THE PRAIRIE TURNIP PARADOX: CONTRIBUTIONS OF POPULATION DYNAMICS, ETHNOBOTANY, AND COMMUNITY ECOLOGY TO UNDERSTANDING *PEDIOMELUM ESCULENTUM* ROOT HARVEST ON THE GREAT PLAINS

By

Lisa Marie Castle

Submitted to the Department of Ecology and Evolutionary Biology
and the faculty of the Graduate School of the University of Kansas
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

____
Kelly Kindscher, Co-chairperson

____
Bryan Foster, Co-chairperson

____
Helen Alexander

____
Maria Orive

____
Stephen Egbert

Date defended: ____________

UMI Number: 3214820

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

The Dissertation Committee for Lisa Marie Castle certifies
that this is the approved version of the following dissertation:

THE PRAIRIE TURNIP PARADOX: CONTRIBUTIONS OF POPULATION DYNAMICS, ETHNOBOTANY, AND COMMUNITY ECOLOGY TO UNDERSTANDING *PEDIOMELUM ESCULENTUM* ROOT HARVEST ON THE GREAT PLAINS

Committee:

____
Kelly Kindscher, Co-chairperson

____
Bryan Foster, Co-chairperson

____
Helen Alexander

____
Maria Orive

____
Stephen Egbert

Date approved ____________

ABSTRACT
Lisa Marie Castle

Pediomelum esculentum (Pursh) Rydberg (Fabaceae), an edible plant native to North American prairies, has a long history of wild harvest. Wild-harvested plants are increasingly of conservation concern, yet demographic data needed to assess the sustainability of harvest are unavailable for most species. Methods used by harvesters and responses to harvest are rarely incorporated into demographic studies. Several of the species' traits, including wide-ranging disperse populations, longevity, and cryptic life stages, make it difficult to accurately monitor population dynamics. However, because the species shares these traits with many wild-harvested species of conservation concern, *P. esculentum* makes a good test case for combining ethnobotanical information with ecological models.

Populations monitored in the absence of harvest are largely stable, with considerable variation in projected growth rates. Challenging life history traits, including the possibility of an entire season spent dormant, and small numbers of hard-to-find individuals in some life stages, add to uncertainty about the accuracy of population projections. Despite this uncertainty, matrix models provide more information about wild-harvested plants that could be of use to conservation practitioners than simpler census techniques could.

Harvest increases adult plant mortality, but *P. esculentum* harvesters paradoxically report that harvest helps populations. Experimental mimicry of traditional harvest led to a pronounced increase in seedling recruitment. Incorporating the observed increase in recruitment into models of harvest led to a nearly three-fold increase in the sustainable yield of roots harvested from the generalized population. This mode of compensation, in which the act of harvest, rather than the removal of competitors, leads to increased recruitment is newly named (harvest induced compensatory recruitment), but likely applies to many other species.

The disturbances caused by harvest of *P. esculentum* and *Echinacea angustifolia* roots lead to changes in prairie plant composition. Forb species diversity increases in harvested plots and grass cover dominance decreases. These subtle changes in plant community composition persist for over a year, even following a homogenizing mowing disturbance. This suggests that as traditional harvesters dug millions of roots from across the prairie, they were creating conditions that favored the category of plant they were harvesting.

ACKNOWLEDGEMENTS

Two people led me into the fascinating realm of prairie turnips, Crow Elder Alma Hogan Snell and my advisor, Kelly Kindscher. Alma Hogan Snell talks about, eats, and talks about eating, prairie turnips with infectious enthusiasm. By inviting me into their home on the Crow Indian Reservation in Montana, Alma and her family graciously welcomed me into a world I found wondrous. My introduction to the Snell family would not have been possible without the forethought of Kelly Kindscher, who has been an exemplary advisor and mentor throughout this fun and sometimes grueling process. The tedium and frustration of graduate life were considerably lessened by constant opportunities to learn about plants, food, Kansas history and so much more.

Committee members Bryan Foster, Helen Alexander, Maria Orive, Barbara Shortridge and Stephen Egbert all offered much needed advice and assistance through this process. They also provided good role models of what it means to be a teacher-scientist. They have been giving with time and expertise, as have so many of the faculty members in the departments of Ecology and Evolutionary Biology and Geography at the University of Kansas and researchers at the Kansas Biological Survey.

Many people with true first-hand knowledge of prairie turnips shared their knowledge. The Snell, WoodenKnife and LoneWolf families took the time to ensure that I learned as they taught me their knowledge. I thank all of the root diggers,

grandchildren of root diggers, Indian art buyers, and gift shop owners who shared information.

This project would not have been possible without financial support in the form of a Lila and Madison Self Graduate Fellowship. Travel assistance from the Department of Ecology and Evolutionary Biology, College of Arts and Sciences and United Plant Savers allowed me to share ideas and results with a much broader audience at national and international meetings.

Tim Dickson, Debbie Baker, Maggie Riggs and Irene Karel Khavin all helped immensely as note-takers and diggers in the field. Jennifer Moody-Weis saved me from hypothermia in 2003 and heat exhuastion in 2004 accompanying me to the field in Nebraska. Erin Questad dug half of the harvest-mimicking disturbances, far beyond the call of duty. Members of the Kindscher Lab Group, the Foster Lab Group, the Alexander Lab Group and the Gorgeous Biologist Knitters counted seeds, read drafts, sewed mesh bags, discussed statistics, forgave me for droning on about my study organism and provided much needed emotional support.

Throughout my life, I have been fortunate to be surrounded by creative discussers of ideas who are supportive of the arts and sciences and my attempts at both. The influences of great teachers Janis Smith, Patti Kincaid, Mike DiSalle, Mr. Brookhart, Jane Bock, Darna Dufour is present in all of my endeavors, as are the good wishes and high hopes of an amazing cast of friends. Perhaps this endeavor will get me one step closer to my mother's dream of me becoming a great novelist so that I can support my plant science habit, and my father's dream of me finding a great paying job so that I can support all of our travel habits. I doubt it will, but I am confidence and appreciative of their constant love and support regardless. My brother John Castle and housemates Elizabeth Wagner and Anna Clarke have provided me with great friendship, ideas, and practice living with a truly brilliant person in preparation for marriage to Jeff Walker. Jeff is to be thanked for the simulations in Java, photos of braided prairie turnips, and meeting me in the midst of this process and deciding he wanted to marry me anyway.

INTRODUCTION

Why study an edible prairie plant?

This project concerns human harvest of prairie turnips, *Pediomelum esculentum* (Pursh) Rydberg. The subject matter falls outside of what I perceive to be currently in vogue in plant science. As I see it, population studies tend to focus on short-lived organisms rather than long-lived organisms. Ethnobotanical studies tend to focus on medicines rather than foods, and tropical, rather than temperate, environments. Community ecologists tend to view humans as entities that may disturb or destruct the study system but remain outside of it.

These prevailing trends in subject matter are completely rational. Studying long lived plants for a long time is incompatible with publishing and funding demands and studying long-lived plants for a short time leads to making conclusions from incomplete data. Conservation biology is a crisis field and the organisms with the smallest numbers are usually the most imperiled. Acres of habitat are being lost in the tropics at incredible rates, as are languages, cultures, and pieces of plant knowledge. Humans in North America have already learned how to raise food, but we have not learned to cure many diseases. Anthropogenic disturbance can, and has, led to rapid loss of ecosystem function.

There are, however, drawbacks to following the prevailing fashion. Short-lived plants may be easier to study, but more plants are long lived. If we concern ourselves only with the organisms that are the most critically imperiled, conservation biology will consistently remain crisis management and humanity will never have the opportunity to make decisions that could prevent “do or die” situations. Acres of habitat have already been permanently altered in temperate grasslands, and the languages, cultures and pieces of plant knowledge are diminishing rapidly. Humans may know how to grow food, but sub-optimal nutritional status, whether from too little, too much or simply the wrong food plagues most of the species. Humans may act differently than other animals, but they are not exogenous to their systems and their actions can be considered part of the ecosystem processes.

I chose to study a long-lived edible plant species, which grows in moderate sized populations in temperate areas and to consider human harvest of the roots of this plant comparable to other animal disturbance. I did this not to dispute the logic of the prominent trends, but rather to help fill gaps of knowledge between the studies of more popular organisms. I also happen to be fascinated by the plants, landscapes and history of the prairies, and I like to eat. Pursuing the subject matter has allowed me to feed these fascinations, and the results of this intellectual pursuit fill the next four chapters.

All four chapters of this dissertation investigate the same process: human harvest of *Pediomelum esculentum*, the prairie turnip. In each chapter I look at this process from a different angle. In chapter one, the emphasis is on the importance of this process to the humans digging the roots, historically, currently and into the future. In chapter two the focus switches to the state of the plant populations in the absence of harvest. This provides information allowing me to simulate the effects of harvest on populations, the focus of chapter three. Finally, in chapter four I investigate the effects this process has not on the two organisms involved, but rather on the surrounding plant community.

Chapter one serves as an extended introduction to the species and the importance of *Pediomelum esculentum* root harvest to people of the prairies. The chapter highlights common and unusual uses of the plant root, considering it both an important food and a cultural indicator. It also addresses the adaptations that make the prairie turnip particularly well suited to life on the prairies and poorly suited to cultivation.

While the entire work addresses questions that can be applied to other organisms, chapter two is designed specifically as a case study to aid others conserving wild-harvested plants. Like many other wild-harvested plants, *Pediomelum esculentum* has poorly studied population dynamics. Matrix population models are among the best mathematical tools available for investigating population dynamics, but can require a great deal of data to be meaningful. Like many other wild harvest plants, *Pediomelum esculentum* individuals are long-lived, reproduce irregularly and can persist in a dormant stage, making the data necessary for a matrix population model difficult to acquire. In chapter two, I report just how much valuable information can be gleaned by creating a matrix population model for a plant with a challenging life-cycle using only four years of data. In doing so, I determine the baseline population status of *Pediomelum esculentum* in the absence of harvest at three sites for the years 2001-2004 and the vital rates with the most effect on projected population growth rates.

In chapter three, The Prairie Turnip Paradox, I add harvest to the models of *Pediomelum esculentum* population growth created in chapter two. Simulations compare the effects of different harvest regimes and include the positive effects of harvest on seedling recruitment that were observed in a manipulated harvest-mimicking experiment. These positive effects, dubbed "harvest induced compensatory recruitment" represent a newly labeled form of partial compensation for harvest and can mathematically more than double the sustainable yield of *Pediomelum esculentum* roots. In chapter three, I discuss how this mode of compensation differs from more commonly reported sustainable harvest practices and speculate on other species for which it may be relevant.

Harvest holes on the prairie, chapter four, considers the effects of root harvest on the surrounding vegetation. Soil disturbances are well known for leading to changes in plant community composition. In this chapter I consider root digging to be an example of soil disturbance and report on changes in plant community composition as a result of experimentally mimicking root harvest in a tallgrass prairie haymeadow. Ethnographic evidence suggests that root harvest has been a widespread activity. By digging roots, harvesters may be subtly altering their environment.

Each chapter is intended not only to contribute to a more holistic view of *Pediomelum esculentum* harvest by approaching it from different angles, but also to provide insights towards answering fundamental biological questions. These studies add small pieces towards collectively solving the great ecological puzzle, “Why are organisms where they are?” and the great conservation biology connumndrum, “How can humans best manage the landscape to simultaneously conserve and utilize natural resources?”

CHAPTER ONE

Root of change: evolving perceptions of the prairie turnip

The phrase “prairie turnip” probably does not conjure images of a highly valued plant species, nutritious and delicious, sacred to some and prized by many. “Prairie turnip” likely just does not sound like a plant anyone would suggest as a viable alternative to wheat and potatoes or would work for hours to extract from rocky soils when tastier food could be bought. When choosing a symbol to represent the freedom of a proud past on the windswept plains, “prairie turnip” would not follow buffalo near the top of the list.

More likely, “prairie turnip” sounds like it might be survival food, what people eat when they are out of other options. The phrase probably does not conjure any images of an actual plant, but the suggestion that it is a tenacious inconspicuous little plant growing on rocky slopes, easy to miss in a sea of taller grasses, might seem fitting. “Bland”, “woody” and “chalk-like” would not surprise as descriptors of the food.

Tasteless survival food and tasty symbolic food; a plant that goes unnoticed growing two feet away and a plant worth completely rearranging summer plans for; an agricultural hope for the future and a reminder of a long gone past; over the last two hundred years, the prairie turnip, *Pediomelum esculentum*, has been all of these things to different people at different times, and occasionally the same people at different times.

In the course of studying the plant from a population ecology perspective, I was surprised by the diversity of opinion such a physically unassuming plant commands. Intrigued by modern internet sales of a plant once promoted by Captain Meriwether Lewis, I set out to learn all I could about the changing use and perceptions of prairie turnips. I also investigated the links between biology of the plant and human use, learning that the very traits that make the species a survivor on the Great Plains make it a poor choice for agriculture improvement. Here I chronicle changing attitudes towards the prairie turnip. I start with the plant's name, discuss European Americans' early reactions to Native American food use and the hopes to make the plant an agricultural commodity, divert to the biology of the plant in addressing the agricultural failure, consider the plant a current cultural indicator, and analyze proposed future uses as past uses re-named.

Misnamed

Half of the prairie turnip name is correct. Prairie turnips do grow on the prairie. The species range spans almost the entirety of the Great Plains and tallgrass prairie in North America. However, they are certainly not turnips. The prairie turnip, *Pediomelum esculentum* (Pursh) Rydberg, is a perennial legume in the Fabaceae, only very distantly related to the garden turnip, *Brassica rapis*, an annual in the Brassicaceae. *Pediomelum esculentum* plants grow 15-30 cm tall and have five-foliate compound leaves in adulthood. They have hairy stems, purple flowers, legume fruits, and hard lentil-sized seeds. They are similar to garden turnips only in that the roots are rounded and edible, and even those are quite different. It takes a wild prairie turnip root several years to become chicken egg sized with a woody white flesh surrounded by a dark brown bark, far from the juicy white and purple roots garden turnips achieve in a single growing season.

Other common names for the species are equally misleading. The French *pomme de prairie*, used by the voyageurs, makes some sense as the "fruit of the prairie" (except the edible part is a root, not a fruit) but none as the direct translation "prairie apple." *Pomme blanche* translated by William Clark as "white apple" conveys nothing about a woody edible root of a small plant in the bean family. Another French name, *pomme de terre* or "apple of the earth" is poetic in direct translation. However, *pomme de terre* is also French for potato, a new world plant of an entirely different family, so the name leads to confusion with Indian potato, a name applied to at least five unrelated plants (Anderson 1990). The official common name from the USDA, "large Indian breadroot," suggests correctly that the root can be used to make bread, but confuses the plant with several other species of the same common name (including *Zamia integrifolia*, *Pediomelum hypogaeum* and several *Lomatium* species more commonly called biscuit roots), not to mention perpetuating the great geographical misnomer dating back to Columbus (USDA 2006). "Breadroot scurfpea", a politically and botanically correct name, is a little too slow to roll off the tongue to receive wide use.

Even the scientific name of the species has been disputed and is slightly misleading. Frederick Pursh named the plant *Psoralea esculenta*, "edible scabby plant", in 1814 based on a specimen collected by Meriwether Lewis near the banks of the Missouri River. In 1919, botanist Per Axel Rydberg revised the group and re-named the species *Pediomelum esculentum* or "edible apple of the plains." Rydberg's work was largely unaccepted and the plant called *Psoralea* until James W. Grimes revised the subtribe in 1990, bringing Rydberg's *Pediomelum* back to botanical correctness.

Native American names reveal more about the peoples using them than the plant. Similarities among names suggest linguistic connections and movement of ideas across wide spaces. The Northern Siouan languages share one term, *ihí*, *ahí* and *wąhe* in Crow, Hidatsa and Mandan. The Southern Plains languages share another. *Dó·le*, *tó·le* and *dógwe* describe the plant in Kansa, Osage and Ioway (Rankin 2006). That the Crow name, *ihí*, is a noun referring only to the plant, rather than a descriptor of the plant, suggests the importance of the plant in Crow life. That a Dakota name, *tipsinna*, translates to "little wild rice of the prairie" implies both that the tribe moved from areas where wild rice was abundant, and that prairie turnips became a staple part of the diet on a wild-rice-like level (Gilmore 1932).

Shorter than the surrounding grasses, visible above ground for less than three months, and never flashy in flower, prairie turnips are easy to miss. Like their plains environment, prairie turnips are often overshadowed by their more vertical and showy neighbors. As with the Great Plains, once humans took notice of their many attributes, the usefulness of prairie turnips became apparent.

Disgust to Delight

> "The white apple appears to me to be a tasteless insipid food of itself."
>
> "They also eat this root roasted and frequently make hearty meals of it without sustaining any inconvenience or injury therefrom."
>
> "I have no doubt but our epicures would admire this root very much, it would serve them in their ragouts and gravies in stead of the truffles morella."
>
> Meriwether Lewis, 1805
> (in Thwaites 1904)

Meriwether Lewis's vacillating attitudes about prairie turnips mirrors the attitudes of European Americans towards much of life on the western frontier, and even the vast treeless areas of the prairie bioregion itself. Fear and disdain mingled with a grudging acceptance of usefulness and then an optimistic view of unbounded promise. Just as ideas of the plains changed from Long's "Great American Desert" to an area well adapted for the "purposes of pasturage," but not "well-suited to agriculture" (Hayden 1859 p. 726), to the "Breadbasket of the World", prairie turnips morphed from inedible to palatable to the next replacement for both bread and potatoes.

Many of the earliest recorded encounters of European and European American with prairie turnips were negative. Besides the prevailing attitude that whatever the Indians did must be savage and unclean, "It may be truly said of some tribes that they reject nothing which their teeth can chew and their stomachs digest, however tasteless, unclean and repulsive," (Havard 1895 p. 98), the turnips themselves were not well-liked. Separate from Lewis, William Clark commented that "it is a large insipid root and very tasteless," (Thwaites 1904, V p. 328). When Captain Palliser first encountered the root at the Red River, he, too, found it "insipid" and added, "unnutricious trash" (Brown 1954). Early reports emphasized that roots' texture, as they "resemble pieces of chalk", a "tough stringy taproot" surrounded by a "thick leathery envelope" (Prescott 1849 p. 22 , Gilmore 1919, Fletcher and La Flesche 1911 p. 431). Several early reports allowed that it was "palatable" (Wedel 1978) and Maximillian went so far as to say that a dish made with prairie turnips "did not taste amiss" (1843 p. 266).

It was not long, however, before recognition spread among the incoming European Americans that, even if the root did not taste great, everybody living on the plains was eating them. Eyewitness and ethnographer accounts mention fresh *Pediomelum esculentum* roots being eaten by members of tribes as far south as the Comanche and Osage, as far north as the Blackfoot and Cree, as far east as the Missouri river and as far west as the Rocky Mountains (Reid 1977). The prairie turnip took on particular significance because it did not need to be eaten fresh. The roots, once peeled, dry very well. Once dry they can be ground into flour as was common among the Arapaho and Assiniboine (Abel 1939, Long 1961), chipped and stored in special pouches, as common among the Cree and Omaha (Fletcher and La Flesche 1911, Mandelbaum 1940) or braided into transportable lengths using their long tap roots, as was common among the Dakota (Gilmore 1926). The ability to store well meant that the roots could be traded. The Cheyenne and Dakota traded great quantities of prairie turnips with the Arikara in exchange for corn (Jablow 1951, Wedel 1978). Complex trading networks brought roots from the Great Plains to the Pacific through the Columbia Valley (Stern 1993) and to supply the fur traders in modern Manitoba and Saskatchewan (Ray 1998). Once they decided prairie turnips were palatable, white hunters and adventures traded for them as well (Bradbury in Thwaites, 1904). Everyone on the plains had heard a story of someone, white or Indian, surviving off the roots alone (Reid 1977). European Americans finally became convinced that prairie turnips were "nourishing." Like so many other things, they just needed a little American ingenuity added and they might be great. Major Long commented in 1823, "had it been seasoned with salt or sugar it would have been considered delicious," (in Parker 1950).

Following acceptance came big dreams. If a prairie turnip root were palatable roasted or boiled, would it not be extraordinary in ragouts or gravies? Early chemical analysis found prairie turnips to have unusually high levels of nitrogen (protein) for a plant root (conducted by Clifford Richardson and reported by Maisch 1899). High in protein and tough in the face of cold and drought, prairie turnips could certainly be cultivated to benefit mankind. "No serious and prolonged attempt has yet been made to develop this tuber by cultivation and selection; such an attempt is certainly desirable and, if successful, would give us a toothsome, wholesome and nutritious vegetable, remarkable for its large proportion of starch and nitrogen, and peculiarly adapted to our arid regions," (Havard 1895 p. 108). "Mr. Lamare Picot, a French naturalist, has lately incurred considerable expense to obtain the seed, which he has carried to France, believing that it is capable of cultivation, and may form a substitute both for potato and wheat," (Prescott 1849 p.22).

As America looked optimistically westward at the end of the nineteenth century, the rain was to follow the plow onto the prairies, and prairie turnips were to be the food to feed the world.

Agricultural Failure

The rain did not follow the plow. Supermarkets shelves stock much wheat and potatoes and no prairie turnips.

Early attempts at cultivation failed, "In the beginning of the present century it was brought to Europe. . . It was cultivated for some time in France where it became known as picquotiane; but the results were not encouraging, and at present it is rarely met with in Europe." (Maisch 1889 p. 346). Lack of positive reports and lack of prairie turnips under current cultivation suggest all later cultivation attempts failed as well.

When it takes at least three years to grow a single edible-sized root, and harvest kills the plant, the space and time required for a cultivated crop become unworkable. The very adaptations that make prairie turnip plants survivors on the plains make them unusable as crop plants.

Resilience and Adaptation

Humans hoped to cultivate prairie turnips because the plants persist in what European American settlers saw as a harsh, uncompromising environment. Inhabitants of the plains must deal with irregular rain and snowfall, great winds, occasional hail, frequent drought, and intense radiation. *Pediomelum esculentum* exhibits specialized ways of storing energy through periods of uncertainty, facing the weather, dealing with wildlife and moving around. As they recognized that human systems needed to be modified in order to succeed in the treeless landscape, settlers began to appreciate the organisms already well adapted to survive the vagaries of the weather (Webb 1931, Kraenzel 1955).

The most obvious adaptation prairie turnips exhibit is a swollen root and accompanying perennial lifestyle. A *P. esculentum* individual can survive dry times and disasters simply by retreating underground. Plants avoid dealing with the intense solar radiation and high evapotranspiration rates of late summer by staying out of the sun entirely. Persisting underground as a swollen root, they cannot take advantage of the light for photosynthesis, but they can avoid its damaging effects. While all individuals retreat underground annually, usually from July to April, some do not emerge at all in a given year. In her seven year study of prairie turnips in Iowa, Hermann (1982) found that adult plants could remain dormant for at least two years and re-emerge looking like healthy individuals. In my four year study of *P. esculentum* populations in three states, I found that, on average, five percent of the population goes unseen aboveground in any given year.

Deeply rooted perennials such as prairie turnips are largely unaffected by short-term droughts and are the last to succumb to and the first to recover from long-term droughts (Weaver 1954). The root storage system has the advantage of helping the plant endure hard times other than drought. If a prairie turnip is grazed, burned, or smashed by hail, the energy stored in the root gives the plant enough nutrition to grow again.

The root storage system is just one of several of the species' adaptations to help plant populations persist in an uncertain environment. White hairs on the leaves, stems, petioles, and corolla help reduce water-loss when the plants are aboveground. The hairs reflect sunlight and trap water vapor in the layer immediately surrounding the leaves, thus increasing humidity and reducing transpiration rates. Buried seeds can also remain viable for at least two years and likely much longer, creating a small seed bank. While seed banks are considered more critical to population persistence of species in which adult survival is more highly variable than it is in prairie turnips, all seed banks are seen as ways for populations to persist in variable environments (Kalisz and McPeek 1993, Doak et al. 2002). In prairie turnips, I observed low seedling recruitment rates among the monitored populations and in experimentally undisturbed areas, but high rates in experimentally disturbed areas. Seeds and seedlings must therefore respond to a specific set of conditions. This suggests that prairie turnips can survive poor conditions by persisting as adults underground and wait to take advantage of good conditions by persisting as a seed.

Prairie turnip populations appear to have yet another “waiting” life stage, a seedling bank. Rather than persisting as seeds until conditions are right growth (as in a seed bank) individual plants in a seedling bank persist as small understory plants until conditions are right for growth to adult size (Marks and Gardescu 1998). Seedling banks serve to reduce the population consequences of seed predation (Breckage and Clark 2005). Herbivory is almost a certainty on the plains. In a land of grazers and insects, a plant is going to be eaten at some point. The stored energy in the swollen root is a way for prairie turnips to survive despite above-ground herbivores. A long life span diminishes the population consequences of outbreaks of specialist fruit predators (Hermann 1983) and a seedling bank could diminish the effects of seed predation.

Legume seeds can often survive drought, cold, and heat. They cannot survive being eaten. As packages rich with protein, seeds are particularly vulnerable to predation (Andersen 1989, Maron and Simms 1997). A plant that has grown into a seedling is less appealing to many herbivores. Remaining a seedling rather than a seed, even when resources are not available to grow to adulthood, may be advantageous to the plant. Lingering as a small plant waiting for a light gap is common in forests but has not been well documented in prairies (Payette et al. 1982, Antos et al. 2005).

During my four years of prairie turnip population observation, many very small plants did not grow at all. Identified as probable new seedlings at first observation, they looked exactly the same at second and subsequent observations. Not only did these plants not gain height or spread from year to year, they also maintained small three-foliate leaves, a morphology specific to newly emerged seedlings and very small plants. Spending at least four years as an apparent seedling is not necessitated by prairie turnip growth rates. Where I planted seeds in unimproved prairie soils and removed competitors, plants quickly grew out of the seedling stage. In the second growing season 25% of the cultivated population exhibited at least some five-foliate or adult leaves. By the third growing season, one plant had flowered, although earliest recorded first reproduction among wild plants is five years (Hermann 1983). Prairie turnips, therefore, are not intrinsically confined to years in the seedling stage. They likely remain in this stage when competition prevents them from growing up, much like the fir trees in the British Columbian forest, which can be one hundred years old and still under three feet tall (Antos et al. 2000).

Like many other plants of the grasslands, prairie turnips take advantage of the persistent winds of the Great Plains. Unlike the grasses, which utilize the wind for pollen dispersal, and many milkweeds and asters which have special structures to loft seeds onto the wind, prairie turnips do not have lightweight parts to disperse through the air. The species rather relies on strong winds to pick up the entire plant and disperse the heavy seeds as the plant tumbles across the prairie.

"Amenogeochory" or tumbleweed dispersal (van der Pijl 1972) is an uncommon method of seed dispersal everywhere but it is most common in places with strong winds and few trees. Investigations into stem abscission in *Psoralea agropyhlla* (now *Pediomelum argophyllum*, a con-generic prairie species shaped similarly to *Pediomelum esculentum*) show the plants changing chemically at the stem-root interface and creating a protective layer, similar to leaf-fall in angiosperm trees (Becker 1968). Once the abscission layer is formed, the plant is free to tumble on the wind.

Very little is still known about the fate of plants and seeds after dehiscence and abscission. It is unlikely that prairie turnips travel as far as the more common and aerodynamic Russian thistle tumbleweed (*Salsola iberica*), which has been documented to move over four km in six weeks. Certainly a single prairie turnip cannot disperse 30,000 seeds in its path, as a Russian thistle can (Stallings et al. 1995). More likely the prairie turnip movements are of the order of those of *Baptisia lanceolata* and *Baptisia lecontei*, two other tumbleweed members of the Fabaceae found in Florida. Observed plants of these species moved an average of 21m and 15m, respectively, with a maximum distance of 119m over a five-month period (Mehlman 1993). I was only able to observe previous year's plant remains at one of our three wild populations (the other two were hayed annually). At the Montana site, every year I found several old plants caught in the bushes one to two meters from the spot where a plant of those dimensions had grown the year before. While the observed plants remained close by, the presumption is that the plants I did not see moved farther. The average distance, however, may not be the critical factor from the species perspective. As with many species, unusual long distance dispersal mechanisms may be critical for defining the range and maintaining dispersed populations: the extremes do count (van der Pijl 1972). While most plants may end up trapped in a tall grass or yucca a few meters from where they started, it does not take many tumbling in a tornado to extend the range of the species. It has become a biological truisms that, given time, uncommon events are not all that rare. This is especially true if that uncommon event is a wind storm on the plains.

What do all of these adaptations have to do with agricultural failure? In a sense, they were the reason for the agriculture hopes. Prairie turnips clearly had the adaptations to survive in the harsh environment of the plains. If they could survive there, they surely could survive almost anywhere, the prevailing logic suggested. A plant that grew slowly into an edible food in a land of intermittent rain could surely bloom quickly into an edible food given regular rain and European care. These adaptations were also indirectly responsible for the plant's failure as an agricultural commodity, for they do not come without cost.

The very short growing season and the long dormant period force the plants to pre-form flower buds almost a full year before blooming. Because of this, even if growing conditions are ideal in the spring, a plant cannot take advantage of the situation and increase its reproductive output (Hermann 1983). Limited time above ground to photosynthesize and a large allocation of the limited sugars produced to root storage leads to plants that can be incredibly slow growing. In a recent phytoremediation experiment, praririe turnips had the lowest relative growth rates among 39 prairie species tested (Robson et al. 2003). Researchers, therefore, labeled the species as “S” or “stress tolerant” based on Grime’s (1979) CSR triangle (competitive, stress tolerant or ruderal) (Robson et al. 2003). Tolerating stress comes at the cost of poor ability to compete and take advantage of resources when times are not tough.

In my studies, planted prairie turnips in a plot that had been weeded grew much more quickly than many small individuals in the wild, but still did not grow quickly. At the end of the fourth growing season, the largest of twenty roots extracted was less than 4cm in diameter and only two plants had flowered. Like the European cultivators 150 years before me, I found that four years was a long time to wait for a single pot of stew.

A Present of Revisited Glories of the Past

Armed with many adaptations to make them well-suited to life on the plains, prairie turnips persist. So does their use. Nobody survives off the little legumes anymore; too many other foods are much more easily available. In a 1996 study of 142 randomly sampled women on the Blackfeet Reservation in Montana, wild foods were listed as the primary source of food in childhood of only one elder. None of the women of any age group listed wild foods as the primary source of food in 1995-1996 (Johnston 2001). When people do use turnips, it is more for their symbolic value than for their food value.

Prairie turnips now connect people to a past and a land that was. In 1954, Annora Brown labeled prairie turnips as the "only vegetable the present Indians of one western reserve could remember when asked about the food of their grandparents," (p. 60). Fifty years later, the majority of young people on the Lake Traverse Reservation in South Dakota could correctly identify a prairie turnip plant, despite generally knowing less than 30% of the plants their elders considered culturally important (Meyer et al. 2005).

In the 1930s, Crow Indian woman Alma Hogan (now Snell) dug roots with her grandmother Pretty Shield to ensure for the winter. Pretty Shield was raising eight grandchildren on a small government pension and whatever they could scrounge. Dried roots provided security. In the 2000s Alma Snell takes her children out digging roots so that she can serve them to young people and they can have a "taste of heritage".

Using food as a cultural marker is a common phenomenon. Foods are relatively inexpensive, temporary, and do not need to displayed publicly (Shortridge and Shortridge 1998). On the Rosebud Reservation in South Dakota in 2003, teenagers I asked about prairie turnips did not dig roots themselves, but became excited as they mentioned eating them at celebratory feasts. Foods can also be a way to experiment with ethnic identity (Tuchman and Levine 1993). Wooden Knife Indian Fry Bread Mix, available at the source at the Wooden Knife Indian Taco Stand in Interior, South Dakota, at tourist gift shops throughout the Northern Plains and on the internet from woodenknife.com, lists timpsula (prairie turnips) as the special ingredient. Last in the list of ingredients, after the baking soda, the small quantity of ground roots is unlikely to greatly influence the taste, but the added timpsula does make the product “an original Sioux recipe”. It is therefore ethnic, exotic, and worth paying over three dollars a pound for biscuit mix.

Prairie turnips connect people to a more glorious past. The root represents wide-open spaces, self-reliance and autonomy. To Pretty Shield, a Crow midwife in the late 1800’s, digging roots represented freedom, the time before the reservation when she still had a soul (Linderman 1972). To her granddaughter Alma Snell, turnip roots in a dream were a clear sign that she must teach young people about the past of the Plains Indian (Snell 2000). The braids of prairie turnips seasonally for sale at Sioux Trading Post in Rapid City, South Dakota are edible, yet Micheal Leckberg, buyer for the store, reports that none of the braids he sells out of each year is intended for food. They end up decorating kitchens and adorning doorframes and representing Native Americans as “Indian Art” (pers. com. 2003).

