

# Journal of Range Management

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# Lessons in developing successful invasive weed control programs

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## Abstract

The development of successful regional or national invasive weed control programs is often hampered by the way the problem is approached. Typically weed control programs are developed and evaluated solely from the perspective of the biological sciences. While this is appropriate from a local or landscape perspective, it will probably not produce the desired results when addressing widespread well-established infestations that impact large regions. The "Ecological Area-wide Management (TEAM) of Leafy Spurge" program was the first U.S. Department of Agriculture (USDA), Agricultural Research Service (ARS) area wide invasive weed program. The 5-year program, funded by the ARS and conducted cooperatively with the USDA Animal and Plant Health Inspection Service, focused on the control of leafy spurge (*Euphorbia esula* L.) in North Dakota and South Dakota, Montana and Wyoming. Now in its final year (2001), the TEAM Leafy Spurge program has made significant progress in controlling leafy spurge, increasing public awareness of the problem and demonstrating the effectiveness of biologically-based integrated pest management. While this is a significant accomplishment, the lessons learned over the course of the project clearly demonstrate that the success of regional weed control programs depends on more than a persistent, marked reduction in the pest population. Effective regional weed control programs need to focus not only on biological issues, but also on the ecological, scientific, economic, social and legal factors that influence the effectiveness of the program. Therefore, the implementation and subsequent evaluation of a weed control program must include all the principal factors that will ultimately determine success and sustainability. This manuscript outlines the history of leafy spurge on the North American continent, the situation currently facing weed managers, and an evaluation of the TEAM Leafy Spurge program's success for each factor listed above. The final analysis indicates that successful biologically-based leafy spurge control is on the horizon, especially when weed managers understand the number of problem areas that must be addressed to achieve a sustained reduction of a weed population. The amount of time it will take to be realized depends on our commitment to solving the problem and our willingness to work together as a cohesive team.

## Resumen

El desarrollo de programas exitosos de control de maleza a nivel nacional o regional es a menudo impedido por la manera en la que se aborda el problema. Los programas de control de maleza son típicamente desarrollados y evaluados solamente desde la perspectiva de las ciencias biológicas. Mientras esto es adecuado desde una perspectiva local o de paisaje, probablemente no producirá los resultados deseados cuando se abordan infestaciones dispersas bien establecidas que impactan grandes regiones. El programa "Ecological Area-wide Management (TEAM) of Leafy Spurge" fue el primer programa de área extensa de maleza invasiva del Servicio de Investigación Agrícola (ARS) - Departamento de Agricultura de Estados Unidos (USDA). El programa de 5 años fue financiado por el ARS y conducido en forma cooperativa con el Servicio de Inspección de Plantas y Animales del USDA y enfocado al control de "Leafy spurge" (*Euphorbia esula* L.) en Dakota del Norte, Dakota del Sur, Montana y Wyoming. Ahora en su año final (2001), el programa TEAM "Leafy spruge" ha hecho avances significativos en controlar el "leafy spruge", incrementando la conciencia pública respecto al problema y demostrando la efectividad del manejo integrado de plagas basado en control biológico. Mientras este es un logro significativo, las lecciones aprendidas en el curso del proyecto demostraron claramente que el éxito de programas regionales de control de maleza depende algo más que una persistente y marcada reducción de la población de la maleza. Los programas regionales efectivos de control de maleza necesitan enfocarse no solo en los problemas biológicos, sino también en los factores ecológicos, científicos, económicos, sociales y legales que influyen en la efectividad del programa. Por lo tanto, la implementación y evaluación subsecuente de un programa de control de maleza debe incluir todos los factores principales que finalmente determinan el éxito y sostenibilidad. Este manuscrito da una perspectiva de la historia del "leafy spruge" en el continente Norteamericano, la situación que actualmente encaran los manejadores de maleza y una evaluación del éxito del programa "TEAM Leafy Spurge" para cada uno de los factores enlistados arriba. El análisis final indica que el éxito del control del "leafy spruge" con bases biológicas está en el horizonte, especialmente cuando los manejadores de maleza entienden el número de áreas problema que deben ser abordadas para lograr una reducción sostenida de la población de maleza. La cantidad de tiempo que tomará para ser realizado depende de nuestro compromiso para resolver el problema y nuestra disponibilidad para trabajar juntos como un equipo unido.

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Biological agents have been used to manage problem weed species for more than 100 years (Gassmann 1996). The goal of biological control is to use diseases, parasites, or predators to increase the mortality of the problem weed species, thus reducing the plant's ability to effectively compete with native vegetation (Krebs 1978). The success or failure of biological control programs has typically been evaluated from the perspective of the agent/host interaction. Perhaps the quintessential definition of biological control success is "a persistent, marked reduction in the pest population" (Lawton 1985).

Presently, 9 of the 15 insects approved in the United States for leafy spurge (*Euphorbia esula* L.) field release have established viable populations. Yet, the best estimates of leafy spurge population change indicate that infestations are doubling every 10 years and in some cases every 5 years (Anderson et al. 1999). Based on Lawton's (1985) definition and the above observations, we conclude that current efforts to control leafy spurge—including biological control—have not yet been successful.

Too often our perception of success or failure is predetermined by how we choose to view the problem. The evaluation of biological control success is both time- and scale-sensitive; it is not independent of the knowledge base and infrastructure supporting the program, and it is closely tied to the socioeconomic conditions existing across the region at any given time. Perhaps we are blurring the line between classical biological control and biological control programs; however, the 2 are codependent. The methodology we use to approach a problem is often as important as the biological interaction in determining the success or failure of a program. Certainly our definition of success should not be limited to a biological evaluation of agent/host interactions, especially when viewing the problem on a national or regional scale.

This paper addresses 2 fundamental questions: Has the leafy spurge control program in North America been successful? And if not, what can be done to make it successful? We take a brief look at the history of the problem and expand our understanding of success beyond that of

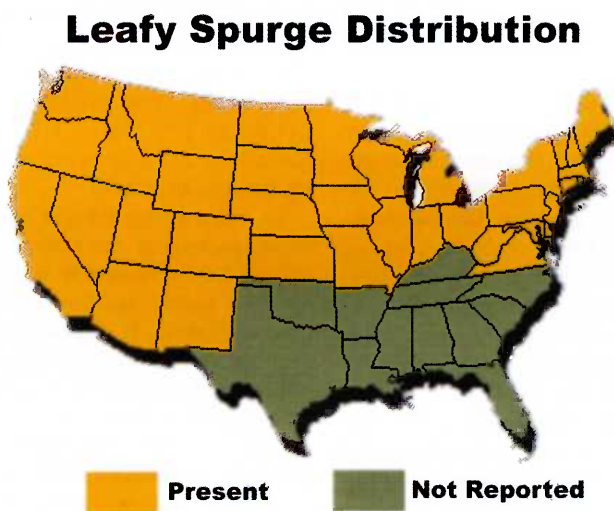
agent/host interactions. Examples from "The Ecological Area-wide Management of Leafy Spurge (TEAM Leafy Spurge)" are presented to expand the concepts presented in this paper. The TEAM Leafy Spurge is a 5-year USDA, Agricultural Research Service (ARS), Area-wide Program funded by the ARS and managed cooperatively with the USDA, Animal and Plant Health Inspection Service.

## Historical Context

Leafy spurge is a deep-rooted perennial weed with erect stems 40 to 80 cm tall (Stevens 1963). The weed reproduces by both vegetative buds and the production of large quantities of seeds. A native of Eurasia, leafy spurge was first reported in the state of Massachusetts in 1827 (Noble et al. 1979). Several sources can be used to document the historical progression of leafy spurge from Massachusetts into the central United States and Canada (key sources include Dunn 1979, Britton 1921, Quimby and Wendel 1997, Selleck et al. 1962, Galitz 1980, and Bangsund and Leistritz 1991). Table 1 provides a short synopsis of the historical facts concerning leafy spurge and key biological control events. This information helps place the current situation facing weed managers within a historical context. Consider that prior to the year 2000, leafy spurge had

existed in North America for at least 173 years. It took almost 100 years before the plant was identified as a weed. Cultural controls and sterilization of the soil were the primary methods for dealing with leafy spurge prior to the development of effective herbicides (late 1940s and early 1950s). Chemical control quickly became the tool of choice for treating leafy spurge infestations because it was relatively cheap and the effects were almost immediate. Chemical control efforts of the last 50 years certainly have affected the distribution and rate of leafy spurge spread; however, chemical costs have continued to rise and the process has proven to be ineffective in achieving sustained long-term control. Negative environmental impacts have also resulted from the use of non-selective chemicals. Today, leafy spurge is believed to infest 2 million hectares throughout 35 states (Fig. 1) and all the Canadian provinces except Newfoundland (Quimby and Wendel 1997).

The introduction of biological control in the mid-1960s provided another tool for the control of leafy spurge. In the 1960s, the concept of biological control for leafy spurge was in its infancy. Demonstrations were made during symposiums where *Hyles euphorbiae* (L), commonly known as the "leafy spurge hawk moth larvae" were released into glass containers containing healthy leafy spurge. By the end of the presentation the hawk moth larvae had



**Source: USDA, NRCS 1999. The plants database (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA**

Fig. 1. The 35 states presently impacted by leafy spurge.



**Table 1. Historical progression of leafy spurge and key biological control events.**

Year	Key Event
1827	Leafy spurge was first documented in Massachusetts.
1876	The plant was found in New York and identified as a "rare plant."
1881	Leafy spurge was found in Michigan.
1913	Leafy spurge was found in at least four states and Canadian provinces.
1921	Leafy spurge was first labeled as a "weed" in a <i>New York Herald</i> editorial.
1933	The plant is found in 19 states and several Canadian provinces.
1949-1950	Leafy spurge is found in all Canadian provinces except Newfoundland.
1940s & 1950s	New herbicides become available and managers begin to use them on a progressively larger scale.
1960s	Efforts to manage leafy spurge with biological control begin.
1964	The first leafy spurge biocontrol agent ( <i>Hyles</i> hawk moth) is released.
1970	Leafy spurge occupies 26 states.
1979	The first leafy spurge symposium was held and participants begin to develop today's local, state and federal leafy spurge management programs.
1979	Leafy spurge occurs in 30 states.
1982	North Dakota reports 350,000 hectares infested with leafy spurge.
1985	The first <i>Aphthona</i> flea beetle ( <i>A. flava</i> ) was released.
1988	The USDA-Animal and Plant Health Inspection Service (APHIS) began their leafy spurge biological control program.
1989	<i>Aphthona nigricutis</i> was approved and released.
1990	Researchers determine that leafy spurge infestations double in area every 10 years.
1991	Agricultural economists at North Dakota State University estimate direct and indirect economic impacts of leafy spurge at \$144 million for North and South Dakota, Montana and Wyoming.
1993	<i>Aphthona lacertosa</i> is approved and released.
1994	Leafy spurge is estimated to infest 650,000 hectares in North and South Dakota, Montana and Wyoming.
1997	Natural Resources Conservation Service reports the presence of leafy spurge in 35 states; the heaviest populations occur in North and South Dakota, Montana, Minnesota, Nebraska, Colorado, Idaho and Wyoming.
1998	Estimates of over 2 million hectares of leafy spurge in the U.S.
1999	North Dakota estimates its leafy spurge infestation to be 450,000 hectares.

devoured the leafy spurge stems and leaves. This type of showmanship excited the leafy spurge control community and the search for additional leafy spurge biological control agents was expanded. Unfortunately for *Hyles*, like so many "prototypes" before it, the species was not destined to become the workhorse of the biological control program. Disease problems prevented *Hyles* from developing population levels substantial enough to impact leafy spurge populations. But the potential demonstrated by the hawk moth energized the search for other biological control agents. Table 2 lists the 15 leafy spurge biological control agents currently approved in the United States for field release on leafy spurge. Presently, 9 of the 15 insects have established; however, control of leafy spurge on a local level within specific habitats has been achieved primarily by *Aphthona nigricutis* (Fondras) and *A. lacertosa* (Rosenhauer) / *czwalinae* (Weise) (Fig. 2). The other 6 biological control agents that have established in the

United States and Canada have enjoyed less success than these 3 *Aphthona* species, however, limited populations are present over large areas dominated by leafy spurge. What role these "lesser" control agents will play as leafy spurge control efforts decrease weed population levels remains to be seen.

So, what is the state of the ecosystem weed managers have to contend with today? Leafy spurge is well established (greater than 2 million hectares in the United States). It displaces most native vegetation, including threatened and endangered species (Sterling et al. 2000) and impacts native ungulates (Trammell and Butler 1995). The deep roots of the plant, along with its ability to reproduce and spread both by vegetative buds and seeds, enable the population to double in size every 10 years or less (Anderson et al. 1999). Chemical control has not produced sustained long-term control, and inappropriate chemical use has caused negative impacts to other components of the envi-

ronment. Cultural control methods such as sheep and goat grazing are not widely accepted as viable control alternatives. Conversely, the acceptance of biological control has increased. Nowierski (1985) attributed the increased acceptance and use of biological control to reduced economic and ecological costs during a period of depressed agronomic income and heightened environmental awareness. *Aphthona* flea beetles have demonstrated the greatest amount of success in controlling leafy spurge populations within specific habitats; however, determining the number of hectares the flea beetles have controlled is more elusive than estimating the amount of leafy spurge in North America. While the overall rate of leafy spurge establishment is still likely greater than the rate of control, the populations of biological control agents are also increasing rapidly. It is very difficult to find leafy spurge stands in western North Dakota that do not have a resident population of *Aphthona* flea beetles (Personal Communication, Donald Kirby, June



Fig. 2. Top to bottom: *Aphthona lacertosa* (Black) and *A. nigriscutis* (Golden Brown).

2000). This leads scientists to believe that control rates will quickly approach and even surpass the rate of leafy spurge establishment as these small resident insect

populations expand to critical density levels and link with other areas where larger insect populations have substantially reduced leafy spurge stem densities.

Table 2. Leafy Spurge Biological Control Agents.

Species and Authority	Order: Family	Date Approved
<i>Hyles euphorbia</i> (L.)	Lepidoptera: Sphingidae	1964
<i>Chamaesphecia empiformis</i> (Esp.)	Lepidoptera: Sesiidae	1975
<i>Chamaesphecia tenthrediniformis</i> (Den. Sch.)	Lepidoptera: Sesiidae	1975
<i>Oberea erythrocephala</i> (Schrank)	Coleoptera: Cerambycidae	1980
<i>Spurgia esulae</i> (Gange)	Diptera: Cecidomyiidae	1985
<i>Aphthona flava</i> (Guill.)	Coleoptera: Chrysomelidae	1985
<i>Aphthona cyarissiae</i> (Koch)	Coleoptera: Chrysomelidae	1986
<i>Aphthona czwalinae</i> (Weise)	Coleoptera: Chrysomelidae	1987
<i>Aphthona nigriscutis</i> (Foundras)	Coleoptera: Chrysomelidae	1989
<i>Dasineura</i> sp. Nr. <i>capsulae</i> (Kieffer)	Diptera: Cecidomyiidae	1991
<i>Aphthona abdominalis</i> (Duftschmid)	Coleoptera: Chrysomelidae	1993
<i>Aphthona lacertosa</i> (Rosenhauer)	Coleoptera: Chrysomelidae	1993
<i>Chamaesphecia hungarica</i> (Tomala)	Lepidoptera: Sesiidae	1993
<i>Chamaesphecia crassicornis</i> (Bartel)	Lepidoptera: Sesiidae	1996
<i>Spurgia capitigena</i> (Bremi)	Diptera: Cecidomyiidae	1998

Based on the above information we conclude that biological control agents have not yet successfully controlled leafy spurge regionally, based on a narrow concept of "success" (Lawton 1985). But control has been established in many local areas, such as hillsides, warm and more open plant communities, and areas where the soils are not too wet or too sandy. Furthermore, the success that has occurred is relatively recent. The first *Aphthona* species of the leafy spurge biological control program (*Aphthona flava*) was cleared for release just 15 years ago. The most recent and potentially most effective agent (*Aphthona lacertosa*) was cleared for release in 1993. The success that leafy spurge biological control has enjoyed is actually quite significant when one considers the large area infested and the huge disparity in time (158 years vs. 15 years) between the introduction of leafy spurge and the introduction of effective biological control agents. While it is premature to label the biological control program a success, current evidence gives us every reason to believe that successful control of leafy spurge in the broad sense is only a matter of time.

## Multiple Dimensions of Success

Some scientists and land managers limit their view of successful weed control to the reduction or elimination of the problem species (biological success). However, other factors that must be con-



Fig. 3. What's left of a leafy spurge stem covered with *Aphthona lacertosa*.

sidered include: ecological, scientific, economic, political, social, and legal success. Each component is an integral part of a comprehensive and sustainable weed control effort.

### Biological Success:

What is success? To most ranchers, farmers and weed control specialists, success is getting rid of leafy spurge or at least having less spurge this year than last. One control methodology is biological control. Biological control agents help control leafy spurge in different ways. Primary methods of attack include consumption of above-ground plant material, consumption of root material, and blocking seed production. *Aphthona* sp. flea beetles have produced the greatest impact on leafy spurge. *A. nigriscutis* and *A. czwalinae/lacertosa* impact the plant by ovipositing at the base of the plant. The resulting larvae feed on leafy spurge roots,

increasing plant morbidity, reducing plant health and creating pathways for the introduction of plant pathogens. We could label this type of success as "botanical or biological success." **Biological success is reducing the density of the problem species to the point that it is a manageable part of the landscape.** Remember, however, that perspective determines the view of success or failure. We cannot simply associate a reduction in the amount of leafy spurge as a success without considering the impact of the pest and the associated treatment(s) in each success component.

### TEAM Leafy Spurge examples:

Research findings from across the 4 state region of North Dakota, South Dakota, Montana, and Wyoming indicate that managers can realize an 85% success rate in site establishment of biological control agents and an average rate of control of approximately .65 ha release<sup>-1</sup> year<sup>-1</sup>

(3,000 *Aphthona lacertosa/czwalinae* and 3,000 *Aphthona nigriscutis* released at each site). The release of 6,000 *Aphthona* spp. at each site was chosen to ensure measurable results over the short 5-year time frame of the project. Operationally, smaller releases of 1,000–2,000 insects released at a greater number of sites can be just as effective (if the sites selected are conducive to insect establishment). In 1998 alone, more than 200 million insects (*Aphthona lacertosa/czwalinae*) were harvested and redistributed from a single area in North Dakota. If 2,000 insects are released at a site with an establishment success of 85%, then the potential exists for 85,000 new release sites with a rate of leafy spurge control of greater than 55,000 ha year<sup>-1</sup>.

The rate of leafy spurge control using flea beetles is, of course, not constant. As flea beetle populations increase exponentially, so will their impact. One researcher in Montana reported a 7-fold increase in flea beetles between 1998 and 2000 (Personal Communication, Jack Butler, October 2000). Control in different geographic areas showed reductions in the foliar cover of leafy spurge that ranged from 35% to 100%. These are substantial reductions considering the insect populations being tracked have only been active for 2 to 3 years. In some older insectaries (areas used to raise harvestable populations of biological control agents) insect populations declined rapidly in 2000. There was nothing wrong with the insects; they simply had reduced the spurge to a level that would no longer sustain high insect populations. The lesson from 2000 is that flea beetles cannot be taken for granted. We now have large numbers of flea beetles (Fig. 3) spread across a wide geographic area, and they must be managed to start new insectaries to ensure that managers have harvestable flea beetle resources over the upcoming years.

Another form of biological control is the use of herbivores, such as sheep or goats that include leafy spurge as part of their daily food intake (Landgraf et al. 1984) (Fig. 4). Rapid reductions in leafy spurge densities were realized when insect biological control agents were used in combination with sheep. Research on one section of land containing approximately 40–50% leafy spurge stands with stem counts approaching 200 stems m<sup>-2</sup>, demonstrated a 31% to 50% reduction in leafy spurge stem densities in less than 3 years (Personal Communication, Timothy





**Fig. 4. Multi-species grazing of leafy spurge infested rangeland near Sentinel Butte North Dakota.**

Faller, June 2000) (Fig. 5). This research indicates that dense stands of leafy spurge can be rapidly controlled using combinations of sheep and insects. This multi-species scenario may not be feasible in all areas, but it does demonstrate what is possible when multiple pest management tools are used together.

Clearly these observations indicate substantial success in reducing leafy spurge, however, how these sites will respond over time will be a function of the ecosystem and controlling agent dynamics.

### **Ecological Success:**

Ecological success is a bit more difficult to define. Ideally, the biological control program will impact only the target pest and the indigenous plants will reestablish much as they were prior to the weed's introduction. Unfortunately, most weed infestations and their associated treatments alter some aspect of the ecosystem. An analogy is the use of surgery, chemotherapy, and radiation to treat a cancerous tumor. The tumor is the immediate threat. Left untreated, it will cause irreparable damage or even kill the host organism. The treatments themselves are usually invasive, causing permanent damage to surrounding tissues and organs and sometimes even contribute to the organism's death. How do you define success or failure under these circumstances? It is not as simple as destroying the tumor or eliminating the infestation. For most patients or ecologists, it is the quality of the life they lead or the health of the entire system that is important. Determining what constitutes a quality life or a healthy ecosystem is dependent on the individual or individuals evaluating the circumstances. Therefore,

we can conclude that the course of action taken by an individual or group will be based on personal reflection and a qualitative assessment of short-term risks versus long-term gains.

While an ecosystem is not a cognitive organism, the individuals who use and

manage these systems are. The decisions they make concerning the use of biological control or other integrated pest management (IPM) strategies are dependent on their perspective, values and aspirations toward the system they are dealing with. From the rancher's perspective, success is the removal of the pest and a subsequent increase in more desirable plant species. Ranch operators are typically not as concerned with the composition of the ecosystem as they are with the quality and quantity of forage available to the operation. Environmental groups are concerned with protecting the quality (health) of the system and its composition (biological diversity). Most federal and state land managers are required to manage the land to maintain or improve productivity and quality and allow for multiple land uses. These differing perspectives often lead to disagreements, protests, and lawsuits (such as against Paterson's curse/salvation Jane, *Echium plantagineum*, in Australia; Cullen and Delfosse 1985, Delfosse 1985, 1990, Delfosse and Cullen 1985) as each group positions itself to



**Fig. 5. Before and after photographs of a rangeland draw treated with biologically-based IPM. Multi-species grazing (cattle and sheep) combined with insect biological control agents reduced leafy spurge stem densities across the pasture by 31% to 50%.**



ensure that its ideologies prevail or that its views are at least considered.

The management guidelines individuals and agencies use on a relatively healthy ecosystem often work together to produce a better system. Unfortunately, as a system deteriorates (e.g., when the condition of a patient worsens or a weed-infestation becomes more pervasive), there comes a point when the rules designed to protect the system (or the individual) can actually interfere with system maintenance and recovery. So it is within this quagmire of emotion, qualitative assessments and conflicting policies that we define exactly what we mean by ecological success. ***Ecological success is stopping or reversing the progression of an invading pest through the use of biological control agents and other IPM tools that have no direct detrimental effect on the system, or whose negative impacts to the ecosystem are outweighed by the overall benefit of their use.*** Notice that this definition does not deal with returning the system to some preconceived notion of health, and it ignores issues such as maximizing biodiversity or preserving threatened and endangered species. These are important issues that must be addressed, but are probably more appropriately dealt within the context of post-control rehabilitation.

### TEAM Leafy Spurge examples:

Herbicides are one of the primary tools used to control leafy spurge. The use of herbicides to treat small new stands of leafy spurge and to prevent the spread of larger stands is extremely important; however, repeated use of herbicides over large infestations will reduce the forb component of the community which ultimately has the effect of reducing overall species richness (Butler 1994). Ecological problems associated with herbicides coupled with increasing chemical costs have reduced their use in many areas. Ward County, N.D. (48.5 N, 101.30 W) sprayed approximately 3,200 ha in 1989. Since then they have reduced herbicide use by 95% and started an aggressive biological control program. The county distributed over 26 million biological control agents during the summer of 2000. Observers in the county indicate that spurge stem densities and foliar cover are being significantly reduced without the extensive use of herbicides. Barnes County, N.D. (47.0 N, 98.0 W) has reduced their cost of herbicide treatment from \$122,117 in 1995 to

\$66,400 in 2000. As producers and land managers come to realize the potential of biological control, they have elected to reduce their dependence on herbicides. This may not be entirely beneficial since herbicides are needed to control outliers and prevent the leafy spurge perimeter from expanding during the period when biological control agents are developing population numbers sufficient enough to control leafy spurge.

More progressive weed management districts have found the availability of multiple management tools combined with the quick kill capability of herbicides has resulted in more judicious use of chemicals while providing adequate control of the weed. In the summer of 2000 Theodore Roosevelt National Park, Medora, N.D. (46.95 N, 103.4 W), saw large blocks of land where spurge was contained and reduced to acceptable levels by large numbers of insect biological control agents and limited chemical use. As a result, the Park is considering a substantial reduction in the amount of herbicides they will use during the summer of 2001.

Environmental groups and managers of natural areas have usually viewed the use of herbicides to control weed populations as bad for the ecosystem. While there are almost always negative impacts resulting from the use of chemicals, they remain an important tool for slowing the expansion of leafy spurge and sometimes they are the only effective tools available to managers of specific biogeographical regions. Biological control has had limited success in areas dominated by sandy soils. The rooting depth of leafy spurge in sandy areas is substantially deeper than loam/clay soils, therefore, flea beetle larva are not able to penetrate deep enough into the soil to inhabit the fine root hairs they depend upon for food and as over wintering sites (Personal Communication, Don Mundal and Robert Carlson, May 2000). In this case, herbicides provide an essential role in controlling vegetative production and minimizing the dominance of leafy spurge. Regions like the Sheyenne National Grassland near Lisbon, N.D. (46.35 N, 97.3 W) are unique in this respect. They are also unique in that this biotype is home to the western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles). The orchid is a federally listed threatened plant species in the United States. Severe restrictions have been placed on the use of herbicides to control leafy spurge, because of the pres-

ence of the orchid. However, the weed itself is more of a problem to the orchid than herbicide treatments. Research indicates that fall herbicide treatments applied over the orchid did not adversely affect orchid growth the following season and there were actually more orchids found in plots treated with herbicides than in untreated plots (Personal Communication, Rodney Lym, June 2000). This is a primary example where conflicting weed treatment and regulatory requirements can interfere with system maintenance and recovery.

Risk assessment must be a part of any comprehensive weed management plan. Leafy spurge crowds out native vegetation, resulting in a monoculture that reduces biodiversity and threatens both abundant and sensitive species. The invasion of exotic weed species in national parks, wildlife refuges and other lands set aside for wildlife and recreation has, in fact, reached epidemic proportions. Dense stands of leafy spurge often have greater than 200 stems m<sup>-2</sup> and a foliar cover approaching 100%. The massive root system and long-lasting seed banks continue to present ecological problems even after the aboveground biomass of the weed has been reduced. This is the case in western North Dakota where the canopy cover of leafy spurge has been reduced by as much as 35–40%; however, more than 90% of the seed bank was made up of undesirable species (Personal Communication, Donald Kirby, June 2000). Research results from Montana and South Dakota indicated even larger reductions in leafy spurge foliar cover, 77% and 76% respectively. However, Montana reported increased grass cover (42%) and both states realized increased species richness (27%) (Personal Communication, Jack Butler, June 2000). Therefore, risk assessment evaluations must be completed in specific regions and under different ecological conditions to determine the best management approach to follow. This type of analysis mandates a basic understanding of the system and how plant communities respond to management.

### Scientific Success:

Another area of success that is often only realized in academia is scientific success. The initiation of a biological control program is often fraught with uncertainty. Successful establishment of an agent in one area does not always translate into success elsewhere. ***Scientific success is***

*the knowledge gained by scientific investigation that improves our understanding of the biological control agent(s), the agent(s) impact on the host plant and what effects the introduction of the agent or changes in the weed population will have on the associated ecosystem.*

Scientific success helps managers improve the potential of achieving effective control; however scientific success can be achieved independent of biological, ecological, economic, social, political, and legal success. Using the North American leafy spurge control effort as an example of an emerging success story, the program does have several areas where our knowledge base has been expanded. Information concerning the additive or synergistic effects of plant pathogens, alternative grazing programs and limited chemical use with biological control agents helps us to understand how weed control programs can be enhanced by the interaction of multiple control tools (biologically-based IPM). Other research helps us understand the complex ecological interactions (ecological barriers) that can influence the establishment or effectiveness of control agents and other IPM tools on leafy spurge. The fact that several issues remain unanswered, especially in the development of models that can guide the complex ecological and socioeconomic decision-making process, indicates that there is still much to learn. However, the scientific progress made to date is certainly a success upon which others will continue to build.

### **Economic Success:**

Economic success seems more straightforward than the other concepts we have looked at, but in fact it is just as complex. The traditional view of economic success is for the benefits of the treatment to exceed treatment costs. While this view is certainly true, quantifying treatment benefits resulting from improved ecosystem health and alternative land uses is difficult. The following discussion assumes that weeds must be controlled (i.e. there is no economic threshold below which weed control should not be attempted). Based on this assumption, economic success depends on minimizing costs. To the rancher it is 1 of 3 things: (1) saving on treatment costs and obtaining the same or a better degree of weed control; (2) improving the quality and/or quantity of a marketable commodity; and (3) improving land quality and sustainability (economic

value and ecological health). Economic success at the federal, state, or local level includes increased revenue from sales and/or taxes, reduced expenditures for weed control and increased consumer satisfaction and utilization of the land for non-agricultural activities. In general, we can say that ***economic success is less cash expended for the same or better weed control and/or an increase in the amount of cash returned for every dollar spent on weed control at the local, state, and federal levels.*** It is generally economic impacts that drive most weed control programs. Unfortunately, the time lag between a weed becoming an ecological problem and its emergence as an economic problem is often decades. This allows the weed to become firmly established, which usually translates into a greater expenditure of resources to achieve control. Perhaps the best alternate definition of economic success is never letting a weed problem reach the level where it has economic impact.

### **TEAM Leafy Spurge examples:**

The economic impact of leafy spurge is staggering. Infestations in the Dakotas, Montana and Wyoming alone are estimated to cost agricultural producers and taxpayers \$130 million a year in production losses (Leitch et al. 1994), control expenses and other impacts to the economy. Every AUM (Animal Unit Month) lost to leafy spurge infestations costs \$167 in lost economic activity. Leitch et al (1994) estimated that the forage loss resulting from leafy spurge infestations could sustain 90,000 additional head of cattle in the 4-state region of North Dakota, South Dakota, Montana, and Wyoming.

The cost of controlling leafy spurge with herbicides on 260 ha of land can be overwhelming. If only 40% of that area were infested with leafy spurge, the standard rate application of Tordon (Picloram) and 2,4-D (2,4-Dichlorophenoxy Acetic Acid) (\$31.50 ha<sup>-1</sup>) would cost the rancher or land manager approximately \$3,300 year<sup>-1</sup>. And, dense population would take a minimum of 10 years to adequately control the leafy spurge and its seeds (\$33,000). Most land managers in North Dakota, South Dakota, Wyoming, and Montana depend on agriculture for a living and do not have the resources necessary to sustain a herbicide control program. Therefore, those that choose to use chemical control alone will never control well established leafy spurge infestations.

Viewing the leafy spurge control program with respect to economic success is much the same as evaluating it with respect to ecological success. Control has been established in many local areas, but the total infestation of leafy spurge continues to grow. Exactly how much land is being improved by biological control and other integrated pest management (IPM) technologies is unknown. Therefore, it is difficult to claim that the program has been an economic success, but it has been successful in many local areas. As biological control agents continue to become an integral part of a biologically-based IPM strategy the cost of control (or at least the rate of increased dollars spent to manage the weed) has become less (as seen in Barnes and Ward Counties of North Dakota). Furthermore, as biological control agents continue to have greater impact, the revenue gained from increased production and utilization increases.

### **Political Success:**

Political success can only be achieved when scientists, community leaders, land managers and special interest groups gain enough support to convince public representatives that it is in the best interest of the state and the country to increase the resources needed to impact the problem. Therefore, ***political success is effective communication of the problem to customers and stakeholders, such as federal and state representatives, who ultimately enact legislation designed to develop and improve weed management efforts.*** A major step toward achieving political success was enacted in 1999 with the issuance of the Executive Order #13112 on Invasive Species. The order establishes an advisory council, mandates agency participation and begins the development of a "National Invasive Species Management Plan." The heightened visibility given to invasive weeds by the Executive Order has definitely been positive, but the success of the initiative depends on the ability of Congress and the administration to directly impact invasive weeds by making more resources available and by implementing changes that improve the efficiency and effectiveness of a national weed control initiative. Landowners and land managers must be proactive in communicating weed issues at the state and federal level to ensure they are not lost among all the other issues.

## Social Success:

Social success is fairly clear-cut. Here we must consider 2 groups. The land manager is the one directly fighting weed infestations. The tools chosen to address a particular weed problem are often based on previous experience. The adoption of new approaches to the problem are often overlooked or dismissed without much thought. Biological control and biologically-based IPM must be demonstrated, and the land manager's faith in its ability to outperform existing tools must be increased, before the majority will use the approach. Sell et al. (1999) conducted a survey in 9 counties of North Dakota, South Dakota, Montana, and Wyoming. They concluded that the most frequent impediment for using biological control is the view that the agents take too long to work and the perspective that access to biological agents is limited. The same group of respondents indicated that environmental, financial, and educational constraints were the primary reason for not using biologically-based IPM control strategies. Therefore, one component of social success is improving the acceptance of biologically-based IPM strategies by land managers and increasing their willingness to actively search for and obtain the additional resources and expertise needed to address weed problems.

The second group of people that must be considered are those not directly connected to the land. Few individuals in our towns and cities realize the impact noxious weeds have on their lives. During the summers of 2000 and 2001, weeds were determined to be a major contributor to the number and intensity of fires in the western United States with suppression costs totaling \$1.8 billion (Healy 2001). Therefore, the impact of improper land management can cost everyone millions of dollars, the loss of a home and even threaten lives.

The reality is that public lands are "our lands" even though states and the federal government act as managers. It is in the best interest of citizens to ensure that their lands are being maintained properly. As any facility manager will tell you, it is more cost-effective to constantly maintain and upgrade a facility than to wait and have to fix everything at once. To date, public land managers allocate far too few resources to manage invasive weeds (maintenance). The primary problem is that limited budgets are stretched too thin to adequately address the myriad of prob-

lems facing our public lands. Other important issues directly impacting individuals working outside the agricultural community are land values and production returns. A reduced amount of revenue results when weeds invade private and public lands and the value of the land and agricultural income decrease. Revenue also decreases as the money spent on alternate uses decreases [e.g. the estimated annual economic impact of leafy spurge in the 4-state region of North Dakota, South Dakota, Montana, and Wyoming is estimated to be \$130 million (Leitch et al. 1994)]. This is a substantial amount of money that impacts one of the most economically depressed regions in the United States. The cost to the public is fewer public services, reduced resources and increased taxes (e.g. Montana acquires noxious weed tax revenue through the allocation of a special surcharge on automobile licenses sold in the state). Therefore, the second component of social success is educating the public concerning the problem, their responsibility to the land and the direct impact inadequate management has on their income. Combining the above components, we can define *social success as increased awareness of the problem, acceptance of individual responsibility in dealing with the issue, improved understanding of biologically-based IPM and how the different tools are used, and the need for individuals to actively search for and obtain the additional resources and expertise needed to address the issue*. Social issues have not been adequately addressed in the past.

## TEAM Leafy Spurge preliminary results:

A major part of TEAM Leafy Spurge is to increase public awareness, demonstrate effective integrated control techniques, and to work directly with ranchers and land managers in implementing current control methodologies. The overall effectiveness of TEAM Leafy Spurge with regard to social success remains to be evaluated; however, the message is getting out. The following quotes were obtained from land managers within the study area:

### North Dakota:

"In the last 3–4 years I have collected and redistributed approximately 6 million flea beetles over 15 sections of rangeland. These 6 million flea beetles are located on approximately 2000 different sites. I have

had more success with the flea beetles than we ever did spraying for the past 40–50 years. USDA, TEAM Leafy Spurge just delivered an additional 3 million insects to me last week. I tell my neighbors that within 3–4 years leafy spurge on this ranch will be reduced 85–90%. Where we are standing right now the insects are working and while I am out haying tomorrow the insects will still be working. Biological control for leafy spurge is definitely the way to go." Roger Myers – February 2002.

### Montana:

"We had sprayed for many years attempting to control leafy spurge with very limited success. Then Neal Spencer brought us some of the brown flea beetles. The flea beetles have reduced the amount of leafy spurge we once had. Since then TEAM Leafy Spurge has given us some of the black flea beetles that appear to be doing very well. There is no doubt the flea beetles are our only chance at getting rid of leafy spurge." Glen Rugg - June 1999

### South Dakota:

"The ranchers are feeling better about the options they now have against leafy spurge. TEAM Leafy Spurge has been a big plus for area producers. As of 3–4 years ago we knew nothing about biocontrol. We didn't know what to do, let alone how to get massive numbers of flea beetles working on the ground. Along with TEAM Leafy Spurge and the Moreau Weed Management Area, we now have more options. TEAM Leafy Spurge has done a remarkable job in getting the word out about those options. People in this area have now contained the spread of leafy spurge and are now seeing the benefits of a biologically-based IPM approach". Larry Nelson - Nov 2000.

We have started to see some changes in the perspective of individual land managers with respect to biologically-based IPM; however, a great deal of work remains in convincing the general public that it is in their best interest to take a proactive stance on controlling weeds. From the perspective of the Northern Great Plains leafy spurge control effort, social awareness of the problem has been increased among land managers; however, the broad-based societal support needed for social success has not been achieved and additional resources must be committed to garner public support and provide the

information needed by land managers to address the problem.

### Legal Success:

*Legal success is the enactment of laws that prevent the introduction of invasive species, mandate effective control programs (e.g. biological control) and assess substantial penalties for failure to comply with existing laws.* Many states have enacted laws designed to limit the spread and mandate the treatment of leafy spurge and other noxious weed populations, but most lack sufficient legal penalties to ensure compliance. In this instance, state and federal programs have not achieved the legal success needed to support the leafy spurge control program.

The TEAM Leafy Spurge has not been a part of the legislative process. We view our part as an information source that law-makers can use to enact the legislation needed to manage noxious weeds and ultimately contribute to the control of noxious weed problems in their area. The effectiveness of the legislation enacted depends on a clear understanding of the problem and its implications. Unfortunately, the laws enacted are often clouded by politics. Therefore, broad-based political support is essential and can only be achieved by addressing the problem in each of the major thrust areas listed above. Only then will all the components needed for effective weed management be in place.

### Conclusions

Leafy spurge has been in the United States for a long time and it will never go away. The best we can hope to do is reduce its impact below ecologically and economically significant levels. There is no one tool adequate to deal with the massive infestations currently plaguing the United States and Canada; however we believe that biologically-based integrated pest management (IPM) offers the best scenario of achieving the desired control level. Has biological control or biologically-based IPM been successful in controlling leafy spurge? The answer depends upon your perspective. Scientifically and politically, the northern Great Plains leafy spurge effort has made significant progress and we believe each can be considered a success, even though a great deal of additional work is still needed. On the national scale, host specific flea beetles

have been collected and moved to many new areas where biological control agents have never been used. Land managers have seen the impacts of biocontrol agents and embraced their use, which has simultaneously reduced their reliance on herbicides and other more expensive control methods. The continued increase and spread of biocontrol agents coupled with a decline in leafy spurge populations, strengthens the interest and support for biologically-based IPM strategies. Success in the biological, ecological, and economic thrust areas has been demonstrated at many sites across the northern Great Plains. Additional work is needed to educate land managers and the public concerning the best methods of treating the

problem, the need for proactively augmenting and managing their biological control agents and allowing additional time for biological control populations to expand and coalesce across regions. Similar progress in the control of other weed species such as spotted knapweed (*Centaurea biebersteinii* DC.), yellow starthistle (*Centaurea solstitialis* L.), melaleuca [*Melaleuca quinquenervia* (Cav.) T. Blake], and salt cedar (*Tamarix ramosissima* Ledeb.) will continue to strengthen the concept of biologically-based IPM. Two problem areas where weed control efforts has been relatively ineffective are the social and legal components of the program. A greater emphasis must be placed on public and land manag-



**Fig. 6. Federal, state and private land managers working together at the Ekalaka, Montana Range Days (June 2000) to distribute biological control agents throughout the region.**



er education, as well as enacting laws that provide significant incentives for public compliance.

The northern Great Plains leafy spurge control effort has contributed a great deal to our understanding of the weed and how it will be controlled in the future. It is important that we acknowledge the contribution of all individuals who have spent their careers, and in some cases their lives, putting in place the control infrastructure we have today. The momentum toward effective management of leafy spurge has rapidly increased because of their efforts. Successful biologically-based leafy spurge control is on the horizon, especially when weed managers understand the number of problem areas (biological, ecological, scientific, political, social, and legal) that must be addressed to achieve a sustained reduction of a weed population. The amount of time it will take to be realized depends on our commitment to solving the problem and our willingness to work together as a cohesive team (Fig. 6).

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# Diets of plains vizcacha, greater rhea and cattle in Argentina

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## Abstract

Food habits of plains vizcacha (*Lagostomus maximus*), greater rhea (*Rhea americana*) and cattle (*Bos taurus*) in the Paraná River Delta, Argentina, were studied over 2 years using micro-histological analysis of faeces. This was the first study of feeding habits of these herbivores grazing in common in a wetland of Argentina. Poaceae was the main diet component throughout the year for all 3 herbivores, with the exception of spring and summer, when greater rhea consumed a higher proportion of *Prosopis nigra* (Griseb.) pods. Botanical composition of plains vizcacha and cattle diets was generally similar for the same season but different from that of greater rhea. *Panicum milioides* Nees., *Dichondra microcalyx* (Hallier) Fabris. and *P. nigra* were the most consumed species for vizcacha, while *P. nigra*, *Plantago myosuroides* Lam., *Solanum* sp. L., *Spilanthes stolonifera* (H. et A.) Baker and *D. microcalyx* dominated the greater rhea diet. The species most consumed by cattle were *Luziola peruviana* Gmel. and *P. milioides*. Similarities between the diets of plains vizcacha and cattle seem to support the ranchers' view that vizcachas compete with domestic herbivores for forage. However, high overlap in food habits would result in competition only if forage is scarce. Greater rhea and cattle have different foraging patterns and hunting of greater rhea is not justified solely on the basis of forage competition with cattle.

**Key Words:** diet composition, herbivory, *Lagostomus maximus*, Paraná River Delta, *Rhea americana*

In farming ecosystems, cattle and other domestic species often co-exist with wildlife. Roughly 80% of Argentina is dedicated to extensive cattle ranching (CONAPA 1991) where cattle interact with a large number of wild species that use the same resources. However, few studies in Argentina have quantified these interac-

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## Resumen

Se estudiaron los hábitos alimenticios de la vizcacha (*Lagostomus maximus*), el ñandú (*Rhea americana*) y el ganado vacuno (*Bos taurus*) durante 2 años en el Delta del Río Paraná, Argentina, utilizando análisis microhistológico de heces. El presente es el primer estudio que focaliza en la comparación de los hábitos alimenticios de estos herbívoros en coexistencia en un área de humedal. Las poáceas fueron el componente principal en la dieta de los 3 herbívoros a lo largo del año, excepto en primavera y verano, cuando los ñandúes consumieron una mayor proporción de vainas de *Prosopis nigra* (Griseb.). La composición botánica de la dieta de la vizcacha y el ganado fue en general similar para una misma estación pero diferente de la del ñandú. *Panicum milioides* Nees., *Dichondra microcalyx* (Hallier) Fabris. y *P. nigra* fueron las especies más consumidas por la vizcacha, mientras que *P. nigra*, *Plantago myosuroides* Lam., *Solanum* sp. L., *Spilanthes stolonifera* (H. et A.) Baker y *D. microcalyx* dominaron en la dieta del ñandú. Las especies más consumidas por el ganado fueron *Luziola peruviana* Gmel. y *P. milioides*. La similitud entre las dietas de la vizcacha y el ganado parecen apoyar la idea de los ganaderos sobre la competencia por el forraje entre estos herbívoros. Sin embargo, un elevado solapamiento dietario no se traduce en competencia a menos que el forraje resulte escaso. Por otra parte, el ñandú y el ganado presentan diferentes patrones de forrajeo y la cacería que sufren estas aves no está justificada únicamente sobre la base de la competencia por el forraje.

tions (e.g., Bonino et al. 1986, Kufner and Pelliza 1987, Martella et al. 1996, Quintana et al. 1998a, 1998b).

Plains vizcacha (*Lagostomus maximus*) and greater rhea (*Rhea americana*) are 2 native species found in these ecosystems. Plains vizcacha are large nocturnal rodents of the Chinchillidae family that dwell in communal burrows ("vizcacheras") of grasslands and semi-arid scrublands from southern Paraguay and Bolivia to central Argentina (Llanos and Crespo 1952, Branch 1993). Greater rhea also live in grasslands and bush country from Brazil and Bolivia to central Argentina. These birds live in polygamous social clusters and are generally associated with farming and cleared fields where native vegetation has been replaced by improved pastures (Martella et al. 1996, Rebores and Fernández 1997).

The plains vizcacha is often considered to be an agricultural pest, damaging soil and vegetation (Weir 1974) due to its burrow-

ing and grazing habits and causing losses in yield of crops such as corn, soybean, pastures, and horticultural species (Rendel 1990, Navarro et al. 1997). It is also hunted for its pelt (Rendel 1990, Bruggers and Zaccagnini 1994) and used as a food resource by humans (Mares and Ojeda 1984). Hunting has severely reduced the numbers of plain vizcachas, and it is now extinct in large tracts of the wet Pampa (Redford and Eisenberg 1992). Greater rhea also have been hunted intensively for meat, feathers and skin, and was declared a harmful species due to its negative impact on crops (Bertonatti 1997) and potential competition with cattle for forage (Martella et al. 1996).

There have been few scientific studies on the feeding habits of these wild herbivores despite their widespread continental distribution. Plains vizcacha are selective grazers (Llanos and Crespo 1952) while greater rhea feed on vegetable matter as well as arthropods and small vertebrates (Bruning 1974).

This study focuses, for the first time, on a wetland area of Argentina (the Paraná River Delta Region) and surveys the food habits of plains vizcachas, greater rheas and cattle sharing the same grazing area.

