Geographic characterization of exotic plant species in Grand Teton National Park, Wyoming
by Deborah Jean Kurtz

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science In Earth Sciences
Montana State University

Abstract:
The study area, located in the southeastern portion of Grand Teton National Park, was sampled to determine the distributions and environmental characteristics of two exotic plant species: Canada thistle (Cirsium arvense) and musk thistle (Carduus nutans).

These data were used to create a model using a Geographic Information System to determine the probability of other areas as suitable habitat for these two species. Measurements of presence/absence, percent cover, and growth stage were recorded and the dominant plants in the plot were noted for two hundred and two 30m x 30m plots randomly distributed throughout the study area. The random sampling layout was created in a Geographic Information System to ensure that seven environmental factors (soil, geology, aspect, slope, elevation, habitat type, and distance from hydrography) were sampled in varying combinations. Canada thistle was present in fifteen sites and musk thistle was present in thirty-three sites, resulting in 7% and 16% presence in the study area for each plant species, respectively.

Chi square tests were performed to determine the association between the environmental factors and the presence/absence of each species. Soil, geology, grazing allotments, elevation, and distance from hydrography were determined to be associated with musk thistle distributions. Soil, geology, grazing allotments, and distance from roads were found to be significantly associated with Canada thistle distributions.

Conditional probabilities were calculated to quantify the frequency of presence and/or absence in each class for each environmental factor with an association. Conditional probabilities were combined using Bayes' probability theorem in a Geographic Information System to produce a map displaying a probability of presence/absence for the exotic species, based on the current distribution. These maps can be interpreted as habitat suitability maps.

The models were validated through a cross-tabulation of the results of the model and Grand Teton National Park data for weeds in areas that have been thoroughly surveyed by the Park. Results of the validation indicate that the Canada thistle model has a 59.8% overall accuracy and the musk thistle model has a 58.5% overall accuracy.

GEOGRAPHIC CHARACTERIZATION OF EXOTIC PLANT SPECIES IN GRAND TETON NATIONAL PARK, WYOMING

by

Deborah Jean Kurtz

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

of

Master of Science

In

Earth Sciences

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana

August 1999

APPROVAL

of a thesis submitted by

Deborah Jean Kurtz

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Dr. Richard Aspinall Richard Aspinall 13 May 1999
(Signature) Date

Approved for the Department of Earth Sciences

Dr. Andrew Marcus Andrew Marcus 17 May 1999
(Signature) Date

Approved for the College of Graduate Studies

Dr. Bruce R. McLeod Bruce R. McLeod 5-18-99
(Signature) Date

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University-Bozeman, I agree that the Library shall make it available to borrowers under rules of the Library.

If I have indicated my intention to copyright this thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may be granted only by the copyright holder.

Signature Deborah J Kurtz

Date 5/13/99

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Richard Aspinall, and the members of my thesis committee, Dr. Kathy Hansen, Dr. Roger Sheley, and Dr. Don Despain for the guidance, suggestions and support provided throughout this study.

I am grateful for assistantships and support provided by the Department of Earth Sciences and for the use of facilities and technical support provided by the Geographic Information and Analysis Center. I thank Grand Teton National Park and the University of Wyoming- National Park Service Research Station for financial and moral support during my field season. I thank the Mountain Research Center, the Biogeography Specialty Group of the Association of American Geographers, the Montana-Idaho GIS Users Group, and the MSU chapter of Sigma Xi for grants and awards that have helped fund this research.

I thank Ray and Cheryl Lougeay for nurturing my love of geography and the outdoors. I give love and thanks to Melany Micozzi for support during the most difficult times of my graduate program. I thank the Earth Science graduate students for all of the support and the distractions they offered (distractions can be a positive thing at times).

Finally, and most importantly, I offer the deepest appreciation to my family and to Brian for always supporting, encouraging, and believing in me during the ups and downs, the good and the bad. Your devoted love and support along the way was more needed and appreciated than I took time to acknowledge.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The study area, located in the southeastern portion of Grand Teton National Park, was sampled to determine the distributions and environmental characteristics of two exotic plant species: Canada thistle (*Cirsium arvense*) and musk thistle (*Carduus nutans*). These data were used to create a model using a Geographic Information System to determine the probability of other areas as suitable habitat for these two species. Measurements of presence/absence, percent cover, and growth stage were recorded and the dominant plants in the plot were noted for two hundred and two 30m x 30m plots randomly distributed throughout the study area. The random sampling layout was created in a Geographic Information System to ensure that seven environmental factors (soil, geology, aspect, slope, elevation, habitat type, and distance from hydrography) were sampled in varying combinations. Canada thistle was present in fifteen sites and musk thistle was present in thirty-three sites, resulting in 7% and 16% presence in the study area for each plant species, respectively.

Chi square tests were performed to determine the association between the environmental factors and the presence/absence of each species. Soil, geology, grazing allotments, elevation, and distance from hydrography were determined to be associated with musk thistle distributions. Soil, geology, grazing allotments, and distance from roads were found to be significantly associated with Canada thistle distributions.

Conditional probabilities were calculated to quantify the frequency of presence and/or absence in each class for each environmental factor with an association. Conditional probabilities were combined using Bayes' probability theorem in a Geographic Information System to produce a map displaying a probability of presence/absence for the exotic species, based on the current distribution. These maps can be interpreted as habitat suitability maps.

The models were validated through a cross-tabulation of the results of the model and Grand Teton National Park data for weeds in areas that have been thoroughly surveyed by the Park. Results of the validation indicate that the Canada thistle model has a 59.8% overall accuracy and the musk thistle model has a 58.5% overall accuracy.

INTRODUCTION

The effects of human introduction of exotic species and human disturbance to natural environments are becoming important issues in conservation biology and natural resource management. Recent scientific literature (Allen and Hansen, 1999; Vitousek et al., 1996; Walker and Smith, 1997) points to increasing concern regarding the spread of invasive exotic plant species. Exotic plants are non-natives that have been introduced by humans accidentally or intentionally, often for ornamental or agricultural purposes, and have adapted to new environments well enough to colonize and spread vigorously and independently. There are several ecological consequences associated with the life history characteristics of these species including increased competition for space, water, and nutrients with native plants (which could result in a decrease in biodiversity), decreased forage quality for native ungulates, and changes in the microenvironments where the establishment occurs (Woods, 1997).

One of the first strategies in protecting an ecosystem from vegetation degradation is to try to prevent the introduction of non-native plants (National Park Service, 1997). Prevention is enhanced with the ability to predict species' distributions and spread. Prediction allows park managers to monitor areas that are most susceptible to invasion. Strategies recommended for preventing spread of exotic species include developing an early warning system to identify and eradicate new infestations of exotic plants in a national park, and inventorying and monitoring non-native plants (National Park Service, 1997). Two goals of the National Park System in relation to managing invasive non-native plants on National Park System lands include 1) an assessment of the distribution and spread of exotic plants and 2) an assessment of trends in time and space (National Park Service, 1997). Actions suggested to facilitate these strategies include supporting the development of remote sensing and Geographic Information Systems (GIS) technologies for detecting and monitoring exotic plants and developing methods and models to predict the invasiveness of exotic plants. It is apparent that a GIS-based model would support and promote the strategies outlined in this plan and provide a means for managing the non-native plant problem on National Park System lands.

Computer models are used to simulate and simplify processes occurring in the natural environment to gain greater understanding of the mechanisms underlying patterns. GIS are useful when linked with models because 1) they allow the spatial component of patterns in landscapes to be incorporated with process understanding and 2) they facilitate geographic representation of model outputs. This type of modeling is beneficial in environmental management as it helps managers to understand processes and predict patterns. Environmental management can also help to determine what affects changes in various environmental factors may have (e.g. prediction of impacts of future environmental conditions).

Prevention of undesirable exotic plants is facilitated by developing the ability to identify habitats that are suitable for invasion by exotic plant populations. Use of a model reduces the need for ground-based surveys of plants across extremely large areas or in hostile environments and may provide insight into the future spread of exotics (Hershey et al., 1997). Application of a model will provide more cost- and time-effective resource management efforts and allow management decisions to be executed in terms of prevention and maintenance, rather than restoration (Sperduto and Congalton, 1996).

OBJECTIVES

In this thesis, I characterize the distribution and environmental factors of exotic plant species within Grand Teton National Park (GTNP) using GIS. Based on this analysis, I determine the probability of suitable habitat for these weeds in other parts of the study area. Canada thistle (*Cirsium arvense)* and musk thistle *(Carduus nutans)* are two of the thirteen highest priority non-native plant species within GTNP (GTNP, 1997b). Data was collected for all of the Park's high-priority species, but Canada thistle and musk thistle were focussed on, based on suggestions by GTNP, to facilitate management of these species within the Park.

According to ecological niche theory, the pattern of species distribution is related to various environmental characteristics (Giller, 1994). Based on this theory, I hypothesized that the current distribution of exotic weeds can be characterized based on environmental factors. It is also hypothesized, therefore, that based on analysis of the species' distributions and these environmental factors, similar areas can be located that will be conducive to future occupation by these weeds. It has been hypothesized that environmental variables such as precipitation (Reichard, 1997), aspect, slope, elevation (Huggett, 1995), soils (Lowell, 1991), temperature, and distance from roads (Tyser and Worley, 1992), trails (Dale and Weaver, 1974), and hydrology (Wilson, 1980) are associated with and influence species' distributions. Steps to test these hypotheses include:

- sampling exotic plants in GTNP using a random sampling methodology to produce a statistically-valid sample of Canada thistle and musk thistle in 1998

- identifying and analyzing the environmental factors underlying the distributions of the species
- correlating the distributions with environmental factors
- determining the probability of the distribution based on the correlation
- testing the accuracy of the results of the probability models

Data management and analysis are carried out with a GIS.

WEED/VEGETATION ECOLOGY

Predicting the Distribution of Weeds

Availability of suitable habitat types along with barriers to dispersal have been argued to be the main factors limiting species' ranges (Cousens and Mortimer, 1995). One of the goals of this study is to find areas that afford suitable habitat for Canada thistle and musk thistle infestation. The word 'habitat' is used here to refer to all the environmental (biotic, abiotic, and human-related) conditions affecting the populations of species that are incidental to where these populations occur (Polunin, 1960). Habitat is comprised of all of the environmental factors and their interactions that influence the flora. In turn, the combination of plant species in an area provides an indication of the specific combination of environmental factors found in a particular location. Plants are long-term occupants of a site, and the characteristics of a site are a result of the integration of all the environmental factors as well as their interactions (Daubenmire, 1947). The area of introduction of a successful plant is often similar to the species biogeographic center of origin in terms of climate, soils, and life forms of the vegetation (Baker, 1986). Therefore, any areas that have a similar environment to those sites that are currently occupied can be identified, giving a fairly conservative estimate of total area that has the potential for invasion by these weeds (Cousens and Mortimer, 1995). Studies with a similar basis as that used in this study to find suitable habitat have been carried out for spotted knapweed in Montana (Chicoine et al., 1985), for *Chondilla juncea* in south-western Australia (Panetta and Dodd, 1987), and for three weed species in New Zealand (Panetta and

Mitchell, 1991). Changes in weed populations can be driven by internal factors, in the case of competition, or by external factors such as the species' environment (Cousens and Mortimer, 1995). The availability of suitable habitats is one important extrinsic factor influencing the spatial distribution of weed populations. Bright (1995) claims that "it is impossible to predict where an exotic will establish itself, or what it will do afterwards, or when it will do it." This study does not try to predict where or when these species will establish themselves, but it determines the probabilities of occurrence of a species based on the similarity of environmental conditions with areas that are presently occupied by the species. Other researchers interested in exotic plants have looked at them in terms of roads (Weaver and Woods, 1986; Meier, 1997) and campgrounds (Allen and Hansen, 1999; Milner, 1995), but have not looked at weeds across a given area away from these disturbance sites.

In addition to the National Park Service policy of excluding non-native species from Park Service lands, there are many other important reasons to prevent invasion by non-native plants. Sheley et al. (1998) list several detrimental impacts of non-native weeds, both ecological and economical including:

-alterations in plant community functioning

-decreases in plant diversity

-changes in riparian area functioning

-loss of wildlife habitat

-competition with endangered and threatened species

-competition with native plant species

-displacement of forage production for livestock and crop production

-decreases in land value

-alteration of recreational value and uses

-and, increases in soil sedimentation and erosion

Several impacts pose serious concerns for National Parks because they directly conflict with Park Service mandate to "conserve the scenery and the natural and historic objects and wildlife therein to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (Seligsohn-Bennet, 1990).

Factors Affecting Vegetation Patterns

Polunin (1960) lists four ecological or environmental factors that individually and/or collectively determine the distribution of plants. Each of these, including 1) Climatic 2) Physiographic 3) Edaphic and 4) Biotic factors, is represented by the environmental factors incorporated in this study.

Edaphic and climatic factors are strongly influenced by physiographic factors such as elevation, aspect, and slope. Therefore, these physiographic factors have an indirect influence on vegetation. Perhaps the greatest example of elevational effects on plants can be seen in vegetational zonation on mountains (Daubenmire, 1943). Although these changes can be correlated with elevation, they are actually a result of interactions of solar radiation, precipitation, and temperature (Huggett, 1995), which are known to create microclimates that impact vegetation and produce strong elevation gradients (Glick et al., 1991). Elevation has been noted as the single most important factor affecting the biogeography of plant species within the Greater Yellowstone Ecosystem (Anderson, 1990). Bian and Walsh (1993) determined that elevation was more important than slope and aspect in terms of vegetation biomass. Despain (1973, 1990) demonstrated that geology is a strong secondary factor in vegetation distribution. Edaphic factors relate to the functions of the soil and, for this study, are encapsulated by the GIS layers for geology and soil. Several studies found climate to be an important factor in plant/weed distributions (Chicoine et al., 1985; Cousens and Mortimer, 1995; Forcella and Harvey, 1983; Hayden, 1934; and Panetta and Mitchell, 1991). However, climatic factors are not incorporated in this study as there is not enough variability in precipitation (Farnes et al., 1999) and temperature data across the study area.

The geology and soil layers are closely related since geological materials and deposits are parent material for soil development. Although soils and geological deposits are not directly equivalent, in some places it is difficult to differentiate the two since their appearances are so similar (Birkeland, 1984). Soils have been defined as "a natural body consisting of layers or horizons of mineral and/or organic constituents of variable thicknesses, which differ from the parent material in their morphological, physical, chemical, and mineralogical properties and their biological characteristics…" (Birkeland, 1984). Furthermore, the significance of soils to plant distributions has been noted repeatedly (Allen and Hansen, 1999; Baker, 1986; Chicoine et al., 1985; Muenscher, 1955; and Stephenson, 1990). Variations of sagebrush community distributions within the valley floor of GTNP have been correlated with soil characteristics (Sabinske and Knight, 1978). These results are because of the fine scale of the study since the authors note that the vegetation on the outwash plains appears to be superficially homogeneous.

Various studies have investigated the susceptibility of ecosystems to weed invasions. Grasslands (especially when disturbed from being overgrazed, trampled, or previously tilled) are highly susceptible to invasions (Baker, 1986; Tyser and Worley, 1992), as are riparian habitats and waterways, roadsides and trampled paths, some light forests, and sand dunes. Baker (1986) considers the most resistant ecosystems to be dense forests, high montane ecosystems, salt marshes, and deserts. Low-montane to dry steppe sites are often more weed infested than higher elevations, although disturbed mid-montane regions (such as those that have been clearcut), may be invaded by weeds (Forcella and Harvey, 1983). With respect to Northern Rocky Mountain forest types, resistance to exotic plants decreases as one increases in elevation from grasslands to forests of Ponderosa pine to Douglas fir to subalpine fir (Forcella, 1992).