The attribution of current symbolic importance to prairie turnips spurs debate of past practical importance. The view of how important prairie turnips once were vacillates along with attitudes about them. Plant foods were considered almost as condiments to break the monotony of a meat-based diet in early reports of Lewis and Clark (McIntosh 2003). To the Blackfoot people, meat was *nutapi waksin*, ‘real food’ and everything else edible was *kistapi waksin*, ‘nothing food’ (Johnston 1970 p. 301). Nineteenth century reports may have listed *Pediomelum esculentum* as a “vegetable staple food” (Maisch 1889 p. 347) but writers devoted volumes to buffalo and sentences to prairie turnips. Much later, serious academics claimed that upland prairies had no vegetation of potential significance to plant-food collectors (Zawacki and Haufster 1969). Re-assessments since have led to a much higher value placed on the importance of plant foods in general and prairie turnips in particular. Historian Richmond Clow concluded that the prairie turnip preserved the Brule and Yankton tribes from death in the spring of 1832, and the late spring turnip harvest ended the starving winter of 1833. He suggests that, through the tribes' histories, the root frequently sustained them through famines (1995). The Piikáni (Piegan) people of southern Alberta no longer dig *Pediomelum esculentum* roots, but, based on the prairie turnip's past importance, chose to include it as sacred in their revitalized sun dance (Peacock 1992). The Sept. 2003 Newsletter of the Native Plant Society of Tyler, Texas informs members to think of eating the food of the now extinct plains grizzly when they eat *Pediomelum esculentum* roots and "eat wild from our historic prairie land," although the plant does not grow in the region (Fleming 2003). Now, even the fry bread box proclaims, "The prairie turnip was probably the most important wild food gathered by Indians who lived on the prairies," and declares, "Prairie turnips were so important, they influenced selection of hunting grounds." (Wooden Knife 2006).

It is impossible to quantify how much of an exaggeration modern suggestions of the past importance of prairie turnips might be. Clearly considering the plants to be indicators of a free and wild past and drivers of whole tribes' location decisions glorifies the roots beyond the level of condiment. However, growing quantities of evidence suggest these ideas may be correct. Just as modern ecological studies indicate the prairies of the past were much more diverse and complex ecosystems than a settler staring at the apparent monotony of the Great American Desert could ever imagine, prairie turnips may have had a greater influence on tribal life than an explorer or early anthropologist could have noticed.

One explanation for this disparity may be gender bias. All accounts suggest that digging roots was a task for women and children (Maximilian 1906, McClintock 1910, Klein 1977). Native American men on the plains hunted and conducted warfare. These loud, grand activities made for good stories to the European American males recording their behavior, and made it easy for the ethnographers to overlook the contributions of women (Klein 1977). However, cross-cultural nutritional studies suggest that even in effective hunting societies, hunted foods only provide 20 to 45 percent of the total calories (Reid 1977). Perhaps if women's work were included, diets of plains Indians would be more in keeping with these figures. The role of the bison in plains life would remain paramount, but the importance of plant foods, particularly *Pediomelum esculentum* would also become obvious (Reid 1977, Wedel 1978, Reichart 1983).

Evidence that the historical importance currently attributed to the species is not all idealization of a more romantic past comes from the long and continued importance of digging sticks. In the 1850's among the Cree, Henry Youle Hind reported that not only did each woman have her own digging stick made out of chokecherry or saskatoon wood specially whittled, but also that each woman "carried it with her constantly during the summer" (in Mandelbaum 1940 p. 202-203). In the ghost-lodge of a Teton Indian, a small altar was created by hanging clothing and food on turnip digging sticks (Dorsey 1889). George Catlin's portrait of Chin-cha-pin, an Assiniboine woman, included her digging stick, which the artist noted, "every woman in this country is suppplied," (1866 p. 56). Crow woman Pretty Shield told stories of chasing wayward bison with her digging stick as if the listeners all knew the implement (Linderman 1972). Pretty Shield's granddaughter tells that Pretty Shield enthusiastically traded for an iron digging stick when they became available, and it became one of her prized possessions (Snell 2004, pers. com). While elk antlers and cherry, bark, ash and amelanchier wood could all be used as effective digging sticks, native women on the plains took quickly to iron (Wedel 1978). By 1889, Dr. Harvard at Fort Lincoln in Dakota was reporting that while the women formerly used "a strong pointed stick to pry the tuber out, now they use a small iron bar, one end of which has been beaten into a narrow blade, (Maisch 1889 p. 347).

Through the changes in materials, digging sticks have remained significant. John Neidhart retold a Lakota legend of a woman digging prairie turnips so vigorously that she fell through the earth and into the prairie sky (1952). Modern Blackfoot sun dance rituals include a holy woman with a digging stick prominent in her sacred bundle (Cowen 1991). Reporting about his 1980s wandering on the plains, Ian Frazier comments "Indians loved crowbars. They used them for digging prairie turnips, bitterroot, tobacco root, and holes for tipi poles." (1989 p. 48). The Baldwin Project, dedicated to "Bringing Yesterday's Classics to Today's Children" by publishing children's literature on the internet, includes "Morning Star", a myth attributed to the Blackfoot. In the story, the digging stick is a gift from the Moon for human benefit, but using it disobediently to dig the Great Turnip leads to banishment from Sky Land and unhappiness for all (Olcott 1917). If prairie turnips were not of great importance, the tool used to dig them would probably not have been described as a loved gift from the Moon and included in paintings, burials, and holy dances.

Novel Future Uses or at Least New Names

While they are celebrating the glorious past prairie turnips have come to represent, many humans are envisioning ways to expand prairie turnip use in the future. Many of these suggestions are not new. Ethnobotanist Nancy Turner writing of prairie turnips as a "gift for the taking" in 1981 was advocating a better appreciation and utilization of the existing resource. Conservationist John Heale similarly wonders if traditional sustainable harvest could bring extra income to his impoverished rural community (pers. com. 2005). One hundred fifty years after early attempts, the idea of prairie turnips as a major food resource has not been entirely abandoned. British non-profit organization Plants for the Future, lists the species as an "Alternative Root Crop" with high potential, even for cultivation in England (Pfaf 2003).

Other ideas only sound new because of new terms being applied to them. Crow healer Alma Hogan Snell recommends prairie turnip gruel to treat irritable bowel syndrome (Snell 2006). At Fort Lincoln in Dakota, Dr. Havard wrote in the

1880s that the plant was used for children while teething and “they are treated in the same manner, with likewise good result, when suffering from bowel complaints,” (Maisch 1889 p. 348). Trading in braided roots is nothing new, but they can reach a new audience as “Native American Art” through expanded distribution on the internet (Table 1.1). Epidemic levels of type II diabetes among the Native American population has led to extensive studies using elements of traditional lifestyles to combat insulin resistance (Gittelsohn et al. 1995, HIS 2004, Hernandez 2005). Using prairie turnips specifically to help combat diabetes may be new, but that the roots might be part of a healthy diet is unsurprising. In the first known chemical analysis of the food, Clifford Richardson in the 1880s found the roots to contain an unknown sugar (Maisch 1889, p. 349). In 1938 Yanovsky and Kingsbury reported unusually high levels of non-reducing sugars and hemi-cellulose in the plant (Wedel 1978). Later analysis found it high in fiber and lysine (Kaldy et al. 1980). Given a complex carbohydrate structure and high levels of fiber, prairie turnips could be a useful addition to anti-diabetes diets. Certainly prairie turnips were part of the diet in the mid-nineteenth century, when Native American men on the Great Plains were taller, and likely had better nutrition, than any other documented population in the world (Prince and Steckel 2003).

Two other uses for prairie turnips truly are new. Ecological field crews in Kansas are using the species as one indicator of high quality prairie. Long known to decrease under grazing pressure (Weaver and Albertson 1956), prairie turnips have been found in enough high quality prairie, and only high quality prairies, to be considered a useful indicator of diverse unplowed grasslands that have not been overgrazed (Jog et al. 2006, K. Kindscher pers. com.). Canadian researchers suggest that prairie turnips show great promise in phytoremediation of hydrocarbon-contaminated soils. It seems that the plants grow so slowly that increasing levels of oil in the soil have very little affect on growth rates (Robson et al. 2003).

While serving as a indicator of grassland quality and remediating oil spills are new uses of prairie turnips, they take advantage of well established traits. Prairie turnips grow very slowly on prairies. What makes the plant a poor choice for agriculture may make it a good choice for toxic clean up.

The varieties of opinion through time are largely a matter of perspective. The fiber that make it the roots "tasteless" make the plant dry well, which makes it a commonly used emergency food and an exceptionally healthful addition to a diet low in fiber. When some saw collecting wild foods as a symbol of degradation, others saw it as noble tradition (Johnston 2001, Snell 2006). The tumbleweed lifestyle that make the plant so hard to find leads to the large root that makes it worth finding. Aspects of prairie turnips make the species worthy of all the praise and derision that have been heaped upon it over time. I, for one, have found boiled *Pediomelum* roots to taste like dirty boiled wood when cooked by fellow scientists on a ranch. When served prairie turnip pancakes with wild chokecherry jam by Crow Indian Elder Alma Hogan Snell, however, I tasted the beaniness and the subtle sweetness of the roots, and felt I was sampling the rich cultural heritage she was offering. The small plant warrants its great image.

	Year	Price	Length of Braid
Retail			
Western Trading Post[a]	1975	$15	47 inches
Museum Gift Shop South Dakota	2002	$35	three feet (93 roots)
Herbal Products Shop South Dakota	2003	$30	three feet
Native American Art Gallery North Dakota	2003	$150	seven feet (141 roots)
Internet, from Native American Gift Store, South Dakota	2006	$60	three feet
Directly from Artisan			
Arikara- Dakota Trade[b]	1890	1 burden basket of shelled corn	4 three foot braids and 1 burdern basket of prairie turnip chips
Rosebud Reservation, South Dakota	1985	$5	three feet
Rosebud Reservation South Dakota	2003	$15	three feet (58 roots)

Table 1.1 Prairie turnip braid prices

[a] from Wedel 1978

[b] from Gilmore 1926

CHAPTER TWO

The role of matrix population models in conservation of wild-harvested plants: a case study of *Pediomelum esculentum*, a long-lived prairie perennial

Analysis of matrix population models has been advocated for use in conservation biology because matrix models and their components can be used to determine population status (growing, stable or declining) and identify life history stages that have the greatest effect on population growth (Schemske et al. 1994). Asymptotic analysis allows for comparisons of current conditions by quantifying what would happen if those conditions were to persist (Caswell 2001). Retrospective examination of variances can elucidate the rates causing populations to behave differently through time or space (Horvitz et al. 1997, Caswell 2001). Prospective perturbation analysis allows for qualitative comparisons of what could happen under different environmental and management scenarios (Reed et al. 2002) and suggest critical life stages for targeted conservation efforts (Crouse et al. 1987, Dixon et al. 1996, Caswell 2000).

Use of matrix population models in conservation applications is not without detractors. Despite, or because of, a great increase in the use of matrix models and resultant population viability analysis, charges of model misuse have escalated in recent years. Applications of matrix populations and their components in conservation biology have been criticized for violating the mathematical assumptions underlying the models (Mills et al. 1999), not including genetic information, metapopulation data or environmental correlations that may be of critical importance for population persistence (Reed et al. 2002, Doak et al. 2002), poorly quantifying uncertainty (Akcakaya and Raphael 1998), and predicting extinction risks contrary to historical observation (Bierzychudek 1999, Lindborg and Ehrlen 2002). Academic skirmishes continue about the superiority of various modeling methods and relative importance of including genetic and spatially explicit data. However, a broad consensus in the conservation and population biology communities agree, that if model assumptions, model limitations and data uncertainties are made explicit and the differences between prediction and projection are understood, matrix population models have a clear place in conservation biology (Menges 2000, Caswell 2001, Reed et al. 2002, Brook et al. 2002, Ellner and Fieberg 2003, Norris 2004).

Results of demographic studies using matrix models could be very helpful in the management and conservation of wild-harvested plant species. In order to best set priorities, conservation managers need to know current population status, life history, and effects of harvest on populations (Brownstein et al. 2003). Knowledge of how fast populations are growing, under which conditions populations grow more quickly, and how sensitive population growth is to vital rate changes would be of great use to policy makers charged with deciding if, where, when, and how, collection of wild plants should be regulated. An understanding of vulnerable life stages would assist conservationists in choosing between planting regimes or among protection, cultivation and augmentation strategies. Matrix population model analysis could provide valuable information towards addressing all of these questions.

Despite their considerable potential, full matrix population models have rarely been applied towards the conservation of wild-harvested plants in North America. Although studies using demographic models comprised less than half of the ecological rare plant studies in the early 1990s (Schmemske et al. 1994), and there have always been far fewer such studies of plants than animals, numbers of demographic studies involving rare plants skyrocketed in the late 1990s (Menges 2000). Such studies involving wild-harvested plants have not kept pace. The United Plant Savers, a non-profit organization dedicated to the conservation of wild-harvested medicinal plants in North America north of Mexico, issued a list in 2000 of 20 species “at-risk” for over harvest and an additional 24 species “to-watch” as they, too, are likely vulnerable (Gladstar and Hirsch 2000). Among the 44 listed species, published demographic studies relating to harvest are available for only a scant few (notably American ginseng, *Panax quinquifolius*, goldenseal, *Hydrastis canadensis.* and echinacea, *Echinacea* sp.) (Nantel et al. 1996, Hurlburt 1999, Van der Voot et al. 2003). At the time of the list creation, so few species had solid demographic data available that the organization had to set conservation priorities based on expert committee opinion. Monitoring studies of other wild-harvested species are underway (PCA 2005), but recent efforts to quantify priorities have been stalled by the continued lack of baseline population knowledge for many wild-harvested plant species (UPS 2005).

The paucity of matrix-based population demography studies in wild-harvested plant conservation can be attributed to two primary factors: “challenging” life history traits exhibited by many wild-harvested plants and the great time commitment required to collect the necessary data. Any trait that makes knowing fates of individuals uncertain, or alters rates between time periods can make matrix models challenging to create and interpret, and wild-harvested plants display many of them.

Seed banks, geophyte dormancy, and other cryptic life stages complicate accurately knowing fates of individuals (Lesica and Steele 1994, Menges 2000, Doak et al. 2002, Kery et al. 2005). Clonal growth confuses the definition of an individual and its fate. A long life span can mask trends in population growth and when either birth or death is an uncommon or irregular event, the time needed to capture necessary transitions becomes long (Hutchings 1991, Elzinga et al. 1998, Menges 2000). A classic study of spider orchids (*Ophrys sphegodes*) revealed that a single population could appear to be plummeting, skyrocketing or remaining stable, depending on which four of the ten years were investigated (Hutchings 1991). More recently, the question of population persistence of a rare Sonoran desert cactus remained unsolvable with 11 years of data from 14 permanent plots (Reed et. al 2002). Wild-harvested plants of conservation concern exhibit many of these traits that make population projection difficult. Of the 44 wild-harvested plant taxa listed as “at-risk” or “to-watch” by the United Plant Savers, many exhibit dormancy, many reproduce vegetatively, at least under some harvest regimes, 42 are perennial, and seed bank dynamics are unknown for most (Klein 2000).

Conservationists setting policy for wild-plant harvest, like other conservation practitioners, rarely have eleven years of data upon which to base a decision or time to wait for the data to arrive. Most population viability models for rare plants are constructed based on four years of data, all of which is time consuming and expensive to acquire (Menges 2000). Together, the difficulties in, and cost of, obtaining critical transition data for plants with challenging life histories has led to recommendations of replacing models requiring fates of individuals with less expensive and time intensive counts and surveys for all but the most rare species (Menges and Gordon 1996, Philippi et al. 2001), using alternative modeling methods (Reed et al. 2002, Silvertown et al. 1996), and avoiding demographic approaches in monitoring populations of plants with challenging life histories altogether (Elzinga et al. 1998).

Most wild-harvested plant species are not federally listed for their rarity. Most do exhibit challenging life cycles. The relatively large population sizes suggest that simpler census data would be appropriate for wild-harvested plants (Menges and Gordon 1996) and the challenging life cycles suggest that demographic data for matrix population models would be difficult to acquire and interpret (Elzinga et al. 1998). However, management decisions regarding wild-harvested plants require an understanding of how different plant life-stages react, data impossible to glean from simple census data (Schmeske et al. 1994). The alternatives to matrix models suggested in the literature either fail to address life stages separately or require basic demographic data to build or interpret the models (Brook et al. 2002). For wild-harvested plants, then, most conservation practitioners are left with a situation that calls for long-term monitoring of individuals and a short time to monitor them. I found myself in this situation with regard to the prairie turnip (*Pediomelum* *esculentum*), a wild-harvested, long-lived perennial species with a huge range and inconspicuous individuals that can remain dormant for a full season. Treating *P. esculentum* as a case study for wild-harvested plant species with challenging life cycles I set out to determine how much information could actually be gained from using matrix population models and four years of data.

My goal was twofold. First, I sought to characterize the basic state of non-harvested *Pediomelum esculentum* populations in order to provide a biological basis for management decisions by answering the following questions: (1) Based on current conditions, are the population sizes projected to increase, decrease or remain stable? (2) Is there significant spatial and/or temporal variation in demographic parameters? and (3) Which demographic transitions have the most impact on population growth? Second, I wanted to provide a case study illustrating the benefits and limitations of conducting a demographic study tracking the fates of individuals given a short (four-year) time frame and a challenging life cycle.

Materials and Methods

Taxon Description

Prairie turnip (*Pediomelum esculentum* (Pursh) Rydberg) is a perennial iteroparous herb in the Fabaceae. Plants emerge in the spring, flower in May or June and abscise at the ground level in early to mid-summer. The above ground structures tumble as a tumbleweed and the plants perenniate by means of a swollen taproot storage organ. Adult plants reach a height of 10 to 50cm, and can have from zero to nine inflorescences. Each inflorescence can have up to 45 flowers, each producing a single seed (Grimes 1992). In a garden setting with competitors removed, I observed flowering in the third growing season, while average first reproduction in the wild is reported at greater than five years (Hermann 1983). *P. esculuntem* leaves are palmately compound. Adult plants usually have five-parted leaves, whereas seedlings and very small juvenile plants have three-parted leaves. A flowering plant does not necessarily flower every year. While all individuals are dormant and invisible above-ground from July to April, adult plants can remain dormant belowground for an entire season, never producing any stems or leaves in a year (Hermann 1983).

The species' extensive native range covers the Great Plains and much of the tallgrass prairie, from Texas north to Manitoba and from the Rocky Mountains east to Wisconsin and Missouri. Prairie turnips do not thrive under intensive grazing or following plowing and in Kansas are considered to be a conservative species and one indicator of high quality prairie (Weaver and Albertson 1956, Freeman and Morse 2002).

Site Descriptions

Kansas

The field studies were conducted in Kansas, Montana and Nebraska from 2001 through 2004. The Kansas site was located in unplowed tallgrass prairie at the north side of Richmond Lake in Franklin County at 38.40° N and 95.22° W. This prairie is dominated by big and little bluestem (*Andropogon gerardii* and *Schizacrium* *scoparium*) and is hayed annually in July. Survey fields were flat to gently sloping. Immediately adjacent to a public recreation area and baseball fields, this site in eastern Kansas receives regular disturbance from humans camping and walking and from occasional off-road traffic. Soils at the site are clay loams over clay, moderately deep, slightly acidic, dark brown soils high in organic matter part of the Eram-Lula complex (Dickey 1981). The nearby weather station at Garnett, Kansas received 983mm, 800mm, 825mm and 1160mm of rain during 2001 to 2004, respectively, compared to an average of 1008mm (High Plains Regional Climate Center 2006). According to the US Drought Monitor (NDMC 2006) the study area experienced drought conditions for 8 weeks in 2000, 4 weeks in 2001, 20 weeks in 2002, 15 weeks in 2003 and no weeks in 2004. The *Pediomelum esculentum* population at the Richmond site was not harvested during the study, and showed no signs of previous harvest.

Montana

Plants were monitored on the Crow Indian Reservation near Fort Smith, Montana in Big Horn County at 45.29° N and 107.92° W. Plots were located on moderate slopes sparsely covered by *Pascopyrum smithii* and *Bouteloua gracilis* among *Yucca glauca*, *Juniperus horizontalis*, *Artemesia frigida* and *Rhus trilobata*. Soils at the site are part of the Abac series, ranging from rock outcrop at the top of the slope to loam at the foot, all derived from shale and red sandstone (USDA 1977). This area in south central Montana is poorly accessible to humans, and thus non-harvested. Cattle range freely in the area, but were seldom observed grazing on the steep slope where study plots were located. The weather station at Fort Smith, Montana, received lower than the average of 462mm of rain each of the study years (Western Regional Climate Center 2006). In 2001 236mm fell, in 2002 338mm, in 2003 369mm, and in 2004 344mm. This low rainfall equated to US Drought Monitor declarations of some level of "drought" for 44 weeks in 2001, every week in 2002, 51 weeks in 2003, and every week in 2004 (NDMC 2006).

Nebraska

Field sampling was conducted at Madigan Prairie in Saunders County, Nebraska at 41.17° N and 96.88° W only in 2002, 2003 and 2004. Dominated by big and little bluestem (*Andropogon gerardii* and *Schizacrium scoparium*), this eastern Nebraksa remnant tallgrass prairie is surrounded by agricultural fields and is inaccessible by road. Prairie turnips have not been harvested at the site since it was donated to the University of Nebraska Foundation in 1978, and the field's isolation and poor road access make prior harvest unlikely. Plots were laid out on gentle to moderate east facing slopes. The soil is composed of Burchard and Selby clay loams that are well-drained with a deep root zone (USDA 1985). The closest weather station in Wahoo, Nebraska received 586mm and 637 mm in 2002 and 2003, compared to an average of 801mm (High Plains Regional Climate Center 2006). Seward, Nebraska the closest station with complete data for 2004, received 639 of a normal 687 mm of precipitation that year (High Plains Regional Climate Center 2006). The study area was declared to be experiencing drought conditions 7 weeks in 2001, 27 weeks in 2002, 44 weeks in 2003, and 3 weeks in 2004 (NDMC 2006). The prairie is typically hayed in July, but was not mowed in 2002 due to droughty conditions.

Plot Establishment

In May 2001, 22 3m x 3m ($9m^2$) plots were laid out along four transects in Richmond Prairie, Kansas. Starting points for transects were located at fixed distances from two fixed points (fence posts and power poles) to facilitate re-location. Plots were laid out at 10m intervals along the transects and were permanently marked with a metal stake pounded flush to the ground at one corner.

Similarly, a random transect of six 3m x 3m was laid out in Montana in July 2001. After these plots yielded only one *Pediomelum* plant in 54 m^2, further plots were not located randomly, but rather were placed surrounding visible *Pediomelum* plants. Six 3m x 3m plots were designated this way in 2001 and an additional two in 2002.

In June 2002, 20 3m x 3m plots were laid out along three parallel transects in one field in Madigan Prairie, Nebraska. Plots were at 10m intervals and transects were located 20m apart. An additional six plots were laid out in areas of visibly high *Pediomelum esculentum* density. All plots at all locations were permanently marked with a length of rebar sunk into the ground at one corner.

Data Collection

The population in Richmond Prairie, Kansas was sampled annually in May-June 2001 to 2004, the Montana population sampled annually in July 2001 to 2004 and the Nebraska population sampled in June 2002, June 2003 and June 2004. At all three sites, I timed sampling to be after plants had reached their full height for the season and flowers had been produced, but before the plants dried and tumbled. At each sampling period, location, number of leaves, numbers of inflorescences, length of inflorescences, overall plant height, plant crown width (widest diameter through the center) and stem diameter were recorded for all individuals. If a plant had more than one stem, was noticeably damaged, or had leaves composed primarily of three leaflets, it was also noted.

Haying, grazing, and the species' tumbleweed lifestyle made marking individual plants impractical. Plants were relocated based on location, recorded as 0.5 dm coordinates on a grid defined by the plot frame. For areas with exceptionally dense clumps of individuals, a bolt was pounded into the ground and locations were recorded as directions and distances 0.5 cm from this point.

Data Analysis

Stage Categorization

I constructed stage based (Lefkovitch) matrix models. There is no way to age a *Pediomelum esculentum* plant based on above ground characteristics and flowering status does not directly correspond with age, (Hermann 1983) so age-based models would be impractical. The multiple measurements taken on individual plants allowed me to create many different stage classes based on leaf morphology, presence and number of flowers, and overall size. However, to keep sample sizes within stage classes as large as possible, I sought to create a biologically meaningful matrix with the fewest dimensions. Because of *Pediomelum esculentum's* longevity and low fecundity, any matrices created would be dominated by stasis in a class or growth to the next class, rather than multiple means of reproduction or transitions that by-pass several stages. These factors make the species a good candidate for a reduced dimensionality matrix (Ramula and Lehtila 2005b). Based on this information, I concluded I needed only four stage classes that were biologically quite distinct: very small, non-flowering, flowering and missing. These stage classes are defined as follows.

"Very small" individuals are morphologically different than adult plants, having three-parted rather than five-parted leaves. In the initial sampling period, very small individuals were considered seedlings. Subsequent sampling periods revealed that while these individuals look like true seedlings (which bear cotyledons), a plant may stay in this stage for at least three years.

Any plant that had dominantly five-parted leaves but no inflorescence was categorized as "non-flowering". This category also included plants that had been grazed (by insect or mammal) prior to sampling and all that remained visible at the location was a stub of adult diameter at sampling time.

Plants with any sign of an inflorescence were considered "flowering." Separating out plants with multiple inflorescences from those with only one led to unusably small sample sizes for several location-years and exacerbated the problem of anonymous reproduction (not knowing the mother of a new plant). The very few plants seen with aborted inflorescences were also considered "flowering". A plant viewed with an aborted inflorescence late in the season may have been recorded as "aborted inflorescence" at that time, but might have been recorded as having a small inflorescence if viewed earlier in the season. Therefore these plants were all added to the flowering category.

In the field, all plants seen the previous year but not found were classified as "missing". There is no way to distinguish a dead plant, a dormant plant, or a plant that whose aboveground parts have been chewed to the ground prior to sampling, so all were grouped into this stage class. While this grouping encompasses considerable uncertainty, I did not want to add to it by including plants that had escaped detection. Therefore, plants that appeared for the first time as full grown adults in subsequent years of the study were not presumed missing the prior year. Only those plants I knew were missing, because I had seen them before and knew exactly where to look for them, were considered missing.

I had hoped to find large numbers of individuals in the plots in all life stages. However, at all sites, "very small" individuals were rare and "missing" individuals could only be counted in second and subsequent years. At each location, I searched for individual plants immediately outside of the plots, hoping to find more individuals in the less represented stage classes, and thus improve the precision of my estimates (as per Munsbergova and Ehrlen 2005). Measurements of these plants outside the plots were taken regardless of whether or not they were in the underrepresented very small class, as the sampling effort had already been taken to find them, and there was a possibility that they might transition to the underrepresented "missing" class. The fates of these out-of-plot individuals were used in calculating the probabilities of transitioning from one stage to another. They were not used in the calculation of the observed stage distribution or reproduction.

Matrix Creation

Four by four Lefkovitch (Lefkovitch 1965) stage matrices were constructed following the methods of Caswell (2001). The matrix form is shown in Table 2.1. The probability of transitioning from stage j to stage i ($P_{(i,j)}$) was calculated by dividing the number of individuals found in stage i at time $t+1$ that had been in stage j at time t by the total number in stage j at time t. The relationship between these measured transition probabilities and their underlying vital rates (survival, growth from one stage to another, regression from one stage to another and stasis in the same stage class) is given in Table 2.2.

If a very small plant was not seen one year, it was not seen again. When making the matrix, I considered these plants to be dead rather than missing. Therefore $P_{(m,v)}$ is zero for all matrices. Similarly, none of the plants missing two years in a row were seen again. Therefore plants missing in consecutive years were considered dead the second year, making $P_{(m,m)}$ equal zero for all matrices. Because flowering and non-flowering plants not seen are considered to be in the missing stage rather than dead, adult plant mortality occurs only through the missing stage in this model. Hermann (1983) documented individual *Pediomelum esculentum* plants remaining dormant for two consecutive growing seasons before re-emerging as healthy plants in subsequent years. Therefore, my assumption that all individuals not observed two years in a row are dead likely over-estimates mortality, leading to a conservative estimate of population growth rate

The average reproductive rate was calculated by totaling the number of very small plants evident in the plots at time $t+1$ that had never been seen before and dividing by the number of plants in the plots flowering at time t. This matrix element is a compound rate that assumes survival of all flowering plants from census through seed production and includes seed production rate, germination rate, and seedling survival from germination until census, none of which I directly calculated. Number of new plants divided by number of flowering plants is an efficient means of estimating anonymous reproduction when a new individual's parentage is unknown (Caswell 2001), but it fails to distinguish contributions from the seed bank.

Eight single transition matrices were created, one for each "location-year" or combination of year and location. Each matrix $\mathbf{A}^{lt}$ is designated by letter of the location (K for Kansas, M for Montana and N for Nebraska) and number of the time period (2 for 2001-2002, 3 for 2002-2003, and 4 for 2003-2004). For example, $\mathbf{A}^{K2}$ is the matrix with transition probabilities for the Kansas population in 2001-2002. Pooled matrices ($\mathbf{A}^{K-}$, $\mathbf{A}^{M-}$, and $\mathbf{A}^{N-}$) for each location were created by pooling the observations of particular transition events at that location over all years. The generalized pooled matrix ($\mathbf{A}^{--}$) was created by pooling the observations of particular transition events over all locations and years. A pooled matrix is a better summary than a matrix of mean rates with regards to less common transitions (Horvitz and Schemske 1995). For example, in a matrix of mean rates, 2 of 6 individuals making a transition at one location one year (0.33) would have the same weight as 16 of 24 making that transition at another location or time (0.67). The rate entered into a matrix of averages would be the mean of the rates, 0.5, while the rate entered in a pooled matrix would be 18 of 30 total individuals, or 0.6. Thus, pooled matrices are averages weighted by the number of individuals.

If there were no plants in a stage at time *t,* I substituted transition probabilities from the pooled matrix for that location. This happened with the very small stage in Montana and Kansas in 2001, and for the missing stage at all locations the first year of sampling. Resulting transition matrices are presented in Table 2.3. Population growth rate (λ), sensitivities, elasticities and stable stage distributions ($\mathbf{w}$, the right eigenvector) were calculated for all matrices using RAMAS EcoLab version 2.0 (Ackakaya and Root 1998).

Bootstrap Confidence Intervals

I used non-parametric bootstrap re-sampling methods to put confidence intervals on my calculated estimates of λ for year-location and pooled matrices (Kalisz and McPeek 1992, Scheiner and Gurevitch 2001). From the population of individuals used to create a matrix, I sampled with replacement and selected a new population of the same size as the original population. From this new population, I created a transition matrix and calculated the dominant eigenvalue (λ). I created 2,000 new populations, matrices, and dominant eigenvalues for each original matrix. I ranked the resulting test statistics (new λ estimates) and placed my original estimate in a 95% confidence interval bounded by test statistics at the 2.5 and 97.5 percentile. The observed growth rate value and the confidence interval were compared to one to determine if the population is projected to grow, decline, or remain stable.

Consistent with the construction of the original matrices, I used individuals from the pooled location matrix for transitions from the very small stage for $\mathbf{A}^{K2}$ and $\mathbf{A}^{M2}$ and from the missing stage for $\mathbf{A}^{K2}$**,** $\mathbf{A}^{M2}$**,** and $\mathbf{A}^{N3}$. However, when a re-sampled population had no individuals in stage *j* at time *t*, due to chance sampling, $P_{(i,j)}$ was defined as zero for the entire column.

Randomization Test for Differences in Growth Rate Among Sites and Years

The null hypothesis that the true population growth rate is the same for all three locations over the duration of the study (i.e. that all differences are due to chance sampling and that $\lambda^{K-} = \lambda^{M-} = \lambda^{N-}$) was tested using repeated randomization following the method described in Caswell (2001). The null hypotheses that the true population growth rate were the same for all years at one location was also tested this way (i.e. $\lambda^{K2} = \lambda^{K3} = .\ \lambda^{K4}$, $\lambda^{M2} = \lambda^{M3} = \lambda^{M4}$, and $\lambda^{N3} = \lambda^{N4}$). Locations and years were tested one pair at a time.

In this test, the observed difference in λ was compared to a sample of 9,999 randomly generated differences. A difference was generated by randomly assigning all individuals from the two observed populations being compared to one of two test populations, keeping the sample sizes the same as in the observed populations. From these new test populations, new transition probabilities, matrices and eigenvalues were calculated, and the absolute difference in eigenvalue recorded. This procedure was done 9,999 times. The resulting sample of differences gives a range of differences in eigenvalue under the null hypothesis that differences in eigenvalue are due to chance alone and therefore group membership of individuals does not matter. Considering the observed difference to be one more possibility under the null hypothesis, the observed difference in eigenvalue was added to the test distribution and the number of differences equal or greater to the observed difference recorded. Dividing the number of equal or more extreme events by 10,000 (the number of total replications) gives a direct estimate of the probability of results as extreme or more extreme than the observed result happening by chance under the null hypothesis (the p-value). In other words,

$P\ [\text{ difference between eigenvalues} \geq \text{observed difference} \mid \text{null hypothesis}] =$

$\#\{\text{difference} \geq \text{observed}\}/\ \text{Number of trials}$

If the calculated probability was less than 0.05, I rejected the null hypothesis. This method was chosen over loglinear analysis because randomization tests directly compare λ values, rather than the transition counts. Bootstrap resampling also includes reproduction, which loglinear analysis cannot (Caswell 2001).