## Materials and Methods

The study area was located on the "Don José" Ranch (1,500 ha, 33°27'S, 58°48'W), 6 km north of Ceibas, Department of Gualaguaychú, Entre Ríos province, Argentina. Mean annual rainfall is 978 mm, and temperature averages 17.4 C° (Servicio Meteorológico Nacional 1972). The study area is situated in one of the 11 wetland landscape units identified for the Paraná River Delta Region. The landscape pattern corresponds to plains with a savanna physiognomy of grasses, patches of xerophytic *Prosopis nigra* (Griseb.) and *Acacia caven* (Mol.) Mol. forest, and baldspots with a large percentage of bare soil and sparse cover of *Portulaca* sp. L. The area is also criss-crossed by small lentic streams covered with floating and rooted aquatic plants (Malvárez 1997).

Unlike its neighboring areas, the study area is free from the periodical floods of the Paraná River. Large areas are waterlogged by rainfall due to the minimum slope of the land (Malvárez 1997) and the type of soils (Pratolongo 2000). During 1998, coincident with an "El Niño" event, both the waterlogged areas and the duration of the waterlogging were longer than for 1996/97.

Soils are composed of a clayey, sodic horizon close to the surface. These sodic clays hamper water penetration because they swell when wet, creating a layer that is effectively impermeable. Trampling by cattle compounds the problem by compressing and hardening the soil, and eroding thin layers of topsoil (Arias 2000). Extensive cattle ranching (0.7 cows per hectare per year), hunting of wildlife species for food and trade, and exploitation of *P. nigra* trees for lumber are the main human activities in this region.

Vizcachas dig their burrows both in the grasslands and the forest patches and their foraging is restricted to the areas surrounding the burrows (Branch and Sosa 1994, Arias 2000). Greater rhea and cattle, on the other hand, graze over extensive areas, including, in the case of cattle, vegetation from the streams. Cattle were always present on the study area and the overall level of forage utilization was moderate.

Fresh faeces of plains vizcachas and cows were collected seasonally for 2 consecutive years, between November 1996 (spring) and August 1998 (winter). Greater rhea fresh faeces were collected only in spring/summer 1997 and fall/winter 1998, when these birds were present on the study area. Collection dates were in the middle of the respective season. All faeces were collected within the single grazing unit that comprised the study area.

Faeces of plains vizcachas were taken from 8 active burrows located on the edge between grassland and forest patches, while faeces of greater rhea and cattle were collected from droppings found both in grassland and forest patches. We verified the vizcachas' burrows were active through direct observation of the animals, or signs of recent activity such as fresh faeces, footprints or diggings (Branch et al. 1994b). Fifty pellets were collected at each vizcacha burrow (a total of 400 pellets per season) to form 8 composite samples (1 sample per burrow with 50 pellets each). This is an adequate number of samples to estimate this rodent's diet (Bontti et al. 1997). For greater rhea and cattle, 32 and 24 samples of faeces of 4 g were collected, respectively, and formed into 8 composite samples for both herbivores (each composed of 4 and 3 faeces).

The botanical composition of the diets was determined by means of microhistological analysis using the William's technique (1969). Four slides were prepared from each of the composite samples and 100 randomly chosen microscopic fields were observed at 400x for each slide

(Holechek and Vavra 1981, Holechek et al. 1982). Frequencies of each consumed item were converted to percentages of the total sample weight (Holechek and Gross 1982, Martella et al. 1996).

Composite samples of greater rhea underwent a special procedure; whole or fragmented pods and seeds of *P. nigra* and arthropods were separated from the herbaceous components and each of these 3 components was dried and weighed. Herbaceous components were then analyzed following the technique described above.

The percent of each food item was calculated for each season. Diet correlations and dietary similarity among seasons and among herbivore species were analyzed using two-tailed Spearman's rank correlation coefficients (Zar 1996) and Kulczynski's similarity index (Smith and Shandruk 1979, Henley et al. 2001), respectively. Data were averaged for the 2 years for plains vizcacha and cattle to compare botanical composition of diets among seasons and herbivores.

## Results

While vizcachas and cattle fed exclusively on plant leaves, greater rhea also fed on *P. nigra* pods and consumed some arthropods (Tables 1, 2, and 3). Plains vizcacha fed on a wide variety of plants during all seasons (Table 1). A total of 45 plant species were identified in vizcacha diets over the length of the study. Grasses were the staple diet of this rodent, both in amount consumed and in number of species, 42.7% of the diet in winter with 20 species to 65.1% of the diet in spring with 17 species. *Panicum milioides* Nees. was the most consumed grass, contributing 8.8% and 16.4% of the diet in winter and spring, respectively. The item "Other Grasses" was at times similar to *P. milioides* (14.8% vs. 15.1% in summer) or even higher (13.4% vs. 8.8% in winter). Other major items were *Dichondra microcalyx* (Hallier) Fabris. (20.4% and 19.3%, fall and winter) and *P. nigra* (18.7% and 13.2% in fall and winter, respectively).

Legumes were the most common component of the greater rhea diet during spring and summer (25.3% and 38.9%; Table 2) while grasses were more common in fall and winter (35.8% and 45.3%). The high content of legumes was due mainly to the consumption of *P. nigra* pods (21.2% and 37.8%, for spring and summer, respectively). *Plantago myosuroides* Lam. (20.5%) and Solanaceae, particularly *Solanum* sp. L. (13.9%) were also important in the spring diet while *Spilanthes*

**Table 1. Botanical composition (%) of plains vizcacha diets in different seasons in the Delta of the Paraná River.**

Food item	Spring			Summer			Fall			Winter		
	1996	1997	$\bar{x}$	1997	1998	$\bar{x}$	1997	1998	$\bar{x}$	1997	1998	$\bar{x}$
----- (%) -----												
<u>Perennial grasses</u>												
<i>Aristida</i> sp.	0.0	9.2	4.6	0.0	0.9	0.4	6.2	0.4	3.3	3.8	0.5	2.2
<i>Briza</i> sp.	0.0	3.6	1.8	0.0	0.0	0.0	2.0	0.0	1.0	2.7	0.0	1.3
<i>Bromus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.2
<i>Cynodon dactylon</i> (L.)	5.5	1.0	3.2	8.3	2.6	5.5	1.2	1.2	1.2	0.3	1.5	0.9
<i>Chloris berroi</i> Arech.	15.2	0.4	7.8	1.2	0.6	0.8	1.0	0.4	0.7	0.7	0.0	0.3
<i>Eleusine tristachya</i> (Lam.) Lam.	5.5	0.4	2.9	1.2	2.6	1.9	0.3	0.6	0.5	0.3	1.5	0.9
<i>Festuca</i> sp.	3.3	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Luziola peruviana</i> Gmel.	0.0	4.5	2.2	6.3	7.8	7.0	10.7	5.4	8.0	5.2	4.0	4.6
<i>Panicum milioides</i> Nees.	16.5	16.4	16.4	11.5	18.6	15.1	12.7	11.6	12.1	9.7	8.0	8.8
<i>Pappophorum</i> sp.	0.0	0.5	0.2	1.2	0.7	1.0	1.8	0.0	0.9	0.5	0.0	0.2
<i>Paspalum</i> spp.	0.0	0.5	0.2	2.2	0.7	1.5	2.8	0.0	1.4	0.3	0.0	0.2
<i>Piptochaetium napostaense</i> Lam.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
<i>Poa</i> sp.	0.0	0.0	0.0	7.7	0.0	3.8	1.3	0.0	0.7	0.3	0.0	0.2
<i>Setaria</i> sp.	0.0	0.6	0.3	0.5	0.1	0.3	2.5	0.6	1.6	0.0	0.4	0.2
<i>Sporobolus indicus</i> (L.) R. Br.	0.0	0.0	0.0	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stipa brachychaeta</i> Godr.	0.0	0.0	0.0	7.5	2.1	4.8	0.2	0.2	0.2	0.0	0.7	0.4
<i>Stipa neesiana</i> Trin. et Rupr.	12.7	0.4	6.5	1.0	1.1	1.1	0.2	1.7	1.0	0.0	0.1	0.1
<i>Stipa</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
<i>Zizaniopsis bonariensis</i> (Balansa et Poir.) Speg.	0.0	1.9	0.9	1.2	5.6	3.4	3.2	1.5	2.3	3.2	0.4	1.8
Total perennial grasses	58.7	39.4	48.7	50.5	43.4	46.9	46.1	23.7	35.0	27.0	17.7	22.4
<u>Annual grasses</u>												
<i>Hordeum euclaston</i> Steud.	2.0	0.0	1.0	0.5	0.0	0.2	0.0	0.2	0.1	0.0	0.1	0.1
<i>Lolium</i> sp.	0.0	0.0	0.0	0.0	2.7	1.4	0.7	6.8	3.8	0.0	7.5	3.7
<i>Phalaris</i> sp.	0.0	0.5	0.2	0.0	0.4	0.2	0.5	0.4	0.4	1.3	0.5	0.9
<i>Polypogon monspeliensis</i> (L.) Desf.	5.3	7.9	6.6	0.7	0.3	0.5	0.2	0.0	0.1	3.3	0.9	2.1
Total annual grasses	7.3	8.4	7.8	1.2	3.4	2.3	1.4	7.4	4.4	4.6	9.0	6.8
<u>Other Grasses</u>	2.8	13.6	8.2	21.5	8.1	14.8	0.0	9.9	4.9	17.5	9.4	13.4
<u>Grass-like plants (Cyperaceae)</u>												
<i>Carex bonariensis</i> Desf.	0.0	3.6	1.8	0.3	5.5	2.9	0.7	3.4	2.0	1.5	4.6	3.0
<i>Eleocharis</i> sp.	0.0	0.0	0.0	0.3	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Other Cyperaceae	3.3	6.5	4.9	0.0	8.7	4.4	6.8	10.1	8.5	9.0	7.1	8.0
Total grass-like plants	3.3	10.1	6.7	0.6	14.2	7.5	7.5	13.5	10.5	10.5	11.7	11.0
<u>Perennial forbs</u>												
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	1.6	0.8
<i>Chenopodiaceae</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.4	0.3	0.0	0.5	0.2
<i>Dichondra microcalyx</i> (Hallier) Fabris.	14.3	15.0	14.7	11.2	14.2	12.7	21.0	19.7	20.4	15.7	22.9	19.3
<i>Eichhornia azurea</i> (Sw.) Kunth.	0.0	0.0	0.0	2.7	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eryngium</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0
<i>Gomphrena pulchella</i> Mart.	0.5	1.2	0.9	3.2	2.2	2.7	0.7	0.0	0.3	2.2	2.5	2.3
<i>Holcheilus hieracioides</i> (Don) Cabr.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.5	0.2
<i>Modiolastrum</i> sp.	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.0	0.1	0.2	0.6	0.4
<i>Oxalis</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1
<i>Pamphalea bupleurifolia</i> Less.	0.0	1.2	0.6	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Phyla canescens</i> (HBK) Greene	2.0	0.7	1.4	4.0	1.5	2.7	2.0	0.4	1.2	0.2	0.0	0.1
<i>Physalis viscosa</i> L.	0.0	0.0	0.0	1.3	0.0	0.7	0.0	0.5	0.2	0.0	0.0	0.0
<i>Solanum</i> sp.	1.7	0.1	0.9	0.7	1.7	1.2	0.3	0.1	0.2	0.2	1.5	0.8
<i>Spergularia levis</i> Camb.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
<i>Spilanthes stolonifera</i> (H. et A.) Baker	0.0	0.0	0.0	0.7	1.4	1.0	0.0	0.6	0.3	0.3	2.2	1.3
<i>Trifolium</i> sp.	0.0	0.1	0.1	0.3	0.1	0.2	2.7	0.9	1.8	0.2	2.9	1.5
Total perennial forbs	18.5	18.3	18.6	24.8	21.2	22.9	27.2	23.5	25.3	19.2	35.3	27.1
<u>Annual forbs</u>												
<i>Gamochaeta</i> sp.	0.0	2.2	1.1	0.0	0.7	0.4	0.5	0.0	0.2	1.2	2.0	1.6
<i>Medicago</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.4	0.0	0.0	0.0
<i>Plantago myosuroides</i> Lam.	3.3	5.0	4.2	0.0	0.6	0.3	0.0	0.1	0.1	0.8	7.0	3.9
Total annual forbs	3.3	7.2	5.3	0.0	1.3	0.7	0.5	1.0	0.7	2.0	9.0	5.5
<u>Shrubs and trees</u>												
<i>Acacia caven</i> (Mol.) Mol.	0.0	0.0	0.0	0.2	0.0	0.1	0.8	0.0	0.4	0.5	0.1	0.3
<i>Prosopis nigra</i> (Griseb.)	6.0	2.7	4.4	1.5	7.7	4.6	16.7	20.7	18.7	18.8	7.6	13.2
Total shrubs and trees	6.0	2.7	4.4	1.7	7.7	4.7	17.5	20.7	19.1	19.3	7.7	13.5

*stolonifera* (H. et A.) Baker was a major item in summer (14.9%) and *D. microcalyx* was the dominant food item in fall (34.7%). In winter, "Other Dicots" sup-

plied 18.2% of the diet. There were traces of arthropod consumption throughout the year, with the highest values in spring (2.9%) and winter (3.0%).

Grasses were also the dominant group in the cattle diet throughout the year, ranging between 78.3% in fall and 87.3% in summer (Table 3). *Luziola peruviana* Gmel.



**Table 2. Botanical composition (%) of greater rhea diets in different seasons in the Delta of the Paraná River.**

Food item	Spring 1997	Summer 1997	Fall 1998	Winter 1998
----- (%) -----				
<b>Perennial grasses</b>				
<i>Aristida</i> sp.	0.0	0.0	0.5	0.0
<i>Bromus</i> sp.	0.0	0.9	0.0	0.0
<i>Chloris berroi</i> Arech.	0.0	0.5	0.2	0.2
<i>Luziola peruviana</i> Gmel.	0.2	0.5	8.1	10.7
<i>Panicum milioides</i> Nees.	0.6	0.0	1.9	2.9
<i>Pappophorum</i> sp.	0.0	0.2	0.0	0.0
<i>Setaria</i> sp.	0.0	0.0	0.5	0.0
<i>Zizaniopsis bonariensis</i> (Balansa et Poitr.) Speg.	0.0	0.0	1.2	6.1
Total perennial grasses	0.8	2.1	12.4	19.9
<b>Annual grasses</b>				
<i>Lolium</i> sp.	0.0	0.0	2.1	2.9
<i>Phalaris</i> sp.	0.0	0.0	0.0	0.7
Total annual grasses	0.0	0.0	2.1	3.6
<b>Other Grasses</b>	7.2	6.0	21.5	21.8
<b>Grass-like Plants (Cyperaceae)</b>				
<i>Carex bonariensis</i> Desf.	0.0	0.0	0.7	3.4
Other Cyperaceae	0.0	1.0	0.0	4.6
Total grass-like plants	0.0	1.0	0.7	8.0
<b>Perennial forbs</b>				
<i>Chenopodiaceae</i>	1.0	0.9	0.2	0.0
<i>Dichondra microcalyx</i> (Hallier) Fabris.	4.8	1.6	34.7	6.3
<i>Gomphrena pulchella</i> Mart.	10.8	13.0	0.0	1.0
<i>Holcheilus hieracioides</i> (Don) Cabr.	0.0	0.0	0.5	0.5
<i>Oxalis</i> sp.	1.1	1.0	0.0	0.0
<i>Pamphalea bupleurifolia</i> Less.	0.0	0.6	0.0	0.0
<i>Phyla canescens</i> (HBK) Greene	9.1	13.1	4.2	1.0
<i>Physalis viscosa</i> L.	0.0	1.1	0.0	0.0
<i>Solanum</i> sp.	13.9	1.7	0.2	0.0
<i>Spilanthes stolonifera</i> (H. et A.) Baker	1.9	14.9	1.9	2.2
<i>Trifolium</i> sp.	1.0	0.0	0.0	0.0
Total perennial forbs	43.6	47.9	41.7	11.0
<b>Annual forbs</b>				
<i>Medicago</i> sp.	0.2	0.0	5.8	3.6
<i>Plantago myosuroides</i> Lam.	20.5	0.3	6.5	8.2
Total annual forbs	20.7	0.3	12.3	11.8
<b>Shrubs and trees</b>				
<i>Acacia caven</i> (Mol.) Mol.	0.0	0.3	0.0	0.0
<i>Prosopis nigra</i> (Griseb.) leaves	3.0	0.8	0.5	2.7
<i>Prosopis nigra</i> (Griseb.) pods	21.2	37.8	6.6	0.0
<i>Lycium</i> sp.	0.8	0.0	0.2	0.0
Total shrubs and trees	25.0	38.9	7.3	2.7
<b>Other Dicots</b>	0.0	1.0	1.4	18.2
<b>Arthropods</b>	2.9	0.8	1.0	3.0

and *P. milioides* were commonly eaten (the former between 13.8% in winter and 25.0% in summer, and the latter ranging from 9.3% in winter and 20.0% in spring) with *Zizaniopsis bonariensis* (Balansa et Poitr.) Speg. somewhat lower (5.8% in spring and 9.8% both in winter and summer). The item "Other Grasses" averaged about 15% over all seasons. *Luziola peruviana* and *P. milioides* together with "Other Grasses", constituted 60%, 63%, and 58% of the spring, summer and winter diets, respectively.

Within seasons, vizcacha and cattle diets differed in botanical composition between years (Table 4). Summer and winter diets

of the vizcacha were significantly correlated between years but the correlation values were low. Similarity index values showed the same trend, except for fall, when similarity was highest (Table 4).

Plains vizcacha and cattle diets were similar among the different seasons, something that matches the rather high values of the similarity index (Table 5). The diet of greater rhea differed among most seasons, being similar only between spring and summer and between fall and winter. Both comparisons also showed the highest similarity values between diets (Table 5).

Botanical composition of the diets of plains vizcacha and cattle was similar

within season and the similarity index values oscillated between 50.5 and 57.9 (Table 6). Inversely, plains vizcacha and greater rhea segregated their grazing resources, without significant associations between diets, except in winter, which again had the highest similarity index value (Table 6). Cattle and greater rhea diets differed most with significant negative correlations; also, the observed similarity index's values showed low values, especially in spring and summer (Table 6).

## Discussion

Grasses were the main forage for plains vizcacha and cattle in all seasons. For greater rhea, grasses were the most important diet component when *P. nigra* pods were lacking. The importance of grasses in the plains vizcacha diet has also been reported by other authors (Giulietti and Jackson 1986, Kufner et al. 1992, Jofré 1994, Branch et al. 1994a, Navarro et al. 1997). Although plains vizcacha grazed on a large variety of plant species, only a few food items composed the bulk of its diet in each season. This last fact was observed in other grassland habitats (Giulietti and Jackson 1986), although we found a greater consumption of dicots compared to that study (23 species versus 3 species). Our results are more similar to those from the semiarid scrub of Central Argentina, where 53% of the species in the diet were dicots (Branch et al. 1994a). The number of items consumed by vizcachas in the Delta Region was 45, while Giulietti and Jackson (1986) and Branch et al. (1994a) record 20 and 62 items in grassland and scrub, respectively. The lower number of items found in the grassland might be explained by higher availability of more palatable species, a fact that might allow the rodents to fulfill their nutritional needs with fewer species, in agreement with classic foraging theory (Stephens and Krebs 1986).

In agreement with other studies (Martella et al. 1996, Comparatore and Martínez 1997), greater rhea had a high intake of greens throughout the year. *P. nigra* pods were an important food item during certain parts of the year. These highly nutritious pods appear in spring, reach their peak during summer, their availability decreases in fall, and they cannot be found in winter (Pratolongo 2000), which correlates with their abundance in the rhea diet.

Variations in digestibility of the different food items could be taking place in the

**Table 3. Botanical composition (%) of cattle diets in different seasons in the Delta of the Paraná River.**

Food item	Spring			Summer			Fall			Winter		
	1996	1997	$\bar{x}$	1997	1998	$\bar{x}$	1997	1998	$\bar{x}$	1997	1998	$\bar{x}$
----- (%) -----												
<b>Perennial grasses</b>												
<i>Aristida</i> sp.	0.0	10.5	5.3	5.0	0.0	2.5	3.5	0.0	1.8	8.0	0.0	4.0
<i>Briza</i> sp.	0.0	5.5	2.7	0.0	0.0	0.0	2.0	0.0	1.0	12.0	0.0	6.0
<i>Cynodon dactylon</i> (L.)	3.5	0.0	1.8	0.5	0.0	0.3	3.0	4.0	3.5	0.0	0.0	0.0
<i>Chloris berroi</i> Arech.	4.0	0.0	2.0	5.5	1.0	3.3	4.0	0.0	2.0	0.0	0.0	0.0
<i>Eleusine tristachya</i> (Lam.) Lam.	0.0	0.0	0.0	4.0	2.5	3.3	0.0	1.5	0.8	0.0	0.0	0.0
<i>Festuca</i> sp.	5.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Luziola peruviana</i> Gmel.	21.5	26.5	24.0	22.0	28.0	25.0	17.5	11.0	14.3	13.0	14.5	13.8
<i>Panicum milioides</i> Nees.	31.0	9.0	20.0	14.0	11.5	12.8	14.0	8.5	11.3	4.0	14.5	9.3
<i>Pappophorum</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	1.8	0.0	0.0	0.0
<i>Paspalum</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.3	0.0	0.0	0.0
<i>Poa</i> sp.	0.0	0.0	0.0	1.5	0.0	0.8	0.0	0.0	0.0	3.0	0.0	1.5
<i>Setaria</i> sp.	0.0	0.0	0.0	0.0	2.5	1.3	5.5	0.0	2.8	0.0	0.0	0.0
<i>Stipa brachychaeta</i> Godr.	0.0	0.0	0.0	1.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stipa neesiana</i> Trin. et Rupr.	4.0	0.0	2.0	0.0	3.5	1.8	2.5	9.0	5.8	0.0	0.0	0.0
<i>Zizaniopsis bonariensis</i> (Balansa et Poitr.) Speg	0.0	11.5	5.8	3.0	16.5	9.8	7.5	8.5	8.0	11.5	8.0	9.8
Total perennial grasses	69.0	63.0	66.1	56.5	65.5	61.4	60.0	46.0	53.4	51.5	37.0	44.4
<b>Annual grasses</b>												
<i>Hordeum euclaston</i> Steud.	1.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lolium</i> sp.	0.0	0.0	0.0	0.0	2.5	1.3	0.0	9.0	4.5	0.0	9.0	4.5
<i>Phalaris</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	3.0	1.5	2.3	0.0	1.0	0.5
<i>Polypogon monspeliensis</i> (L.) Desf.	3.5	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total annual grasses	4.5	0.0	2.3	0.0	2.5	1.3	3.0	10.5	6.8	0.0	10.0	5.0
<b>Other Grasses</b>	6.5	25.0	15.8	35.5	14.5	25.0	16.0	21.0	18.5	37.5	31.5	34.5
<b>Grass-like Plants (Cyperaceae)</b>												
<i>Carex bonariensis</i> Desf.	0.0	6.0	3.0	0.0	12.5	6.3	0.0	7.5	3.8	1.0	5.5	3.3
Other Cyperaceae	0.5	2.5	1.5	0.0	0.0	0.0	3.0	8.5	5.8	0.0	4.0	2.0
Total grass-like plant	0.5	8.5	4.5	0.0	12.5	6.3	3.0	16.0	9.6	1.0	9.5	5.3
<b>Perennial forbs</b>												
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	0.5	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Chenopodiaceae</i>	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.5	0.0	1.0	0.5
<i>Dichondra microcalyx</i> (Hallier) Fabris.	7.0	1.5	4.3	1.0	0.0	0.5	4.0	0.0	2.0	2.5	5.0	3.8
<i>Gomphrena</i> sp.	0.0	0.0	0.0	1.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Phyla canescens</i> (HBK) Greene	0.5	0.0	0.3	2.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Solanum</i> sp.	0.0	0.0	0.0	1.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Spergularia levis</i> Camb.	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.5	0.0	0.0	0.0
<i>Spilanthes stolonifera</i> (H. et A.) Baker	0.5	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.0
<i>Trifolium</i> sp.	0.0	0.0	0.0	0.5	0.0	0.3	5.5	0.0	2.8	1.0	0.0	0.5
Total perennial forbs	8.5	1.5	5.2	5.5	0.0	2.8	11.5	0.0	5.8	3.5	8.0	5.8
<b>Annual forbs</b>												
<i>Gamochaeta</i> sp.	0.0	0.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Plantago myosuroides</i> Lam.	0.5	0.0	0.3	2.5	0.0	1.3	0.0	0.0	0.0	0.5	0.0	0.3
Total annual forbs	0.5	0.5	0.6	2.5	0.0	1.3	0.0	0.0	0.0	0.5	0.0	0.3
<b>Shrubs and trees</b>												
<i>Prosopis nigra</i> (Griseb.)	10.5	1.5	6.0	0.0	5.0	2.5	6.5	6.5	6.5	2.5	4.0	3.3
<b>Other Dicots</b>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	0.0	1.8

digestive tract. Plant parts in the rhea faeces were hardly degraded. There were only traces of arthropods in the faeces, in spite of their high abundance in the field throughout the year. As with Martella et al. (1996), these traces were highly digested, unlike the plant material. This seems to indicate that this method for diet quantification is unsuitable to analyze the food habits of the greater rhea, because differences in digestibility produce a bias in establishing the true proportion of each item in its diet (Moreby 1988, Rosenberg and Cooper 1990, Martella et al. 1996).

Although the results obtained by com-

paring the diet compositions by means of correlations and similarity indices showed on the whole a similar trend, the former were clearer when comparing between years, seasons and species.

Differences observed in botanical composition of the diets of plains vizcacha and cattle between the 2 years could be due to environmental variability. Observed differences in rainfall might account for variability in both vegetation abundance and grazing area because of the waterlogging, resulting in changes in forage availability. Plains vizcacha avoid waterlogged areas. Waterlogging may also provoke changes

in the vegetation which may in turn influence changes in the grazing patterns from one year to the next. While some grasses were eaten less in the wettest year (e.g. *Chloris berroi*, *Stipa neesiana*, *Polypogon monspeliensis*), intake of Cyperaceae grew (See Tables 1 and 3). Despite the yearly changes in the foraging patterns, however, the staple components of the diet kept their high values between the 2 years of the study (e.g. *Dichondra microcalyx* and *Panicum milioides* for both vizcachas and cattle and *Luziola peruviana* for cattle). Thus, these environmental changes corresponded to changes in the grazing patterns

**Table 4. Comparison of the composition of plains vizcacha and cattle diets (Spearman's rank correlation coefficient,  $r^s$  and Kulczynski's similarity index, K) between the same season of different years in the Paraná River Delta.**

Comparison <sup>a</sup>	Plains vizcacha				Cattle			
	n <sup>b</sup>	$r_s$	P	K	n	$r_s$	P	K
SP 96 – SP 97	28	0.10	0.61	51.7	21	0.01	0.96	40.5
SU 97 – SU 98	36	0.35	0.04	54.7	21	0.17	0.47	54.5
F 97 – F 98	39	0.30	0.07	68.5	22	0.23	0.30	59.5
W 97 – W 98	39	0.42	<0.01	61.4	18	0.21	0.41	62.5

<sup>a</sup>SP = Spring; SU = Summer; W = Winter; F = Fall.

<sup>b</sup>n = Number of food items.

of both herbivores. Something similar was observed for wild and domestic herbivores in central Entre Ríos (Quintana et al. 1998b). This underscores the need to conduct surveys for at least 2 years, as proposed by Hansen and Lucich (1978).

Variations observed in the greater rhea diet throughout the year may be explained by changes in basic nutritional requirements associated with reproductive activities (Bruning 1974, Robbins 1981, Lombardi 1994, Martella et al. 1995,

of greater rhea were collected in 1997, while the fall and winter samples were from 1998, one might think that variation of intake of *Prosopis nigra* pods between spring/summer and fall/winter could also be due to environmental changes that took place from one year to the next. Yet, intake of these pods corresponded to the availability of *Prosopis nigra* fruits through the year in this region (Burkart 1976, Pratolongo 2000), supporting our previous argument.

*europaeus*) (Bonino et al. 1986). Increased intake of *P. nigra* leaves by plains vizcacha in fall and summer did not coincide with the results for cattle (except for a slight intake in fall) and this may be due to the wider range of movement of cattle as compared to that of the rodents. Cattle had easy access to areas with more tender, palatable grass, a preferred forage (Hansen and Gold 1977, Vavra et al. 1977, Samuel and Howard 1982). This forage was not as available for vizcachas because their foraging was restricted to the surroundings of their burrows (Branch and Sosa 1994, Arias 2000). Greater rhea diet was more similar to those of the other 2 species in seasons where the intake of *Prosopis* seeds decreased.

According to Kufner et al. (1992), the larger number of items in the diet of plains vizcachas seems to indicate better adapted grazing habits than those of greater rhea and cattle, when faced with the resources available in their habitat. However, the

**Table 5. Comparison of the composition of plains vizcacha, greater rhea and cattle diets (Spearman's rank correlation coefficient,  $r^s$  and Kulczynski's similarity index, K) among seasons in the Paraná River Delta.**

Comparison <sup>a</sup>	Plains vizcacha				Cattle				Greater rhea			
	n <sup>b</sup>	$r_s$	P	K	N	$r_s$	P	K	n	$r_s$	P	K
SP – SU	38	0.38	0.02	63.1	29	0.48	<0.01	71.2	24	0.58	<0.01	56.6
SP – F	41	0.47	<0.01	56.9	30	0.47	<0.01	67.9	25	0.17	0.42	34.1
SP – W	41	0.51	<0.01	61.6	27	0.48	0.01	63.3	25	-0.17	0.43	30.6
SU – F	43	0.61	<0.01	62.0	28	0.50	<0.01	68.0	30	0.07	0.72	23.3
SU – W	44	0.50	<0.01	64.6	27	0.31	0.11	69.0	28	-0.17	0.36	14.9
F – W	43	0.60	<0.01	76.6	26	0.48	0.01	68.6	25	0.56	<0.01	58.2

<sup>a</sup>SP = Spring; SU = Summer; W = Winter; F = Fall.

<sup>b</sup>n = Number of food items.

Reboreda and Fernández 1997). Intake of insects, small vertebrates, and seeds satisfy the need of minerals, vitamins, proteins, or specific nutrients in larger or lesser demand according to the season (Robbins 1981, Martella et al. 1996). This intake was higher during spring and summer, the mating season for this species (Reboreda and Fernández 1997). Consequently, the similar diets observed in these seasons and their difference with the fall/winter intake is logical. Since spring and summer faeces

Grazing on common grounds explains the similarity observed in botanical composition of diet observed throughout the year between plains vizcacha and cattle, including a few common dominant species (mainly grasses) and a wide range of less relevant species (<3%). Diet similarities between cattle and medium-sized wild herbivores such as the plains vizcacha have also been reported for mara (*Dolichotis patagonum*) (Kufner and Pelliza 1987) and European hares (*Lepus*

relevance of grasses as a resource shared by this rodent and cattle implies a significant dietary overlap that might be a negative factor for the remaining populations of vizcacha in this area. Plains vizcacha and cattle had similar diets, which supports the ranchers' view that vizcachas compete with domestic herbivores for foraging resources and leads to their being hunted as pests. However, high overlap in the use of resources implies competition only if the resources are scarce (Wiens 1989). Hunting of greater rhea on ranches

**Table 6. Comparison of the composition of plains vizcacha (PV), greater rhea (GR) and cattle (CA) diets (Spearman's rank correlation coefficient,  $r^s$  and Kulczynski's similarity index, K) in different seasons in the Paraná River Delta.**

	PV vs CA				PV vs GR				GR vs CA			
	n <sup>a</sup>	$r_s$	P	K	N	$r_s$	P	K	n	$r_s$	P	K
Spring	30	0.70	<0.01	56.7	35	-0.19	0.29	23.3	30	-0.38	0.04	16.1
Summer	36	0.57	<0.01	53.6	41	0.01	0.98	19.0	32	-0.38	0.04	10.8
Fall	40	0.82	<0.01	57.9	43	0.22	0.16	43.3	32	-0.04	0.83	36.2
Winter	40	0.64	<0.01	50.5	42	0.41	<0.01	49.6	24	0.34	0.11	59.6

<sup>a</sup>n = Number of food items.

and farms has been justified for the same reason: its perceived competition with cattle for the grazing resources. Our results suggest that greater rhea and cattle have different foraging patterns during the year, with little potential for diet competition.

Both native herbivores may have important ecological roles in this wetland area: greater rhea in forest regeneration, not only dispersing *P. nigra* seeds but also speeding up the germination process as the seeds pass through their digestive tract and improving seed germination rates (Pratolongo 2000). Plains vizcachas help recycle nutrients, increase soil water infiltration through their burrowing activities, which could improve these already degraded soils, and add to the creation of a new habitat type that is used by other wildlife species (Arias 2000).

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# Date and plant community effects on elk sedge forage quality

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## Abstract

Elk sedge (*Carex geyeri* Boott) is one of the most important livestock and big game forages in many areas of the western U.S. It is one of the most prominent forage species in the diets of cattle and elk utilizing forested rangelands. Despite its acknowledged ecological and economical importance, very little is known about the factors influencing the forage quality of elk sedge. Effects of sampling date, plant community, and their interaction on the neutral detergent fiber, acid detergent fiber, and crude protein levels of elk sedge are reported for samples collected at the Starkey Experimental Forest and Range and the Bridge Creek Wildlife Management Area, both in northeastern Oregon, during January, April, July, and October of 1997 and 1998. Neutral detergent fiber levels in elk sedge were lowest in mid-October ( $\bar{x}$  = 71.3%) and highest in mid-July ( $\bar{x}$  = 76.1%). Acid detergent fiber was lowest in elk sedge collected in mid-October ( $\bar{x}$  = 37.3%) and highest in mid-July ( $\bar{x}$  = 39.0%) and mid-January ( $\bar{x}$  = 39.2%). Elk sedge from the Douglas-fir/ninebark community was lowest in acid detergent fiber ( $\bar{x}$  = 38.1%). Crude protein was highest ( $\bar{x}$  = 8.0%) in mid-July elk sedge samples and lowest ( $\bar{x}$  = 5.7%) in mid-January samples. Elk sedge from the ponderosa pine/fescue community was lowest in crude protein ( $\bar{x}$  = 5.9%). All forage quality parameters exhibited variability between years. Although sampling date and plant community effects were detected, the forage quality of elk sedge appeared relatively stable compared to other native forages. A more intensive spring sampling campaign is needed to characterize the relationship between elk sedge phenology and forage quality dynamics.

**Key Words:** *Carex geyeri*, cattle, graminoids, nutrition, phenology, season

Elk sedge (*Carex geyeri* Boott) is one of the most important forages for livestock and big game in northeastern Oregon (Pickford and Reid 1943, Edgerton and Smith 1971, Skovlin et al. 1976, Skovlin and Vavra 1979) and other areas of the western U.S. (Kufeld 1973). Elk sedge has been noted as the most prominent forage species in the diets of cattle (*Bos taurus* L.) on summer range in northeastern Oregon (Skovlin et al. 1976). Cattle may consume from 4 to 23% of their summer diet as elk sedge

## Resumen

En muchas áreas del oeste de Estados Unidos el "Elk sedge" (*Carex geyeri* Boott) es uno de los forrajes mas importantes para el ganado y la fauna mayor. Es una de las especies forrajeras mas prominentes en las dietas del ganado y alces que utilizan los pastizales boscosos. A pesar de su conocida importancia económica y ecológica se sabe muy poco respecto a los factores que influyen en la calidad del forraje del "Elk sedge". Se reportan los efectos de la fecha de muestreo, comunidad vegetal y sus interacciones en los niveles de fibra neutro detergente, fibra ácido detergente y proteína cruda de "Elk sedge" de muestras colectadas en la Estación Experimental Forestal y de Pastizales Starkey y en el área de Manejo de Fauna Silvestre de Bridge Creek, ambas situadas en el nordeste de Oregon. Los muestreos se realizaron durante Enero, Abril, Julio y Octubre de 1997 y 1998. Los niveles mas bajos de fibra neutro detergente del "Elk sedge" se presentaron a mediados de Octubre ( $\bar{x}$  = 71.3%) y los mas altos a mediados de Julio ( $\bar{x}$  = 76.1%). Los niveles mas bajos de fibra ácido detergente presentaron en el "Elk sedge" colectado a mediados de Octubre ( $\bar{x}$  = 37.3%) y los mas altos en el colectado a mediados de Julio ( $\bar{x}$  = 39.0%) y mediados de Enero ( $\bar{x}$  = 39.2%). El "Elk sedge" colectado en comunidades de "Douglas-fir/ninebark" fue el que presento los niveles mas bajo de fibra ácido detergente ( $\bar{x}$  = 38.1%). El contenido de proteína cruda mas alto se obtuvo en las muestras colectadas a mediados de Julio ( $\bar{x}$  = 8.0%) y el mas bajo en las colectadas a mediados de Enero ( $\bar{x}$  = 5.7%). El "Elk sedge" proveniente de la comunidad de "Pine/fescue" fue el mas bajo en proteína cruda ( $\bar{x}$  = 5.9%). Todos los parámetros de calidad de forraje mostraron variabilidad entre años. Aunque se detectaron efectos de la fecha de muestreo y la comunidad vegetal, la calidad del forraje del "Elk sedge" parece relativamente estable comparada con otros forrajes nativos. Se necesita una campaña de muestreo mas intensiva durante la primavera para caracterizar las relaciones entre la fonología del "Elk sedge" y la dinámica de la calidad del forraje.

while fall diets may contain 17 to 24% elk sedge (Holechek et al. 1982). Seasonal diets of Rocky Mountain elk (*Cervus elaphus nelsoni* Bailey) may contain 11 to 21% elk sedge in spring, 12 to 24% in summer, 18 to 46% in fall and from 0 to 30% in winter (McArthur 1977, McReynolds 1977, Sheehy 1987). Despite this acknowledged importance, little is known about the variability in elk sedge forage quality or the factors influencing this variability.

Forage quality greatly influences rangeland carrying capacity and forage and habitat utilization patterns of livestock (Pinchak et al. 1991, Bailey et al. 1996) and big game (Hobbs and Swift 1985, Larter and Gates 1991). Forage quality of nearly all herbage varies throughout the year. A limited amount of seasonal forage quality data has been collected for elk sedge in northeast-

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ern Oregon (Skovlin 1967, Clark et al. 2000) and central Washington (McArthur 1977, McReynolds 1977). Our understanding of the forage quality trends of elk sedge, however, has been confined to late spring through fall.

By definition, biotic and abiotic conditions differ between vegetation or plant communities and these conditions may influence the forage quality of component species. Researchers in Montana have compared total nonstructural carbohydrate levels in elk sedge from different vegetation types (Krueger and Bedunah 1988), but the forage quality responses of elk sedge to differing vegetation or plant communities have not been evaluated. The objective of this study was to examine the influence of sampling date, plant community, and their interaction on the neutral detergent fiber (NDF), acid detergent fiber (ADF), and crude protein (CP) levels of elk sedge.

## Materials and Methods

### Study Areas

The study was conducted at 2 study areas; Starkey Experimental Forest and Range (hereafter referred to as Starkey; 45° 35' N, 118° 30' W) near La Grande, Ore., and Bridge Creek Wildlife Management Area (hereafter referred to as Bridge Creek; 45° 03' N, 118° 55' W) near Ukiah, Ore. Starkey is a USDA Forest Service research area (101 km<sup>2</sup>) where forage and habitat use by livestock, elk, and mule deer (*Odocoileus hemionus hemionus* Rafinesque) have been monitored since 1940 (Skovlin 1991). Bridge Creek (33 km<sup>2</sup>) has been owned by the Oregon Department of Fish and Wildlife since 1961 and is primarily managed as an elk range where late spring grazing by livestock has been closely-monitored since 1964 (Anderson and Scherzinger 1975).

Climate at both study areas is continental with maritime influences. Winters are cold and wet with more than half of the annual precipitation falling as snow between November and March (Fig. 1). Summers are warm and dry. The growing season is about 120 days but frost can occur during any month of the year.

Elevation at Starkey ranges from 1,150 to 1,700 m while Bridge Creek lies between 850 and 1,200 m. The landscape at both study areas consists of a dissected basaltic plateau with broad ridges and steep, narrow drainages typical of the interior Blue Mountains and much of the Columbia Basin at mid elevations (800 to

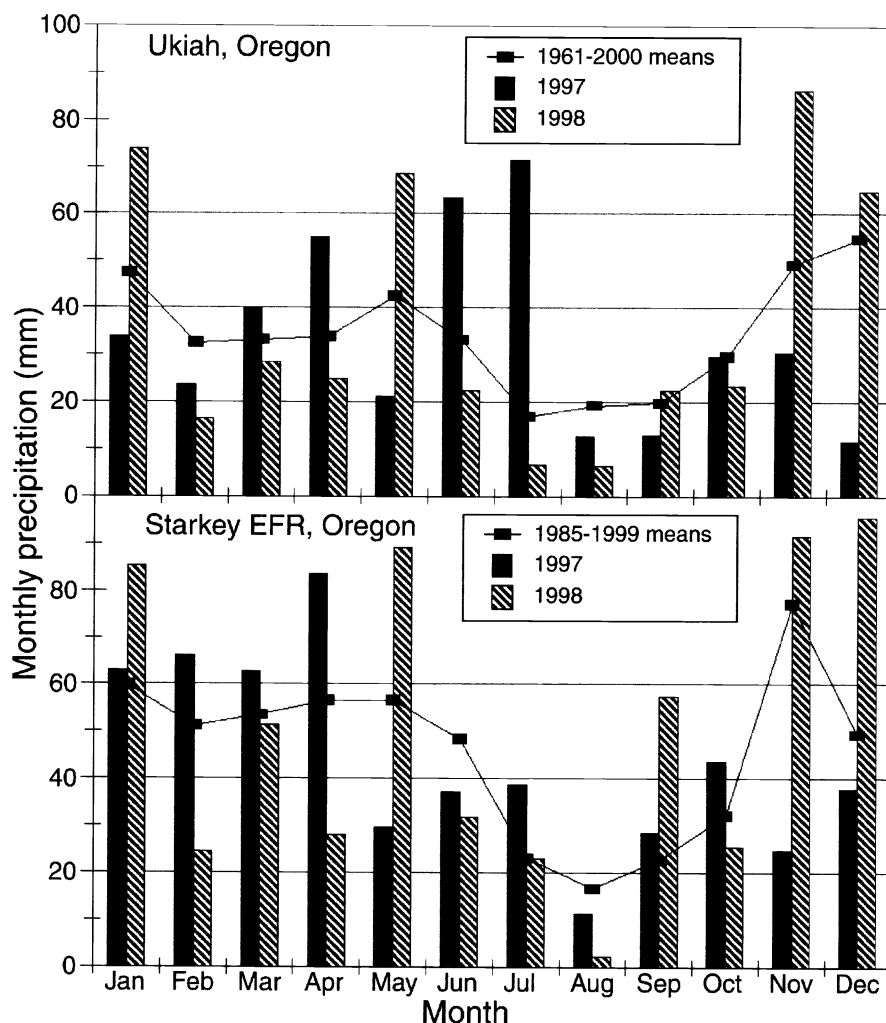
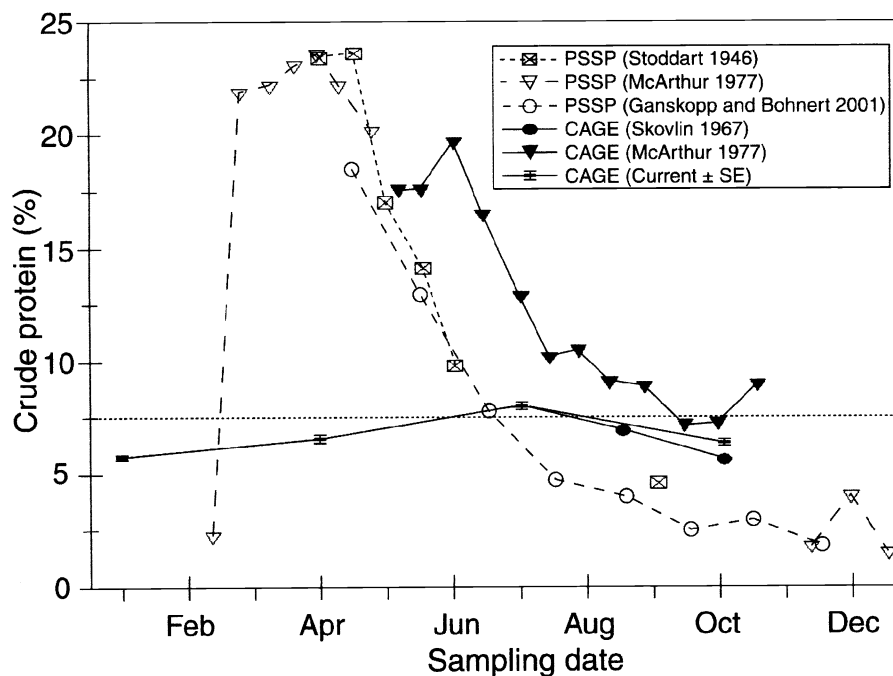


Fig. 1. Monthly precipitation for 1997-1998 and long-term mean monthly precipitation for Ukiah, Oregon, and Starkey Experimental Forest and Range, Oregon.

1,800 m). Soils at Starkey range from shallow silty clay loams and heavy clays on the ridges to silty clays and clay loams of variable depth on the steep, forested drainage slopes (Skovlin 1991). At Bridge Creek, ridgetop soils are shallow, very stony loams or relatively deep silt loams overlying basalt. Soils on the steep slopes range from shallow, stony loams to deep silt loams depending on exposure (Anderson and Scherzinger 1975).