Vegetation and plant community composition present internal factors such as competition which affects the availability of nutrients, water, and space, and can change the humidity of the immediate air and even the composition, development, and structure of the soil (Polunin, 1960). An important internal factor of vegetation type is the amount of open canopy and resultant light availability (Allen and Hansen, 1999; Marcus et al., 1998; and Milner, 1995). Allen and Hansen (1999) found Canada thistle infestations in Yellowstone National Park beneath 20% or less canopy cover ranging from Big sagebrush/ bluebunch wheatgrass habitat types to subalpine fir/ Grouse whortleberry habitat.

Exotic Plants and Disturbances

Disturbances are known to facilitate and are sometimes necessary for weed invasions (Bright, 1995; Cook and Fuller, 1995; Marcus et al., 1998; Walker and Smith, 1997; Weaver et al., 1989; Weaver and Woods, 1986). Generally, without an adequate disturbance of the natural vegetation, newly introduced plants cannot compete successfully with the dominant native plants to become more than a minor constituent of the plant community (Polunin, 1960). It has been noted that the human-related disturbance that is the most often cited is because of heavy grazing and trampling by domestic livestock (Woods, 1997; Glick et al., 1991). Plant communities in the Northern Rockies evolved without heavy livestock grazing which was not introduced into the northwestern United States until the late 1800s (Bedunah, 1992). Grazing and trampling can change the taxonomic composition and phenology of grassland communities, possibly to the point of creating an entirely new vegetation structure. A single period of heavy grazing or a summer's worth of repeated grazing at a moderate level can decrease litter and vegetation cover, reduce grass stem counts, and increase bare soil, possibly resulting in a shift in plant community composition (Olson-Rutz et al., 1996). Hansen et al. (1995) link forest invasions into grasslands and shrublands with periods of cattle and sheep grazing. Effects of trampling, grazing, and previous tillage of grasslands in Glacier National Park in northwestern Montana were determined to encourage invasions by weeds (Tyser and Worley, 1992). Not only do disturbances provide a bed for non-native weeds, but weeds that reproduce vegetatively, such as Canada thistle, may have a faster recovery after a disturbance (Amor and Harris, 1974; Whitson et al., 1996; and Reicherd, 1997).

Besides the effects of grazing and trampling, rangeland may also be disturbed by irrigation. Various researchers that have studied the ability of irrigation ditches to disperse non-native seeds, including Canada thistle, have found that these waterways can be an efficient means for transporting numerous seeds to new locations (Bruns, 1965; Bruns and Rasmussen, 1953; Bruns and Rasmussen, 1957; Kelley and Bruns, 1975; and Wilson, 1980). Wilson (1980) compared the amount of weed seed transport between a natural waterway and a manmade irrigation canal in the North Platte River Project and found that more seeds were collected from the irrigation canals than from the North Platte River as it entered Nebraska. However, although most of the plant seeds collected in the canals were found in smaller quantities in the river, Canada thistle was one of the seeds that had a higher quantity in the river than in the canal. Canada thistle was found both along the bottom of the canal and floating along the surface. Of the Canada thistle seeds collected, 52% of them were viable. Wilson (1980) determined that roughly 10,000- 94,000 seeds per hectare could be dispersed by irrigation waters. As a result, surface irrigation water is both a way of introducing new weed species into fields as well as another mechanism for dispersing weed seeds that are already present.

Bruns and Rasmussen (1953, 1957) looked at the viability of Canada thistle seeds after being submerged in fresh water for extended periods of time. They determined that the germination of Canada thistle seeds increased after four months in wet storage. This suggests that short-term water storage because of seeds being trapped or carried in irrigation waters is beneficial to Canada thistle seeds and aids in water dispersal (Bruns, 1965).

Kelley and Bruns (1975) examined weed seed dissemination in irrigation project canals in Washington State and concluded that irrigation waters can be a major source of weed seed on irrigated lands. Although the amount of seeds collected depended on the time of seed production, they found that the irrigation waters were dispersing an average of 10,350 seeds per hectare of land. The combination of seed transport and duration of viability make irrigation waters a possible dispersal mechanism for weed seeds.

MAPPING AND MODELING VEGETATION

Introduction

The value of Geographic Information Systems (GIS) for large-scale studies in ecology is increasingly being recognized as researchers are expanding their use of GIS from a simple data storage and mapping tool, to a way of applying statistical equations for more intricate analysis of interdependence and spatial relationships (Burrough and McDonnell, 1998). In this sense, GIS is becoming a significant component of ecological modeling, particularly as ecologists attempt to explain the relationship between vegetation patterns and processes occurring at the landscape scale. Furthermore, ecologists and vegetation managers are beginning to experiment with these models as predictive tools.

Processes and patterns in nature occur at varying scales and, depending on the scale used for the study, the results of the scientific investigation may differ for the same place at the same time (Levin, 1992). Levin notes that in order to make predictions in nature, one must understand and be able to explain the mechanisms underlying the observed patterns. The following is a review of different scientific approaches for mapping current distribution or predicting future distribution of vegetation or habitat at a variety of scales.

Predictive vegetation mapping has been defined as "predicting the geographic distribution of the vegetation composition across a landscape from mapped environmental variables" (Franklin, 1995) and can be approached in many ways involving the use of 1) math (statistics) 2) remote sensing and GIS and 3) biology.

Quantitative Approaches to Vegetation Mapping

Mathematical models have become useful for determining the implications of multi-scaled environmental processes on observed landscape patterns (Bartell and Brenkert, 1991). Biogeographers and landscape ecologists are interested in understanding and quantifying how environmental and ecological processes result in various landscape patterns. Remote sensing and GIS can greatly enhance landscape studies by facilitating spatial analysis. Although these technologies have been available throughout the last decade, some researchers have still not taken advantage of the full utility of their capabilities. For example, Hershey et al. (1997) created a map of sugar maple trees in New York and Pennsylvania using sample survey-data and kriging to extrapolate across these two states. The goal was to predict the distribution of sugar maple trees without executing a complete ground-based survey of the area. Although the authors mention that remotely sensed data could be used and “overlaid” for further analysis, they did not apply any remote sensing or GIS techniques to their project beyond kriging. Lenihan and Neilson (1993) also excluded the use of GIS and remote sensing tools when they created a vegetation model for Canada based on current and future climatic conditions using a binary classification tree. Chicoine et al. (1985) predicted suitable habitats for spotted knapweed using a light table to overlay maps showing weed infested sites in their respective counties onto maps of each edaphic and climatic characteristic. This form of overlay is a classic operation facilitated by GIS (Burrough and McDonnell, 1998). Lindenmayer et al. (1991) used bioclimatic analysis (using climate to set the limits of distribution for a species) to predict the distribution of a rare marsupial, Leadbeater’s possum, by applying the BIOCLIM model, based on the concept of homocline matching. In this case, a series of climatic variables were used to define the habitat (bioclimate) of a species. These variables are summarized by a set of descriptive statistics for the frequency histogram of values for climatic variables in areas where the species is found. Walker and Cocks (1991) created a similar model, HABITAT, using mathematical programming and computer induction to delineate an "environmental envelope" which bounds all sites where the presence of a species had been recorded to locate similar areas of habitat for a kangaroo in Australia. In their example, the concept of an "environmental envelope" is restricted to the "climate envelope" where only the climates in which the species is believed to be able to persist are mapped based on the set of climates at areas of known presence in addition to areas of similar climates. They compared their model, HABITAT, to BIOCLIM, the difference between the two models being that BIOCLIM used orthogonal projections to create the initial envelope, while HABITAT created an environmental envelope from the climatic conditions at sites where observations found the species. The HABITAT method assumes that the potential range of a species is not expressed as a linear combination of the orthogonal projections on each environmental dataset. GIS was not used in the above studies, even though for efficient stratified field sampling, the use of digital geographic databases is necessary (Franklin, 1995).

Daehler and Strong (1996) published a study in which they identified sites that were vulnerable to invasion by a non-native cordgrass on the U.S. Pacific Coast. The study, which incorporated current vegetation patterns, involved identifying two specific criteria for identification of potential sites of invasion. Native climatic and latitudinal ranges were used to determine what particular species of *Spartina* would be most likely to invade. Although GIS was not used in this study, the authors noted a GIS could be useful in their research. Daehler and Strong were not the only researchers to recognize that the use of GIS can enhance a study. Noest (1994) presented a model that predicted the probability of occurrence of 100 dune slack species under different environmental conditions. Although her approach was to use logistic regression implemented through the procedure CATMOD from the SAS package, she mentioned that she will incorporate the model into a GIS in the future to facilitate the evaluation of the spatial pattern of the model output.

Statistical Methods

Franklin (1995) notes that predictive vegetation mapping is founded in niche theory. General ecological theory states that the shape of a species' response to a number of environmental factors is often Gaussian. Although this may not always be true, it is a base assumption for much statistical analysis. Use of statistics and visual components, such as graphs, often are used even if a GIS is not incorporated into analysis. Generalized Linear Modeling (GLM) has been used successfully for predictive modeling as demonstrated by Austin et al. (1990). This project studied *Eucalyptus* in Australia to determine the qualitative environmental niche as a function of four environmental variables. They used GLM to demonstrate how complex response patterns can be selected and modeled. Since predictive modeling using statistics is based on correlation, they demonstrate how a descriptive correlation model is essential before any explanatory model can be formulated or tested.

GIS for Data Storage and Mapping

Several studies, although they incorporate GIS, do not use it to its full extent (as a modeling and analytical tool) since they simply use it for mapping or data storage. For example, Martinez-Taberner et al. (1992) used existing information on physico-chemical dynamics of water, combined with the environmental tolerances of the species studied, to predict the most probable macrophyte species composition for the different areas of the Albufera of Majoca in the Balearic Islands. They then developed a GIS for sites capable of being rehabilitated as open water areas. Jensen et al. (1992) used GIS for predicting the future distributions of aquatic macrophytes such as cat-tail and water-lily, but they only used the GIS for data storage. The rest of the study consisted of using Boolean logic to query the data within the GIS. Prentice et al. (1992) modeled global vegetation patterns in relation to climate change. The study predicts global patterns in vegetation physiognomy based on current climate conditions and remaps these under conditions associated with predicted climate changes. Prentice et al. based their model on a small number of plant functional types applied with an environmental sieve and dominance hierarchy, with the environmental limits of each plant type being defined with reference to physiological constraints. They then used kappa statistics to compare the global biome maps derived from the model with data from a previous study. The only reference that this paper makes to the use of their GIS is to state that the mapping and manipulation of the data was carried out within a specially written GIS, but further detail is omitted. Finally, Stoms et al. (1992) compare two approaches, deduction and induction, to GIS-based modeling of species habitat associations for the California Condor. The deductive approach of the GIS output produces a map that depicts levels of habitat suitability, therefore identifying "potential" habitat without implying that the species is present. With the inductive approach, habitat requirements are not well known, so GIS is used to induce them from a sample of observations. The output is a map and a tabular or textual summary describing the variables most notably associated with the species' observed distribution. Results from the induction can be extrapolated to predict the spatial distribution of suitable habitat using the deductive method.

GIS and Remotely Sensed Data

Many studies that involve modeling vegetation use remotely sensed data and incorporate it with a GIS but, again, the GIS is often used more as a data storage technique rather than as a method of analysis. Franklin (1995) provides a thorough discussion of the development of predictive vegetation mapping, focusing a section on those studies that are based on remote sensing. For example, Dewey et al. (1991) wanted to identify areas within the Cache National Forest in northern Utah that have not been invaded by an exotic plant, Dyer's woad, but that are suitable for invasion based on specific landcover types. This study incorporated satellite data with spectrally homogeneous land-cover classes into a GIS to correlate species' locations with the spectral classes. In order to determine significant differences between "expected" and "observed" occurrences among land-cover classes, a Chi square test of population homogeneity was used. Again, this study utilized the data storage capabilities of GIS more than its analysis abilities for the predictive project. Homer et al. (1993) also combined remote sensing and GIS techniques to model winter habitat of sage grouse in Rich County, Utah. In this case, these two techniques were combined to link fine-scaled structural and compositional attributes of animal habitat to macro-scale remote sensing habitat assessments. Methods included the use of log-linear analysis to develop statistical models that best describe habitat use by sage grouse, followed by a determination of the best fit of the model by using conditional tests. Finally, they attempted to indicate "preference" or "avoidance" for each habitat class by using standardized lambda estimates for each cell. The GIS was used to create infrastructure data layers and for data storage, and it provided a method for expanding wildlife habitat research capabilities while distributing information and data to natural resource managers. Another example of this method is offered by Sperduto and Congalton (1996), who use traditional overlay methods in GIS to investigate natural history, present distribution, and potential habitat for whorled Pogonia, a rare orchid that occurs in New Hampshire and Maine. They developed two predictive GIS overlay models: 1) an equal-weight model where each habitat characteristic is equally weighted and 2) a Chi square model where the importance of each habitat parameter was evaluated with a Chi square test at sites both with and without an established orchid population. The GIS was useful in providing a framework to collect habitat information, to question the importance of each habitat characteristic, and to assess how best to combine the characteristics. It was also useful in visualizing the results of the initial decisions, refining ideas, and evaluating changes to the model. Remote sensing and GIS were also used by Breininger et al. (1991) for habitat modeling of Florida scrub jay at the Kennedy Space Center in Florida. In this case, comprehensive field studies could not be performed so remote sensing and GIS applications were applied to map areas that vary according to their potential for Scrub Jay habitat. Aerial color infrared photography was incorporated into a GIS and all analysis used GIS functions such as overlay, recode, matrix, and search. The GIS analyses were carried out using ERDAS 7.3 GIS software. Remote sensing and GIS were also combined by Clark et al. (1993) in a model of habitat for female black bears in the Ozark Mountains of Arkansas. The model uses habitat data and black bear radio-collar locations and is based on the Mahalanobis distance statistic, executing calculations within a GIS. They tested the model by characterizing habitat use by female bears based on individual map layers through a Chi square goodness-of-fit test.

Modeling with GIS

Several models have been successful in using an integrative collection of methods for modeling vegetation and/or habitat where the model was implemented within the GIS. Aspinall and Veitch (1993) used Landsat TM imagery in a GIS based model to map the habitat of curlew in northeast Scotland. In this case, wildlife survey data indicating presence/absence of the species was used to classify the satellite image. Combined with a Digital Elevation Model (DEM), this data was then incorporated into a GIS where analysis was performed using Bayesian statistics. By classifying the digital image as part of the model they created an "information surface" that represented the probability of the presence of the curlew. The output probability values were treated as a measure of habitat suitability. Modeling with Bayes' theorem is used in various studies by Aspinall (1992a, 1992b, and 1994), Pereira and Itami (1991), and Milne et al. (1989). Aspinall (1992a) modeled the winter distribution of red deer in the Grampian region of northeast Scotland based on Bayes' theorem incorporated in a GIS. In this case, the output is a probability model that describes the distribution of the species based on a relationship between the distribution of deer and predictor data set used as a process of inductive learning. Not only does this method measure the statistical significance of model inputs, but it also incorporates an assessment of error propagation based on the combined data sets within the GIS. The model provides a framework for combining relative values of right or wrong with the probabilities of being right or wrong (Aspinall, 1992a). Aspinall also uses point-pattern analysis and an inductive learning process for pattern analysis based on Bayesian statistics applied through a GIS to generate hypotheses using bioclimatic mapping for wildlife in Scotland (Aspinall, 1994).

Pereira and Itami (1991) developed a model for determining suitable habitat for the Mt. Graham red squirrel. A GIS is used for data analysis and input to create two logistic multiple regression models. These models are integrated with Bayesian statistics to create a digital map of the combined outcome as a model of habitat potential of this species.