Stochastic Growth Projections

Populations of *Pediomelum esculentum* were projected for ten and fifty time steps into the future using four methods: deterministic simulation, demographic stochasticity added, environmental stochasticity added in the form of varying matrix elements, and environmental stochasticity added in the form of entire transition matrices being drawn from a pool of choices at each time step. All four forms of simulation are density independent. In the deterministic simulation, matrix elements remain the same at each time step. Adding demographic stochasticity keeps the probabilities of transitions constant, but forces each individual to live, die, grow and reproduce as a whole number, leading to variation in projected population sizes. Pooled location and generalized pooled matrices were used in the deterministic and demographic stochasticity simulations. In a varying matrix element projection, matrix elements are considered random variables. For each time step they are drawn from a normal distribution of possible values that has a mean and variance of the mean and variance observed for each element across the eight location-year transition matrices. The variation in matrix elements among observed locations and years represents the variation in environments experienced by *Pediomelum esculentum* populations. Illogical (survival over 100% for a given stage) rates are not accepted, but otherwise rates do not co-vary. Both the demographic stochasticity and the varying matrix element simulations were run in Ramas EcoLab (Ackykaya and Root 1998).

In order to simulate years with highly correlated transition rates, I projected the population by randomly drawing one of the observed transition matrices for each time step. In this simulation, the eight year-location matrices represent environmental variability as a suite of conditions that act on all rates simultaneously. Rates co-vary as they do in the observed transitions.

Simulations were run for individual locations as well as for the generalized population, represented by all years and all sites. For the single location varying matrix element simulations, transition rates were those of the pooled matrix for a location, and the standard deviations were the standard deviations of the rates among years at that location. For the random matrix simulation for a location, the matrices were drawn from among the single year matrices for that location. Random matrix simulations were programmed in Java.

For all of the simulations, I started with a population of 200 individuals, representing the size of a very small natural *Pediomelum esculentum* population, one that might be of conservation concern. Initial proportions of individuals in each stage followed the observed average proportions for each site and overall. Each simulation was run with 1,000 simulated replications. Mean population size was recorded after 10 and 50 time steps, as was the number of the 1,000 trials in which the population was driven to extinction. Populations with fewer than one individual were considered extinct.

The realized growth rate was calculated from the mean final population size of the 1,000 simulated replicates. The realized growth rate is the average annual growth rate experienced by the population, a shorter-term version of the long-term stochastic growth rate described by Tuljapurkar (1997) and a means of comparing growth experienced by a simulated population with the projected growth rate of a matrix (λ). It is calculated based on the following population equations:

$$N_t = N_0e^{rt}$$

$$\ln\lambda = r$$

$$\ln \lambda_{realized} = \ln(N_t/N_0) \times 1/t$$

(Tuljapurkar 1997, Silvertown and Chatsworth 2001, Gurevitch et al. 2002). In order to compare projections of small populations over short time horizons, transitory dynamics were not excluded from the simulations.

Determination of Importance of Matrix Elements

I addressed the issue of which matrix elements are most important to growth rates through both prospective and retrospective methods. Prospectively, in order to compare effects of potential future perturbations, I analyzed sensitivities and elasticities. Sensitivities compare how a very small change in one matrix element would change the growth rate. Elasticities are proportional sensitivities and can be interpreted as proportional contributions of matrix vital rates to λ (van Groenendael et al. 1994). Matrix elements of zero can have a high sensitivity (e.g. *if* non-flowering plants could be made to reproduce, this *would* have a great effect on the population growth rate) whereas the elasticity of a zero element is zero (i.e. increasing the number of non-flowering plants reproducing by 10% has no effect on growth rate because 110% of zero is still zero). Elasticities sum to one across a matrix (de Kroon et al. 1986, Caswell 2001).

For these prospective perturbation analyses, my model is based on a time invariant matrix model

$$\mathbf{n}_{(t+1)} = \mathbf{A}\mathbf{n}_{(t)}$$

in which **A** is the population projection matrix and $\mathbf{n}_{(t)}$ is a vector giving the abundances of the stages in the population at time t. The dominant eigenvalue λ gives the population growth rate, the associated right and left eigenvectors **w** and **v** give the stable stage distribution, and the stage-specific reproductive value. Letting <**w**,**v**> represent the scalar product of **w** and **v**, the sensitivity of λ to a change in the matrix element a_{ij} is given by

$$s_{ij} = \partial\lambda/\partial a_{ij} = v_i w_j / \langle \mathbf{w},\mathbf{v} \rangle$$

I use "sensitivity" only in this narrow sense throughout. The elasticity or proportional sensitivity of λ to a change in the matrix element a_{ij} is given by

$$e_{ij} = a_{ij}/\lambda * \partial\lambda/\partial a_{ij}$$

(Caswell 2001).

Looking retrospectively, to determine which rates had led to the greatest variation in observed growth rates, I used Life Table Response Experiment (LTRE) methods. As with a traditional analysis of variance (ANOVA), the variation observed in a LTRE can either be considered the result of random effects or the result of fixed treatment effects. Considering the years and locations to be a random sample of all environments *Pediomelum esculentum* faces, I decomposed the variance into contributions from specific rates, hereafter referred to as random effects contributions. Following Horvitz et al. (1997 p. 252-253), I let V(λ) equal the variance of λ among treatments and approximated λ as a linear function of the matrix elements, and used the sensitivities (s_{ij})as slopes.

When this is the case, the general equation for a linear combination of variables x and y,

$$\mathrm{V}(ax + by) = a^2\mathrm{V}(x) + b^2\mathrm{V}(y) + 2ab\mathrm{C}(x,y)$$

where $\mathrm{C}(x,y)$ is the covariance of x and y, and $\mathrm{V}(x)$ is the variance of x, can be approximated,

$$\mathrm{V}(\lambda) \approx \sum_{ij} \sum_{kl} \mathrm{C}(ij, kl)\, s_{ij}\, s_{kl}$$

The covariances of each pair of matrix elements, $\mathrm{C}(ij, kl)$ were calculated from the data for each location-time matrix, and the sensitivities were evaluated at the mean matrix for the generalized population. In this equation, each element is a contribution of one pair of matrix elements to $\mathrm{V}(\lambda)$. From this, the contribution of a single element to the variation in growth rate was calculated by summing all of the contributions involving that element:

$$\mathrm{X}_{ij} = \sum_{kl} \mathrm{C}(ij, kl)\, s_{ij},\, s_{kl}$$

Considering year and location to be fixed treatment effects, I calculated how much each vital rate contributed to the main treatment effects and the interaction following Horvitz et al. (1997) and Caswell (2001). The two way model is analogous to analysis of variance. Population growth at location l in year t can be described as:

$$\lambda^{(lt)} = \lambda^{(--)} + \alpha_l + \beta_t + (\alpha\beta)_{lt}$$

where $\lambda^{(--)}$ is the calculated growth rate at the generalized population matrix (all sites, all years pooled), and $\alpha_{l,}$ β_t, and $(\alpha\beta)_{lt}$ are the location, year and interaction effects.

Letting $\lambda^{(l-)}$ represent the growth rate calculated at the pooled matrix at location *l* over all years and $\lambda^{(-t)}$ represent the growth rate calculated at the pooled matrix for year *t* over all locations, I can estimate the effects as:

$$\alpha_l = \lambda^{(l-)} - \lambda^{(--)}$$

$$\beta_t = \lambda^{(-t)} - \lambda^{(--)}$$

$$(\alpha\beta)_{lt} = \lambda^{(lt)} - \alpha_l - \beta_t - \lambda^{(--)}$$

These treatment effects can be decomposed into contributions of each matrix element:

$$\alpha_l \approx \sum_{ij} (a_{ij}^{(l-)} - a_{ij}^{(--)})\, s_{ij}$$

$$\beta_t \approx \sum_{ij} (a_{ij}^{(-t)} - a_{ij}^{(--)})\, s_{ij}$$

$$(\alpha\beta)_{lt} \approx \sum_{ij} (a_{ij}^{(lt)} - a_{ij}^{(--)})\, s_{ij}$$

where the sensitivities, s_{ij}, for each element, a_{ij}, are calculated at an intermediate matrix. For α_l this intermediate matrix is $(\mathbf{A}^{(l-)} + \mathbf{A}^{(--)})/2$ for β_t it is $(\mathbf{A}^{(-t)} + \mathbf{A}^{(--)})/2$ and for $(\alpha\beta)_{lt}$ $(\mathbf{A}^{(lt)} + \mathbf{A}^{(--)})/2$. Contributions of rates to effects can be positive or negative and the mean contribution of a rate over the levels of a factor is approximately zero. I am interested in magnitude of contribution, so I opted to use mean of absolute value of contribution as my summary measure (Horvitz et al. 1997).

Finally, I compared results of elasticity, sensitivity and LTRE methods to simple comparisons of variation within and correlations among rates. Statistical calculations were conducted using Mintab for windows version 12 (1998) and Microsoft Excel (2000).

Results

Observed Population Changes

I tracked the fates of a total of 302 individuals in Kansas, 102 individuals in Montana and 218 individuals in Nebraska. The vast majority of these plants were non-flowering and flowering adults, with the proportion flowering varying across sites and years (Fig. 2.1). Through the years of the study, I observed 59 new very small individuals in Kansas, 7 in Montana and 10 in Nebraska while 9 very small and two adult plants died in Kansas, 5 very small and 3 adult plants died in Montana and 10 very small and 3 adult plants died in Nebraska. Figure 2.1 compares the observed stage distributions to the stable stage distributions calculated from the pooled matrix for each location along with the pooled matrix (all sites, all years) for the generalized population.

Population Growth Rate (λ)

The λ values for a transition period at an individual location ranged from 0.957 for Montana 2003-2004 to 1.172 for Kansas 2001-2002 (Figure 2.2). λ greater than one for all transitions at the Kansas site indicates the population will grow if conditions remain the same. While λ was less than one for all but one transition at the Montana and Nebraska sites, the bootstrap 95% confidence interval included one for all transitions and the locations pooled over the years (Fig. 2.2). This indicates that based on the observed years, the Montana and Nebraska populations are projected to decline, but that the projected growth rates are not statistically different from those I would expect for a stable population. All three populations fared more poorly over the 2003 to 2004 transition than they had in previous years.

Based on the results of the randomization test, I was able to reject the null hypotheses that $\lambda_{\mathbf{K}p} = \lambda_{\mathbf{M}p}$ and $\lambda_{\mathbf{N}p} = \lambda_{\mathbf{K}p}$ (Table 2.4). Given the distribution of results of 10,000 randomizations, the observed difference in eigenvalue would have happened by chance with a probability of 0.0014 under the null hypothesis for Kansas and Montana and 0.0002 for Kansas and Nebraska. I was unable to reject the null hypothesis that $\lambda_{\mathbf{M}p} = \lambda_{\mathbf{N}p,}$ because differences as great as or greater than the observed difference would happen with a probability of 0.8392 under the null hypothesis.

Within sites, differences in λ were significant for most, but not all, pairs of years (Table 2.4). At the Kansas location, λ for the poor year 2003-2004, was significantly different from λ for the better years, 2001-2002 and 2002-2003. In Montana, λ for the poor years 2003-2004 and 2001-2002 were statistically indistinguishable from each other, but both differed significantly from λ for the good year at that site, 2002-2003. In Nebraska, λ for 2002-2003 and 2003- 2004 were not significantly different than the expectation under the null hypothesis. I conclude that there are significant spatial and temporal differences in growth rate for *Pediomelum esculentum* populations.

Stochastic Growth Projections

All three forms of stochastic simulations projected a lower mean population size for the generalized population after ten and fifty years than did a deterministic simulation (Table 2.5). The varying matrix element simulation presented the most pessimistic population projections. In this simulation, in ten or fewer years, 37 of the 1000 replicate populations went extinct, and by 50 years, 971 of 1000 replicate populations were extinct. While demographic and random matrix simulations projected growth for the generalized population, mean final sizes very near the initial sizes suggests that this population should be considered stable, rather than rapidly increasing.

Even with the addition of uncertainty, the Kansas population is projected to grow. In most projections, stochasticity accelerated the projected decline of the Montana and Nebraska populations. A surprising exception is the random matrix simulation for Nebraska, which, like the random matrix simulation for Kansas, projected larger final populations than did a deterministic simulation. Mathematically this is possible because the pooled matrices, which form the basis of the deterministic simulation, are weighted by numbers of individuals. In the random matrix simulation, a matrix with a high value for a matrix element, based on a small sample of individuals will, on average, be drawn as frequently as a matrix with a low value for that element based on a larger sample. This leads to an overall higher rate for that transition than found in the pooled matrix, where rates are weighted by numbers of individuals.

Important Transitions

Different measures of "importance" lead to different assessment of the most critical life transitions for population growth. Among the 16 matrix elements, population growth rate measured at the generalized pooled matrix $\mathbf{A}^{--}$ is most sensitive to small changes in the percentage of plants transitioning from non-flowering to flowering (Figure 2.3). Elasticity analysis reveals that a small proportional change in the number of plants remaining in the non-flowering stage would have the greatest effect on growth rate (Figure 2.4). Considering retrospective random effects analysis, differences in the proportion of flowering plants remaining flowering make the greatest positive contribution to observed variation in growth rate and differences in the proportion of flowering plants regressing to the non-flowering stage make the greatest negative contribution (Figure 2.5). Considering variation from λ^{--} to be treatment effects of the year, location, and year by location interaction, I find that differences in the matrix element representing the number of flowering plants remaining in the flowering stage made the greatest contribution to the location effect, while differences in non-flowering to flowering transitions made the greatest contribution to the year and interaction effects (Figures 2.6, 2.7, 2.8).

The rate of growing from missing to non-flowering had the greatest variance across location-year matrices (Figure 2.9). Increases in λ across matrices were most closely correlated with increases in the reproductive rate (Figure 2.10). λ is also significantly positively correlated with the rate of flowering plants remaining flowering stasis, and negatively correlated with transitions from the adult stages to missing and with flower to non-flower regression (Figure 2.10). Most matrix elements are correlated with each other, several strongly so (Table 2.6). The five “most important” transitions as determined by each method are summarized in Table 2.7.

Discussion

Population Status

Growth rates near one and populations in near stable stage distribution suggest that the populations in Kansas and Montana are largely stable. For these sites, none of the 1,000 simulated replicate populations with an initial size of 200 plants went extinct in ten years. The Nebraska site, on the other hand, exhibits considerable variation in stage distribution, percentage of adults flowering, and simulated fate, from near stable to completely doomed.

The variation in simulation outcomes stems from the different assumptions inherent in the simulations. All simulations assume density independence. This is a reasonable assumption for a small dispersed population with a growth rate near one (as with the initial populations) but it makes little sense to assume it holds after the populations have grown considerably (as with the 50 year projections of the Kansas population) (Bierzychudek 1999). A varying matrix element type of simulation does not assume that the years and locations observed represent the possible extremes of growth rate, a definite advantage over the random matrix simulation, which does (Kaye and Pyke 2003). However, this simulation assumes that rates vary independently. In my simulation, as with other demographic studies, ignoring the correlations among rates led to overly pessimistic projections (Ramula and Lehtila 2005a). Among the transition matrices, P(n,f) and P(f,f) were highly variable, which led to a high standard deviation for these rates, and high variability in the simulation. These rates, however, are products of underlying survival, growth and regression probabilities (Table 2.2). There was no variation in non-flowering and flowering plant survival among my populations (if an adult plant transitioned to the missing stage, it was still considered to have survived). If survival is constant, all changes to P(n,f) and P(f,f) will be based on the underlying growth, stasis and regression rates. By definition, any variation in the flowering to non-flowering regression R(n,f) or flowering to missing regression R(m,f) rate was offset by an equal and opposite change to the rate of flowering remaining flowering (1-R(n,f)- R(m,f)). The varying rates simulation does not maintain this structure, so a lower than average P(f,f) could occur with a lower than average P(n,f). Because the simulation rejects sets of rates which combine to over 100% survival for a stage, and P(n,f) + P (f,f) + P (m,f) already equal 1, a larger than average P (n,f) could not occur with a larger than average P (f,f) and P (m,f). Allowing rates to have "bad-bad" combinations not seen in the field, but disallowing equivalent "good-good" combination leads to the varying matrix element simulations projecting overly pessimistic outcomes. This type of simulation is among the easiest ways for a conservation practitioner to include variability while projecting population growth. Before basing a decision on a projection from a varying rates simulation, practitioners are advised to look at the structure of their underlying matrix. If rates are highly negatively correlated, a varying rates simulation which assumes independence or positive correlation of rates will be pessimistic (Ramula and Lehtila 2005a) and a poor choice for decision making. More sophisticated software which allows the practitioner flexibility in determining the distribution rates are drawn from and how rates are correlated, or a random matrix simulation might be a preferred choice.

In contrast to the varying matrix element simulation, the random matrix simulation assumes that I captured not only the average in rates, but also the maximum and minimum in rates. This model gains verisimilitude by maintaining the observed strong covariance structure, but at the cost of never allowing for better or worse years than those observed. This is an especially dangerous assumption for the single site simulations, which are based on only two or three transition matrices.

Policies regarding wild-harvested plants are often implemented across broad geographical areas concerning the overall state of the species. In order to set such policies based on actual data, a determination must be made as to whether or not spatial and temporal variation can act as surrogates for each other. If spatial and temporal variation are not surrogates for each other, Kansas, Montana and Nebraska populations must be considered separately, and models pooling sites make little sense. If they can serve as surrogates for each other, policies can be set range-wide based on pooled data.

For the case of *Pediomelum esculentum*, I argue that temporal and spatial variation are suitable surrogates for each other. Between the site with the highest growth rate (Kansas) and the site with the lowest growth rate (Nebraska) the biggest environmental difference over the course of my study was drought. Constrained by their very short growing season, flower buds are formed before a *Pediomelum esculentum* individual emerges in the spring, and flowering rate is thus strongly affected by environmental conditions during the previous growing season (Hermann 1983). When drought levels during the prior season were normal, flowering rates in Nebraska were on par with those in Kansas. At both sites, as drought severity increased, flowering rate decreased (Figure 2.11). It happens that the years of my study covered exceptionally droughty years in Nebraska.

Besides also suffering through exceptionally dry years during my study, the Montana site additionally suffered a "micro-catastrophe" in 2004 when a very small landslide buried half of a plot and all of the prairie turnip plants within it. None of the buried plants were seen in 2004, but given an individual plant's ability to remain dormant, I suspect many of them re-emerged in later (unobserved) years. This micro-catastrophe led to unusually high flowering and non-flowering to missing transition probabilities for that year.

Given these observations, I believe that my transitions together form a reasonable estimate of possible conditions across the range of *Pediomelum esculentum*. Kansas will suffer from drought at some time and Nebraska will receive more rain. A small landslide or other disturbance could happen anywhere. I am not proposing that the three populations fared as well as each other over my observed years, but rather that such variation could occur with time across the range. Similarly, variation in time at one site could represent variation in location at a given time. Longer-term range-wide data are needed to determine if populations in particular habitats or at the edges of the range consistently perform differently, and are thus in need of area specific conservation efforts. In the absence of even more data, I believe considering all the available data together to be the most reasonable approach to making conservation decisions.

If I consider temporal variation and spatial variation surrogates for each other, and my sites and years representative of the conditions that *Pediomelum esculentum* faces, my results suggest that the species is stable, with considerable spatial and year to year variation.

Conservation Implications of Matrix Element Importance

The differences in "most important" vital rates illustrated by Figures 2.3 to 2.10 and Table 2.7 may at first be bewildering to a conservation practitioner. All of the information has applications to conservation biology, however, as demonstrated by my *Pediomelum esculentum* case study.

Elasticity and sensitivity analysis demonstrate that small changes in adult survival (as non-flowering to flowering or non-flowering, and flowering to non-flowering or flowering transitions) would have the most effect of *P. esculentum* growth rate. Sensitivity analysis also illustrates that conservation efforts designed to promote survival of very small individuals would have only a very limited effect on population growth rate. However, if one could alter growth rates of very small plants, increasing the number of plants transitioning from very small to flowering (in my study an extremely uncommon event, with thus a very low rate and a low elasticity), it would have a greater effect on population growth rate than a similar change on the transition from very small to not-flowering.

The random effects contribution analysis answers a different question. Rather than explaining which rates would have the greatest impact on population growth rate if changed slightly, this retrospective LTRE analysis explains which rates contributed most to the observed differences in λ across years and locations. The percentage of adult plants flowering (non-flowering to flowering growth and flowering to flowering stasis) had the greatest positive contribution and the percentage of adult plants not flowering (non-flowering to non-flowering stasis and flowering to non-flowering regression) had the greatest negative contribution.

In order to relate observed differences in λ to particular environmental conditions, I use the fixed effect analysis. To answer "What demographic transitions led to the Kansas population growing more quickly than the Nebraska and Montana populations?" I look to the location treatment effects and find that the percentage of flowering plants remaining flowering drives the overall difference. Wondering what rates contributed to worse years across the range leads to the year treatment effects and I find temporal differences are largely due to the proportion of plants progressing from non-flowering to flowering stages. These types of questions are the first step in correlating environmental conditions and growth rates. While the questions do not directly lead to answers of causes of growth or decline, they do point toward sensible solutions. The Kansas site differs from the Nebraska site in disturbance and rainfall.

Higher levels of disturbance could not logically lead to increased percentage of flowering plants remaining flowering. However, it could explain higher levels of successful reproduction via increased seedling recruitment, and rainfall might be a causal factor in level of flowering consistency. Across the range, 2003-2004 was a year of below normal rainfall, which could explain the lower percentage of plants moving from non-flowering to flowering.

Conservation practitioners may want to consider different importance analyses in combination. Caswell (2001) warns against using retrospective analysis to answer prospective questions. For instance, that a rate has not varied in the past does not mean it will not in future, and if the change in a rate contributed to a decline in a population, reversing the change is not the only or necessarily most efficient means of reversing the decline. However, it seems imprudent not to consider the past levels of variation when suggesting future changes. Targeting conservation efforts towards rates with both high elasticities and high contributions to observed variation seems like an efficient starting point. It also is important to consider ability of a rate to change and negative correlations with other rates (Ehrlen and van Groenendael 1998, Ramula and Lehitla 2005a).

In *Pediomelum esculentum* conservation, for instance, a first glance at sensitivities and LTRE contributions would suggest conservation efforts focus on the four visible adult transitions ($P_{(f,f)}$, $P_{(f,n)}$, $P_{(n,n)}$, and $P_{(n,f)}$) because λ is very sensitive to all of them and they contribute to observed differences in λ. However, these rates are strongly negatively correlated with each other (Table 2.6). In my model in which mortality is through the missing stage, survival of flowering and non-flowering plants (S_f and S_n) equals one, and I observed all adult mortality to be very low. Therefore increases in the number of visible adult plants transitioning to the flowering stage is off-set by decreases in the number of adult plants transitioning to the non flowering stage (Table 2.2). If efforts are aimed at increasing population growth, increasing reproduction might be a more efficient use of resources, as increase in reproductive rate does not have a direct trade-off cost and is highly correlated with λ.

If preventing population decline is the goal, than the focus should be on preventing erosion of adult survival. While S_n and S_f have no room to improve from my observed data, they can certainly decline. A decline in either would lead to a decline in several transition probabilities (Table 2.2), all of which have high elasticity values. Knowledge of the importance of survival for separate life stages is critical for setting harvest policy. In the case of *Pediomelum esculentum*, both non-flowering and flowering plants are harvested and the harvest kills the plant. With an understanding of how much survival of these stages influences overall population growth, conservative harvest policies should encourage only very low levels of harvest.

Another use of perturbation analysis is for focusing further studies. *Pediomelum esculentum* rates for the transitions from missing to flowering and missing to non-flowering exhibit the most variance across matrices, largely due to having fewer year-locations from which to measure these rates and fewer individuals at each time step. Before planning a targeted study to reduce this uncertainty, it would be worth looking at the sensitivity analysis. That λ is largely insensitive to changes in fate of missing plants suggests that spending great effort to reduce this uncertainty would be ill advised if population conservation is the top priority.

Death, Dormancy and Detection

From tracking the fate of individual plants, I confirmed earlier reports that *Pediomelum esculentum* plants can be dormant or undetected. In the years of my study, about 5.3% percent of the adult plants were seen one season and not the next. Of these, 73% were seen again the following year. The stable stage distribution of the pooled matrices suggest that 4 to 5% of the population is in the missing stage at any one time (Fig. 2.1). Because I did not see any very small individuals reappear after being missing for a year or more, I considered very small plants not seen again to be dead, rather than missing, which concurs with earlier estimates of much higher mortality rates among seedlings and small juveniles (Hermann 1983).

I also learned that my ability to detect plants is not consistent. In the second year of the study, I found 80 adult plants in the plots in Kansas that I had not seen in 2001. Assuming that 9 of these (5.3% percent of the population) were missing in 2001, that leaves 71 plants that were aboveground and undetected. While it is possible that many more plants were dormant in 2001 than in other years of the study, it seems more likely that my ability to spot individuals increased with experience. Most plant monitoring schemes assume 100% detection of aboveground plants (Kery et al. 2005, but see Alexander et al. 1997 and Slade et al. 2003). This seems to be an unrealistic assumption for *Pediomelum esculentum*, and is most likely so for other small, dispersed, under-story plants, particularly when monitoring (or harvesting) is conducted by different individuals. My study does not assume 100% detectability of aboveground plants, which is why the plants not seen the first year but seen as adults the second year were omitted for the first transition rather than being considered missing the first year. I wanted to distinguish from those plants that were known to be missing (because I knew exactly where to look for them and they were not there) and those plants that I missed seeing. My methods do assume 100% detectability of above ground plants previously located. That I found 2cm stem remnants when attempting to relocate known plants confirms my ability to re-locate an above ground plant if it is there, and validates that those labeled as "missing" were not visible aboveground.

"Missing" individuals could be dormant, eaten to the ground, or dead. My model does not distinguish between the former, but does consider unseen adult plants to be alive while categorized as missing. Those adult plants that do die in my model die transitioning from the first to second year in the missing stage, even if death happened immediately following the last aboveground observation. If the latter is true, my method slightly overestimates population size at a particular time by delaying death a year. If precise estimates of population size at a given year are important, mark-recapture methods could provide better estimates than my model does (Alexander et al. 1997, Kery et al. 2005). My model, however, is not used for precise estimates at a given time and I cannot imagine a plant harvest scenario where the distinction between “dead” and “undetectable and soon-to-be-dead” would be critical.

While the specifics of the missing stage are not critical to the matrix population models, the recognition that the stage exists is. If a population is modeled without a missing stage and all individuals not observed in time 2 are considered dead, as would be predicted with only two years of data, mortality is overestimated and a dramatic decline is projected. With three years of data on fates of individuals, it is clear that some plants become missing and then reappear aboveground the following year. An investigator assuming that all plants not found are in the missing stage would underestimate mortality (effectively modeling plants as immortal, if perhaps trapped in a missing stage) and project erroneously large population growth.

Uncertainties and Benefits

Despite four years of data collection, large uncertainties remain in my knowledge of *Pediomelum esculentum* dynamics. I am uncertain about the representativeness of the sites and years studied. I did capture years of very low levels of flowering, years of high levels of flowering, years of very poor reproduction, years of drought, and one micro-catastrophe. I did not capture a bonanza year, nor a genuinely catastrophic year. From my data, I remain uncertain how often which sets of conditions prevail. To truly alleviate this uncertainty, I would need many more years of data from many more field locations. My data set, however, could serve as an excellent starting point for finding environmental correlates of growth rates and then using climate data to suggest periodicity of good and bad years. I also remain uncertain as to the suite of environmental conditions that would lead to a bonanza year or a catastrophic year.

Reproductive dynamics remain uncertain. Because of the way I measured reproduction as an observed average, rather than tracking the component rates, I cannot deconstruct how changes in germination rate or seedling survival rate would affect population growth rate independently. Uncertainties also remain about the role of the seed bank. Following my study, however, I am more certain that under the conditions experienced in the study years, the overall role of the seed bank is minor. Based on *Pediomelum esculentum* adults' longevity and low variation in adult survival, I assumed *a priori* that the role of the seed bank was not important to the question of *P. esculentum* population persistence (Doak et al. 2002). The observed low levels of recruitment from seeds of all sources and low sensitivity and elasticity to reproduction confirm that the presence or absence of a seed bank did not dramatically affect population growth for the years observed. A *Pediomelum esculentum* plant's ability to survive through adverse times as a small adult or an underground root suggest considerable investment in strategies for buffering environmental variation other than a seed bank. However, a long term seed bank might still be important for dispersal and for persistence through catastrophes. It is conceivable that a long term seed bank could lead to bonanza years of new growth following regional disturbance and the removal of other competitors. Seed bank studies, by their nature destructive, need to be conducted apart from *in situ* demographic studies (Kalisz and McPeek 1993) and could not be performed in the intact prairies where my demographic studies took place.

I remain uncertain as to the long term fates of missing plants, largely because of my small sample. A longer duration of study could alleviate some of this uncertainty, but documenting time of death would require destructive sampling outside of my study areas.

These uncertainties are not insignificant, and given the huge time cost to conduct a four-year, multi-site study, force one to reassess the benefits of such a study. Here is an accounting of what I would have lost had I conducted a simpler study.

Had I not tracked the fates of individuals, I would not know of the existence of the missing stage, nor of *Pediomelum esculentum* plants' ability to remain in what I would have called a seedling stage for several years. Unless I marked plants, changes in detectability following haying and grazing would most likely have led to erroneously large fluctuations in growth rate (and once plants are marked, the additional effort required to track fates of individuals is minimal).

Had I used three years of data instead of four, I would have missed catching the transition with fastest projected growth (Kansas 12) or the transition with the fastest projected decline (Montana 34). Three years would also have drastically cut down my sample of missing individuals. If I had any fewer location-years, my assumption that I captured the environmental variation experienced by *Pediomelum* would be considerably more presumptuous.

From tracking the fates of individuals, I have created a model that I feel accurately represents the demographics for the transitions observed. From this model, I can project how changes in matrix elements due to harvest, changing policies or changing environmental conditions might affect my population. A census based model would require all the same assumptions and bring all the same uncertainties, but with it I would not be able to model changes to specific life stages.

Conclusion

Observed *Pediomelum esculentum* populations are largely stable but do vary temporally and spatially. Retrospective and prospective analyses of the matrix elements that have the most impact on population growth rate, lead to different results, because each analysis answers a different question. However, transitions associated with adult survival are important in all analyses. Because the matrix elements associated with adult survival are negatively correlated and cannot increase independently, reproduction may be equally important for conservation efforts aimed at increasing population size.

Pediomelum esculentum does have a life history making population demography challenging. However, the case of this species suggests that, as laborious and time consuming as fate-of-individual data can be to collect, the matrix population models created from them provide conservation practitioners with a useful tool other simpler methods cannot provide.

	From $_{(j)}$			
to $_{(i)}$	**very small**	**non-flowering**	**flowering**	**missing**
very small	$P_{(v,v)}$	$P_{(v,n)}$	Reproduction	$P_{(v,m)}$
non-flowering	$P_{(n,v)}$	$P_{(n,n)}$	$P_{(n,f)}$	$P_{(n,m)}$
flowering	$P_{(f,v)}$	$P_{(f,,n)}$	$P_{(f,,f)}$	$P_{(f,,m)}$
missing	$P_{(m,v)}$	$P_{(m,n)}$	$P_{(m,f)}$	$P_{(m,m)}$

Table 2.1: Matrix model form

$P_{(i,j)}$ represents the probability of transitioning from stage *j* to stage *i* over a one year time step.

	From $_{(j)}$			
to $_{(i)}$	**very small**	**non-flowering**	**flowering**	**missing**
very small	$S_v(1- G_{(n,v)} - G_{(f,v)})$	0	Seed production* seed survival* germination* $S_{\text{seedling to cenus}}$	$S_m(1- G_{(n,m)} - G_{(f,m)})$
non-flowering	$S_vG_{(n,v)}$	$S_n(1- G_{(f,n)} - R_{(m,n)})$	$S_f\, R_{(n,f)}$	$S_mG_{(n,m)}$
flowering	$S_vG_{(f,v)}$	$S_nG_{(f,,n)}$	$S_f(1- R_{(n,f)} - R_{(m,f)})$	$S_mG_{(f,,m)}$
missing	0	$S_nR_{(m,n)}$	$S_fR\ _{(m,f)}$	0

Table 2.2: Relationship of matrix elements and underlying rates

S= survival G = growth R= regression

Reproduction as written here assumes 100% survival of flowering plants from census to seed release and no long-term seed bank.

Structurally impossible transitions are listed as zero.