Bunchgrass grasslands occupy the broad ridges of both study areas while ponderosa pine (*Pinus ponderosa* Dougl.), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco.) and grand fir (*Abies grandis* [Douglas] Forbes) forests occur in the drainages and on the highlands. Plant communities of interest for the current study were: 1) ponderosa pine/fescue (*Festuca* spp.), 2) Douglas-fir/ninebark (*Physocarpus malvaceus* [Greene]

Kuntze), and 3) mixed conifer/pinegrass (*Calamagrostis rubescens* Buckl.) communities. These communities occur extensively throughout the region and contain elk sedge as an understory dominant or co-dominant. The ponderosa pine/fescue community occupies the upper slopes of the study area drainages, forming a pine/bunchgrass savanna at the interface between ridgetop grasslands and coniferous forest. Vegetation in this community consists of a ponderosa pine overstory and an understory of Idaho fescue (*Festuca idahoensis* Elmer), elk sedge, and blue-bunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) (Hall 1973: CP-G1-12). The Douglas-fir/ninebark community occurs on canyon slopes and is more extensive on the drier aspects. The Douglas-fir/ninebark community supports Douglas-fir, ponderosa pine, and grand fir with a shrub layer of ninebark, common



**Fig. 2. Sampling date trends in crude protein (%) for elk sedge (CAGE) collected in central Washington and northeastern Oregon and for bluebunch wheatgrass (PSSP) collected in northern Utah, central Washington, and southeastern Oregon. The dashed horizon line represents the 7.5% crude protein threshold for maintenance diets.**

snowberry (*Symphoricarpos albus* [L.] Blake), and oceanspray (*Holodiscus discolor* [Pursh] Maxim.) with a herbaceous layer of elk sedge and pinegrass (Hall 1973: CD-S7-11). The canyon bottoms and north slopes of the study areas are occupied by the mixed conifer/pinegrass community. Douglas-fir, grand fir and ponderosa pine form the overstory in this community with elk sedge and pinegrass making up the understory. No shrub layer occurs in the mixed conifer/pinegrass community (Hall 1973: CW-G1-11).

### Sample Collection

Digital plant community maps of Starkey and Bridge Creek were developed in a GIS using 1:12,000 scale, color aerial photographs and extensive ground-truthing. At each of the 2 study areas, 3 plant community mapping units were randomly selected as sampling sites for each of the ponderosa pine/fescue, Douglas-fir/ninebark, and mixed conifer/pinegrass plant community types. A randomly located base line was established within each sampling site. During each sampling campaign, elk sedge at a site was sampled along 4 transects originating from 4 random locations along the baseline. At 5 random points along each transect, all the elk sedge standing crop within 0.5 m<sup>2</sup> cir-

cular sampling frames was hand clipped to a 2.5-cm stubble height and collected. Elk sedge from all 4 transects per site was pooled into 1 composite sample for laboratory analysis.

Samples were collected on 4 sampling dates during both 1997 and 1998: 1) January 15<sup>th</sup> (late dormancy), 2) April 15<sup>th</sup> (new leaf emergence), 3) July 15<sup>th</sup> (seed shatter), and 4) October 15<sup>th</sup> (early dormancy). New transects were used for each sampling campaign. These sampling dates were chosen to target what were assumed to be critical points in the phenological development and seasonal forage quality trends of elk sedge (Skovlin 1967, Krueger and Bedunah 1988). Logistical constraints prevented the temporally-intensive sampling needed to completely characterize the forage quality dynamics of elk sedge within each season. Consequently, sampling date rather than season was analyzed as a factor influencing elk sedge forage quality. Forage quality of cool-season graminoids is typically most dynamic between early spring and early summer. Some data describing the forage quality trends of elk sedge from late spring to early fall are available (Skovlin 1967, McArthur 1977, McReynolds 1977). Forage quality of elk sedge during early spring (April) has never been characterized and the timing of

peak forage quality in elk sedge is unknown. The mid-April sampling campaign of the current study was an attempt to capture elk sedge during its expected annual peak in forage quality. The timing of this campaign was selected by examining the forage quality trends of elk sedge, pinegrass, and bluebunch wheatgrass using data collected by McArthur (1977) and McReynolds (1977) in central Washington and bluebunch wheatgrass data collected in northern Utah by Stoddart (1946) (Fig. 2).

### Laboratory Analysis

Samples were oven dried at 45° C, ground to pass a 1-mm screen, and stored in air-tight bags. Neutral detergent fiber (Robertson and Van Soest 1981) and ADF (Goering and Van Soest 1970) analyses were conducted using procedures modified for use in an Ankom 200 Fiber Analyzer (Ankom Co., Fairport, N.Y.<sup>1</sup>). Neutral detergent fiber describes the cell wall content of a forage including cellulose, lignin, and hemicellulose (Van Soest 1982). Acid detergent fiber is a measure of the cellulose and lignin content of a forage and is inversely related to the digestible dry matter (DDM) content (Van Soest 1982). Crude protein was determined in duplicate using a LECO carbon/nitrogen analyzer (LECO Corp., St. Joseph, Mich.). Crude protein, NDF, and ADF values were reported on a dry matter basis.

### Statistical Analysis

Forage quality data were analyzed with a split-plot in time analysis procedure (PROC MIXED; SAS 1997) where study areas ( $n = 2$ ), years ( $n = 2$ ), and plant communities ( $n = 3$ ) were assigned as whole plot factors and sampling dates ( $n = 4$ ) were subplot factors. The sites within year, study area and plant community term with 24 degrees of freedom (Satterthwaite 1946) was designated as a random effect in the mixed model and became the error term for testing the main effects of year, study area, plant community and their interactions. The residual with 72 degrees of freedom (Satterthwaite 1946) was used as the error term for date and all interactions involving date. Where significant main effects or interactions were detected, Tukey's HSD procedure was used for all mean separations (Tukey 1953). All differences reported were significant at  $P < 0.05$  unless stated otherwise.

<sup>1</sup>Mention of manufactures or trade names is for the convenience of the reader only and implies no endorsement on the part of the author or USDA.



## Results

### Neutral Detergent Fiber

Neutral detergent fiber of elk sedge was influenced by sampling date ( $P < 0.01$ ,  $SE = 0.33\%$ ) and year ( $P < 0.01$ ,  $SE = 0.24\%$ ) but was unaffected by plant community ( $P = 0.99$ ,  $SE = 0.29\%$ ) or study area ( $P = 0.18$ ,  $SE = 0.24\%$ ). Samples collected in mid-October ( $\bar{x} = 71.3\%$ ) were lowest in NDF. Elk sedge harvested in January ( $\bar{x} = 73.6\%$ ) and April ( $\bar{x} = 73.2\%$ ) had similar NDF levels but was lower than that collected in July ( $\bar{x} = 76.1\%$ ). Levels of NDF were lower in 1998 ( $\bar{x} = 72.5\%$ ) than in 1997 ( $\bar{x} = 74.6\%$ ). No significant interactions for NDF were detected between any of the 4 main effects.

### Acid Detergent Fiber

Differences in ADF of elk sedge were detected between sampling date ( $P < 0.01$ ,  $SE = 0.20\%$ ), among plant communities ( $P = 0.02$ ,  $SE = 0.17\%$ ), and between years ( $P < 0.01$ ,  $SE = 0.14\%$ ). Mid-October samples of elk sedge contained the lowest ADF levels ( $\bar{x} = 37.3\%$ ) while April levels were intermediate ( $\bar{x} = 38.4\%$ ) and July ( $\bar{x} = 39.0\%$ ) and January ( $\bar{x} = 39.2\%$ ) levels were highest. Elk sedge in the Douglas-fir/ninebark plant community was lowest in ADF ( $\bar{x} = 38.1\%$ ). Acid detergent fiber levels were similar in the ponderosa pine/fescue ( $\bar{x} = 38.7\%$ ) and mixed conifer/pinegrass ( $\bar{x} = 38.6\%$ ) communities. Elk sedge collected in 1998 ( $\bar{x} = 37.6\%$ ) was lower in ADF than in 1997 ( $\bar{x} = 39.4\%$ ). A significant interaction between plant community and study area was detected for ADF ( $P = 0.03$ ,  $SE = 0.24\%$ ) (Table 1).

### Crude Protein

Crude protein of elk sedge was affected by sampling date ( $P < 0.01$ ,  $SE = 0.11\%$ ), plant community ( $P < 0.01$ ,  $SE = 0.10\%$ ), study area ( $P < 0.01$ ,  $SE = 0.08\%$ ), and year ( $P < 0.01$ ,  $SE = 0.08\%$ ). Samples collected in mid-July were highest in CP ( $\bar{x} =$

**Table 2. Mean crude protein (CP) in elk sedge samples collected at Starkey Experimental Forest and Range and Bridge Creek Wildlife Management Area, Ore., during 1997 and 1998 as affected by sampling date-plant community interactions.**

Plant Community	Sampling Date			
	Mid-Jan	Mid-Apr	Mid-Jul	Mid-Oct
	------(%)-----			
P. Pine/fescue <sup>1</sup>	5.5cd <sup>2</sup>	5.8cd	7.0b	5.4d
D-fir/ninebark	5.7cd	6.9b	8.6a	6.7b
M. Conifer/pinegrass	5.9c	6.8b	8.4a	6.6b

<sup>1</sup>P. Pine/fescue represents the ponderosa pine/Idaho fescue community, D-fir/ninebark represents the Douglas-fir/ninebark community, and M. Conifer/pinegrass represents the mixed conifer/pinegrass community.

<sup>2</sup>Means sharing a common letter are not significantly different ( $P > 0.05$ ).

8.0%) while mid-April ( $\bar{x} = 6.5\%$ ) and mid-October ( $\bar{x} = 6.3\%$ ) samples were similar but higher than elk sedge collected in mid-January ( $\bar{x} = 5.7\%$ ). Crude protein levels in the Douglas-fir/ninebark ( $\bar{x} = 7.0\%$ ) and mixed conifer/pinegrass ( $\bar{x} = 6.9\%$ ) plant communities were similar but higher than in the ponderosa pine/fescue community ( $\bar{x} = 5.9\%$ ). Elk sedge collected at Bridge Creek ( $\bar{x} = 6.9\%$ ) was higher in CP than at Starkey ( $\bar{x} = 6.3\%$ ). Percentage crude protein in samples harvested in 1998 ( $\bar{x} = 6.9\%$ ) was higher than in 1997 ( $\bar{x} = 6.3\%$ ). Sampling date by plant community ( $P = 0.03$ ,  $SE = 0.19\%$ , Table 2) and study area by year ( $P = 0.05$ ,  $SE = 0.12\%$ ) interactions affected CP levels of elk sedge. Elk sedge at Bridge Creek contained higher CP levels during 1998 ( $\bar{x} = 7.3\%$ ) than 1997 ( $\bar{x} = 6.5\%$ ) while elk sedge at Starkey exhibited no CP differences between 1998 ( $\bar{x} = 6.5\%$ ) and 1997 ( $\bar{x} = 6.2\%$ ).

## Discussion

### Forage Quality and Phenology

Seasonal trends in ADF and CP of elk sedge at Starkey and Bridge Creek appear to differ from other dominant graminoids such as bluebunch wheatgrass. Forage quality of bluebunch wheatgrass tends to increase sharply from an annual low in late winter to a peak in early spring during the early vegetative growth stage (mid-

April), declines rapidly in late spring/early summer during reproductive stages (mid-June), then more gradually declines through summer and fall back to the winter low (Stoddart 1946, McArthur 1977) (Fig. 2). Favorable soil moisture conditions may promote a fall peak in forage quality of bluebunch wheatgrass but this is uncommon in the Blue Mountains (Bryant 1993). Results from the current study suggest the forage quality of elk sedge in the Blue Mountains exhibits very slight peaks during summer or fall but generally is relatively stable. These results, however, may not fully reflect the forage quality dynamics of elk sedge. Although the phenology of elk sedge at Starkey and Bridge Creek was well advanced during mid-April (most plants were in the spikelet emerging or anthesis stages), the mid-April sampling date may have been too early to capture the actual peak in forage quality of elk sedge. Data presented by McArthur (1977) and McReynolds (1977) suggest the forage quality of elk sedge in central Washington probably peaks at levels somewhat lower than bluebunch wheatgrass and may do so in mid-June rather than in mid-April. The phenology of elk sedge was not reported in the central Washington studies, however, elk sedge at Starkey is typically nearing the ripe seed phenological stage by mid June (Driscoll 1957, Skovlin 1967). Given these observations, the relationship between forage quality and phenology of elk sedge appears to differ considerably from that of bluebunch wheatgrass and possibly other dominant graminoids in the region. Additional research is needed to investigate the relationships between forage quality and phenology in elk sedge.

### Plant Community Effects

Although NDF levels in elk sedge were unaffected by plant community, ADF was lowest in the Douglas-fir/ninebark community and CP was highest in the Douglas-fir/ninebark and mixed conifer/pinegrass

**Table 1. Mean acid detergent fiber (ADF) in elk sedge samples collected at Starkey Experimental Forest and Range and Bridge Creek Wildlife Management Area, Ore., during 1997 and 1998 as affected by a plant community-study area interaction.**

Study Area	Plant Community		
	P. Pine/fescue <sup>1</sup>	D-fir/ninebark	M. Conifer/pinegrass
	------(%)-----		
Starkey	38.3bc <sup>2</sup>	38.1c	38.8ab
Bridge Creek	39.2a	38.0c	38.4bc

<sup>1</sup>P. Pine/fescue represents the ponderosa pine/Idaho fescue community, D-fir/ninebark represents the Douglas-fir/ninebark community, and M. Conifer/pinegrass represents the mixed conifer/pinegrass community.

<sup>2</sup>Means sharing a common letter are not significantly different ( $P > 0.05$ ).

communities. The Douglas-fir/ninebark and mixed conifer/pinegrass plant communities provide a more mesic growing season microclimate for elk sedge than the drier sites occupied by the ponderosa pine/fescue community. The understory in these 2 communities is typically well shaded and accumulated snow and soil moisture is likely conserved later into the year than in the ponderosa pine/fescue community. As observed in other studies (Clark et al. 2000), elk sedge in the more open ponderosa pine/fescue community appears to suffer more from desiccation and exposure, exhibiting more withered leaves or leaf tips, than elk sedge in the communities with denser tree canopies. More favorable growing conditions may allow elk sedge in the Douglas-fir/ninebark and mixed conifer/pinegrass communities to be more vigorous, nutritious and sustain high forage quality longer through the year than elk sedge in the ponderosa pine/fescue community.

Plant community effects on ADF levels in elk sedge differed between Starkey and Bridge Creek (Table 1). Although elk sedge at Starkey and Bridge Creek exhibited similar ranges in ADF among plant communities, ADF was highest in the ponderosa pine/fescue community at Bridge Creek while the ponderosa pine/fescue community and mixed conifer/pinegrass communities were similar and highest in ADF at Starkey. This interaction of plant community and study area might be explained by differences in snow and soil moisture patterns. Bridge Creek is lower in elevation than Starkey and probably receives a lower and more spatially variable snowpack. Possible plant community effects on snow accumulation and soil moisture conservation may be more pronounced at Bridge Creek and may contribute to the greater forage quality variability observed among plant communities at Bridge Creek.

### Sampling Date by Plant Community Interactions

Crude protein in elk sedge was similar among plant communities during mid-January, but CP in elk sedge collected during all other sampling dates was higher in the Douglas-fir/ninebark and mixed conifer/pinegrass plant communities than in the ponderosa pine/fescue community (Table 2). Additionally, elk sedge in the Douglas-fir/ninebark and mixed conifer/pinegrass communities exhibited significant increases in CP by mid-April and maintained these increases through mid-October while CP increases for elk sedge in the ponderosa

pine/fescue community were only detected at the mid-July sampling date. If the earlier, higher, and longer lasting CP increases observed in elk sedge from the Douglas-fir/ninebark and mixed conifer/pinegrass communities were due to moister, more favorable microclimatic conditions in these communities, then these moister conditions may also promote increased rates of degradation and nutrient leaching during the winter months compared to those in the ponderosa pine/fescue community. Hence, differences in elk sedge CP levels observed among plant communities during the growing season would likely even out, as observed, during winter.

### InterAnnual Variability

Forage quality differences, particularly in NDF and ADF levels, detected between years may be related to differences in the amount and timing of precipitation. Weather stations at Starkey and within 8 km of Bridge Creek experienced above normal precipitation during the early spring months of 1997 (Fig. 1). May of 1997, however, was abnormally dry. Spring precipitation in 1998 was generally below average at both stations except during May 1998 which was far above average. The spike in precipitation during May 1998 may have stimulated a late surge of new growth in elk sedge, increasing the forage quality of mid-July 1998 samples at both study areas. Additionally, early to mid winter (November–January) precipitation was at or below average in 1997 but well above average in 1998 at both stations. High winter precipitation may have impacted the mid-January forage quality of elk sedge during 1998. The year effect on CP noted at Bridge Creek but not at Starkey may be related to station differences in early summer precipitation. Precipitation amounts near Bridge Creek during June and July of 1997 were much higher than the long-term means but were near normal at Starkey.

### Conclusions

Although sampling date and plant community effects were detected, the forage quality of elk sedge appeared relatively stable compared to other native forages. Elk sedge has been considered as a “level component” forage or a forage that maintains at least moderate forage quality through all seasons and may help sustain herbivore diet quality during dormancy of other forage species (Huston and Pinchak 1991, p. 48). Crude protein is commonly regarded as an effective index of overall nutritional quality in forages (Van Soest

1982). Crude protein of 7.5% has been considered a nutritional threshold for maintenance of wild and domestic herbivores (Ganskopp and Bohnert 2001). Spring-early summer CP content in the dominant grasses of the interior Pacific Northwest and northern Great Basin is generally elevated well above this threshold. Crude protein levels rapidly decline, however, as these grasses enter reproductive phenological stages (Fig. 2). By July, CP in these species typically drops below 7.5% and continues to decline through summer and fall (Ganskopp and Bohnert 2001). Crude protein in elk sedge from the Blue Mountains of Oregon remains above 7.5% at least through mid July, allowing cattle, elk and other herbivores to continue on a maintenance diet later into the season. Elk sedge may also serve as a critical forage source during late fall and winter when the CP content of other graminoids is extremely low (3 to 4%) (Clark et al. 2000, Ganskopp and Bohnert 2001).

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# Prescribed fire effects on erosion parameters in a perennial grassland

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## Abstract

A 2-year field experiment was undertaken to quantify the interacting effects of a late-spring prescribed burn and summer rainfall on seasonal runoff and erosion in a southern Arizona grassland. Six blocks with walled subplots ( $n = 24$ ) were installed on a hillslope to measure changes to plant, soil, and hydrologic variables in response to treatments. Increased bulk density, erosion, and runoff volumes; and lowered plant cover and water intake rates were observed within the burned plots following the first summer season. In the second year, higher bulk density, runoff volumes, and erosion measures were again observed within the burned plots, as well as lower plant cover, aggregate stability, and water intake rates. The results of this study indicate that following late-spring burning, semi-desert grasslands are susceptible to greater summer runoff and erosion compared to unburned grasslands.

**Key Words:** Arizona, sediment yield, summer rainfall

Following decades of active suppression, fire is being reintroduced in to the grasslands of southern Arizona as a management tool to achieve some of the landscape values attributed to wildfire. Fire within these systems has historically preceded the start of the summer rainy season (Wright and Bailey 1982), restructuring the plant community by reducing woody plant numbers and increasing herbaceous plant diversity and abundance (Martin 1983, McPherson 1995, Wright and Bailey 1982). Within various Southwest perennial grass communities, the response of many aboveground plant attributes (i.e. biomass, seedling establishment, percent cover) has been either positive or neutral to burning (Biedenbender and Roundy 1996, Bock et al. 1995, Ford 1999, Wilson 1999). However, localized climatic conditions (i.e. winter drought) either preceding or following burning have been associated with the notable delay in community recovery (Wright 1979), as well as in the recovery of specific grass species (Wright and Bailey 1982).

The removal of vegetation soil cover by fire is an important driver of surface runoff and erosion processes, as it reduces the frequency and size of vegetated areas over the landscape (Baker 1988, Simanton and Renard 1981). Removal of vegetation exposes the soil surface to the energy of raindrop impact (Bennett

## Resumen

Se condujo un estudio de campo de 2 años para cuantificar los efectos interactuantes del fuego prescrito a fines de primavera y la lluvia de verano en el escurrimiento estacional y erosión en un pastizal del sur de Arizona. En la ladera de la montaña se instalaron 6 bloques, subdivididos en subparcelas ( $n=24$ ), para medir los cambios en planta, suelo y variables hidrológicas en respuesta a los tratamientos. En el primer verano después de la quema se observó en las parcelas quemadas una mayor densidad aparente del suelo, una mayor erosión y mayores volúmenes de escurrimiento así como una menor cobertura vegetal y menor tasa de infiltración. En el segundo año nuevamente se observó dentro de las parcelas quemadas mayores valores de densidad aparente, erosión y volumen de escurrimiento, así como menor cobertura vegetal, estabilidad de los agregados y consumo de agua. Los resultados de este estudio indican que después de un fuego a fines de primavera, los pastizales semidesérticos son susceptibles a una mayor erosión y escurrimiento en comparación con los pastizales sin quemar.

1974, Hester et al. 1997), affecting surface aggregate stability (Armstrong and Stein 1996, Gang et al. 1998, Warren 1987) and the permeability of surface soil layers to water infiltration (Baker 1988, Smith et al. 1990). In grasslands of the southwestern U.S., little is known about the interchanges between soil erosion and grassland community dynamics following a prescribed fire. A 2-year field experiment was undertaken to quantify the effects of prescribed fire and summer rainfall interactions on plant and soil parameters that affect summer runoff and erosion in a southern Arizona grassland.

## Materials and Methods

The Elgin, Arizona study area ( $31^{\circ} 62' N 110^{\circ} 52' W$ ), with an average elevation of 1,450 m, was characterized by perennial bunchgrasses occupying the uplands, oak woodlands in the drainages, and more than 30 years of livestock exclusion. The grass genera *Eragrostis*, *Bouteloua*, *Lycurus*, and *Muhlenbergia* dominated the site. Mimosa (*Mimosa biuncifera* Benth.), rabbit brush (*Chrysothamnus nauseosus* (Pall.) Britton), and various cacti were also present. The soil is a White House gravelly loam (Fine, mixed, superactive, thermic Ustic Haplargids) (Richardson et al. 1979), and the study site has a 1 to 3% slope.

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The study was a randomized complete block (block = replication) with 6 replications in a split-strip plot arrangement. The 4 treatment variations were a control, a prescribed burn, a rainfall simulation, and a rainfall simulation x prescribed burn interaction. Each block was established on a hillslope and contained 4 walled runoff subplots (3 m by 10 m) with sediment catchments. Sediment catchments were sheet metal boxes, each having covers to prevent rainfall contributions to runoff measures, set into the ground at the base of each plot. The seams of the boxes were sealed with silicone. A prescribed fire treatment was randomly applied to half of the plots in late May 1998. The plots were then split into strips for the application of a simulated summer rainfall event (63.5 mm hour<sup>-1</sup> for 40 min. for an average depth of 43.2 mm  $\pm$  0.4mm) using a rotating-boom rainfall simulator (Swanson 1965) at the end of June 1998. The rainfall simulation represented a storm return interval of approximately 3.5 years. Given the unpredictable timing of the summer rainy season, the simulated rainfall treatment was applied to ensure that surface erosion and sediment production would occur at the start of the growing season. Experimental design and weather limitations did not allow for the collection of sediment produced during rainfall simulation.

Permanent sampling points were established within each subplot to measure plant ( $n = 3$ ) and soil parameters ( $n = 6$ ). Sampling followed the summer growing seasons of 1998 and 1999. Vegetation variables were measured within quadrats (0.5 m by 0.5 m) centered upon the point marker. Percent aerial cover was ocularly estimated, gramineous ramets and seedlings were counted, and ground-level grass clump caliper was used for basal area calculations. Within a quadrat subset (0.25 m by 0.25 m) annual herbaceous dicot cover was also ocularly estimated. Bulk density (Blake and Hartge 1986), percent water-stable aggregates (PSA) (Kemper and Rosenau 1986), and surface intake rates were measured. Soil cores (2cm by 10cm) were collected for PSA measurements, and bulk density measurements were taken for depths of 0–5 cm and 6–10 cm. Water intake rates were used as surrogate measures of infiltration under unsaturated soil conditions (Perroux and White 1988, Sullivan et. al. 1996, White and Sully 1987). Measurements were conducted using a CSIRO designed disc permeameter at a single tension (negative pressure) 1.5 kPa, on a debris-cleared and leveled bed of silica sand within a soil embedded steel

ring (unpublished, CSIRO 1988). Aggregates, sized 0.15–0.30 mm, were used as measures of aggregate stability as they represented the mean PSA of the soil samples. Informal tests with water droplets shows no evidence of post-burn hydrophobicity at the soil surface.

Runoff volumes and dried sediment weights were recorded for each subplot 1 July through 1 October. Runoff volumes were calculated from the runoff depth captured in the catchments following the rainfall simulation event and natural storms. There was no adjustment for potential evaporation or pan leakage. Catchments were drained after the sediment had settled out. The sediment was air-dried in the field, collected, oven dried at 90°C for 24 hours, and then weighed. Due to logistical limitations sediment yield was not determined for the simulation events. Sediment yields reflect the total sediment collected for the summer season. Summer rainfall data were collected on the research site for 2 years following treatment application. Additionally, local long-term (10-year average) rainfall data were available from the Audubon Research Ranch, Elgin, Ariz. located approximately 2.4 kilometers from research site. Summer rainfall totals for 1998 (100.0 mm) and 1999 (106.0 mm) were above average (10-year average = 86.8 mm). Rainfall totals were below average (10-year average = 29.1 mm) for the falls of 1998 (12.5 mm) and 1999 (6.3 mm), and well below average (10-year average = 37.3 mm) for the winter of 1999 (2.0 mm) (O'Dea 2000).

There was no significant block by treatment interaction, and subplots were used as replicates. Effects of prescribed fire and simulated rainfall on plant (seedling and ramet numbers) and soil (bulk density, PSA) response variables were analyzed using analysis of variance (ANOVA). Water intake rates, plant cover, and basal area were analyzed with repeated mea-

sures ANOVA (SAS Institute, Inc. 1990). Soil depth increments (i.e. 0–5 cm and 6–10 cm) were used as covariates in tests of treatment effect on bulk density. Comparisons of treatment means for each year were made using least-squares means (Steel and Torrie 1980).

## Results

### Plant Parameters

There were significant ( $p \leq 0.01$ ) treatment effects on measured plant response variables in 1998 and 1999, results are summarized in Table 1. For both years, perennial grass cover and basal area were greater on unburned plots (i.e. control and rainfall simulation) than on burned plots. Recovery of the perennial grasses following the prescribed burn was slow, with little difference between 1998 and 1999. Plots treated with rainfall simulation only in 1998 had the greatest percent perennial grass cover, an effect of the additional watering and not in evidence in 1999. Mean basal area within the simulation X burn treatment was 2 to 4 times lower than values for the prescribed burn only treatment, and at least 4 times lower than the unburned treatments (Table 1). A significant within-subjects effect for time was found ( $p = 0.001$ ) for both perennial cover and basal area, prompting the expected conclusion that cover and basal area changed with time in the population from which the sample was drawn. In 1998, while there was a reduction in perennial grass cover compared with unburned plots, annual dicot cover increased. All treated plots had greater annual cover compared with the control, with the greatest dicot increase within the simulation x burn plots. In the second post-treatment year, burned plots continued to have greater annual cover and less perennial cover than the unburned plots (Table 1).

Table 1. Comparison of means among treatments for plant variables<sup>1</sup>.

		1998		1999	
		Cover	Basal Area	Cover	Basal Area
		(%)	(cm <sup>2</sup> )	(%)	(cm <sup>2</sup> )
Perennial grasses	Control	20.4 <sup>b</sup>	254.8 <sup>a</sup>	31.9 <sup>a</sup>	285.5 <sup>ab</sup>
	Prescribed burn	9.0 <sup>c</sup>	185.3 <sup>ab</sup>	19.0 <sup>b</sup>	158.2 <sup>ab</sup>
	Rainfall simulation	29.8 <sup>a</sup>	319.8 <sup>a</sup>	30.8 <sup>a</sup>	332.6 <sup>a</sup>
	Simulation x burn	11.2 <sup>c</sup>	45.7 <sup>b</sup>	15.0 <sup>b</sup>	80.3 <sup>b</sup>
Annual dicots	Control	0.9 <sup>c</sup>	-----	5.3 <sup>b</sup>	-----
	Prescribed burn	1.9 <sup>b</sup>	-----	10.1 <sup>a</sup>	-----
	Rainfall simulation	1.9 <sup>b</sup>	-----	3.8 <sup>b</sup>	-----
	Simulation x burn	3.2 <sup>a</sup>	-----	9.5 <sup>a</sup>	-----

<sup>1</sup>Significant ( $p < 0.05$ ) differences among treatment means for each plant variable are denoted with different letters.

**Table 2. Comparison of means among treatments of soil variables (10 cm depth)<sup>1</sup>.**

	1998			1999		
	Bulk density	Aggregate stability	Water intake rate	Bulk density	Aggregate stability	Water intake rate
	(g cm <sup>-3</sup> )	(PSA)	(mm hr <sup>-1</sup> )	(g cm <sup>-3</sup> )	(PSA)	(mm hr <sup>-1</sup> )
Control	1.53 <sup>b</sup>	0.74 <sup>a</sup>	14.4 <sup>a</sup>	1.50 <sup>b</sup>	0.64 <sup>ab</sup>	12.8 <sup>a</sup>
Prescribed burn	1.65 <sup>a</sup>	0.75 <sup>a</sup>	9.7 <sup>b</sup>	1.59 <sup>ab</sup>	0.59 <sup>b</sup>	8.0 <sup>b</sup>
Rainfall simulation	1.70 <sup>a</sup>	0.82 <sup>a</sup>	15.3 <sup>a</sup>	1.54 <sup>b</sup>	0.73 <sup>a</sup>	13.8 <sup>a</sup>
Simulation x burn	1.64 <sup>a</sup>	0.83 <sup>a</sup>	10.0 <sup>b</sup>	1.62 <sup>a</sup>	0.58 <sup>b</sup>	8.9 <sup>b</sup>

<sup>1</sup>Significant ( $p < 0.05$ ) differences among treatment means for each plant variable are denoted with different letters.

The perennial grasses regenerated primarily through the re-sprouting of residual grass clumps, with few new recruits becoming established. Seedlings were found within all treatments in 1998 and 1999, yet none survived the proceeding fall and winter droughts. In 1998, a significant treatment effect was observed for seedling number that was not observed the second year ( $P = 0.040$ ). In 1998, the greatest number of seedlings counted was within the simulation x burn plots (3.4 seedlings m<sup>-2</sup>) compared to the other treatments ( $< 1$  seedling m<sup>-2</sup>) ( $P \leq 0.05$ ). Counts were less than 1 seedling m<sup>-2</sup> for all treatments with no treatment effect in 1999. There was no treatment effect on ramet number in either 1998 or 1999. Ramets were only observed within the simulation x burn plots (0.4 ramet m<sup>-2</sup>) in 1998, and there were none found in 1999. Ramet number did not appear to be affected by either prescribed burning or the rainfall simulation.

### Soil Parameters

Differences among treatments were observed for soil bulk density, aggregate stability (PSA), and water intake rates in 1998 and 1999 (Table 2). A significant treatment effect was observed for bulk density in 1998 ( $P = 0.014$ ) and 1999 ( $P = 0.031$ ), including a significant depth x treatment interaction in 1998 ( $P = 0.01$ ). Increased bulk density with depth (i.e. 0-5 cm and 6-10 cm) ( $P \leq 0.05$ ) was observed in plots treated with rainfall simulation, but these changes were not evident in 1999. In 1998, bulk density (0-10 cm) was lowest within the control plots compared with the other treatments. In the following year, only bulk density within the simulation x burn plots was greater than the control (Table 2). There was a significant treatment effect on aggregate stability in 1999 ( $P = 0.009$ ), but not in 1998. In 1999, aggregate stability was lower in the burned plots compared to the rainfall simulation only plots, but not with the control (Table 2). Significant treatment effects on

water intake rates were observed in 1998 ( $P = 0.0001$ ) and 1999 ( $P = 0.0001$ ), with intake rates lower both years in the burned plots compared with the unburned (Table 2). A significant within-subjects effect for time was found ( $P = 0.001$ ) for water intake rates, suggesting intake rates changed with time in the population from which it was sampled.

### Surface Runoff and Sediment Yield

The simulated rainfall treatment contributed approximately 40% of the total summer rainfall and 52% of the total summer runoff volume for 1998. Simulator-generated runoff volumes were greater in the burned plots than in the rainfall simulation only plots ( $P = 0.05$ ). Excluding the contributions of the simulation treatment, total summer runoff from natural rainfall events was greatest for the simulation x burn treatment compared to the other treatments (Table 3).

In comparing total rainfall (simulation + natural) for the summer months, a significant treatment effect for runoff volume was observed in 1998 ( $P = 0.0001$ ) and 1999 ( $P = 0.0001$ ). In 1998, total summer runoff volumes were higher for plots treated with the rainfall simulation, with the greatest measured runoff on the simulation x burn plots. Runoff volumes in the simulation only treatment were not significantly different the control under natural rainfall, when the simulation was excluded. In 1999, total summer runoff volumes con-

tinued to be greater for the simulation x burn plots compared with the others (Table 3). Runoff in all treatments was higher in 1999 than in 1998 because of above average rainfall in the summer of 1999. There was a significant treatment effect on sediment production in 1998 ( $P = 0.011$ ) and in 1999 ( $P = 0.004$ ), with the greatest amount of sediment produced in the simulation x burn plots. Sediment production was lowest in the control plots; with no difference between the prescribed burn only and the rainfall simulation only plots. In 1998, sediment yields from all of the treated plots were greater than the control, with no significant difference between the prescribed burn only and the simulated rainfall only plots. In 1999, sediment yields from the burned treatments continued to be greater than the control, with the greatest yields coming from the simulation x burn plots (Table 3).

### Discussion

Prescribed burns preceding the summer rainy season affect not only the perennial bunchgrass community, but also structural features of the surface soil layers. The perturbation of these grassland attributes affected runoff and erosion, as soil loss after a burn is strongly influenced by the frequency and size of exposed areas (Baker 1988, Meeuwig 1970). The decline in perennial grass cover, along with the lack of new recruits increased the frequency and size of non-vegetated area within the burned plots. The increased bare area exposed the soil surface to raindrop impact, and removed barriers to overland flow and sediment transport (Hester et al. 1997, Smith et al. 1990), as well as the localized zones of greater infiltration associated with vegetation (Blackburn 1975, Thurow et al. 1986). While annual dicot cover increased in the burned plots, it did little to mitigate runoff volumes or sediment yield. The higher dicot cover in con-

**Table 3. Comparison among treatments of mean summer runoff volumes and sediment yields<sup>1</sup>.**

	1998			Sediment Yield	1999	
	Runoff Volume		Total		Runoff Volume	Sediment Yield
	Simulation	Natural			Total	Total
	-----	(liters)	-----	(kgm <sup>-2</sup> )	(liters)	(kgm <sup>-2</sup> )
Control	----	175 <sup>b</sup>	175 <sup>c</sup>	1.7 <sup>c</sup>	443 <sup>b</sup>	1.8 <sup>c</sup>
Prescribed burn	----	182 <sup>b</sup>	182 <sup>c</sup>	2.8 <sup>b</sup>	452 <sup>b</sup>	2.2 <sup>ab</sup>
Rainfall simulation	279 <sup>b</sup>	264 <sup>ab</sup>	543 <sup>b</sup>	2.9 <sup>b</sup>	592 <sup>b</sup>	1.9 <sup>cb</sup>
Simulation x burn	414 <sup>a</sup>	394 <sup>a</sup>	808 <sup>a</sup>	4.1 <sup>a</sup>	828 <sup>a</sup>	2.6 <sup>a</sup>

<sup>1</sup>Significant ( $p < 0.05$ ) differences among treatment means for each plant variable are denoted with different letters.

junction with lower perennial grass cover on areas burned and artificially eroded (i.e. simulation x burn) appeared to have a positive effect on runoff yields.

The slow recovery of the perennials was unexpected following 2 years of above-average summer rainfall, as well as moist pre-burn soil conditions that was expected to mitigate plant damage and support a greater post-fire growth response (Wright 1979, Wright and Bailey 1982). Additionally, there was no notable grass mortality following the burn. Vegetative sprouting occurred almost immediately following the fire and was well established before the rainfall simulation. The delayed recovery of the grasses may have been a combination of 4 uncontrollable factors: a week of storms (total rainfall = 37.5 mm) immediately following the rainfall simulation, lack of grass recruitment, winter and fall droughts, and fire effects on the mycorrhizal community. Two days after the simulation treatment, the summer rains began. Storms came in every afternoon for 6 consecutive days, accounting for 40% of the season's natural rainfall and with the simulation, approximately 60% of the summer total. While a storm of similar intensity to the simulation had occurred the previous year, it had not been in conjunction with a series of storms. With so much of the rainfall occurring in a short period, the large volumes of runoff and sediment produced in the burned plots may have damaged residual plants by exposing portions of the root system. Burning alone may damage aboveground growing points (Steuter and McPherson 1995), while erosion around the plant (i.e. pedestalling) exposed previously protected plant parts. Desiccation of exposed roots, as well as damage to belowground growing points may explain the disproportionate decline of the perennials within burned plots treated with the rainfall simulation.

Recruitment of new individuals within the grass community appeared to be predominantly influenced by environmental factors (e.g. drought) rather than only by treatment characteristics. The largest seedling counts were recorded in 1998 within plots treated with the rainfall simulation, although seedlings were found within all treatments both years. However, none of the counted seedlings were able to survive the fall and winter droughts (Biedenbender and Roundy 1996). Gramineous ramets were also observed in 1998, but none were observed in the following year's survey. Many grasses common to southern Arizona, such as blue grama (*Bouteloua gracilis* (H.B.K.)), side-

oats grama (*B. curtipendula* (Michx.) Torr.), and wolftail (*Lycurus phleoides* H.B.K.) have been reported to be harmed by spring fires that were followed by winters of below-average rainfall (Wright and Bailey 1982). Additionally, the mycorrhizal nature of these grasses is another important factor in their recovery. Prescribed burning inhibits the potential colonization of these grasses by mycorrhizal fungi (O'Dea 2000). Differential plant responses to colonization occur between and within different grass genera (Smith et al. 1999, Wilson and Hartnett 1998), influencing species growth and regeneration. Both plains lovegrass (*Eragrostis intermedia* Hitchc.) and Lehmann lovegrass (*E. lehmanniana* Nees.) were common to this study site, and were found to produce significantly greater biomass under greenhouse conditions when they were not colonized compared to when they were. In contrast, grama (*Bouteloua* spp.) and wolftail (*Lycurus phleoides* H.B.K.) grasses produced substantially less biomass when they were not colonized (O'Dea 2000). These results infer that the slow regrowth of the perennial grasses, specifically that of the wolftail and grama grasses were in part mitigated by a belowground response to the burn.

Within this grassland, prescribed burning appears to affect the structure of surface soil layers. Soil structure influences water infiltration, runoff, and erosion through aggregate size distribution and stability (Armstrong and Stein 1996, Blackburn et al. 1992, Granger 1992). First year increases in bulk density and lowered water intake rates within the burned plots infer a treatment effect on the stability of surface soil layers, yet results indicate aggregate stability did not differ after treatment. The removal of vegetation cover promotes the erosion process by exposing surface aggregates and structures to destruction by raindrop impact (Bennett 1974, Hester et al. 1997, Smith et al. 1990, Thurow et al. 1986). Observed increases in bulk density and decreases in water intake rates may be a function of fine particle illuviation and subsequent surface sealing, common to bare or sparsely vegetated surfaces (Bresson and Cadot 1992, Stolte et al. 1997).

By the second year, aggregate stability was lower within the burned plots compared to the unburned. However, high variability between means did not allow for significant differences to be observed. Greater bulk density, runoff volumes and sediment production were also observed.

The decline in aggregate stability may be a function of low levels of soil organic carbon (SOC), as well as declines in root growth and rhizosphere activity. As soil organic matter may be considered limiting in the more arid ecosystems of the southwestern U.S. (Whitford 1986), its removal through burning may result in the loss of water stable aggregates (Tate 1987). However, changes in aggregate stability and bulk density were not found correlated to the paucity of SOC, which was on average 1.1% (O'Dea 2000). Nor were there significant differences in SOC levels among treatments in either year. While changes in SOC levels do not appear to fully answer questions regarding declines in aggregate stability, reductions in below-ground plant growth may. The mechanical binding of soil particles and aggregates by roots, as well as the production of root exudates are important mechanisms by which soil aggregates are stabilized (Tisdall and Oades 1982). Slow grass regrowth within the burn treatments, along with evidence of pedestal formation and post-treatment death of some remnant individuals may have resulted in the overall decline of root biomass, growth rates, and exudate production. However, these root properties were not measured in this study, and this hypothesis was not tested.

First year comparisons of burn effects showed declines in water intake rates on burned plots appeared to be the result of surface sealing associated with the loss of vegetation cover. Second year declines, while possibly affected by a surface seal may also be the result of structural changes to surface soil layers. More specifically, the result of a decline in aggregate stability affiliated with the decline in perennial grass cover. For both years, the declines in intake rates and perennial grass cover resulted in increased sediment yield from the burned plots, but not in runoff volumes.

Perturbation of the southern Arizona perennial grasslands, such as with spring-time burning, whether by lightning ignitions or prescription, appears to create an environment that enhances typical erosion rates. Natural erosion rates are enhanced following burning because of the loss of vegetation cover and the high intensity of the unpredictable convective summer storms. In this study, with the use of artificial erosion (ie. rainfall simulation), soil loss in two-thirds of the simulation x burn plots had exceeded their T-values or soil loss tolerances of 11.2 tonnes ha<sup>-1</sup> year<sup>-1</sup> (5 tons acre<sup>-1</sup> year<sup>-1</sup>) by the fall of 1998 (Richardson et al. 1979). Unfortunately,

neither experimental method nor weather safety concerns allowed the measurement of the simulation's sediment contributions or the analysis of the effects of the consecutive storms on the sediment yields observed in the first season. However, it may be inferred that if like storms commonly occur, they may have the potential to initiate a large erosion event, which in turn may extend the long-term effects of prescribed burning. Moreover, we were not able to determine if the effect of the rainfall simulation was an increase in sediment yield that would correspond to the site receiving 30% more summer rainfall, or if the simulation itself created unaccounted for factors that confounded the study's results. However, it may be inferred from study results that the amount of soil loss on unburned areas (i.e., simulation only plots) is similar to what that area would lose had it received 30% more summer rainfall.

## Summary

The perennial grasslands of southern Arizona have historically burned primarily in the late spring. Fires are ignited by the dry lightning strikes that precede the summer convective storms, the major source precipitation in the grasslands. Land managers attempting to reintroduce fire into these systems often ignite fires in the spring to mimic the natural fire regime reported for the semi-desert grasslands (Wright and Bailey 1982). Following prescribed burning, results indicate that the reduction in perennial grass cover strongly contributes to increases in runoff volumes and sediment yield the first post-burn year. However, without further disturbance the site appears to return to erosion and runoff rates observed in unburned conditions, even without vegetation cover reaching pre-burn levels. Initial declines in surface water intake rates were attributed to sediment alluviation and surface sealing, the affects of which appeared to disappear after the first year. The adverse affects of prescribed burning occurred after large (i.e. rainfall simulation for this study) or sequential storm events, with the interaction of the burn and storms creating an environment of increased erosion. The interaction appeared to adversely affect plant and soil structural components, perpetuating above-average runoff and erosion events in relation to unburned conditions. The stochastic nature of the summer storms (i.e., return intervals, intensity, and timing) contributes to the risks associated


with prescribed burning, and therefore there is a need for these storm effects to be investigated further to provide information for the planning of prescribed burns.

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# A method for determining the onset year of intense browsing

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## Abstract

A survey based on browsing related architectures indicated that browsing level had increased at the Mt. Haggin Wildlife Management Area. We describe a technique for determining the year in which the increase in browsing level occurred. The technique is based on the analysis of stems old enough to have experienced the early period of light browsing; the onset year of intense browsing was determined by using dendrochronology to date the formation of twig clusters produced by intense browsing. Stems from 20 Geyer willow (*Salix geyeriana* Anderss.) plants were analyzed from each of 6 study sites. Mean onset years at the 6 sites ranged from 1983.1 to 1988.4; the mean onset year for all 6 sites was  $1985.4 \pm 0.5$  SE ( $N = 120$ ). The reconstructed history was used to evaluate the relationship between moose (*Alces alces*) number and browse trend. From 1976 to 2000, the winter trend census of moose increased from 7 to 56. The onset of intense browsing in 1985 occurred when 23 moose were counted.

**Key Words:** *Alces alces*, architecture, browse-use history, moose, ungulate, willow

A browsing history describes levels of browsing that existed over time. Such histories have many management applications. For example, a browsing history has contributed to philosophical discussions on "what is natural" in Yellowstone National Park (YNP) (Despain et al. 1986, Kay and Wagner 1994, Keigley and Wagner 1998). Where there is historic information on ungulate population size, a historic browse condition can be associated with the ungulate population size that was present at the time (Keigley 1997b, 1998); the reconstructed history may allow a manager to attribute a historic browse condition to one ungulate species rather than another.

Despite the potential management applications, the widespread use of browsing histories is uncommon. In part, the uncommon use may be due to the relatively youthful state of technique development. As we describe below, the application of different techniques has resulted in the inconsistent reconstruction of browsing histories. In part, uncommon use may arise out of lack of appreciation for the potential management applications.

There are 4 principal sources of information from which to reconstruct browse-use histories: 1) scientific reports that document browse use at different points in time, 2) comparison of photographs taken at different points in time, 3) age structure

## Resumen

Un reconocimiento basado en arquitecturas relacionadas de ramoneo indicó que el nivel de ramoneo en el Área de Manejo de Fauna Silvestre Mt. Haggin ha aumentado. Describimos las técnicas para determinar el año en el que ocurrió el nivel de ramoneo aumento. La técnica es basada en el análisis de los tallos lo suficientemente viejos para haber experimentado el periodo inicial del ramoneo ligero; el año inicial del ramoneo intenso se determinó usando la dendrocronología para determinar la fecha de formación de los racimos de ramas producidas por el ramoneo intenso. Se analizaron tallos de 20 plantas de "Geyer willow" (*Salix geyeriana* Anderss.) colectadas en cada uno de los 6 sitios de estudio. La media de los años iniciales en los 6 sitios varió de 1983.1 a 1988.4; la media del año final para todos los sitios fue  $1985.4 \pm 0.5$  SE ( $N = 120$ ). La historia reconstruida se usó para evaluar la relación entre el número de Alces (*alces*) y la tendencia de ramoneo. De 1976 al 2000, la tendencia invernal del censo de alces se incrementó de 7 a 56. El inicio del ramoneo intensivo en 1985 ocurrió cuando se contaron 23 alces.

analysis, and 4) the analysis of browsing-related architectures. Browse-use histories typically draw on a combination of sources. For example, Houston (1982) reconstructed a browse-use history of the northern elk winter range of YNP based on scientific reports and the comparison of historic photographs with more-recent photographs. Kay (1990) reconstructed a browse-use history of aspen (*Populus tremuloides* Michx.) based on scientific reports, photographs, and age structure analysis. Working in the same area as Houston and Kay, Romme et al. (1995) and Ripple et al. (2001) reconstructed a browsing history of aspen based on age structure. Keigley (1998) reconstructed a browse-use history of a cottonwood stand (*Populus angustifolia* James) on the YNP northern range based on the dendrochronologic analysis of browsing related architectures. An architecture-based browse-use history of a second YNP cottonwood stand was reconstructed using a combination of height and age data (Keigley 1997b).