Davis and Goetz (1990) created a model to predict the distribution of live oak in California. Their model was based on simple GIS operations of spatial sampling, patch size analysis, and a combination of map weighting and overlay to incorporate digital maps of geology, topography, and calculated clear-sky radiation. They validated their results by overlay with a distribution map for live oak processed from remotely sensed data. They argued that the ability to overlay predicted and observed patterns was very helpful for both applying and improving the model, and the combination of GIS and remotely sensed data greatly aided in the success of their model.

Brown (1994) modeled the relationship between four vegetation types and variables representing topography and biophysical disturbance gradients at treeline in Glacier National Park. A number of methods were used in this study, including the use of remotely sensed data, GIS, and statistics. A logistic model was constructed by combining GLM and Generalized Additive Modeling (GAM) techniques. Satellite imagery was processed to characterize the spatial pattern of the observed alpine ecotone at treeline. With the aid of a GIS, spatial coverages were processed and integrated to derive variables that represented sets of biophysical processes and disturbances. The expected positions of the ecotone were mapped using the models. Finally, spatial auto-correlation was used to assess the ordering of values as a function of location. Brown went beyond predictive modeling by incorporating residual analysis to identify and assess unexplained spatial patterns in the predicted vegetation and to determine the performance of the model as a function of scale.

Several studies that attempt to predict or map vegetation patterns or the suitability of habitat have been cited. The studies that did not incorporate a GIS recommended it and felt that the success of their research would have been aided by it. The studies that used GIS as a data management system noted that its utility could have been enhanced had they used it for analysis, also. Those who used the GIS as a greater part of their model had fewer recommendations and generally, more successful results, as did those who combined GIS techniques with remotely sensed data. These studies also demonstrate that GIS can be a powerful tool for modeling vegetation patterns and habitat availability, with both inductive and deductive strategies.

Spatially distributed ecological data is the basis for assessing patterns of ecosystem structure and function and is gathered at different temporal and spatial scales (Stow, 1993). A tool such as GIS is ideal for handling these data as it can deal with data at varying scales in terms of storage, management, and analysis. GIS are readily integrated with ecosystem models to facilitate the analysis of observed spatial data and the prediction of future distributions. This full use of a GIS as part of a model, rather than a system for data storage, should be the direction that large-scale ecological studies take in the future.

For this review, the Bayesian method has been determined to be the most successful and most applicable method for use in this study. Bayes' method involves a probability equation based on conditional probabilities. There are six reasons for using this method:

1) continuous and categorically measured data can be synthesized in one analysis

2) numerous maps can be incorporated into the model

3) the inductive nature of the method incorporates objectivity (this allows the model to be constructed for available data)

4) the method can be implemented in GIS with relative ease, allowing for spatial

analysis

5) associations between dependent and independent variables can be quantified statistically

6) the conditional probabilities provide data on the relationships in the data and are relatively easy to interpret

STUDY AREA

Introduction

The study area is located at the southern part of GTNP at the lower elevations of the valley known as Jackson Hole (Figure 1). GTNP was established by Congress in 1929 “to protect the area’s spectacular scenic values, as characterized by the geologic features of the Teton Range and Jackson Hole, and to protect the native plant and animal life” (Grand Teton National Park, 1987). Located south of Yellowstone National Park in the northwestern corner of Wyoming, GTNP consists of 310 thousand acres and rises from the lowest elevation of 6,350 feet (1,935 meters) at the southern end of the park to the highest elevation of 13,770 feet (4,197 meters) at the top of the Grand Teton. A variety of physiographic features are contained within the park including Jackson Lake, several moraine lakes and other glacial features, the Snake River, the sagebrush flats of the valley, and the magnificent Teton Range for which the park is most famous.

Vegetation in Grand Teton National Park

The Tetons are the youngest mountains in the Rocky Mountain chain, forming from an active fault-block where the mountains are being uplifted and the valley of Jackson Hole is being down-dropped (Love and Reed, 1995). The Teton range contains eight peaks above 12,000 feet and ten active glaciers. Vegetation within the mountains is typical of Central-Northern Rocky Mountain forests and consists primarily of seven

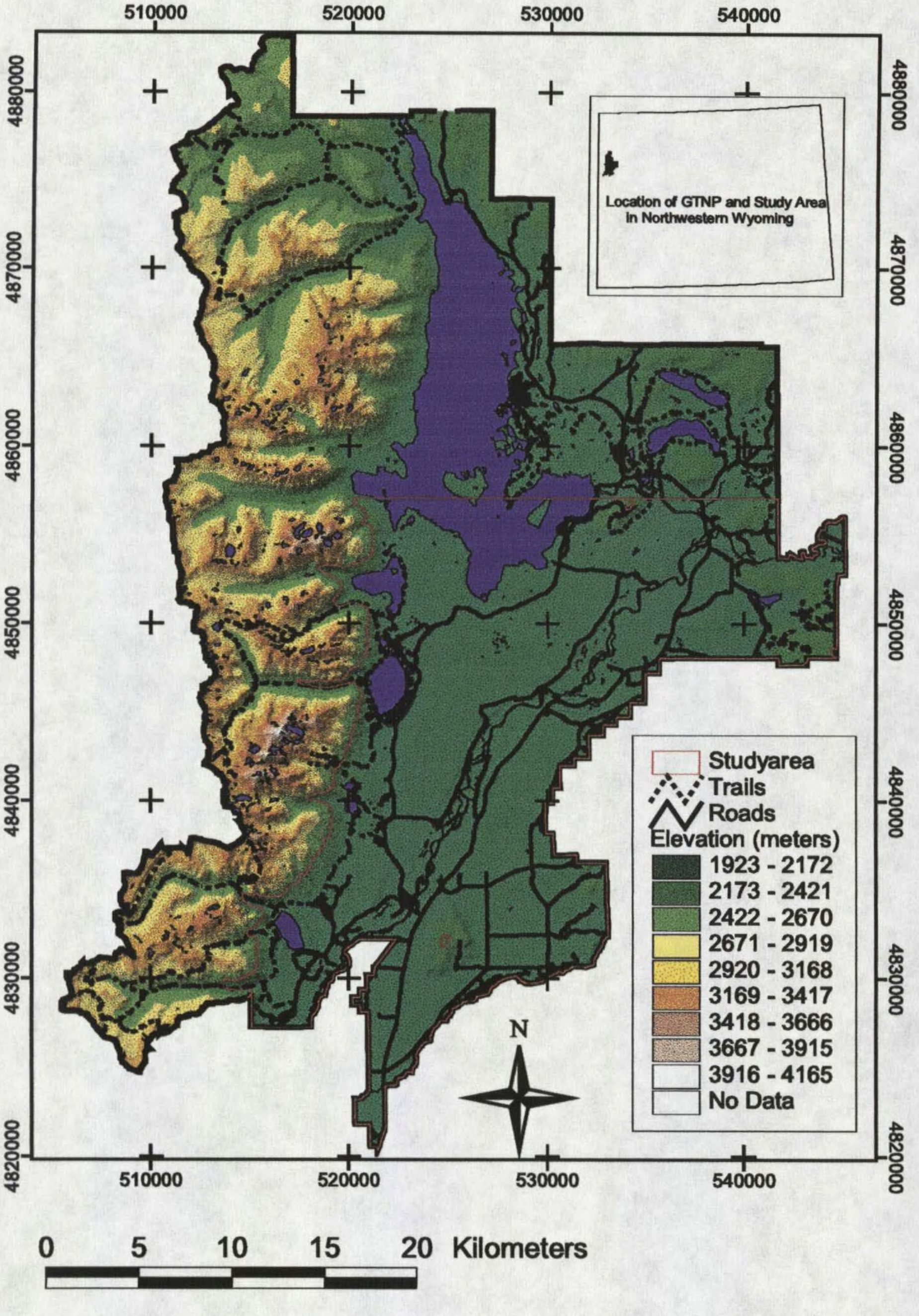


Figure 1.
Grand Teton National Park

coniferous tree species: limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), and whitebark pine (*Pinus albicaulis*), Englemann spruce (*Picea engelmannii*) blue spruce (*Picea pungens*), sub-alpine fir (*Abies lasiocarpa*) and Douglas fir (*Pseudotsuga menziesii*) (Grand Teton National Park, 1987; Shaw, 1981; National Park Service, 1936). Plant nomenclature is based on Hitchcock and Cronquist (1973). The valley floor is dominated by sagebrush while the Snake River and its tributaries are lined with willows (*Salix* spp.), cottonwoods (*Populus* spp.), and blue spruce (Grand Teton National Park, 1987).

The presence of exotic plant species within GTNP conflicts with the National Park Service's goal of preserving the land in its natural state. Exotic species are becoming a great concern for park managers (National Park Service, 1997), as well as an economic burden (Campbell, 1997). To add to the intensity of this problem, out of the 1,000 species of flowering plants within the park, there are also four (possibly five) rare plants within GTNP that may be threatened as a result of competition with exotics (Wyoming Rare Plant Technical Committee, 1994). These are *Draba borealis* (boreal draba), *Epipactis gigantea* (giant helleborine), *Lesquerella carinata* var. *carinata* (keeled bladderpod), *Lesquerella paysonni* (Payson's bladderpod), and possibly *Draba densifolia* var. *apiculata* (rockcress draba). The need for continued survival of these sensitive plants in the study area increases the need for management of exotic plants.

GTNP is home to several wildlife species including a number of rare, threatened and endangered species such as bald eagles, peregrine falcons, whooping cranes, trumpeter swans, grizzly bears, river otters, the endemic Snake River cutthroat trout, and numerous other sensitive birds, mammals, and reptiles (Clark et al., 1989). Several of these species depend on the protected, natural habitats within the Greater Yellowstone Ecosystem for survival within the lower 48 states. The area is also an important component of migratory routes for avian species that fly through the United States to their summer and winter homes.

GTNP has implemented a classification system for exotic plant species that consists of three priority levels (GTNP, 1997b). Priority 1 weeds are aggressive invaders that are established in small areas but also expand into surrounding disturbed areas. Priority 2 species are less aggressive than Priority 1 species and are established only in small, localized areas. Priority 3 species are found throughout the Park and require extensive control measures, beyond that possible with current funding and staffing, to eliminate. Currently, there are thirteen exotic plant species with a Priority 1 status within GTNP (Table 1). Nomenclature follows Hitchcock and Cronquist (1973).

History of Grand Teton National Park

Natural history is only one constituent of the significance of GTNP. The Park also has an intriguing cultural history relating to early homesteaders and the concept of 'dude ranching'. Settlers moved into the valley of Jackson Hole in the late 1800s and began to ranch the land. GTNP was established in 1929. The original Park consisted of 96,000 acres and did not include the valley floor. Jackson Hole National Monument, consisting of 221,610 acres of public and private lands adjacent to the national park was designated in 1943. Most of the land in the monument was added to GTNP in 1950, enlarging the Park to its current boundaries (GTNP, 1987). Acquisition of land for GTNP took place over an extended period of time as Jackson Hole property owners released their land from ranching. As a result, much of the park contains agricultural and ornamental vegetation that is non-native to a western montane ecosystem and that appears to be thriving under present environmental conditions. The increasing number of park visitors has also contributed to a high rate of plant introductions as seeds are unknowingly being transported across the park boundaries via footwear, camping gear, and vehicles (Reinhart, 1998).

Table 1. Grand Teton National Park's list of priority 1 exotic plant species

(Source: Grand Teton National Park, 1997)

Carduus nutans	musk thistle
Centaurea diffusa	diffuse knapweed
Cirsium arvense	Canada thistle
Centaurea maculosa	spotted knapweed
Chrysanthemum leucanthemum	oxeye daisy
Tanacetum vulgare	common tansy
Verbascum thapsus	common mullein
Linaria vulgaris	butter and Eggs
Cynoglossum officinale	houndstongue
Hyoscyamus niger	black henbane
Linaria dalmatica	Dalmation toadflax
Isatis tinctoria	Dyer's woad
Euphorbia esula	leafy spurge

Controversy in Grand Teton National Park

Various aspects of GTNP make it one of the more anomalous and controversial parks in the National Park System. Approximately twenty years prior to the establishment of the original GTNP, a dam was built on the Snake River for irrigation purposes that resulted in an enlargement of Jackson Lake (Grand Teton National Park, 1987). Today, the dam is still present and scars from the irrigation ditches continue to line the sage covered valley as a cultural and physical reminder of previous land uses. Jackson Hole Airport is in the southern portion of the park. Not only does this contradict original purposes stated for establishment of National Parks, but it is also located in an area known to have several sage grouse leks. Finally, the eastern part of GTNP is still used for grazing by cattle being corralled from ranch land south of the Park to the Forest Service land east of the Park. Several tracts of privately owned or leased land consisting of just under 1,000 acres are also found scattered throughout the park, including a number of commercial dude ranches and private residences. Included in this land are several grazing allotments (some of which are currently irrigated). The presence of these allotments within a National Park is both unusual and controversial.

The existence of exotic plant species in GTNP is also controversial. Unlike the presence of Jackson Hole Airport and the allowance of domestic grazing, exotic plants will not be tolerated within GTNP boundaries (Grand Teton National Park, 1987). The lack of tolerance for presence of exotic plants is demonstrated with the primary resource management goal of "...perpetuating the indigenous plant and animal associations of the

Teton Range and Jackson Hole…" in as natural a condition as possible (Grand Teton National Park, 1976).

METHODS

This study was conducted based on analysis of 1) vegetative data from previous researchers, 2) data collected through field work during the summer of 1998, and 3) use of a Geographic Information System for management, analysis, and modeling of data.

GIS Development

The first step in establishing a geographic database is creation and compilation of the data layers. The geographic database was compiled from data available from three sources: the GTNP GIS database, the Greater Yellowstone Area Data Clearinghouse, and the United States Geological Survey's World Wide Web site for Digital Line Graph data. All digital data are at a scale of 1:24,000 except geology which has a scale of 1:62,500. Data for Canada thistle and musk thistle within GTNP from the past seven field seasons are also available (Appendix A).

Eight environmental layers were determined to be necessary for this study based on previous studies noted earlier including:

1) geology,
2) soils,
3) cover types,
4) grazing allotments,
5) hydrography,
6) roads,
7) trails,
8) and elevation

General examples of these layers are provided in Appendix B.

Elevation is in raster format with 30 meter pixel size. Data for slope and aspect were derived from the elevation layer. Temperature and precipitation data throughout the

Park are available from previous studies (Farnes et al., 1999) however, the area of study within the park is small enough that there is not enough variability in these data to make them useful in analysis.

Based on statistical analysis of the contributing variables, a model has been developed that demonstrates the geographic controls on plant establishment and locates similar habitats that are assigned a probability for the suitability of colonization by musk thistle and Canada thistle.

Developing a Random Sample

To develop a statistically valid sampling regime, it was necessary to assure that all environmental factors were sampled. This was accomplished by basing the sample sites on the pattern of environmental factors. Before this could be done, the data layers had to be processed. Slope and aspect were derived from the digital elevation model. Slope, elevation, and aspect were recoded to create layers of twenty slope classes (with 5 degree intervals), eighteen elevation classes (with 25 meter intervals), and thirty-six aspect classes (with 10 degree intervals). The roads and trails layers were processed to create two individual layers representing distance from roads and distance from trails in increments of 480 meters for each layer respectively.

Because of the large amount of data to be processed and the limited time available during one field season, the study area does not comprise all of GTNP, but encompasses 127,028 acres of the front country where the lowest elevations in the park are located and the greatest number of visitors travel. A straight line through the southern portion of Jackson Lake, the middle of Signal Mountain, and just north of the town of Moran determines the northern border of the study area. The western boundary was determined by the 2,300 meter elevation level, thereby confining the study area to the southeastern portion of the Park (Figure 2).