Kansas

2001-2002

	v* (70)	n (64)	f (30)	m* (7)
v	0.5286	0.0000	0.7000[a]	0.1429
n	0.3429	0.6250	0.2333	0.4286
f	0.0000	0.3594	0.7667	0.1429
m	0.0000	0.0156	0.0000	0.0000

2002-2003

	v (28)	n (109)	f (92)	m (2)
v	0.3214	0.0000	0.2581	0.0000
n	0.6071	0.6422	0.2717	0.5000
f	0.0000	0.3119	0.7283	0.5000
m	0.0000	0.0459	0.0000	0.0000

2003-2004

	v (11)	n (141)	f (113)	m (6)
v	0.6667	0.0000	0.2750	0.1667
n	0.1667	0.7518	0.3451	0.3333
f	0.0000	0.2340	0.6195	0.1667
m	0.0000	0.0142	0.0354	0.0000

All Years Pooled

	v (70)	n (314)	f (235)	m (7)
v	0.5286	0.0000	0.3430	0.1429
n	0.3429	0.6879	0.3021	0.4286
f	0.0000	0.2866	0.6809	0.1429
m	0.0000	0.0255	0.0170	0.0000

Table 2.3a Transition matrices for Kansas
Initial sample size for the stage class given in parentheses.
* Where no individuals in a stage were seen at a site in a year, data from the pooled matrix for that site were used.
[a] Only very small individuals and flowering individuals in the plots were considered for reproductive rate, so these rates are based on a different sample size.
In all tables and figures v= very small, n= non-flowering, f=flowering, and m=missing.

Montana

2001-2002

	v* (11)	**n (23)**	**f (18)**	**m* (13)**
v	0.1818	0.0000	0.0556[a]	0.0769
n	0.2727	0.6087	0.4444	0.3077
f	0.0909	0.1739	0.4444	0.3846
m	0.0000	0.2174	0.1111	0.0000

2002-2003

	v (5)	**n (50)**	**f (29)**	**m (7)**
v	0.2000	0.0000	0.2105	0.0000
n	0.2000	0.5800	0.5172	0.1429
f	0.2000	0.3600	0.4483	0.7143
m	0.0000	0.0600	0.0345	0.0000

2003-2004

	v (6)	**n (52)**	**f (38)**	**m (13)**
v	0.1667	0.0000	0.0769	0.1667
n	0.3333	0.5577	0.5263	0.5000
f	0.0000	0.3077	0.3421	0.0000
m	0.0000	0.1346	0.1316	0.0000

All Years Pooled

	v (11)	**n (125)**	**f (72)**	**m (10)**
v	0.1818	0.0000	0.1111	0.0769
n	0.2727	0.5760	0.5059	0.3077
f	0.0909	0.3040	0.4000	0.3846
m	0.0000	0.1200	0.0941	0.0000

Table 2.3b Transition matrices for Montana
Initial sample size for the stage class given in parentheses.
* Where no individuals in a stage were seen at a site in a year, data from the pooled matrix for that site were used.
[a] Only very small individuals and flowering individuals in the plots were considered for reproductive rate, so these rates are based on a different sample size.
In all tables and figures v= very small, n= non-flowering, f=flowering, and m=missing.

Nebraska

2002-2003

	v (8)	n (62)	f (86)	m* (10)
v	0.2500	0.0000	0.0615[a]	0.0000
n	0.3750	0.1774	0.4419	0.6000
f	0.0000	0.7742	0.4767	0.1000
m	0.0000	0.0484	0.0814	0.0000

2003-2004

	v (14)	n (122)	f (72)	m (10)
v	0.5000	0.0000	0.1429	0.0000
n	0.0000	0.8607	0.8333	0.6000
f	0.0000	0.0492	0.1389	0.1000
m	0.0000	0.0902	0.0278	0.0000

All Years Pooled

	v (22)	n (184)	f (158)	m (10)
v	0.4091	0.0000	0.0935	0.0000
n	0.1364	0.6304	0.6203	0.6000
f	0.0000	0.2935	0.3228	0.1000
m	0.0000	0.0761	0.0570	0.0000

Generalized Population

All Sites All Years Pooled

	v (103)	n (623)	f (465)	m (27)
v	0.4660	0.0000	0.2222	0.0667
n	0.2913	0.6485	0.4435	0.4333
f	0.0097	0.2921	0.5126	0.2333
m	0.0000	0.0594	0.0439	0.0000

Table 2.3c and 2.3d Transition matrices for Nebraska and transition matrix for the generalized population

Initial sample size for the stage class given in parentheses.

* Where no individuals in a stage were seen at a site in a year, data from the pooled matrix for that site were used.

[a] Only very small individuals and flowering individuals in the plots were considered for reproductive rate, so these rates are based on a different sample size.

In all tables and figures v= very small, n= non-flowering, f=flowering, and m=missing.

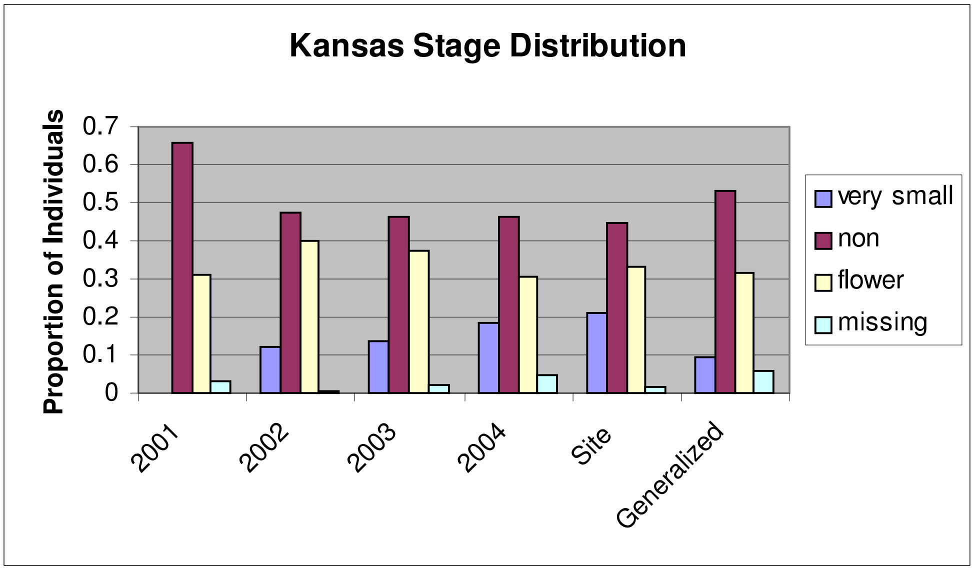


Figure 2.1a Observed and calculated stage distribution for the Kansas population
Comparison of the observed stage distributions to the calculated stable stage distribution for each site and for the generalized population. Stable stage distributions calculated from the pooled matrices (all years pooled at the Kansas site and all years all sites pooled for the generalized population).

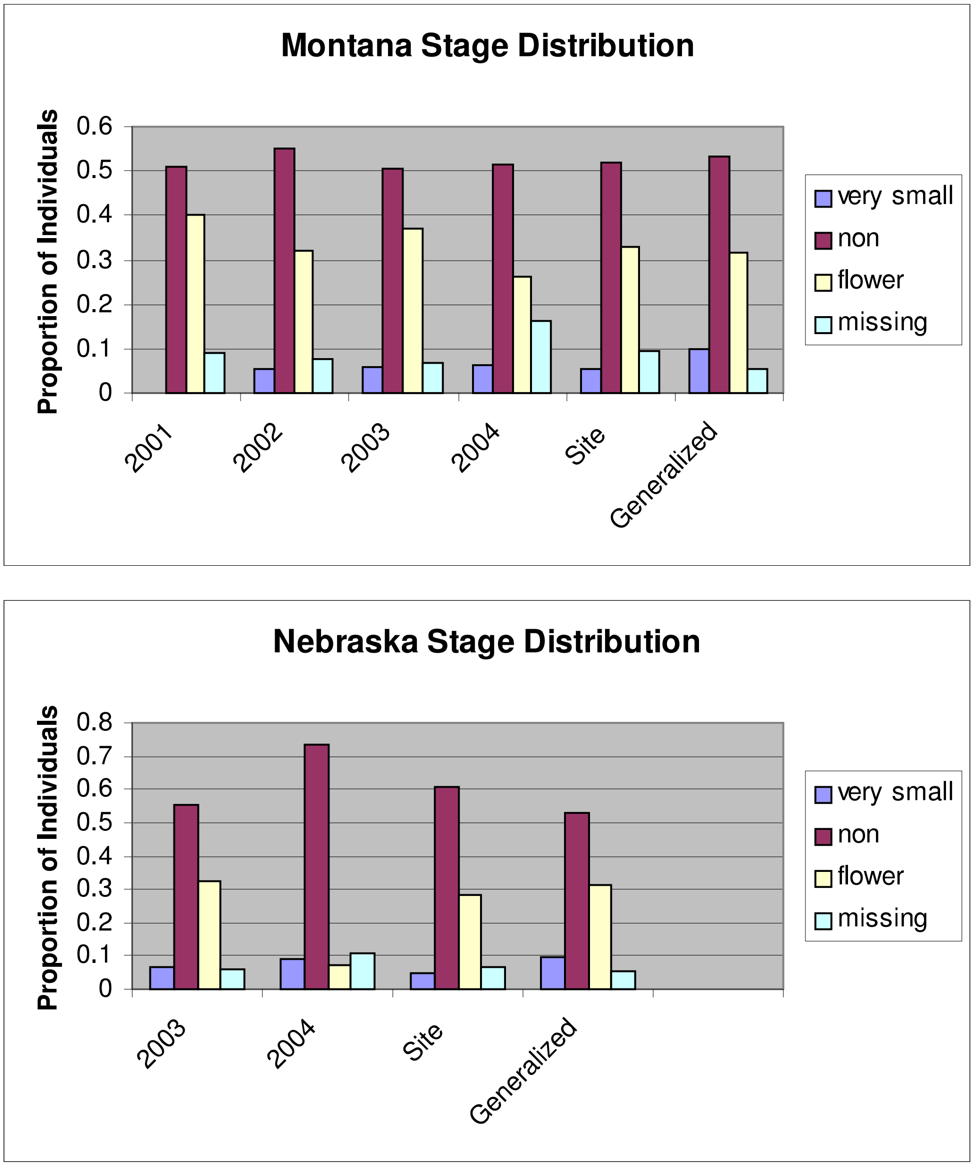


Figure 2.1b and 2.1c Observed and calculated stage distribution for the Montana and Nebraska populations

Comparison of the observed stage distributions to the calculated stable stage distribution for each site and for the generalized population. Stable stage distributions calculated from the pooled matrices (all years pooled at each site and all years all sites pooled for the generalized population).

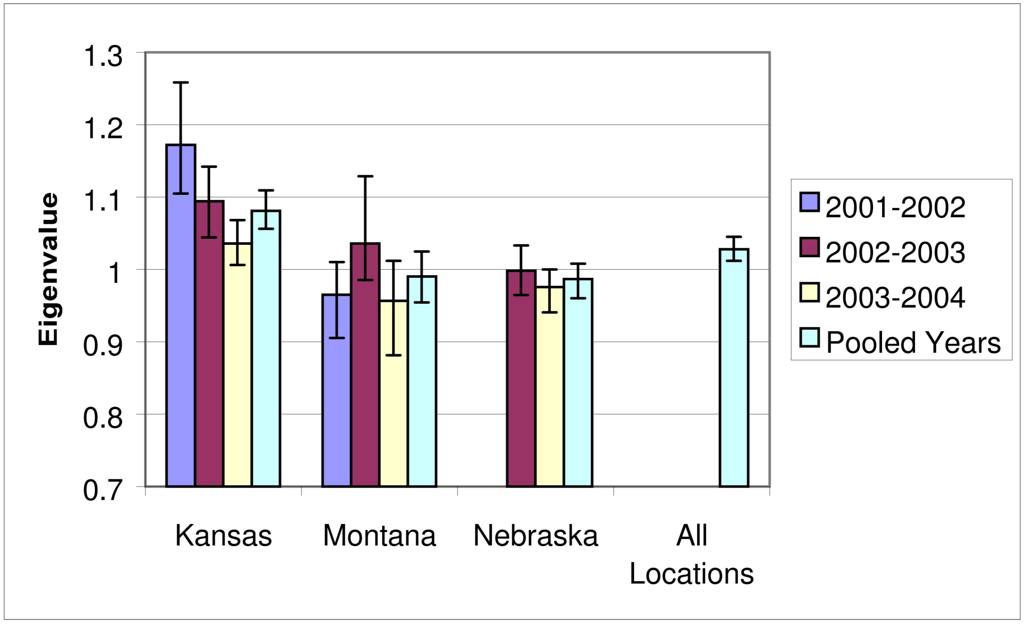


Figure 2.2 Calculated *Pediomelum esculentum* growth rates
Projected growth rate (λ) calculated from the eight location-year transition matrices as well as the pooled years at each location and generalized (all locations all years) pooled matrices. The 95% confidence interval shown is the result of 2,000 bootstrap re-sampling trials per λ.

Pooled Years				**Kansas**		
	Nebraska	Kansas			2003-2004	2001-2002
Kansas	0.0002			2001-2002	0.0002	
Montana	0.8392	0.0014		2002-2003	0.0331	0.0539
Montana				**Nebraska**		
	2003-2004	2001-2002			2003-2004	
2001-2002	0.8159			2002-2003	0.2414	
2002-2003	0.0341	0.0407				

Table 2.4 Statistical differences among growth rates
Probability that observed differences between pairs of calculated growth rates happened by chance under the null hypothesis that $\lambda_1 = \lambda_2$ computed directly from 10,000 random permutations of observed individuals.

	Ten Years			Fifty Years		
Type of Simulation	Mean Population Size	Realized Growth Rate	Number of 1000 replicate populations extinct	Mean Population Size	Realized Growth Rate	Number of 1000 replicate populations extinct
Kansas						
Deterministic	465	1.0880	0	10,472	1.0824	0
Demographic	369	1.0632	0	5,603	1.0689	0
Varying Elements	252	1.0233	0	664	1.0243	0
Random Matrix	570	1.1104	0	31,561	1.1065	0
Montana						
Deterministic	187	0.9933	0	176	0.9974	0
Demographic	134	0.9604	0	134	0.9919	360
Varying Elements	80	0.9123	0	1	0.8954	646
Random Matrix	178	0.9882	0	108	0.9878	0
Nebraska						
Deterministic	164	0.9804	0	99	0.9860	0
Demographic	123	0.9529	0	3	0.9199	462
Varying Elements	20	0.7958	275	0	0.7833	1000
Random Matrix	180	0.9898	0	137	0.9924	0
Generalized						
Deterministic	261	1.0270	0	756	1.0269	0
Demographic	205	1.0024	0	218	1.0017	0
Varying Elements	60	0.8860	37	0	0.8502	971
Random Matrix	236	1.0162	0	606	1.0206	0

Table 2.5 Stochastic simulation results

Comparisons of results of deterministic and three types of stochastic projections after ten and fifty years. The initial population size for all projections is 200 individuals which represents a small population of potential conservation concern. Stochastic results are based on the mean of 1000 replications.

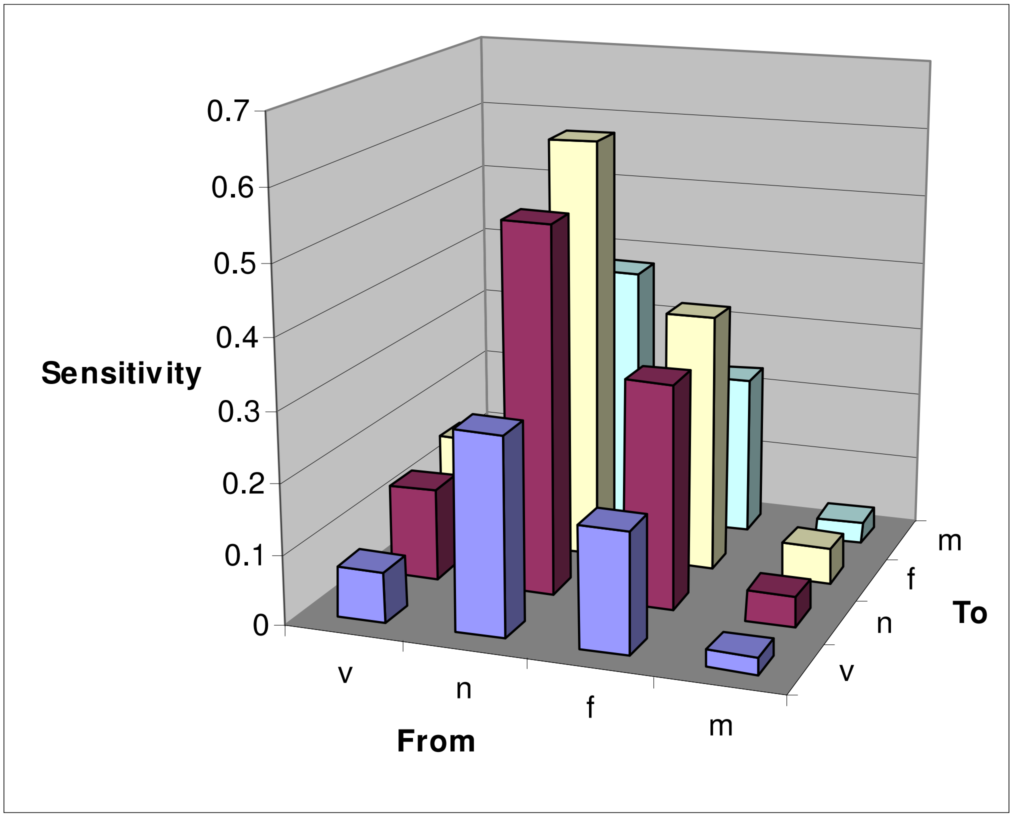


Figure 2.3 Sensitivity of Matrix Elements
Sensitivity of projected growth rate to changes in matrix elements calculated at A^{--}, the all sites all years pooled matrix representing the generalized population.

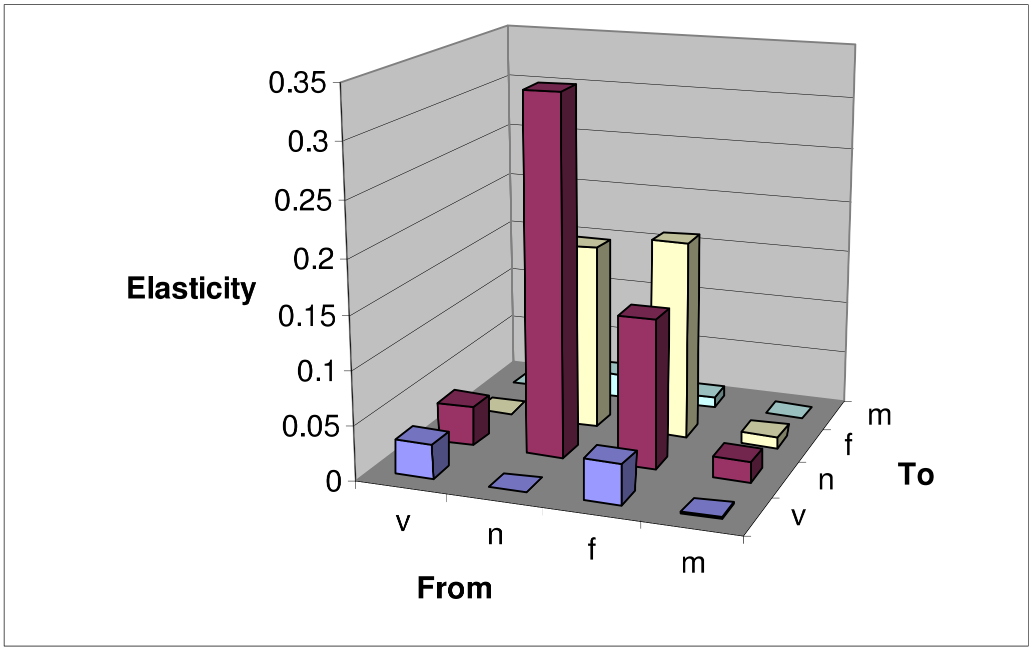


Figure 2.4 Elasticity of matrix elements
Elasticity calculated at $\mathbf{A}^{--}$, the all sites, all years, pooled matrix representing the generalized population.

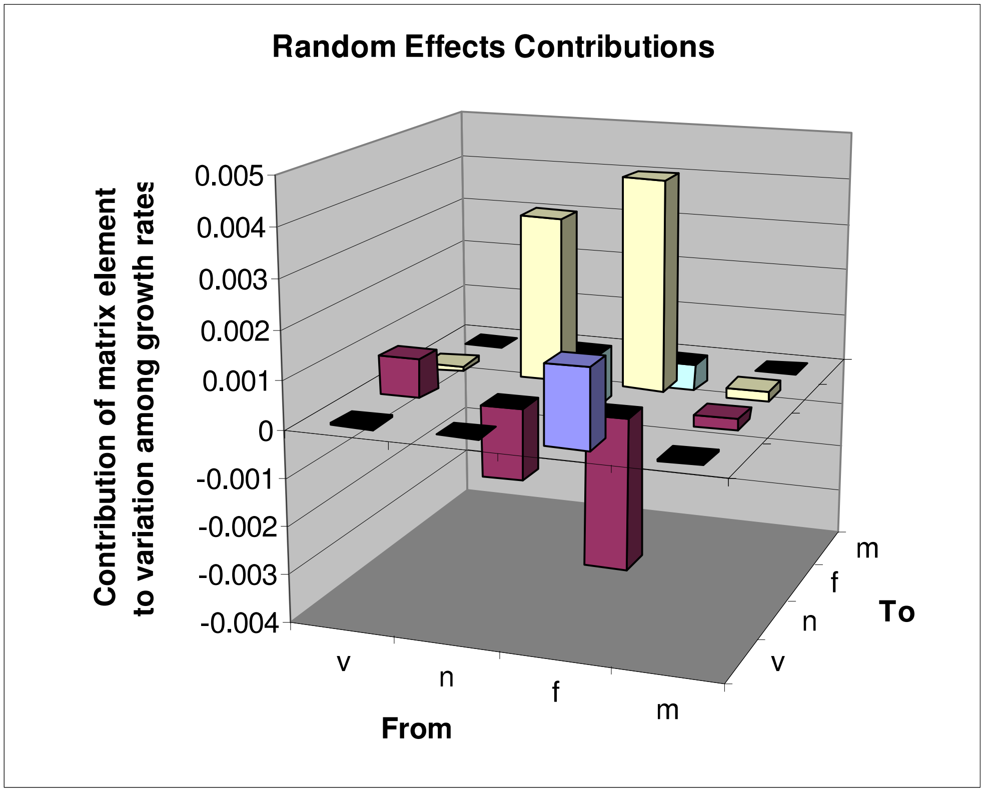


Figure 2.5 Random effects contributions of matrix elements to variation in projected growth rate among the eight location-year matrices

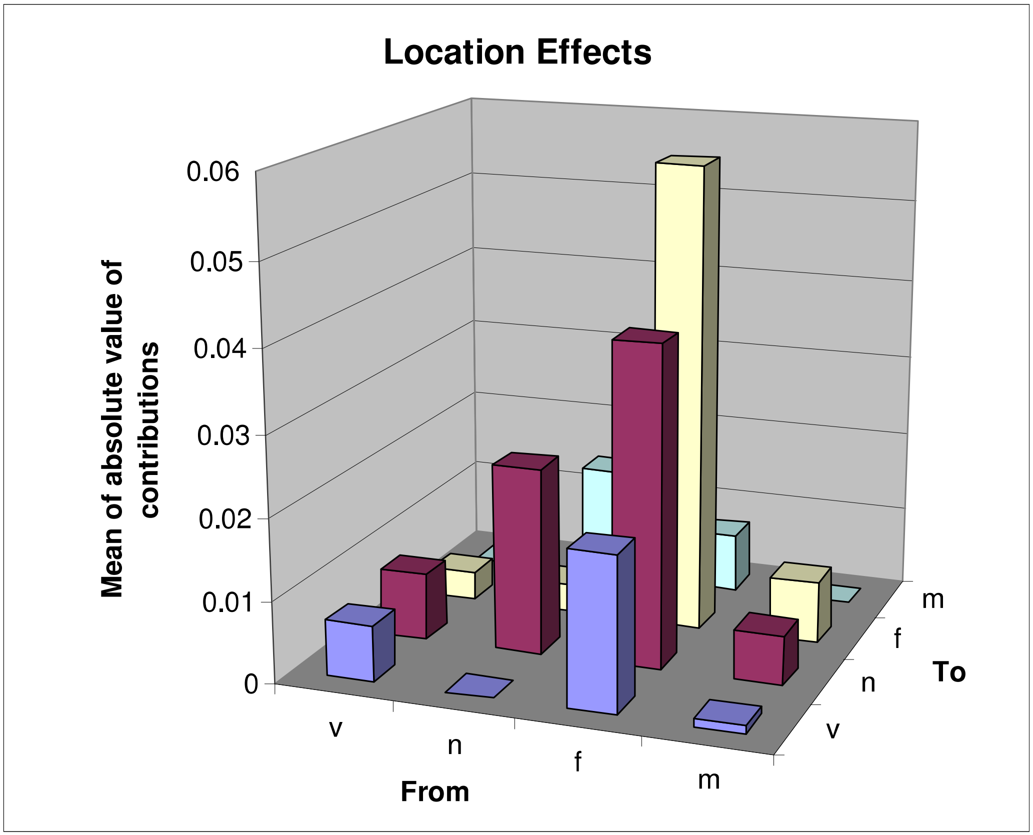


Figure 2.6 Contribution of matrix elements to location effects

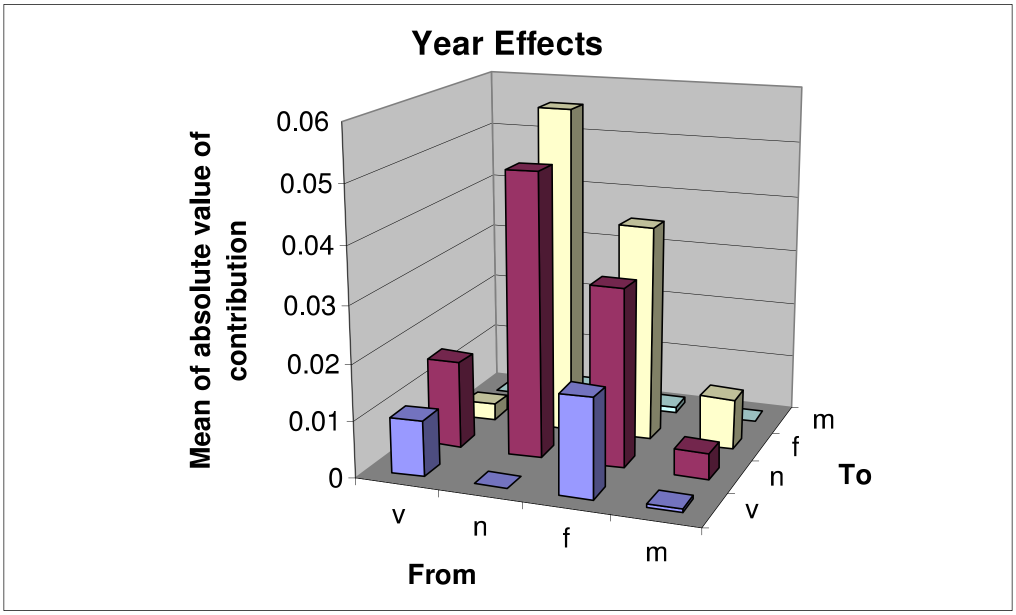


Figure 2.7 Contribution of matrix elements to year effects

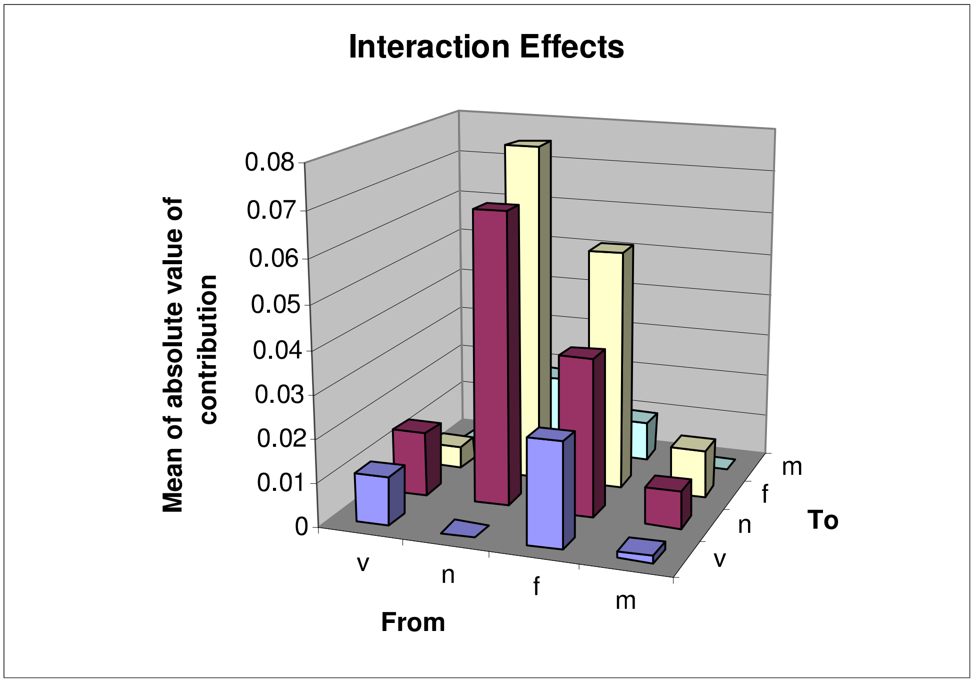


Figure 2.8 Contribution of matrix elements to interaction effects

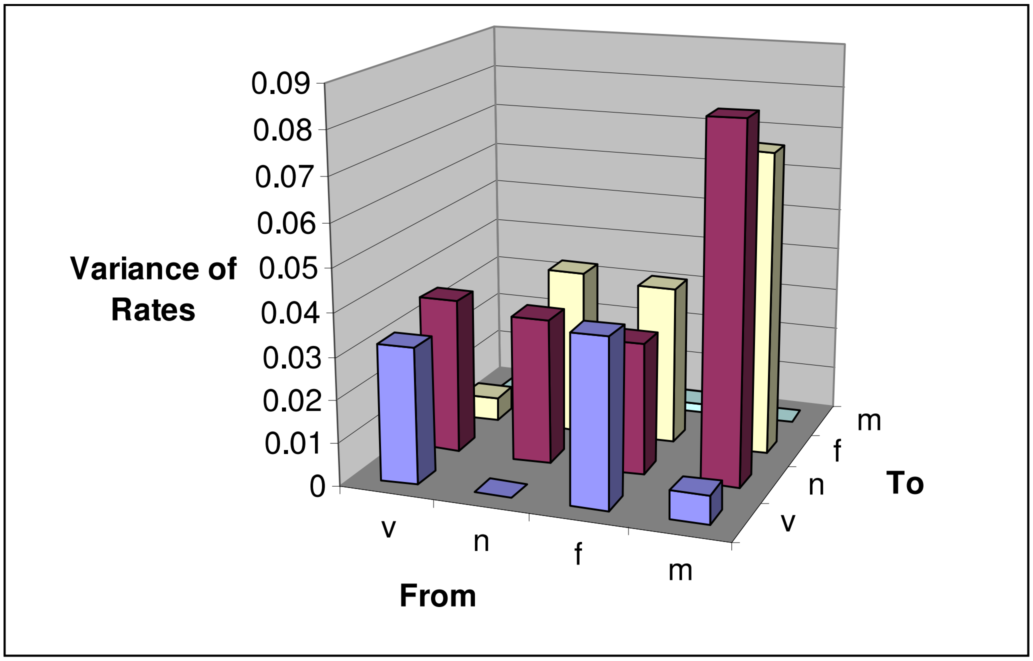


Figure 2.9 Variance of matrix elements among location-year matrices

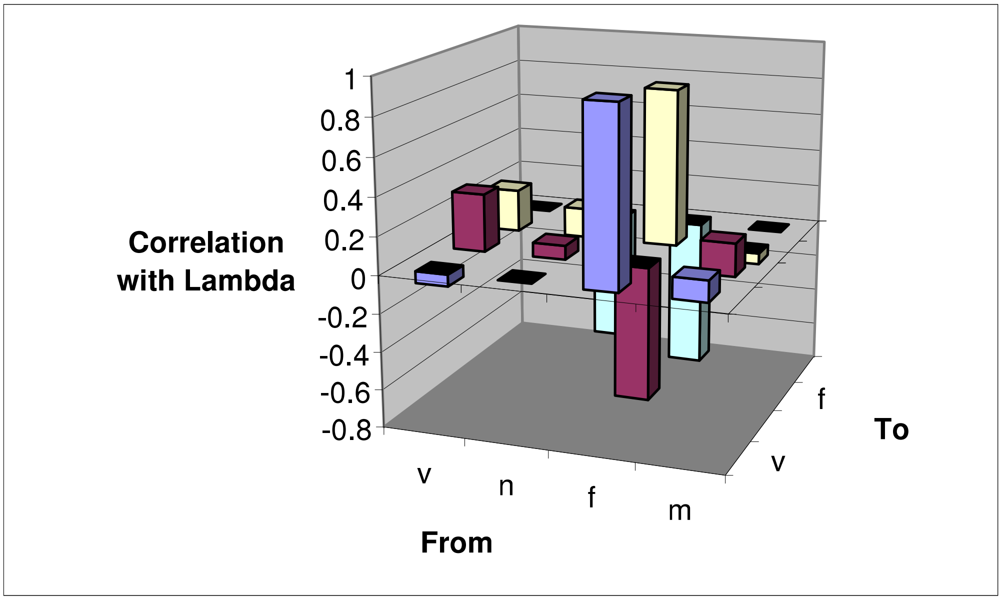


Figure 2.10 Correlation of changes in matrix elements with changes in projected growth rate (λ) among eight location-year matrices

	v to v	v to n	v to f	n to n	n to f	n to m
v to n	-0.350					
v to f	-0.472	-0.206				
n to n	0.516	-0.510	-0.009			
n to f	-0.276	0.512	-0.074	**-0.946		
n to m	-0.625	-0.123	0.257	0.061	-0.380	
f to v	0.577	0.141	-0.161	0.176	0.035	-0.611
f to n	-0.098	*-0.744	0.116	0.332	-0.422	0.353
f to f	0.247	0.693	-0.122	-0.216	0.365	-0.509
f to m	-0.632	-0.059	0.066	-0.345	0.076	*0.753
m to v	0.323	-0.057	-0.324	0.186	-0.177	0.013
m to n	0.033	0.593	-0.647	-0.068	0.125	-0.191
m to f	-0.289	-0.336	**0.968	0.024	-0.076	0.168

	f to v	f to n	f to f	f to m	m to v	m to n
v to n						
v to f						
n to n						
n to f						
n to m						
f to v						
f to n	-0.498					
f to f	0.629	**-0.97				
f to m	-0.701	0.236	-0.465			
m to v	0.340	-0.336	0.241	0.264		
m to n	-0.034	-0.136	0.191	-0.269	-0.327	
m to f	-0.055	0.097	-0.087	-0.007	-0.252	*-0.760

Table 2.6: Pearson correlation coefficients illustrating correlation among matrix elements across the eight location-year matrices

*significant at the $p < 0.05$ level
** highly significant at the $p < 0.01$ level

	Prospective Analyses		Retrospective Analyses (Life Table Response Experiments)				Basic Statistics	
			Random Effects	Fixed Effects				
Rank	**Sensitivity**	**Elasticity**	**Covariance Method**	**Location**	**Year**	**Interaction**	**Correlation with Eigenvalue**	**Variance**
1	f,n	n,n	f,f (+)	f,f	f,n	f,n	v,f (+)	n, m
2	n,n	f,f	f,n (+)	n,f	n,n	n,n	f,f (+)	f, m
3	f,f	f,n	n,f (-)	n,n	f,f	f,f	m,f (-)	v, f
4	m,n	n,f	v,f (+)	v,f	n,f	n,f	n,f (-)	f, n
5	n,f	n,v	n,n (-)	m,n	v,f	v,f	m,n (-)	f, f

Table 2.7: "Importance" of matrix elements
Five most important matrix elements as determined by sensitivity, elasticity, life table response experiments and basic statistical measures. Elements listed (to *i*, from *j*).
f = flowering, n= non-flowering, v = very small and m = missing.

