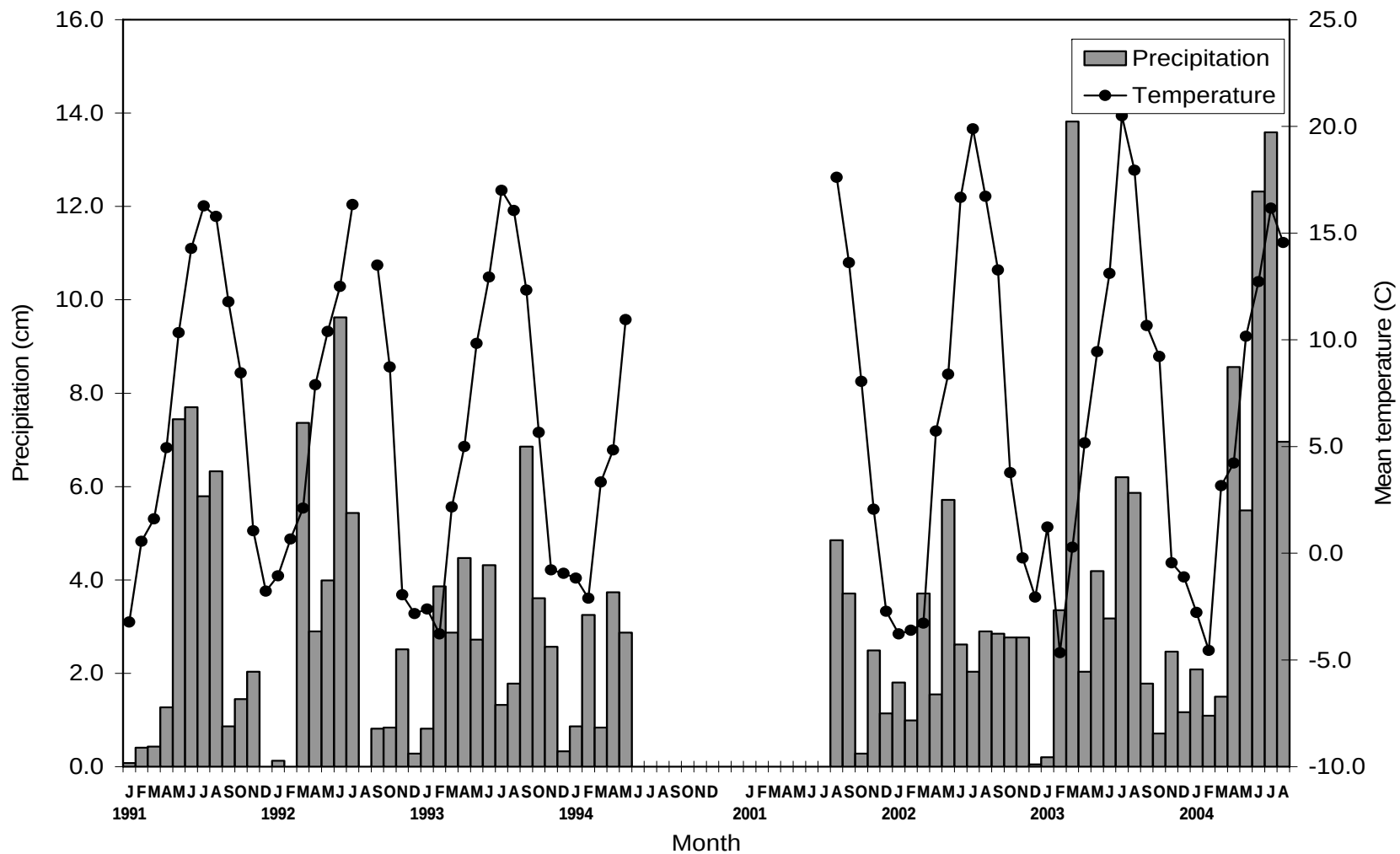


Figure 1. Summary of available mean monthly temperature and total monthly precipitation data for Estes Park, Colorado. Station 052759, 1991-1994; station 052761, 2001-2004; elevation 2280 meters. (NCDC 2005).