The remaining data layers were processed to consolidate the number of classes within each layer to examine the number and distribution of combinations of environmental data. The resultant combination provided a layer of all combinations of terrestrial environmental factors consisting of 87,370 unique combinations of classes. Many of these were slivers and some 143,699 pixels were in combinations each larger than 200 pixels.

A program was written to create a computer-generated random sample of points from the study area. This sampling strategy samples in proportion to the area that they constituted within the study area. The output of this processing resulted in a map of the study area with the locations of 249 randomly selected sites (Figure 3), and a table providing UTM's and attribute information for each of the study sites.

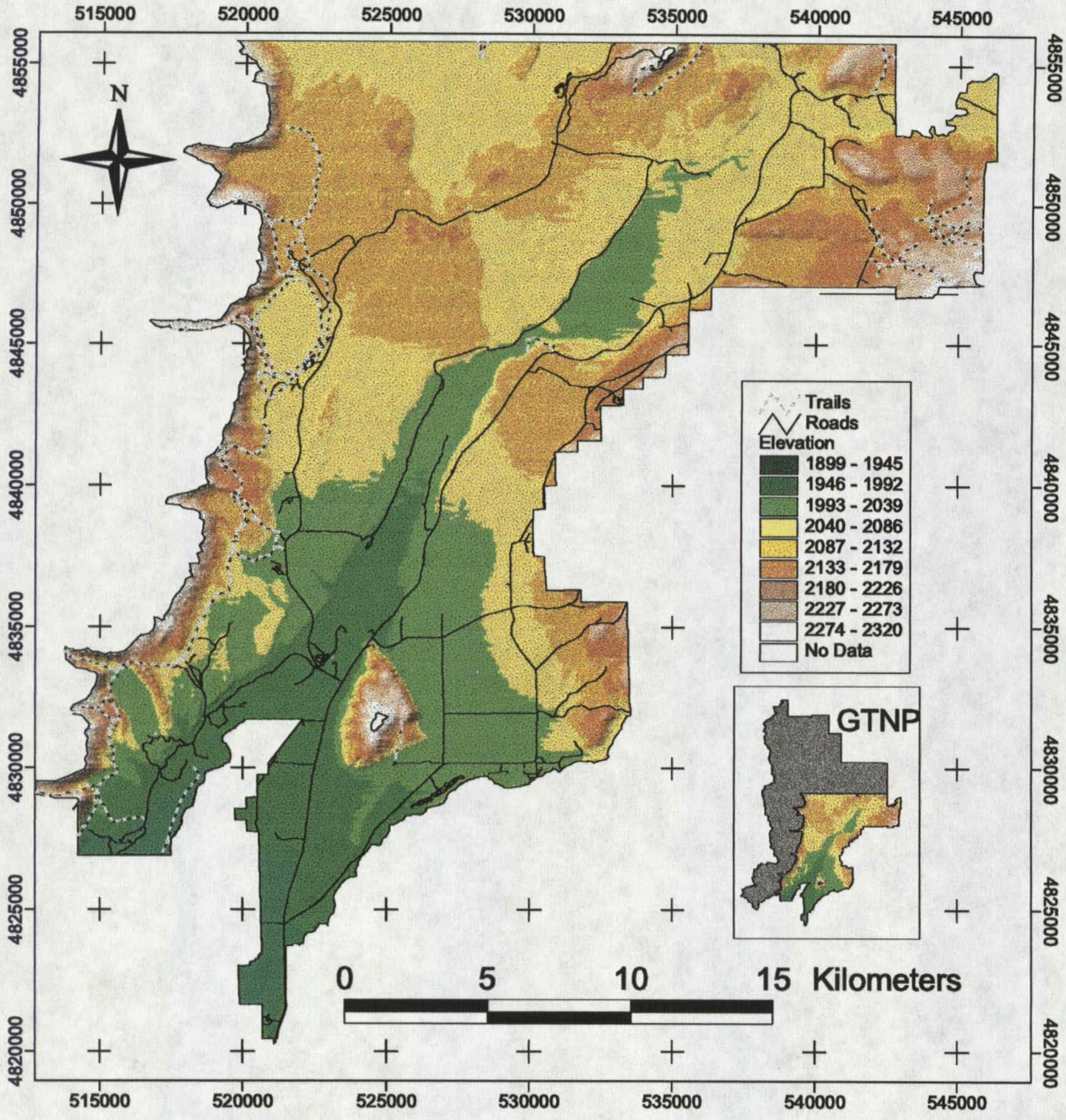


Figure 2.
Study Area

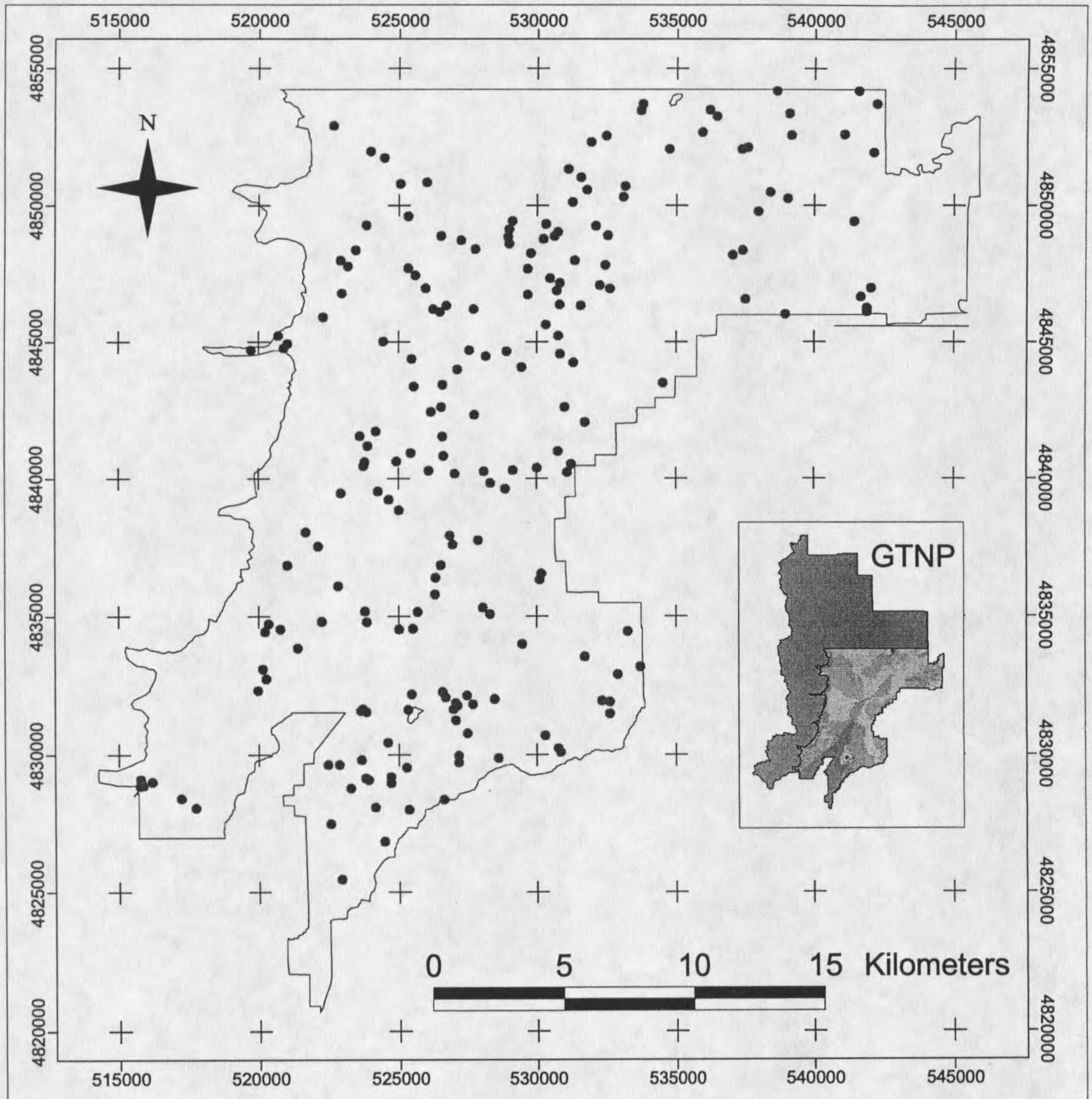


Figure 3.
Location of the study sites in the study area

Data Collection

Field sampling was completed during the period of July to early-September, 1998. Sampling did not begin in June due to cool, wet weather conditions that inhibited plant growth and made identification difficult. Sampling began at the southern end of the study area and progressed northward since the southern end of the area is a lower elevation and the plants appeared to be at a more advanced phenological stage than in the northern part of the study area. Sample sites were located with the aid of topographic maps, a compass, and a Garmin GPS 12 global positioning system. Upon locating the position of a site, a 30m x 30m plot was laid out. Starting at the southwest corner, one tape measure was run to 30 meters north and one tape measure was laid out 30 meters east to delineate two sides and three corners of the plot. After walking through the plot in a systematic zig-zag (Figure 4), data were recorded. Recorded data consisted of :

1) a general description of the location
2) vegetation type and/or dominant plants in the plot
3) the presence or absence of the weeds with estimates of the percent cover and growth stage of the weeds that were present (Appendix C).

Data on all thirteen of the Park's priority weeds were recorded although not all weeds were intended for modeling. Data collection methods were based on Mapping Noxious Weeds in Montana published by the Department of Plant, Soil, and Environmental Sciences at Montana State University (Cooksey and Sheley, 1998). Cover estimates were based on the percent of the ground covered by a particular weed species and are presented

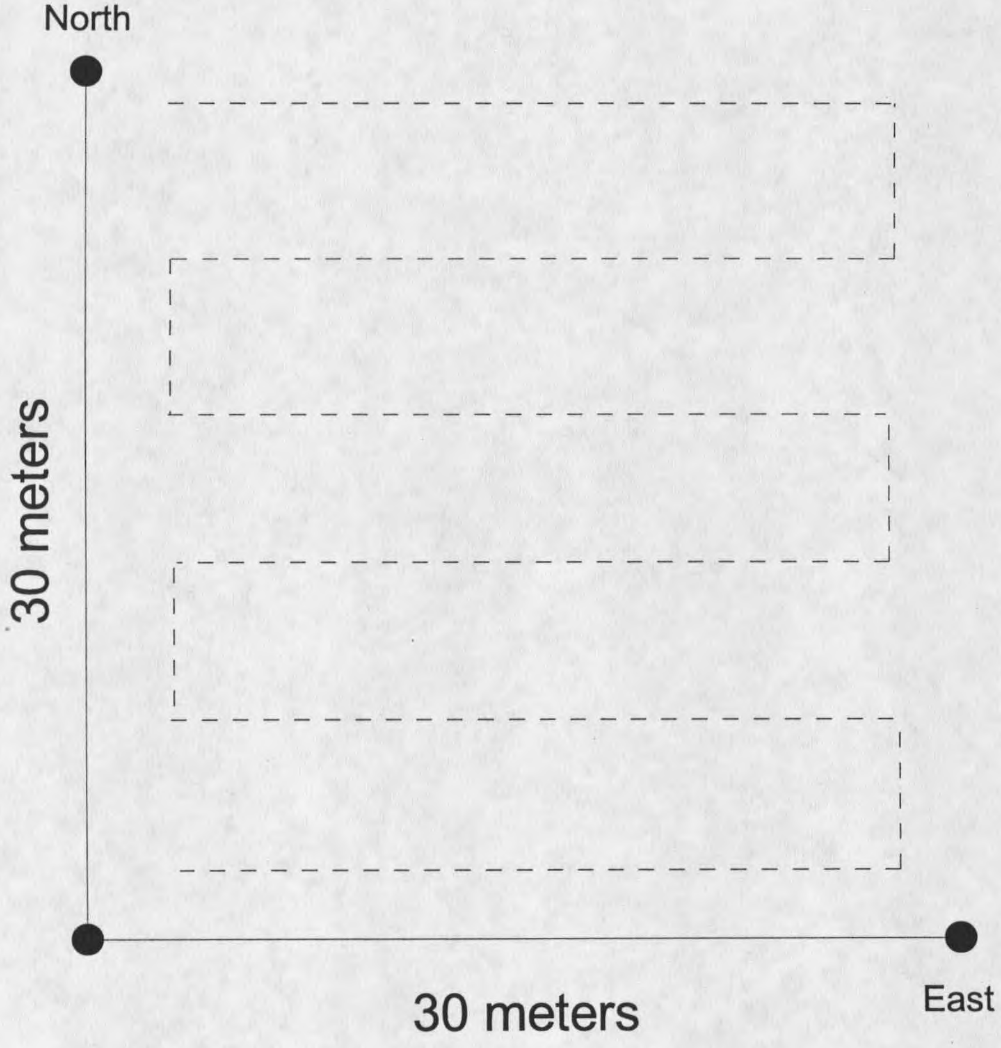


Figure 4. The method of data collection along a transect through each study site

As 1 of 4 cover classes broken down into Trace (<1% cover), Low (1-5% cover), Moderate (5-25% cover), and High (25-100% cover). Growth stage classifications were also based on Cooksey and Sheley (1998) and consist of Seedling, Bolt, Bud, Flower, Seed Set, and Mature. Percent cover and growth stage data were not necessary for modeling, but were collected for thoroughness. Field data results are located in a table in Appendix D.

ANALYSIS

The original intent of this research was to model Canada thistle (*Cirsium arvense*) and spotted knapweed (*Centaurea maculosa*) based on suggestions by employees of GTNP. Of the 202 sites visited, spotted knapweed was found in only one site. This was not enough presence data to model. Fortunately, data was collected for all thirteen Priority 1 species. The greatest amount of presence data was collected for musk thistle, so musk thistle (*Carduus nutans*) was modeled in place of spotted knapweed.

Prior to creating the model, data were analyzed to determine the statistical association between the weed presence/absence and each environmental factor. This was accomplished using a Chi square test of independence with a 95% confidence level to identify significant differences (Jaeger, 1990). This analysis suggests the usefulness of each environmental factor for predicting the likeliness of future occurrences of these species by determining whether the presence or absence of a weed is associated with a particular environmental factor. Factors (for which the null hypothesis of no association between presence/absence and the environmental variables was rejected) were used as input for the Bayesian model. It is assumed that the predictor data sets are independent, although environmental data are often related to each other (Aspinall, 1992a).

Conditional probabilities are proportionally calculated as the total area of presence and/or absence in each class of each environmental factor. This is accomplished by determining the frequency of association between each environmental factor and the sampled weed distribution. The area of overlap between the weed sample and each of the classes of the environmental factors is used to calculate the conditional probability.

Using the conditional probabilities, predictor data sets are combined within Bayes' theorem for discriminating between presence and absence. Given the particular combination of attributes from the predictor data set, the probability of the presence of the weed is provided as a single probability value. Therefore, at any given location, there is a measure of the probability of the area being suitable habitat for these weeds based on the environmental variables used in the model.

The Bayes' theorem model equation is as follows:

$$Pp=\frac{(Ppp*Pcp)}{(Ppp*Pcp)+(Ppa*Pca)}$$

where

Pp = the probability of presence
Ppp = a priori probability for presence*
Ppa = a priori probability for absence/random
Pcp = the product of conditional probabilities for presence
Pca = the product of conditional probabilities for absence

Output is in the form of a map showing a range of probabilities of the suitability of weeds throughout the area, based on the environmental factors.

Model Validation

The utility of a model can not be known until the model is validated. Bayes' model results in the probability of potential habitat for musk thistle and Canada thistle, and does not imply that the plants are actually present at these sites. Therefore, the model can not

---

[*] A priori probabilities were set to .5 due to an original assumption that there is an equal probability for presence and absence (Aspinall, 1992a).

be validated by looking for presence and absence of these weeds in the field.