Browsing-related scientific reports describe firsthand accounts of browse use. In the Yellowstone National Park (YNP) reports over the period 1935–1957 primarily include descriptions of the effect of browsing on growth form and mortality; beginning in 1958, areal distribution and plant height were measured (unpublished data, YNP). The use of reports for history reconstruction is limited to locations for which information was recorded. In an area such as YNP, much information is available, but in many areas, browse-related studies were not conducted historically.

A comparison of photographs taken at different points in time provides a visual perspective of browse use. As in the case of sci-

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entific reports, the use of photographs is limited to sites for which they are available. The interpretation of historic photographs is subjective, and as a result, interpretations may vary. For example, in an examination of early photographs taken in YNP, Houston (1982) found that conifers were highlined, indicating that intense browsing had occurred since the earliest EuroAmerican presence. In an examination of the same photographs, Kay and Wagner (1994) found that conifers were not highlined indicating that, prior to the establishment of YNP in 1872, browsing was light.

While reports and photographs provide a perspective on gross historic changes, neither source of information provides the resolution of data with which to reconstruct a year-by-year history of browse use. To accomplish this requires the ability to document the year-by-year state of a parameter over an extended period. One parameter in common use is the growth of an aspen stem to breast height. Based on the assumption that growth to breast height corresponds to a year of light browsing pressure, browsing histories are reconstructed by describing the age classes of stems that are present at a site (e.g., Kay 1990, Romme et al. 1995, Ripple et al. 2001).

In an age-structure-based history reconstruction, growth to breast height is a tangible form of evidence, while the evidence for intense browsing is intangible (i.e., intense browsing is inferred from the absence of an age class). The intangible nature of this evidence can lead to difficulties in 2 ways. First, evidence of growth may be missed. Based on the absence of older age-class aspen, Romme et al. (1995) concluded that aspen were intensely browsed prior to the 1870s. In a further examination of YNP aspen, Ripple et al. (2001) discovered evidence for these older age classes, leading to an interpretation that aspen was lightly browsed during that period. Even if evidence for the older age classes had not been found, the significance of that absence would be uncertain because factors unrelated to browsing may have been responsible for the lack of recruitment.

Architectural analysis is the process of reconstructing past browsing conditions based on the dendrochronologic dating of morphologic features; some features are produced by light browsing, others by intense browsing (Keigley 1997a, Keigley and Frisina 1998). The morphologic features provide tangible evidence of both light and intense levels of browsing that occurred in the past (Keigley 1997b, 1998).

We describe a method for reconstructing a history of browsing applicable to sites where browsing pressure has increased from a light-to-moderate level to an intense level. We describe how, during a preliminary reconnaissance, a manager can use gross architectural evidence to identify the condition that browsing intensity increased at some time in the past. We then describe methods for determining the year in which the increase occurred. The paper also describes an application of that reconstructed history.

## Materials and Methods

### Study Area

The study took place on a portion of the 22,743-ha Mt. Haggin Wildlife Management Area located in southwest Montana about 19 km south of the town Anaconda (45° 58' N, 113° 4' W). The study area consists of a combination of wet and dry meadows. Willows (*Salix* spp.) are common along numerous stream courses and in wide riparian areas created by beaver dams. Elevation of the study area is about 1900 meters; annual precipitation is about 51 cm (Frisina 1992).

Prior to 1976, the area was privately owned (Newell and Ellis 1982). Domestic livestock grazed pastures continuously and intensively; willow was sprayed, dozer-piled, and burned to create more grassland for livestock. In 1976, the Montana Fish,

Wildlife & Parks (MFWP) purchased the land and established Mt. Haggin Wildlife Management Area to provide habitat for wildlife and public recreational opportunities (Frisina 1982). The reduction of willow stopped. Populations of moose (*Alces alces* L.), elk (*Cervus elaphus* L.), mule deer (*Odocoileus hemionus* Merriam), and pronghorn antelope (*Antilocapra americana* Ord) increased (Frisina 1982, Kuntz 1993). Recently, whitetail deer (*Odocoileus virginianus* Merriam) began using the study area during the summer.

Moose are the only large ungulate present on the study area during winter; they concentrate in willow bottoms as snow accumulates. Deer, elk, and antelope inhabit the area during snow-free months, when herbaceous plants are generally preferred and all habitat types are available for foraging. After establishment of the wildlife management area, livestock numbers were reduced (Frisina 1992). A restoration grazing system was established in 1984, in which cattle are allowed access to a pasture during the growing season once every third year. Under the new grazing system, livestock were excluded from a 30 ha area; since that time, this area has only been used by wildlife.

### Detecting an increase in browsing pressure

Keigley and Frisina (1998) distinguish between 2 browsing levels: a) light-to-moderate, and b) intense. Light-to-moder-

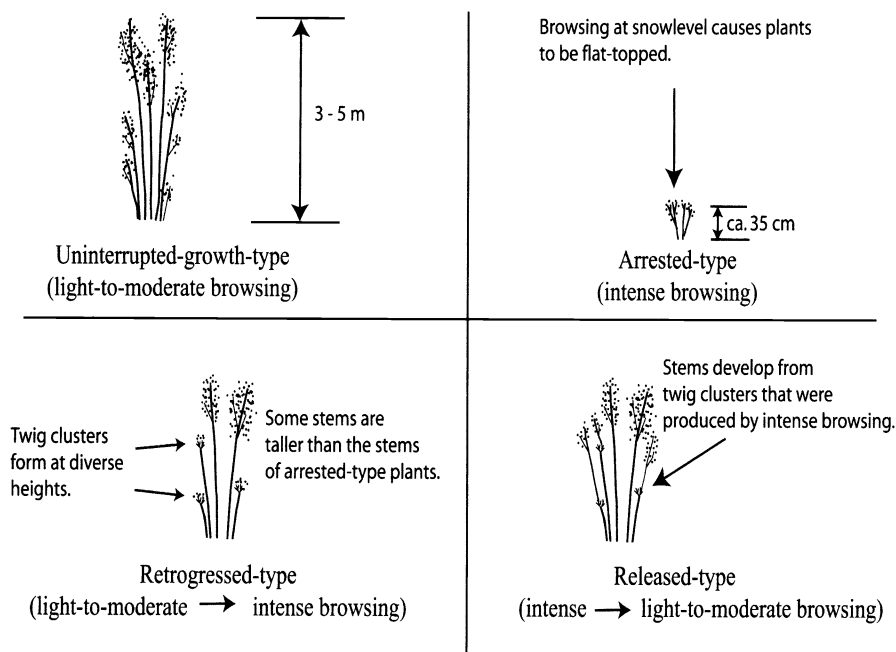
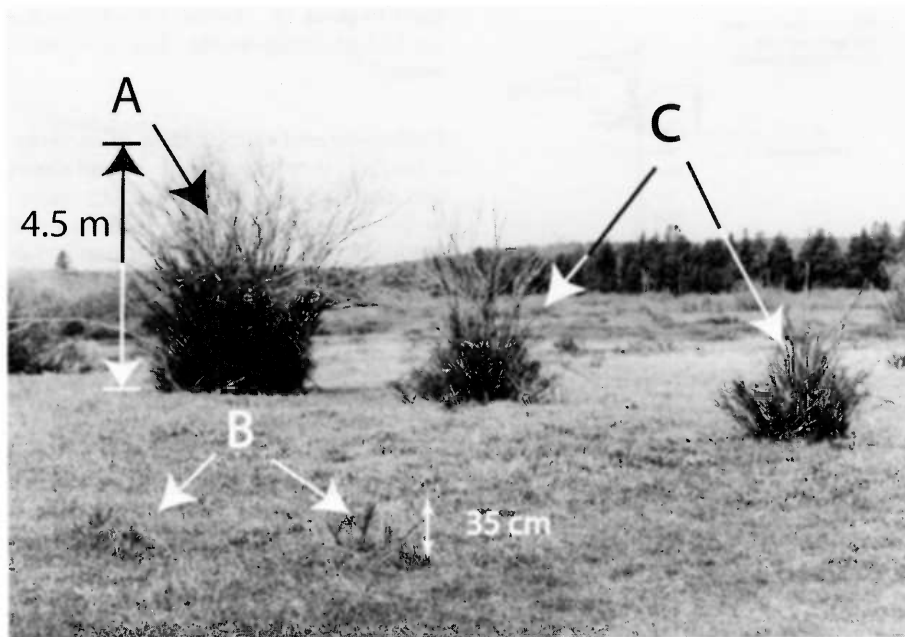


Fig. 1. Four architecture types that are produced by 4 browsing regimes. The architectures are produced during the time that the terminal leader grows within the browse zone.



**Fig. 2.** Older willow plants (A) have grown to heights of 4.5 m tall, while the youngest plants (B) are browsed to within 35 cm above ground level. The ability of the older plants to grow taller than 35 cm indicates that browsing was less intense in the past. At the time browsing level increased, many stems on plant A were out of ungulate reach. The stems of plants of intermediate age (C) were browsed at the height present at the time the increase in browsing pressure occurred. Plants A and C have retrogressed-type architecture; plant B has arrested-type architecture.

ate browsing is defined to occur when current-year-growth develops from the previous-year's-growth. Intense browsing is defined to occur when browsing causes the death of a complete annual segment. In this case, current-year-growth develops from a segment that is older than the previous-year's-growth.

At the whole-plant level, the effect of browsing is expressed in the form of 4 general types of architectures (Fig. 1). The architectures are produced during the period of time that the terminal leader is exposed to browsing. The 4 architecture-types correspond with 4 browsing regimes:

- 1) Uninterrupted-growth-type architecture is produced by light-to-moderate browsing as the terminal leader grows through the browse zone.
- 2) Arrested-type architecture is produced by intense browsing since establishment.
- 3) Retrogressed-type architecture is produced by a change from light-to-moderate browsing to intense browsing.
- 4) Released-type architecture is produced by a change from intense browsing to light-to-moderate browsing.

In general, similar-aged plants of the same species and site should have experienced a similar level of browsing over their lifetime, and should have the same architecture. On sites where browsing

pressure has changed, plants of different age may have different architectures; those architectures should express a similar history. For example, at a site where browsing pressure has increased from light-to-moderate to intense, one might find older retrogressed-type plants and younger arrested-type plants. Given the difference in plant ages, both architectures are consistent with an increase in browsing pressure. At Mt. Haggin, the relationship between willow age and architecture indicated such a history (Fig. 2). The objective of this study was to determine the year in which the increase occurred.

Geyer willow (*Salix geyeriana* Anderss.) is widely distributed and is substantially used by ungulates at Mt. Haggin. We stratified segments of Deep Creek, Sullivan Creek, and Dry Creek into 6 sample sites; the sites were distributed along a total distance of 3 km. Using the methods described below, we determined the onset year of intense browsing of Geyer willow for each of the six, 0.2 ha sample sites.

### Determining the onset year of intense browsing

#### Overview

The stem morphology produced by light-to-moderate browsing is distinctly different from the morphology produced

by intense browsing. Stems that have experienced an increase in browsing level would have the light-to-moderate browsing morphology at the base (where the stem first elongated) and intense-browsing morphology at the distal end. Using dendrochronology, we determined the year in which those morphologic changes occurred.

The stem morphologies are produced as follows. The annual segments of a light-to-moderately browsed stem develop from stem segments produced during the previous year. The new segment may develop either from the previous-year's terminal bud or, if that bud aborted, from lateral buds slightly lower down the stem. Ungulates typically consume segments produced the most recent growing season (current-year-growth). The browsing removes the terminal bud insuring that, if subsequent growth occurs, it must arise by activation of a lateral bud. The stem dies between the point where it was bitten and the point where new growth emerges the following growing season. If ungulates repeatedly consume a minor portion of each year's current-year-growth, the stem grows in a zigzag manner, with dead stubs located at intervals on the stem.

Under heavy browsing pressure, ungulates consume major portions of current-year-growth, leaving behind a stub of the current annual segment. Because the dead stub is tough and unpalatable, it mechanically protects stems that may subsequently grow beneath it. If ungulates repeatedly browse current-year-growth to a point even with the dead stubs from preceding years, a compact cluster of twigs develops (Fig. 3). Browsed twigs are abruptly terminated by bite marks that are easily distinguishable from other sources of disturbance such as disease or insect infestation. A compact cluster of twigs with bite marks is morphologic evidence of intense browsing. We used dendrochronology to determine the year in which twig clusters formed.

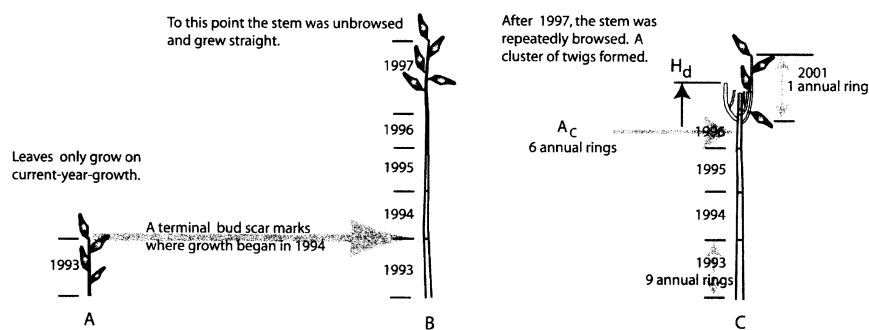
#### Determining the year of twig cluster formation

The dendrochronologic dating of morphologic features involves determining the year in which a given stem segment was a terminal leader. For a stem segment collected from the beginning of a growing season through the end of the calendar year, the formula for determining the year of initial elongation is:

$$Y_E = \text{Collection year} - A + 1, \quad (1)$$

where  $Y_E$  is the year that the stem elongated and  $A$  is the number of annual rings in





**Fig. 3. Stem with live twig cluster. The year of browsing can be directly determined. Stems A, B, and C show how plant would appear in during the growing seasons of 1993, 1997, and 2000, respectively.**

the stem segment. For example, a current-year-growth segment collected in August 2001 would have a single annual ring. The year of elongation is:

$$Y_E = 2001 - 1 + 1 = 2001. \quad (2)$$

The +1 corrects for the annual ring produced during the current calendar year. If the segment had 9 annual rings,  $Y_E$  would equal 1993. To determine the year of elongation when the stem segment is collected the next calendar year, but before the growing season (e.g., in February), the +1 correction would not be made. The stem segment must be live at the time of collection.

Stem C in Fig. 3 records 2 periods: a period of light-to-moderate browsing (in which the lower stem grew straight) and a period of intense browsing (in which the cluster of twigs formed). Using the formula above, the number of annual rings just below the twig cluster ( $A_C$ ) can be used to determine the last year in which the terminal leader grew under light-to-moderate browsing ( $Y_C = \text{Collection year} - A_C + 1$ ). Because the stem at point  $A_C$  is live (and by our definition, light-to-moderately browsed), we assume that intense browsing began the following year ( $Y_I = Y_C + 1$ ). To use this method of dating, the twig cluster must be live; we refer to it below as the "live twig cluster method."

Protracted browsing often causes stem dieback of the original stem, with the development of new terminal leaders from the base of the stem (Fig. 4). Because the base of the twig cluster is dead, the annual rings there cannot be directly associated with a given year. To make that association, one must link the dead twig cluster to a live segment of the stem. The onset year of intense browsing is determined from 3 sections:

1. Section L from the primary stem just below the point where the live secondary stem originates. The year that this stem segment was a terminal

leader is determined from the number of annual rings. Ring development in section L may be asymmetrical depending on how close the section is to the dead primary stem above it; when counting annual rings, care must be taken to include those produced during the most recent growing season.

2. Section DB from the dead primary stem immediately above the point where the live secondary stem originates. An assumption is made that the stem at point DB was a terminal leader the same year as at point L. When making collections, the length between points L and DB was typically 2–5 cm, so it is likely that the sections were produced the same growing season.
3. Section DC from the base of the dead twig cluster. The difference in the number of annual rings in sections DB and DC indicates the number of years it took for the stem to grow to the base of the cluster. It is assumed that cluster formation began the following year.

The year of twig cluster formation is calculated as follows:

$$Y_I = [\text{Collection year} - A_L + 1] + [A_{DB} - A_{DC}] + 1. \quad (3)$$

The first bracketed term indicates the year that the linking section was a terminal leader;  $A_L$  is the number of annual rings in the linking segment. As above, +1 may or may not be added depending on when the collection was made. The second term,  $[A_{DB} - A_{DC}]$ , indicates the number of years it took the stem to grow to the base of the cluster. The first 2 terms added together indicate the year that the stem at the base of the cluster was a terminal leader. As above, the second +1 is added because browsing intensity is assumed to have increased the year after the stem

grew to point DC. Below we refer to this method of dating as the "linked segment method."

### Collection and examination of sections

Sections were collected with hand shears and examined under a dissecting microscope. Sections of live segments were not sanded; sanding of soft (moist) wood tended to collapse the vessel walls, obscuring the view. In cases where the annual rings were not clear, a thin slice was removed with a razor blade. Sections of dry, dead segments were sanded; the view was clarified with a razor as necessary.

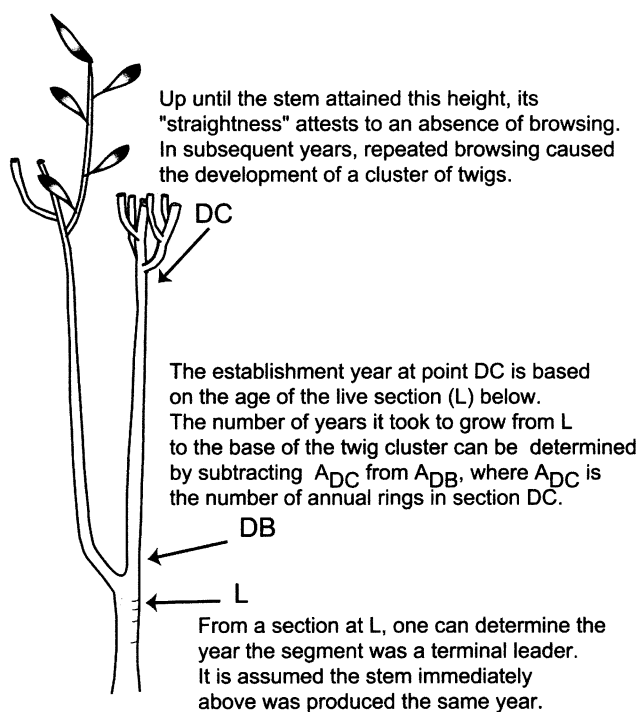
### Selection of stems for dating

We determined the onset year of intense browsing from 20 Geyer willow stems at each of the 6 study sites. Each stem was collected from a different shrub.

At sites where browsing level increases from light-to-moderate to intense, all shrubs will eventually have either arrested- or retrogressed-type architecture. Plants with arrested-type architecture may be established after the increase occurred. The dating of twig cluster formation on such plants would indicate a time subsequent to that establishment, not when the initial area-wide increase in browsing occurred. The year of the area-wide increase is only recorded in stems old enough to have experienced both the early period of light-to-moderate browsing and the subsequent period of intense browsing. Such stems are found on retrogressed-type plants.

With respect to suitability for dating, retrogressed-type shrubs can be placed in 2 categories. In one category are retrogressed-type plants that, at the time browsing level increased, had stems that were tall enough to escape ungulate browsing (ca 2.5); these tall stems would not develop morphologic evidence of the increased browsing. After browsing increased, such shrubs would continue to produce stems, some of which would be mechanically protected from browsing within the interior of the shrub. Stems that were within ungulate reach at the time browsing increased would develop twig clusters indicative of the onset year. However, stems that have been mechanically protected within the interior of the shrub may elongate beyond mechanical protection and develop twig clusters. These clusters would not indicate the onset year. Because there is no sure way to distinguish between those possibilities, we avoided this category of retrogressed-type plant.

The second category of retrogressed-type plants consist of those whose tallest termi-



**Fig. 4.** Stem in which dieback has occurred; the initial twig cluster is dead. To determine the initial year of browsing, the dead twig cluster must be linked to a live stem segment.

nal leaders were within the browse zone at the time browsing increased. When possible, we selected retrogressed-type plants that were 75–200 cm tall; height was measured to the tip of dead twigs in the cluster ( $H_d$  in Fig. 3). The 200 cm height is well within the reach of moose. We were concerned that plants less than 75 cm tall might be too young to have experienced the area-wide increase in browsing. Stems within the 75–200 cm height range were fully exposed to browsing, and were likely old enough to have been present when the area-wide increase occurred. When enough plants within this height range could not be located within the sample area, stems from plants somewhat shorter than 75 cm were included in the sample.

We sampled the oldest live stem from the selected plant. We assessed stem age in 2 ways. First, we selected stems having large basal girth in comparison to other stems in the shrub. Second, when possible, we selected stems having dead twig clusters. Because protracted browsing kills the upper stem, stems with dead twig clusters are most likely to record the earliest browsing events. The effect of including stems shorter than 75 cm tall and stems with live twig clusters was analyzed by comparing the results of the full data set with results obtained when plants not meeting the above criteria were removed.

## Results and Discussion

### Dating the onset year of intense browsing

In a preliminary survey we found that all Geyer willow exposed to browsing had either arrested- or retrogressed-type architecture. The lack of uninterrupted-growth-type individuals indicated that the current browsing level was intense. Older Geyer willows had retrogressed-type architecture, while younger plants had arrested-type architecture (see Fig. 2). This relationship between age and architecture indicates that browsing level has increased. Using the methods described above, we determined that the onset year of intense browsing averaged across sites was  $1985.4 \pm 0.5$  SE ( $N = 120$ ) (Table 1).

**Table 1.** Location of sample sites, year intense browsing began, and lifespan of heavily browsed twigs.  $N = 20$ .

Site	Year intense browsing began		Age at base of dead stem	
	Mean $\pm$ SE $N = 20$		Mean $\pm$ SE $N = 20$	
			(Years)	
1	1986.9	$\pm 0.7$	10.6	$\pm 0.5$
2	1988.4	$\pm 0.9$	8.2	$\pm 0.7$
3	1983.1	$\pm 1.5$	10.2	$\pm 0.8$
4	1983.7	$\pm 0.9$	11.4	$\pm 0.5$
5	1986.9	$\pm 1.1$	10.1	$\pm 0.7$
6	1983.6	$\pm 1.3$	11.5	$\pm 0.7$

### Effect of including live twig clusters and plants less than 70 cm tall

For the following reason, we were concerned that the use of live twig clusters might skew the result to a more-recent date. The formation of twig clusters indicates when a stem was first exposed to intense browsing. In the case of the oldest stems, twig cluster formation indicates an area-wide increase in browsing pressure. In the case of younger stems, such as those with live twig clusters, cluster formation may indicate when the stem grew taller than some form of mechanical protection. Out of the total sample of 120, 4 dates were obtained from stems with live twig clusters. We examined the effect of including live-twig-cluster data by excluding those data and recalculating a pooled mean. The resulting date was identical:  $1985.4 \pm 0.5$  ( $\pm$  SE).

The average age of the stem at the base of the dead twig clusters was  $10.2 \pm 0.3$  years ( $\pm$  SE) (Table 1). This age suggests that live twig clusters may reliably indicate the onset of intense browsing for periods up to about 10 years. To document an onset of browsing that occurred more than 10 years in the past, one should sample stems with dead twig clusters and determine the onset date by the linked segment method.

We were concerned about the potential effect of including plants less than 75 cm tall. Because the age of the plants was not known at the time of sampling, we were concerned that short plants might be too young to accurately reflect the earliest increase in browsing pressure. We examined the effect of sampling 11 such plants by excluding them from the data set. The resulting mean onset year was  $1985.4 \pm 0.5$  SE, a value identical to those above.

### Comparison with other methods of history reconstruction

Architectural analysis and age structure analysis can be used to document past levels of browsing at any site where shrubs of suitable age are present; scientific reports

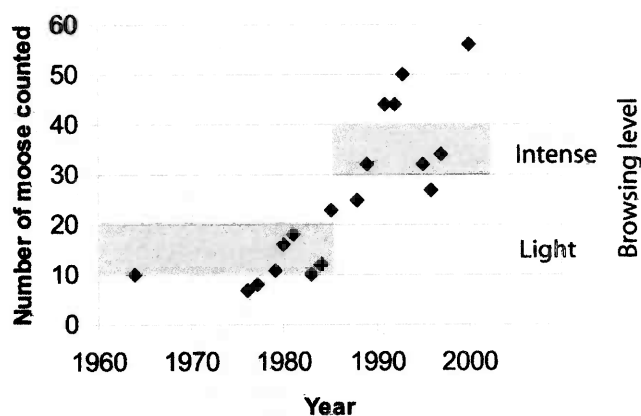


Fig. 5. Relationship between moose census number and browsing intensity. Based on the pooled data, browsing intensity changed from a light-to-moderate level to an intense level in 1985. The horizontal line indicates the range of onset dates that occurred over the 6 study sites.

and photographs can only be used where this information was recorded in the past. Age structure analysis can only document periods of light browsing in which stems grew; because the absence of an age class can be caused by multiple factors, periods of intense browsing and transitions in browsing levels cannot be dated. Architectural analysis dates the transition from a morphology produced by light browsing to a morphology produced by intense browsing; as a result, periods of intense browsing are documented and a history is reconstructed that has fewer gaps.

The technique described above provides a repeatable method of determining a date at a given site. Because ungulates prefer some browse species over others, the date applies only to the browse species on which it was based. By measuring the onset dates of other species, one can examine interspecific patterns of browse use.

### An application of the reconstructed history

The study area lies within Montana Fish, Wildlife and Parks (MFWP) moose Hunting District 325. Moose population data collected during winter aerial surveys of Hunting District 325 from 1964 through 2000 were used to determine population trend (Fig. 5). In any census, the data represent the actual number of moose observed; the total number of moose in the population is greater (Anderson and Lindzey 1996). We view the census data as an index of trend.

Three lines of evidence indicate that moose are primarily responsible for the recent impacts on browse plants. First, heavy browsing occurs at a site where livestock have been excluded since 1984 (Site 1). Browsing within this 30 ha area must

have been due to wild ungulates. Second, the average onset years for intense browsing (1983–1988) coincide with the period in which the HD 325 moose population was increasing most dramatically. During this period, a grazing system was established that lessened the impact of livestock (Frisina 1992). Third, because of mid-winter snow conditions, moose are the only ungulate to occupy the area year-round. These factors suggest that moose played an important role at all 6 sites.

The lack of willow with uninterrupted-growth type architecture suggests that the willow carr is in the process of conversion to a meadow-like condition. The fact that this conversion began during period of a moose population increase suggests that, to reverse the trend, the population must be reduced.

The reconstructed history indicates the magnitude of the required reduction. The increase in browsing pressure first occurred in 1983 (at Site 3) when 10 moose were counted. The latest year to mark the increase in browsing was 1988 (at Site 2) when 25 moose were counted. In the mean onset year of 1985, 23 moose were counted. We conclude that, to reverse the trend to a meadow-like condition, the moose population must be reduced by about half. In 2000, the moose harvest quota was increased by 50%. A monitoring program has been instituted to determine the effect of moose reductions.

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# Changes in shrub fecundity in fourwing saltbush browsed by cattle

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## Abstract

Shrub fecundity is critical to long term persistence of fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) populations at our research site on the shortgrass steppe in Colorado. We conducted a 2-year experiment to test hypotheses concerning the impact of cattle-browsing on fecundity-related variables in fourwing saltbush. Protection from cattle browsing was significantly associated with floral phenotype shifts toward femaleness, occurring mostly in monocious shrubs (1% and 13% of grazed and protected shrubs, respectively). Sex shifts observed at the individual shrub level did not translate into detectable alterations of sex ratios at the pasture level. Shrubs exhibiting no flowers were considerably more abundant in browsed pastures (26.5%) than in exclosures (1.5%). Nonflowering occurred as frequently in female (3.6%) as it did in male (1.8%) phenotypes. Percent utricule fill was not related to previous year's cattle browsing regime (39% and 44% in protected and grazed shrubs, respectively) but rather to crown volume of the fruiting female and to the gender of and distance to the nearest neighboring shrub. The influence of cattle-browsing on reproductive output of fourwing saltbush occurred mainly through its inhibition of flowering.

**Key Words:** *Atriplex canescens*, sex change, nonflowering, utricule fill, cattle browsing

Herbivores can affect plant fecundity (sensu Richards [1997]) in a number of ways. In most cases they reduce or suppress flowering and fruiting, yet they can also stimulate it by promoting compensatory fruiting responses (Paige and Whitham 1987, Hendrix 1988, Lowenberg 1994, Crawley 1997). Fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) populations at our research site on the shortgrass steppe in Colorado appear to persist mainly through sexual reproduction, therefore, factors that reduce shrub fecundity can have significant effects on the long term persistence of this critical forage resource.

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## Resumen

La subsistencia de poblaciones de *Atriplex canescens* (Pursh) Nutt. en nuestro sitio de estudio en la estepa de pastos cortos de Colorado depende en gran medida de los índices de fecundidad de los individuos que las componen. Se condujo un experimento de 2 años de duración para poner a prueba hipótesis relacionadas con el impacto del ramoneo bovino sobre variables asociadas a la fecundidad de arbustos de *A. canescens*. La exclusión del ramoneo bovino estuvo significativamente asociada a cambios de fenotipo floral de arbustos masculinos o monoicos que produjeron flores femeninas (13% y 1% en clausuras y potreros pastoreados, respectivamente). Los cambios en el fenotipo sexual observados a nivel de individuos no se tradujeron en alteraciones detectables en las proporciones fenotípicas de sexos a nivel de potreros. La ausencia de floración se observó en mayores proporciones en arbustos ramoneados (26,5%) que en arbustos en clausuras (1,5%). Dicho fenómeno ocurrió en frecuencias similares en fenotipos femeninos (3,6%) y masculinos (1,8%). El porcentaje de frutos llenos en arbustos hembra no estuvo asociado al régimen de ramoneo del año anterior (39% y 44% en arbustos protegidos y ramoneados, respectivamente) sino al volumen de copa de la hembra evaluada y al sexo y la distancia del arbusto más cercano. El ramoneo bovino afectó el desempeño reproductivo de arbustos de *A. canescens* principalmente inhibiendo de la floración.

Stresses such as severe winters, droughts, crowding (in transplant gardens), and heavy seed production in the previous growing season may trigger sex shifts toward maleness in sexually labile fourwing saltbush shrubs (McArthur 1977, McArthur et al. 1978, 1992, McArthur and Freeman 1982). Since fourwing saltbush has been described as being fairly sensitive to defoliation (Trlica et al. 1977, Pieper and Donart 1978, Price et al. 1989), herbivory may be a significant source of stress to this shrub. It is not known, however, whether cattle browsing can trigger floral phenotype shifts toward maleness in this species.

Besides inducing sex phenotype shifts, herbivory could have other equally important effects on shrub fecundity either by suppressing flowering or reducing fruit fill (Hendrix 1988, Milton 1995). Nonflowering occurs frequently in dioecious species of the genus *Atriplex*, and is considerably more common in male and female genotypes of fourwing saltbush than in monocious genotypes (Freeman and McArthur 1984), however, the relation

between nonflowering and cattle-browsing is largely ignored. Artificial defoliation is known to reduce seed set of fourwing saltbush (Trlica et al. 1977), and while utricule fill is generally low (40 to 60% [Springfield 1970]), the direct effects of cattle-browsing on viable utricule production are unknown.

We conducted an experiment to test hypotheses related to the impacts of cattle-browsing on sex expression, suppression of flowering, and fruit fill (sensu Springfield 1970) of the subdioecious tetraploid shrub fourwing saltbush. We tested the hypotheses that: 1) cattle-browsing would produce sex shifts toward maleness in fourwing saltbush, and that release from browsing would promote shifts in the opposite direction; 2) increasing levels of cattle-browsing would promote higher frequency of nonflowering shrubs; and 3) increasing levels of browsing by cattle would promote lower utricule fill percentages.

## Materials and Methods

### Experimental design and data collection

Our study site was located on the USDA-ARS Central Plains Experimental Range (CPER), approximately 60 km northeast of Fort Collins, Colo. (40°49' N 107° 47'W) at 1,650 m elevation. We conducted our research on a floodplain area, close to Owl Creek. Major soil types of our study site were Remmit loamy sands and Edgar loams. Fourwing saltbush, blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths) and western wheatgrass (*Agropyron smithii* Rydb.), are the dominant plant species at the site (Liang et al. 1989). Mean annual precipitation is 320 mm, 50 to 80% of which occurs between April and September (Hart and Ashby 1998). Rainfall during and immediately before our experiments was above the historical average, particularly in 1997 (559 mm). Late spring and summer rainfall (May–September) was also considerably higher in 1997 (436 mm) relative to 1996 (294 mm) and 1998 (275 mm).

We measured sex change, percent flowering and utricule fill on fourwing saltbush shrubs in 14, 0.5 ha experimental grazing pastures. The pastures were built in the fall of 1996 in 2 parallel blocks of 7 adjacent units each, within a pasture that had been moderately browsed by cattle in winter for approximately 20 years. At the

beginning of the experiment, pastures within a block were assigned randomly to each treatment (3 seasons x 2 stocking densities + ungrazed control). Randomization was performed within each block of experimental pastures, subject to the constraint that no 2 adjacent pastures were grazed on the same date. Four different pastures were browsed with cattle for periods of 4 days in winter (January), early spring (April), and late summer (September) in 1997 and 1998. At each season, 2 pastures were browsed moderately with 4 heifers (weighing 400 to 520 kg) and 2 were browsed heavily with 12 heifers. Moderate stocking densities (32 heifer days ha<sup>-1</sup>) simulated historical moderate grazing intensity used at the CPER (approximately 5.3 ha AUM-1 over a 6 month grazing season, 34 AU days ha<sup>-1</sup>). Heavy stocking rates were set at 3 times (96 heifer days ha<sup>-1</sup>) the moderate rates to ensure levels of defoliation likely to promote shrub fecundity alterations (Buwai and Trlica 1977, Trlica et al. 1977). Cattle used in the experiments were randomly assigned to the 0.5-ha pastures and were always taken from herds grazing pastures with abundant fourwing saltbush, to minimize dietary and social adjustment.

Twenty female and 20 male shrubs were randomly selected and labeled in each 0.5-ha grazing pasture prior to the grazing treatment. In the second year (1998), we marked 20 randomly selected monocious shrubs as well. We were prevented from identifying monocious shrubs in the first season (1997) because inflorescences were badly damaged by a hail storm that occurred while we were in the process of marking shrubs in 1996. Shrubs with pistillate flowers were classified as females, those with staminate flowers were classified as males, and those with close-to-equal proportions of pistillate and staminate flowers were considered monocious. Occasionally, at the end of the flowering phase, we found solitary utricles on shrubs that had been classified as males. These were possibly shrubs that had flowered as males, yet carried sexually labile genotypes. The identification of shrub genotype, however, went beyond the scope of this study so our classification was qualitative and made exclusively on the basis of the observed phenotype. On each shrub we measured utilization of marked leaders by cattle, greatest crown diameter, crown diameter perpendicular to the greatest diameter, crown height, and distance to closest shrub. In the late fall of 1997, we

collected utricles from 3 randomly selected female shrubs in each of the 14 grazing pastures. On each of the 42 female shrubs we measured crown dimensions (as described above), distance to closest and second closest shrub, and sexual phenotype of the closest shrub. We examined 100 utricles per plant to estimate the percentage of utricles containing embryos (utricule fill).

Utilization was determined by measuring differences in lengths (immediately before and after each 4-day browsing event) on 4 marked primary leaders on each labeled shrub. Base diameters and lengths of eaten secondary stems remaining on portions of utilized marked leaders were also measured. On female shrubs we marked both reproductive (with utricles) and non-reproductive leaders. Prior to each browsing event we harvested primary and secondary leaders from non-labeled female, male, and monocious (in 1998) shrubs in the experimental pastures. Each primary leader was labeled and sectioned into 6 cm long segments (approx) that were numbered sequentially from tip to base and placed in separate containers. Sectioned primary leaders were oven-dried separately at 60°C for 48 to 72 hours. Secondary stems were also labeled, placed in separate containers, and oven-dried in the same manner as were primary stems. We then recorded weights and lengths of the oven-dried segments from each primary stem, and base diameter, weight and length of each oven-dried secondary stem. Mean length-weight distributions of stems were used to construct a length-weight curve that was used to transform percent length measurements obtained in the field into percent biomass utilization estimates. A regression equation, relating total length of pooled male, female, and monocious primary leaders (predictor) to their total biomass (response), was also developed to calculate biomass of marked primary stems when necessary. Secondary stem measurements were also pooled and used to develop 2 regression equations: one relating base diameter (predictor) to stem length (response), and another relating stem length (predictor) to stem biomass (response). The first equation was used to estimate original length of eaten secondary stems. The second was used to estimate biomass of the length removed from utilized secondary stems. Length removed from a particular browsed secondary stem was calculated by subtracting the residual



length measured in the field from the total estimated length (calculated using secondary stem base diameters measured with a dial caliper). Finally, total biomass removed from browsed secondary stems on a given marked primary leader was expressed as a percentage of its total estimated biomass. Thus, we obtained an overall estimate of utilization for each marked leader expressed in terms of percent biomass removed by cattle.

### Sex change

We studied sex change in fourwing saltbush at the level of: a) experimental pastures; and b) individual marked shrubs. To evaluate sex change at the pasture level we set up 2 parallel transects in June of 1997 and 1998 in each grazing plot and determined sexual phenotype of the closest shrub to each 3-m interval point along the transect. If the closest shrub at a given interval point was either a young shrub or a nonflowering adult, the second closest shrub was selected. The transects were not permanent, but were set up in the same general area in both years. Shrubs were classified as either females, males, or monocious. We examined a total of 100 shrubs per grazing plot each year, and obtained sex ratio estimates for each of the 14 grazing plots in 1997 and 1998. Sex change at the level of grazing plots was analyzed using contingency tables, to determine whether sex ratios were significantly related to grazing treatments. The

significance of the factors included in the experimental design (block, season, and stocking density) was assessed in a preliminary analysis using a 4-way contingency table. Since effects of none of the factors were significant, the data were pooled into 2 classes (grazed and ungrazed) and collapsed into 2-way contingency tables. A separate table was constructed for 1997 and 1998, and then both of these were related using the Cochran-Mantel-Haenszel test of general association (Ott 1993). Sex ratios for grazed and ungrazed classes (in 1997 and 1998) were also compared to the 35 male:55 female:10 monocious tetraploid fourwing saltbush sex ratio described by McArthur (1977). Data were analyzed using PROC CATMOD and FREQ of SAS version 6.12 (1996) package. Statgraphics Plus (1994) was used to perform the  $\chi^2$  goodness of fit tests.

At the individual plant level we utilized permanently marked plants in each pasture. The previous season's floral phenotype of marked shrubs was compared to the floral phenotype of the current season. If a shrub exhibited flowers it was placed into 1 of 3 categories on the basis of its current season's floral phenotype, namely: a) changing toward maleness; b) changing toward femaleness; and c) constant sexual phenotype expression. Nonflowering shrubs were not included in this analysis. Once floral phenotype of marked shrubs was determined in June 1997, nonflower-

ing and labile shrubs were replaced by newly marked shrubs to maintain a balanced number of flowering individuals ( $n = 20$ ) in each sex phenotype class. Sex change at the individual shrub level was analyzed following 2 approaches. First, we analyzed counts of shrubs exhibiting either constant or labile (changing toward femaleness or maleness) sex expression in relation to browsing regime, to determine whether sex change and grazing treatments were significantly associated. Again, we used contingency tables and followed the same path of analysis described above for sex ratios. While the 1997 analysis included only shrubs that had been male or female in the previous year, in 1998 we analyzed counts from previously male, female and monocious individuals. The second analysis approach consisted of conducting discriminant analysis with data collected in 1998 to identify the variables that weighed most heavily on changes in shrub floral phenotype. Shrubs were grouped a priori into 2 categories: 1) those exhibiting shifts in sexual phenotype; and 2) those exhibiting sex phenotype constancy. Crown volume (CV), crown height:width ratio (HWR), distance to closest shrub (D1), percent utilization by cattle (U), length of rest between browsing event and onset of flowering in June (R), and sexual phenotype (S) were the variables used to construct the discriminant function. This set

**Table 1. Sex ratios and sex phenotype shifts in fourwing saltbush shrubs in relation to cattle grazing.**

a) Pooled sex ratios							
Year	Treatment	Sexual phenotype			Cochran-Mantel-Haenszel	$\chi^2$	p
		Male	Female	Monecious			
		----- (%) -----					
1997	Grazed	41	45	14	5.3	0.07	
	Ungrazed	36	54	11			
1998	Grazed	41	45	1	1.1	0.30	
	Ungrazed	37	49	14			
Overall					5.3	0.07	

b) Sex phenotype shifts							
Year	Treatment	Phenotypic shift			Cochran-Mantel-Haenszel	$\chi^2$	p
		Toward femaleness	Toward maleness	Constant			
		----- (%) -----					
1997 <sup>1</sup> ([ ♂ ♀ ] excluded)	Grazed	1	9	90	0.80	0.670	
	Ungrazed	1	13	86			
1998 ([ ♂ ♀ ] included)	Grazed	1	30	69	60.93	0.001	
	Ungrazed	13	20	67			
Overall					48.43	0.001	

<sup>1</sup>In 1997 monocious shrubs ([ $\sigma$  ♀]) were not included in the analysis.

of variables was chosen to assess the relative impacts of shrub size (CV), shrub age (HWR), shrub density (D1), cattle-browsing (U, R), and floral phenotype (S) on sex-change. The HWR of woody plants tends to decrease over the lifetime of an individual (Horn 1971) and was used as the best surrogate for shrub age. Length of rest period was expressed as a proportion of a year (days of rest/365). We constructed 2 discriminant functions, one for shrubs capable of shifting toward maleness and another for shrubs capable of shifting toward femaleness. The first function was developed using a subset of the data including flowering females and monocious shrubs that exhibited either constancy or a shift toward male floral phenotype. The second function was developed using a subset of data including flowering male shrubs, and monocious shrubs that exhibited either constancy or a shift toward female floral phenotype. Wilk's Lambda was used to test for significant differences between groups. Level of significance for all tests was set at  $P \leq 0.05$ . We used PROC CATMOD, FREQ, and DISCRIM of the SAS version 6.12 (1996) package to perform the statistical analyses.

### Nonflowering

Nonflowering was studied at the individual plant level only. Counts of labeled nonflowering shrubs were analyzed following the same 2 approaches used for the analysis of sex-change at the individual plant level. Contingency tables were used to determine whether nonflowering was significantly related to grazing regime and to floral phenotype (male or female). Discriminant analysis was used to determine the variables weighing most heavily on shrub nonflowering. Contingency tables and discriminant functions were constructed in the same way as in the sex-change analysis, except that in this case contingency tables included only male and female shrubs. For the discriminant analysis, data were separated a priori into 2 groups: a) flowering shrubs; and b) nonflowering shrubs. Wilk's Lambda was used to test for significant differences between groups in the discriminant analysis. Level of significance for all tests was set at  $P \leq 0.05$ . We used PROC CATMOD, FREQ, and DISCRIM, of the SAS version 6.12 package (1996) to perform the statistical analyses.

**Table 2. Discriminant analysis for fourwing saltbush shrubs on the basis of sex phenotype lability.**

<b>a) Discriminant scores</b>		
Shrubs capable of shifting	Constant	Labile
Toward maleness	4.3 a <sup>1</sup>	3.5 b
Toward femaleness	1.9 a	0.1 b
<b>b) Discriminant coefficients</b>		
	Shrubs capable of shifting	
	Toward maleness	Toward femaleness
Crown volume	0.03	0.59
Distance to closest shrub	0.21	-0.30
Crown height : width ratio	0.11	0.05
Percent utilization by cattle	-0.02	0.28
Length of rest period	0.16	-0.79
Sexual phenotype	1.40	2.03
<b>c) Correct classification</b>		
Shrubs capable of shifting	Constant	Labile
	----- (%) -----	
Toward maleness	77	80
Toward femaleness	83	95

<sup>1</sup> Different letters indicate significant differences at  $P = 0.05$  between constant and labile groups in shrubs shifting toward maleness and shrubs shifting toward femaleness.

### Utricle fill

Utricle fill was also analyzed at the individual plant level only. We conducted multiple regression analysis to determine which variables were significant predictors of fruit-fill at our experiment site. The predictors included in the model were: a) log crown volume (LCV); b) length of rest period between browsing event and onset of flowering in June (R); c) distance to closest shrub (D1); d) distance to second closest shrub (D2); e) sexual phenotype of closest shrub (dummy variables expressed by S1=1 if male, else 0, and S2= 1 if female, else 0). In addition to these, we also included 2 interactions of interest, namely: D1\*S1, and LCV\*S1. Crown volume was log-transformed in order to meet regression assumptions. Level of significance was set at  $P \leq 0.05$ . We used PROC GLM of the SAS version 6.12 (1996) package to perform the statistical analyses.

## Results

Mean shrub utilization in moderately grazed pastures was 35% in January, 15% in April, and 17% in September. In heavily grazed pastures, mean utilization was 54% in January, 25% in April, and 50% in September.

### Sex change Pasture level

Shrub sex ratios exhibited little annual variation in ungrazed exclosures or grazed pastures. Shrub sex-change and cattle-

browsing were only marginally related at the level of experimental grazing plots (Table 1.a). Neither grazed nor ungrazed shrub sex ratios differed significantly ( $P \leq 0.05$ ) from the 35 male:55 female:10 monocious frequency described for tetraploid fourwing saltbush (McArthur 1977).

### Individual shrubs

Sex change on individual shrubs was not significantly associated with browsing in 1997 when monocious shrubs were excluded from the analysis (Table 1b). However, when monocious shrubs were included in 1998, the association was highly significant (Table 1b). Whereas sex shifts towards maleness were more frequent, only change toward femaleness was significantly associated with presence or absence of browsing; the shift toward femaleness occurred much more frequently ( $P = 0.001$ ) in exclosures than in the grazed plots (13% vs 1%; Table 1b).