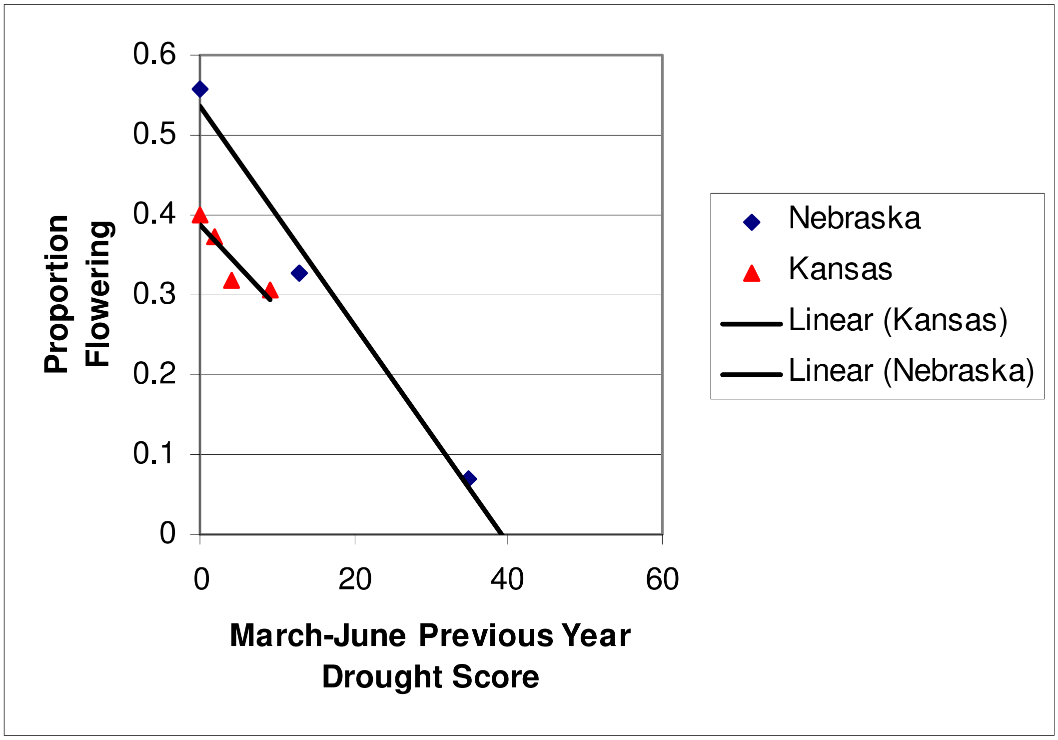


Figure 2.11 Flowering rate by drought severity
March through June drought score calculated by assigning numbers to the US Drought Monitor (NDMC 2006) weekly drought reports and summing all weekly scores for the period.
“Abnormally dry” =1, “Drought moderate” = 2, “Drought severe” = 3, “Drought extreme” = 4, “Drought exceptional” = 5
Least squares line shown.

CHAPTER THREE

The prairie turnip paradox: how harvest induced compensatory recruitment increases the sustainable harvest of a long-lived prairie legume

The prairie turnip, *Pediomelum esculentum* (Pursh) Rydberg, a perennial legume with an edible taproot, has a long history of human harvest. Use of the plant by people on the Great Plains of North America dates into pre-history (Reid 1977, Wedel 1978), and the plant was considered a staple food of many tribes of Plains Indians at the time of European-American settlement (Maisch 1889). While no longer a primary food source, the plant is still wild-harvested and has become iconic of Plains Indian culture (Wedel 1978, Wooden Knife 2006). Contemporary harvesters of prairie turnip roots often believe that they are helping the plant population as they dig the roots. Some harvesters actively scatter seeds as they collect while others feel they are helping the population simply by digging holes and leaving the tops of the plants with seeds attached (Reid 1977, Snell 2006). In discussing prairie turnips with harvesters, I have heard many comments stating that there are fewer plants than there used to be. While some harvesters ascribe this to destruction of the plant's prairie habitat or over-grazing, others also comment that prairie turnips are diminishing on prairies. They feel that there are fewer plants because fewer people dig them "properly", and that there are more plants where people dig them "properly".

Higher plant abundance where the plants are removed seems paradoxical. Prairie turnips are long-lived perennial plants and reproductive adults are killed when harvested. Removal of reproductive adults of long-lived organisms generally hinders, rather than helps population growth. In this paper I examine this paradox, investigating how prairie turnips are harvested and under what conditions this harvest is biologically sustainable. To begin, I compare prairie turnip harvest to established modes of sustainable harvest, including those in which increased growth and survival of remaining individuals compensates for the loss of harvested individuals. I describe a new mode of partial compensation for harvested individuals: harvest induced compensatory recruitment, and test for it in *Pediomelum esculentum* populations.

Established Modes of Sustainable Harvest

While the term "sustainable harvest" can incorporate economic factors and ecosystem processes, here I consider only the sustainability of the population size of the harvested species. Harvest practices are considered sustainable when the harvested population maintains a growing population size and thus a population growth rate (λ) of greater than one. This condition can be met when births outpace deaths and there is a resulting reproductive surplus, when harvested individuals are unimportant to population growth, and when the remaining population can compensate for harvested individuals through increased survival or reproduction (Hilborn et al. 1995).

Harvesting populations with reproductive surpluses (births outpacing deaths) is common among fast growing organisms. Our agriculture system is entirely dependent on creating environments where food plants and animals produce far more off-spring than merely replacing themselves (Hilborn et al. 1995). While prairie turnip have been suggested as a "food of the future" in both the 1890s and 2000s because the plants are drought tolerant and the are roots high in protein (Havard 1895, Pfaf 2003), they have not been cultivated on an agricultural scale. Because of the species' very slow growth rates, populations cannot be made to produce the necessary reproductive surplus quickly enough to be cost-effective.

Sustainable harvest levels have also been set for other slow growing organisms without consideration of compensation. Under optimal conditions in the 1980s, polar bear harvest was calculated to be sustainable if no more than 1.6% of the adult female population was harvested annually (Taylor et al. 1987). Annual harvest of less than 8% of the American ginseng (*Panax quinquefolium*) plants with more than three leaves has been calculated to be sustainable in Quebec, even though the plant is long-lived and the population growth rate in the absence of harvest is only slightly greater than one (1.045, Nantel et al. 1996). A low level of harvest of prairie turnips might be sustainable following this mode.

In many populations, only certain individuals contribute to reproduction, and the remaining individuals are considered "surplus". Surplus individuals may be post-reproductive. Surplus individuals may not have the opportunity to mate. For example, harvest of male deer often has insignificant effects on the remaining population. As long as there are some bucks around, the does will become impregnated, and if harvest is to control populations, females must be taken (Jensen

2000, Clutton-Brock et al. 2002). Surplus individuals may also be part of a stage largely doomed to death before they reach reproduction, such as plant seeds or fish eggs. For example, the tropical shrub *Grias peruviana* produces large quantities of seeds, but germination and survival rates of seedlings are extremely low. Peters (1990) calculated that *G. peruviana* could withstand harvest of 73% of the fruits without driving the population to extinction. The removal of reproductive adults, with potential for many more future reproductive episodes, as is the case with *Pediomelum esculentum* harvest, certainly does not fall into the category of removal of surplus individuals.

Sustainable harvest can also take place when the increased survival or reproduction of the remaining individuals compensates for the removal of harvested individuals. If competition for shared resources limits population growth, reducing the number of individuals through harvest leads to increased survival and reproductive rates for the remaining individuals (Smith 1990). Waterfowl management has long been based on this idea (Poysa et al. 2004), and release from density dependence may also increase sustainable harvest yields for long-lived perennial plants (Titkin 2002). Small cormlets of blue dicks, *Dichelostemma capitatum,* grow rapidly following traditional harvest of the larger plants. Based on these increased growth rates, Anderson and Rowney (1999) calculated that annual removal of up to half of the adults of this edible species could be sustained.

In theory, compensation is also possible for harvest of organisms competing for limited space. In these populations, the finite number of suitable habitats limits the overall population size. When an individual is harvested, another individual that otherwise could not have survived will occupy the patch of suitable habitat. Many mussel culture operations were founded on this principle. To an extent, lack of suitable substrate, rather than lack of mussel propagules or nutrients, limits mussel population growth. If ropes for mussels to attach to are provided during the annual spatfalls, mussels will attach and grow (Incze and Lutz 1980). Sustainable timber harvest can be viewed as a combination of these compensatory mechanisms, as trees compete for resources in an environment with limited suitable habitats. When a tree is removed, direct resource competition is reduced and one of a finite number of patches of canopy becomes available. Remaining trees increase growth and reproduction as a result (Smith 1990).

The death of an individual prairie turnip does not dramatically alter resource availability for the remaining plants. *Pediomelum esculentum* is not a dominant species and rarely are individual prairie turnips each other's nearest neighbor. Therefore, removal of an adult would not likely result in diminished competition and increased growth in the remaining population. However, harvester's references to "leaving the seeds for new plants" in the process of harvesting led us to question if there might be some compensatory recruitment following prairie turnip harvest. Harvest might not lead to decreased intra-specific competition among remaining individuals, but might create conditions suitable for growth of new individuals. At the population level, increased mortality due to harvest may be partially off-set by increased seedling recruitment induced by the act of harvest.

Addressing the prairie turnip paradox, how there can be more individuals where they are harvested than where they are not, involves determining if a mechanism exists to compensate for loss of harvested individuals through increased recruitment. I did this through a two-stage study. In the experimental stage, I conducted a harvest mimicking experiment and a small seed bank experiment. From these experiments I hoped to learn 1) how harvest affects seedling recruitment and 2) if *Pediomelum esculentum* seeds can persist in a seed bank. Following the experimental stage, I created models of population growth under different harvest regimes. Using matrix models created from non-harvested populations as a foundation (Chapter 2), I added harvest at different intensities and the results of my harvest-mimicking experiment to the projections. By simulating population growth with these models, I sought to learn 1) how harvest intensity, timing, and frequency affect population growth and harvest yield and 2) if harvest induced recruitment compensates for loss of adults. My overall goal was to determine the level of harvest of prairie turnips that can be considered sustainable.

Stage 1: Field Studies Methods

Before I designed my harvest mimicking experiment, I observed harvesters extracting roots in Kansas, South Dakota and Montana. Prior to the experiment, I also monitored the fates of individual plants in three populations in Kansas, Nebraska and Montana (Chapter 2). These observations provided us with basic information on harvest methodology and plant densities critical to my experimental design.

Harvest Mimicking Experiment

In order to determine the effects of harvest on seedling recruitment and survival, I experimentally mimicked harvest in a tallgrass prairie meadow and tracked the prairie turnip population the following two years. This experiment was conducted in an unplowed prairie dominated by big and little bluestem (*Andropogon gerardii* and *Schizachyrium scoparium*) in Franklin County, Kansas.

Sixty 1m x 1m plots five meters apart were laid out in a grid of ten transects ten meters apart in June, 2004. Within each transect, plots were randomly assigned a disturbance treatment (no hole, three holes or six holes per square meter) and a seed treatment (*Pediomelum esculentum* seeds added or not).

Average prairie turnip density in an adjoining prairie haymeadow was 1.2 turnips per m^2, with dense patches containing over 10 individuals per m^2. Therefore, creating three holes per plot mimics the harvest of all adult plants in a moderately dense population or a fraction of the plants in a dense population. Creating six holes per plot mimics the harvest all plants in a dense population, or a fraction of the plants in a very dense population. Modern harvesters listed using crow bars, spades, shovels, and pick axes to dig roots, while historical accounts include birch, chokecherry and service berry sticks as well as deer and elk antlers (Wedel 1978). Among these harvest methods, I chose to mimic root harvest using a spade, because spade holes were the disturbance simplest to replicate and the visible soil disturbances they created were of intermediate size. This method of harvest exposes bare soil, but does not deliberately overturn the soil. I timed the disturbances for the peak of prairie turnip harvest in Kansas, late June, which coincides with seeds ripening. I mimicked the usual harvest practice of leaving adult plants with ripe seeds by scattering thirty seeds in and around the harvest disturbances in half of the plots. Thirty seeds represent the average annual reproductive output of one large healthy individual (Grimes 1992, P. Allen pers. com. 2002) or six individuals in a population highly infested with weevils (Hermann 1983).

Within each plot, disturbances were randomly located on a 10cm grid system. Three "non-disturbance points" were chosen for each undisturbed plot in the same way. I created disturbances by using a spade to cut through the sod, and then lifted the vegetation, mimicked removing a root and placed the turf back in its hole. No attempts were made to reduce trampling while making disturbances, because the harvest process involves both digging and walking around. Each disturbance hole was intended to be square, 15cm on a side. Following digging, each disturbance was marked with a metal tag, as was each non-disturbance point. *Pediomelum esculentum* seedlings were counted, measured, and located on a grid defined by the plot frames in spring 2004 and again in spring 2005.

Because many plots had no seedlings in 2004 and 2005, the mean and within treatment variance for a whole treatment was zero, which violates the assumptions of a standard analysis of variance (ANOVA). Statistical analyses were therefore conducted using a non-parametric Kruskal-Wallis test in Minitab for Windows (version 12.21, 1998).

Seed Bank Experiment

Holes created by harvest could create suitable sites for germination of both newly produced seeds and seed from the seed bank. A first step in assessing the importance of potential compensation due to increased recruitment was to determine whether or not *Pediomelum esculentum* seeds could persist in the seed bank. If at least some seeds can persist in the seed bank, the magnitude of the potential effects of harvest on recruitment could be much greater, as enhanced recruitment would not be entirely dependent on the current season's seed production.

We set up an experiment to determine if *Pediomelum esculentum* seeds can persist for more than one year in the soil and how age of seed and depth of burial affect seed persistence. Prairie turnip seeds are produced in summer and germinate the following April, often requiring scarification to germinate (Reichart 1983, Spessard 1988). Mesh bags containing 20 seeds each were buried just below the surface and at a depth of 10cm, (to represent scattering seeds near the surface or burying seeds in the harvest hole) in an abandoned field eastern Kansas in late winter 2003. The seeds had been produced in summer 2000 and summer 2002 and purchased clean from a wildflower seed company in Nebraska. Seeds were stored in a freezer from the time of purchase (spring 2001 and late fall 2002) until burial. Only visibly whole seeds were included, those that had noticeable chips or holes were excluded from the experiment. One replicate of each treatment (seed age and depth of burial) was randomly assigned to a location in each of ten transects. Mesh bags

10cm x 10cm square allowed for gas and moisture exchange and for recovery of seeds.

Bags were excavated in spring 2004. At this time I could distinguish seeds that had not germinated in 2003 but were germinating in 2004 from seeds that had not germinated in 2003 and were not germinating in 2004. These categories were labeled “sprouts” and “hard seeds.” The hard seeds were further tested for potential viability using tetrazolium as an indicator (2,3,5-tri phenyl-tetrazolium chloride).

Stage 1: Field Studies Results

Harvest Mimicking Experiment

The number of seedlings found in spring 2004 on the experimental plots varied from no seedlings in any of the undisturbed plots without additional seeds to an average of 6.7 for the highly disturbed plots with seeds added (Figure 3.1). Both seed treatment and disturbance treatment had a significant effect on seedling recruitment rate.

Of the seedlings found in 2004, 76% of them survived to spring 2005, and another small batch of new seedlings appeared in spring 2005 (Figure 3.2).

These results suggest that seedling recruitment is both disturbance and seed limited and that traditional harvest disturbing the ground when the seeds are ripe may result in increased numbers of young plants.

Seed Bank

A small seed bank developed in the course of my short study. Of the seeds buried in the late winter of 2003, most germinated or disintegrated during the 2003 growing season. However, almost 25% of the original seeds were either newly germinating or still intact in the spring of 2004, after over a full year in the ground (Figure 3.3). Older seeds persisted less often than newer seeds ($p < 0.05$ for a two sample t-test), but depth of burial did not have a significant effect on either number or sprouts or persistent seeds. Tetrazolium tests indicated 100% of the remaining intact seeds were potentially viable.

From these limited results I can conclude that *Pediomelum esculentum* seeds can persist at least two years in the ground. The ability of *P. esculentum* to persist as seeds is supported by the 2005 seedlings in the harvest mimicking experiment. In the highly disturbed plots 1.7 new seedlings were found in 2005 beyond those seen in 2004, which indicates that 6% of the original seeds waited a full year to germinate and successfully recruited, even though 2004 was a good year for germination and recruitment. In a garden patch where I planted seeds only in spring 2001, cotyledon-bearing seedlings were found in 2003, again suggesting seed persistence.

Both experimental and field results confirm that seeds can persist for at least 22 months prior to germination, and likely more, but reveal little about the long term importance of the seed bank.

Stage 2: Model Methods

Existing Matrix Population Models

I previously monitored non-harvested populations of *Pediomelum esculentum* in grasslands in Kansas, Nebraska and Montana (Chapter 2). In brief, I tracked the fates of individual plants from 2000 to 2004 in Kansas and Montana and from 2001 to 2004 in Nebraska. Individual plants were classified into four morphologically distinct life stages: very small individuals with three-parted leaves, non-flowering plants, flowering plants and missing plants. The "very small" stage included new seedlings and those plants that maintained a seedling-like size and leaf-shape. "Non-flowering" plants possessed adult (five-parted) leaves, but no flowers. Transitioning back and forth between "non-flowering" and "flowering" was common. The "missing" stage included all plants that I had seen the previous year as adults but could not be seen in the present year. Prairie turnips can remain fully dormant for over a year (Hermann 1983) and could be grazed early in the season. The "missing" stage includes both types of individuals.

Eight stage based (Lefkovitch) transition matrices were created based on the number of individuals at one location transitioning from one stage to another over the course of a year (Lefkovitch 1965, Caswell 2001). The reproductive rate for each matrix was calculated by dividing the new very small individuals at time t+1 by the number of flowering plants at time t. General matrix form is given in Table 3.1. Observed transition matrices, along with the associated dominant eigenvalue (λ, or projected growth rate) are given in Table 3.2.

Simulation Models

Starting with the basic matrix population models for non-harvested populations, I added harvest and incorporated the results of my harvest-mimicking experiment. I used long run (1,000 year) stochastic simulations to compare stochastic growth rates under different continued harvest regimes and short term stochastic simulations to compare harvest yield and population status at ten years.

For all simulations, I started with the observed transition matrices for the generalized population and the Kansas site. The generalized population includes populations from across the species' range through years of greatly varying environmental conditions. This represents my best estimate of how the population is faring "overall" and is my most useful tool for making general statements about harvest of the species. The Kansas monitoring site is immediately adjacent to the harvest simulation experiment and therefore experienced the same environmental conditions over the course of the study. The Kansas population was also included as a "best case scenario" in the simulations. Unlike the other study sites (and thus the generalized population), which had good and bad years for population growth during my study, conditions in Kansas led to projected population growth every year of the monitoring study. While I do not propose that these conditions will prevail indefinitely, harvest estimates for the Kansas population provide a high-end estimate of the number of prairie turnips that could be harvested if good growing conditions could be maintained.

For each time step in the stochastic simulations for the generalized population, the population vector was multiplied by one of the eight observed transition matrices, selected randomly with replacement. Likewise, for the Kansas population, one of the three observed transition matrices was drawn at random for each time step. Simulations were programmed in Java. All simulations started with a population size of 1,000 individuals, which represents a moderate sized population large enough to be harvested. These individuals were distributed among stage classes based on the observed average stage distributions.

Stochastic projections were run with harvest rates of 0, 0.01, 0.05, 0.10, 0.30 and 0.50, representing harvest of none, one percent, five percent, thirty percent and half of the visible adults (those in the "non-flowering" and the "flowering" stages). Harvest intervals were set at 1, 2, 3 and 5 years. For each type of simulation, four harvest methods were compared: pre-reproductive and post-reproductive harvest with no compensation, harvest with observed compensation and harvest with qualified compensation. All projections are based on density-independent models. The assumption of density independence likely fits small, dispersed plant populations with growth rates near one (as *Pediomelum esculentum* populations were observed generally), but is an increasingly erroneous assumption as population density increases (as in the case of long-run Kansas projections) (Bierzychudek 1999).

Pre-reproductive and post-reproductive harvest

By convention, harvest is usually modeled as occurring immediately after reproduction (Getz and Haight 1989), yet timing of harvest can play a crucial role in modeling plant harvest (Freckleton et al. 2003) and may in *Pediomelum esculentum* models. *P. esculentum* is a tumbleweed with a very short growing season. Individual plants emerge in late spring and flower in May or June. The entire aboveground plant structures dry and tumble by late June or July, after which time the roots impossible to locate. Plants are only visible, and thus harvestable, for a short time, and most of this time is prior to seed-set. Harvesters, however, overwhelmingly report waiting until seeds are produced to harvest, either because of perceived benefit to the plant population or improved palatability of the root once it is starting to store, rather than expend, nutrients (Toineeta 1970, Wedel 1978, Kindscher 1987, Snell 2006). In order to assess the effect of timing of harvest, I compared a pre-reproductive harvest to a post-reproductive harvest. In the pre-reproductive model, harvested individuals are subtracted from the population before the population is multiplied by the transition matrix:

$$\mathbf{x}\,(t+1) = \mathbf{A}\,(\mathbf{x}(t) - \mathbf{u}\,(t))$$

In the post-reproductive model, the harvested individuals are subtracted after the population is multiplied by the transition matrix.

$$\mathbf{x}\,(t+1) = \mathbf{A}\mathbf{x}(t) - \mathbf{u}\,(t)$$

In both cases, **x** represents the population vector, **A** the transition matrix and **u** is a vector containing the number of individuals harvested in each stage class (following Getz and Haight 1989 and Nantel et al. 1996).

Formally, $\mathbf{u}(t) = h\mathbf{a}\mathbf{x}(t)$ where h is the harvest rate and a is a vector identifying the proportion of each stage class harvestable. In these simulations, $\mathbf{a} = [0\ 1\ 1\ 0]$ indicating that very small and missing individuals are not harvested and non-flowering and flowering individuals are. For this series of simulations, therefore, I assume that non-flowering and flowering plants are equally likely to be harvested.

Addition of compensatory recruitment

In my harvest mimicking experiment, I found higher levels of seedling recruitment on harvest-holes than I had observed in the undisturbed populations I was monitoring. In order to include this increase in seedlings following harvest, I added an element of compensatory recruitment to my post-reproductive harvest model by means of a different reproductive rate for harvested adults. This rate, $\text{Reproduction}_{\text{compensation}}$ (R_c), was calculated by dividing the average number of seedlings (6.8) in a high disturbance seed addition plot, by the number of disturbances, 6. The resulting rate 1.1333 is the average reproduction per disturbance.

In the observed compensation simulations, R_c was multiplied by the proportion of flowering and non-flowering adults harvested, representing the observed situation that in the presence of seeds, disturbances themselves lead to increased seedling recruitment. Because plants frequently vary between flowering and non-flowering stages, and seeds can persist in the seed bank, it is reasonable to believe that seeds would be present where a non-flowering adult had been dug. Seeds could also easily be scattered as harvesters shake nearby flowering plants.

In the qualified compensation simulation, R_c was multiplied only by the number of flowering adults harvested, directly representing the situation where only the flowering plants removed lead to increased seedling production. In so qualifying this rate, the number of new seedlings projected is decreased by more than half (as less than half of the harvested adults are flowering in any given year) from the level I observed. Indirectly, therefore, the qualified compensation simulations also represent a scenario in which survival of new seedlings on harvest holes is lower than average due their presence in high density.

Mathematically, models of the four harvest methods vary only in the calculation of the number of individuals in the "very small" stage at time t+1. Based on multiplying a population vector [v n f m] where v, n, f and m are the numbers of very small, non-flowering, flowering and missing individuals at time t, by the transition matrix given in Table 1, the number of very small individuals at time t+1 in the absence of harvest is calculated:

No harvest $v_{t+1}= v_t(P_{v,v}) + n_t(P_{v,n}) + f_t(P_{v,f}) + m_t(P_{v,m})$

$P_{v,f}$ is the average reproductive rate and $P_{v,n}$ equals zero because non-flowering plants do not reproduce.

For post-reproductive harvest, this equation is unchanged.

Post-reproductive $v_{t+1} = v_t(P_{v,v}) + n_t(P_{v,n}) + f_t(P_{v,f}) + m_t(P_{v,m})$

When harvest occurs before reproduction, only those individuals not harvested can reproduce:

Pre-reproductive $v_{t+1} = v_t(P_{v,v}) + n_t(1-h)(P_{v,n}) + f_t(1-h)(P_{v,f}) + m_t(P_{v,m})$

At observed compensation, harvested individuals in the non-flowering and flowering classes lead to increased recruitment at a different rate (R_c)

Observed Compensation $v_{t+1} = v_t(P_{v,v}) + n_t(1-h)(P_{v,n}) + n_t(h)(R_c) + f_t(1-h)(P_{v,f}) + f_t(h)(R_c) + m_t(P_{v,m})$

and at qualified compensation only the harvested flowering plants lead to increased recruitment

Qualified compensation $v_{t+1} = v_t(P_{v,v}) + n_t(1-h)(P_{v,n}) + f_t(1-h)(P_{v,f}) + f_t(h)(R_c) + m_t(P_{v,m})$

Population Size and Harvest Yield

One thousand replications of ten-year simulations were run for both Kansas and the generalized populations, for each of the four methods of harvest, at each of six levels of harvest and each of the four harvest intervals. The mean population size and the mean number of individuals harvested were recorded. Those harvest regimes that resulted in a population size at ten years equal to or greater than the initial population size were considered sustainable. These regimes were ranked by total yield over the ten-year period.

Stochastic Growth Rate

Following Tuljapurkar (1990, 1997), the stochastic growth rates were calculated by long-run simulation. Rates were calculated for both Kansas and overall, for each of the four methods of harvest, at each of 6 levels of harvest and each of the four harvest intervals. Each simulation was run for 1,000 trials for 1,000 year time steps. One of the observed transition matrices was drawn at random for each time step. Estimated stochastic growth rates were calculated from the median final population size of the 1,000 simulations using the equation:

$$\text{Log } \lambda_{\text{stochastic estimate}} = \frac{\log N(T) - \log N(0)}{T}$$

In this equation, N represents the population size and T the number of time steps (Tuljapurkar 1997, Caswell 2001). Following Nantel et al. (1996), I plotted the estimated stochastic growth rates vs. proportion harvested and calculated the equations of the lines as a means of determining the mathematical relationship between growth rate and harvest level and harvest interval.

Maximum Sustainable Harvest Level

Maximum sustainable harvest is defined as the level of harvest at which $\lambda_{\text{stochastic estimate}}$ equals one (Nantel et al. 1996). Plotting the stochastic growth rate vs. proportion harvested for each treatment and harvest interval, I solved for x when y equals one. The resulting level of harvest is the average proportion of non-flowering and flowering adults that can be removed while maintaining the population size (Nantel et al. 1996).

Stage 2: Model Results

Ten Year Harvest Yield

Adding compensatory recruitment to the model greatly increases the number of individual plants that can be sustainably harvested from a population with an initial size of 1000 individuals. For the overall population, an observed compensation, 5 year interval, 30% harvest regime yielded 523 turnips in ten years, almost three times as many as the best-yielding regime without compensation (post-harvest, 10% every five years, yielding 179 individuals) (Table 3.3). As expected, sustainable yields are considerably higher under the best-case Kansas scenario (Table 3.4). Here, too, timing of harvest, addition of compensation and a recovery period between harvests increases the sustainable yield.

Stochastic Growth Rates

Although the observed compensation model of harvest led to considerably higher growth rates than the same levels of uncompensated harvest, all harvested populations averaged slower growth than the unharvested population (Figures 3.4 and 3.5). The slope of the linear decline of growth rate along the gradient of harvest pressure varied with method of harvest and harvest interval with pre-reproductive harvest every year leading to the steepest decline. Harvest with observed compensation every five years led to the gentlest decline.

Realized growth rate with harvest is a function of both the proportion harvested (h) and the years between harvests (t). For generalized population at a pre-reproductive harvest, this relationship can be described as:

$$\lambda_{\text{harvest}} = \lambda_{\text{noharvest}} - 0.903\, h\, t^{-0.908}$$

and for the observed compensation harvest as:

$$\lambda_{\text{harvest}} = \lambda_{\text{noharvest}} - 0.320\, h\, t^{-0.650}$$

The longer the harvest interval and the greater the level of harvest, the more pronounced the difference between harvest methods.

Maximum Sustainable Yield

For the generalized population without compensation, less than three percent of the visible adults can be sustainably removed from the population each year. (Figure 3.6). Even with high compensation, less than 7% can be removed. A longer recovery time between harvests leads to higher sustainable yields and greater differentiation among models of harvest.

Sustainable harvest levels were considerably higher for the Kansas population, where, mathematically, all of the visible adults can be sustainably removed every five years under the high compensation model (Figure 3.7).

Discussion

Harvest Implications

Our models suggest that very low levels of prairie turnip harvest may be sustainable in fluctuating environments and that traditional harvest practices increase the yield that is sustainable. Harvesting the plants when the seeds are ripe increases the sustainable yield over pre-reproductive harvest. The practice of leaving plant tops, with seeds attached, at the harvest holes leads to the possibility of increased recruitment to partially compensate for the harvested individuals. Even with good timing and compensation, however, only very low levels of harvest are sustainable.

Similar to harvesters of other wild plants, prairie turnip diggers informed us that their concerns for the plant populations and future harvest led them to either only take a fraction of the plants available or harvest in one area only infrequently. The "rules" of wild harvesting vary substantially, from taking one in twenty individuals to taking half (Endholm and Wilder 1998, Hatter 2005, Seward 2005, Lemmerman 2006). A typical figure is one-third or every three years, a suggestion reported by Crow Elder Alma Hogan Snell as advice from her Grandmother Pretty Shield, a traditional Crow Indian who harvested prairie turnips from the 1860s to 1920s (2006).

Based on my projections, removing one third of the adults from the generalized population every year will lead to population decline even with compensation from the high levels of recruitment I observed. In fact, only taking one third of the visible adults and waiting for three years will still lead to population decline. In the terms of the most common uses of prairie turnips, these numbers suggest that a moderately sized (1,000 plant) population will not recover from an annual harvest large enough for a Crow Indian feast (100 roots) or a decorative

Lakota braid (50-100 roots). These activities could be sustained on an annual basis if the harvesters were to rotate among at least five different patches. Longer intervals between harvests also lead to larger long-term yields from each population. With compensation, harvesting 30% of the visible adults every five years and harvesting 5% every year are both sustainable, but at the end of ten years, the yield of the former is 125 individuals more than the latter. The difference is real: two braids worth of roots or an extra large tribal feast.