GTNP weed managers have done thorough surveys of the roadsides and trailsides of GTNP for the past eight field seasons (1991-1998). Although GTNP managers did not collect this weed data with the intentions of it being used in this particular model, it is assumed that the maps produced by GTNP have accurate presence/absence data of weeds for a 200 meter buffer (100m from each side) along the roads and trails. These data are sufficient to compare to the results of the Bayes' probability maps for musk thistle and Canada thistle suitable habitat within the surveyed area.

The study area portion of GTNP's weed data was isolated for the validation. The roads and trails were merged and a 200 meter buffer was placed around the weed presences to accommodate error in mapping. The two sets of data were cross-tabulated to determine the amount of overlay for presence and absence of the Park's data compared with the probabilities provided by Bayes' theorem.

Results of the models were also compared to the data used to create the model to see how well the models could predict themselves. This was done by looking at how many sites of presence and absence fell on each of the probability values determined by the models (in the sense of conditional probabilities).

RESULTS

Field Sampling

Results of the field work determined that of the thirteen Priority 1 exotic species recorded, only five different species were found in any of the study sites, and these were found in a very low number of sites. Musk thistle was found most frequently, being present in 16% of the study sites, followed by Canada thistle which was present in 7% of the study sites. The other three weeds that were found present in any of the study sites had a very low percentage of presence. Houndstongue was found in three sites (1.5%), while spotted knapweed and common mullein were each only found in one site (.5% of the sites visited, each).

Results of the fieldwork demonstrate the rarity of these weeds in a random sample of the southeast part of the Park. Although the weeds are observed along roads and trails, a survey across the lower elevations of GTNP determines exotic plants to be a low percentage of the entire vegetative composition of the valley floor. This conclusion can be viewed as a positive finding for GTNP weed managers.

Chi Square Test Results

The Chi square tests suggest that five factors have a significant association with musk thistle infestations and four factors have a significant association with Canada thistle (Table 2). Elevation, geology, soil, grazing allotments, and distance from hydrography were all significantly associated with musk thistle distributions. Geology,

Table 2: Results of the Chi square tests of association

MUSK THISTLE

Environmental Factor	Chi Square Value	Degrees of Freedom	Critical Value	Statistical Significance
Elevation	**30.084**	**15**	**24.990**	**Significant difference at 95%**
Slope	4.707	7	14.060	Insignificant difference at 95%
Aspect	40.176	35	48.800	Insignificant difference at 95%
Geology	**39.965**	**24**	**36.410**	**Significant difference at 95%**
Habitat Cover	7.847	7	14.067	Insignificant difference at 95%
Soil	**51.974**	**31**	**44.985**	**Significant difference at 95%**
Grazing Allotments	**20.906**	**1**	**3.842**	**Significant difference at 95%**
Distance from Roads	6.268	6	12.592	Insignificant difference at 95%
Distance from Trails	10.919	6	12.592	Insignificant difference at 95%
Distance from Hydrography	**14.520**	**4**	**9.488**	**Significant difference at 95%**

CANADA THISTLE

Environmental Factor	Chi Square Value	Degrees of Freedom	Critical Value	Statistical Significance
Elevation	18.012	15	24.996	Insignificant difference at 95%
Slope	4.017	7	14.067	Insignificant difference at 95%
Aspect	30.468	35	49.802	Insignificant difference at 95%
Geology	**40.479**	**24**	**36.415**	**Significant difference at 95%**
Habitat Cover	8.320	7	14.067	Insignificant difference at 95%
Soil	**93.651**	**31**	**44.985**	**Significant difference at 95%**
Grazing Allotments	**7.093**	**1**	**3.842**	**Significant difference at 95%**
Distance from Roads	**23.773**	**6**	**12.592**	**Significant difference at 95%**
Distance from Trails	7.128	6	12.592	Insignificant difference at 95%
Distance from Hydrography	7.108	4	9.488	Insignificant difference at 95%

soil, grazing allotments, and distance from roads were determined to be significantly associated with Canada thistle distributions.

Conditional Probabilities

The conditional probabilities reveal patterns of presence or absence on particular classes of each of the environmental factors (Appendix E). Musk thistle was present most often in sample sites within the 1976-2000m elevation range. It was most absent in three elevation intervals ranging from 2026-2100m. The greatest number of musk thistle samples occurred on the same geologic type as the greatest number of absences, namely the "Outwash gravel forming terraces graded to Jackson Lake Moraine," which also happened to be one of the highest occurrences of presence. The two geologic types with the highest occurrences of musk thistle presence were "Alluvial Fan Deposits" and "Alluvial, Gravel, and Sand and Floodplain Deposits." Some prominent patterns were displayed with the conditional probabilities of soil. The greatest amount of samples were taken on "Tineman Gravelly Loam" and "Tineman-Bearmouth Gravelly Loams, 0-3% slopes," with the greatest number of absences occurring on the latter soil type and the greatest number of presences occurring on the first type. The "Taglake-Sebud Association" and the "Leavitt-Youga Complex, 0-3% slopes" had the second and third highest amounts of presence, respectively. The "Buffork Tongue Association" had a much greater occurrence of presence than absence, and the "Greyback-Thayne Complex, 3-6% slopes" soil type is a perfect predictor since musk thistle was found on every site visited with this soil type.

Although the majority of sites were located on lands that were not allocated as grazing allotments for domestic cattle or horses, the greatest number of musk thistle absences occurred on the ungrazed lands. Therefore, the conditional probabilities for the presence or absence of grazing allotments demonstrate that it is more likely that there will be absences of musk thistle on ungrazed land and that musk thistle will be present on grazed land. The greatest number of presences within grazing allotments fell on the Gros Ventre allotment. The most apparent pattern is seen with the distance of hydrography layer. Although the majority of sites sampled were relatively near water, the number of sites where musk thistle was present were also near water, especially in the 0-500m range, while the absences tapered off with the increase of distance.

Canada thistle is only found on six of the twenty-four geologic types sampled. The two geologic types with the greatest amount of presence were “Alluvium, Gravel, and Sand and Floodplain Deposits” and “Alluvial Fan Deposits,” followed by “Debris of the Jackson Lake Moraine” and “Swamp Deposits.” Canada thistle also displays a strong affinity for soil type with the greatest amount of presence on the “Taglake-Sebud Association” and the “Slocum-Silas Loams.” The conditional probabilities for the soil type are very important for Canada thistle because they reveal three perfect predictors. The soil types "Leavitt Variant Loam", "Slocum-Silas Loams", and "Tetonia-Lantonia Silt Loams, 6-10% slopes" were found to have Canada thistle growing on them for every site visited. This information is important when creating a model of prediction. The conditional probabilities for Canada thistle and grazing allotments revealed a similar pattern as the musk thistle. Although there were more sites on areas that were not set aside for grazing, there was still evidence of weeds on the East Elk, Gros Ventre, and West Elk grazing allotments, and the proportion of presences to absences demonstrates that it is more likely that Canada thistle will be present on grazed land than on ungrazed land. The conditional probability for distance from roads shows that more Canada thistle was found at shorter distances from roads, particularly within 500m of the roads. However, there is also evidence of weeds between 2500-3000m from the roads. This may be a result of other factors that were present at these sites.

Bayesian Probability

Results of Bayes' probability models are in the form of maps showing the probability of suitable habitat for musk thistle (Figure 5) and for Canada thistle (Figure 6). The map for musk thistle shows the areas with the greatest probabilities of musk thistle as being south and east of Blacktail Butte, west of the town of Kelly and both north and south of Antelope Flats Road in the southeast corner of the study area. High probabilities (indicating suitable habitat) are found along the Snake River as a corridor, but not within the meanders, braids, and islands of the river. The shores of Phelps, Taggart, Bradley, and Leigh lakes are all high-probability areas, while the portion of Jackson Lake's shore that is in the study area is moderately high. The area around the southern part of Signal Mountain and west-southwest of Uhl Hill are also areas of high probability for suitable habitat for musk thistle.

The Canada thistle map exhibits larger areas with a high probability for suitable habitat. High-probability areas for Canada thistle are within the braids and meanders of

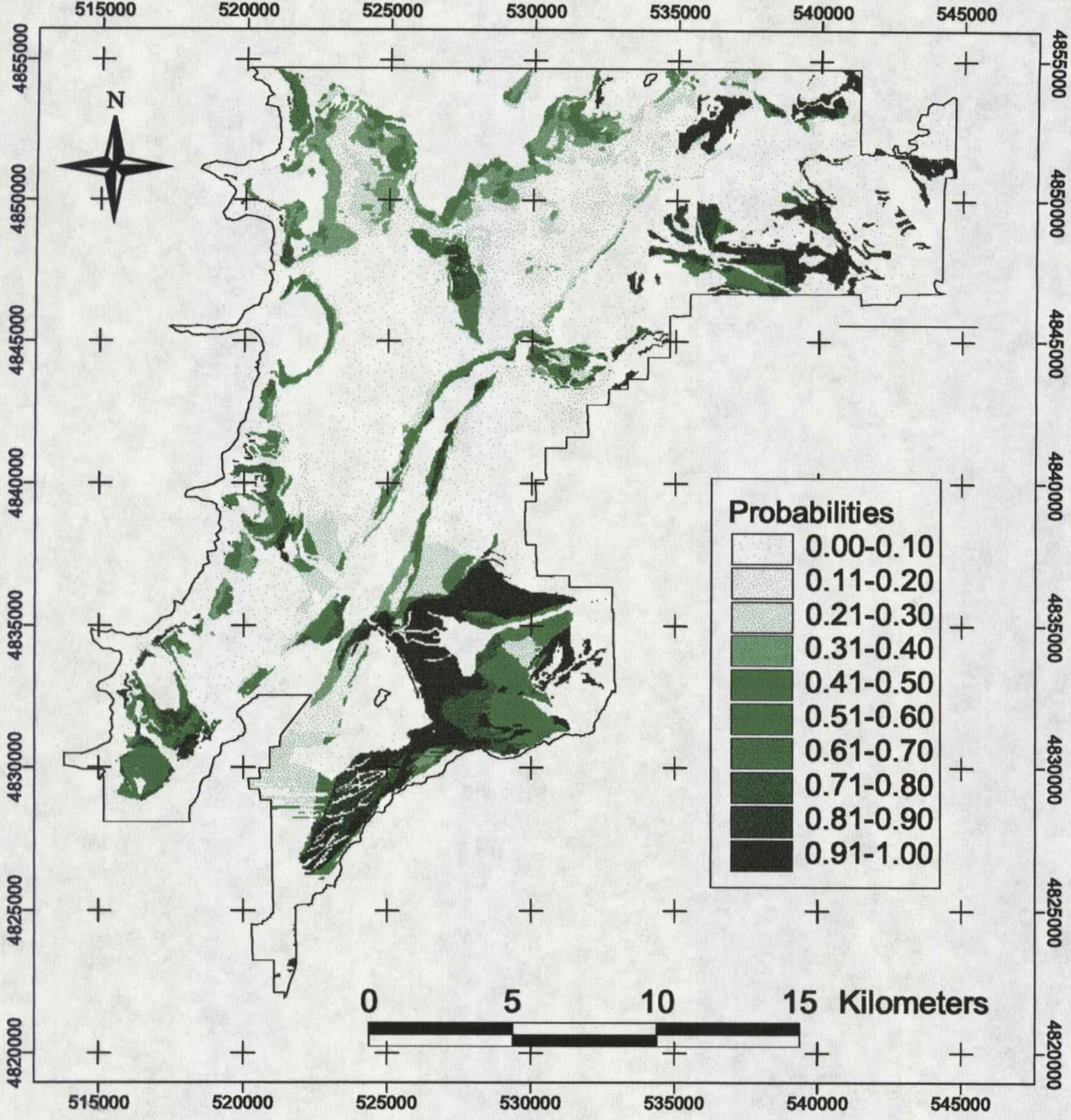


Figure 5.
Probability of suitable habitat
for Musk thistle

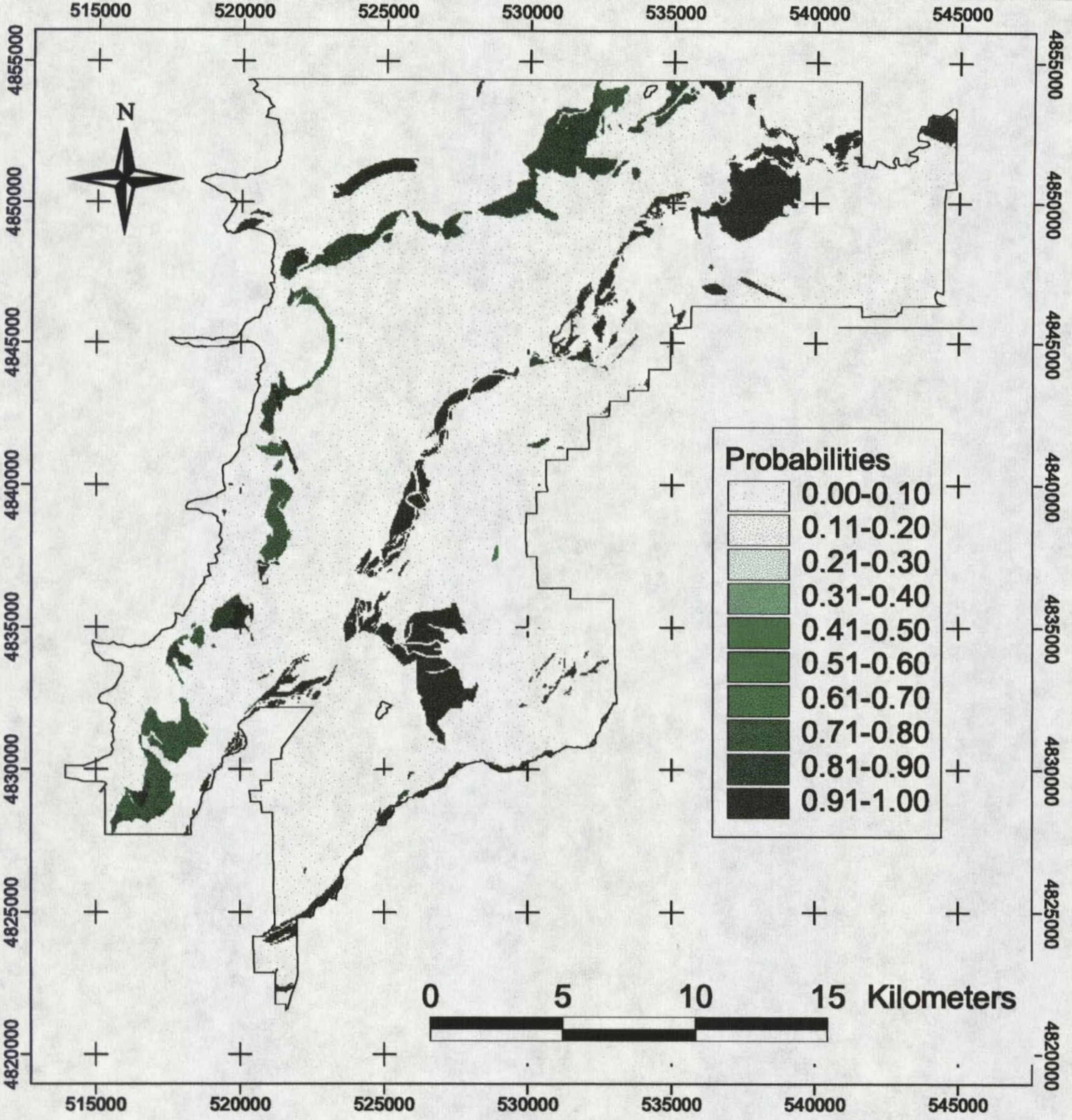


Figure 6.
Probability of suitable habitat
for Canada thistle

the Snake and Gros Ventre rivers' floodplains. The Valley Trail, shores of the moraine lakes, and the southern shores of Jackson Lake are areas that have a high probability of being suitable Canada thistle habitat. Other suitable areas are east and northeast of Blacktail Butte, Moran Junction, and the western side of Signal Mountain.