Shrubs discriminated into the a priori defined classes on the basis of sexual phenotype constancy produced groupings that were significantly different from each other (Table 2a). Mean discriminant scores for shrubs exhibiting shifts in sexual phenotype were significantly lower (both in shrubs shifting toward maleness and femaleness) than mean scores of shrubs exhibiting constancy. Sex phenotype was the variable that weighed most heavily on both discriminant functions (Table 2b). Monocious shrubs tended to have smaller discriminant scores and were more likely to be placed in the sex-changing group. Distance to closest shrub, per-

**Table 3. Effect of distance to closest shrub, length of rest period, and percent utilization on the classification of labile female, labile male, and monocious fourwing saltbush shrubs.**

Variable	Magnitude	Labile female	Labile male	Monocious
Distance to closest shrub	Large	constant	→ ♀ <sup>1</sup>	→ ♀
	Small	→ ♂ <sup>2</sup>	constant	→ ♂
Length of rest period	Long	constant	→ ♀	→ ♀
	Short	→ ♂	constant	→ ♂
Percent utilization by cattle	High	→ ♂	constant	→ ♂
	Low	constant	→ ♀	→ ♀

<sup>1</sup>Shifts toward femaleness.

<sup>2</sup>Shifts toward maleness.

cent utilization by cattle, and length of rest period exhibited opposite signs in the discriminant functions corresponding to shrubs capable of shifting toward maleness and those capable of shifting toward femaleness (Table 2b). The discriminant functions correctly classified 80% of shrubs capable of shifting toward male-

ly different from each other (Table 5a). Mean discriminant scores for flowering shrubs were significantly lower than mean scores of nonflowering ones. Percent utilization by cattle was the variable weighing most heavily upon the discriminant function (Table 5b). High levels of utilization produced high discriminant scores,

**Table 4. Percentages of fourwing saltbush that flowered or did not flower.**

Year	Treatment	Flowered	Did not flower	Cochran-Mantel-Haenszel	$\chi^2$	P
		----- (%) -----				
1997	Grazed	82	18		5.0	0.03
	Ungrazed	97	3			
1998	Grazed	65	35		16.9	0.01
	Ungrazed	100	0			
Overall				21.07		0.01

ness and 95% of shrubs capable of shifting toward femaleness (Table 2c). Distance to closest shrub, percent utilization by cattle, and length of rest period had opposite effects on the sex phenotype status of labile females, labile males, and monocious shrubs (Table 3).

### Nonflowering

Nonflowering and cattle-grazing were significantly associated (Table 4). Almost all labeled shrubs in exclosures (all of them in 1998) flowered, but up to approximately one third of labeled shrubs did not flower in browsed pastures (Table 4). Nonflowering was not significantly associated with shrub floral phenotype, it occurred as often among female shrubs as it did among male shrubs.

Shrubs discriminated into the classes defined a priori by the presence of flowers produced groupings that were significant-

causing an individual to be classified in the nonflowering group. The opposite occurred with individuals undergoing low levels of utilization. Crown volume was the second most influential variable. Shrubs with large crowns tended to obtain

small discriminant scores and were, thus, classified as flowering; the opposite occurred with shrubs exhibiting small crowns. The discriminant functions correctly classified about 70% of both flowering and nonflowering shrubs (Table 5c). Overall, increasing levels of utilization by cattle and/or decreasing crown sizes were associated with increasing levels of nonflowering in fourwing saltbush at our site.

### Utricle fill

Mean utricle fill of protected and grazed shrubs was similar. In both cases there was a large amount of among-shrub variation (Table 6). We found a significant relation between utricle fill and the overall set of variables included in our model ( $df = 39$ ,  $F = 2.41$ ,  $P = 0.04$ ,  $R^2 = 0.38$ ). However, sexual phenotype of closest shrub, and the interactions both with distance to closest shrub and with log crown volume of the sampled female, were the only significant terms ( $P < 0.05$ ) in the multiple regression model (Table 6). Since the interaction terms were significant, we conducted separate regression analyses for shrubs with female or male neighbors. As distance to closest shrub increased, utricle fill decreased significantly if the closest shrub was a male ( $\beta_1 = -0.42$ ;  $t = -2.2$ ;  $P = 0.02$ ), and increased if the closest shrub was a female ( $\beta_1 = 0.38$ ;  $t = 2.30$ ;  $P = 0.04$ ). If the closest shrub was a male, utricle fill increased with increases in log crown volume ( $\beta_1 = 66.9$ ;  $t = 5.76$ ;  $P < 0.01$ ) but not if the closest shrub was a female ( $\beta_1 = -2.84$ ;  $t = -0.19$ ;  $P = 0.85$ ).

### Discussion

Sex expression in tetraploid fourwing saltbush is genetically constrained (McArthur 1977, McArthur et al. 1992).

**Table 5. Discriminant analysis for flowering and nonflowering fourwing saltbush shrubs.**

a) Discriminant scores		
	Flowering	Nonflowering
	1.62 a <sup>1</sup>	1.93 b
b) Discriminant coefficients		
Crown volume		-0.38
Distance to closest shrub		0.23
Crown height : width ratio		-0.30
Percent utilization by cattle		0.90
Length of rest period		0.13
c) Correct classification		
	Flowering	Nonflowering
	----- (%) -----	
	70	73

<sup>1</sup>Different letters indicate significant differences at  $P = 0.05$ .

**Table 6. Utricle fill as affected by grazing**

Grazing regime	Utricle fill		
	Mean	SE	Range
	----- (%) -----		
Grazed	44	± 2.6	15 - 78
Ungrazed	39	± 7.5	10 - 60
Multiple regression coefficients			
	Parameter estimate	t	P
Length of rest period (R)	< -0.01	-0.01	0.99
Log crown volume (LCV)	8.06	0.50	0.62
Distance to closest shrub (D1)	0.12	0.81	0.43
Distance to second closest shrub (D2)	-0.09	-0.63	0.54
Sexual phenotype of closest shrub (S 1) (if male = 1, else = 0)	70.20	3.18	< 0.01
Sexual phenotype of closest shrub (S 2) (if female = 1, else = 0)	14.48	1.89	0.07
D1 * S1	-0.41	-2.44	0.02
LCV * S1	46.05	2.25	0.03

An estimated 55% of all shrubs carry sexually labile genotypes; the remaining 45% exhibit genotypic sex constancy. Within a season, approximately 2/3 of shrubs with labile genotypes produce female flowers, 1/6 produce male flowers, and the remaining 1/6 exhibit both male and female flowers (i.e. monocious shrubs). Shrubs with sex constant genotypes always flower as either males or females in close-to-equal proportions. Whereas overall phenotypic sex ratios are female biased with fairly constant proportions of female (55%), male (35%), and monocious (10%) shrubs (McArthur 1977, McArthur and Freeman 1982, Barrow 1987, Petersen et al. 1987, Cibils et al. 2000), sex shifting can trigger changes in phenotypic sex ratios of fourwing saltbush populations over time (Freeman and McArthur 1984). Shrubs with sexually labile genotypes are able to shift sex expression on a year-to-year basis as a response to environmental stress. Therefore, all 3 sex phenotypes are capable of sex shifting on a yearly basis, but such changes (given the phenotypic frequencies of labile genotypes mentioned above) are more frequent in shrubs that exhibit either monocious or female phenotypes (McArthur 1977, McArthur and Freeman 1982, Freeman and McArthur 1984).

Sex change in fourwing saltbush at our research site was significantly related to browsing at the level of individual shrubs. Exclosures exhibited a larger number of shrubs that shifted toward femaleness than did pastures that were browsed. Sex-shifts observed at the level of individual shrubs, however, did not translate into deviations of overall phenotypic sex ratios (as measured by the transect method we used) at the level of experimental pastures. The

significant association between browsing regime and floral shifts was due primarily to the tendency of monocious shrubs (all of which carry labile genotypes) to change sexual phenotype (McArthur 1977, McArthur et al. 1992). The frequency of labile genotypes in our sample of marked shrubs, particularly in the 1997/98 season, may have been higher than that of the population as a whole. This would account for the difference in response to browsing-regime measured at the different levels at which we conducted the sex change study. In a plantation stand, McArthur and Freeman (1982) reported that 91% of monocious shrubs, 49% of females, and 15% of males changed sex over a 7-year period. Stress conditions (severe winters, droughts, crowding and heavy seed sets in the previous growing season) generally promoted changes toward maleness. Conversely, release from stress produced a return toward femaleness in labile shrubs (Gamarth 1972, McArthur and Freeman 1982). We observed a somewhat similar pattern at our site; small distance to closest shrub (~crowding) was associated with shifts towards maleness and large distance to closest shrub was associated with changes toward femaleness.

Removal of leaves or flowers, or crown pruning have been reported to produce changes toward femaleness in sexually labile plants of at least 8 species (Freeman et al. 1980). Removal of storage organs, on the other hand, produced the opposite shift in at least 2 plant species (Freeman et al. 1980). Sex shifts toward maleness in fourwing saltbush at our site were weakly associated with very high utilization by cattle and short rest periods. Conversely, sex shifts toward femaleness were highly

associated with low (or no) utilization by cattle and long rest periods. This trend is somewhat consistent with the reserve organ removal responses mentioned above, yet is opposite to sex shift trends reported in the defoliation and crown pruning examples. This apparent inconsistency may be explained by the fact that woody plants store reserve carbohydrates in perennial stems (Coyne et al. 1995), and that cattle browsing involves removal of leaves, fruits, and a considerable amount of stems (storage organs).

While shifts toward maleness were weakly associated with very high utilization by cattle (up to 53.6% in heavily grazed pastures) and short rest periods, they occurred in all the experimental pastures irrespective of browsing regime. Since our experiment was conducted in a shrub stand historically browsed by cattle in winter (when shrub utilization is highest [Shoop et al. 1985]), it is likely that the level of stress imposed by our browsing treatments was not greater than the stress to which the shrubs were already subjected. Release from previous browsing stress, on the other hand, may have promoted a return toward femaleness in shrubs within exclosures. This would be consistent with the post-stress sex change reversal trends in fourwing saltbush reported by McArthur and Freeman (1982).

Shrubs with small crown volumes were more likely to be classified in the sexually labile groups, especially in the case of shrubs shifting sex expression toward femaleness. Changes toward femaleness were far more frequent in the exclosures. Reproductive output of small plants is affected more negatively by herbivory than is that of large plants (Marquis 1984). Therefore, it is not surprising that this variable weighed so heavily on the discriminant function for plants capable of shifting toward femaleness.

The association between cattle-browsing and nonflowering was highly significant. Nonflowering was much more frequent in browsed fourwing saltbush shrubs than in protected ones. Almost all shrubs in exclosures flowered in both years. Freeman and McArthur (1984) reported that occasionally (in 1 year of a 7-year study), nonflowering was slightly more common among female plants than among males. At our experimental site, nonflowering occurred as frequently in females as it did in males, both in 1997 and in 1998. Reduction in seed set is often reported as a direct consequence of herbivory or defoliation in

plants (Edwards 1985, Elmqvist and Gardfjell 1988, Milton 1995), including fourwing saltbush (Trlica et al. 1977); but cases of nonflowering as a consequence of herbivory are uncommonly reported. Our results suggest that this more severe response may occur in fourwing saltbush grazed by cattle.

In annual agricultural crops, reduction in seed (fruit) production is proportional to amount of biomass removed by herbivores (Hendrix 1988). The relation between herbivory and fruit set in perennial plants is not as clear cut and is, in many instances, associated both with intensity and timing of herbivory events (Hendrix 1988, and references therein, Milton 1995). Length and number of fruit-bearing stems in female fourwing saltbush shrubs can be reduced by defoliation (Buwai and Trlica 1977, Trlica et al. 1977). Number and total weight of utricles increases exponentially with increasing crown volume (Stapp, unpublished data). Hence, cattle herbivory can be expected to cause overall reductions in fruit set, both directly, by reducing length and number of fruit stalks, and indirectly, by reducing crown size. Variation in fruit fill, however, was not significantly related to cattle browsing regime in our experiment. Crown volume was a significant predictor of fruit fill only when floral phenotype of the closest shrub was taken into account. The relatively wide range of percent utricule fill values we observed is consistent with previous reports (Springfield 1970, Gerard 1978). Springfield (1970) speculated that the large fruit fill variability among the fourwing saltbush shrubs he sampled could be governed by either genetic or site specific factors. Gerard (1978), who also observed a considerable degree of utricule fill variation among fourwing saltbush shrubs, reported no significant correlation between cumulative precipitation for various periods, or between total weight of fruit produced and percent utricule fill.

Sexual phenotype of the closest shrub and the interaction of floral phenotype of the closest shrub with both crown volume of the sampled female and distance to the closest shrub were the only significant explanatory variables of the set of predictors included in our model. Since fourwing saltbush is wind pollinated, it is likely that pollen flow dynamics may have been responsible for these interactions. If the closest shrub was a male (pollen source), fruit fill decreased with increasing distance to closest shrub. If, on the other

hand, the closest shrub was a female (pollen flow interference factor), fruit fill increased with increasing distance to closest plant. Increases in crown volume were associated with increases in utricule fill when the closest shrub was a male. Larger crowns probably enabled sampled females to intercept larger amounts of pollen. If the closest shrub was a female, increases in crown volume were associated with close-to-zero changes in percent utricule fill.

Because pollen is thought to be rarely limiting in local populations of fourwing saltbush (McArthur et al. 1978) we did not expect these results. Strawbridge et al. (1997) reported that in plantations of river saltbush (*Atriplex amnicola* P.G. Wilson), optimum seed fills were obtained with a relatively wide range of shrub sex ratios (11 to 50% males). However, McArthur et al. (1978) found that, while pollen was abundant, the number of pollen grains captured down-wind from a solitary male shrub was 7 times larger than that captured at an equally distant spot in the opposite direction (44.2 vs 6.5 grains/mm<sup>2</sup>). Spatial arrangement of male and female shrubs across the landscape interacting with crown volumes and the direction of predominant winds should, in turn, control the efficiency of pollen flow and indirectly affect utricule fill (Freeman et al. 1993).

## Conclusions

Short-term cattle-browsing effects on shrub fecundity at our research site were mostly associated with increases in non-flowering. The magnitude of sex shifts (toward femaleness) associated with protection from browsing were not large enough to promote detectable alterations in shrub sex ratios. Consequently, previously observed differences in sex ratios between browsed stands and long-term exclosures (Cibils et al. 2000) could be a product of gender-specific shrub mortality rather than sex shifting. While release from the stress imposed by cattle-browsing was clearly associated with shifts toward femaleness in labile plants, the level of detail at which we addressed sex-change questions did not allow a quantification of this process. Our results, however, may merit further studies of a quantitative nature with greater control of environmental stress to assess the magnitude and importance of herbivory in promoting sex shifts in labile fourwing saltbush shrubs.

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# Female-biased herbivory in fourwing saltbush browsed by cattle

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## Abstract

Female fourwing saltbush (*Atriplex canescens* Pursh [Nutt.]) shrubs are more abundant in exclosures than in adjacent grazed pastures at our research site on the shortgrass steppe in Colorado. We hypothesized that female shrubs at this site were being browsed more heavily by cattle than were male shrubs. We conducted a series of 2-year experiments (1997 and 1998) with cattle to measure levels of cattle utilization of male and female shrubs. Overall, utilization of marked leaders was 43.5% in January, 19.7% in April, and 33.4% in September. Percent utilization of marked leaders was consistently and significantly higher on female shrubs both in January (females: 46.5%, males: 40.2%), and September (females: 36.9%, males: 29.9%). In April, differences in utilization of shrub sexes were not significant (females: 20.3%, males: 19.2%). The female-bias in cattle herbivory increased significantly with increasing overall utilization of shrubs. Gender-biased herbivory may have promoted higher mortality among female shrubs, leading to the sex ratio alteration previously observed at this site.

**Key Words:** *Atriplex canescens*, cattle-browsing, dioecious shrubs, gender-biased herbivory

Interest in studying patterns of animal-plant interactions in dioecious plants has increased steadily over the past 35 years (Boecklen and Hoffman 1993, Watson 1995), although the subject has received little attention (28 case studies published since 1960) compared to other aspects of plant-herbivore interactions. Whereas male-biased herbivory appears to be the most common pattern (and is therefore assumed to be the rule), a number of studies report the occurrence of no bias or female-biased her-

## Resumen

La abundancia de arbustos hembra de *Atriplex canescens* Pursh [Nutt.] es mayor en clausuras que en potreros pastoreados en nuestro sitio de estudio en la estepa de pastos cortos de Colorado. Se postuló que los arbustos hembra estaban siendo ramoneados mas intensamente por bovinos que los arbustos macho. Se condujeron una serie de experimentos de 2 años de duración (1997 y 1998) para determinar niveles de ramoneo bovino en arbustos hembra y macho. En general, los niveles de utilización medidos sobre tallos marcados fueron de 43.5% en enero (invierno), 19.7% en abril (primavera) y 33.4% en septiembre (verano). El porcentaje de utilización de tallos marcados en arbustos hembra fue consistente y significativamente mayor que la utilización registrada en arbustos macho, tanto en enero (hembras: 46.5%; machos: 40.2%) como en septiembre (hembras: 36.9%; machos: 29.9%). En abril dichas diferencias no fueron significativas ( hembras: 20.3%; machos:19.2%). El sesgo femenino de heborivoria tendió a acentuarse con niveles crecientes de intensidad de ramoneo bovino. Dicho sesgo podría haber promovido mayores tasas de mortalidad en arbustos hembra provocando la alteración de proporciones de sexos de la población de arbustos observada previamente en este sitio.

bivory (Graetz 1978, Williams et al. 1978, Lovett Doust and Cavers 1982, Lovett Doust and Lovett Doust 1985, Danell et al. 1985, Alliende 1989, Boecklen et al. 1990, Krischik and Denno 1990, Danell et al. 1991, Hjalten 1992, Maywald 1998, Maywald et al. 1998).

We conducted our research in a stand of tetraploid fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) that had been browsed by cattle for at least 20 years. Tetraploid fourwing saltbush is sub-dioecious, with female, male, and monocious individuals occurring in fairly constant proportions (McArthur 1977, McArthur and Freeman 1982). At our research site on the Central Plains Experimental Range, Cibils et al. (2000) found that female shrubs were less abundant in browsed stands than in long-term exclosures. These authors also found that female shrubs in browsed stands were apparently younger than their male counterparts. Such apparent age differences, however, did not exist in stands that had received long-term protection from cattle. This evidence suggested that female shrubs at this site were being impacted more heavily by cattle-browsing than were male shrubs. Preferential browsing of female shrubs by cattle could have been responsible for this phenomenon. Our first hypothesis, therefore,

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was that female fourwing saltbush shrubs at our research site were being browsed more heavily than were male shrubs.

Since herbivory bias tends to disappear under either very low or very high herbivore densities (Boecklen et al. 1990, Danell et al. 1991), we manipulated stocking rates to test our second hypothesis that female-biased herbivory would tend to disappear under very low and very high grazing intensity (sensu Vallentine 1990) by cattle.

## Materials and Methods

Our study site was located on the USDA-ARS Central Plains Experimental Range (CPER), approximately 60 km north-east of Fort Collins, Colo. (40°49' N 107° 47' W) at 1,650 m elevation. We conducted our experiments at a shrub-dominated site, on a floodplain area close to Owl Creek. Major soil types of our study site were Remmit loamy sands and Edgar loams. Fourwing saltbush, blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), and western wheatgrass (*Agropyron smithii* Rydb.) are the dominant plant species at the site (Liang et al. 1989). Mean annual precipitation is 320 mm (ranging from 150 to 500 mm), 50 to 80% of which occurs between the months of May and September (Hart and Ashby 1998). Rainfall during and immediately before our experiments was above the historical average, particularly in 1997 (559 mm). Late spring and summer rainfall (May–September) was also considerably higher in 1997 (436 mm) relative to 1996 (294 mm) and 1998 (275 mm).

Fourwing saltbush shrubs at our site at the CPER begin rapid growth in the month of May, flower during the month of June, and generally complete seed set by the end of August. Utricle maturity and shedding of current year's leaves occur in the month of October. Female shrubs exhibit mature utricles throughout the quiescent period that usually begins in November (Trlica et al. 1977).

To test the first and second hypotheses, we measured percent utilization of marked leaders on female and male fourwing saltbush shrubs in 0.5-ha experimental pastures. The pastures were built in 2 parallel blocks of 7 adjacent units each (one pasture was ungrazed in each block), within a pasture that had been moderately grazed by cattle in winter for approximately 20 years (approximately 5.3 ha AUM<sup>-1</sup> over a 6-month grazing season; 34 AU days ha<sup>-1</sup>). Moderately grazed pastures at the CPER

have historically been stocked to leave an ungrazed residue equal to 60% of peak standing crop (Hart and Ashby 1998).

Cattle diets on the shortgrass steppe change throughout the year as a consequence of seasonal variation in the quality and availability of dietary items (Schwartz and Ellis 1981, Shoop et al. 1985). In moderately stocked pastures with abundant fourwing saltbush, cattle diets contained 13 and 55% fourwing saltbush in November and March, respectively (Shoop et al. 1985). Therefore, shrubs are subjected to contrasting levels of utilization throughout a given year. We conducted 3 browsing experiments in 1997 and 1998: one in winter (January), another in early spring (April), and another in late summer (September). By repeating the experiment at different dates we were able to assess the impact of season (associated with plant phenology) on shrub utilization patterns.

Each experiment consisted of browsing 4 pastures with cattle (Hereford heifers weighing 400 to 520 kg) for a period of 4 days. Two pastures were browsed moderately (4 heifers; 32 heifer days ha<sup>-1</sup>) and 2 were browsed heavily (12 heifers; 96 heifer days ha<sup>-1</sup>). Pastures were assigned randomly to each combination of season and stocking density at the beginning of the study. Randomization was performed within each block of experimental pastures, subject to the constraint that no 2 adjacent pastures were grazed on the same date. Cattle used in the experiments were randomly assigned to the 0.5 hectare pastures and were always taken from herds grazing pastures with abundant fourwing saltbush, to minimize dietary and social adjustment.

Twenty female and 20 male shrubs were randomly selected and labeled in each 0.5 ha grazing pasture. Each shrub was at least 3 m away from any other marked shrub, and was labeled by placing a numbered stake under the shrub crown, a marking technique inconspicuous to cattle. In the weeks prior to each experiment, 4 primary leaders were marked on each labeled shrub. On female shrubs we marked both reproductive (with utricles) and non-reproductive leaders. Lengths of marked leaders were measured prior to introducing the cattle. Immediately after each experiment we re-measured the lengths of marked leaders, and the base diameters and lengths of eaten secondary stems remaining on portions of utilized marked leaders.

Prior to each browsing event we harvested 30 primary and 30 secondary leaders, 15 from non-labeled female and 15

from non-labeled male shrubs in the experimental pastures. Each primary leader was labeled and sectioned into 6 cm long segments that were numbered sequentially from tip to base and placed in separate containers. Sectioned primary leaders were oven-dried separately at 60°C for 48 to 72 hours. Secondary stems were also labeled, placed in separate containers, and oven-dried in the same manner as were primary stems. We then recorded weights and lengths of the oven-dried segments from each primary stem, and base diameter, weight and length of each oven-dried secondary stem. Primary stem segment measurements were transformed into cumulative relative (%) expressions of length and biomass. Using linear regression we developed length-weight relationships for each of the 30 primary leaders. Mean length-weight distribution of female (n = 15) and male (n = 15) stems were used to construct a length-weight curve, later used to transform percent length measurements obtained in the field into percent biomass utilization estimates. A regression equation, relating total length of pooled male and female primary leaders (predictor) to their total biomass (response), was also developed to calculate biomass of marked primary stems when necessary. Secondary stem measurements were pooled and used to develop 2 regression equations: one relating base diameter (predictor) to stem length (response), and another relating stem length (predictor) to stem biomass (response). The first equation was used to estimate original length of eaten secondary stems. The second was used to estimate biomass of the length removed from utilized secondary stems. Length removed from a particular eaten secondary stem was calculated by subtracting the residual length measured in the field from the total estimated length (calculated using secondary stem base diameters measured with a dial caliper). Finally, total biomass removed from eaten secondary stems on a given marked primary leader was expressed as a percentage of its total estimated biomass. Thus, we obtained an overall estimate of utilization for each marked leader expressed in terms of percent biomass removed by cattle.

Mean percent utilization of marked leaders was calculated for each experimental pasture following each grazing trial. Data from each experiment were analyzed separately using repeated measures analysis of variance (ANOVAR). The statistical model selected for the analysis was a mixed effects repeated measures factori-

al experiment design. Shrub gender (male and female), stocking density (moderate and heavy), year (1997 and 1998), and block (1 or 2) were the factors studied. Year was repeated within shrub gender, stocking density, and block. Shrub gender and stocking density were considered fixed effects. Block was considered a random effect. We included all possible 2-way and 3-way interactions between fixed effects in the final model. We explored interactions between fixed and random main effects, and included significant interactions in the final model. The diagnostic plots of studentized residuals of raw utilization data showed slight deviations from the assumption of homogeneity of variances. We therefore arcsin-transformed our data and re-ran the residual diagnostic tests. The transformed data set did not exhibit any significant deviations from the ANOVA assumptions so all analyses were performed on the transformed data set. The overall level of significance was set at  $P \leq 0.05$ . We used proc GLM and proc MIXED from the SAS Version 6.12 (1996) package to perform the statistical analyses.

We calculated herbivory bias for each treatment at each of the experiment dates ( $n = 12$ ) by subtracting mean utilization of marked leaders on male shrubs from that of females. We then calculated the Pearson Correlation Coefficient ( $r$ ) and performed linear regression analysis (Ott 1993) using mean overall utilization of marked leaders and herbivory bias as the independent and dependent variables, respectively. We used proc CORR and proc GLM from the SAS Version 6.12 (1996) package to perform the statistical analysis. The level of significance used to test statistical hypotheses regarding the regression model and the slope of the function ( $\beta_1$ ) was set at  $P \leq 0.05$ .

## Results

In relation to the first hypothesis, utilization of marked leaders on female shrubs was significantly higher than that of male shrubs in January and September (Fig. 1). In April, no significant gender bias in shrub herbivory was observed (Fig. 1). Overall shrub utilization was greater in the snowy winter of 1997 than in the mild winter of 1998, probably because understory vegetation was covered in 1997. In all 3 experiments there were significant differences in overall utilization of shrubs between years and stocking density treatments; heavily stocked pastures exhibited consistent overall higher shrub utilization

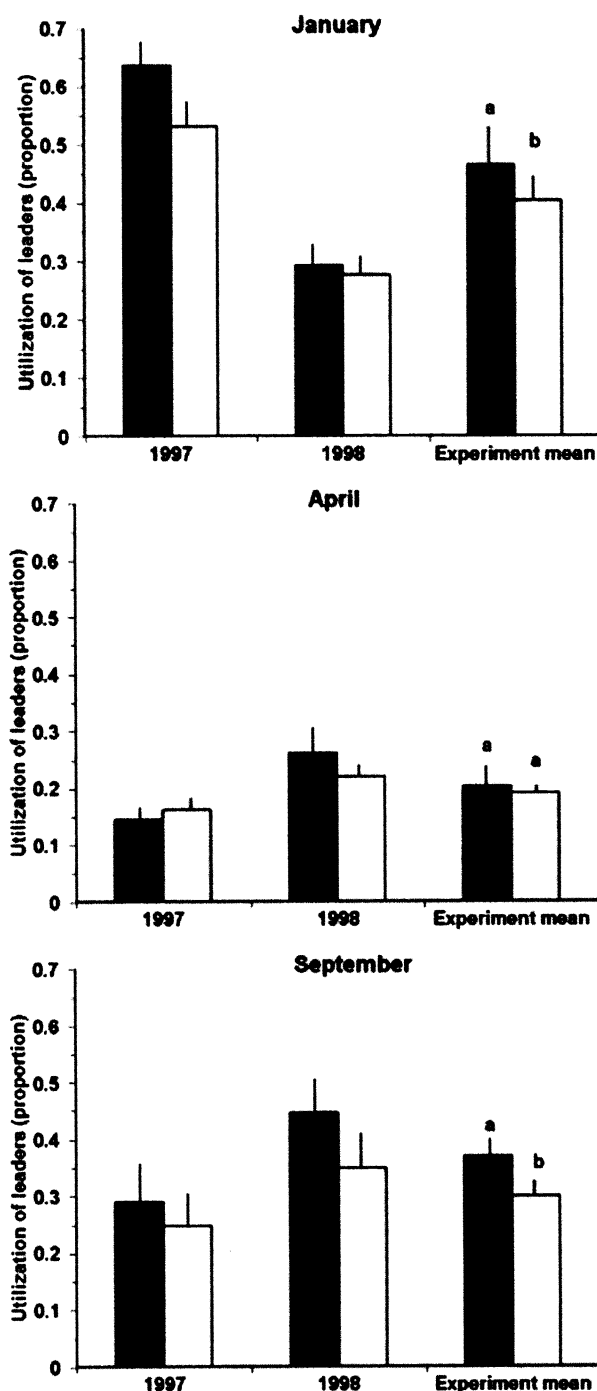


Fig 1. Mean utilization of marked leaders on female (solid bars) and male (empty bars) shrubs in: January (Winter), April (early Spring), and September (late Summer). Different letters indicate significantly different means ( $P = 0.05$ ). Error bars indicate standard errors of means ( $n = 2$ ).

levels (Table 1). Shrub gender, however, affected utilization significantly, irrespective of stocking density, in 2 (January and September) of the 3 experiments.

In relation to the second hypothesis, female biased browsing increased as overall shrub utilization increased ( $r = 0.82$ ,  $P$

$= 0.01$ , Fig. 2). The gender-biased browsing pattern tended to disappear when overall shrub utilization was low. Contrary to what we had hypothesized, sex-biased herbivory persisted under the highest levels of utilization imposed by our experimental treatments.

**Table 1. Overall utilization of marked leaders in moderate and heavy stocking density treatments.**

Month	1997		1998	
	Moderate	Heavy	Moderate	Heavy
	-----(-%)-----		-----(-%)-----	
January	45.9 b <sup>1</sup>	70.9 a	20.7 b	36.3 a
April	11.6 b	19.1 a	17.9 b	30.3 a
September	10.0 b	43.9 a	23.3 b	56.3 a

<sup>1</sup>Different letters within a row and year indicate significantly different means (P = 0.05).

## Discussion and Conclusions

Cattle browsed female fourwing saltbush shrubs more intensely than male shrubs both in winter and late summer. Utilization of female and male shrubs was similar in early spring. Cattle exhibited consistent preferences across stocking density treatments and years. While our results depart from the general pattern of male-biased herbivory found in the literature, they are consistent with findings from most studies of large herbivores grazing dioecious plants (Williams et al. 1978, Graetz 1978, Maywald 1998). Sheep preferentially browse female shrubs of bladder saltbush (*Atriplex vesicaria* Heward ex. Benth.) irrespective of season or phenological stage (Maywald 1998). This pattern apparently results in higher mortality of female shrubs that leads to alterations of shrub sex ratios (Williams et al. 1978). Our results, however, agree only partially with a recent study conducted with sheep in a transplant garden with male and female fourwing saltbush shrubs (Maywald et al. 1998). Similarly to our findings, in late winter (March), a date roughly equivalent to our early spring (April) experiment, these authors found no sex-related differences in shrub biomass

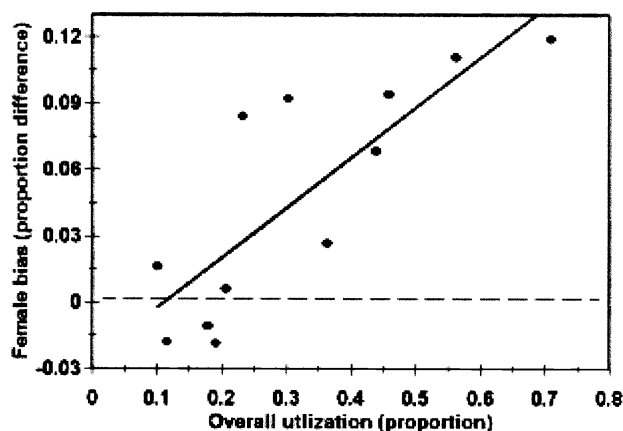
removal. However, during flowering in late spring (June), Maywald et al. (1998) reported that sheep consumed significantly more biomass from male shrubs as compared to females.

When overall shrub utilization by cattle was low (in April), possibly because new green herbaceous vegetation was available, we did not detect any gender-related bias in herbivory irrespective of stocking density. The female-biased pattern became more pronounced under increasing levels of overall shrub utilization by cattle. It is possible that the highest level of utilization imposed by our experiments (in January 1997) was not sufficient to alter cattle preferences and cause the herbivory-bias to disappear, as suggested by studies conducted with other herbivores (Danell et al. 1991).

Differences in overall levels of shrub utilization by cattle between years were possibly influenced by weather fluctuations. Overall utilization in the January experiment (58% and 28% in 1997 and 1998, respectively) apparently reflected weather-driven variations in understory forage availability. A heavy snowfall reduced grass availability severely during our January experiment in 1997. Conversely, a mild winter of 1998 with abundant grass residue from the previous

growing season (a particularly moist summer in 1997) was associated with higher levels of understory availability and lower shrub utilization. A somewhat similar pattern occurred in the September experiment; the very high summer rainfall of 1997 (436 mm) compared with the relatively dry summer of 1998 (275 mm) had a visible effect on understory growth presumably producing contrasting browsing levels (27% and 40% shrub utilization in 1997 and 1998, respectively). In April, between-year variations in shrub utilization (15% and 24% in 1997 and 1998, respectively) may have been related to differences in the onset of cool-season grass and forb growth. Thus, overall browsing pressure on fourwing saltbush in our experiments appeared to be inversely related to understory forage availability.

Heavy defoliation or continuous grazing can promote mortality in fourwing saltbush stands (Cibils et al. 1998 and references therein). For example, single browsing events involving the removal of 100% of current year's growth led to high fourwing saltbush mortality rates (37 to 100%) over a 5-year period in an experiment conducted in Israel (Benjamin et al. 1995). At our research site, fourwing saltbush shrubs can take 14 to 26 months to recover from a single heavy artificial defoliation event involving the removal of 90% of current year's growth (Trlica et al. 1977). If defoliation occurs in August (near maturity) or if shrubs are subjected to multiple defoliations, recovery may take even longer (Trlica et al. 1977). Because cattle in our experiments removed woody stems from previous growing seasons together with current year's growth, our utilization estimates were based on total (primary) leader biomass. Therefore, removal of current year's growth at dates when shrub utilization was highest (January 1997 and September 1998), particularly in the case of the heavier-browsed female shrubs, was possibly comparable to levels of defoliation known to promote shrub mortality. Additionally, since females of dioecious plant species generally grow slower than their male counterparts (Jing and Coley 1990), female shrubs may need more time than males to recover from a defoliation event (Cibils et al., unpublished data), and would consequently be more vulnerable to future defoliations. Therefore, it would be reasonable to expect higher mortality in the slower-growing female shrubs subjected to higher levels of defoliation. Differences in shrub utilization levels between years in our experiments suggest that heavy browsing events in moderately



**Fig 2. Female bias in utilization of marked leaders (female utilization - male utilization) in relation to overall level of shrub utilization. Points above the horizontal line indicate female bias, points below the horizontal line indicate male bias.**



stocked pastures do not occur every year. Consequently, mortality rates of shrubs (females, in particular) can be expected to be less severe than those described by Benjamin et al. (1995).

Although the study of palatability factors influencing female-biased browsing patterns was beyond the scope of this study, preliminary data on nitrogen content of leaves and thin stems of female and male shrubs at our site (Cibils et al. unpublished data) suggest that differences in N content were possibly not important in driving cattle preferences in our experiments. Fourwing saltbush can synthesize carbon-based secondary compounds such as triterpenoid saponins (Nord and Van Atta 1960, Sanderson et al. 1987) and oxalates (Davis 1981). Saponins, common in many genera of the Chenopodiaceae (Cibils et al. 1998 and references therein), can deter herbivores, and have been shown to influence patterns of herbivory in stands of fourwing saltbush (Otsyina 1983, Sanderson et al. 1987). Utricle bracts of fourwing saltbush can contain large concentrations of saponins, 10% of the weight of original bract chaff (Nord and Van Atta 1960). Preliminary observations of within-shrub browsing patterns in our experiments suggest that cattle preferred to consume non-flowering stems when browsing female shrubs (Cibils et al. unpublished data). It would be reasonable to speculate that gender-specific differences in levels of defensive compounds (mainly saponins) may have been responsible for the browsing pattern we observed, however further studies on aspects of the defensive ecology of fourwing saltbush will be needed to test these hypotheses.

Differences in fourwing saltbush sex ratios between exclosures and adjacent grazed pastures previously reported at our site (Cibils et al. 2000) may have been the result of greater mortality rates in female shrubs. Female-biased browsing by cattle may have promoted larger mortality of females relative to males, thus altering sex ratios and promoting gender-specific age differences.

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# In vivo digestibility of kleingrass from fecal nitrogen excretion

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## Abstract

It was proposed that the digestibility of organic matter (OMD) can be estimated from the relationship between total fecal nitrogen (TFN, as a % of organic matter intake (OMI)) and fecal nitrogen concentration (FNc) through the equation:  $OMD = 1 - TFN / FNc$ . Two assumptions are critical to this equation, total fecal nitrogen (as a % of OMI) is a constant and does not change within a range of diet crude protein and fecal nitrogen concentration is proportional to digestibility of organic matter. The objective of this study was to test if total fecal nitrogen (as a % of OMI) remains constant over 3 feeding levels, and if fecal nitrogen concentration decreases with decreasing organic matter digestibility of maturing forages. Total fecal nitrogen did not change ( $P = 0.94$ ) with feeding level, but increased ( $P < 0.05$ ) with evaluation period. The fecal nitrogen concentration correlated ( $r = 0.60$ ;  $P < 0.001$ ) to digestibility of organic matter. The results show that digestibility of organic matter cannot be estimated from total fecal nitrogen, unless time of the year is considered.

**Key Words:** fecal index, nutritive value, N fecal, rams.

Simple estimates of nutritive value are often of little value if there is no information regarding the amounts that will be consumed (Ørskov and Ryle 1990). The estimation of forage intake in grazing systems is, perhaps, the most challenging question of animal production.

The determination of individual intake can be obtained from fecal production (F) and diet digestibility. The precision of organic matter digestibility (OMD) determination is affected by the accuracy with which the forage samples represent the actual diet of the animals (Burns et al. 1994, Coates and Penning 2000). The use of the in vitro technique to estimate forage digestibility is associated with several errors, including the effects of diet composition, between animal variations, intake level and physiological status of animals (Schneider and Flatt 1975). The fecal index technique, alternatively, does not require diet samples, but only routine chemical determinations of fecal material, and is currently being used to estimate intake of wild and domestic herbivores (Caughley and Sinclair 1996, Hodgman et al. 1996, Mésochina et al. 1998). Fecal N concentration (FNc) has been widely used as a fecal index (Le Du and Penning 1982), due to its easy determination and low variation within 24-hour periods (Bartiaux-Thill 1980).

## Resumen

Se ha propuesto que la digestibilidad de la materia orgánica (DMO) puede ser estimada a partir de la relación entre el nitrógeno total fecal (NTF, como un % del consumo de materia orgánica (CMO)) y la concentración de nitrógeno fecal (cNF), en la ecuación:  $DMO = 1 - NTF / cNF$ . La aplicación de esta ecuación se sustenta en dos supuestos, el nitrógeno total fecal permanece constante dentro de un rango de proteína bruta de la dieta y la concentración de nitrógeno fecal es proporcional a la digestibilidad de la materia orgánica. El objetivo de este estudio fue determinar si el nitrógeno total fecal (como un % del CMO) permanece constante sobre tres niveles de alimentación y si la concentración de nitrógeno fecal disminuye con la disminución de la digestibilidad de la materia orgánica. El nitrógeno total fecal no se modificó ( $P = 0.94$ ) con el nivel de alimentación, pero incrementó ( $P < 0.05$ ) con el período de evaluación. La concentración de nitrógeno fecal se correlacionó ( $r = 0.60$ ;  $P < 0.001$ ) con la digestibilidad de la materia orgánica. Los resultados demuestran que no es posible estimar la digestibilidad de la materia orgánica, a partir de la utilización del nitrógeno total fecal, sin la consideración del período del año.

Lancaster (1949a, 1949b) proposed that OMD can be estimated from the relationship between total fecal nitrogen (TFN, as a % of organic matter intake (OMI)) and FNc through the equation:  $OMD = 1 - TFN / FNc$ . Two assumptions are critical to this equation: (1) TFN (as a % of OMI) is a constant and does not change within a range to diet crude protein, and (2) FNc is proportional to OMD. The objective of this study was to test: a) if TFN (as a % of OMI) remains constant over 3 feeding levels, and b) if FNc decreases with decreasing organic matter digestibility of maturing forages.

## Materials and Methods

The study was performed at the Facultad de Agronomía, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina (36° 46' S, 64° 16' W, 210 m ASL), during 1995. The forage was obtained from a pasture sown in spring 1994, of pure Kleingrass (*Panicum coloratum* L.) cv. Verde. At the beginning of each growth season (early October), the pasture was cut at 5 cm above ground to eliminate all standing dead forage, and fertilized with 60 kg urea/hectare.

Measurements of intake and digestibility were carried out during 4 experimental periods (I to IV), each one lasting for 16 days, with 11 days of adaptation and 5 days of data collection. Beginning day of each period was: 21 March, 2 May, 13 June,

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and 25 July, 1995. This was done to obtain forage of different nutritive value for each trial.

Seventeen Pampinta rams in each period ( $51.3 \pm 5.1$  kg,  $56.7 \pm 2.9$  kg,  $66.4 \pm 11.7$  kg and  $74.0 \pm 6.7$  kg in period I to IV, respectively) were grouped by weight, and then randomly assigned within weight group, to 3 feeding levels (treatments): 0.5 maintenance level (feeding level = **L1**; 5 rams), 1.0 maintenance level (feeding level = **L2**; 5 rams), and ad libitum, 1.5 the actual intake of 2 days previous to feeding (feeding level = **L3**; 7 rams). Maintenance level was estimated according to the energy requirements (AFRC 1993) of rams, and the in vitro DM digestibility of the forage (Stritzler et al. 1996). All animals were dewormed 15 days before the beginning of the study and housed in individual pens under continuous light, with free access to water.

The forage, accumulated from the beginning of the growing season, was cut by sickle at 5 cm above ground, before each feeding time (0800 and 1730 hours). Samples of offered forage were obtained before feeding. Refused forage of each experimental animal was removed from the manger every day, and weighed immediately. The animals were fitted with feces bags, secured to harnesses. Total fecal production was measured for each animal by weighting feces twice daily. Samples of forage offered and refused, and feces produced were obtained twice a day, dried at 55° C for 72 hours and ground through a 1-mm screen in a Wiley mill.

Organic matter intake (OMI) was determined by difference between offered and refused OM of food (Burns et al. 1994). In vivo organic matter apparent digestibility (OMD) was estimated by the method of total fecal collection, using the following equation 1:

$$\text{OMD} = [1 - F / \text{OMI}] \times 100 \quad (1)$$

Where:

OMD = In vivo OM apparent digestibility,  
F = daily OM feces output, and  
OMI = OM intake.

#### Chemical analyses and in vitro OM digestibility

Dry matter was determined at 105° C for 48 hours, and ash content was measured gravimetrically by igniting samples in a muffle furnace at 550° C for 12 hours in forage and fecal samples. Aliquots of dried samples were analyzed for total N concentrations by the semi-micro Kjeldahl procedure (2040 Digestion Unit and 1026 Distilling Unit, Tecator, Höganäs,

**Table 1. Chemical composition and in vivo organic matter digestibility of deferred Kleingrass at 4 periods of evaluation.**

	Period <sup>1</sup>			
	I	II	III	IV
	----- (%) -----			
Ash	8.4	8.5	7.4	7.6
Crude protein	9.7	6.8	6.6	5.9
Neutral-detergent fiber	65.4	69.4	71.1	70.6
Acid-detergent fiber	37.7	39.1	40.0	40.5
Acid-detergent lignin	5.2	3.7	4.9	3.6
In vivo organic matter digestibility	56.0	54.3	48.6	51.0

<sup>1</sup>I = 21 March to 6 April; II = 2 to 18 May; III = 13 to 29 June; IV = 25 July to 10 August.

Sweden). Forage samples were additionally analyzed for crude protein (CP, N x 6.25), neutral-detergent fiber (NDF), acid-detergent fiber (ADF), and acid-detergent lignin (ADL), as described by Van Soest and Robertson (1985). In vitro organic matter digestibility (IVOMD) was estimated as described by Tilley and Terry (1963) and modified by Alexander and McGowan (1966). Samples were incubated at 39° C for 48 hours in a rumen fluid-artificial saliva solution, followed by an additional 48-hour period in 20% hydrochloric acid-pepsin solution. Inoculum for the procedure was obtained from rumen cannulated steers fed alfalfa hay. The in vitro values were adjusted by in vivo standards in each batch. The IVOMD values of consumed forage were estimated for each experimental animal, from the amount of OM and IVOMD of offered and refused forage (Meijs et al. 1982).

The total fecal nitrogen (as a % of OMI) was estimated from the nitrogen concentration, feces production and OMI.

#### Statistical analysis

The trial was carried out within a randomized block design, with a factorial arrangement of treatments. To test for differences in total fecal nitrogen as influenced by feeding levels and periods, the following model was used: Y = mean + block + period + levels + period x levels +

error, where Y = total fecal nitrogen (as a % of OMI); period = Periods I to IV, replications of feeding trial, in which 17 rams, different between periods, were fed at 3 different levels (L1, L2, and L3), as explained above, and error = residual error (Steel and Torrie 1980). Statistical significance was determined using the GLM procedure (SAS Institute Inc. 1999). Mean separations were made using LSD at P = 0.05. Simple correlation coefficients between fecal nitrogen concentration and organic matter intake were determined using PROC CORR procedure of SAS Institute Inc. (1999). Paired t-test compared in vitro organic matter digestibility and predicted in vivo organic matter digestibility from total fecal nitrogen and fecal nitrogen concentration.

## Results and discussion

The chemical composition and in vitro organic matter digestibility of the forage offered in each evaluation period are shown in Table 1. All analyses were performed on pooled samples of all days of data collection. The feed quality declined with evaluation period (from I to IV), but the highest differences were found between periods I and II (Table 1).