New Mode of Compensation

Partial compensation for the removal of harvested individuals by means of reducing competition and increasing survival and reproduction among the remaining individuals has been well documented in both plant and animal species (Hilborn et al. 1995, Anderson and Rowney 1999, Boyce et al. 1999, Ticktin 2002). The compensation suggested here for *Pediomelum esculentum*, however, does not follow this pattern. My experimental results suggest that the act of harvesting, rather than the removal of individual competitors, leads to increased recruitment. To my knowledge, this form of harvest-induced compensatory recruitment has not been previously addressed in the harvest literature. Harvest-induced compensatory recruitment is distinguished by increased seedling recruitment following harvest. It is different from mowing or coppice systems, wherein harvest stimulates increased growth rates within the harvested individual, and thinning systems, wherein harvest removes competitors.

Although I cannot imagine a situation in the animal kingdom where the act of hunting, rather than the removal of competitors, leads to new births of game species, harvest induced compensatory recruitment is probably not unique to *Pediomelum esculentum* among plants. Lack of disturbance limits seedling recruitment among many prairie species (Foster et al. 2004). For these species, too, harvesting of roots may create suitable sites for recruitment of new individuals. In deciduous forests in the eastern U.S., American ginseng (*Panax quinquefolium*) harvesters are encouraged to sprinkle seeds as they dig roots and to only harvest when the berries are ripe. The expectation of better population persistence when harvest disturbance coincides with seed ripening (McGraw et al. 2005) suggests to us that this species may also benefit from harvest induced compensatory recruitment when collected using traditional methods. This mode of compensation could also influence population recovery of dispersed understory plants extracted from tropical forests. Research by M. Kat Anderson and colleagues among California Indians has found traditional harvest practices to increase populations through thinning, coppicing and fire (Anderson 1990, Anderson 1996, Anderson and Rowney 1999). Statements by California Indian harvesters that traditional harvest of bulbs, roots and tubers leads to more young plants suggests that harvest induced compensatory recruitment may also be a factor for these species as well (Anderson 1990, Anderson and Nabham 1991, Anderson 1996, Anderson and Rowney 1999).

Harvest induced compensatory recruitment may also thwart efforts to control invasive species. Many invasive species are prolific seed producers and thrive on disturbance (Rejmanek 2000, Clements et al. 2004). When plants are “harvested” or pulled for control, the resulting disturbance could lead to increased recruitment. Preliminary results from woodlands in eastern Kansas demonstrate marked increases in recruitment where garlic mustard (*Alliaria petiolata*) is controlled by pulling alone (J. Moody-Weis, pers. com). Longer term *Pediomelum esculentum* studies and research into other species should reveal how pronounced and prevalent harvest induced compensatory recruitment is.

Density and Thinning

That seedling recruitment increased on harvest holes was clear from my experimental results. How to quantify the harvest induced compensatory recruitment was much less clear, because I do not know the long-term fates of the seedlings that were recruited. The observed compensation model possibly overstates the long-term survival of compensatory seedlings, as they are closer together than adult plants in the wild. As a result, these close-together seedlings may experience higher mortality rates and individuals will likely be thinned. On the other hand, the model does not directly include any positive effects on the seeds in the seed bank. It also does not include the continued positive effects of disturbance beyond the first year. The qualified compensation model understates the experimentally observed compensatory recruitment, reducing it by more than half, in an attempt to correct for possible future increased seedling mortality. As with the observed compensation model, it also does not include any of the long-term benefits of harvest disturbances.

An increase in seedling recruitment does not necessarily lead to a real increase in population growth rate. Just as most seeds never germinate, in many species most seedlings never grow up to reproduce. The marked increase in seedling recruitment in the harvest mimicking experiment leads to the question as to how many of the additional seedlings can survive to adulthood when they are germinating in close proximity to one another on the disturbance holes. Without following the seedlings to adulthood, I cannot answer this question directly, but I do have some suggestive evidence. Those seedlings that died between sampling in 2004 and sampling 2005 were, on average, closer to their nearest neighbor in 2004 than those that survived, (fatalities averaging 7.0cm from a neighbor and survivors 12.2cm, $p = 0.063$ for a two-sample t-test). The seedlings in the experimental plots are also on average nearer to each other than the plants in the densest 3m x 3m plot in the in monitoring study (11.0cm vs. 21.9cm, $p < 0.01$ for a two-sample t-test).

Conclusions about self-thinning, however, should be made with caution. Despite the death of 24% of their cohort, seedlings that survived to 2005 were no further to their nearest neighbor in 2005 than they had been in 2004. The experimental seedlings are about the same distance from each other as plants in one square meter of a nearby monitoring plot, which, rather than thinning itself, actually became denser through the years of monitoring.

Seedling survival from 2004 to 2005 in the experimental population (76.5%) is on par with overall survival of very small individuals in the wild population over all years (76.7%) (Chapter 2). The "very small" stage in the wild population, however, includes individuals of multiple ages, and survivorship tends to increase with age (Hermann 1983, Chapter 2). The survival rate of true seedlings in the experiment, therefore, is higher than the survival rate of true seedlings in the monitored wild populations. This is consistent with Hermann's (1983) finding that prairie turnip seedlings survive better on disturbances than undisturbed prairie. These results suggest that my method of modeling compensatory recruitment as a pulse in recruitment followed by a return to the observed un-harvested transition rates in subsequent years is not altogether unreasonable.

The continued effects of disturbance are not trivial. The changes in conditions caused by harvest may increase recruitment beyond the initial surge. Twenty-two months after mimicked harvest, highly disturbed plots had an average of 1.7 new prairie turnip seedlings. This rate of 0.2833 new seedlings per old hole was higher than the observed reproductive rate (seedling per flowering plant) in all but one of the eight transitions in the populations I monitored (Chapter 2). I did not try to include this "seedlings per old hole" rate in my models, but it is worth noting that harvest-like disturbance was followed by an immediate spike in recruitment the next spring as well as an elevated level of recruitment from the seed bank a year later.

The study also does not address the effects of very high levels of disturbance on seedling recruitment and population growth. Among levels of disturbance tested, which are realistic mimics of harvest-like disturbance, higher levels disturbance led to higher levels of seedling recruitment. *Pediomelum esculentum*, however, has been labeled as a "decreaser" under increasing grazing pressure (Weaver and Albertson

1956) and given a “conservative” coefficient of conservatism for Kansas (Freeman and Morse 2002). Both labels suggest that the species does not tolerate extreme levels of disturbance. Therefore it is likely that at some increased level, harvest-like disturbances would have detrimental rather than positive effects on *P. esculentum* establishment. Further empirical studies would be needed to elucidate whether or not this detrimental level of disturbance is outside of the range of reasonable harvest levels.

Conclusion

Paradox Solved?

These results do not provide a complete solution to the paradox of larger populations where plants are traditionally harvested. These results suggest a partial solution. Certainly my models project that traditionally harvested populations will fare better than those harvested off-season or by removing entire plants from the site. I suspect that the full solution to the paradox may be part biological and part sociological. Biologically, harvest induced compensatory recruitment promotes the recruitment of new individuals. Sociologically, traditionally harvested areas have higher plant densities because traditional harvesters chose to dig in the areas with the most plants.

Altogether, I note that traditional harvest does not directly compensate for the removal of *Pediomelum esculentum* adult plants. According to my models, unharvested populations fare better than harvested populations. However, the disturbances caused by traditional harvest do provide excellent seed beds for prairie turnips and seedling recruitment is markedly higher on these disturbances than in undisturbed prairie. When harvest is timed so that seeds are present on the plants and left in the field, the resulting harvest induced compensatory recruitement nearly triples the number of plants that can be sustainably harvested. This mode of compensation, where the very act of harvest, rather than the removal of an individual competitor, increases reproductive rates, is first documented here. Because many plants are disturbance limited for recruitment, similar forms of compensation are likely for other root-harvested plants.

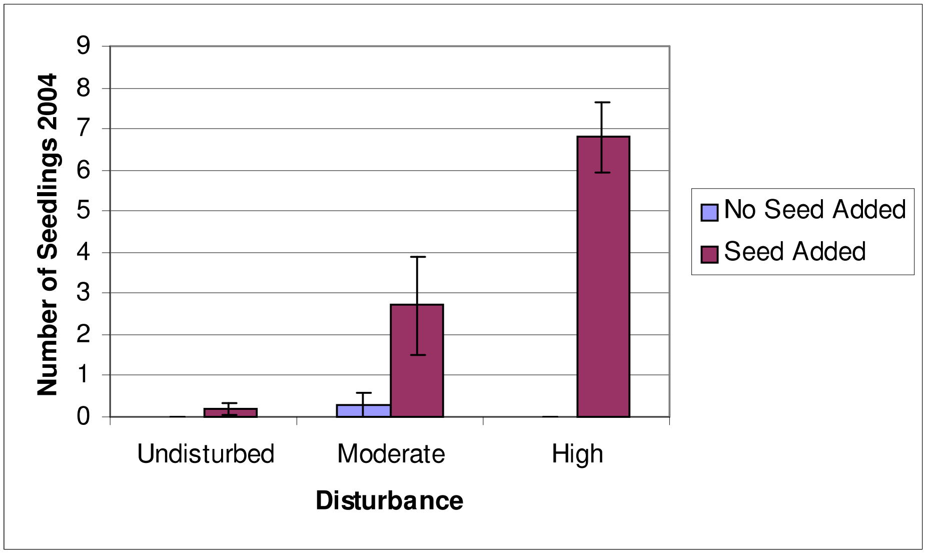


Figure 3.1 Average number of *Pediomelum esculentum* seedlings on plots by treatment in spring 2004
Differences among treatments highly significant ($p < 0.01$) based on a non-parametric Kruskal-Wallis test. Error bars represent the standard error of the mean.

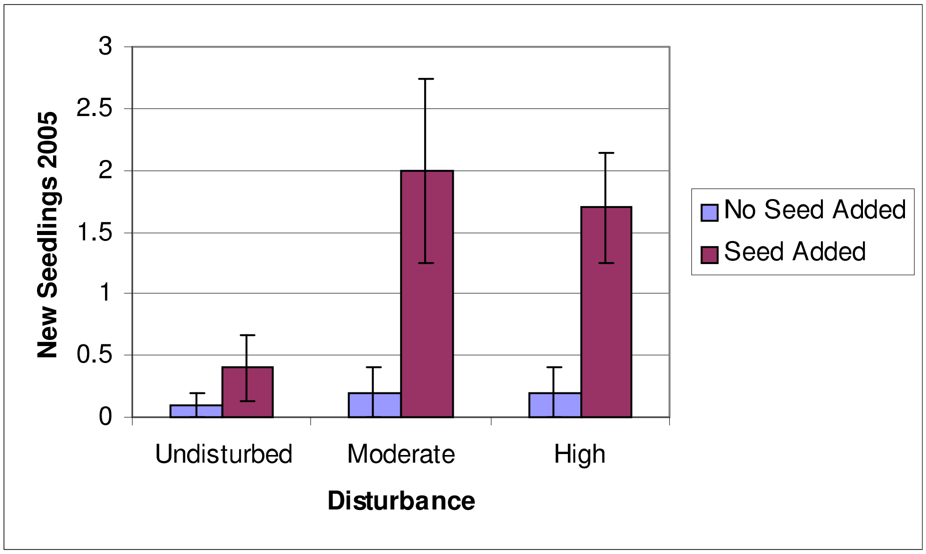


Figure 3.2 Average number of new *Pediomelum esculentum* seedlings on plots by treatment in spring 2005.
Differences among treatments highly significant ($p < 0.01$) based on a non-parametric Kruskal-Wallis test.

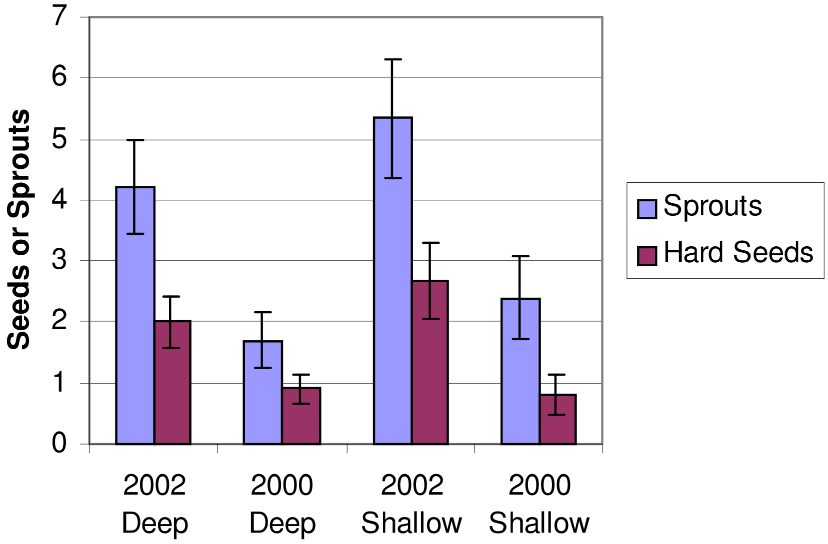


Figure 3.3 Seed bank study results
Average number of 20 seeds buried in late winter 2003 that were sprouting ("sprouts") or remaining as a seed ("hard seed") when removed in April 2004. 2000 or 2002 represents the year the seed was produced. Differences in both mean number of sprouts and hard seeds significant ($p < 0.05$) between seed years but not between depths when analyzed with a non-parametric Kruskal-Wallis test

All hard seeds viable based on tetrazolium test.

	From $_{(j)}$			
to $_{(i)}$	**very small**	**non-flowering**	**flowering**	**missing**
very small	$P_{(v,v)}$	$P_{(v,n)}$	Reproduction	$P_{(v,m)}$
non-flowering	$P_{(n,v)}$	$P_{(n,n)}$	$P_{(n,f)}$	$P_{(n,m)}$
flowering	$P_{(f,v)}$	$P_{(f,,n)}$	$P_{(f,,f)}$	$P_{(f,,m)}$
missing	$P_{(m,v)}$	$P_{(m,n)}$	$P_{(m,f)}$	$P_{(m,m)}$

Table 3.1: Matrix model form

$P_{(i,j)}$ represents the probability of transitioning from stage *j* to stage *i* over a one year time step.

Kansas

2001-2002 **λ = 1.8822**

	v	n	f	m
v	0.4625	0.0000	0.7000	0.1429
n	0.4250	0.6250	0.2333	0.4286
f	0.0000	0.3594	0.7667	0.1429
m	0.1286	0.0156	0.0000	0.2857

2002-2003 **λ = 1.0916**

	v	n	f	m
v	0.3214	0.0000	0.2581	0.0000
n	0.6071	0.6422	0.2717	0.5000
f	0.0000	0.3119	0.7283	0.5000
m	0.0714	0.0459	0.0000	0.0000

2003-2004 **λ = 1.0349**

	v	n	f	m
v	0.6667	0.0000	0.2750	0.1667
n	0.1667	0.7518	0.3451	0.3333
f	0.0000	0.2340	0.6195	0.1667
m	0.1667	0.0142	0.0354	0.3333

Table 3.2a Observed transition matrices for an unharvested population in Kansas and the dominant eigenvalue (projected asymptotic growth rate) for each

Montana

2001-2002 **λ = 0.9657**

	v	n	f	m
v	0.1818	0.0000	0.0556	0.0769
n	0.2727	0.6087	0.4444	0.3077
f	0.0909	0.1739	0.4444	0.3846
m	0.0000	0.2174	0.1111	0.0000

2002-2003 **λ = 1.0355**

	v	n	f	m
v	0.2000	0.0000	0.2105	0.0000
n	0.2000	0.5800	0.5172	0.1429
f	0.2000	0.3600	0.4483	0.7143
m	0.0000	0.0600	0.0345	0.0000

2003-2004 **λ = 0.9558**

	v	n	f	m
v	0.1667	0.0000	0.0769	0.1667
n	0.3333	0.5577	0.5263	0.5000
f	0.0000	0.3077	0.3421	0.0000
m	0.0000	0.1346	0.1316	0.0000

Table 3.2b Observed transition matrices for an unharvested population in Montana and the dominant eigenvalue (projected asymptotic growth rate) for each

Nebraska

2002-2003 **λ = 0.9985**

	v	n	f	m
v	0.2000	0.0000	0.2105	0.0000
n	0.2000	0.5800	0.5172	0.1429
f	0.2000	0.3600	0.4483	0.7143
m	0.0000	0.0600	0.0345	0.0000

2003-2004 **λ = 0.9867**

	v	n	f	m
v	0.5000	0.0000	0.1429	0.0000
n	0.0000	0.8607	0.8333	0.6000
f	0.0000	0.0492	0.1389	0.1000
m	0.0000	0.0902	0.0278	0.0000

Table 3.2c Observed transition matrices for an unharvested population in Nebraska and the dominant eigenvalue (projected asymptotic growth rate) for each

Model of Harvest	Harvest Interval	Proportion Harvested	Population Size at Ten Years	Number Harvested
observed compensation	5	0.30	1,075	523
observed compensation	2	0.10	1,035	408
observed compensation	1	0.05	1,023	397
observed compensation	3	0.10	1,087	259
observed compensation	2	0.05	1,127	214
qualified compensation	2	0.05	1,034	209
observed compensation	5	0.10	1,175	183
qualified compensation	5	0.10	1,079	180
post-reproductive	5	0.10	1,028	179
pre-reproductive	5	0.10	1,016	178
observed compensation	3	0.05	1,155	133
qualified compensation	3	0.05	1,101	131
post-reproductive	3	0.05	1,073	130
pre-reproductive	3	0.05	1,066	130
observed compensation	5	0.05	1,200	93

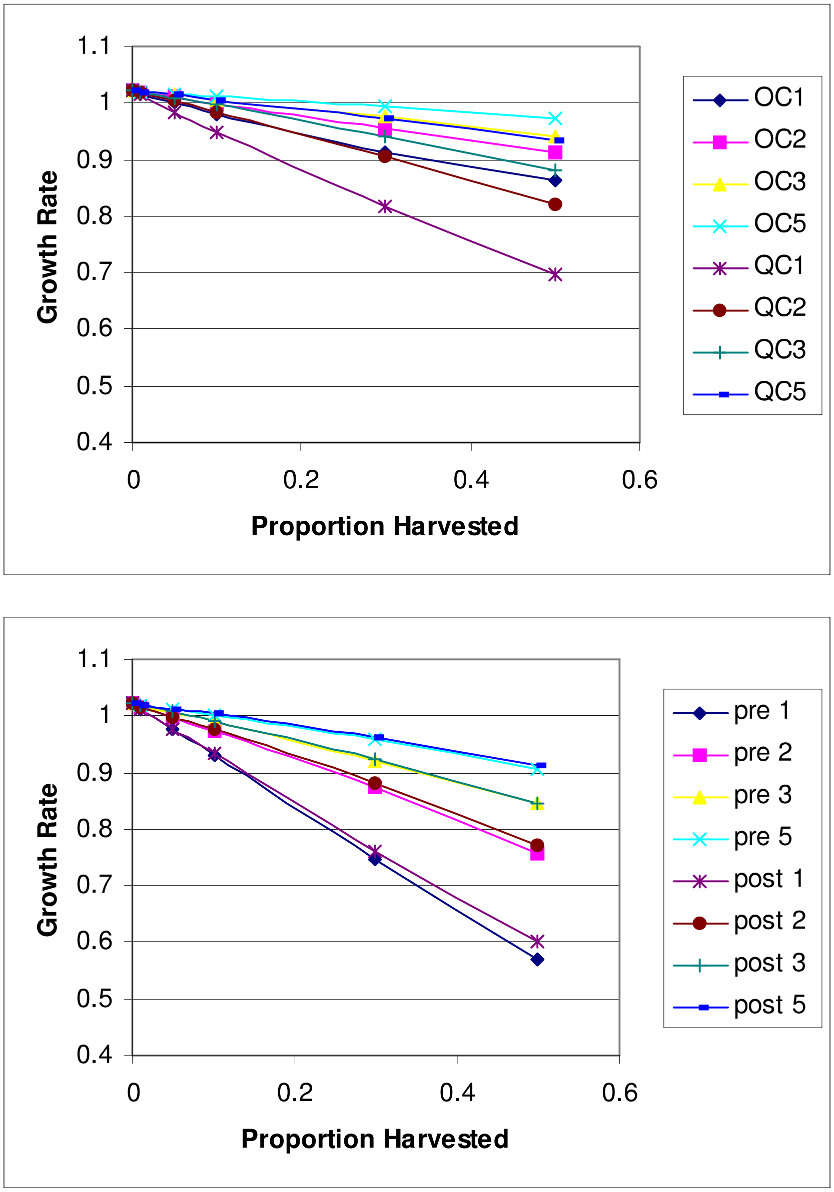
Table 3.3 Fifteen highest yielding sustainable harvest regimes for the generalized population

Of the 96 harvest regimes (combinations of model of harvest, harvest interval, and proportion of the visible adult plants harvested) simulated, those with a projected population size at ten years as large as the original population size of 1,000 individuals were considered sustainable. The fifteen highest yielding of these regimes are listed, in descending order by yield.

Model of Harvest	Harvest Interval	Proportion Harvested	Remaining Population at Ten Years	Number Harvested
observed compensation	2	0.5	1,382	2,108
observed compensation	1	0.3	1,275	2,021
observed compensation	3	0.5	1,685	1,685
observed compensation	2	0.3	1,819	1,522
observed compensation	5	0.5	2,266	1,388
qualified compensation	2	0.3	1,033	1,262
qualified compensation	5	0.5	1,471	1,257
post-reproductive	5	0.5	1,145	1,191
observed compensation	3	0.3	2,092	1,055
observed compensation	1	0.1	2,088	1,020
qualified compensation	3	0.3	1,527	953
qualified compensation	1	0.1	1,510	910
post-reproductive	3	0.3	1,301	905
pre-reproductive	3	0.3	1,180	878
observed compensation	5	0.3	2,499	876

Table 3.4 Fifteen highest yielding sustainable harvest regimes for the Kansas population

Of the 96 harvest regimes (combinations of method of harvest, harvest interval, and proportion of the visible adult plants harvested) simulated, those with a projected population size at ten years as large as the original population size of 1,000 individuals were considered sustainable. The fifteen highest yielding of these regimes are listed, in descending order by yield.



Figures 3.4a and 3.4b Stochastic growth rates from long run simulations for the generalized population

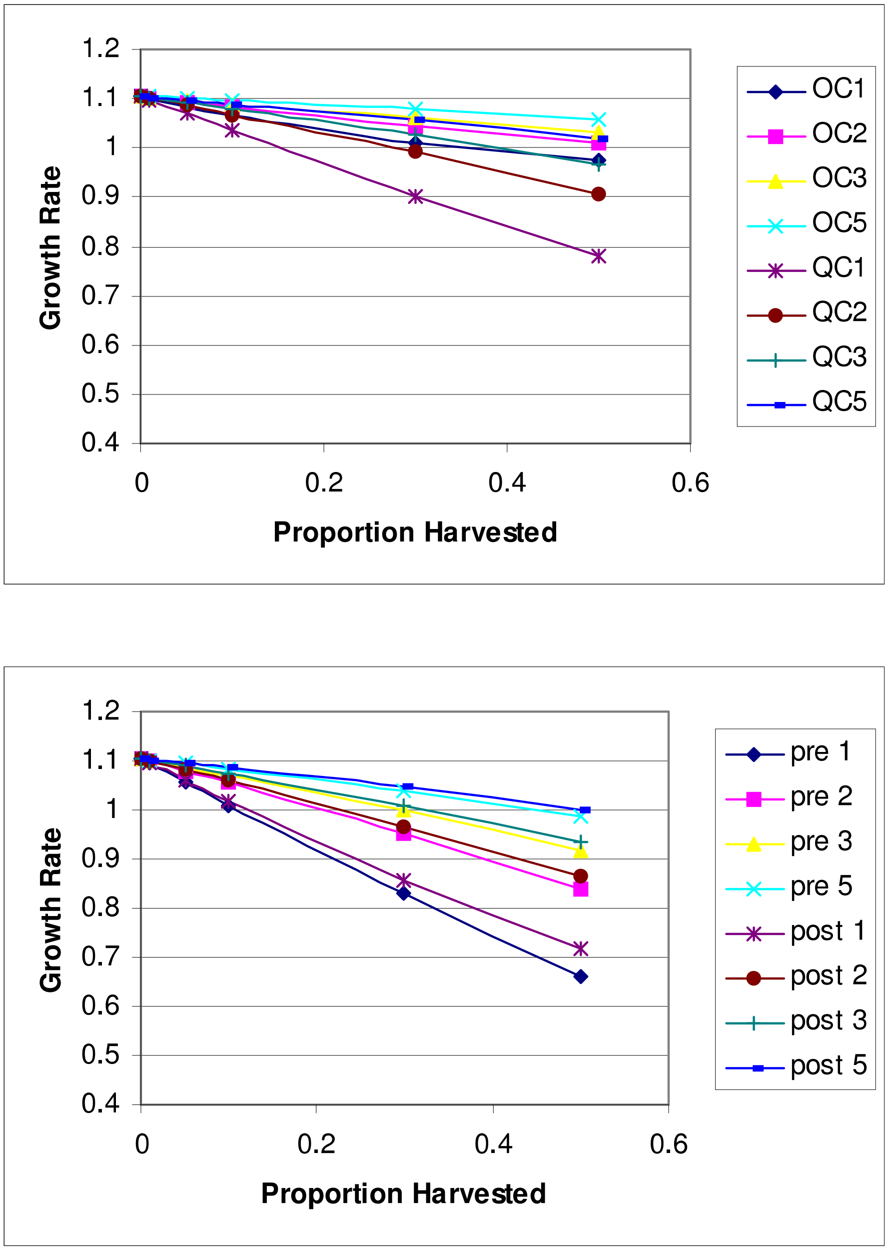
Realized growth rate of overall population at different levels of harvest, methods of harvest and harvest intervals.

“OC” = observed compensation, “QC” = qualified compensation

“Pre” = pre-reproductive and “Post” = post-reproductive

1, 2, 3, 5 represent the harvest interval

Growth rate calculated from median population size of 1,000 simulated 1,000 year runs per treatment interval and proportion combination.



Figures 3.5a and 3.5b Stochastic growth rates from long run simulations for Kansas

Realized growth rate of overall population at different levels of harvest, methods of harvest and harvest intervals.
“OC” = observed compensation, “QC” = qualified compensation
“Pre” = pre-reproductive and “Post” = post-reproductive
1, 2, 3, 5 represent the harvest interval
Growth rate calculated from median population size of 1,000 simulated 1,000 year runs per treatment interval and proportion combination.

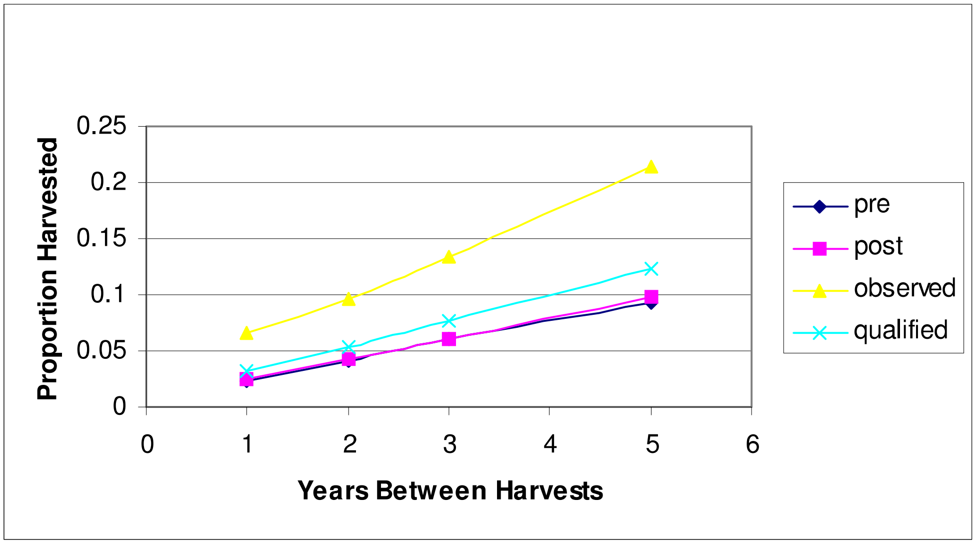


Figure 3.6 Maximum sustainable harvest yield for the generalized population
Proportion harvested is the proportion of visible adults that can be sustainably removed, on average.

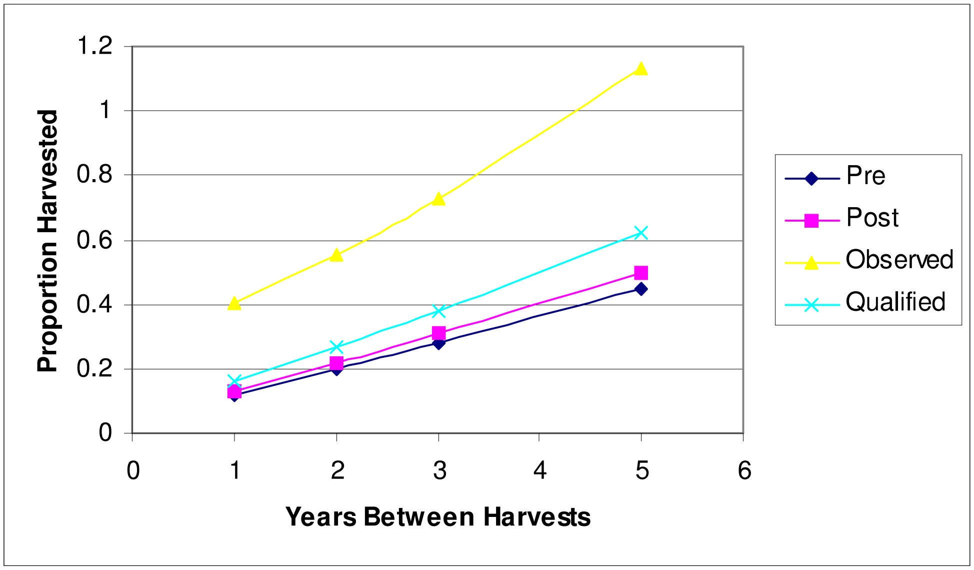


Figure 3.7 Maximum sustainable harvest yield for the Kansas population
Proportion harvested is the proportion of visible adults that can be sustainably removed, on average.

CHAPTER FOUR

Harvest holes on the prairie: the effects of root-digging disturbances on plant community composition

Introduction

Anthropogenic disturbances have been credited with the maintenance of prairie systems and blamed for their destruction. Through both consciously and inadvertently igniting fires, humans stifled woody plant growth and allowed grasslands to flourish (Anderson 1990, Laughlin 2004). Through plowing, overgrazing, and building cities, humans directly destroyed the prairies and indirectly altered their function by creating conduits for invasion by exotic species (Howe 1994, Samson and Knopf 1994). In this paper, I examine a different anthropogenic disturbance, the holes caused by the extraction of plant roots for food and medicine, and investigate the effects it has on prairie plant community composition.

Disturbance is important in shaping prairie plant communities. Two large-scale disturbances, fire and herbivory, maintained the prairies of North America as grasslands. Regular burning leads to conditions that favor grasses over woody vegetation (Wright and Bailey 1982). In the absence of other disturbances, fire favors dominant grasses to the point of excluding forb species and reducing overall diversity (Howe 1994, Collins et al. 1998). In recognition of this, smaller disturbances have received attention as mechanisms promoting overall diversity in grasslands by reducing the competitive domination of the grasses and increasing heterogeneity of the landscape. Increased plant richness relative to undisturbed patches has been documented on buffalo wallows (Polley and Collins 1984, Polley and Wallace 1986), badger mounds (Platt 1975, Gibson 1989) and rodent holes (Martinsen et al. 1990, Hobbs and Mooney 1991). Despite the relatively small scale of a rodent hole, the change in light levels, resource competition, and soil factors on such holes alters the system enough to affect species diversity at much larger spatial scales (Klaas et al. 2000).

Human-caused disturbances similarly alter grassland plant communities. Human ignited fires have kept woody growth in check for millennia (Denevan 1992, Anderson 1996, Umbanhowar 1996). Increased species diversity has been documented in association with trails, roads, and military maneuvers (Larson 2002, Hansen and Clevenger 2005, Leis et al. 2005). However, not all human actions are of this grand of scale. Every year, millions of small holes are created across the North American grasslands when people dig plant roots to be used for food, craft and medicine. The resulting soil disturbances, measured on the scale of centimeters rather than meters or kilometers, share more in common with rodent holes than with roads.

This paper addresses the effects of such harvest-holes on the surrounding vegetation. I wondered, if rodents alter prairie plant communities by digging holes, might not human digging holes to harvest echinacea or prairie turnips also change the community? What would the effects be? How long would they last? Would the effects even be evident in a community that also experiences larger-scale disturbances? Would the disturbance affect the populations of the harvested species and root resources for the future? In order to answer these questions, I experimentally mimicked root harvest in a tallgrass prairie haymeadow in Eastern Kansas and tracked changes in plant community composition.