Model Validation Results

Cross-tabulation of GTNP's data for Canada thistle and musk thistle with the results from Bayes' model suggest a 59.8% overall accuracy for the Canada thistle model and a 58.5% overall accuracy for the musk thistle model. A probability of 0.70 or higher was arbitrarily chosen to differentiate between suitable and unsuitable habitat. Table 3 provides a summary of the cross-tabulation results. A table containing the entire results of the cross-tabulations is located in Appendix F. Results of these cross-tabulations determine that the models are useful for identifying suitable habitat in the study area.

Table 3. Summary of Cross-tabulation Results

Probability of Presence	Actual Absence	Actual Presence
0-30	42.90	34.72
31-69	28.26	13.16
70-100	28.83	52.12
Musk Thistle Model Overall Accuracy: 58.5		

Probability of Presence	Actual Absence	Actual Presence
0-50	58.98	43.21
51-100	41.02	56.79
Canada Thistle Model Overall Accuracy: 59.8		

Results of a comparison of the model to the data used to create it are found in Appendix G. These results show that 100% of the sites where Canada thistle was present are predicted by the Canada thistle model with a probability of greater than or equal to .70. 76% of the sites where Canada thistle was present are predicted with a probability of .98 or higher. The model for musk thistle predicted 60% of the sites where musk thistle was present at greater than or equal to .70 probability and 47% of the sites with a probability greater than or equal to a probability of .98. The Canada thistle model may have been more successful because there were fewer environmental factors and fewer sites where presence was recorded which results in a simpler, more specific model.

DISCUSSION

The objectives of this study were to characterize exotic weeds in Grand Teton National Park based on environmental factors and to determine other areas in the Park suitable for weed infestations. Models have been constructed for Canada thistle and musk thistle. GTNP has mapped its Priority 1 weeds, but the main trajectory for this mapping was roads and trails. It is believed that the use of GTNP's data would have introduced a bias to the distance from roads and distance from trails factors. Steps taken in this study included collecting Canada thistle and musk thistle presence and absence data based on a random sample as input for a model to find similar areas as suitable habitat, and to test the results of the model using data collected by GTNP.

Characterizing the Environments of Canada Thistle and Musk Thistle Distributions

Results of this study indicate that particular environmental factors have an association with the distributions of Canada thistle and musk thistle, and that those factors can be used in a model to determine the probability of a site to support a population of Canada thistle or musk thistle. Five environmental factors were found to be associated with musk thistle distribution and four environmental factors were found to be associated with the distribution of Canada thistle. Three of these factors were important to both weeds (geology, soil, and grazing allotments).

The GIS layers for geology and soil have already been identified as being closely related and proven to be significant to plant distributions. Therefore, it is not surprising that both of these two layers were found to be significant to both exotic species in the study.

The effects of grazing and trampling, both of which are concentrated within grazing allotments, were discussed earlier. The effects of these activities combined with irrigation may contribute to the explanation of the significant association of grazing allotments with musk thistle and Canada thistle. Natural disturbances are as habitable for weeds as human-induced disturbances. Although not quantified, weeds (musk thistle in particular) were often seen growing along game trails, bison wallows, and pocket gopher mounds and tunnels. Pocket gopher mounds differ in physical and chemical properties from undisturbed soil, as the flora growing on them often differs from the surrounding vegetation (Huntley and Inouye, 1988). Gophers disrupt the soil and disturb surface vegetation enough to affect the plant species and reset the period of succession that occurs in a particular area (Glick et al., 1991). Unfortunately, the scale of these features is smaller than the 30 meter resolution of this project. Although a measure of disturbance could have been used within the study sites, data on these types of disturbances are not available for the study area as a whole, and could not be incorporated into the model.

Distance from hydrography had a significant association with musk thistle. It was surprising that there was not a similar association with Canada thistle (based on studies mentioned earlier and personal field observations), although the map produced from Bayes' equation shows the banks of the rivers and the shores of the lakes as areas of highest probability for Canada thistle suitable habitat. Although quantitative methods were not used to measure this, Canada thistle was observed growing along irrigation ditches in grazing allotments on GTNP land in areas where there were not populations of Canada thistle away from the ditches.

The fifth significant environmental factor for musk thistle was elevation. Elevation is known to be an important abiotic factor for plant distribution (Bian and Walsh, 1993) and has been proven elsewhere to be a significant environmental factor for Canada thistle (Allen, 1996) and spotted knapweed (Marcus et al., 1998) (although Chicoine et al. (1985) determined that elevation was not a restrictive factor for Spotted knapweed in western Montana). Musk thistle was found only on elevations between 1926-2175m although field sites ranged from 1875-2300m.

The fourth significant factor for Canada thistle was distance from roads. Prior to field work for this project, GTNP weed data sets (Appendix A) indicated that roadsides and Gros Ventre River/Snake River riparian areas were infested by various non-native weeds, which was not unusual since these areas are typical seed transport pathways for weeds. Most of GTNP's weeds can be found growing along roads (Weaver and Woods, 1986) or on currently or historically developed sites. Roadside vegetation is often contaminated with weedy species (Tyser and Worley, 1992) because of seed transport and deposition by automobiles (Meier, 1997) and also because roadsides are often disturbed due to road construction and snowplowing during the winter. As in Yellowstone National Park, it is believed that some weeds have been brought into GTNP through contaminated sand and soil used for construction or for winter road maintenance (Allen and Hansen, 1999; Villalobos, 1998). In 1986, Weaver and Woods documented 53 exotic plant species along GTNP roadsides, including Canada thistle and musk thistle in small numbers.

Environmental Factors Determined Insignificant to Canada Thistle and Musk Thistle Distributions in Grand Teton National Park

Four environmental factors out of the nine incorporated were determined not significantly associated with musk thistle or Canada thistle distributions in GTNP including aspect, slope, habitat cover, and distance from trails. Each of these factors has been documented as being significant to vegetation patterns, but was not determined to have an association with Canada thistle or musk thistle distributions in the study area within GTNP. Relationships between the species' distributions and the scale of this study were not determined. The scale of this study may not have been fine enough, and the ranges of each of these factors may not have been large enough to identify or establish relationships within the study area.

It is important to note that statistical tests are limited in the information that they are capable of providing and, therefore, can only be used as a guide. Although the Chi square test is the best statistical method for associating the data layers with the weed distributions as used here, it is not necessarily the best overall method. For example, if a species is only present or only absent on one particular soil type, this results in several empty cells in the spread sheet that are not very effective when performing a Chi square test. However, in the case of prediction, this type of data presents itself as a perfect predictor in which it can be assumed that if a species is only found on one specific type of soil, then it is very likely to be found on that type in other areas. Therefore, the conditional probabilities of the model are the best overall method for associating the data, and the Chi square is simply used as a guide.

It is surprising that distance from roads is not a contributing factor in the distribution of musk thistle, although the Chi square test determined it to be insignificant. The Chi square test results are questionable, however, as there were many empty cells within the analysis. GTNP weed data displays musk thistle as being along the roads, and direct observation during the 1998 field season showed musk thistle lining the roadsides, especially in the southern part of the park. Since roadsides are visible to the greatest number of visitors and are easily accessible, GTNP management efforts have been primarily aimed at eradication of roadside weeds. Chemical spraying and hand-pulling efforts along the roadsides may help explain why the distance from roads factor was not determined to be a contributing factor to the distribution of musk thistle in GTNP. The scale of the distance from roads layer may also have contributed to this. The distance intervals were in 480 meter increments. If the weeds were found mostly within 50 meters of the roads, this may not have been captured by the sampling. However, musk thistle may be randomly dispersed in relation to roads as it was often observed growing in areas away from roads as well. Although roads may be a vector of transport, other agents of dispersal are also at play and it is likely that this species is dispersed randomly throughout the study area, without regard to the roads.

The biotic factor included in this study was the habitat cover layer, which was not significantly associated with Canada thistle and musk thistle distributions in the study area. Since the study area was restricted to the valley floor of Jackson Hole, the primary vegetation type sampled was sagebrush-grassland on the outwash plains, dominated mainly by big sage (*Artemisia tridentata*) or, in localized areas, by low sage (*Artemisia arbuscula*). The moraines within the study area were forested with coniferous trees dominated by lodgepole pines (*Pinus contorta*) (Oswald, 1966), although most of the sites were within the sagebrush-grassland. It may be due to this low variability in vegetation types sampled that there is no significant association between the habitat cover and the musk thistle or Canada thistle distributions in the study area.

Unlike distance from roads, distance from trails did not have a statistically significant association with either Canada thistle or musk thistle distributions in the park. However, trails have been documented as a corridor for weed travel as seeds get caught in, and transported by people's clothing and in the fur of horses and wild animals using the trails (Benninger-Truax et al, 1992; Tyser and Worley, 1992). Within GTNP, weeds can be found along various trails, as represented on the maps of GTNP weed data in Appendix A. Distance from trails was probably not associated with Canada thistle and/or musk thistle distributions because there were not many trails in the study area (12.2 kilometers of trails for 514 square kilometers of land) or because of the same scale issue discussed in terms of the distance from roads factor for musk thistle.

Management of Weeds in Grand Teton National Park

The National Park Service defines exotic species as those that occur outside their range as a result of human activities (NPS, 1997). In order to deal with the removal of these species, the National Park Service designed and implemented an Integrated Pest

Management Program that coordinates the use of environmental information and pest control methods to control non-native plant populations. GTNP is one of over 535 projects costing the NPS over $80 million to eliminate exotics on National Park Service lands (NPS, 1997). GTNP incorporates four methods of control for this program: 1) chemical spraying, 2) hand-pulling, 3) biocontrol, and 4) cultural control. The Park is also working with the University of Wyoming and the University of Wyoming Cooperative Extension service to test the ability of native perennial grasses to out-compete musk thistle (GTNP, 1997a). Studies are done by GTNP personnel to measure the effectiveness of chemical spraying. Mechanical controls, although time-consuming due to lack of personnel, provide immediate aesthetic improvements. Biocontrol used in GTNP consists of a stem-boring weevil, *Rhinocyllus conicus*, that infects musk thistle blossoms. These insects are released at specific locations in the park and monitored. Cultural controls consist of education, prevention, and environmental management efforts involving quarantines or closures, rehabilitation, and changes in livestock and wildlife management practices (GTNP, 1997b).

Recommendations for Grand Teton National Park

Based on the results of this study, the exotic plant species sampled are rare within the study area in the southeastern part of GTNP. However, it is suggested that GTNP continue their efforts in mapping, preventing, controlling, and eradicating non-native weeds as there are populations present within the Park. Results of this study suggest that

GTNP is still at a point of prevention in terms of weed management. Attention should be given to all areas determined to have high probabilities of suitable habitat throughout the park, not just to roadsides and trailsides, as non-native weeds have permeated beyond these features. Caution should be taken that the focus is not only on more easily controlled species as this may eventually result in the Park becoming overgrown with exotics that are more resistant to control (Westman, 1990). As exotic plant species are removed, erosion control methods should be applied and efforts should be taken to encourage restoration of native plant species. The probability maps produced in this study may aid weed managers by directing them to monitor areas with high probabilities of suitable habitat for Canada thistle and musk thistle.

It is recommended that grazing allotments be monitored as possible sites of new weed introductions or explosions of current weed populations. Irrigation ditches should also be monitored for weed seed content. If irrigation ditches are found to be carrying weed seed, weed seed screens may aid in preventing further dispersal (Bruns, 1965).

Commercial vendors within the Park, particularly those that provide horseback riding, should be mandated to monitor their horse corrals and the trails they ride on, and they should also be responsible for weed control in these areas. This responsibility would include prevention of any introduction of weed seed via their horses and control of weed infestations should they occur. Prevention methods should include mandatory weed seed free hay and a thorough cleaning of the horses (and the trailers they are transported in) prior to entry into the Park to rid the animals of any seeds that may be clinging to their coats.

Further Research

Several actions could be taken to further and continue this research. The areas of greatest error or uncertainty could be mapped to create an error surface for the outcome by mapping standard deviations of the probabilities (Aspinall, 1992a). Using the UTM coordinates and developing a permanent monitoring framework, sites could be resurveyed and the percent cover of bare ground and/or disturbances could be measured to quantify effects of disturbance on populations and possibly to map disturbances to include as an environmental factor in the model. It is hypothesized that natural disturbances such as game trails, bison wallows, pocket gopher mounds, etc. are an important factor in determining suitable habitat for weeds, and that incorporation of this information would enhance the utility of the model. Soil samples could be taken and weed seed content examined at each site to determine if the weed seeds are everywhere but are only able to grow in certain places, or if the seeds are only found where the weeds are actually growing. Soil moisture could be tested at each site to determine the effect (if any) of soil moisture on weed locations.

Alternative data sets could be included in the model to supplement data collected through fieldwork. Although costly, remotely sensed data including aerial photographs and satellite-acquired digital imagery could be used to map the larger populations of exotic plants in the study area.

Now that a model of suitable habitat has been created for the lower elevations of GTNP, management could be further aided by incorporating models of life history characteristics along with suitable habitats as conditional probabilities in Bayes' probability theorem. Additional models could be made using the same methods used here to determine probable dispersal patterns and competition probabilities. Results of these three models could be combined with Bayes' model to produce a map showing the probability of invasions or, a predictive map based on suitable habitat, dispersal patterns, and competition rates that would predict the spread of these species. The areas with the highest probabilities of invasions should also be the earliest sites to be invaded.

Results of this model would be most useful if the model was updated periodically over several years to eliminate sites that have been eradicated through control methods and to add sites of new invasions until, if possible, all weeds are under control.

CONCLUSIONS

Canada thistle and musk thistle distributions in GTNP were characterized. Other sites in the study area were assigned probabilities of suitable habitat based on these characterizations. Chi square test results determined elevation, geology, soil, grazing allotments, and distance from hydrography as having significant associations with musk thistle presence and absence. Results of the Chi square tests indicate geology, soil, grazing allotments, and distance from roads as having significant associations with the distribution of Canada thistle. Incorporation of the conditional probabilities of these attributes into a model based on Bayes' theorem produced two maps of the probability of an area as suitable habitat for Canada thistle or musk thistle. The model method used, Bayes' probability theorem, was successful in determining suitable habitats for the two exotic species studies, with a validation accuracy of 58.5% for musk thistle and 59.8% for Canada thistle. Therefore, the models are helpful in aiding management to areas that are most likely to be habitable to Canada thistle and musk thistle.

REFERENCES CITED

Allen, K. and K. Hansen. (in press, 1999 expected). The geography of exotic plants adjacent to campgrounds, Yellowstone National Park, USA. Great Basin Naturalist.

Amor, R.L. and R.V. Harris. 1974. Distribution and seed production of *Cirsium arvense* (L.) Scop. in Victoria, Australia. Weed Research, 14: 317-323.

Anderson, J. 1990. Vegetation and Vegetation Dynamics in the Greater Yellowstone Ecosystem: An Introduction. manuscript prepared for Greater Yellowstone Coalition Science Council.

Aspinall, R.J. and N. Veitch. 1993. Habitat mapping from satellite imagery and wildlife survey data using a Bayesian modeling procedure in GIS. Photogrammetric Engineering and Remote Sensing 59: 537-543.