The interaction between feeding level and evaluation period, for total fecal nitro-

**Table 2. Total fecal nitrogen (as a % of OMI) at 3 feeding levels and 4 evaluations periods.**

Feeding Level <sup>2</sup>	Period <sup>1</sup>				Mean
	I	II	III	IV	
	----- (% of OMI) -----				
L1	0.569	0.627	0.746	0.705	0.662
L2	0.523	0.592	0.773	0.743	0.647
L3	0.523	0.605	0.757	0.707	0.653
Mean <sup>3</sup>	0.537 <sup>c</sup>	0.608 <sup>b</sup>	0.758 <sup>a</sup>	0.715 <sup>a</sup>	
SEM				0.016	

<sup>1</sup>I = 21 March to 6 April; II = 2 to 18 May; III = 13 to 29 June; IV = 25 July to 10 August.

<sup>2</sup>L1 = 0.5 maintenance, L2 = 1.0 = maintenance, L3 = ad libitum.

<sup>3</sup>Means followed by a common superscript are not significantly different at (P > 0.05).

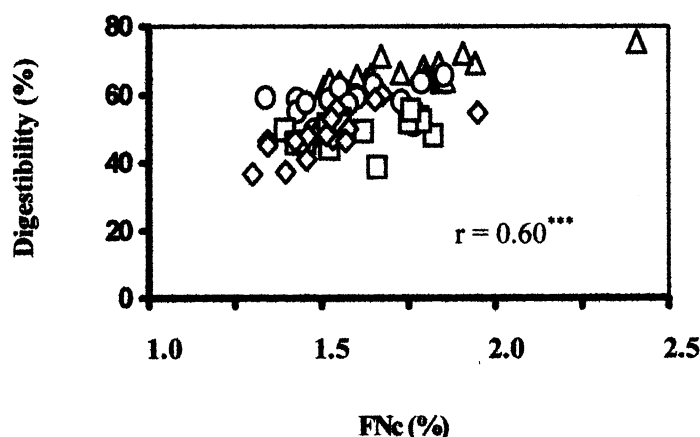


Fig. 1. Relationship between the fecal nitrogen concentration (FNc) and digestibility organic matter. Triangles correspond to 21 March to 6 April, circles 2 to 18 May, squares 13 to 29 June, and rhombus 25 July to 10 August period evaluation.

gen, was not significant ( $P = 0.70$ ; Table 2). The total fecal nitrogen did not change ( $P = 0.94$ ) with feeding level. This finding is in agreement with the results found by Lancaster (1949a) and Barrow and Lambourne (1962) and confirms Lancaster's first assumption that total fecal nitrogen (as a % of OMI) is constant and directly proportional to intake.

Insoluble N in feces comes largely from feed (Ørskov 1982), although a small contribution of N bound to indigestible cell wall of rumen bacteria should be also taken into account. The soluble N present in feces is mostly microbial, and includes considerable ammonia produced by cecum-colon bacteria (Van Soest 1994). Although much of the fecal N may originally have been endogenous, before excretion it has been converted to microbial N through fermentation in the hindgut (Mason 1969). The amount of excreted N depends, partially, on the microbial N yield (Van Soest 1994), on the digestion

site (rumen or cecum-colon) (Ørskov et al. 1972) and the digestion extent (Arman et al. 1975). When forages of similar nutritive value are considered, total fecal nitrogen (as % of OMI) keeps constant with feeding level because microbial N yield is proportional to intake.

The total fecal nitrogen, however, increased ( $P < 0.05$ ) from evaluation periods I to III. It seems likely that this increase is associated to changes in digestion site; according to Thomas (1988), with good-quality forages, 5–15% of cell wall carbohydrates are fermented in the cecum-colon. As forages mature, this proportion increases; Hogan et al. (1969) found that up to 25% of the total digestion of low quality grasses occurs in the hindgut. Rumen microbes, but not colon-cecum microbes, are exposed to the host animal's enzymes (Mason 1969); therefore the fermentation site might affect the amount of total fecal nitrogen (Ørskov et al. 1972). The increasing proportion of

feed carbohydrates fermented in cecum-colon would affect mostly the soluble N in feces (Ørskov et al. 1972), whilst the insoluble N should not be changed.

The fecal nitrogen concentration was correlated with organic matter digestibility ( $r = 0.60$ ;  $P < 0.001$ ; Fig. 1) across all 4 periods. Correlations within

each period were also obtained; they were all significant ( $P < 0.05$ ) but not high ( $r = 0.77, 0.67, 0.50$ , and  $0.66$  for period I, II, III and IV, respectively), due to large between experimental animals variations of total fecal nitrogen excretion.

Although fecal nitrogen concentration increased with organic matter digestibility, the correlation across the 4 periods was not high. This would allow us to infer that total fecal nitrogen, as determined in this study, changes with period. In other words, for a given value of fecal nitrogen concentration obtained in different periods, the organic matter digestibility would be different. When analyses were run within each experimental period, the correlations were significant.

The estimations of digestibility by the in vitro technique and the fecal N index were not different ( $P > 0.05$ ; Table 3) in 3 of the 4 periods. The means of both methods across periods were different ( $P < 0.05$ ). However, this difference was only of 1.5%.

The comparison of indirect techniques to predict in vivo digestibility of consumed forage presents limitations. The main problem of the in vitro technique is the collection of samples representative of the diet consumed by the animal. The fecal N index technique requires a feeding trial to estimate total fecal nitrogen (as % of OMI), using the same forage to be grazed. The nitrogen fecal concentration is then assessed in fecal samples from the grazing animals, and diet digestibility can be predicted from the equation:  $OMD = 1 - TFN / Nfc$ . The usefulness of this technique is restricted to situations where the forage to be grazed can also be cut to run a feeding trial simultaneously. The main advantages of the technique are that the analytical requirements are low and simple, and does not require diet sampling.

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Table 3. Estimated organic matter digestibility (OMD) of consumed herbage using either in vitro organic matter digestibility or fecal N index in Periods I to IV ( $n = 17$ ).

Period <sup>1</sup>	In vitro OMD	Fecal N index <sup>2</sup>
	OMD = $(1 - TFN / FNc) * 100$	
	(%)	
I	59.5 <sup>b</sup>	62.5 <sup>a</sup>
II	54.6 <sup>a</sup>	56.3 <sup>b</sup>
III	49.3 <sup>a</sup>	50.3 <sup>a</sup>
IV	51.5 <sup>a</sup>	51.9 <sup>a</sup>
Media	53.8 <sup>b</sup>	55.3 <sup>a</sup>

Means in the same row followed by a common superscript are not significantly different at ( $P > 0.05$ ).

<sup>1</sup>I = 21 March to 6 April; II = 2 to 18 May; III = 13 to 29 June; IV = 25 July to 10 August.

<sup>2</sup>TFN, total fecal nitrogen; FNc, fecal nitrogen concentration.

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# Available water influences field germination and recruitment of seeded grasses

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## Abstract

Periodic summer rainstorms in some semi-arid regions result in variable soil moisture and differential establishment of seeded species. A 2-year study investigated soil water effects on germination and survival of 6 native and 2 non-native southwestern U.S. grass species. Bags of seeds were buried and retrieved before and during the summer rainy season. High field germination in seed bags (20–100%) and limited germination in the laboratory of seeds that were ungerminated in seedbags (0–45%) were exhibited by 6 native grasses following initial rainfall events in which the surface soil was saturated for 2 days or water potential (1–3 cm depth) was above  $-1.5$  MPa for more than 9 days. Fewer Lehmann lovegrass (*Eragrostis lehmanniana* Nees) seeds germinated in response to initial and subsequent rainfall events (0–49%), but this species retained more residual germinable seeds (49–99%) than all other species studied. For 2 sowing dates, the soil drying front exceeded estimated seminal root depth 13 days after germination. Lack of recruitment for some species sown on these dates was probably due to seedling desiccation before adventitious roots had sufficient time to develop. The ability of Lehmann lovegrass to retain a viable seedbank when rainstorms are separated by long dry periods allows it to establish better than some native grasses that germinate quickly and are then subject to seedling desiccation. During a summer with more consistent rainfall, native species recruitment was greatest when seeds were planted during, rather than before the summer rainy season.

**Key Words:** warm-season, desert grassland, rangeland revegetation, drought tolerance, *Bouteloua curtipendula*, *Bothriochloa barbinodis*, *Leptochloa dubia*, *Digitaria californica*, *Muhlenbergia porteri*, *Eragrostis lehmanniana*, *Eragrostis intermedia*, *Eragrostis lehmanniana* X *tricophora*

In semi-desert grasslands of the southwestern United States, native warm-season perennial grass seedlings often fail while those of perennial non-native species are successful (Cox et al. 1982, Roundy and Biedenbender 1995). Lehmann lovegrass (*Eragrostis lehmanniana* Nees), a warm-season perennial bunchgrass introduced from South Africa, is commonly used for revegetation because of its reliable establishment (Cox et al. 1982).

Summer precipitation in the southwestern United States is spo-

## Resumen

Las tormentas periódicas de verano que ocurren en algunas regiones semi-áridas resultan en una humedad del suelo variable y un establecimiento diferencial de las especies sembradas. Un estudio de 2 años investigó los efectos del agua del suelo en la germinación y sobrevivencia de 6 especies de pastos nativos del sudoeste de Estados Unidos y 2 introducidas. Bolsas con semilla se enterraron y recuperaron antes y durante la estación de lluvias de verano. La alta germinación en campo en las bolsas de semilla (20–100%) y la germinación limitada en el laboratorio de las semillas que no germinaron en las bolsas (0–45%) se presentó en las 6 especies de zacates nativos después de los eventos iniciales de lluvia en los cuales la superficie del suelo se saturó por 2 días o el potencial del agua (1–3 cm de profundidad) estuvo arriba de  $-1.5$  MPa por mas de 9 días. Pocas semillas de “Lehmann lovegrass” (*Eragrostis lehmanniana* Nees) germinaron en respuesta de los eventos de lluvia iniciales y subsecuentes (0–49%), pero esta especie retuvo mas semillas germinables residuales (49–99%) que cualquier otra de las especies estudiadas. En dos fechas de siembra el frente de secado del suelo excedió la profundidad estimada de las raíces seminales a los 13 días después de la germinación. La falta de establecimiento de algunas especies sembradas en estas fechas probablemente se debió a la desecación de la plántula antes de que las raíces adventicias tuvieran suficiente tiempo para desarrollarse. La habilidad del “Lehmann lovegrass” para mantener un banco de semilla viable cuando las tormentas son separadas por periodos secos largos le permite establecerse mejor que algunos zacates nativos que germinan rápidamente y entonces están sujetos a la desecación de la plántula. Durante un verano con lluvia mas consistente, el establecimiento de especies nativas fue mayor cuando las semillas se sembraron durante, en lugar de antes, la estación lluviosa de verano.

radic (Humphrey 1958, McClaran 1995), resulting in variable soil water availability during the growing season. Where soil water drying is rapid, strategies to avoid, rather than tolerate drought, may be most useful. The fate of seeds and seedlings is the result of 1) whether or not seeds germinate during a wet period, and 2) the length of water availability during the subsequent dry period (Frasier and Lopez 1990). If wet periods are short and infrequent, fast-germinating species are likely to fail because their seminal roots will not stay ahead of the soil drying front long enough for adventitious roots to develop and supply water to the seedling. One to several weeks of soil water availability at the location of

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the coleoptilar node near the soil surface is generally required for warm-season grass seedlings to develop adventitious roots (Wilson and Briske 1979, Ries and Svejcar 1991, Roundy et al. 1993, Abbott 1999). Depending on ambient conditions, short, infrequent rainstorms may not even wet the seedling root zone for longer than a few days (Roundy et al. 1997). Slower-germinating species may not germinate but remain germinable during short wet periods. This may increase their probability of establishment by delaying germination until sufficient rain has fallen to ensure longer water availability to roots. Slower germination may favor recruitment, if initial summer rainfall is less consistent than later summer rains. Although rainfall patterns are highly variable from year to year, long-term records from southeastern Arizona indicate that storms are generally less frequent in the beginning of the summer rainy season than later in the season (Smith and Schreiber 1973, Frasier and Lopez 1990, Roundy et al. 1996).

In southeastern Arizona, the recommended time to reseed warm-season grasses has been in May or June, prior to the beginning of the summer rainy season (Jordan 1981). Utilizing these seeding practices, successful rangeland reseeding in this region can be expected in 1 of 10 years (Cox and Jordan 1983). In greenhouse studies in sandy soil, Frasier et al. (1984, 1985) and Frasier (1989) found that slower-germinating warm-season grasses were more likely to establish than faster-germinating native grasses when initial short wet periods and subsequent long dry periods were followed by long wet periods.

These results led us to predict that recruitment of fast-germinating native grasses could be improved by seeding them during, rather than before the onset of summer rains. We tested the effects of sowing date on field germination, residual

germination (percentage of seeds not germinating in the field but still able to germinate), and seedling recruitment.

## Materials and Methods

### Study Site

Studies were conducted in a semi-desert grassland site at the Santa Rita Experimental Range, approximately 40 km southwest of Tucson, Ariz. (31° 47' N. lat., 110° 37' W. long.). The site is located on an alluvial fan with a maximum slope of 5%; elevation is 1,075 m (Cox et al. 1990). Annual precipitation averaged 415 mm over the last 30 years, and varied between 205 and 765 mm (SRER 1999). Precipitation is bimodally distributed, with approximately 60% falling as rain between July and September, and most of the remaining 40% falling as rain or snow between October and April (Cox et al. 1990, Roundy et al. 1997). Air temperatures range annually between 0° and 40° C (Green and Martin 1967).

Soils are classified as coarse-loamy, mixed, superactive, nonacid, thermic Typic Ustic Torrifluvents and coarse-loamy, mixed, superactive, thermic Ustic Haplargids of the Combate-Diaspar complex, and the site is classified as a complex of sandy loam upland and deep sandy loam range sites in the 305 to 406 mm precipitation zone (Breckenfeld and Robinett 1997). Research was conducted within a livestock enclosure that had been fenced since 1984. The area inside the enclosure supports a herbaceous community dominated by Lehmann lovegrass. Nearby vegetation is typical semi-desert grassland with an overstory of velvet mesquite (*Prosopis velutina* Woot.) and a shrubby understory of burroweed (*Happlopappus tenuisectus* [Green] Blake), catclaw aca-

cia (*Acacia greggii* Gray), false mesquite (*Calliandra eriophylla* Benth.), and prickly pear *Opuntia* Miller spp. Common native perennial grasses include three-awns (*Aristida* L. spp.), Arizona cottontop (*Digitaria californica* [Benth.] Chase), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), Rothrock grama (*B. rothrockii* Vasey), black grama (*B. eriopoda* Torr.), slender grama (*B. filiformis* [Fourn.] Griffiths), and sprucetop grama (*B. chondrosioides* [H.B.K.] Benth.) (Martin 1966). Experimental plots were mowed, raked, and sprayed with glyphosate (N-[phosphonomethyl] glycine, a non-selective herbicide) and were maintained relatively free of non-study vegetation by mowing, hoeing, and raking.

Two field studies were conducted concurrently during the summers of 1992 and 1993 using 8 warm-season perennial grass species (Table 1). Prior to sowing all seeds were mechanically cleaned to remove appendages from caryopses. Seeds were sown before summer rains on 16 June 1992 and 15 June 1993, and after summer rains began on 30 July 1992 and 2 August 1993. Experiments were replicated in 3 blocks.

### Germination Study

This experiment employed a randomized complete block design in a split-split-split-plot factorial arrangement, with year as the main factor, sowing date as level 2, species as level 3, and retrieval date as level 4. Seeds were retrieved twice after each sowing to determine changes in germination over time. The first retrieval occurred as the top 1 cm of soil was drying after the initial rainfall event. The second retrieval followed after at least 1 subsequent rainfall and drying event.

Seeds were placed in nylon mesh bags prior to burial to facilitate recovery of all

**Table 1. Common and scientific names of species used in germination and recruitment studies.**

Scientific Name	Common Name	Seed Source
<u>Native:</u>		
<i>Bouteloua curtipendula</i> (Michx.) Torr.	Sideoats grama	Native Plants, Inc., Arizona
<i>Leptochloa dubia</i> (H.B.K.) Nees	Green sprangletop	Granite Seed Co., Utah; Texas origin
<i>Bothriochloa barbinodis</i> (Lag.) Herter	Cane beardgrass	Tucson Plant Materials Center, Arizona, Natural Resource Conservation Service
<i>Digitaria californica</i> (Benth.) Chase	Arizona cottontop	Granite Seed Co., Utah; Arizona origin
<i>Muhlenbergia porteri</i> Scribn.	Bush muhly	Collected Jornada Expt. Range, New Mexico
<i>Eragrostis intermedia</i> Hitchc.	Plains lovegrass	Native Plants, Inc., Arizona
<u>Non-native:</u>		
<i>Eragrostis lehmanniana</i> Nees	Lehmann lovegrass	Native Plants, Inc., Arizona
<i>Eragrostis lehmanniana</i> Nees x	Cochise lovegrass	Native Plants, Inc., Arizona
<i>E. trichophora</i> Coss and Dur.		

planted seeds. Individual bags contained 10 pure live seeds of 1 species and were buried at 3–5 mm depth; bags contained seeds only, and did not contain soil. Sample sizes differed in the 2 years. Six bags of each species were buried in each block on each sowing date in 1992 (N = 18), resulting in a sample size of 9 bags per sowing date/species/retrieval date. In 1993, 4 bags of each species were buried on each sowing date in each of three blocks (N = 12), resulting in 6 bags per sowing date/species/retrieval date.

Seeds in retrieved bags were inspected for germination; a seed was considered germinated if the radicle visibly protruded beyond the testa. Ungerminated seeds were placed on wetted filter paper in petri dishes and placed in a 25° C constant-temperature germination chamber. Seeds were checked daily for germination, and those that germinated in the germination chamber were considered germinable. Seeds that did not germinate after 14 days in the germination chamber were considered dead or dormant. Due to difficulties in differentiating between dead and dormant seeds following this procedure, dead or dormant seeds were excluded from analysis and interpretation; subsequent analyses were conducted on the proportion of seeds that had germinated in the field or were germinable after retrieval.

### Recruitment Study

This experiment employed a randomized complete block design in a split-split-plot factorial arrangement, in which year was the main factor, sowing date was level 2, and species was level 3. Within each sowing date/species treatment combination there were 10 circular sub-plots (cylinders), each of which was 15 cm in diameter. Cylinders were constructed by

excavating 15 x 15 cm pits to a depth of approximately 5 cm, placing a 15-cm diameter by 7.5-cm deep cylinder of PVC pipe into the pit, and backfilling around the outside of the cylinder. Each cylinder was then filled with sandy loam soil. Precautions were taken to reduce the potential of contamination of the cylinders with seeds of the extant seedbank. In 1992, cylinders were filled with autoclaved soil collected from the study site. In 1993, off-site soil was imported from an undisturbed location where the soil profile supported a deep layer of sandy loam very similar to the soil at the study site; the surface 10 cm of soil was not used in the study. On each sowing date, 25 pure live seeds of a single species were planted into each cylinder. Consistent with typical recommendations for the species (Jordan 1981), small-seeded species (lovegrasses) were covered with approximately 0.5 cm of soil, and larger-seeded species were covered with approximately 1 cm of soil. The number of surviving seedlings in each cylinder was recorded at the end of each season. Recruitment was calculated as a percentage of seeds sown.

### Environmental Data

Throughout the observation period, soil moisture and temperature were recorded in each block, as described by Roundy et al. (1997). Soil moisture was estimated with calibrated Colman fiberglass soil cells (Colman and Hendrix 1949) at 5 depths in the soil: 1–3, 4–6, 8–10, 12–14, and 18–20 cm. Temperature was measured with copper-constantan thermocouples buried at 1, 2, 5, 9, 13, and 19 cm. At each depth, soil moisture measurements were replicated with 5 soil cells in each of 3 blocks, and temperature measurements were replicated using 3 thermocouples. Ambient climatic

data (precipitation, air temperature, relative humidity, wind speed, and incident solar radiation) were measured on site. Measurements were recorded every minute using dataloggers (CR-10, Campbell Scientific Inc., Logan, Utah) and stored as an hourly sum for precipitation and as hourly means for all other variables.

### Data Analysis

Germination response and seedling establishment data were analyzed using likelihood-based methods appropriate for general linear mixed models (MIXED procedure in SAS; Littell et al. 1996). Blocks were considered random effects, whereas all other factors (year, sowing date, species, and retrieval date) were considered fixed effects. The data were not normally distributed, and consequently were rank-transformed prior to analysis (Conover and Iman 1981). Nylon bags served as replicates in the germination response study; cylinders served as the replicates in the seedling establishment study.

## Results and Discussion

### Rainfall and Soil Moisture Patterns

Total precipitation and distribution of precipitation during the summer months differed between 1992 (Fig. 1a) and 1993 (Fig. 1b). Total rainfall between 1 July and 10 September was greater in 1992 (219 mm) than 1993 (157 mm), but rainfall was more frequent in 1993 than 1992. Therefore, available water in the surface soil (matric potential > -1.5 MPa at 1–3 cm) was 2.3 days greater in 1993 (39.7 days) than in 1992 (37.4 days) for this same period. Seeds for each sowing date and retrieval were exposed to different ini-

**Table 2.** Wet (soil matric potential at 1–3 cm deep > -1.5 MPa) and dry periods associated with 8 seed bag retrieval dates for warm-season grasses in southeastern Arizona.

Available Water Period	Date Sown	Date Retrieved	Total time of seed bag burial beginning with first wet period			Total Time Wet	Initial Wet Period	Chronological wet-dry times						
			Wet	Dry	Total			Dry	Wet	Dry	Wet	Dry	Wet	Dry
			----- Days) -----			(%)	----- Days) -----							
S 1	16 Jun 1992	10 Jul 1992	2.3	0.0	2.3	100	2.3							
L 2	16 Jun 1992	20 Jul 1992	9.3	3.0	12.3	76	9.3	3.0						
L 3	30 Jul 1992	12 Aug 1992	11.1	1.9	13.0	85	11.1	1.9						
L 4	30 Jul 1992	9 Sep 1992	20.3	20.8	41.1	49	11.1	7.2	0.8	4.7	8.3	8.9		
S 5	15 Jun 1993	5 Jul 1993	2.8	1.0	3.8	74	2.8	1.0						
S 6	15 Jun 1993	20 Jul 1993	11.1	7.1	18.2	61	2.8	4.4	1.6	0.1	2.8	0.3	3.9	2.3
L 7	2 Aug 1993	16 Aug 1993	12.7	1.3	14.0	91	12.0	1.3	0.7					
L 8	2 Aug 1993	28 Aug 1993	22.6	3.4	26.0	87	12.0	1.3	5.8	2.1	4.8			

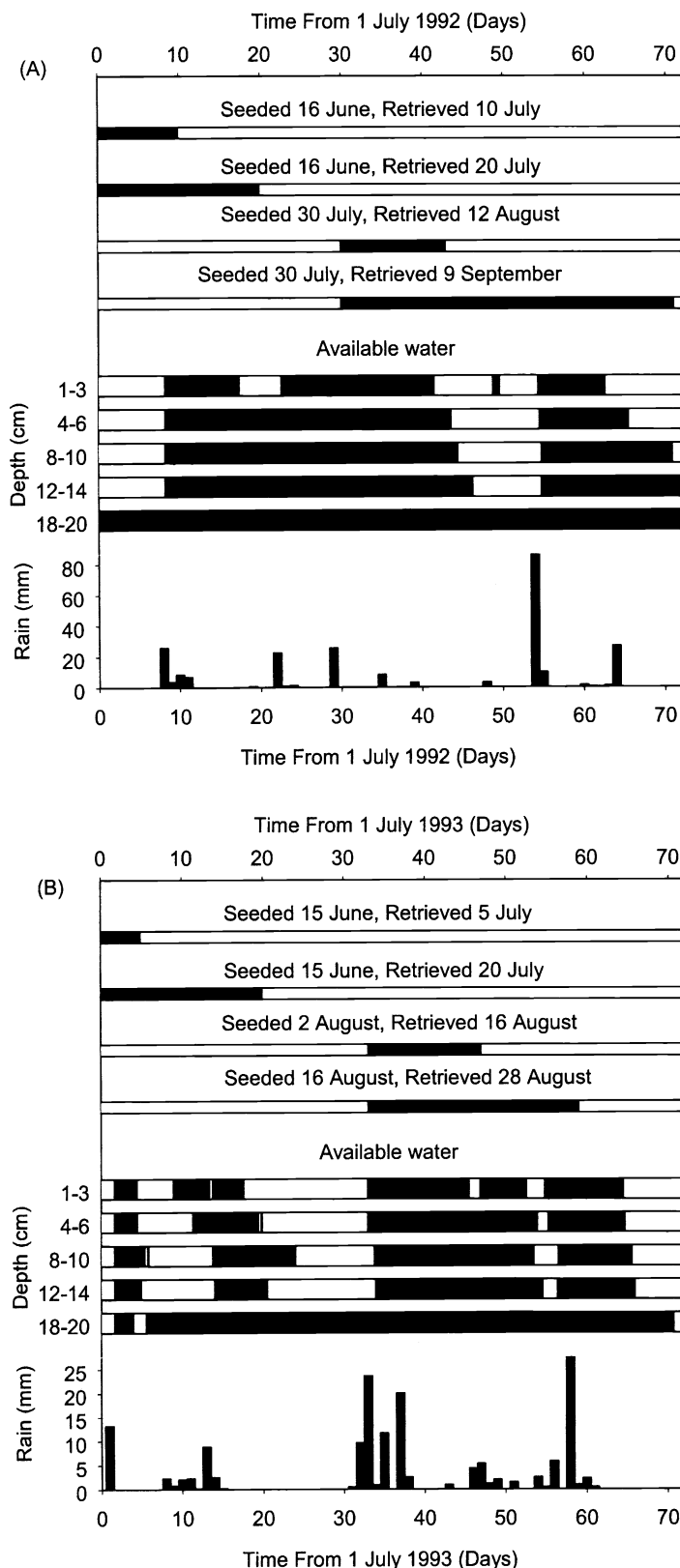


Fig. 1. Daily precipitation (vertical bars), time of seed exposure to soil, and soil moisture availability patterns when volumetric soil water content > a matric potential equivalent of  $-1.5$  MPa (dark horizontal bars indicate periods of available soil moisture) at the Santa Rita Experimental Station field site for the summers of 1992 (A) and 1993 (B).

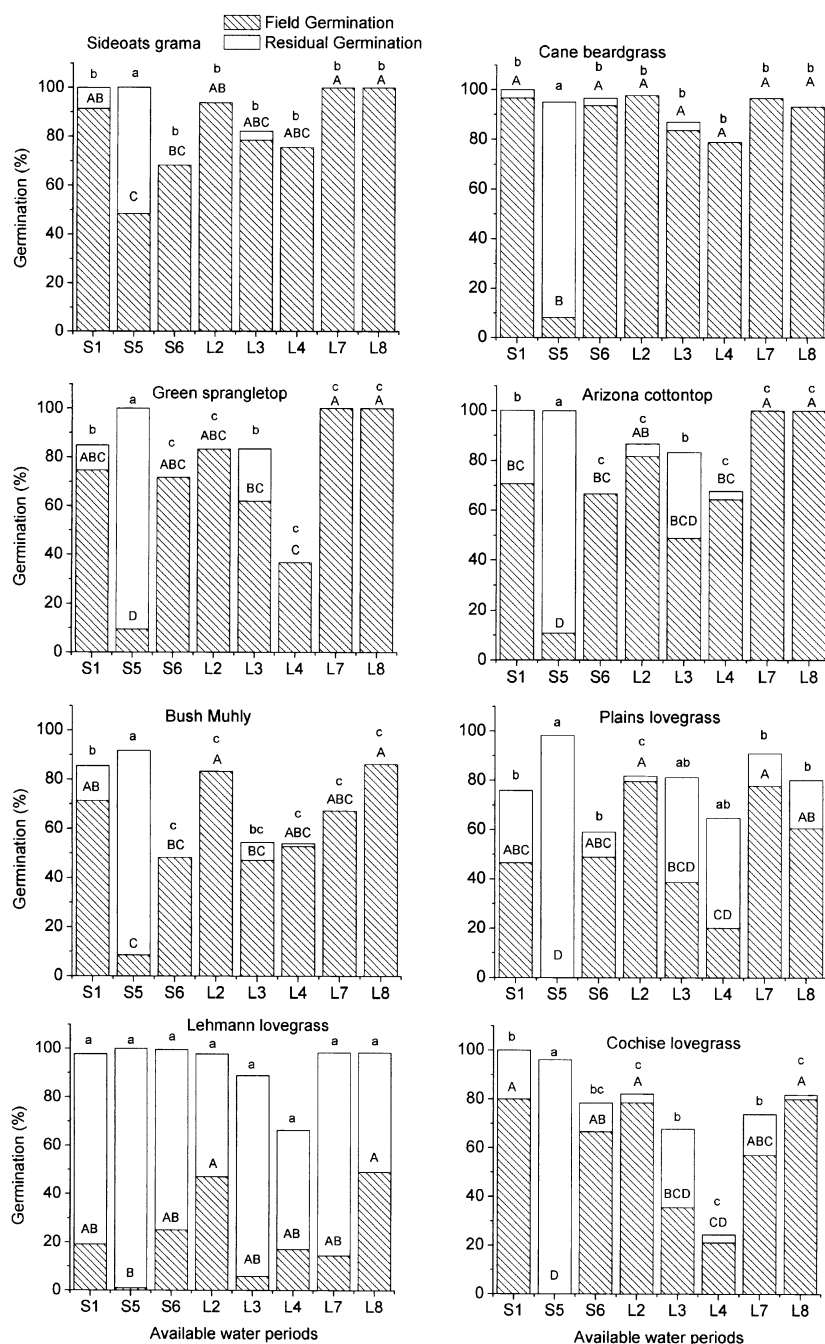
tial and subsequent available water periods (Table 2). Out of the 8 different retrievals (2 years  $\times$  2 sowing dates  $\times$  2 retrievals), seeds in 3 retrievals had short initial available water periods of 2.3–2.8 days (S1, S5, S6-Table 2), while seeds in 5 retrievals were exposed to much longer initial wet periods of 9.3–12 days (L2, L3, L4, L7, L8-Table 2). Subsequent to the initial wet period, seeds in the different retrievals were exposed to a range of dry periods lasting from 0 to 7.2 days. Total exposure to available water while seeds were buried ranged from 2.3 to 22.6 days across the 8 retrievals. Percentage of burial time that seeds were exposed to available water beginning with initial wetting ranged from 49–100%. For the 2 years of this study, seeds sown in the middle of the rainy season (30 July 1992 and 2 August 1993) were exposed to longer initial periods of available water (11.1 and 12 days) than those sown prior to the rainy season (16 June 1992–2.3 days and 15 June 1993–2.8 days). Greater precipitation in 1992 than 1993 resulted in more continuous periods of available water at soil depths of 4–14 cm for 1992 than 1993, but water was continuously available at 18–20 cm from 8 July through 8 September in both years (Fig. 1).

### Germination Study

For field germination, all main effects except year ( $df = 1,64$  for year and sowing date,  $df = 7, 64$  for species), and all 2 and 3-way interactions of year, sowing date, species, and retrieval ( $df = 7, 64$ ) were significant ( $P < 0.05$ ) except for species  $\times$  sowing date. The significance level of the 4-way interaction of year  $\times$  sowing date  $\times$  species  $\times$  retrieval date for field germination was  $p = 0.079$  ( $df = 7,64$ ). For residual germination, all main effects ( $df = 1,64$  for year and sowing date,  $df = 7, 64$  for species) and 2, 3, and 4-way interactions ( $df = 7,64$ ) were significant ( $P < 0.05$ ) except for the interaction of year  $\times$  species  $\times$  retrieval. The significance of these interactions suggests that field and residual germination responses might best be understood in terms of the response of each species to the 8 different available water periods experienced. Therefore, for each species, 28 pair-wise  $t$ -tests were conducted for field and residual germination among these 8 periods using a significance level of  $P < 0.05/28$  (Fig. 2)

### Short initial available water periods

For 2 of the 3 retrievals that had initially short available water periods (S1, S6), most species had high to moderate field



**Fig. 2.** Field (hatched bars) and residual (open bars) germination percentages of warm-season grasses sown on 4 dates and experiencing 8 different available water periods (Table 2). Means for different available water periods with the same letter are not significantly different ( $p = 0.05/28$ ) for a species. Means separation for field germination indicated with upper-case letters; means separation for residual germination indicated with lowercase letters.

germination and moderate to limited residual germination (Fig. 2). In contrast, the retrieval that most differed in germination from all others was that associated with available water period S5, which produced limited to no field germination and high residual germination. Seeds for this retrieval experienced 2.8 days of available

water followed by 1 day when the soil was dry (Table 2). Seeds experiencing 2.3 days of available water and no dry days (S1) had similar total germination as those from S5, but evidently germinated more quickly. Seeds from S1 received at least 30 mm precipitation and soil water content at 1-3 cm was near saturation for the 2.3

days prior to retrieval. In contrast, seeds from S5 received 13 mm rainfall and soil water content was near saturation for about 0.8 days, decreased to a matric-potential equivalent of  $-1.5$  MPa over the next 2 days, and were dry for the last day prior to retrieval. Seeds retrieved after available water period S6 were exposed to 4 wet-dry periods before retrieval, with the first dry period being 4.4 days long (Table 2). Total germination for some species was less for this available water period than for S1 and S5, suggesting that some seeds germinated and died during the dry periods.

#### Long initial available water periods

Most species had moderate to high field germination and limited to moderate residual germination after initial exposure to long wet periods ( $> 9$  days; L2, L3, L4, L7, L8- Table 2). For all species, field germination that was maximum or not significantly different from the maximum occurred for seeds sown 2 August 1993 and retrieved 14 or 26 days later (L7, L8, Table 2). These seeds experienced 12 days of available water immediately after sowing and had limited exposure to dry soil ( $< 2.1$  days). Field germination was also maximum for seeds with available water period L2, consisting of 9.3 days of available water and 3 dry days. Total or field germination for some species was less for available water periods L3 and L4 than for L2, L7, and L8 (Fig. 2). For available water period L4, seeds were exposed to a 7.2-day dry period after initial exposure to 11.1 days wet. Some seeds may have died or gone dormant during that long dry period.

#### Species responses

The different species exhibited specific germination behavior in relation to the different available water periods (Fig. 2). Most obvious was the conservative germination behavior of Lehmann lovegrass compared to the other species. Lehmann lovegrass had less than 50% field germination and very high residual germination for all retrievals. Except for seeds associated with available water period S5, most other species had much higher field than residual germination. Sideoats grama, cane beardgrass (*Bothriochloa barbinodis* [Lag.] Herter), and bush muhly (*Muhlenbergia porteri* Scribn.) especially had very limited residual germination. Green sprangletop (*Leptochloa dubia* H.B.K.), Arizona cottontop, plains lovegrass (*Eragrostis intermedia* Hitch.), and Cochise lovegrass (*Eragrostis lehmanni-*

*ana* Nees x *E. trichophora* Coss and Durr.) all had residual germination of > 20 % for certain available water periods. Besides available water period S5, period L3 produced the highest residual germination in these species. Seeds for this retrieval were sown in wet soil 30 July 1992 and retrieved after 11.1 days of wet soil and 1.9 days of dry-soil exposure. These seeds sown in wet soil may not have imbibed as fast as those exposed to the saturating conditions of initial rain (L2, L7, L8) and may have had slower germination and therefore higher residual germination for this retrieval.

#### *Sowing dates*

Overall, field germination was about 10% lower and residual germination about 16 % higher for seeds sown prior to, rather than in the middle of the rainy season. This could be attributed to the longer initial wet periods for the mid-season sowing dates (Table 2). Seeds from the second retrievals should be more indicative of potential field establishment than those from the first retrievals because they experienced a longer period of exposure to subsequent wet and dry periods. For the second retrievals, seeds sown prior to the rainy season in 1992 (L2) had greater field germination (80.6%) than those sown in the middle of the rainy season (L4-45.8%). The reverse was true for 1993 where seeds sown prior to the rainy season (S6) had 61.2% field germination and those sown in the middle of the season (L8) had 83.6%. Germination responded more to actual available water patterns after sowing than to the date of sowing.

#### *Germination and hydrotime*

Seed requirements for a critical minimum level of hydration necessary for germination are species-specific and vary widely (Collis-George and Sands 1959, Hegarty 1978). Gummerson (1986) and Bradford (1990) developed germination models that incorporate dynamic seed water potentials as would be encountered under field conditions of variable soil moisture availability. These models incorporate 2 components of hydration: base water potential (i.e., potentials below which fewer than 50% of seeds germinate), and hydrotime (i.e., accumulated time that seed water potential is above the base water potential). Using grass species common to the present study, Adams (1997) developed parameters for a hydrotime model conceptualized by Gummerson (1986) and Bradford (1990). He found that Lehmann lovegrass and sideoats grama are

capable of initiating germination at relatively low water potentials, but Lehmann lovegrass required much longer exposure time than sideoats grama to complete germination. Whereas sideoats grama and Cochise lovegrass both required relatively short exposure to base water potentials to germinate, Cochise lovegrass required more available water (higher base water potential) than sideoats grama (Adams 1997).

Relative rates of germination under field conditions are in general agreement with previous studies of emergence. Maximum emergence of sideoats grama was reached in 2–3 days in greenhouse and growth chamber studies (Olmsted 1941, Frasier et al. 1984, 1985, Adams 1997); this pattern is expected for a species that has a short hydrotime requirement and the potential to germinate at a wide range of soil water potentials. Similarly, delayed emergence of Lehmann lovegrass has been observed in greenhouse and growth-chamber emergence studies (Frasier et al. 1985, 1987, Adams 1997), and is predicted for a species capable of germinating at a wide range of soil water potentials with a long hydrotime requirement.

Species-specific differences in hydration requirements are most clearly demonstrated by examination of the 15 June 1993 sowing; the first rainfall after sowing was scant and seeds were retrieved after approximately 2 days from a drying soil (matric potential at 1–3 cm above –1.5 MPa). Germination for the first retrieval date of that sowing (S5) was relatively low (0–11%) for all species except sideoats grama (48%), yet by the second retrieval (S6), germination ranged from 48% to 94% for all species except Lehmann lovegrass. In a growth chamber study, cane beardgrass, bush muhly, and Cochise lovegrass reached 50% germination in 1.7 days (Roundy and Biedenbender 1996); thus, field germination after the first retrieval was less than expected for these species.

Low germination in the present study would result if soil matric potentials at the depth of seeds were lower than the base water potentials for those species. It is likely that soil drying occurred more quickly at the < 1.0-cm depth of seed burial than at the 1–3-cm depth of the soil moisture sensors. Under drying soil conditions, species with high base water potentials probably did not have sufficient time to complete germination; sideoats grama germination could proceed as long as the soil matric potential did not drop below –1.68 MPa (Adams 1997). Residual germinability following the first retrieval of

the 15 June 1993 sowing was generally high (> 83%) for all species except sideoats grama. The second period of favorable moisture conditions lasted approximately 8.3 days with 2 intermittent dry periods of 0.1 and 0.3 days (S6-Table 2, Fig. 1b). By the second retrieval date 48–94% of seeds for all species except Lehmann lovegrass had germinated (Fig. 2). Thus, expected species-specific germination responses were in agreement with hydrotime parameter values of Adams (1997).

Lehmann lovegrass field germination was generally lower than expected based on germination rates and moisture requirements determined in laboratory studies. Roundy and Biedenbender (1996) found 50 % of germinating Lehmann lovegrass to germinate in 2.2 to 3.7 days under summer seedbed temperatures. Lehmann lovegrass total germination and germination rate vary widely within and among seed lots (Hardegree and Emmerich 1991), and germination response varies with temperature, water stress, light, seed priming, seed age, and wet-dry sequences (Knipe and Herbel 1960, Tapia and Schmutz 1971, Frasier 1989, Jordan and Haferkamp 1989, Hardegree and Emmerich 1992a, 1992b, Roundy et al. 1992a, 1992b). Lehmann lovegrass germination was low in constant darkness, but increased with exposure to red light and with exposure to fluorescent light and alternating temperature (Tapia and Schmutz 1971, Roundy et al. 1992a). Lehmann lovegrass germination in the field may have been limited by conditions of low light associated with burial of the seed bags, and subsequent high residual germinability was expressed after exposure to light in the laboratory. However, a small percentage of seeds of Lehmann lovegrass germinate in darkness (Roundy et al. 1992a) and some seeds germinated after burial in soil at a depth of 0.6 cm (Winkel et al. 1991). The highly variable germination responses of Lehmann lovegrass to a variety of environmental conditions (Hardegree and Emmerich 1991), helps explain why some subpopulations germinate under initial rainfall conditions and others delay germination. This hypothesis is supported by the observation that Lehmann lovegrass produced multiple cohorts of emerged seedlings after sowing directly into soil at this field site (Abbott 1999).

#### **Recruitment Study**

Seedling survival at the end of the growing season was significant for all possible 2-way interactions of year, sowing date,



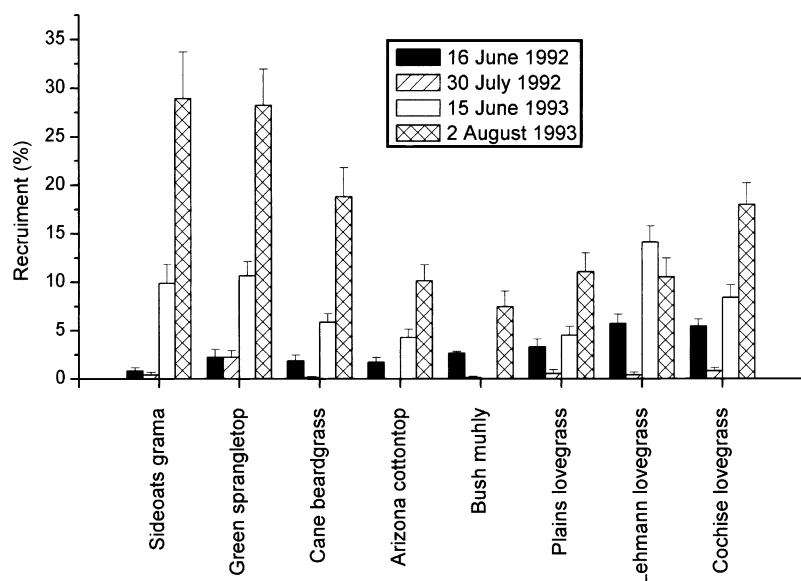


Fig. 3. Mean recruitment as a percentage of number of seeds sown for warm-season grass species seeded on 4 dates on a sandy loam upland site in southeastern Arizona. Error bars represent standard errors of the means.

and species (year  $\times$  sowing date  $df = 1,4$ , for all others  $df = 7,56$ ) but was not significant for the 3-way interaction of those factors ( $df = 7,56$ ,  $P = 0.33$ ). Of all possible 2-way interactions, the interaction of year and sowing date was strongest ( $p = 0.0002$ ). In 1992, more seedlings established from the 16 June sowing (2.6%) than from the 30 July sowing (0.6%); in 1993, the 15 June sowing (7.2%) resulted in fewer established seedlings than did the 2 August sowing (16.7%). In general, more seedlings established for each species in 1993 than in 1992, but the magnitude of the difference among years differed among species (Fig. 3). For example, seedling recruitment was lowest for bush muhly in 1992 (0.2%) and in 1993 (3.7%). In 1992, Lehmann lovegrass (3.1%) and Cochise lovegrass (3.1%) had the highest seedling establishment, whereas in 1993 green sprangletop had the highest seedling recruitment (19.5%). When considering the interaction of species and sowing date, bush muhly had the lowest seedling recruitment for all species in both the pre-summer (0.1%) and mid-summer (3.8%) sowings. Lehmann lovegrass had the highest seedling recruitment for the pre-summer sowings (9.9%), and green sprangletop had the highest seedling recruitment for the mid-summer plantings (15.3%). In general, the number of established seedlings for the mid-summer sowings was either greater or not different than the pre-summer sowings for all species except Lehmann lovegrass.

Successful recruitment requires envi-

ronmental conditions that promote germination and support continued seedling growth. Once seeds have germinated, seedling survival is compromised if the soil drying front surpasses the advancing seminal root depth in the absence of additional rain (Roundy et al. 1997). Seminal roots must supply water to the seedling until adventitious roots develop near the soil surface. That requires 9 days to 3 weeks of available water at the soil surface for these warm-season grasses (Roundy et al. 1993, Abbott 1999). Knowing the time of germination, estimating seminal root growth, and knowing the soil water availability by depth, it should be possible to predict seedling success or failure (Roundy et al. 1997). Seminal root growth varies with species, soil moisture, and ambient conditions (Abbott 1999, Olmsted 1941, Sosebee and Herbel 1969, Simanton and Jordan 1986, Roundy et al. 1993), but could be liberally estimated at 1 cm day<sup>-1</sup>.

Using this approach, seminal root depth would have been exceeded by the soil drying front before substantial adventitious root development for seeds sown 30 July 1992 and 15 June 1993. Establishment failure was predicted for these sowing dates, while actual establishment in the sub-plots averaged 0.6 % for the 1992 date and 7.2% for the 1993 date. An associated study conducted at the same time on nearby plots where these same species were sown in rows resulted in limited seedling establishment of native grasses when sown on similar dates (Biedenbender and Roundy 1996). In contrast, seedling suc-

cess would be expected to be higher for the 16 June 1992 and 2 August 1993 sowing dates where the soil drying front would not have exceeded the depth of seminal roots, thereby allowing over 3 weeks of available water for adventitious root development. Actual establishment for these dates averaged 2.6% for the 16 June 1992 sowing date and 16.7% for the 2 August 1993 sowing date. Seeds of native grasses sown in rows where Lehmann lovegrass was controlled on this site produced 5.6 seedlings m<sup>-2</sup> when sown in mid June 1992 and 12.7 seedlings m<sup>-2</sup> when sown early August 1993 (Biedenbender and Roundy 1996).