I predicted that human harvest holes would affect plant community composition, but that these effects would diminish with time and repetition of mowing, a homogenizing larger-scale disturbance. I expected greater species diversity on disturbed plots and greater numbers of annual and invasive forbs on disturbed plots.

Methods

Harvest Methods and Timing

I concentrated my efforts on the harvest of prairie turnips (*Pediomelum esculentum*) and echinacea (*Echinacea angustifolia*), two of the most widely harvested roots on the Great Plains (Kindscher 1987, Kindscher 1992). In order to best mimic harvest of these roots, I studied traditional and modern root harvest. I extracted prairie turnips and echinacea roots with collectors in Kansas, South Dakota and Montana, interviewed other harvesters and read the historic literature. Root digging implements included spades, shovels, pick axes, iron prying bars, hardened chokecherry sticks and elk antlers (Chapter 1). The size of the soil disturbance varied with implement and soil type, but most strongly with harvester experience and care (Figure 4.1). An experienced and careful digger using a pry bar on sandy soils created the smallest disturbance. The pry bar needs to be inserted at least 20cm into the ground, usually on two sides of the root, but the scars on the soil surface can be less than 10cm by 10cm, and scarcely visible the next day. A careless digger using a shovel will often completely overturn the soil and leave a surface scar 30cm by 30cm and still apparent after a year has past. Echinacea and prairie turnips are dug using the same tools and can be harvested at the same time (Snell 2006).

Harvesters mentioned personal strategies of taking only a portion of the individuals plants they encounter or harvesting more completely but revisiting an area infrequently. Echinacea roots are harvested whenever the plants are visible, beginning with June flowering. For prairie turnips, the above ground parts of the plants dehisce and tumble by mid-summer, so harvest usually takes place in June when the plants are full size and most visible. All prairie turnip harvesters report leaving the top of the plant in the field, and some harvesters bury the top or shake out the seeds onto the disturbance.

Among the harvest methods described, I chose to mimic root harvest using a spade, because spade holes were the disturbance simplest to replicate and were intermediate in the size of disturbance they created. I timed the disturbances for the peak of prairie turnip harvest in Kansas, which coincides with prairie turnip seeds ripening and echinacea plants flowering.

Study Site

Our study site was located in an unplowed prairie hay meadow in a public park near Richmond in Franklin County, Kansas, USA at 38.393 °N and 95.226 °W.

The study field and all nearby fields in the park are hayed annually in July. Surrounding the city property are agricultural fields and pastures. Plots were located on the west side of Richmond Lake in a prairie dominated by big bluestem and little bluestem (*Andropogon gerardii* and *Schizachyrium scoparium*), part of the tall sod temperate grassland of the *Andropogon gerardii* (*Sorghastrum nutans*) herbaceous alliance (Lauver et al. 1999). Species found in at least one third of the plots are listed in Table 4.1.

The Richmond Site has moderately deep, slightly acidic, dark brown soils high in organic matter. They are part of the Eram-Lula complex and are composed of a crumbly layer of clay loam about 25cm thick over a B horizon composed of clay (Dickey 1981). The years of the study 826 and 1160mm of precipitation fell at the site, 82 and 115 percent of the average of 1012mm. (High Plains Regional Climate Center 2006).

Experimental Design

Sixty plots were laid out in ten transects. Transects running east to west were located 10m apart (with transect 2 being 10m south of transect 1) and 6 1m x 1m plots were positioned at 5m intervals along the transects. Within transects, plots were randomly assigned a disturbance level (no holes, three holes or six holes per plot) and a seed treatment (*Pediomelum esculentum* seeds added or not). Results of the seed addition portion of the experiment are discussed in chapter 3. Average prairie turnip density in an adjoining prairie haymeadow was 1.2 turnips per m^2, with dense patches containing over 10 individuals per m^2. Where it is harvested in Rooks County, Kansas, *Echinacea angustifolia*, occurs at similar densities, with fields averaging as many as 10 adult plants per m^2 (Hurlburt 1999). Therefore, creating three holes per plot mimics the harvest of all adult plants in a moderately dense population or a fraction of the plants in a dense population for either species. Creating six holes per plot mimics the harvest all plants in a dense population, or a fraction of the plants in a very dense population.

Within each plot, disturbances were randomly located on a 10cm grid system. Because of physical constraints, no disturbances were located within 10cm of the plot edge or closer than 20cm apart. Three "non-disturbance points" were chosen for each undisturbed plot in the same way. I created disturbances by using a spade to cut through the sod, lift the vegetation, mimic removing a root and place turf back in its hole. While the purpose was not to overturn the soil, many of the disturbances created did leaves some bare soil exposed. No attempts were made to reduce trampling while making disturbances, because the harvest process involves both digging and walking around. Each disturbance hole was intended to be square, 15cm on a side, and located such that the northeast corner of the hole was at the randomly selected disturbance point. Following digging, each disturbance was marked with a metal tag, as was each non-disturbance point.

For each plot, I randomly chose one of the disturbances or non-disturbance points to locate a 30cm x 30cm subplot to sample in each plot. Subplots in moderately and highly disturbed plots were all centered on a single harvest-mimicking disturbance and were therefore combined into a single “disturbed subplot” category for smaller scale analyses.

Data Collection

Visual estimates of percent cover (live plus standing dead) were recorded for all species in each plot and subplot as well as for the amount of bare ground (Daubenmire 1959). Plants were identified to species where possible and to genus where not possible (e.g. non-reproductive *Carex* species). Plot level estimates were made prior to disturbance in June 2003 and then in autumn 2003, spring 2004, summer 2004, and autumn 2004. Subplots were sampled immediately following the disturbances in June 2003 and then in the week following plot-level sampling in the following four seasons.

Data Analysis

Statistical calculations were completed using Minitab version 12 for Windows (1998) and Microsoft Excel (1997). Diversity indices were calculated using PC Ord (McCune and Mefford 1999). For cover comparisons, cover values were standardized to 100% for each plot. Prior to analysis percentages were arcsine square root transformed to correct for non-normality of variances.

For each subsequent time period after disturbance, comparisons were made to the pre-disturbance state for each plot and analyses were performed on the difference. Plot level results were compared using analysis of variance (ANOVA) to determine is differences among group means for all treatments were statistically significant. Where differences were not statistically significant, results from the "moderately disturbed" and "highly disturbed" treatments were pooled and compared to the undisturbed treatment.

Species were assigned to categories: forb, graminoid (including grasses and sedges), annual, perennial, exotic and native (following the Flora of the Great Plains 1986). Exotic species and those species with a Kansas coeffiecient of conservatism of 3 or lower were catergorized as "weedy" (Freeman and Morse 2002).

Processes were analyzed at a smaller scale using "appearances" and "disappearances" at the subplot level. A plant species not found in a subplot in June 2003 but found in that plot at a later time, counted as an "appearance" of that species. The absence of a plant species in a subplot that had been present in that subplot in summer 2003 was counted as a "disappearance". The number of disturbed or undisturbed subplots in which a species appeared or disappeared was summed for each species and then pooled by species category (graminoid, forb, exotic, native, annual, perennial). I compared the observed number of appearances in undisturbed and disturbed subplots to the number expected if appearance were independent of disturbance status using a chi-squared test with one degree of freedom. Forty of the sixty subplots were disturbed (those in both the three hole and six hole plots). Therefore, if likelihood of appearance is independent of disturbance status, one would expect 40/60 or 2/3 of the total number of appearances to be on disturbed subplots and 1/3 to be on undisturbed subplots. The expected values for the chi-squared test were calculated as follows, where E_A is the expected number of appearances, E_D the expected number of disappearances, N_A the total number of observed appearances, and N_D is the total number of observed disappearances.

$E_{A,\text{Disturbed}} = N_A \cdot 2/3$

$E_{A,\text{Undisturbed}} = N_A \cdot 1/3$

$E_{D,\text{Disturbed}} = N_D \cdot 2/3$

$E_{D,\text{Undisturbed}} = N_D \cdot 1/3$

Results

Presence of Effects

The change in bare ground cover is the most direct way to determine if harvest holes have any noticeable effect on plant community composition. Judging by change in bare ground cover, the effects of harvest are detectable three months after the initial disturbances, even in the presence of larger scale disturbance (mowing) (Figure 4.2). Not surprisingly, those plots that were more disturbed in June had more bare ground in October. The magnitude of this difference diminished with time as plants re-colonized the disturbances. Somewhat surprisingly, following summer 2004, during which abundant grass growth overwhelmed the plots to the extent that few plots had any bare ground, in the autumn of 2004 disturbances were again easily detectable in the form of increased bare ground. This increased bare ground cover comes at the expense of graminoid cover at both the plot (Figure 4.3) and subplot scale (Figure 4.4).

Species Diversity

Harvest-like disturbances led to greater species richness (Table 4.2). The seasonal loss of early season species and competitive exclusion of weaker competitors leads to a decline in species richness from June to October. All plots had fewer species in fall 2003 than they did prior to the disturbance in June, but the net reduction in species number was greater in the undisturbed plots. A spring surge in recruitment and reemergence leads to an annual peak in species richness in late spring. All plots contained more species in spring 2004 than they had the previous summer, but the net increase in species number was greater in the disturbed plots than the undisturbed plots. In the seasons following disturbance, disturbed plots exhibited greater evenness than did undisturbed plots. Because of this, changes in species diversity as measured by the Shannon Diversity Index followed the same pattern as species richness at a greater level of statistical significance (Figure 4.5).

Consistent with our expectations, disturbed plots had a greater increase in annual, exotic and weedy species. Disturbed plots, however, also showed increases in perennial forb diversity while grass species richness remained largely unaffected by disturbance (Table 4.2). Appearances of plant species in spring 2004 not found in summer 2003 illustrate these trends at the smaller subplot level. Other than prairie turnips (*Pediomelum esculentum*, which had added seeds), only one species, oxeye daisy (*Leucanthemum vulgare),* appeared on disturbed subplots more than undisturbed subplots in a statistically significant manner, suggesting that no one species is driving the effects. As groups, however, exotic species, native species, forb species, annual forb species and all species together all appeared in disturbed subplots more often than would have been expected by chance if appearance were independent of disturbance (Table 4.3). Disappearances of annual forbs between summer 2003 and spring 2004 happened less often on disturbed subplots than would be expected by chance (Table 4.4).

Discussion

Implications for Human Harvest

Our results suggest that where roots are harvested on the Great Plains, the disturbing act of root extraction creates conditions that favor the forb plants desirable for harvest at the expense of grass dominance.

Prior to modern agriculture, the majority of edible and medicinal plants harvested from the North American prairie were forbs (Kindscher 1987, Kindscher 1992, Turner 1997). Species used by humans were concentrated in a few families now known to have active chemical constituents and edible storage organs. Far fewer grass and sedge species were used than would be expected by chance (Moerman 1996, Moerman and Estabrook 2003). Many of these forb species benefit from disturbance at some stage in their life history. Experimental results with prairie turnips suggest that seedling recruitment for this commonly used prairie forb increases with harvest-like disturbances (Chapter 3).

Root harvest cannot be dismissed as an isolated occurrence. The thousands of people who lived on the Great Plains prior to European settlement collected roots in abundance. As a food harvested primarily by women for consumption within the family setting, records of prairie turnip harvest numbers are hard to find. It is known that members of the Cheyenne, Blackfoot and Crow tribes ate prairie turnips as a major food source prior to settlement (Jablow 1951, Johnston 1970, Snell 2006) and that they were mentioned in the writings of Lewis, Clark, and Fremont (Reid 1977). Prairie turnip braids served as a unit of commerce among the Dakota and Arikara, with each one requiring fifty to seventy roots, and thus fifty to seventy holes on the landscape (Gilmore 1926). In the early 1800's, roots from the Great Plains made it as far west as the Pacific Ocean through the Columbia River trading networks (Stern 1993) and to trappers in Northern Saskatchewan through a complex series of exchanges surrounding the fur trade (Jablow 1951, Ray 1998).

Even in modern times, after most of the prairie has been plowed or converted to fenced cattle pasture, roots are extracted in quantity. Prairie turnips sold as braids containing dozens to hundreds of roots are for sale at museum shops, trading posts, herb shops, and native art galleries in North and South Dakota, on the internet and as the special ingredient in Woodenknife Company's widely distributed Indian Fry Bread Mix. The echinacea market fluctuates wildly. In 2001 the American Herbal Products Association reported 33,554 pounds of dry *Echinacea angustifolia* root and 14,092 pound of dry *E. pallida* roots being traded by regional buyers. That figure is down from a recent high of 237,572 pounds in 1998, but at an average of 100 to 120 roots per pound, that still translates to almost 5 million holes (Kindscher et al. in prep.). These numbers certainly underestimate the total number of holes dug by humans for root harvest, because much harvest is done surreptitiously or for personal use, well outside of the market economy. Others species being dug from North American prairies include wild onions (*Allium* sp.), American licorice (*Glycyrrhiza lepidopta*), rattlesnake master (*Eryngium yuccafolium*), groundnuts (*Apios americana*). lomatium (*Lomatium* sp.) and Jerusalem artichokes (*Helianthus tuberosa*) (Kindscher 1987, Kindscher 1992, Turner 1997).

In light of the extent and magnitude of root harvest, the implication of our experimental results is that root-diggers may alter the composition of the surrounding plant community. Native Americans prior to European settlement, in particular, were dramatically affecting their surroundings. Not only were they altering the landscape through fire, they were also changing local species composition through the everyday action of digging a root. By decreasing grass dominance, forb root harvest led to increased safe sites for forb recruitment and conditions that favored forb species. The act of exploiting a natural resource promotes the conditions that enhance that resource.

To more fully understand the effects of harvest holes on prairie plant communities, sites across the range of Great Plains ecosystems should be studied, as soil type, surrounding vegetation and other disturbance regimes may alter how root-harvest affects community composition.

Mechanisms

Small soil disturbances such as pocket gopher mounds can be revegetated through seed bank, seed rain, clonal growth from surrounding plants and re-growth of buried plants. Experimentally, these modes of growth have been shown to occur concurrently but have very different effects on community composition (Rogers and Hartnett 2001). The sharp increase in grass cover in the disturbed subplots following disturbance (Figure 4.4) and lack of apparent grass seedlings, suggest that clonal growth of existing surrounding or partially buried grasses is largely responsible for visible changes in overall composition. Re-growth of existing grass species however, does not lead to differences in species richness.

Of processes that do lead to differences in diversity, the one most evident in this experiment is that soil disturbance leads to increased safe sites for seedling recruitment. Our dramatic increase in spring colonizations on the disturbed plots lends credence to this process, although I did not distinguish between seed bank and seed rain colonizations. This process is further supported at a finer scale by the spring 2004 subplot data. Within subplot disappearances of annuals happened far more on undisturbed subplots than would be expected by chance if "disappearance" was independent of disturbance (Table 4.4). On the disturbed subplots, the annuals present in 2003 reappeared in the spring of 2004 (and thus did not disappear). On the undisturbed subplots, many annual species present in 2003 did not reappear in 2004 (and thus disappeared). Seed availability should not have differed between the disturbed and undisturbed subplots because the species were present in each in summer 2003, and annual plants could not have re-grown clonally, therefore the difference between groups must be the more favorable conditions for seedling establishment on the disturbed subplots.

The recruitment of prairie turnips only on those plots both disturbed and with seed addition demonstrates how this community process plays out at the population level. The dual requirement suggests that local prairie turnip populations are both seed and safe site limited. Seed addition studies in nearby prairie restorations suggest that this is true of many other forb species as well (Foster and Dickson 2004, Foster et al. 2004).

While increased safe sites for seedling recruitment may explain much of the differences in diversity in spring of 2004, it cannot explain all of the differences for other time periods. At both the plot and subplot level, for instance, disturbed plots experienced fewer local extinctions than undisturbed plots between June and October 2003. By October, all plots have fewer species than they had in June. This might be due to the presence of spring ephemerals in June, but also suggests that the dominant plants (C-4 grasses in this system) are competitively excluding locally rare species through the course of the growing season. The reduced competition around the disturbances allowed non-dominant plants to persist longer or be out-competed less quickly.

Interactions of Disturbances

White and Harrod (1997) noted that large-scale disturbances can homogenize otherwise patchy environments, for example fires erase fine-scale patchiness caused by grazing. Experimentally, the effects of gopher mounds on *Medicago lupulina* germination and distribution in a tallgrass prairie were nullified in years with fires (Wolfe-Berlin and Moloney 2000), and differences in species richness on badger mounds compared to the surrounding area diminished in a burned field relative to an unburned field (Gibson 1989).

I anticipated that differences caused by small root-harvest disturbances would become insignificant following the apparently homogenizing disturbance of mid-summer haying. This did not happen. While differences between disturbed and undisturbed plots were scarcely detectable a year after disturbance in the summer of 2004, they were again clearly noticeable in the fall of 2004 following the summer mowing.

The grass canopy had fully closed over the disturbances in summer 2004. I expect that the canopy closure prevented any new seedling recruitment on the disturbances, and that, in absence of further disturbance, the overhanging grasses would have out-competed other species for light and fully re-colonized the disturbances at all levels. After mowing, however, it was clear that the disturbances had not yet been fully colonized at the ground level. Mowing re-exposed the bare ground, leading to increased light levels, reduced competition and possible seed germination. Through slowing the progress of clonal re-colonization by dominant grass species, the mowing disturbance increased the light levels and allowed more chances for seedling colonization and survival on the disturbances. In this experiment, it seems that an apparently homogenizing disturbance extended the duration of the effects of the patchy smaller disturbance.

Mowing had previously been associated with an increase in grass diversity and no change in forb diversity in a long term experiment (Fynn et al. 2004) and an increase in forb diversity due to increased light availability and reduced competition in a shorter term study (Collins et al. 1998). Both studies considered mowing as a smaller disturbance in the context of fires, but not as a large disturbance in the context of small holes. Experiments controlling for different combinations of disturbances at varying scale over different lengths of time are needed to test how the interactions of disturbances alters community composition.

Implications for Exotic Invasion

Discussions of anthropogenic disturbances on grasslands have almost become synonymous with discussion of invasion by exotic invasive species (see, for instance, Hobbs and Huenneke 1992, Kotanen 1997, Hayes and Holl 2003, Larson 2003). While not the focus of our work, our results demonstrate that root harvest disturbances, like other anthropogenic disturbances, do create conditions increasing the chances of invasion by exotic species. In spring 2004, exotic species such as *Leucanthemum vulgare*, made many more appearances on disturbed subplots than undisturbed subplots. Level of disturbance alone, however, did not predict plot level cover by exotics. Our results show a significant (p = .028), if weak (R-squared =

8.0%), correlation between species richness prior to disturbance and lower cover of exotic species the following spring. The plot most species rich in June 2003 had only 5.4% exotic cover in spring of 2004, while exotics covered 26.1% of the least species rich plot. This adds a small piece of evidence in support of Tilman's 1997 paper supporting Elton's 1958 hypothesis that diverse systems are less invasible.

Root harvest disturbances may create conditions ripe for invasive species seedling recruitment, but successful invasion requires a source of exotic seeds. In our study, disturbances were only invaded by those species already found in the local species pool. The close proximity of our study site to agricultural fields and a road meant that the field had previously been invaded, and propagules of exotic species already existed in the seed bank or local seed rain. During the times of the greatest root extraction from the Great Plains, Eurasian species were not present in the local pool. While modern root digging may open the door for increased exotic invasion as well as creating safe sites for native forbs, prior to European contact, Native Americans extracting roots from the plains were only creating conditions favoring the forbs, the category including the plant species they were harvesting.

Conclusion

By conducting an experiment investigating the population and community effects of a human action, I found that human root harvest disturbances created conditions that favored the class of plants being harvested. Perhaps as importantly, I affirmed the belief that the fields of ethnobotany and ecology can benefit from further exploration of their intersection, and that experimental ecological methodologies can apply to ethnobotanical questions (Anderson 1997, Salick et al. 2003, Ticktin 2004). I look forward to seeing more investigations combining techniques from multiple disciplines to better understand the role humans play in shaping our environment.

Size of Disturbance	**Small**	**Large**
Harvester	Careful and Experienced	Careless and Inexperienced
Soil	Sandy Soil	Rocky Soil
Digging Implement	Pry Bar	Shovel

Figure 4.1 Factors affecting size of root-harvest disturbance

	Summer 2003	**Fall 2003**	**Spring 2004**	**Summer 2004**	**Fall 2004**
Total Species					
Undisturbed	19.4 (0.54)	12.0 (0.47)	21.3 (0.63)	18.6 (0.67)	10.7 (0.48)
Moderately	17.7 (0.72)	12.9 (0.56)*	22.9 (0.75)**	19.2 (0.73)**x**	12.1 (0.44)**
Highly	18.2 (0.68)	12.7 (0.57)	24.3 (0.82)	20.1 (0.60)	11.7 (0.49)
Perennial Graminoids					
Undisturbed	4.0 (0.19)	3.4 (0.15)	4.6 (0.18)	4.7 (0.22)	3.7 (0.13)
Moderately	3.9 (0.25)	3.8 (0.25)	4.8 (0.18)	4.6 (0.20)*	4.4 (0.21)*
Highly	3.8 (0.17)	3.9 (0.22)	5.0 (0.21)	4.5 (0.21)	4.1 (0.16)
Annual Graminoids					
Undisturbed	0.4 (0.11)	0.0	0.0 (0.00)	2.0 (0.00)	0.0 (0.00)
Moderately	0.3 (0.11)	0.0	0.1 (0.07)	2.0 (0.00)	0.0 (0.00)
Highly	0.2 (0.08)	0.0	0.1 (0.07)	2.0 (0.00)	0.5 (0.05)
Perennial Forbs					
Undisturbed	10.9 (0.43)	6.1 (0.38)	11.8 (0.50)	10.2 (0.54)	6.1 (0.36)
Moderately	9.9 (0.53)	6.4 (0.48)**x**	11.7 (0.50)	9.7 (0.47)	6.9 (0.38)*
Highly	10.0 (0.52)	6.2 (0.38)	12.3 (0.55)	9.9 (0.60)	6.4 (0.29)
Annual Forbs					
Undisturbed	4.0 (0.32)	0.9 (0.20)	4.4 (0.36)	3.5 (0.29)	0.7 (0.17)
Moderately	3.7 (0.25)	1.0 (0.18)	5.7 (0.29)*	4.6 (0.41)*	0.6 (0.15)
Highly	4.3 (0.42)	1.0 (0.22)	6.2 (0.43)	5.6 (0.44)	1.0 (0.16)
Weedy Species					
Undisturbed	8.3 (0.55)	3.6 (0.35)	7.5 (0.37)	8.8 (0.53)	3.5 (0.26)
Moderately	7.3 (0.42)	3.8 (0.40)	8.4 (0.37)**	9.3 (0.67)**xx**	4.2 (0.31)**x**
Highly	8.2 (0.53)	3.9 (0.41)	10.3 (0.50)	10.2 (0.45)	4.4 (0.32)
Exotic Species					
Undisturbed	2.6 (0.29)	1.2 (0.09)	2.3 (0.19)	2.7 (0.24)	1.9 (0.07)
Moderately	2.5 (0.27)	1.3 (0.13)	3.4 (0.20)**	3.2 (0.22)**xx**	2.0 (0.05)
Highly	2.4 (0.24)	1.2 (0.16)	3.7 (0.22)	3.0 (0.24)	2.1 (0.07)

Table 4.2 Average number of species per category present in plots at different time periods for each disturbance treatment
(standard error of mean)
Significance based on a one-way ANOVA,
among all three treatments: * $p < 0.05$, ** $p < 0.01$;
between “undisturbed” and pooled “disturbed” treatment **x** $p < 0.05$, **xx** $p < 0.01$

	Number of appearances on disturbed subplots	Number of appearances on undisturbed subplots	Expected appearances on disturbed (total*2/3)	Expected appearances on undisturbed (total*1/3)	*p*-value for χ^2 test
Total Appearances	378	129	338	169	< 0.001
Graminoids	82	35	78	39	0.433
Forbs	290	89	252.7	126.3	< 0.001
Annual forbs	133	38	114	57	0.002
Perennial forbs	157	51	138.7	69.3	0.007
Exotic species	72	21	62	31	0.028
Native species	300	103	268.7	134.3	0.001
Native perennial forbs	123	45	112	56	0.072
Native perennial forbs with prairie turnips excluded	106	44	100	50	0.299

Table 4.3 Number of appearances at the subplot level in spring of 2004 compared to the expected number if appearance were independent of disturbance.

The presence of a species in a subplot in spring 2004 that was not present in that subplot in summer 2003 counts as one appearance. Number of appearances for a category is the number of subplots in which a given species was found in spring 2003 but not summer 2004 summed for all species in the category.

Expected frequencies for disturbed sites calculated by multiplying total number of appearances by 2/3 (because 2/3 of the subplots were disturbed, if appearance is independent of disturbance, we would expect 2/3 of the appearances to be found on these subplots.)

	Disappearances on disturbed suplots	Disappearances on undisturbed subplots	Expected on disturbed	Expected on undisturbed	*p*-value for $\chi 2$ test
Total	91	64	103.33	51.67	0.035
Graminoid	13	5	12.00	6.00	0.617
Forb	78	59	91.33	45.67	0.015
Annual Forb	26	27	35.33	17.67	0.007
Perennial Forb	52	32	56.00	28.00	0.354
Exotics	19	9	18.67	9.33	0.894

Table 4.4 Number of disappearances at the subplot level in spring of 2004 compared to the expected number if disappearance were independent of disturbance.

Number of disappearances for a category is the number of subplots in which a given species was not found in spring 2003 but had been found in summer 2004 summed for all species in the category.

Expected frequencies for disturbed sites calculated by multiplying total number of disappearances by 2/3 (because 2/3 of the subplots were disturbed, if appearance is independent of disturbance, we would expect 2/3 of the appearances to be found on these subplots.)

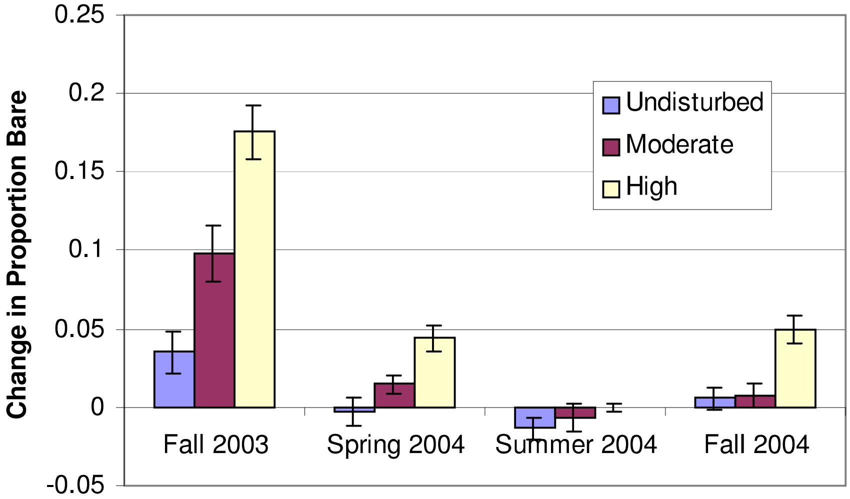


Figure 4.2 Change in relative proportion of bare ground cover from the proportion bare before disturbance in Summer 2003.

Differences among treatments highly significant (*p* < 0.01 for a one-way ANOVA) in Fall 2003, Spring 2004 and Fall 2004.

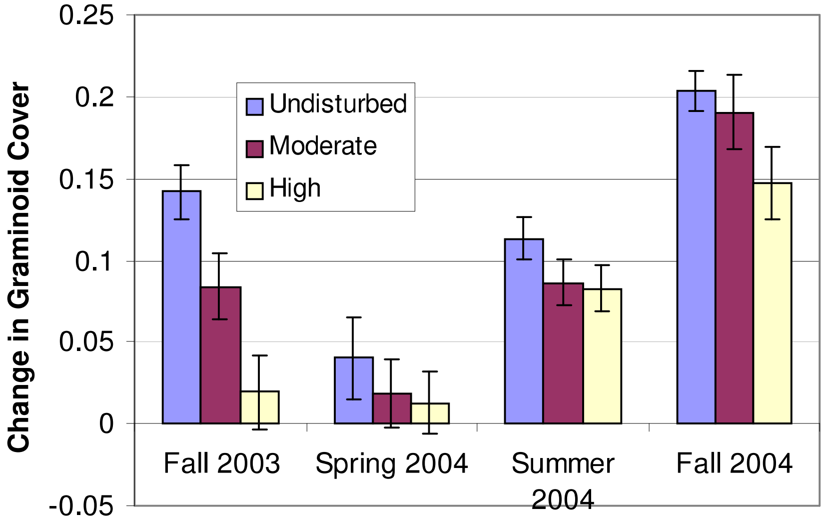


Figure 4.3 Change in relative proportion of graminoid cover from proportion graminoid before disturbance in Summer 2003.

Differences among treatments highly significant ($p < 0.01$) in Fall 2003 and significant ($p = 0.011$) in Fall 2004 when analyzed with a one-way analysis of variance.

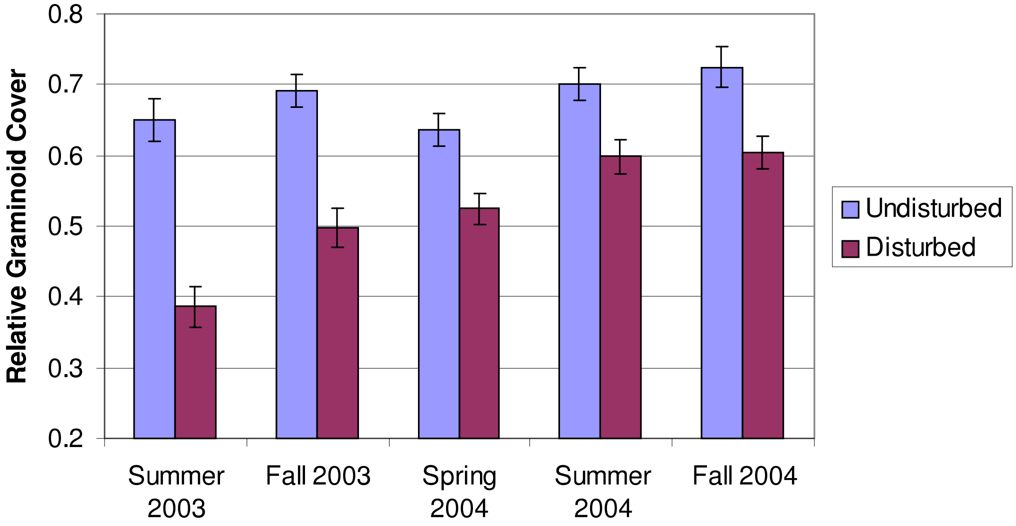


Figure 4.4 Relative proportion of graminoid cover on subplots.
Summer 2003 sampling for subplots conducted immediately after disturbance.
Differences between groups highly significant ($p < 0.01$) at all time periods based on a one-way ANOVA

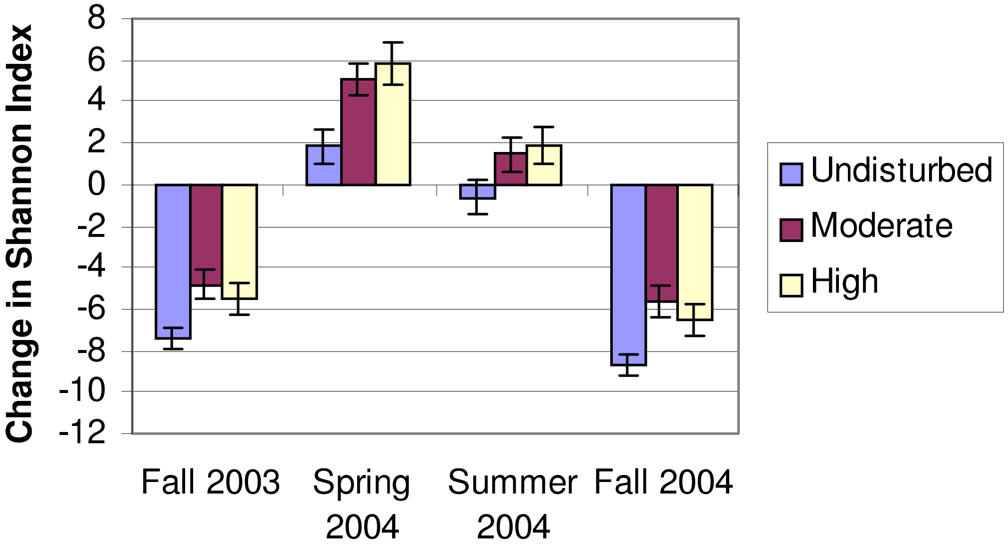


Figure 4.5: Change in Shannon Diversity Index from before disturbance value
Differences among treatments significant ($p < 0.05$) for a one-way ANOVA for Fall 2003 and Spring 2004 and highly significant ($p < 0.01$) for Summer 2004 and Fall 2004.

CONCLUSION

What is gained from this project?