Aspinall, R.J. 1992a. An inductive modelling procedure based on Bayes' theorem for analysis of pattern in spatial data. International Journal of Geographical Information Systems, 6: 105-121.

Aspinall, R.J. 1992b. Spatial analysis of wildlife distribution and habitat in a GIS. Proceedings of the 5th International Symposium on Spatial Data Handling, Charleston, S.C.

Aspinall, R.J. 1994. Exploratory spatial analysis in GIS: Generating geographical hypotheses from spatial data, in Innovations in GIS 1. Worboys, M., ed. Taylor-Francis.

Austin, M.P., A.O. Nicholls, and C.R. Margules. 1990. Measurement of the realized niche: Environmental niches of five *Eucalyptus* species. Ecological Monographs, 60: 161-177.

Baker, H.G. 1986. Patterns of plant invasion in North America in, Ecology of Biological Invasions of North America and Hawaii. H.A. Mooney and J.A. Drake, eds. Springer-Verlag, New York.

Bartell, S.M. and A.L. Brenkert. 1991. A spatial-temporal model of nitrogen dynamics in a deciduous forest watershed, in Quantitative Methods in Landscape Ecology. M.G. Turner and R.H. Gardner, eds. Springer-Verlag.

Bedunah, D.J. 1992. The complex ecology of weeds, grazing, and wildlife. Western Wildlands, 18: 6-11.

Benninger-Truax, M., J.L. Vankat, and R.L. Scheafer. 1992. Trail corridors as habitat and conduits for movement of plant species in Rocky Mountain National Park, Colorado, USA. Landscape Ecology, 6: 269-278.

Bian, L. and S.J. Walsh. 1993. Scale dependencies of vegetation and topography in a mountainous environment of Montana. Professional Geographer, 45: 1-11.

Birkeland, Peter W. 1984. Soils and Geomorphology. Oxford University Press, N.Y.

Breininger, D.R., M.J. Provancha, and R.B. Smith. 1991. Mapping Florida Scrub Jay habitat for purposes of land-use management. Photogrammetric Engineering & Remote Sensing, 57: 1467-1474.

Bright, C. 1995. Bioinvasions: the spread of exotic species. World Watch, 18:10-19.

Brown, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. Journal of Vegetation Science, 5: 641-656.

Bruns, V.F. 1965. The effects of freshwater storage on the germination of certain weed seeds. Weeds, 13:38-40.

Bruns, V.F. and L.W. Rasmussen. 1953. The effects of freshwater storage on the germination of certain weed seeds. I. White top, Russian knapweed, Canada thistle, Morning glory, and Poverty weed. Weeds, 2: 138-147.

Bruns, V.F. and L.W. Rasmussen. 1957. The effects of freshwater storage on the germination of certain weed seeds. II. White top, Russian knapweed, Canada thistle, Morning glory, and Poverty weed. Weeds, 5: 20-24.

Burrough, P.A. and R.A. McDonnell. 1998. Principles of Geographical Information Systems. Oxford University Press. Oxford.

Campbell, F.T. 1997. Exotic pest plant councils: Cooperating to assess and control invasive nonindigenous plant species. In, Assessment and Management of Plant Invasions. J.O. Luken and J.W. Thieret (eds.) Springer, New York.

Chicoine, T.K., P.K. Fay, and G.A.Nielsen. 1985. Predicting weed migration from soil and climate maps. Weed Science, 34: 57-61.

Clark, J.D., J.E. Dunn, and K.G. Smith. 1993. A multivariate model of female black bear habitat use for a Geographic Information System. Journal of Wildlife Management, 57: 519-526.

Clark, T.W., A.H. Harvey, R.D. Dorn, D.L. Genter, and C. Groves, eds. 1989. Rare, Sensitive and Threatened Species of the Greater Yellowstone Ecosystem. Northern Rockies Conservation Cooperative, Montana natural Heritage program, The Nature Conservancy, and Mountain West Environmental Services. 153 pp.

Cook, Q.C.B. and J.L. Fuller. 1995. Plant Invasions: The Threat to Natural Ecosystems. A ‘People and Plants’ Conservation Manual. Chapman and Hall, London.

Cooksey, D. and R. Sheley. 1998. Mapping Noxious Weeds in Montana. Department of Plant, Soil and Environmental Sciences, Montana State University. Bozeman, Montana 59717.

Cousens, R. and M. Mortimer.1995. Dynamics of Weed Populations. Cambridge University Press, Great Britian.

Daehler, C.C. and D.R. Strong. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biological Conservation, 78: 51-58.

Dale, D. and T. Weaver. 1974. Trampling effects on vegetation of the corridors of Rocky Mountain forests. Journal of Applied Ecology, 11: 767-772.

Daubenmire, R.F. 1947. Plants and Environment. John Wiley & Sons, Inc. New York.

Daubenmire, R.F. 1943. Vegetational zonation in the Rocky Mountains. The Botanical Review, 9:325-393.

Davis, F.W. and S.Goetz. 1990. Modeling vegetation pattern using digital terrain data. Landscape Ecology, 4: 69-80.

Despain, D.G. 1990. Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting. Roberts Rinehart, Inc. Boulder, CO.

Despain, D.G. 1973. Vegetation of the Big Horn Mountains, Wyoming, in relation to substrate and climate. Ecological Monographs, 43: 329-355.

Dewey, S.A., K.P. Price, and D. Ramsey. 1991. Satellite remote sensing to predict potential distribution of Dyers Woad (*Isatis tinctoria*). Weed Technology, 5: 479-484.

Farnes, P., Heydon, C. and K. Hansen. 1999. Snowpack Distribution in Grand Teton National Park. Final Report. Proposal No. 97-059. Department of Earth Sciences. Montana State University. Bozeman, MT.

Forcella, F. 1992. Invasive weeds in the northern Rocky Mountains. Western Wildlands, 18: 2-5.

Forcella, F. and S.J. Harvey. 1983. Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Madrono, 30: 102-109.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography, 19: 474-499.

Giller, P.S. 1984. Community Structure and the Niche. Chapman and Hall, London.

Glick, D., M. Carr, and B. Harting. 1991. An Environmental Profile of the Greater Yellowstone Ecosystem. The Greater Yellowstone Coalition. Bozeman, Montana 59771.

Grand Teton National Park. 1997a. Annual Report for the Non-Native Plant Management Program in Grand Teton National Park. Office of Science and Resource Management. Grand Teton National Park. Moose, WY 83012.

Grand Teton National Park. 1997b. Invasive Plant Management Plan. Draft Copy. Office of Science and Resource Management. Moose, Wyoming.

Grand Teton National Park. 1987. Land Protection Plan. Biennial Review. Moose, Wyoming.

Grand Teton National Park. 1976. Master Plan. United States Department of the Interior/National Park Service. Wyoming.

Hansen, K. W. Wycoff, and J. Banfield. 1995. Shifting forests: Historical grazing and forest invasion in southwestern Montana. Forest & Conservation History, 39: 66-76.

Hayden, A. 1934. Distribution and reproduction of Canada thistle in Iowa. American Journal of Botany, 21: 355-373.

Hershey, B.R., M.A. Ramirez, and D.A. Drake. 1997. Using geostatistical techniques to map the distribution of tree species from ground inventory data, in Modelling Longitudinal and Spatially Correlated Data: Methods, Applications and Future Directions. Lecture Notes in Statistics. Vol. 122. Gregoire, T. et al, eds. Springer-Verlag.

Hitchcock, C.L. and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Homer, C.G., T.C. Edwards, R.D. Ramsey, and K.P. Price. 1993. Use of remote sensing methods in modelling sage grouse winter habitat. Journal of Wildlife Management, 57: 78-84.

Huggett, R.J. 1995. Geoecology: An Evolutionary Approach. Routledge, London.

Huntley, N. and R. Innouye. 1988. Pocket gophers in ecosystems: Patterns and mechanisms. BioScience, 38: 786-793.

Jaegar, R.M. 1990. Statistics: A Spectator Sport. Sage Publications. Newbury Park, California. pp. 236-238.

Jensen, J.R., S. Narumalani, O. Weatherbee, K.S. Morris, Jr., and H.E. Mackey, Jr. 1992. Predictive modeling of cattail and waterlily distribution in a South Carolina reservoir using GIS. Photogrammetric Engineering & Remote Sensing, 58: 1561-1568.

Kelley, A.D. and V.F. Bruns, 1975. Dissemination of weed seeds by irrigation water. Weed Science, 23: 486-493.

Lees, B.G. and K. Ritman, 1991. Decision-tree and rule-induction approach to integration of remotely sensed and GIS data in mapping vegetation in disturbed or hilly environments. Environmental Management 15: 823-831.

Lenihan, J.M. and R.P. Neilson. 1993. A rule-based vegetation formation model for Canada. Journal of Biogeography 20: 615-628.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Lindenmayer, D.B., H.A. Nix, J.P. McMahon, M.F. Hutchinson, and M.T. Tanton. 1991. The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): A case study of the use of bioclimatic modelling. Journal of Biogeography, 18: 371-383.

Love, J.D. and J.C. Reed, Jr. 1995. Creation of the Teton Landscape. Grand Teton National History Association. Moose, Wyoming 83012.

Lowell, K.E. 1991. Utilizing discriminant function analysis with a geographical information system to model ecological succession spatially. International Journal of GIS 5: 175-191.

Marcus, W.A., G. Milner, and B. Maxwell. 1998. Spotted knapweed distribution in stock camps and trails of the Selway-Bitterroot Wilderness. Great Basin Naturalist, 58: 156-166.

Martinez-Taberner, A., M. Ruiz-Perez, I. Mestre, and V. Forteza. 1992. Prediction of potential submerged vegetation in a silted coastal marsh, Albufera of Majorca, Balearic Islands. Journal of Environmental Management, 35: 1-12.

Meier, G.A.. 1997. The Colonization of Montana Roadsides by Native and Exotic Plants. Master's These. Department of Biological Sciences. Montana State University. Bozeman, MT 59717.

Milne, B.T., K.M. Johnson, and R.T.T. Forman. 1989. Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. Landscape Ecology, 2: 101-110.

Milner, G.M. 1995. The Relationships Between Disturbances in Stock Camps and the Occurrence of Spotted Knapweed (*Centaurea maculosa*) in the Selway-Bitterroot Wilderness in Montana and Idaho. Master's Thesis. Department of Earth Sciences, Montana State University. Bozeman, MT 59717.

Muenscher, W.C. 1955. Weeds. The MacMillan Company. New York.

National Park Service. 1936. Summary of Vegetation Types of Grand Teton National Park. National Park Service, Branch of Forestry, C.C.C.

National Park Service. 1997. Preserving Our Natural Heritage- A Strategic Plan for Managing Invasive Nonnative Plants on National Park SystemLands. http://www.nature.nps.gov/natnet/wv/strat_pl.htm

Noest, V. 1994. A hydrology-vegetation interaction model for predicting the occurrence of plant species in dune slacks. Journal of Environmental Management, 40: 119-128.

Olson-Rutz, K.M., C.B. Marlow, K. Hansen, L.C. Gagnon, and R.J. Rossi. 1996. Recovery of a high elevation plant community after packhorse grazing. Journal of Range Management, 49: 541-545.

Oswald, E.T. 1966. A Synecological Study of the Forested Moraines of the Valley Floor of Grand Teton National Park, Wyoming. PhD Thesis in Botany. Montana State University. Bozeman, MT 59717.

Panetta and Dodd. 1987. Bioclimatic prediction of the potential distribution of Skeletonweed *Chondrilla juncea* L. in western Australia, in Dynamics of Weed Populations. Cousens, R. and M. Mortimer (eds.). Cambridge University Press, Great Britian.

Panetta, F.D. and N.D. Mitchell. 1991. Homocline analysis and the prediction of weediness. Weed Research 31: 273-284.

Pereira, J.M. and R.M. Itami. 1991. GIS-Based habitat modeling using logistic multiple regression: A study of the Mt. Graham red squirrel. Photogrammetric Engineering & Remote Sensing, 57: 1475-1486.

Polunin, N. 1960. Introduction to Plant Geography. Longmans Green and Co, Ltd. London.

Prentice, I.C., W. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud, and A.M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties, and climate. Journal of Biogeography,19: 117-134.

Reichard, S.E. 1997. Prevention of invasive plant introductions on national and local levels. In, Assessment and management of Plant Invasions. J.O. Luken and J.W. Thieret (eds.) Springer, New York.

Reinhart, D.1998. "Lake Trout and Other Non-Natives: Their Effects on the Yellowstone Ecosystem." Emerson Cultural Center, Bozeman, MT.

Sabinske, D.W. and D.H. Knight. 1978. Variation within the sagebrush vegetation of Grand Teton National Park, Wyoming. Northwest Science, 52: 195-204.

Seligsohn-Bennet, K. 1990. Mismanaging endangered and "exotic" species in the national parks. Environmental Law, 20: 415-440.

Shaw, R.J. 1981. Plants of Yellowstone and Grand Teton National Parks. Wheelwright Press, LTD. Salt Lake City, Utah.

Sheley, R.L., B.E. Olson, and C. Hoopes. 1998. What is so Dangerous about the Impacts of Noxious Weeds? EB#152. Montana State University Extension Service.

Sperduto, M.R. and R.G. Congalton. 1996. Predicting rare orchid (small whorled Pogonia) habitat using GIS. Photogrammetric Engineering & Remote Sensing, 62: 1269-1279.

Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. The American Naturalist, 135: 649-670.

Stoms, D.M., F.W. Davis, and C.B. Cogan. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogrammetric Engineering & Remote Sensing, 58: 843-850.

Stow, D.A. 1993. The role of geographic information systems for landscape ecological studies, in Landscape Ecology and GIS. Haines-Young, R., D.R. Green, and S.H. Cousins, eds. Taylor & Francis, Ltd. London.

Tyser, R.W. and C.A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). Conservation Biology, 6: 253-262.

Villalobos, B. 1998. Personal Communication. Seasonal Weed Scientist. Grand Teton National Park.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84: 468-478.

Walker, L.R. and S.D. Smith. 1997. Impacts of invasive plants on community and ecosystem properties in, Assessment and Management of Plant Invasions. J.O. Luken and J.W. Thieret (eds.). Springer, New York.

Walker, P.A. and K.D. Cocks. 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. Global Ecology and Biogeography, 1: 108-118.

Walker, R.E., D.M. Stoms, F.W. Davis, and J. van Wagtendonk. 1992. Modeling potential natural Vegetation from a topographic gradient in the southern Sierra Nevada, California. Proceedings GIS/LIS 92. Bethesda, MD: ASPRS, 794-803.

Weaver, T., D. Gustafson, J. Lichthardt, and B. Woods. 1989. Distribution of Exotic Plants in the N. Rocky Mountains by Environmental Type and Disturbance Condition. MSU Biology Report #41. Bozeman, MT 59717.

Weaver, T. and B. Woods. 1986. Roadside Distribution of Exotic Plants in Grand Teton National Park. MSU Biology Report #39. Bozeman, MT 59717.

Westman, W.E. 1990. Park management of exotic plant species: Problems and issues. Conservation Biology, 4: 251-260.

Whitson, T.D., L.C. Burrill, S.A. Dewey, D.W. Cudney, B.E. Nelson, R.D. Lee, and R. Parker. 1996. Weeds of the West. The Western Society of Weed Science.

Wilson, R.G. Jr. 1980. Dissemination of weed seeds by surface irrigation waters in western Nebraska. Weed Science, 28: 87-92.