A review of the chronology of germination and seedling growth in relation to available water patterns for each sowing date helps clarify reasons for success or failure. For the 16 June 1992 sowing date, initial rains resulted in 9.3 days of available water near the surface (L2- Table 2) and high field germination (Fig. 1a, Fig. 2). Soil drying proceeded for approximately 10 days between the end of the initial rainy period and beginning of the next rain. The drying front did not exceed the estimated seminal root depth (Fig. 1a) and seedlings would be expected to have survived until the second rainy period. In contrast, seeds that germinated after the 30 July 1992 sowing were exposed to 11 days of available water, 7.2 days of dry soil, 0.8 days of wet soil, and then 4.7 days of dry soil (L4- Table 2). The depth of the drying front exceeded the estimated seminal root depth within 13 days of germination. The next wet period of 8.3 days (Table 2) would only benefit seedlings that survived the previous 12 days of dry soil conditions or those seeds that remained ungerminated yet germinable. Residual germination after the first retrieval date of the 30 July 1992 sowing varied from 3.3 to 42.5% for all species except Lehmann lovegrass (83.0%). Therefore, less than half of the planted seeds for all species except Lehmann lovegrass had the potential to germinate during that second, 8-day moist period. Furthermore, the subsequent dry period lasted over 8.9 days, during which time the survival of recently emerged seedlings would have been unlikely.

Moisture conditions following the 15 June 1993 sowing resulted in low initial germination (S5- Table 2, Fig. 2). Relatively high germination of all species except Lehmann lovegrass occurred by the second retrieval date (S6). However, the second retrieval date was followed by a 15-day dry period (Fig. 1b). During this rainless period, the drying front exceeded

the estimated seminal root depth 12.5 days after germination. In contrast, in the 32 days following the 2 August sowing, only 2 short drying periods occurred, the drying front never exceeded the estimated seminal root depth, and seedling establishment was high. There was sufficient time of available water near the soil surface to support development of adventitious roots for all the sowing dates (17–26 days). The lack of available water to allow seminal roots to support seedlings during intermittent dry periods for the 30 July 1992 and 15 June 1993 sowing dates best explains the failure of those seedlings.

### Management Implications

Our investigation of germination response of seeds planted under field conditions clearly revealed species-specific response patterns to dynamic soil moisture conditions. Smith et al. (2000) also found intraspecific responses of Arizona cotton-top seedling emergence to soil water. Many native grass species exhibit high and rapid germination, and would be favored by rainfall and long periods of available water subsequent to germinating rains. For these species, the planted seedbank can be depleted after the initial rain event. The risk of seeding failure is high if lengthy dry periods occur after germination. The seedbank of Lehmann lovegrass with more conservative germination would not be depleted by initial rain events. The occurrence of lengthy dry periods following initial rains imposes less risk to reseeding success of this species. This is due to the potential for subsequent rain events to promote germination and growth of remaining germinable seeds. Successful recruitment of Lehmann lovegrass in rows on both pre- and mid-rainy season sowing dates supports this conclusion (Biedenbender and Roundy 1996).

Rainfall and soil moisture patterns widely vary between and within years. Environmental conditions during 1 growing season may favor establishment of 1 or more species, whereas different environmental conditions may favor the establishment of a different suite of species. Thus, years in which summer soil moisture conditions are highly variable would tend to favor Lehmann lovegrass over faster-germinating native species.

The tendency for Lehmann lovegrass to germinate a small proportion of seeds in response to individual rainfall events, yet retain a residual seedbank typifies a bet-hedging strategy that is favorable in variable environments (Venable 1989), and is 1 reason for the relative success of

Lehmann lovegrass reseeds in regions characterized by low precipitation (Cable 1971, Cox et al. 1982). Long-term summer precipitation records in southeastern Arizona indicate that the probability of rain sequences in which the initial rain event is followed by dry periods lasting 5 days or less is maximized between the third week of July and the first week of August (Frasier and Lopez 1990, Roundy et al. 1996, 1997). Given the rapid germination response and concomitant depletion of seedbank reserves exhibited by native species in this study, chances for successful establishment of native grass species in revegetation projects in southeastern Arizona may be increased by delaying sowing until at least the third week of July.

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# Diffuse knapweed and bluebunch wheatgrass seedling growth under stress

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## Abstract

Growth characteristics of diffuse knapweed (*Centaurea diffusa* Lam.) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith) seedlings were evaluated in 2 temperature regimes, 10 and 16°C, and 2 moisture regimes, - 0.01 and - 0.03 MPa, in an environmental chamber. In cool, wet conditions, root penetration was greater for diffuse knapweed roots than bluebunch wheatgrass roots, but penetration was equal in warm, dry conditions. Root lengths for both species were equal in cool, wet conditions; but, bluebunch wheatgrass root length was greater in warm, dry conditions. Leaf area of diffuse knapweed was greater than bluebunch wheatgrass in warm, dry conditions. Drier, but not cooler, conditions favored diffuse knapweed leaf area over bluebunch wheatgrass leaf area. Root:shoot ratios for bluebunch wheatgrass were greater than diffuse knapweed in all environmental conditions. Results suggest that bluebunch wheatgrass should be more competitive than diffuse knapweed for nutrients and water at lower depths in warmer, drier conditions. Diffuse knapweed should be more competitive for nutrients and water in wetter conditions.

**Key Words:** Noxious weeds, *Centaurea diffusa*, *Pseudoroegneria spicata*, seedling growth, water, temperature

Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith) is a common native perennial grass of western North America that has been developed as a commercial seed source through the varieties 'Whitmar', and 'Goldar'. Seedling establishment is the first step for natural plant spread or seeding efforts in range environments. Successful bluebunch seedling establishment is a function of root penetration (Nelson et al. 1970), soil temperature (Miller et al. 1986), and soil water content (Johnson and Aguirre 1991). Early root development and penetration are essential for bluebunch wheatgrass establishment (Johnson and Aguirre 1991, Hassenyar and Wilson 1978). Root branching of bluebunch wheatgrass is decreased by a reduction in soil water availability (Johnson and Aguirre 1991).

Invasive weeds have the ability to reduce the productive capacity of native grasslands (Olsen 1999). Annual weeds may have an advantage in competition with bluebunch seedlings through faster root growth and soil penetration. Cheatgrass (*Bromus tectorum* L.) has demonstrated greater root and leaf growth than 'Whitmar' bluebunch wheatgrass (Harris 1967).

## Resumen

Se evaluaron las características de crecimiento de plántulas de "Diffuse knapweed" (*Centaurea diffusa* Lam.) y "Bluebunch wheatgrass" (*Pseudoroegneria spicata* (Pursh) Scribn. & Smith) en dos regímenes de temperatura 10 y 16°C y 2 de humedad, - 0.01 y -0.03 MPa, para lo cual se uso una camara ambiental. En condiciones frías y húmedas la penetración de raíz fue mayor para "Diffuse knapweed" que para "Bluebunch wheatgrass", pero la penetración fue igual en condiciones calientes y secas. La longitud de raíz de ambas especies fue igual en condiciones frías y húmedas, pero la longitud de raíz del "Bluebunch wheatgrass" fue mayor en condiciones calientes y secas. En condiciones calientes y secas, el área foliar de "Diffuse knapweed" fue mayor que la de "Bluebunch wheatgrass". Condiciones secas, pero no frías, favorecieron el área foliar de "Diffuse knapweed" sobre el área foliar del "Bluebunch wheatgrass". En todas las condiciones ambientales evaluadas la relación tallo:hoja del "Bluebunch wheatgrass" fue mayor que la del "Diffuse knapweed". Los resultados sugieren que el "Bluebunch wheatgrass" debe ser mas competitivo que el "Diffuse knapweed" por nutrientes y agua a bajas profundidades en condiciones secas y calientes. "Diffuse knapweed" debe ser mas competitivo por nutrientes y agua en condiciones húmedas.

Invading noxious weed species such as diffuse knapweed (*Centaurea diffusa* Lam.) are most likely to pose a competitive problem in bitterbrush (*Purshia tridentata* (Pursh) DC.) /bluebunch wheatgrass community types (Talbot 1987). The density of diffuse knapweed has been suggested as an indicator of range degradation (Roche and Roche 1999). Diffuse knapweed exists in a wide variety of environments (Roche and Roche 1991) and exhibits life cycles ranging from annual to triennial (Thompson and Stout 1991). Seed production from plants with this range of environmental plasticity is variable (Schirman 1981).

Seedling establishment is a critical phase of knapweed invasion. Studies have shown water stress increases knapweed seedling mortality in field plots (Berube and Myers 1982). Other studies suggest that competitive grass seedlings can initiate water stress (Larson and McInnis 1989, Huston et al. 1984).

Understanding the growth response of seedlings in varying environmental conditions can help explain establishment success and invasion potential of weedy species. The objective of this study was to compare seedling growth responses of diffuse knapweed and bluebunch wheatgrass combinations to varying regimens of water and temperature.

## Methods and Materials

Mature diffuse knapweed plants were collected near LaGrande, Ore. (45°18'N, 118°04'W) and stored for 3 months in plastic grain sacks at 22° C before seed heads were removed. After shattering the seed heads, seeds were cleaned in a mechanical seed cleaner and shriveled seed discarded. Foundation 'Goldar' bluebunch wheatgrass was obtained from Grassland West (Cul-de-sac, Ida.). Seeds of both species were rinsed with 5% sodium hypochlorite solution for 30 seconds followed by 3 distilled water rinses (15 ml).

Diffuse knapweed and 'Goldar' bluebunch wheatgrass were grown for 30 days in an environmental chamber in 4 temperature/water regimes: 10° C and -0.01 MPa (cool/wet), 16° C and -0.01 MPa (hot/wet), 10° C and -0.03 MPa (cool/dry), and 16° C and -0.03 MPa (hot/dry). Individual plants of each species were established in vertically split, taped polyvinyl chloride tubes (80 cm in height x 81 cm<sup>2</sup> cross section area) filled with a Walla Walla silt loam (coarse-silty, mixed, mesic Typic Haploxeroll). Soil water levels were attained by batch-mixing soil with water until a tensiometer reading was constant at -0.01 MPa or -0.03 MPa. As soil was added to the tubes, they were tapped on concrete to facilitate soil settling. Tubes were arranged in a randomized-complete-block design in an environmental chamber (10° C or 16° C, 12 hours daylength, 500  $\mu\text{Em}^{-2}\text{sec}^{-1}$  spectral light), with blocks as locations within the chamber.

Harvest occurred at 10, 20, and 30 days after emergence. At harvest, tubes were split, soil washed away, and root depth penetration measured. Roots were separated from shoots, and total root length was measured using a root length scanner (CI-203RL, CID, Inc., Vancouver, Wash.). Leaf area was measured using the same instrument. Leaves and roots were dried at 60° C for 48 hours and weighed. Growth data were analyzed in a 2 x 2 x 2 factorial using ANOVA with mean differences separated using Fisher's protected LSD test ( $P = 0.05$ ).

## Results and Discussion

Growth at 10 and 20 days was not significantly different among treatments. The results reported are for 30 days of growth. Interactions between water and temperature were not significant, therefore only species by water and species by temperature interactions will be discussed.

**Table 1. Means and standard errors for growth parameters of diffuse knapweed and bluebunch wheatgrass as influenced by soil water regimes.**

	Soil Water Potential	
Species	-0.01 MPa	-0.03 MPa
<hr/>		
Root Penetration		
<hr/>		
----- (cm) -----		
Diffuse knapweed	60 (3) <sup>1</sup>	53 (4)
Bluebunch wheatgrass	41 (3)	51 (1)
LSD (P = 0.05)	11 <sup>2</sup>	
<hr/>		
Root Length		
<hr/>		
----- (cm) -----		
Diffuse knapweed	432 (97)	578 (80)
Bluebunch wheatgrass	554 (25)	1090 (138)
LSD (P = 0.05)	340	
<hr/>		
Root Biomass		
<hr/>		
----- (mg) -----		
Diffuse knapweed	43 (7)	88 (7)
Bluebunch wheatgrass	90 (22)	133 (5)
LSD (P = 0.05)	45	
<hr/>		
Leaf Area		
<hr/>		
----- (cm <sup>2</sup> ) -----		
Diffuse knapweed	30 (2)	19 (2)
Bluebunch wheatgrass	19 (2)	11 (1)
LSD (P = 0.05)	6	
<hr/>		
Root:shoot Ratio		
<hr/>		
Diffuse knapweed	0.6 (0.04)	1.2 (0.13)
Bluebunch wheatgrass	1.2 (0.23)	2.1 (0.12)
LSD (P = 0.05)	0.4	

<sup>1</sup>Values in parentheses are standard errors.

<sup>2</sup>LSD for comparisons between species or water potentials.

Roots of diffuse knapweed penetrated soil deeper than roots of bluebunch wheatgrass at -0.01 MPa, but not at -0.03 MPa (Table 1). Greater penetration of diffuse knapweed roots was also evident at 10° C (Table 2). Rooting depth of both species increased at 16° C compared to 10° C, with depths being equal between species at 16° C.

Root lengths of species were equal at -0.01 MPa (Table 1). Length of bluebunch wheatgrass roots was increased with increased water stress, whereas, length of diffuse knapweed roots was not. Root biomass of both species increased with water stress. Apparently diffuse knapweed produced thicker roots than bluebunch wheatgrass with the water stress encountered in our experiment. Secondary root growth of dicotyledonous plants may account for this difference in root morphology between diffuse knapweed and bluebunch wheatgrass. Bluebunch wheatgrass produced greater root biomass than diffuse knapweed in both moisture regimes. Root lengths and biomass were equal between species at 10° C, but both were greater for

bluebunch wheatgrass than for knapweed at 16° C (Table 2). Additional root length at warmer soil temperatures would favor increased nutrient uptake by bluebunch wheatgrass over diffuse knapweed.

Leaf area for each species was reduced by increased water stress (Table 1), and increased by a warmer temperature (Table 2). Leaf area of diffuse knapweed was greater than bluebunch wheatgrass at each water regime. Diffuse knapweed leaf area increased about 20-fold when grown in 16° C as compared to 10° C, while bluebunch wheatgrass leaf area increased about 10-fold.

The root:shoot ratio of bluebunch wheatgrass was greater than diffuse knapweed in all environmental regimes; root:shoot ratios increased for both species with higher water stress (Table 1). Each species put more resources into root growth and less into leaf production at -0.03 MPa compared to -0.01 MPa. The root:shoot ratio for bluebunch wheatgrass decreased with increasing temperature (Table 2). These findings agree with those of Klepper (1991) that higher root:shoot

**Table 2. Means and standard errors for growth parameters of diffuse knapweed and bluebunch wheatgrass as influenced by temperature regimes.**

Species	Temperature	
	10° C	16° C
Root Penetration		
	----- (cm) -----	
Diffuse knapweed	48 (2) <sup>1</sup>	65 (5)
Bluebunch wheatgrass	34 (1)	58 (3)
LSD (P = 0.05)	11 <sup>2</sup>	
Root Length		
	----- (cm) -----	
Diffuse knapweed	83 (7)	927 (126)
Bluebunch wheatgrass	191 (12)	1,460 (140)
LSD (P = 0.05)	338	
Root Biomass		
	----- (mg) -----	
Diffuse knapweed	13 (1)	118 (24)
Bluebunch wheatgrass	46 (3)	176 (8)
LSD (P = 0.05)	45	
Leaf Area		
	----- (cm <sup>2</sup> ) -----	
Diffuse knapweed	2 (0.2)	46 (3)
Bluebunch wheatgrass	3 (0.4)	26 (2)
LSD (P = 0.05)	6	
Root:shoot Ratio		
Diffuse knapweed	1.0 (0.05)	0.8 (0.12)
Bluebunch wheatgrass	1.9 (0.05)	1.4 (0.08)
LSD (P = 0.05)	0.4	

<sup>1</sup>Values in parentheses are standard errors.

<sup>2</sup>LSD for comparisons between species or temperature.

ratios are generally found in stressed compared to non-stressed plants.

Rooting characteristics influence the competitive effectiveness of range plants (Johnson and Aguirre 1991). In many situations resource preemption is determined primarily by rapid germination and root growth (Harper 1977). Results from this study suggest diffuse knapweed derives a root penetration advantage over bluebunch wheatgrass in cool, moist conditions but not in warm, dry conditions. Bluebunch wheatgrass seedlings grew numerous adventitious roots in the 0-10 cm soil depth in moist conditions, while a singular seminal root extended into the deeper soil depths in dry conditions. This apparent transition in root morphology resulted in greater root length for bluebunch wheatgrass compared to diffuse knapweed in drier conditions. Plummer (1943) suggested that root length of bluebunch wheatgrass may play a role in its competitive ability in the seedling stage. These results appear to support conclusions by Berube and Myers (1982) and Sheley et al. (1997) that diffuse knapweed establishment is enhanced with above normal precipitation in spring (i.e., cool and moist conditions).

Poorter and Remkes (1990) indicate that faster growing species, given ideal conditions, tend to maximize shoot function while slower growing species generally maximize root function. Leaf area data and root:shoot ratios suggest that diffuse knapweed is the faster growing species in comparison to bluebunch wheatgrass.

We speculate that a shift to a warmer, drier climate would result in bluebunch wheatgrass being more competitive for nutrients and water at deeper soil depths (> 50 cm). However, in wetter conditions, with deeper root penetration and similar root lengths, diffuse knapweed would be more competitive than bluebunch wheatgrass for water and nutrients.

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# Understory species response to Utah juniper litter

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## Abstract

A greenhouse study was conducted to determine the effects of litter leachate and litter depth of Utah juniper [*Juniperus osteosperma* (Torr.) Little] on seedling emergence and emergence rate of 8 common herbaceous understory species. Species tested were: 'Secar' bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Love], bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], cheatgrass (*Bromus tectorum* L.), 'Paiute' orchardgrass (*Dactylis glomerata* L.), 'Appar' Lewis flax (*Linum lewisii* Pursh), 'Delar' small burnet (*Sanguisorba minor* Scop.), antelope bitterbrush [*Purhsia tridentata* (Pursh) DC.], and mountain big sagebrush [*Artemisia tridentata* spp. vaseyana (Rydb.) J. Boivin]. Three water treatments (distilled water, 1%, and 10% litter leachates) and 3 litter depths (0, 3, and 5 cm) were tested. Leachates decreased seedling emergence of orchardgrass and small burnet. Emergence rate was unaffected by leachate treatments. Seedling emergence of all species tested decreased significantly with increasing litter depth. Emergence rate was initially slower in pots with litter, but after 2 weeks no differences were found.

**Key Words:** leachate, litter depth, allelopathy, plant competition, *Juniperus osteosperma*, emergence

The pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) woodland is an important ecosystem of the western United States, comprising about 25 million hectares throughout Nevada, Utah, Colorado, New Mexico, and Arizona (Hurst 1987). In pre-settlement days, juniper was most abundant in the southwestern U.S., but distinct populations could be found on rocky mid-elevation foothills of the Great Basin (Welch et al. 1987). Since the mid-1800's, juniper has slowly encroached into the valleys of the Great Basin. As juniper becomes the dominant species in these communities, elements of both the biotic and abiotic environments have been modified (Tausch et al. 1981). This has created a serious problem for land managers, because as these trees come to dominate a site, the herbaceous understory is severely reduced (Tausch and Tueller 1977). Increased runoff and soil erosion have been reported as a result of the plant community shift (Farmer 1995). Hypotheses to explain how junipers are able to dominate a site include: 1) increased canopy cover which creates shading (Schott and Pieper 1985) and intercepts precipitation (Skau 1964, Gifford 1970), 2) deep litter accumulation (Jameson 1966) 3) allelopathy (Lavin et al. 1968, Peterson 1972), 4) changes in the soil nutrient composition (Doescher et al. 1987, Tiedemann 1987), and 5) competition for soil moisture (Miller et al. 1987, Breshears et al. 1997)

Litter affects the understory either due to its depth (Everett and Koniak 1981) or to allelopathy (Lavin et al. 1968, Jameson 1970). In a mature stand of one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.], Jameson (1966) stated that litter

## Resumen

Se condujo un estudio de invernadero para determinar los efectos del lixiviado del mantillo y la profundidad del mantillo de "Utah juniper" [*Juniperus osteosperma* (Torr.) Little] en la emergencia de plántulas y la tasa de emergencia de 8 especies herbáceas comunes. Las especies evaluadas fueron: 'Secar' "Bluebunch wheatgrass" [*Pseudoroegneria spicata* (Pursh) A. Love], "Bottlebrush squirreltail" [*Elymus elymoides* (Raf.) Swezey], "Cheatgrass" (*Bromus tectorum* L.), 'Paiute' "Orchardgrass" (*Dactylis glomerata* L.), 'Appar' "Lewis flax" (*Linum lewisii* Pursh), 'Delar' "Small burnet" (*Sanguisorba minor* Scop.), "Antelope bitterbrush" [*Purhsia tridentata* (Pursh) DC.] y "Mountain big sagebrush" [*Artemisia tridentata* spp. vaseyana (Rydb.) J. Boivin]. Se probaron tres tratamientos de agua (agua destilada y lixiviados del mantillo al 1% y 10%) y tres profundidades de mantillo (0, 3 y 5 cm). Los lixiviados disminuyeron la emergencia de plántulas del "Orchardgrass" y "Small burnet". La tasa de emergencia no fue afectada por los tratamientos de lixiviado. La emergencia de plántulas de todas las especies disminuyó significativamente al incrementar la profundidad del mantillo. La tasa de emergencia inicialmente fue lenta en macetas con mantillo, pero después de dos semanas no se encontró diferencia.

accumulation was more detrimental than shading. He found blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths] basal area and production were not affected by the roughly 40% shading, but litter accumulation did adversely affect them both. Johnsen (1962) demonstrated that a significant reduction occurred in blue grama emergence with as little as 2.5 cm of litter.

It has been reported that juniper litter may be allelopathic (Lavin et al. 1968, Peterson 1972). Allelopathy is defined "...as any direct or indirect harmful effect of one plant on another through production of chemical compounds that escape into the environment" (Rice 1984). With respect to allelopathy in juniper species, the literature contains conflicting evidence as to whether or not it really occurs. Jameson (1970) identified 2 compounds from Utah juniper that were considered possible growth inhibitors. Peterson (1972) found that Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) produced both water soluble and volatile inhibitors that reduced germination of several herbaceous species. Lavin et al. (1968) reported that allelopathy in Utah juniper was species specific. Johnsen (1962) found that one seed juniper extracts did not significantly reduce blue grama germination.

This study was conducted to better understand the effects Utah juniper litter depth and allelopathy have on seedling emergence and emergence rate of 8 potential understory plant species of central Utah.

## Materials and Methods

This study tested the effects of 3 water treatments [distilled water (control), 1% and 10% leachate concentrations made from Utah juniper litter] and 3 litter depths (0, 3 and 5 cm) on seedling emergence and emergence rate on the following species: 'Secar' bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Love], bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], cheatgrass (*Bromus tectorum* L.), 'Paiute' orchardgrass (*Dactylis glomerata* L.), 'Appar' Lewis flax (*Linum lewisii* Pursh), 'Delar' small burnet (*Sanguisorba minor* Scop.), antelope bitterbrush [*Purhsia tridentata* (Pursh) DC.], and mountain big sagebrush [*Artemisia tridentata* var. *vaseyana* (Rydb.) J. Boivin].

Seed for all of the species, except mountain big sagebrush and cheatgrass, were purchased from a local seed dealer. Mountain big sagebrush seed was obtained from the USDA Forest Service Shrub Research Lab in Provo, Ut. Cheatgrass seed was collected in the summer preceding the study in Spanish Fork Canyon, Utah Co., Ut. Seeds were visibly inspected and used in the study if they had adequate seed fill and lacked any evidence of predation or parasitism. Seed viability, based on germination trials, ranged from 56% for orchardgrass to 99% for mountain big sagebrush, with most species in the 80–90% range.

Allelopathic potential is usually tested using leachates made from plant material (Jameson 1970, Jobidon 1986). Leachate used in this experiment was made from juniper litter collected beneath Utah juniper trees in Spanish Fork Canyon. Litter was sifted through #20 hardware mesh to separate soil from litter. A 1% leachate solution was prepared by soaking 1 g of litter in 100 ml of distilled water for 24 hours at 20° C. The leachate was then filtered through a #60 mesh filter. A 10% leachate was made in the same fashion except that 10 g of litter per 100 ml of water was used (Jobidon 1986).

Twenty centimeter diameter pots were filled with a soil mixture of 1 part sand and 1 part standard potting soil (Sunshine Mix #3). Litter treatments of 3 depths (0, 3, and 5 cm) were applied using litter collected beneath Utah juniper trees in Spanish Fork Canyon. The litter was placed in the pots on the soil surface at depths representative of the those found in the interspace (0 cm), the mid-canopy area (3 cm), and near the trunk (5 cm), respectively. Each pot was seeded with 1 of the 8

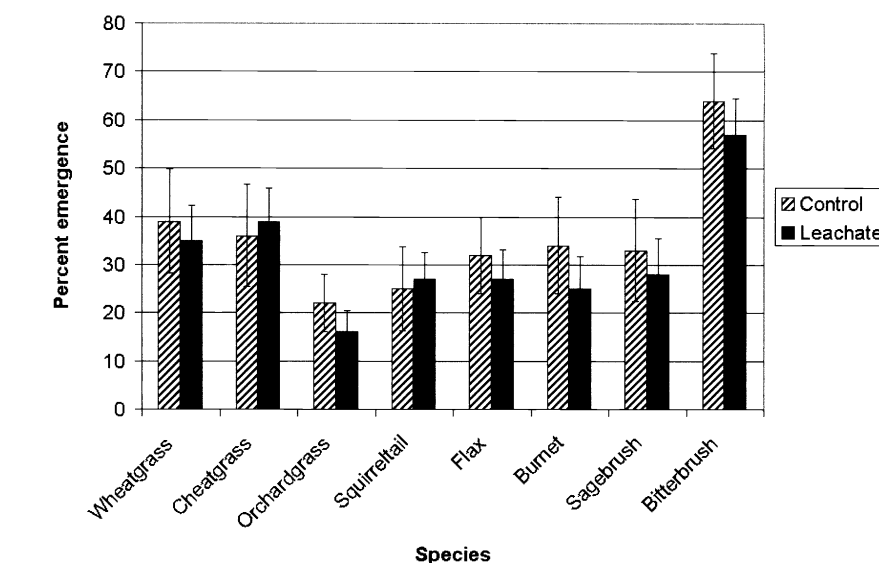


Fig. 1. Response of understory species to imposed Utah juniper litter leachate.

species, with 50 seeds per pot. The seeds were broadcast on top of the surface material, either soil or litter, and then covered by lightly raking them into the surface material. Antelope bitterbrush was planted in 10 caches of 5 seeds at a depth of 2.5 to 3 cm beneath the surface material. This was done to simulate rodent caching, a common form of antelope bitterbrush seed dispersal (Vander Wall 1994). The pots were then watered until the soil was saturated with the respective water treatments (distilled water, 1% or 10% leachate) and placed outside in a lath house for 6 weeks (late December 1996 to early February 1997), to simulate a short wintering period. To prevent precipitation diluting the leachate, pots were placed beneath benches whose tops were covered with clear plastic. No additional watering occurred during this time, since soils were frozen. In February 1997, the pots were moved into a greenhouse with a 12 hour diurnal 20°/15° C temperature regime. Supplemental lighting was provided in order to increase existing photoperiod to spring-time conditions of approximately 12 hours, using 400 watt sodium vapor lamps. Inside the greenhouse, the pots were watered to saturation with their assigned water treatment once a week. The experiment was a 2 factor complete factorial design with 3 litter depths (0, 3, and 5 cm) and 3 leachate concentrations [distilled water (control), 1%, and 10% leachates] replicated 4 times in a randomized block design. Seedling density was counted daily for the first 3 weeks and then every 3 days for the remaining 5 weeks of the study.

An ANOVA analysis was performed, by

species, using SAS (SAS 1999) statistical package and a Fisher's protected LSD was used for mean separation (Ott 1993). Differences were deemed significant at  $P < 0.05$  unless otherwise noted.

## Results & Discussion

The results of the 2 leachate treatments were not significantly different and were pooled for presentation. No significant interactions occurred, thus only the main effects (litter and water treatments) are presented here.

Of the 8 herbaceous understory species tested, only small burnet and Lewis flax showed any response to the leachate treatments (Fig. 1). Seedling emergence of small burnet and Orchard grass were reduced by 25% and 23% compared to the control treatment, respectively.

Emergence rate was defined as the total number of emerged seedlings per week. The leachate treatments had no significant effect on emergence rate (data not shown).

These results indicate that allelopathic effects of Utah juniper are species specific. Similar findings were reported for Rocky Mountain juniper by Peterson (1972) and for 1-seed juniper by Lavin et al. (1968).

The differences in the results of this study as compared to those indicating that juniper is allelopathic, may be due to methodology. The majority of allelopathy studies (Jameson 1961, Lavin et al. 1968, Peterson 1972) have tested leachates made from fresh foliage. It is possible that the negative effects observed in those studies

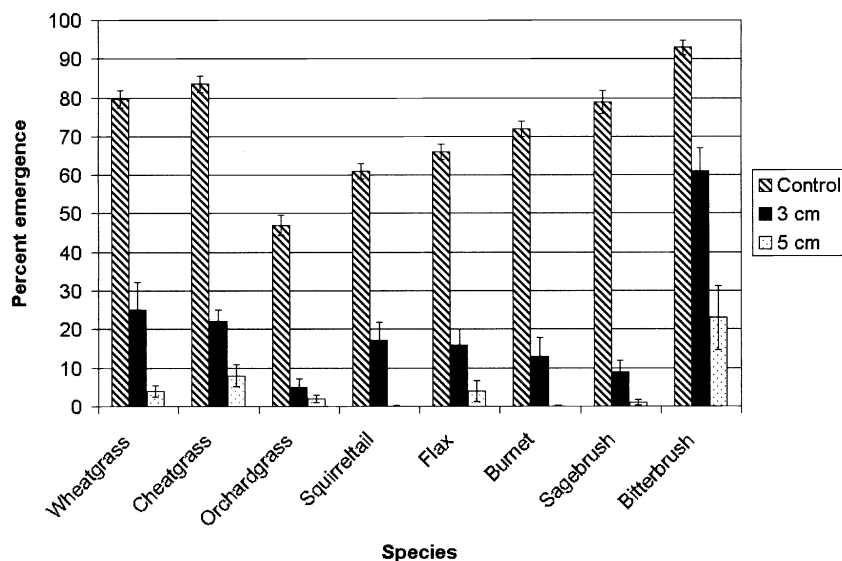


Fig. 2. Response of understory species to imposed Utah juniper litter depth.

may have been due to compounds that may be allelopathic, but are quickly degraded and lost once the foliage begins to decompose. Jameson (1966) identified 2 potentially allelopathic compounds in Utah juniper foliage and litter that behaved in just such a manner. The first compound, although allelopathic, degraded quickly enough that it never reached toxic concentration. The second compound had a slower decomposition rate and could accumulate if the right conditions occurred. This same thing may apply to other compounds in Utah juniper litter. When extracts from fresh foliage are used,

they may contain compounds that may be harmful, but since they decompose or volatilize quickly they never reach toxic levels in a natural setting. This may explain the weak allelopathic response of the species tested to leachates made of decomposing litter.

Litter depth was found to have a more profound effect on seedling emergence than did leachates. All 8 species exhibited decreasing emergence with increasing litter depth (Fig. 2). The impact of as little as 3 cm of litter was quite dramatic across all species, except for antelope bitterbrush, with a 70–90% decrease in emergence

compared to control pots. A 90–100% decrease in emergence occurred in pots with 5 cm of litter compared to pots with no litter, except for antelope bitterbrush. Though not as severe as the other species, emergence of antelope bitterbrush was still strongly impacted by litter depth with a 34% and 75% decrease in emergence in pots with 3 cm and 5 cm of litter, respectively, compared to pots with no litter.

Emergence rate was also affected by litter depth. The response of bluebunch wheatgrass, shown in Figure 3, was typical of all species tested. During the first week of the study, seedling emergence was faster in pots with no litter than in pots with 3 or 5 cm of litter. However, by the end of the second or third week very little subsequent emergence occurred in any of the 3 litter treatments.

These findings support those of other researchers both in the laboratory and field. Johnsen (1962) reported that blue grama emergence was significantly reduced by as little as 2.5 cm of one-seed juniper litter. Jameson (1966) likewise reported that litter depth, not canopy shading, was responsible for low blue grama basal area and production in pinyon-juniper stands of Arizona. Schott and Pieper (1985) found that litter depth was negatively correlated with grass basal cover around one-seed juniper trees in New Mexico.

There are 2 possible reasons why litter depth reduces emergence. First, the litter may drain and dry out quickly which would limit moisture for imbibition. This would especially be the case if the seeds were at or near the litter surface as they were in this study, representing natural dispersal. The antelope bitterbrush results appear to support this hypothesis. The seeds were planted 2.5 to 3 cm below the surface material. In pots with 3 cm of litter, seeds were deposited at the soil-litter interface. While seeds in pots with 5 cm of litter were planted at the same depth, they still had about 2 cm of litter beneath them. The fact that emergence in the pots with 3 cm of litter was relatively higher compared to the other species was probably due to the seeds having adequate imbibition because of contact with the soil and the litter acting as a protective mulch. Whereas, antelope bitterbrush seeds in the pots with 5 cm of litter did poorly because they were in a much drier environment due to their placement in the middle of the litter profile.

This explanation may be influenced by the intensity and duration of a precipitation event. In the greenhouse the pots were

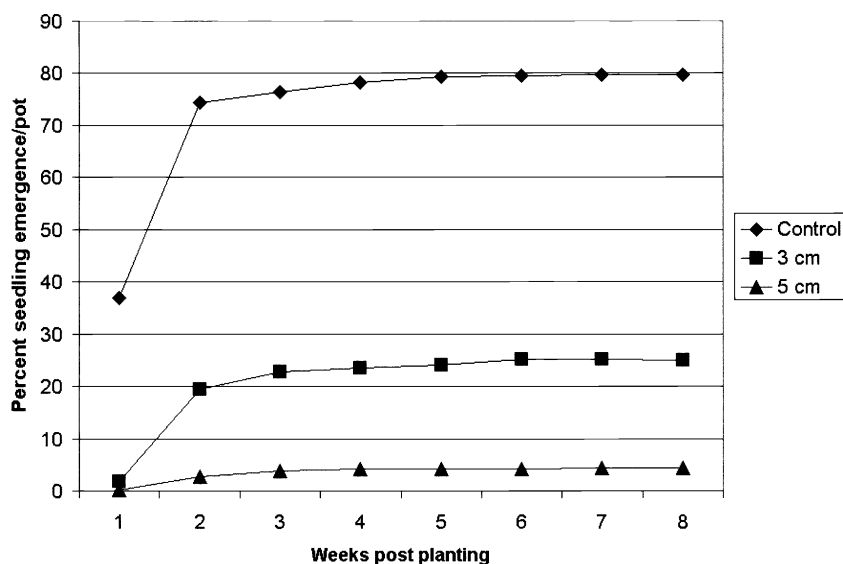


Fig. 3. Response of bluebunch wheatgrass emergence rate to increasing depth of Utah juniper litter.

watered with a watering can which dispensed the water rather quickly, much like a high intensity, short duration thunder storm. In this type of storm the litter would probably drain and dry rather quickly creating the aforementioned conditions. If, however, the storm was of a low intensity and long duration then the litter would stay moist longer which would allow for more imbibition to occur and subsequent higher germination.

The second possible explanation for the effect of litter depth is that the litter may simply be too deep creating an establishment barrier. It is possible that the emerging radicle may never be able to reach mineral soil in order to obtain water and nutrients. In trying to reach mineral soil the seedling uses up all of its energy stores and dies. The depth and physical structure of the litter may be a critical factor in determining seedling success for extremely small seeded species, such as sagebrush, that have limited energy reserves for radical growth. If the seedling radicle can reach mineral soil, then the litter ceases to be a barrier.

## Conclusion

In summary, this study showed that Utah juniper litter leachates had a limited allelopathic effect on emergence of orchardgrass and small burnet under greenhouse conditions, supporting previous research that any allelopathic effects are species specific.

Litter depth was shown to drastically affect emergence and emergence rate. All of the understory species used in the investigation had a reduction in emergence as litter depth increased. Emergence rates of all 8 species were initially lower. However, by the end of the second week this effect was not noticeable. These findings indicated that litter beneath Utah juniper trees has a much stronger affect on plant emergence than does allelopathy.

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# Converting mesquite thickets to savanna through foliage modification with clopyralid

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## Abstract

Honey mesquite (*Prosopis glandulosa* Torr.) is a problem plant in much of the southwestern USA because it reduces forage production for livestock, interferes with livestock handling and reduces off-site water yield. Aerial spraying a 1:1 mixture of clopyralid (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt) and triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid, butoxyethyl ester) at 0.28 kg ae ha<sup>-1</sup> + 0.28 kg ae ha<sup>-1</sup> usually achieves high above-ground (top-kill) and whole plant (root-kill) mortality, but limits multiple-use options of livestock and wildlife production because little mesquite foliage is left to provide screening cover for wildlife. In addition, most surviving plants resprout from basal meristems and will become multi-stemmed plants. Some managers treat mesquite in strips or blocks, leaving untreated areas for screening cover, but these areas become increasingly non-productive for livestock and wildlife forage. The objective of this study was to evaluate the potential of aerial sprays of clopyralid alone at 0.28 kg ha<sup>-1</sup> to convert thickets of mature, multi-stemmed mesquite to savannas by reducing mesquite foliage amount to an intermediate level (by 50–70%), yet preserving apical dominance and limiting basal sprouting. The clopyralid treatment was compared to an untreated control and aerial sprays of 0.28 kg ha<sup>-1</sup> clopyralid + 0.28 kg ha<sup>-1</sup> triclopyr on 2 sites. The clopyralid treatment reduced foliage amount tree<sup>-1</sup>, canopy area tree<sup>-1</sup>, and stand-level mesquite cover by > 57% when compared untreated areas, and 73% of surviving trees maintained apical dominance. Apical dominance was maintained in > 70% of trees not totally top-killed if at least 20% of the original canopy survived and produced foliage following the spray year. Percent root-kill in the clopyralid-only treatment differed between sites (34 and 10%). The lower root-kill on one site was attributed to rainfall that occurred 2 days before and one day after spraying. The clopyralid+triclopyr treatment reduced foliage on original canopies by > 96% and mesquite cover by 82% on both sites. Root-kill was > 52% on both sites but only 37% of surviving plants maintained apical dominance. Results suggest that clopyralid at 0.28 kg ha<sup>-1</sup> may be effective for converting mesquite thickets to savanna and may aid in multiple-use management.

**Key Words:** Brush management, brush sculpting, canopy cover, multiple use, *Prosopis glandulosa*, shrubs, triclopyr, woody plants

## Resumen

El “Mezquite” (*Prosopis glandulosa* Torr.) es una planta problema en gran parte del sudoeste de Estados Unidos porque reduce la producción de forraje para el ganado, interfiere con el manejo del mismo y reduce los rendimientos de agua del sitio. La aspersión aérea de una mezcla en proporción 1:1 de clopiralid (ácido 3,6-dicloro-2-piridinecarboxílico, sal monoetanolamina) y triclopí (ácido 3,5,6-tricloro-2-piridiniloxiacético, butioxiel ester) en dosis de 0.28 kg i.a. ha<sup>-1</sup> + 0.28 kg i.a. ha<sup>-1</sup> usualmente logra una alta mortalidad de la parte aérea y mortalidad total (muerte de raíz) de la planta, pero limita las opciones de uso múltiple de ganado y producción de fauna porque queda poco follaje de “Mezquite” para proveer una cubierta de protección para la fauna. Además, la mayoría de las plantas sobrevivientes rebrotan de meristemos basales creando plantas multi-tallos. Algunos manejadores tratan el mezquite en franjas o bloques, dejando áreas sin tratar para tener una cubierta de protección, pero estas áreas poco a poco llegan a ser improductivas de forraje tanto para el ganado como para la fauna. El objetivo de este estudio fue evaluar el potencial de aspersiones aéreas de clopiralid solo en dosis de 0.28 kg ha<sup>-1</sup> para convertir poblaciones densas de plantas de “Mezquite” maduras multi-tallos en savanas reduciendo la cantidad de follaje a un nivel intermedio (50–70%), pero preservando la dominancia apical y limitando el rebrote basal. El tratamiento de clopiralid se comparó con un control sin tratar y con aspersiones aéreas de 0.28 kg ha<sup>-1</sup> clopiralid + 0.28 kg ha<sup>-1</sup> triclopí, la comparación se efectuó en 2 sitios. El tratamiento de clopiralid redujo la cantidad de follaje árbol<sup>-1</sup>, el área de copa árbol<sup>-1</sup> y el nivel de cobertura de la población de mezquite en > 57% en comparación con las áreas sin tratar y 73% de los árboles sobrevivientes mantuvieron la dominancia apical. La dominancia apical se mantuvo en mas del 70% de los árboles en los que la parte aérea no se murió totalmente y que al menos 20% de la copa original sobrevivió y produjo follaje en el año siguiente de la aplicación. El porcentaje de árboles muertos de raíz en el tratamiento de clopiralid solo difirió entre sitios (34 y 10%). El porcentaje mas bajo de muerte de raíz en uno de los sitios se atribuyó a la lluvia que ocurrió 2 días antes y uno después de la aplicación. El tratamiento de clopiralid + triclopí redujo el follaje de la copa original en mas del 96% y la cobertura de mezquite en 82%, la respuesta fue similar en ambos sitios. La muerte de raíz fue mas de 52% en ambos sitios, pero solo el 37% de las plantas sobrevivientes mantuvieron la dominancia apical. Los resultados sugieren que el clopiralid en dosis de 0.28 kg ha<sup>-1</sup> pueden ser efectivos para convertir las áreas con invasiones densas de “Mezquites” en savanas y puede ayudar en el manejo de uso múltiple.

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Honey mesquite (*Prosopis glandulosa* Torr.) is considered a problem plant in much of the southwestern USA because it reduces forage production for livestock, interferes with livestock handling and reduces off-site water yield (Dahl et al. 1978, Bedunah and Sosebee 1984, Teague et al. 1997). Treatments that only top-kill mesquite, such as chaining, shredding, high-intensity fires, or herbicides such as triclopyr (3,5,6-trichloro-2-pyridinyloxy-acetic acid, butoxyethyl ester), compound the problem by stimulating regrowth from stem bases, thus increasing stem numbers and the competitive effects of mesquite (Fisher et al. 1959, Scifres et al. 1974, Jacoby and Ansley 1991, Ansley and Jacoby 1998).

A widely used aerial herbicide treatment for mesquite control is a 1:1 mixture of clopyralid (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt) and triclopyr applied at 0.28 kg ae ha<sup>-1</sup> + 0.28 kg ae ha<sup>-1</sup>. This treatment achieves high levels of top-kill and root-kill (Bovey and Meyer 1985, Bovey and Whisenant 1991, 1992), although most surviving mesquite have basal regrowth and will become multi-stemmed trees. While viewed as a "best management option" by many livestock producers, this treatment initially leaves so little mesquite foliage remaining that live-tree screening cover for many wildlife species is inadequate. To achieve multiple-use goals of livestock and wildlife production, patterned spraying or mechanical treatments are often employed that leave alternating treated and untreated strips or blocks (Scifres et al. 1985, Scifres and Koerth 1986, Fulbright 1996, 1997, Rollins et al. 1997). However, areas left untreated become increasingly non-productive for livestock and wildlife forage.

We evaluated an alternative strategy to achieve multiple-use goals: aerial spraying thickets of mature, multi-stemmed mesquite with clopyralid alone at 0.28 kg ha<sup>-1</sup>. This treatment achieves moderate root-kill (30-50%) (Jacoby et al. 1991, Bovey and Whisenant 1991), but there is no quantitative information available regarding foliage responses of surviving plants. We have observed that most surviving plants have a ragged appearance called "stem flagging" in which portions of the tree canopies survive (Jacoby and Ansley 1991, Ansley et al. 1996). Stem-flagged mesquite often have little or no basal regrowth, yet canopy foliage is reduced substantially. The reduced foliage, coupled with few or no basal sprouts, shifts the physiognomy of multi-stemmed mesquite to an arborescent

"savanna" appearance, similar to that of few- or single-stemmed mesquite that have never experienced a top-killing disturbance. Use of clopyralid at 0.28 kg ha<sup>-1</sup> may enhance multiple-use goals by reducing the competitive ability of mesquite and, thereby, increasing forage production for livestock and wildlife, yet leaving adequate foliage for wildlife cover. In addition, apical dominance exerted by stem-flagged mesquite may limit multi-stemmed basal regrowth and thus extend treatment effects.

The first objective of this study was to evaluate the potential of aerial sprays of clopyralid at 0.28 kg ha<sup>-1</sup> to convert mesquite thickets to savannas by reducing mesquite foliage amount to an intermediate level (by 50–70%), yet preserving apical dominance and limiting basal sprouting. We compared responses in this treatment to those in an untreated control and to aerial sprays of clopyralid + triclopyr at 0.28 + 0.28 kg ha<sup>-1</sup>. Our hypothesis was that the clopyralid treatment would reduce mesquite foliage amount by at least 50% and maintain apical dominance in surviving trees to a greater degree than would the clopyralid+triclopyr treatment. A second objective was to determine amount of foliage in partially top-killed (i.e., "stem-flagged") plants needed to maintain apical dominance. Apical dominance was maintained in multi-stemmed mesquite partially top-killed by fire if 40% of foliage remained intact (Ansley et al. 1997b, Ansley and Jacoby 1998). We hypothesized that this relationship would be the same in mesquite partially top-killed by clopyralid.

## Study Sites

Research was conducted on 2 private ranches in the northern Rolling Plains ecological area of Texas: Kite Trap on the Waggoner Ranch south of Vernon (33° 53' N, 99° 02' W; elev. 352 m), and Windmill pasture on the Y Ranch west of Crowell (33° 54' N, 100° 03' W; elev. 488 m). The sites are 80 km apart and differ in herbaceous species composition and soils. Kite Trap has an equal mixture of cool- and warm-season grasses, while Windmill pasture is dominated by warm-season grasses. Primary cool-season grass species at Kite Trap are perennial Texas wintergrass (*Nassella leucotricha* Trin. and Rupr.) and the annual, Japanese brome (*Bromus japonicus* Thunb. ex. Murray). Primary warm-season grasses are buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.),

meadow dropseed (*Sporobolus asper* [Michx.] Kunth var. *drummondii* [Trin.] Vasey), silver bluestem (*Bothriochloa laguroides* [DC.] Herter. Subsp. *torreyana* [Steud.]), and sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.). Primary grass species at Windmill pasture are buffalograss, sideoats grama, and tobosagrass (*Hilaria mutica* [Buckl.] Benth), with lesser amounts of Texas wintergrass and Japanese brome.