The most far-reaching conclusion of this project is that that there is a great deal to be gained in merging techniques from different disciplines and sub-disciplines. The combination of observational, experimental and modeling procedures, ethnobotanical and ecological methods, and population and community scales allow us far greater insight into the effects of prairie turnip harvest than any single approach could. Far beyond the scope of *Pediomelum esculentum*, this project suggests that there is still a great deal of knowledge to be gained through investigating "out of fashion" subjects. Much can be learned from study of food plants, temperate plants, and long-lived and challenging but not federally listed plants and by listening to the people who interact with the plants on a regular basis.

The prairie-turnip-specific conclusions of the component pieces can be summarized as follows. 1) Prairie turnips, once a staple plant food of many peoples of the plains are currently wild-harvested for their cultural significance. While specific adaptations make the plant well suited to prairie survival and poorly suited to agriculture, new or re-named uses for the plant continue to be suggested. 2) In the absence of harvest, populations of *Pediomelum esculentum* are largely stable with variation in both space and time. Projecting populations of the species using matrix models involves making considerable assumptions, but reveals more stage-specific information useful in modeling harvest scenarios than more simple techniques could. 3) Harvest holes create good conditions for *P. esculentum* recruitment, particularly when harvest is timed to coincide with seed ripening and the seed-bearing tops of plants are left near the holes, as is traditionally done. The partial compensation for the removal of harvested adults through increased recruitment is now named "harvest induced compensatory recruitment" and is likely to be a factor in root harvest of other disturbance-limited plants. 4) Not only do harvest holes lead to increased prairie turnip recruitment, they also subtlety change the character of the surrounding plant community. Following harvest, grass dominance is reduced near the holes and forb species diversity increases relative to undisturbed areas. Harvesters digging roots across the grassland landscapes would have been creating conditions that favored many of the species that they were harvesting.

We add all these bits of information to the ever-growing pile of ecological and anthropological science. We hope that the greater collective of scientific information can elucidate a real understanding of the basic issue, how our species can co-exist on the planet with prairie turnips and everything else.

LITERATURE CITED

Abel, A. H. (1939). Tabeau's Narrative of Loisel's Expedition to the Upper Missouri. Norman, University of Oklahoma Press.

Akcakaya, H. R. and M. Raphael (1998). "Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA." Biodiversity and Conservation 7: 875-894.

Akcakaya, H. R. and W. Root (1998). RAMAS Ecolab: Applied Ecology Laboratory. Setauket, Applied Biomathmatics.

Alexander, H. M., N. A. Slade, et al. (1997). "Application of mark-recapture models to estimation of the population size of plants." Ecology 78(4): 1230-1237.

Andersen, A. N. (1989). "How important is seed predation to recruiment in stable populations of long-lived perennials?" Oecologia 81(3): 310-315.

Anderson, M. K. (1990). "Plant Gathering as a Conservation Strategy: Learning From California's Earliest Resource Managers." Yosemite Centennial Symposium Proceedings: Natural Areas and Yosemite: Prospects for the Future October 13-20: 472-481.

Anderson, M. K. (1992). "At Home in the Wilderness." News from Native California Special Reports 1: 17-40.

Anderson, M. K. (1997). "From Tillage to Table: The Indigenous Cultivation of Geophytes for Food in California." Journal of Ethnobiology 17(2): 149-169.

Anderson, M. K. and G. P. Nabhan (1991). "Gardeners in Eden." Wilderness Fall: 27-30.

Anderson, M. K. and D. L. Rowney (1999). "The Edible Plant Dichelostemma capitatum: Its Vegetative Reproduction Response to Different Indigenous Harvesting Regimes in California." Restoration Ecology 7(3): 231-240.

Anderson, R. C. (1990). The Historic Role of Fire in the North American Grassland. Fire in North American Tallgrass Prairies. S. L. Collins and L. L. Wallace. Norman, University of Oklahoma Press: 19-27.

Antos, J. A., H. J. Guest, et al. (2005). "The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat." Journal of Ecology 93(3): 536-543.

Antos, J. A., R. Parish, et al. (2000). "Age structure and growth of the tree-seedling bank in subalpine spruce-fir forests of south-central British Columbia." American Midland Naturalist 143(2): 342-354.

Association, G. P. F. (1986). Flora of the Great Plains. Lawrence, Kansas, University Press of Kansas.

Becker, D. A. (1968). "Stem abscission in the tumbleweed, Psoralea." American Journal of Botany 55(7): 753-756.

Bierzychudek, P. (1999). "Looking backwards: assessing the projections of a transition matrix model." Ecological Applications 9(4): 1278-1287.

Boyce, M. S., A. Sinclair, et al. (1999). "Seasonal compensation of predation and harvesting." Oikos 87(3): 419-426.

Breckage, B. and J. S. Clark (2005). "Does predation contribute to tree diversity?" Oecologia 143(3): 458-469.

Brook, B. W., M. A. Burgman, et al. (2002). "Critiques of PVA ask the wrong questions:throwing the baby out with the numerical bath water." Conservation Biology 16(1): 262-263.

Brook, B. W., J. J. O'Grady, et al. (2000). "Predictive accuracy of population viability analysis in conservation biology." Nature 404: 385-387.

Brown, A. (1954). Old Man's Garden. Toronto, J.M. Dent and Sons.

Brownstein, C., M. Lee, et al. (2003). "Harnessing consumer power for ocean conservaiton." Conservation in Practice 4(4).

Caswell, H. (2000). "Prospective and retrospective perturbation analyses: their role in conservation biology." Ecology 81: 619-927.

Caswell, H. (2001). Matrix Population Models. Second Edition. Sunderland, Massachusetts, Sinauer.

Catlin, G. (1866). Illustrations of the Manners, Customs and Conditions of the North American Indians, with Letters and Notes Written During Eight Years of Travel and Adventure Among the Wildest and Most Remarkable Tribes Now Existing. London, H. Bohn.

Clements, D. R., A. DiTommaso, et al. (2004). "Adaptability of plants invading North American cropland." Agriculture Ecosystems and Environment 104(3): 379-387.

Clow, R. (1995). "Bison Ecology, Brule and Yankton Winter Hunting and the Starving Winter of 1832-33." Great Plains Quarterly 15: 259-70.

Clutton-Brock, T. H., T. N. Coulson, et al. (2002). "Sex differences in emigration and mortality affect optimal management of deer populations." Nature 415: 633-637.

Collins, S. L., A. K. Knapp, et al. (1998). Modulation of Diversity by Grazing and Mowing in Native Tallgrass Prairie. Science. 280: 745-747.

Cowen, R. (1991). "The Sacred Turnip." Science News 139(20): 316-317.

Crone, E. E. and J. L. Gehring (1998). "Population viability of Rorippa columbiae: Multiple models and spatial trend data." Conservation Biology 12(5): 1054-1065.

Crouse, D. T., L. B. Crowder, et al. (1987). "A stage-based population model for loggerhead sea turtles and implications for conservation." Ecology 68: 1412-1423.

Daubenmire, R. (1959). "A Canopy-Coverage Method of Vegetational Analysis." Northwest Science 33(1): 42-65.

de Kroon, H., A. Plaisier, et al. (1986). "Elasticity: the relative contribution of demographic parameters to population growth rate." Ecology 67: 1427-1431.

Denevan, W. M. (1992). "The pristine myth: the landscape of the Americas in 1492." Annals of the Association of American Geographers 82(3): 369-385.

Dickey, H. P. (1981). Soil Survey of Franklin County, Kansas, United States Department of Agriculture Soil Conservation Service and Kansas Agricultural Experimental Station.

Dorsey, J. O. (1889). "Teton Folk-Lore." American Anthropologist 2(2): 143-158.

Dunn, C. P., G. R. Guntenspergen, et al. "Effects of Site Landscape Features and Fire Regime on Vegetation Patterns in Presettlement Southern Wisconsin USA."

Edholm, S. and T. Wilder (1998). "A developing gathering ethic." Bulletin of Primitive Technology(16): 13-19.

Ehrlen, J. and J. V. Groenendael (1998). "Direct Perturbation Analysis for Better Conservation." Conservation Biology 12(2): 470-474.

Elton, C. S. (1958). The Ecology of Invasions by Animals and Plants. London, UK, Methuen.

Elzinga, C. L., D. W. Salzer, et al. (1998). Measuring and Monitoring Plant Populations. BLM Technical Reference 1730-1, Bureau of Land Management.

Fieberg, J. and S. P. Ellner (2001). "Stochastic matrix models for conservation and management: a comparative review of methods." Ecology Letters 4(3): 244-266.

Fleming, K. (2003). "Timpsula, Turnip of the Prairie." Native Plant Society of Tyler Texas Newsletter: September 2003: 4-5.

Fletcher, A. C. and F. LaFlesche (1911). "The Omaha Tribe." Smithsonian Institution: Bureau of American Ethnology 27: 76-78.

Foster, B. L. and T. L. Dickson (2004). "Grassland diversity and productivity: The interplay of resource availability and propagule pools." Ecology 85(6): 1541-1547.

Foster, B. L., T. L. Dickson, et al. (2004). "Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient." Journal of Ecology 92(3): 435-449.

Frazier, I. (1989). Great Plains. New York, Penguin Books.

Freckleton, R. P., D. M. Silva Matos, et al. (2003). "Predicting the inpacts of harvesting using stage structured population models: the importance of density-dependence and timing of harvest for a tropical tree." Journal of Applied Ecology 40: 846-858.

Freeman, C. C. and C. A. Morse (2002). Kansas floristic quality assessment: coefficients of conservatism. Lawrence, R.L. McGregor Herbarium and Kansas Biological Survey.

Fynn, R. W. S., C. D. Morris, et al. (2004). "Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment." Applied Vegetation Science 7: 1-10.

Getz, W. M. and R. G. Haight (1989). Population Harvesting: Demographic Models of Fish, Forest, and Animal Resources. Princeton, Princeton University Press.

Gibson, D. J. (1989). "Effects of Animal Disturbance on Tallgrass Prairie Vegetation." American Midland Naturalist 121(1): 144-154.

Gilmore, M. R. (1919). "Uses of Plants by the Indians of the Missouri River Region." Bureau of American Ethnology 33: 14-17.

Gilmore, M. R. (1926). "Arikara Commerce." Indian Notes 3: 13-18.

Gilmore, M. R. (1932). "Importance of Ethnobotanical Investigation." American Anthropologist 34(2): 320-327.

Gittelsohn, J., S. B. Harris, et al. (1995). "Developing diabetes interventions in an Ojibiwa-Cree community in Nothern Ontario: linking qualitative and quantitative data." Chronic Diseases in Canada 16(4).

Gladstar, R. and P. Hirsch, Eds. (2000). Planting the Future: Saving Our Medicinal Herbs. Rochester, Vermont, Healing Arts Press.

Grime, J. P. (1979). Plant Strategies and Vegetation Processes. New York, John Wiley and Sons.

Grimes, J. W. (1990). "A Revision of the New World Species of Psoraleeae (Leguminosae: Papiliondeae)." Memoirs of the New York Botanical Garden 61: 1-114.

Gurevitch, J., S. M. Scheiner, et al. (2002). The Ecology of Plants. Sunderland, Massachusetts, Sinauer Associates.

Hansen, M. J. and A. P. Clevenger (2005). "The influence of disturbance and habitat on the presence of non-native plant species along transport corridors." Biological Conservation 152(2): 249-259.

Harrison, S., B. D. Inouye, et al. "Ecological heterogeneity in the effects of grazing and fire on grassland diversity."

Hatter, I. (2005). Wildcrafting: "Just What is Wildcrafting". posted Feb. 2005, Viewed March 2006.

Havard, V. (1895). "Food Plants of the North American Indians." Bulletin of the Torrey Botanical Club 22: 98-123.

Hayden, F. V. (1859). "Botany." Report of the Secretary of War 1859: 726-747.

Hayes, G. F. and K. D. Holl (2003). "Site-specific responses of native and exotic species to disturbances in a mesic grassland community." Applied Vegetation Science 6(2): 235-244.

Hermann, S. M. (1983). The Life History and Evolutionary Biology of a Long-Lived Herbaceous Legume, Psoralea esculenta. Biological Sciences. Chicaho, University of Illinois at Chicago.

Hernandez, D. (2005). "Got tradition? American Indians use native foods to fight diabetes and revive Indian Culture." Colorlines Magazine: Race, Action, Culture Summer 2005.

High Plains Regional Climate Center (2006). "Monthly Precipitation" http://hprcc.unl.edu. Accessed 1/12/06.

Hilborn, R., C. J. Walters, et al. (1995). "Sustainable exploitation of renewable resources." Annual Review of Ecology and Systematics 25: 45-67.

Hobbs, R. J. and L. F. Huenneke (1992). "Disturbance, diversity, and invasion: implications for conservation." Conservation Biology 6: 324-337.

Hobbs, R. J. and H. A. Mooney (1991). "Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics." Ecology 72(1): 59-68.

Horvitz, C. and D. Schemske (1995). "Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis." Ecological Monographs 66: 155-192.

Horvitz, C., D. Schemske, et al. (1997). The Relative "Importance" of Life-History Stages to Population Growth: Prospective and Retrospective Analyses. Structured-Population Models in Marine, Terrestrial and Freshwater Systems. S. Tuljapurkar and H. Caswell. New York, Chapman and Hall.

Howe, H. F. (1994). "Managing Species Diversity in Tallgrass Prairie: Assumptions and Implications." Conservation Biology 8(3): 691-704.

Howe, H. F. (1994). "Response of Early- and Late-Flowering Plants to Fire Season in Experimental Prairies." Ecological Applications 4(1): 121-133.

Howe, H. F. (1995). "Succession and Fire Season in Experimental Prairie Plantings." Ecology 76(6): 1917-1925.

Howe, H. F. (1999). "Dominance, Diversity and Grazing in Tallgrass Restoration." Ecological Restoration 17:(1 & 2): 59-66.

Hurlburt, D. P. (1999). Population Ecology and Economic Botany of Echinacea angustifolia, a Native Prairie Medicinal Plant, University of Kansas (Lawrence, Kansas): 154.

Hutchings, M. J. (1991). Monitoring plant populations: census as an aid to conservation. Monitoring for Conservation and Ecology. B. Goldsmith. London, Chapman and Hall.

IHS (2004). Appendix: Epidemic of Type 2 Diabetes. Interim Report to Congress Special Diabetes Programs for Indians, United States Department of Health and Human Services. http://www.ihs.gov/MedicalPrograms/diabetes/resources/irc2004_apndx1.pdf: 173-180. Accessed March 12, 2006.

Incze, L. S. and R. A. Lutz (1980). Mussel culture: an east coast perspective. Mussel culture and harvest: a North American perspective. R. A. Lutz. Amsterdam, Elsevier: 99-140.

Jablow, J. (1951). The Cheyenne in Plains Indians Trade Relations 1795-1840. New York, J.J. Augustin.

Jakobsson, A. and O. Eriksson (2000). "A comparative study of seed number, seed size, seedling size and recruitment in grassland plants." Oikos 88(3): 494-502.

Jensen, A. L. (2000). "Sex and stage structured matrix model applied to harvesting a white tailed deer population." Ecological Modelling 128: 245-249.

Jog, S. K., K. Kindscher, et al. (2006). "Floristic Quality as an Indicator of Native Species Diversity within Managed Grasslands." Natural Areas Journal in press.

Johnston, A. (1970). "Blackfoot Indian Utilization of the Flora of the Northwestern Great Plains." Economic Botany 24: 301-324.

Johnston, S. L. (2001). "Food choice is shaped by accessibility: how sources of food have changed over time for the Blackfeet." Nutritional Anthropology 24(2): 3-9.

Kaldy, M. S., A. Johnston, et al. (1980). "Nutritive Value of Indian Bread-root, Squaw-root, and Jerusalem Artichoke." Economic Botany 34(4): 352-357.

Kalisz, S. and M. A. McPeek (1992). "Demography of an age-structured annual: resampled projection matrices. elasticity analysis, and seed bank effects." Ecology 73: 1082-1093.

Kalisz, S. and M. A. McPeek (1993). "Extinction dynamics, population growth and seed banks." Oecologia 95: 314-320.

Kaye, T. N. and D. A. Pyke (2003). "The effect of stochastic technique on estimates of population viability from transition matrix models." Ecology 84(6): 1464-1476.

Kindscher, K. (1987). Edible Wild Plants of the Prairie. Lawrence, Kansas, University Press of Kansas.

Kindscher, K. (1992). Medicinal Wild Plants of the Prairie, An Ethnobotanical Guide. Lawrence, Kansas, University Press of Kansas.

Klaas, B. A., K. A. Moloney, et al. (2000). "The tempo and mode of gopher mound production in a tallgrass prairie remnant." Ecography 23(246-256).

Klein, M. A. (1977). Adaptive Strategies and Process on the Plains: The Nineteenth Century Cultural Sink. Anthropology. Buffalo, State University of New York, Buffalo: 507.

Klein, R. (2000). Wise Old Plants. Planting the Future. R. Gladstar and P. Hirsch. Rochester, Vermont, Healing Arts Press.

Korzeniak, J. (2005). "Species richness and diversity related to anthropogenic soil disturbance in abandoned meadows in the Bieszczady Mts. (Eastern Carpathians)." Acta Societatis Botanicorum Poloniae 74(1): 65-71.

Kotanen, P. M. (1997). "Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows." Journal of Applied Ecology 34(3): 631-644.

Kraenzel, C. F. (1955). The Great Plains in Transition. Norman, Oklahoma, University of Oklahoma Press.

Larson, D. L. (2003). "Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie." Plant Ecology 169(2): 317-333.

Laughlin, D. C. (2004). "Woody plant invasion and the importance of anthropogenic disturbance within xeric limestone prairies."

Lauver, C. L., K. Kindscher, et al. (1999). "A Classification Of The Natural Vegetation Of Kansas." The Southwestern Naturalist 44: 421-443.

Lefkovitch, I. P. (1965). "The study of population growth of organisms grouped by stages." Biometrics 21: 1-18.

Leis, S., D. Engle, et al. (2005). "Effects of Short- and Long-Term Disturbance Resulting from Military Maneuvers on Vegetation and Soils in a Mixed Prairie Area." Environmental Management 36(6): 849-861.

Lemmerman, K. (2006). Suriving on a backyard bounty, Homestore.com. 2006.

Lesica, P. and B. M. Steele (1994). "Prolonged dormancy in vascular plants and implications for monitoring studies." Natural Areas Journal 14: 209-212.

Lindborg, R. and J. Ehrlen (2002). "Evaluating the extinction risk of a perennial herb: demographic data versus historical record." Conservation Biology 16(3): 683-690.

Linderman, F. B. (1972). Pretty-Shield, Medicine Woman of the Crows. Lincoln, University of Nebraska Press (Previously published as Red Mother, 1932).

Long, J. L. and M. S. Kennedy (1961). The Assiniboines. Norman, University of Oklahoma Press.

Maisch, J. M. (1889). "Useful plants of the genus Psoralea." American Journal of Pharmacy 61: 345-352.

Mandelbaum, D. G. (1940). "The Plains Cree." Anthropological Papers: American Museum of Natural History 37: 202-203.

Marks, P. L. and S. Gardescu (1998). "A case study of sugar maple (Acer saccharum) as a forest seedling bank species." Journal of the Torrey Botanical Society 124(4): 287-296.

Martinsen, G. D., J. H. Cushman, et al. (1990). "Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community." Oecologia 83: 132-138.

Maximilian, P. o. W. (1906). Maximilian's Travels. Travels in the Interior of North America. R. G. Thwaites. Cleveland, The Arthur H. Clark Company. 24: 18-19,30-35,80-83.

McClintock, W. (1923). Old Indian Trails. Boston, Houghton Mifflin Company.

McCune, B. and M. J. Mefford (1999). PC-ORD for Windows. Gleneden Beach, Oregon, MjM Software.

McGraw, J. B., M. A. Furedi, et al. (2005). "Berry Ripening and Harvest Season in Wild American Ginseng." Northeastern Naturalist 12(2): 141-152.

McIntosh, E. N. (2003). The Lewis and Clark Expedition: Food, Nutrition and Health. Sioux Falls, South Dakota, The Center for Western Studies, Augustana College.

McIntyre, S., S. Lavorel, et al. (1995). "Plant Life-History Attributes - Their Relationship to Disturbance Responses in Herbaceous Vegetation." Journal of Ecology 83(1): 31-44.

Meffe, G. K. and C. R. Carroll (1997). Principles of Conservation Biology. Sunderland, Massachusetts, Sinauer Associates.

Mehlman, D. W. (1993). "Tumbleweed dispersal in Florida sandhill Baptisia (Fabaceae)." Bulletin of the Torrey Botanical Club 102(1): 60-63.

Menges, E. S. (2000). "Population viability analyses in plants: Challenges and opportunities." Trends in Ecology and Evolution 15(2): 51-56.

Menges, E. S. and D. R. Gordon (1996). "Three levels of monitoring intensity for rare plant species." Natural Areas Journal 16(3): 227-237.

Meyer, K. M., K. Witt-Lowe, et al. (2005). Preserving traditional botanical knowledge among the Dakota People. Society for Economic Botany Annual Meeting, Fort Worth, Texas.

Microsoft (1996). Microsoft Excel 97.

Milchunas, D. G., K. A. Schulz, et al. (2000). "Plant Community Structure in Relation to Long-Term Disturbance by Mechanized Military Maneuvers in a Semiarid Region." Environmental Management 25(5): 525-539.

Mills, L. S., D. F. Doak, et al. (1999). "Reliability of conservation actions based on elasticity analysis of matrix models." Conservation Biology 13: 815-829.

Minitab (1998). Minitab for Windows, Minitab Inc.

Moerman, D. E. (1996). "An Analysis of the Food Plants and Drug Plants of Native North America." Journal of Ethnopharmacology 52: 1-22.

Moerman, D. E. and G. F. Estabrook (2003). "Native Americans' choice of species for medicinal use is dependent on plant family:confirmation with meta-significance analysis." Journal of Ethnopharmacology 87(1): 51-59.

Munzbergova, Z. and J. Ehrlen (2005). "How best to collect demographic data for population viability analysis models." Journal of Applied Ecology 42: 1115-1120.

Nantel, P., D. Gagnon, et al. (1996). "Population Viability Analysis of American Ginseng and Wild Leek Harvested in Stochastic Environments." Conservation Biology 10(2): 608-621.

NDMC (2006). "The Drought Monitor." National Drought Mitigation Center http://drought.unl.edu/dm/monitor.html. Updated 2/7/2006.

Neidhart, J. G. (1952). When the Trees Flowered. New York, Macmillan Company.

Norris, K. (2004). "Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm." Journal of Applied Ecology 41: 413-426.

Olcott, F. J. (1917). The Red Indian Fairy Book, The Baldwin Project: http://www.mainlesson.com/display.php?author=olcott&book=indian&story=bride.

Parker, D. D. (1950). Major Long's Visit to Lake Big Shore and Traverse in 1823. Early Explorations in Fur and Trading in South Dakota. Pierre, South Dakota History Collections Report. XXV: 1-211.

Payette, S., J. Deshaye, et al. (1982). "Tree seed populations a the treeline in Riviere-aux-Feuilles area of northern Quebec Canada." Arctic and Alpine Research 14(3): 215-222.

PCA (2005). Medicinal Plant Working Group- Papers, Reports and Articles, Plant Conservation Alliance. http://www.nps.gov/plants/medicinal/pubs/index.htm#im Accessed 3/7/2006.

Peacock, S. L. (1992). Piikani Ethnobotany: Traditional Plant Knowledge of the Piikani Peoples of the Northwestern Plains. Department of Archeaelogy. Calgary, Alberta, The Univeristy of Calgary.

Peters, C. M. (1990). Population ecology and management of forest fruit trees in Peruvian Amazonia. Alternatives to deforestation: steps towards sustainable use of the Amazon rain forest. A. B. Anderson. New York, Columbia University Press: 86-98.

Pfab, M. F. and M. A. Scholes (2004). "Is the collection of Aloe peglerae from the wild sustainable? An evaluation using stochastic population modelling." Biological Conservation 118(5): 695-701.

Pfaf (2003) “Alternative Root Crops” Plants for a Future. http://www.pfaf.org/leaflets/altroots.php. Accessed 4/27/06.

Platt, W. J. (1975). "The Colonization and Formation of Equilibrium Plant Species Associations on Badger Disturbances in a Tall-Grass Prairie." Ecological Monographs 45: 284-305.

Polley, H. W. and S. L. Collins (1984). "Relationships of Vegetation and Environment in Buffalo Wallows." American Midland Naturalist 112(1): 178-187.

Polley, H. W. and L. L. Wallace (1986). "The relationship of plant species hererogeneity to soil variation in buffalo wallows." Southwestern Naturalist 31(1): 493-502.

Poysa, H., J. Elmberg, et al. (2004). "Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid?" Oikos 104(3): 612-615.

Prescott, P. (1849). "Farming Among the Sioux Indians." United States Patent Office Department of Agriculture 1849: 451-455.

Prince, J. M. and R. H. Steckel (2003). "Nutritional success on the Great Plains: nineteenth century equestrian nomads." Journal of Interdisciplinary History 33(3): 353-384.

Ramula, S. and K. Lehtila (2005a). "Importance of correlations among matrix entries in stochastic models in relation to number of transition matrices." Oikos 111(1): 9-18.

Ramula, S. and K. Lehtila (2005b). "Matrix dimensionality in demographic analyses of plants: when to use smaller matrices?" Oikos 111(3): 563-573.

Rankin, R. L. (2006). Cultivated Plants in the Siouan Language Family. Lawrence, Kansas. Feb. 2006 Lecture Notes.

Ray, A. J. (1998). Indians in the Fur Trade. Toronto, University of Toronto Press.

Reed, J. M., L. S. Mills, et al. (2002). "Emerging Issues in Population Viability Analysis." Conservation Biology 16(1): 7-19.

Reichart, M. (1983). "Psoralea esculenta in Northeast Kansas." Journal of the Kansas Anthropological Association 4: 103-121.

Reid, K. C. (1977). "Psoralea esculenta as a Prairie Resource: An Ethnographic Appraisal." Plains Anthology 22(78): 321-327.

Rejmanek, M. (2000). "Invasive plants: approaches and predictions." Austral Ecology 25(5): 497-506.

Robson, D. B., J. D. Knight, et al. (2003). "Ability of cold-tolerant plants to grow in hydrocarbon-contaminated soil." International Journal of Phytoremediation 5(2) 105-123.

Rogers, W. E. and D. C. Hartnett (2001). "Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie." American Journal of Botany 88(9): 1634-1643.

Salick, J., C. Asa, et al. (2003). Intellectual Imperatives in Ethnobiology: NSF Biocomplexity Workshop Report. St. Louis, Missouri Botanical Garden.

Samson, F. and F. Knopf (1994). "Prairie conservation in North America." BioScience 44(6): 418-421.

Scheiner, S. M. and J. Gurevitch, Eds. (2001). Design and Analysis of Ecological Experiments. New York, Oxford University Press.

Schemske, D., B. C. Husband, et al. (1994). "Evaluating approaches to the conservation of rare and endangered plants." Ecology 75: 584-606.

Seward, C. (2005). As the ramps sprout, so do new rules. Washington Post. Washington D.C.: A19.

Shortridge, B. and J. Shortridge (1998). Food in American Culture. The Taste of American Place. B. Shortridge and J. Shortridge, Rowman and Littlefield.

Silvertown, J. and D. Charlesworth (2001). Introduction to Plant Population Biology. London, Blackwell Science.

Silvertown, J., M. Franco, et al. (1996). "Interpretation of elasticity matrices as an aid to the management of plant populations for conservation." Conservation Biology 10(2): 591-597.

Slade, N. A., H. M. Alexander, et al. (2003). "Estimation of population size and probabilities of survival and detection in Mead's milkweed." Ecology 84(3): 791-797.

Smith, R. L. (1990). Ecology and Field Biology. New York, Harper and Row.

Snell, A. H. (2000). Grandmother's Grandchild. Lincoln, University of Nebraska Press.

Snell, A. H. and L. M. Castle, Ed. (2006). A Taste of Crow Hertitage. Lincoln, University of Nebraska Press.

Spessard, L. L. (1988). "Seed-germination studies of Psoralea esculenta Pursh (Indian Turnip) and Psoralea argophylla (Silver Scurfpea)." Transactions of the Nebraska Academy of Sciences XVI: 123-126.

Stallings, G. P., D. C. Thill, et al. (1995). "Plant movement and seed dispersal of Russian thistle (Salsola iberica)." Weed Science 43(1): 63-69.

Stern, T. (1993). Chiefs and Chief Traders: Indian Relations at Fort Nez Perces 1818-1855. Corvallis, Oregon State University Press.

Taylor, M. K., D. P. Demaster, et al. (1987). "Modelling the sustainable harvest of female polar bears." Journal of Wildlife Management 51(4): 811-820.

Thwaites, R. G. (1904). Bradbury's Travels in the Interior of America: 1809-1811. Early Western Travels: 1748-1846. R. G. Thwaites. Cleveland, The Arthur H. Clark Company. 5.

Thwaites, R. G. (1904). Original Journals of the Lewis and Clark Expeditionn: 1804-1806. New York, Dodd, Mead and Company.

Thwaites, R. G. (1905). S.H. Long's Expedition. Early Western Travels. R. G. Thwaites. Cleveland, The Arthur H. Clark Company. 14: 128-129,184-199,210-215,260-261,288-289,294-295,308-309.

Ticktin, T. (2004). "The ecological implications of harvesting non-timber forest products." Journal of Applied Ecology 41(1): 11-21.

Ticktin, T., P. Nantel, et al. (2002). "Effects of variation on harvest limits for nontimber forest species in Mexico." Conservation Biology 16(3): 691-705.

Tilman, D. (1997). "Community invasibility, recruitment limation, and grassland biodiversity." Ecology 78: 81-92.

Toineeta, J. Y. (1970). Absorag-issawa. Education. Bozeman, Montanta State University: 146.

Tuchman, G. and H. G. Levine (1993). "New York Jews and Chinese Food: The Social Construction of Ethnic Pattern." Journal of Contemporary Ethnography 22(3): 382-407.

Tuljapurkar, S. (1990). Population Dynamics in Variable Environments. New York, Springer-Verlag.

Tuljapurkar, S. (1997). Stochastic matrix models. Structered-Population Models in Marine, Terrestrial, and Freshwater Systems. S. Tuljapurkar and H. Caswell. New York, Chapman and Hall.

Turnbull, L. A., M. J. Crawley, et al. (2000). "Are plant populations seed-limited? A review of seed sowing experiments." Oikos 88(2): 225-238.

Turner, N. J. (1981). "A Gift for the Taking: The Untapped Potential of Some Food Plants of North American Native Peoples." Canadian Journal of Botany 59(11): 2331-2357.

Turner, N. J. (1997). Food Plants of Interior First Peoples. Vancouver, B.C., University of British Columbia Press.

Umbanhowar, C. E. (1996). "Recent fire history on the Northern Great Plains." American Midland Naturalist 135: 115-121.

UPS (2005). "At-Risk Update", United Plant Savers. 2006.

USDA (1965). Soil Survey of Saunders County Nebraska. Lincoln, Nebraska ?, United States Deparment of Agriculture Soil Conservation Service and University of Nebraska Conservation and Survey Division.

USDA (1977). Soil Survey of Big Horn County Area, Montana, United States Department of Agriculture Soil Conservation Service and United States Department of the Interior Bureau of Indian Affairs.

USDA and NRCS (2006). The PLANTS Database 6 March 2006. Baton Rouge, LA, National Plant Data Center.

van der Pijl, L. (1969). Principles of Dispersal in Higher Plants. New York, Springer-Verlag.

Van der Voort, M. E., B. Bailey, et al. (2003). "Recovery of Populations of Goldenseal (Hydrastis canadensis L.) and American Ginseng (Panax quinquefolius L.) Following Harvest." The American Midland Naturalist 149(2): 282-292.

Weaver, J. E. (1954). The North American Prairie. Lincoln, Nebraska, Johnsen Publishing.

Weaver, J. E. and F. W. Albertson (1956). Grasslands of the Great Plains. Lincolon, Nebraska, Johnsen Publishing Co.

Webb, W. P. (1931). The Great Plains. Boston, Ginn and Company.

Wedel, W. R. (1978). "Notes on the Prairie Turnip (Psoralea esculenta) Among the Plains Indians." Nebraska History 59(2): 1-25.

Western Regional Climate Center (2006). “Monthly Precipitation” http://www.wrcc.dri.edu. Accessed 1/12/06.

White, P. S. and J. Harrod (1997). Disturbance and diversity in a landscape context. Wildlife and landscape ecology: effects of pattern and scale. J. A. Bissonette. New York, Springer.

Wolfe-Berlin, K. S. and K. A. Moloney (2000). "The effect of gopher mounds and fire on the spatial distribution of a short-lived legume in tallgrass prairei." Canadian Journal of Botany 78: 1299-1308.

Wooden Knife, A. (2006). Fry Bread's Secret Ingredient, Wooden Knife. 2006.

Wright, H. A. and A. W. Bailey (1982). Fire Ecology. New York, Wiley.

Zawacki, A. A. and G. Hausfater (1969). Early vegetation of the Lower Illinois Valley. Springfield, Illinois State Museum.