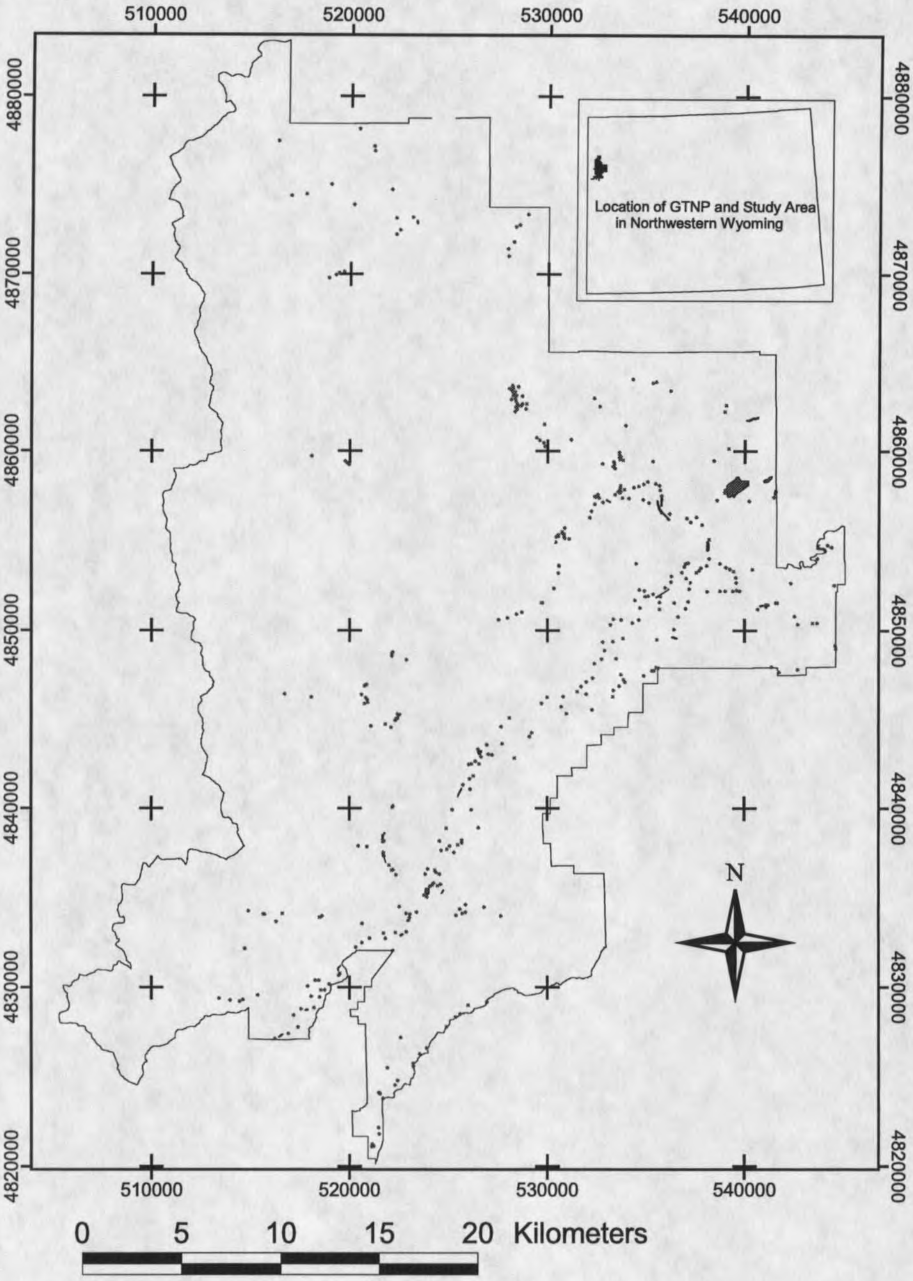
Woods, K.D. 1997. Community response to plant invasion. In, Assessment and Management of Plant Invasions. J.O. Luken and J.W. Thieret (eds.). Springer, New York.

Wyoming Rare Plant Technical Committee. 1994. Wyoming Rare Plant Field Guide. United States Department of the Interior. Bureau of Land Management.

APPENDICES

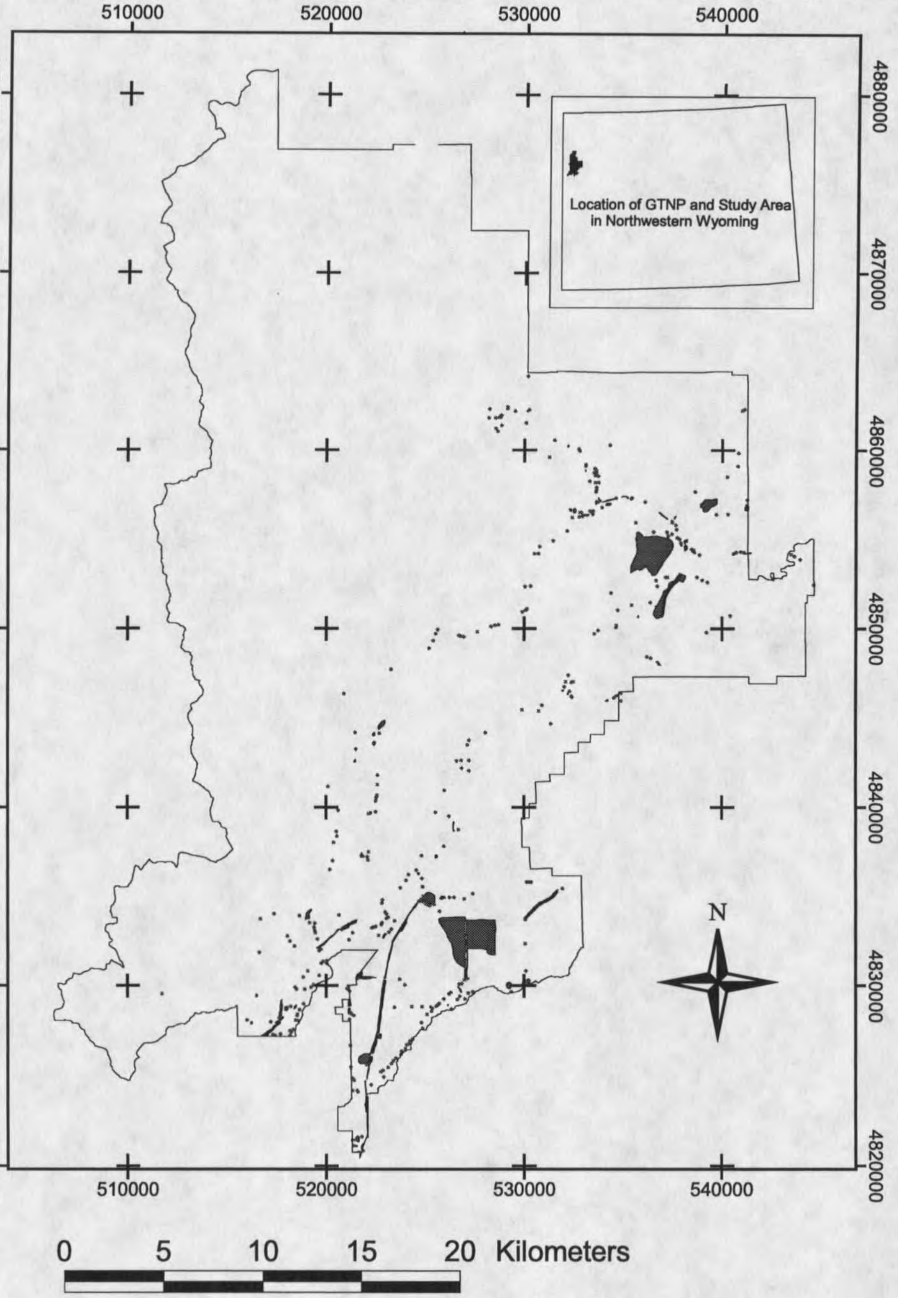
APPENDIX A

MAPS OF GRAND TETON NATIONAL PARK WEED DATA



Grand Teton National Park Weed Data: Canada Thistle

Source: Grand Teton National Park

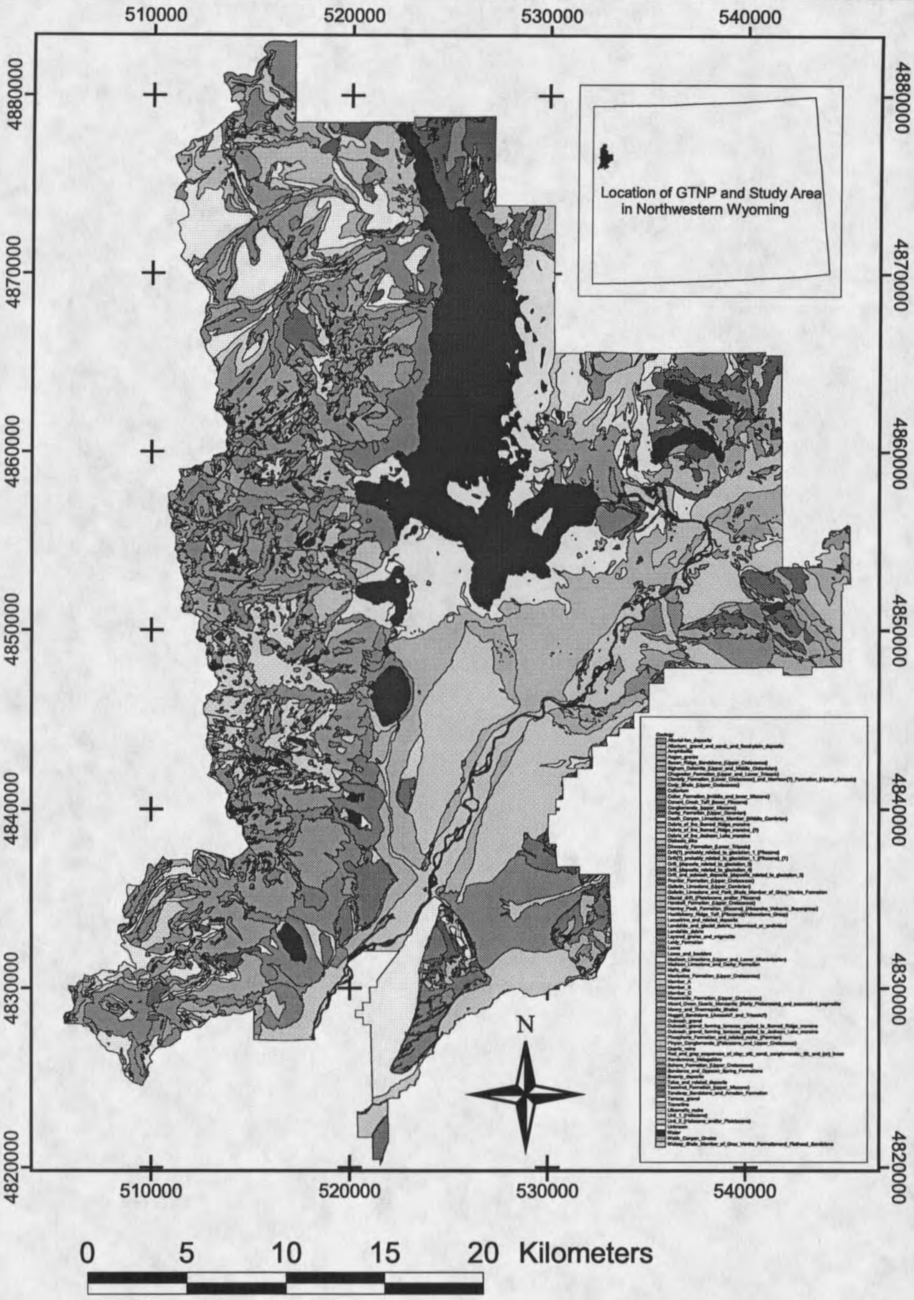


Grand Teton National Park
Weed Data: Musk Thistle

Source: Grand Teton National Park

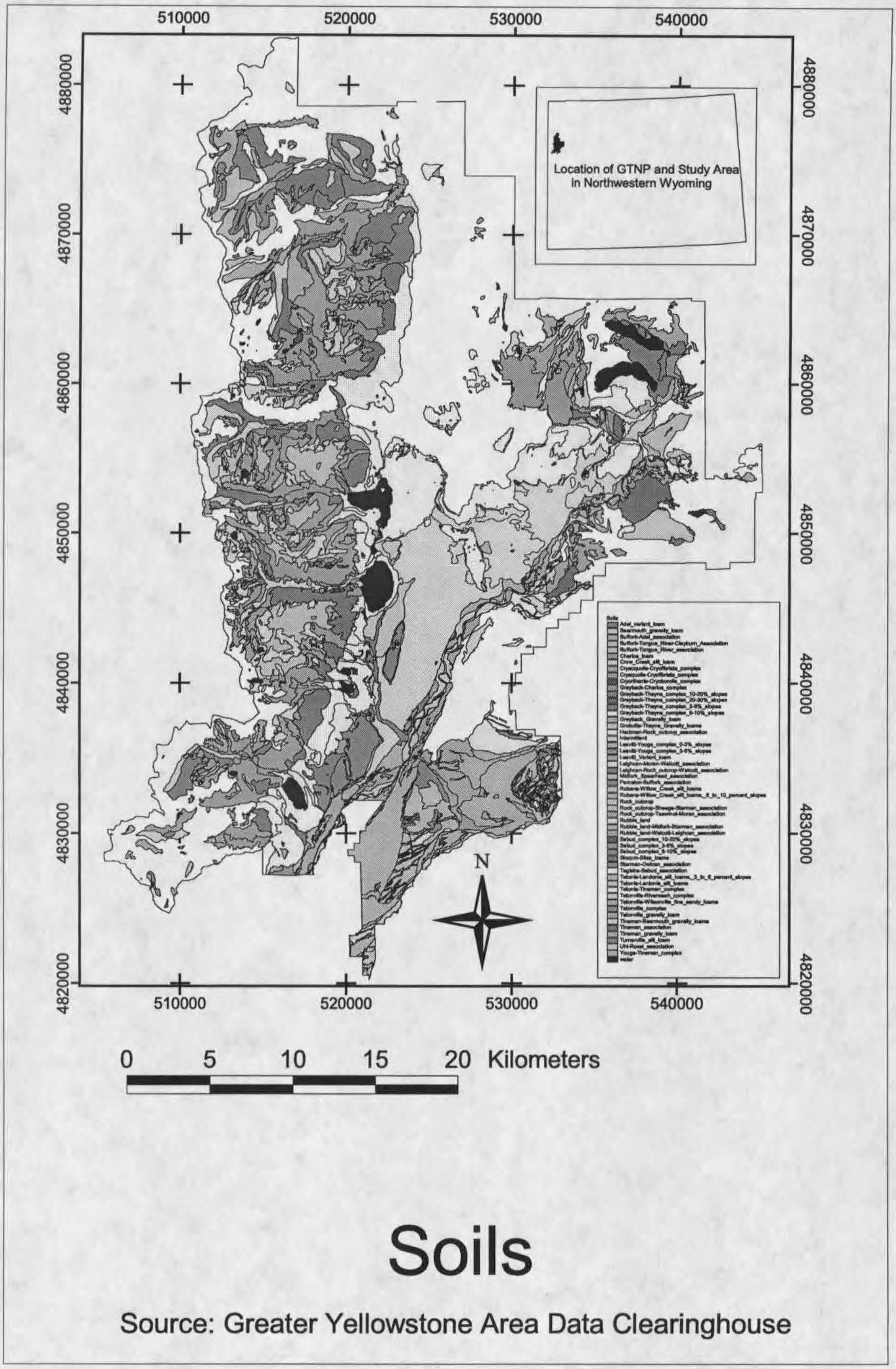
APPENDIX B

MAPS OF DATA LAYERS



Geology

Source: Greater Yellowstone Area Data Clearinghouse



Soils

Source: Greater Yellowstone Area Data Clearinghouse