Mean annual rainfall at Kite Trap is 653 mm. Soils are fine, mixed, thermic Typic Paleustolls of the Tillman series which are alluvial clay loams from the surface to 3–4 m depth, underlain by Permian sandstone/shale parent material (Koos et al. 1962). Mean annual rainfall at Windmill pasture is 630 mm. Soils are fine-silty, mixed, thermic Typic Calcicustolls of the Quanah series, and fine, montmorillonitic, thermic Typic Haplusterts of the Hollister series (NRCS-Vernon, pers. comm). Soils at Windmill pasture are not as deep as those at Kite Trap and are underlain by calcareous limestone or gypsum rock.

Both sites were dominated by multi-stemmed, regrowth mesquite due to previous top-killing treatments. Mean tree height was 2.4 m (± 0.3) at Kite Trap and 2.2 m (± 0.1) at Windmill pasture. Mean number of basal stems tree<sup>-1</sup> was 5.7 (± 0.6) at Kite Trap and 6.3 (± 0.6) at Windmill pasture. Less than 20% of trees had >10 basal stems tree<sup>-1</sup>, and 38% of the mesquite at each site were classified as few-stemmed (1–3 basal stems tree<sup>-1</sup>), possibly due to ongoing recruitment of new plants after treatment. Basal stem diameter ranged from 5–10 cm at both sites. Livestock grazing was continuous at moderate stocking rate at Windmill pasture and sporadic with variable stocking rates for short intervals at Kite Trap.

## Materials and Methods

Herbicide plots were established at Windmill pasture on 08 July 94, and at Kite Trap on 02 July 96 using fixed-wing aircraft (Hardcastle Ag-Air, Inc., Vernon, Tex.). Treatments were (1) untreated, (2) clopyralid alone at 0.28 kg ha<sup>-1</sup> (clopyralid), and (3) clopyralid + triclopyr at 0.28 + 0.28 kg ha<sup>-1</sup> (clopyralid+triclopyr), arranged in a randomized complete block design at each location with 4 replications per treatment. Plot size at Windmill pasture was 120 m x 610 m (7.2 ha) with 6 spray swaths per plot (each swath 20 m). Plot size at Kite Trap was 100 m x 366 m (3.6 ha) with 5 swaths per plot. Herbicide



treatments were applied in 37.4 liters total volume ha<sup>-1</sup> (4 gallons acre<sup>-1</sup>) in a 1:7 diesel fuel-to-water emulsion (4.7 liters of diesel ha<sup>-1</sup>). At Windmill pasture, herbicide treatments were applied between 0800 and 1000 hours with air temperatures 22–27° C, wind speed 11–16 km hour<sup>-1</sup> and soil temperature 27° C at 46 cm depth. At Kite Trap treatments were applied between 0700 and 900 hours with air temperatures 25–31° C, wind speed 3–11 km hour<sup>-1</sup>, and soil temperature 29° C at 46 cm depth. Mesquite foliage conditions at both sites were rated as good to excellent. Soil moisture conditions were dry at Kite Trap. A 3.9-cm rain occurred 2 days prior to spraying and a 3.0 cm rain occurred 1 day after spraying at Windmill pasture.

In 2001, at 5 and 7 years post-treatment at Kite Trap and Windmill pastures, respectively, 60 randomly selected mesquite trees were evaluated in each plot to determine foliage responses at both the stand- and tree-level. Stand-level response variables included: percent of trees with complete above-ground mortality that had basal regrowth (top-kill), percent of trees with foliage on original stems only and no basal regrowth (SF-only), percent of trees with stem foliage and basal regrowth (SFBR), percent of trees with complete mortality (root-kill), percent aerial cover, vertical distribution of foliage with respect to original woody canopies, and percent of the total population (live+dead trees) and of live-only trees that maintained apical dominance. Tree-level response variables included percent foliage reduction per tree, foliage height, live canopy area (determined by measuring foliage radius (r) in 2 perpendicular directions, averaging the 2 values and calculating area by  $\pi r^2$ ) and height of basal regrowth. Foliage reduction per tree was a visual estimate of the amount of foliage present at 5–7 years after spraying as a percentage of foliage estimated to be present before spraying (based on the spatial distribution of the original woody canopy). Height of basal regrowth was measured in the 2 herbicide treatments only.

Mesquite aerial cover was determined using the line intercept method in spring 2001 (Canfield 1941). Canopy intercept was measured along three, 60-m line transects in each plot. In addition, pre-treatment mesquite cover was determined from color-infrared aerial images of each site taken 1 year prior to treatment (field data were not available). Images were scanned and geo-referenced in Arcview GIS (Ansley et al. 2001), and cover was determined using a variation of the line inter-

cept method. Five computer-generated lines (each scaled to 60 m length on the images) were established in each plot at approximately the same position as where the field data were obtained. Intercept was measured manually along each line using the distance measure feature in Arcview. To compare the accuracy of field-determined and image-determined cover, computer generated transects were located on aerial images of Kite Trap taken in September 2000 in each of the 12 plots where line-intercept was field-measured in 2001 (assuming cover had not changed significantly from 2000 to 2001). These data were closely related ( $r^2 = 0.94$ ;  $y = 0.97x - 0.98$ ;  $n = 12$ ). Post-treatment aerial images were not available for Windmill pasture.

Vertical distribution of foliage within mesquite canopies was determined at the stand level by visually dividing the original woody canopy of each tree into 3 equal horizontal layers (upper, middle and lower) and noting whether foliage was present or absent in each layer. Basal sprouting, if present, was assigned to the lower layer. Percent of trees having foliage in each canopy "layer" was then determined.

Mesquite apical dominance was estimated by establishing a level of basal regrowth above which it was assumed apical dominance was lost. During evaluations, it was noticed that many trees in untreated plots had a few basal sprouts (usually < 3), yet these trees were obviously allocating most of their resources to growth of apical tissue. In addition, nearly all trees that were completely top-killed in

the treated plots had numerous (> 5) basal sprouts. Therefore, to identify apical/basal dominance trends in partially top-killed trees, we defined trees with 5 or more basal sprouts as having "many" sprouts. A tree with "many" sprouts was assumed to have lost apical dominance in favor of basal regrowth. Trees without "many" sprouts were assumed to have maintained apical dominance.

### Statistical Analysis

All mesquite response variables were analyzed using a split-plot analysis of variance with site as the whole plot and herbicide treatment as the subplot (4 replicates per treatment at each site). We used the replicate by site mean square as the error term to test for effects of site, and the pooled error to test for treatment effect and site by treatment interaction (SAS 1987). If a site by treatment interaction was significant, differences between treatments were analyzed within each site (Freund and Russell 1981). Means were compared using LSD ( $P \leq 0.05$ ). Percentage data were subjected to arcsin transformation prior to analysis.

## Results

### Mesquite Stand-level Responses

Analysis indicated a significant ( $P \leq 0.05$ ) main effect of treatment for 12 of the 14 post-treatment response variables evaluated (Table 1). Effect of site was significant for 2 variables, percent top-kill and percent of trees with foliage in the upper

**Table 1. Effect of treatment and site as sources of variation on variables measured at the stand and individual tree levels. P values are shown where effects are significant ( $P \leq 0.05$ ; ns = not significant).**

Variable	Trt	Site	Trt x Site
<b>Stand Level</b>			
Trees with basal sprouts only (top-kill) (%)	.0001	.0389	ns
Trees with stem foliage only (SF-only) (%)	.0001	ns	ns
Trees with stem foliage and basal sprouts (SFBR) (%)	ns	ns	ns
Trees root-killed (root-kill) (%)	.0001	ns	.0065
Mesquite cover, pre-treatment (%)	ns	ns	ns
Mesquite cover, post-treatment (%)	.0001	ns	ns
Live trees with foliage in upper canopy layer (%)	.0001	.0355	ns
Live trees with foliage in middle canopy layer (%)	.0001	ns	ns
Live trees with foliage in lower canopy layer (%)	.0006	ns	ns
% of total population (live+dead) with "many" basal sprouts	.0001	ns	ns
% of live-only trees with "many" basal sprouts	.0001	ns	ns
<b>Tree Level</b>			
Foliage reduction per tree (%)	.0001	ns	.0493
Foliage height (m)	.0001	ns	ns
Live canopy area per tree (m <sup>2</sup> )	.0001	ns	ns
Height of basal regrowth (m)	ns	ns	ns

**Table 2. Mesquite percent top-kill, stem foliage only (SF-only) trees and stem foliage+basal regrowth (SFBR) trees in response to herbicide treatments, 2001 (Kite Camp and Windmill sites pooled). Values in parentheses are 1 standard error (n = 8; 4 reps x 2 sites). Means with similar letters are not significantly different (P ≤ 0.05).**

Treatment	Rate (kg ha <sup>-1</sup> )	Top-kill	SF-Only	SFBR
		(%)	(%)	(%)
Untreated	–	0 (0) c	87.5 (4.1) a	12.5 (4.1) a
Clopyralid	0.28	17.1 (2.2) b	51.7 (6.4) b	9.4 (1.8) a
Clopyralid + Triclopyr	0.28 + 0.28	35.8 (3.6) a	5.8 (1.8) c	4.0 (0.7) a

canopy layer. There was a significant site by treatment interaction for percent root-kill and percent foliage reduction per tree.

Percent top-kill was twice as high in the clopyralid+triclopyr treatment than the clopyralid treatment (Table 2), and was greater at Kite Trap (20%) than Windmill (15%) (Table 1). Percent of trees with stem foliage only and no basal sprouts (SF-only) was over 8 times greater in the clopyralid than the clopyralid+triclopyr treatment (52 vs. 6%) (Table 2). Percent

Pre-treatment mesquite cover ranged from 44 to 50% across all treatments (Table 4). Cover increased in the untreated plots by an average of 6 percentage units from 1993 (Windmill) or 1995 (Kite Trap) to 2001, an average of about 0.8 to 1 percentage unit year<sup>-1</sup>. Mesquite cover in 2001 was slightly over half that of pre-treatment cover (23 vs. 44%) in the clopyralid treatment and 1/5th pre-treatment cover in the clopyralid+triclopyr treatment (10 vs. 50%). The clopyralid treatment

**Table 3. Mesquite percent root-kill and foliage reduction per tree in response to herbicide treatments on 2 sites, 2001. Values in parentheses are 1 standard error (n = 4). Means with similar letters within a column and site are not significantly different (P ≤ 0.05).**

Site	Treatment	Rate (kg ha <sup>-1</sup> )	Root-kill	Foliage Reduction Per Tree
			(%)	(%)
Kite Trap	Untreated	–	0 (0) b	5.3 (1.4) c
	Clopyralid	0.28	33.8 (7.8) a	74.4 (7.0) b
	Clopyralid + Triclopyr	0.28 + 0.28	52.1 (4.5) a	98.2 (0.7) a
Windmill	Untreated	–	0 (0) c	8.8 (2.8) c
	Clopyralid	0.28	10.0 (1.8) b	58.8 (1.9) b
	Clopyralid + Triclopyr	0.28 + 0.28	56.7 (5.8) a	96.4 (1.5) a

of trees having stem foliage and basal regrowth (SFBR) did not differ among treatments. Root-kill was similar for the 2 herbicide treatments at Kite Trap, but was different at Windmill pasture (Table 3), explaining the site by treatment interaction. Root-kill was over 52% in the clopyralid+triclopyr treatment at both sites. Root-kill in the clopyralid treatment was greater at Kite Trap (34%) than at Windmill (10%).

reduced mesquite cover by 57% (54 to 23%) when compared to the untreated control.

Vertical foliage distribution within the original woody canopy structure on surviving trees differed among treatments and, in the upper canopy layer only, among sites. As expected, nearly all of the untreated trees at each site had foliage present in the upper and middle canopy layers, but foliage was absent in the lower

**Table 4. Pre- and post-treatment mesquite canopy cover in response to treatments (Kite Camp and Windmill sites pooled). Values in parentheses are 1 standard error (n = 8; 4 reps x 2 sites). Means with similar letters within a column are not significantly different (P ≤ 0.05).**

Treatment	Rate (kg ha <sup>-1</sup> )	Pre-treatment Cover	Post-treatment Cover
		(%)	(%)
Untreated	–	48.2 (5.1) a	53.9 (4.9) a
Clopyralid	0.28	43.8 (3.5) a	23.2 (2.0) b
Clopyralid + Triclopyr	0.28 + 0.28	50.4 (4.0) a	9.5 (1.5) c

layer in almost one-third of the trees (Table 5). About 70% of live trees in the clopyralid treatment had foliage in upper and middle canopy layers, while only 12 and 18% of live trees in the clopyralid+triclopyr treatment had foliage in the upper and middle layers, respectively. A greater percentage of live trees in the clopyralid+triclopyr treatment had foliage in the lower canopy layer than occurred in the other 2 treatments. The significant site effect (Table 1) occurred in the upper layer only. A greater percentage of trees at Windmill pasture (66%) than at Kite Trap (55%) had foliage present in this layer.

### Mesquite Tree-level Responses

Foliage reduction per tree was >96% in the clopyralid+triclopyr and >58% in the clopyralid treatment at both sites (Table 3). Differences between the 2 herbicide treatments were greater at Windmill pasture than at Kite Trap, possibly explaining the site by treatment interaction that was just significant (P = 0.049) (Table 1). Live foliage height and canopy area were significantly reduced by both herbicide treatments, but to the greatest extent by the clopyralid+triclopyr treatment (Table 6). Basal regrowth height was not different between the 2 herbicide treatments and averaged 0.9 m after 5 (Kite Trap) or 7 (Windmill) years post-treatment.

### Basal Sprouts and Apical Dominance (Objective 2)

Percent of the total population of trees (live + dead) with “many” (≥5) basal sprouts was slightly greater in the clopyralid+triclopyr treatment than the clopyralid treatment (Table 7). However, percent of live plants with many basal sprouts was considerably greater in the clopyralid+triclopyr than the clopyralid treatment. The reciprocals (100% – % with many basal sprouts) of these data suggest that apical dominance was maintained in 73 and 37% of surviving trees in the clopyralid and clopyralid+triclopyr treatments, respectively. None of the untreated trees had “many” basal sprouts, but about 13% had “few” basal sprouts (the SFBR plants in Table 2).

Partially top-killed trees from the clopyralid treatment were used to determine the amount of foliage needed on original woody canopies to maintain apical dominance. At both sites, over 70% of trees (y axis) that had >20% of foliage remaining on the original woody canopy structure maintained apical dominance (Fig. 1). As foliage remaining decreased below 20%, responses differed among the 2 sites in

**Table 5. Vertical distribution of foliage on surviving mesquite in each treatment (Kite Camp and Windmill sites pooled). Values in parentheses are 1 standard error (n = 8; 4 reps x 2 sites). Means with similar letters within each group are not significantly different (P ≤ 0.05).**

Treatment	Rate	Trees with Foliage in Upper Layer	Trees with Foliage in Middle Layer	Trees with Foliage in Lower Layer
	(kg ha <sup>-1</sup> )	----- (%) -----		
Untreated	—	100.0 (0) a	97.5 (1.6) a	68.8 (5.5) b
Clopyralid	0.28	69.3 (6.7) b	72.8 (5.0) b	82.5 (2.3) b
Clopyralid + Triclopyr	0.28 + 0.28	12.0 (3.0) c	18.1 (3.2) c	97.0 (1.8) a

**Table 6. Individual mesquite tree responses to herbicide treatments when evaluated in 2001 (Kite Camp and Windmill sites pooled). Values in parentheses are 1 standard error (n = 8; 4 reps x 2 sites). Means within a column with similar letters are not significantly different (P ≤ 0.05).**

Treatment	Rate	Foliage Height	Live Canopy Area	Basal Regrowth Height
	(kg ha <sup>-1</sup> )	(m)	(m <sup>2</sup> )	(m)
Untreated	—	2.9 (0.1) a	47.7 (3.9) a	—
Clopyralid	0.28	2.0 (0.1) b	17.6 (1.9) b	0.89 (0.05) a
Clopyralid + Triclopyr	0.28 + 0.28	1.2 (0.1) c	7.7 (0.6) c	0.93 (0.05) a

that a greater percentage of trees at Kite Trap maintained apical dominance.

## Discussion

### *Use of Clopyralid for Savanna Development (Objective 1)*

For the purposes of mesquite savanna development from multi-stemmed thickets, clopyralid at 0.28 kg ha<sup>-1</sup> achieved the targeted “intermediate” response with respect to overall foliage reduction with >58% foliage reduction per tree (Table 3), 57% reduction in cover (Table 4), and 63% reduction of canopy area of individual plants (Table 6). Apical dominance was maintained in 73% of surviving plants (Table 7). As expected, the clopyralid+triclopyr treatment killed more mesquite plants and caused greater foliage reduction than the clopyralid treatment and also triggered most surviving plants into a basal regrowth mode. We thus fail to reject our first hypothesis that the clopyralid treatment would reduce mesquite foliage amount by at least 50%, but would maintain apical dominance in most surviving trees to a greater degree than would the clopyralid+triclopyr treatment.

The lower root-kill in the clopyralid treatment at Windmill pasture than at Kite Trap may be explained by the inherent variability in response of mesquite to this treatment (Bovey and Whisenant 1992) and/or by the rainfall events that occurred both prior to and following spraying at

Windmill. The site was in an extended drought for several months prior to the spray date and mesquite metabolism was likely suppressed. Rainfall that occurred near the spray date may have stimulated the trees to translocate stored carbohydrates toward leaves for new shoot, leaf or reproductive growth. This upward movement of carbohydrates may have inhibited clopyralid translocation to the root system (Dahl and Sosebee 1984). Apparently, enough clopyralid was absorbed by leaves and stems to modify foliage in a way similar to results found at Kite Trap. The fact that there were more trees at Windmill pasture (66%) than at Kite Trap (55%) with foliage in the upper layer of the original woody canopies supports this hypothesis because it suggests that clopyralid was not translocated as far downward in trees at Windmill pasture compared to Kite Trap. Other factors may have affected root-kill such as differences in soil type and mesquite genetics. In addition, it

should be noted that rainfall did not reduce root-kill in the clopyralid+triclopyr treatment.

The literature indicates a fairly consistent range of mesquite root-kill responses to the 0.28 kg ha<sup>-1</sup> rate of clopyralid with one notable exception. Jacoby et al. (1991) found a range of 29-52% root-kill, Bovey and Meyer (1985) reported 37%, and Bovey and Whisenant (1991) reported 33% root-kill. The exception was a study by Bovey and Whisenant (1992), who found root-kills of 0 and 93% in 2 consecutive years with this clopyralid rate. Further tests are needed to determine factors that affect root-kill using this rate. In addition, other higher rates should be tested, although a rate of 0.56 kg ha<sup>-1</sup> clopyralid has been found to yield results similar to the 0.28 kg ha<sup>-1</sup> clopyralid + 0.28 kg ha<sup>-1</sup> triclopyr treatment (Jacoby et al. 1991, Bovey and Whisenant 1991, 1992) and may remove too much foliage from the landscape for wildlife screening cover.

Root-kill, while certainly important, may not be the most important variable with respect to savanna development. Reduction of the overall foliage amount is probably more critical and that was achieved at both sites. In addition, it is important to note that evaluations were conducted 5–7 years after treatment, indicating that the foliage reduction effects had reasonable longevity.

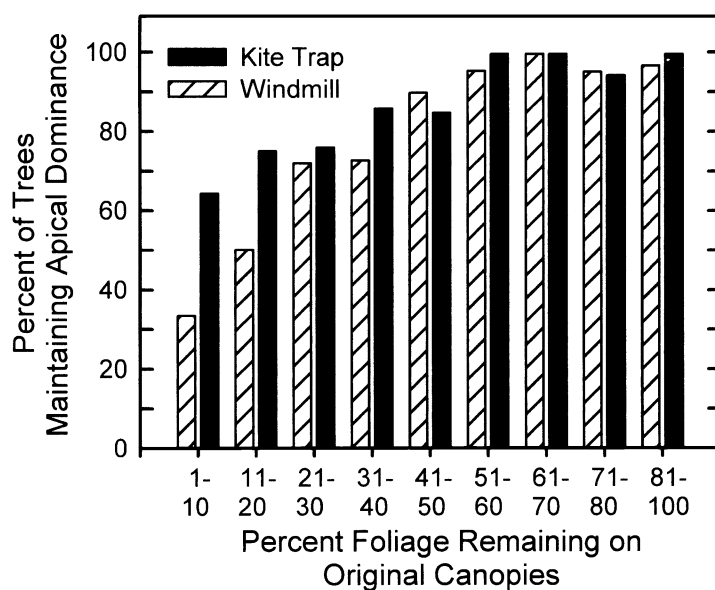
### *Stem Flagging and Apical Dominance (Objective 2)*

The minimum of 20% of original canopy foliage required to maintain apical dominance in partially top-killed trees in the clopyralid treatment was lower than the 40% required by mesquite that had been partially top-killed by low-intensity fires (Ansley et al. 1997b, Ansley and Jacoby 1998) (Fig. 1). Thus, we reject our hypothesis that 40% of original foliage is needed to maintain apical dominance.

Differences in responses between fire- and clopyralid-mediated apical dominance may reflect differences between physical

**Table 7. Percent of total population (live +dead) and of live trees only that had “many” (≥5) basal sprouts in response to herbicide treatments when evaluated in 2001 (Kite Camp and Windmill sites pooled). Values in parentheses are 1 standard error (n = 8; 4 reps x 2 sites). Means with similar letters within a column are not significantly different (P ≤ 0.05).**

Treatment	Rate	Total Pop. with “Many” Basal Sprouts	Live Trees with “Many” Basal Sprouts
	(kg ha <sup>-1</sup> )	(%)	(%)
Untreated	—	0 (0) c	0 (0) c
Clopyralid	0.28	20.8 (1.8) b	27.4 (3.1) b
Clopyralid + Triclopyr	0.28 + 0.28	28.8 (3.8) a	63.0 (6.3) a



**Fig. 1.** The percent of trees maintaining apical dominance (y axis) as a function of amount of foliage remaining on original woody canopies 5–7 years after being partially top-killed by aerial sprays of clopyralid at 0.28 kg ha<sup>-1</sup> at Kite Trap and Windmill pastures. Number of plants evaluated in each x axis group ranged from 20 to 30.

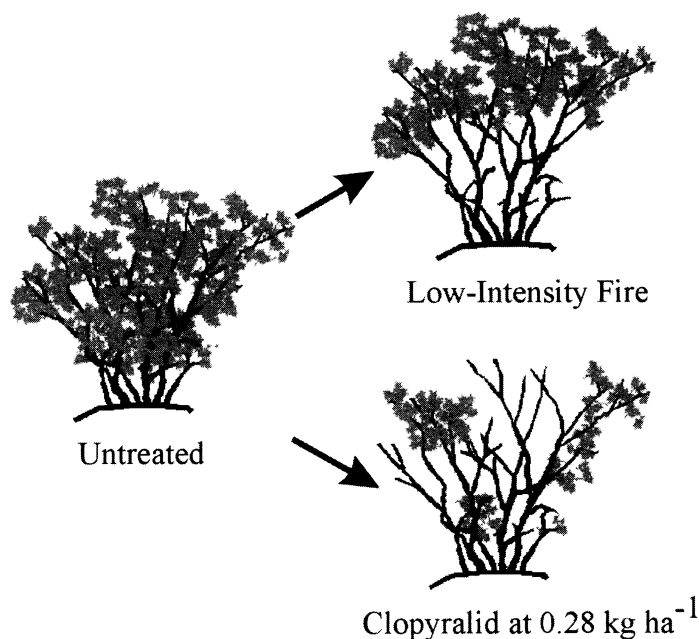
effects of fire and physiological effects of clopyralid. Most subterranean meristem that produces basal regrowth is protected from fire effects by the soil (Ansley and Jacoby 1998). Additionally, few main support stems with rough bark are killed by fire because of the protective bark layer. Because heat is generated from beneath mesquite canopies as herbaceous fuel burns, growing points on small branches and twigs in middle and lower canopy regions are killed but nearly all main support stems retain foliage in upper portions of the canopy (Fig. 2). The resulting relationship between percent foliage remaining per tree following fire and degree of basal sprouting follows a reverse sigmoidal curve. When remaining foliage is less than 30% of pre-burn levels, nearly all the trees produce “many” basal sprouts. When foliage remaining exceeds 40%, sprouting is almost completely eliminated (Ansley et al. 1997b).

In contrast to the response to low-intensity fires, stem-flagging from clopyralid occurred throughout the vertical length of the canopy. Most stem-flagged trees had a combination of partially defoliated stems and other stems that were completely killed (Figs. 2 and 3). Most dead stems had no evidence of sprouting at the stem base, suggesting that clopyralid was translocated to stem bases and killed the meristematic tissue (Bovey et al. 1986, Meyer and Bovey 1986). By killing some

support stems and associated basal meristems, the clopyralid treatment eliminated the potential for resprouting from that portion of the base of the tree. If the remaining live stems retained enough foliage to

maintain apical dominance at each of their respective stem bases, this would produce the appearance that very little foliage in the original woody canopy was needed to maintain apical dominance for the entire tree. Indeed, many clopyralid-treated plants with less than 20% foliage remaining per tree maintained apical dominance (Fig. 1). More trees at Kite Trap may have maintained apical dominance at <20% foliage remaining levels than at Windmill because more support stems within a tree may have been killed at Kite Trap, although we have no data to substantiate this. Adding further support to the assumption that some support stems were killed and others survived is the observation that the clopyralid treatment reduced live canopy area to a greater degree (63%) than it reduced foliage height (31%) (Table 6).

The contrasting responses of partially top-killed trees in low-intensity fire and clopyralid treatments support a general hypothesis that basal sprouting is controlled within each support stem rather than at the organismal or “whole tree” level and explains why efforts to prune multi-stemmed mesquite to a few-stemmed physiognomy by mechanically removing stems results in vigorous sprouting from those stem bases (Patch et al. 1998). Further investigation into physio-



**Fig. 2.** Conceptual illustration of a mature, multi-stemmed mesquite tree partially top-killed by a low-intensity fire (adapted from Ansley and Jacoby 1998) or an aerial spray of clopyralid at 0.28 kg ha<sup>-1</sup>. Number of basal stems depicted is similar to the mean of all trees measured.



Fig. 3. Ground-level view of a mesquite plot at Kite Trap in 2000 treated with clopyralid at  $0.28 \text{ kg ha}^{-1}$  in 1996. None of the mesquite in view have basal regrowth. Vegetation at the base of the large tree on the left is grass growth.

logical mechanisms is needed.

#### *Clopyralid+Triclopyr Mixture*

Clopyralid was initially marketed to be sprayed alone or in combination with picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) for mesquite control (Bovey et al. 1981, Jacoby et al. 1981, 1990, 1991). However, after its commercial release in 1990, many livestock producers expressed dissatisfaction with these treatments because of excessive stem-flagging (Jacoby and Ansley 1991). The combination of clopyralid with triclopyr was developed as an industry response to this dissatisfaction. It is believed that the triclopyr ester provides the top-killing action in those plants not top-killed by clopyralid alone. Because the monoethanolamine salt of clopyralid has low volatility, it may not produce the vapors or small particles that increase coverage within a canopy as do ester herbicide formulations, such as triclopyr. However, laboratory tests have also found that the addition of triclopyr to clopyralid increases clopyralid deposition, absorption, and translocation in mesquite when compared to clopyralid applied alone (Bovey et al. 1988).

The  $0.28 \text{ kg ha}^{-1}$  clopyralid +  $0.28 \text{ kg ha}^{-1}$  triclopyr treatment was moderately successful in converting mesquite thickets to open grassland by yielding > 52% root-kill, 36% top-kill and > 96% canopy reduction (Tables 2 and 3). There is little field research of this treatment combination in the literature, although Bovey and

Whisenant (1991) found that this treatment yielded 49% root-kill and 92% canopy reduction. Their study used hand sprayers that applied the equivalent of 187 liters  $\text{ha}^{-1}$  (20 gallons  $\text{acre}^{-1}$ ) total spray volume on relatively small (1–2 m tall) mesquite. However, efficacy was comparable to that in our study that used 37 liters  $\text{ha}^{-1}$  (4 gallons  $\text{acre}^{-1}$ ) total spray volume.

Our data indicate that 63% of the surviving plants in the clopyralid+triclopyr treatment produced “many” basal sprouts (Table 7). Regrowth from basal meristems presents several problems which may increase in economic importance over time (Fisher et al. 1959, Scifres et al. 1974, Jacoby and Ansley 1991). Because regrowth mesquite are multi-stemmed, they have greater foliage density and may be more competitive with grasses and create greater visual and physical barriers than do few-stemmed mesquite of equivalent height. Multi-stemmed mesquite are also more resistant to subsequent herbicide applications (Jacoby et al. 1990). From a long-term management perspective, once a mesquite plant has been top-killed and produces multi-stemmed regrowth, it may take decades before this plant attains an arborescent physiognomy. Thus, long-term consequences of treatments that induce basal regrowth should be considered prior to treatment.

The level of root-kill produced by the clopyralid+triclopyr treatment reduced effects of basal regrowth in surviving plants when projected to the landscape level. As noted in Table 7, while the percent of surviving mesquite with many basal sprouts was much greater in the clopyralid+triclopyr than the clopyralid treatment, this percentage, when averaged over all trees (live + dead), was more similar between treatments, although it remained significantly different (29 vs. 21%; Table 7). Recent studies suggest the clopyralid+triclopyr treatment has an effective treatment life of at least 20 years if increased herbaceous production for livestock is the management goal (McMullen 2000, Teague et al. 2001). Conversely, in the same studies, herbicide treatments that only top-killed mesquite and induced basal regrowth were not economical.

Basal regrowth rate of 0.9 m in 5–7 years was not nearly as rapid as that found by Hamilton et al. (1981) in south Texas after a top-killing fire, or by Scifres et al. (1974), who found in north Texas, that mesquite regrowth attained 1.6 m height 8 years after 2,4,5-T (2,4,5-trichlorophenoxy acetic acid) application. Our lower regrowth rates were possibly due to drought conditions that occurred during much of the period between application of the herbicide treatments in 1994 or 1996 and final evaluations in 2001. They may also indicate that clopyralid and clopyralid+triclopyr treatments have a negative impact on the growth rate of basal regrowth.

It should be noted that this study was conducted on sites where the majority of mesquite were mature, multi-stemmed regrowth that had been top-killed by earlier treatments. As such, our results may not apply to stands dominated by undisturbed mesquite, although 38% of the trees evaluated were few-stemmed (1–3 stems  $\text{tree}^{-1}$ ) and mean basal stems  $\text{tree}^{-1}$  was only 6. Much of the mesquite in Texas has experienced a prior disturbance. This assumption is supported by survey data that indicates that about 20 million ha of Texas rangelands are infested with mesquite (NRCS 1985) and total acreage of all brush species treated in Texas from 1940–1984 was > 26 million ha (Welch 1985). While Welch’s report did not specify the acreage of mesquite treated, it can be assumed that a significant portion of this total was mesquite and that most of the treatments were non-lethal and produced regrowth. Thus, we believe the pre-treatment physiognomy of mesquite in our study was typical of the majority of mature mesquite that currently exist. Research is needed to determine if similar responses occur in single-stemmed mesquite.

## Management Implications

There is much evidence to suggest that on areas with uniform soil types, mesquite savannas will transition to thickets if left unmanaged (Archer 1995, Ansley et al. 2001). This process is accelerated by a variety of factors, including distribution of mesquite seeds by livestock and the reduction of naturally occurring fires (Archer et al. 1988, Brown and Archer 1989, Kramp et al. 1998). Within this north Texas ecosystem, mesquite savanna is most likely the "transition" phase between true grassland and woodland thicket "states". There is little doubt that maintaining a site as a mesquite savanna will require periodic management inputs.

Treating mesquite thickets in strips or blocks, or thinning stands by selectively killing individual mesquite plants, are options that provide spatial discontinuity and may achieve multiple-use goals (Jacoby 1985, Scifres et al. 1985, Scifres and Koerth 1986). However, there are some problems associated with these "brush sculpting" treatments, including high cost of implementation and maintenance, especially if mechanical treatments are used (Rollins et al. 1997), or if the mesquite is allowed to thicken and mature before control is attempted. A disadvantage of leaving untreated strips is that these strips decline in productivity for livestock and wildlife grazing and hinder attempts to gather livestock and harvest wildlife. Use of low-cost maintenance treatments such as prescribed fire are often not practical because discontinuity of herbaceous fine fuel in areas supporting dense mesquite disrupt movement of the flame front (Ansley et al. 1997a).

Aerial sprays of clopyralid at 0.28 kg ha<sup>-1</sup> may facilitate conversion of mesquite thickets to savannas and enhance opportunities for multiple-use management for livestock and wildlife. This treatment maintains some screening cover for wildlife, yet surviving mesquite will have less leaf area per tree and will likely be less competitive with forage grasses than before treatment, thereby increasing forage production for livestock and wildlife (Fig. 3). In addition, most surviving mesquite will largely have elevated, rather than basal regrowth foliage that theoretically could be maintained using low-intensity fires (Ansley et al. 1996, 1997b).

Twenty years ago, the results of the low rate of clopyralid, as documented in this study, would have been perceived as an unsatisfactory control because of the stem flagging. However, societal perceptions of human manipulations of the landscape

have changed and there is increasing interest in maintaining diversity and multiple-use options on rangelands (Cairns and Lackey 1992, Fulbright 1996). Effects of clopyralid at 0.28 kg ha<sup>-1</sup> alone or in combination with other "brush sculpting" treatments, such as patterned spraying or individual plant thinning, on floral and faunal diversity and forage responses for both livestock and wildlife need further investigation.

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# Vegetation of chained and non-chained seedlings after wildfire in Utah

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## Abstract

After wildfires in 1996 in the sagebrush (*Artemisia* spp.) and pinyon-juniper (*Pinus* spp.—*Juniperus* spp.) zones of west-central Utah, the USDI-BLM attempted to reduce soil erosion and cheatgrass proliferation (*Bromus tectorum* L.) through rehabilitation treatments. We compared the vegetation of aerially seeded, chained treatments with aerially seeded but non-chained treatments for 3 years following seeding. Vegetation cover increased significantly in both treatments between the first and second year, concurrent with above-average precipitation. By the second year, seeded grasses, primarily crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] and intermediate wheatgrass [*Elymus hispidus* (Opiz) Meld. and *Elymus elongatus* (Host) Runem.], dominated the chained treatment while cheatgrass dominated the non-chained treatment. Seeded grass establishment in non-chained areas was highest beneath dead trees on steep northeast-facing slopes. The first year following the fires, frequency of most annual species and some native perennial species was higher in the non-chained than chained treatment. Native species richness and diversity declined in both treatments between the first and third year following the fires due to the loss of early-seral native annuals and probably because of climatic factors and competition from seeded grasses and cheatgrass. This study reaffirmed the utility of aerial seeding followed by chaining as a rehabilitation technique for rapid establishment of standard plant materials and suppression of cheatgrass, although the implications for soil protection were less clear. Maintenance of native biodiversity on public lands will require greater development and use of native plant materials for wildfire rehabilitation. Planning for future rehabilitation needs is important in light of continuing wildfire risks.

**Key Words:** Bureau of Land Management, rehabilitation, chaining, aerial seeding, plant materials, cheatgrass

Wildfire rehabilitation via the Emergency Fire Rehabilitation program has been widely used by the USDI Bureau of Land Management (BLM) in the Intermountain West with primary pur-

## Resumen

Después de los fuegos sin control ocurridos en 1996 en las zonas de "Sagebrush" (*Artemisia* spp.) y "Pinyon-Juniper" (*Pinus* spp.—*Juniperus* spp.) de la región central - oeste de Utah, el USDI-BLM intentó reducir la erosión y la proliferación del "Cheatgrass" (*Bromus tectorum* L.) a través de tratamientos de rehabilitación. Comparamos la vegetación de áreas sujetas a cadeneo y siembra aérea contra áreas sin cadeneo y con siembra aérea, la comparación se realizó durante 3 años después de la siembra. Entre el primer y segundo año la cobertura vegetal se incrementó significativamente en ambos sitios, concordando con precipitación arriba del promedio. Para el segundo año los zacates sembrados, principalmente "Crested wheatgrass" [*Agropyron cristatum* (L.) Gaertn.], "intermediate wheatgrass" [*Elymus hispidus* (Opiz) Meld. y *Elymus elongatus* (Host) Runem.], dominaron en el tratamiento con cadeneo, mientras que el "Cheatgrass" dominó las áreas sin cadeneo. El establecimiento de los zacates sembrados en las áreas sin cadeneo fue mayor debajo de los árboles muertos en las pendientes pronunciadas con exposición nordeste. En el primer año después de los fuegos, la frecuencia de la mayoría de las especies anuales y de algunas especies nativas perennes fue más alta en el tratamiento sin cadeneo que en el tratamiento con cadeneo. La riqueza y diversidad de especies nativas disminuyó en ambos tratamientos entre el primer y tercer años después del fuego, debido a la pérdida de especies anuales nativas de las primeras etapas serales y probablemente a causa de los factores climáticos y la competencia entre los zacates sembrados y el "Cheatgrass". Este estudio reafirma la utilidad de la siembra aérea seguida de un cadeneo como una técnica de rehabilitación para el establecimiento rápido de material vegetal estándar y la supresión del "Cheatgrass", aunque las implicaciones para la protección del suelo fueron menos claras. El mantenimiento de la biodiversidad nativa en terrenos públicos requerirá un mayor desarrollo y uso de material vegetal nativo para la rehabilitación a fuegos no prescritos. La planeación de las necesidades futuras de rehabilitación es importante por el riesgo continuo de fuegos no prescritos.

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poses to reduce soil erosion, protect property and life, and prevent the spread of weeds (BLM 1999a, Roberts 1999). One rehabilitation goal on semiarid sites may be to prevent site dominance by the exotic annual cheatgrass (*Bromus tectorum* L.) by establishing perennial species (BLM 1999b, MacDonald 1999).

In areas where rangeland drills cannot be used, rehabilitation can be accomplished through aerial broadcast seeding, often fol-

**Table 1. Characteristics of study sites that burned in the summer of 1996 in west-central Utah.**

Site Name	Location (Reference Marker)	Elevation (m)	Slope and Aspect	Soils
Dog Slopes	110m at 195° from Tidwell Spring enclosure, T13S R2W S19	1,650–1,690	20–34% slopes; north- to east-facing	Saxby very cobbly loam: Loamy-skeletal, mixed, mesic Lithic Xerollic Calciorthids <sup>1</sup>
Gilson	Section marker T13S R3W S35 T14S R3W S1 S2	1,615–1,645	4–15% slopes; mainly northeast- to southeast-facing	Borvant cobbly loam: Loamy-skeletal, carbonatic, mesic, shallow Aridic Petrocalcic Paleoxerolls <sup>1</sup>
Jericho	Milemarker 124, US Hwy. 6, T12S R3W S28	1,650–1,670	4–16% slopes; east, south-, and west-facing	Jericho gravelly fine sandy loam: Loamy-skeletal, mixed, mesic, shallow Xerollic Durorthids <sup>1</sup>
Paul Bunyan	Near Paul Bunyan's Woodpile road, T12S R3W S23	1,800–1,810	5–11% slopes; mainly west- and south-facing	Jericho gravelly fine sandy loam: Loamy-skeletal, mixed, mesic, shallow Xerollic Durorthids <sup>1</sup>
Railroad	151m at 195° from section marker T12S R3W S15 S16 S21 S22	1,670–1,680	5–7% slopes; north-, south-, and west-facing	Wales loam: Fine-loamy, mixed (calcareous), mesic Xeric Torrifluvents <sup>1</sup>
Twin	Quarter-section marker T25S R7W S29 S32	1,800–1,810	1–6% slopes; north- to northeast-facing	Kessler-Penoyer very cobbly loam: Fine-silty, carbonatic, mesic Xerollic Calciorthids; and/or coarse-silty, mixed (calcareous), mesic Typic Torriorthents <sup>2</sup>

<sup>1</sup>Trickler and Hall (1984)

<sup>2</sup>Stott and Olsen (1976)

lowed by chaining (Vallentine 1989, BLM 1999b, MacDonald 1999). Chaining has been widely used on rangelands to eliminate unwanted trees and brush (Vallentine 1989), but in wildfire rehabilitation its primary role is to create a suitable seedbed including coverage of seed by soil (BLM 1999b). Although the BLM has accumulated much corporate knowledge of wildfire rehabilitation using chaining through years of practical experience, few formal

studies have been conducted. See Clary (1988) for some Utah chaining and seeding study examples and results.

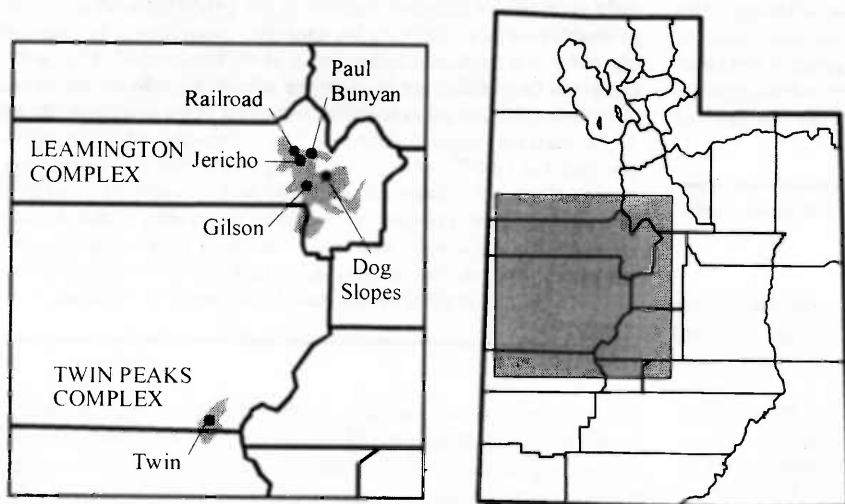
This paper presents a comparative study in which vegetation of chained and non-chained seedlings was monitored for 3 years following 1996 Utah wildfires. Controversy over the impact of chaining treatments on archeological sites, wilderness resources, and native vegetation dynamics following these fires stimulated

this research. Our objective was to document the effects of these rehabilitation treatments, particularly in relation to seed-plant establishment, exotic annual suppression, and consequences to native species.

### Study Area and Rehabilitation Description

The Twin Peaks Complex fire was ignited by lightning on 5 July 1996 and was controlled on 12 July 1996 (BLM, personal communication). The area affected by this fire lies between 38° 30'–45'N and 113° 35'–50'W in Millard and Beaver counties, Utah (Fig. 1; Table 1), primarily between 1,580–1,950 m elevation, on plains and low ridges composed primarily of basalt flows and alluvium (Hintze 1975). Pre-burn vegetation was dominated by mature Wyoming big sagebrush [*Artemisia tridentata* var. *wyomingensis* (Beetle & A. Young) Welsh] and Utah juniper [*Juniperus osteosperma* (Torr.) Little], in a precipitation regime averaging 30 to 41 cm per year over a 30-year period (USDA-NRCS 1999). Pre-burn understory vegetation varied but included substantial amounts of cheatgrass.

Another fire, the Leamington Complex, occurred in an area about 120 km to the



**Fig. 1. Location of 1996 fire complexes (shaded) and rehabilitation study sites in west-central Utah.**

north of the Twin Peaks Complex, in Juab county, Utah, between 39° 24'-50'N and 111° 50'-112° 20'W (Fig. 1; Table 1). The Leamington Complex fire began with a lightning strike on 1 August 1996 and was controlled on 17 August 1996 (BLM, personal communication). Most of this fire occurred between 1,520–2,100 m elevation, on topography characterized by alluvial plains, foothills, and fault-block mountains composed of volcanic rocks and limestone (Hintze 1975). Pre-burn vegetation was a mosaic of seral stages of sagebrush steppe and pinyon (*Pinus* spp.)-juniper and juniper woodlands as well as stands of cheatgrass and seeded grasses. Precipitation in this area ranges from a 30-year average of 25 to 30 cm per year in lower valley areas to 41 to 46 cm per year on lower mountain slopes (USDA-NRCS 1999).

Seed mixes were prepared primarily using 'Hycrest' and 'Nordan' crested wheatgrass [*Agropyron cristatum*(L.) Gaertn.], 'Oahe' intermediate wheatgrass [*Elymus hispidus* (Opiz) Meld.], 'Luna' pubescent wheatgrass [*Elymus hispidus* (Opiz) Meld.], 'Alkar' tall wheatgrass [*Elymus elongatus* (Host) Runem.], 'Bozoisky' Russian wildrye (*Elymus junceus* Fisch.), 'Magnar' Great Basin wildrye (*Elymus cinereus* Scribn. & Merr.), 'Lincoln' smooth brome (*Bromus inermis* Leysser), 'Ladak' alfalfa (*Medicago sativa* L.), and fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.]. Seed mix composition, seeding rates, and timing of application differed for different locations and treatments (Table 2). An Ely anchor chain was used at all sites considered in this study. The Ely chain is a modification of the standard anchor chain (rail segments are welded to some of the chain links to provide added weight and additional soil disturbance—Vallentine 1989).

Aerial seeding followed by chaining was carried out as weather conditions permitted from autumn 1996 until 31 March 1997, when chaining was halted by a temporary court restraining order (BLM, personal communication). This was the result of legal proceedings led by citizens concerned with the impact of these chaining treatments on archeological sites (Haase 1983) and on the integrity of wilderness resources and native vegetation (SUWA 1997, SUWA personal communication). At the time of this order, aerial seeding treatments had been completed but chaining treatments were only partially completed and were not pursued further by the Utah BLM during that year (BLM, personal communication). Thus, some lands had

been seeded and chained and some had been seeded but not chained. No further chaining occurred on the 1996 burns until 1998 after legal restraints were lifted. Livestock grazing was restricted from rehabilitated sites for 2 growing seasons following treatment.

## Methods

During the summer of 1997, we selected 6 study sites, 5 within the burned area of the Leamington Complex, and 1 within the Twin Peaks Complex (Fig. 1; Table 1). Sites were selected based on accessibility and the presence of treatments of interest on comparable topographic settings. All sites included a chained treatment (aerially seeded followed by Ely chaining) adjacent to an aerially seeded, non-chained treatment. Site selection resulted in 5 different seed mixes being represented (Table 2). The non-chained treatment area at the Railroad site was inadvertently reseeded and chained by the BLM during a 1998-1999 operation. We relocated plot markers following this chaining and collected plot data in 1999—see Ott (2001) for further details.

At 3 sites, cadastral survey markers were used as reference points. Metal rebar stakes were placed to mark reference points at sites lacking such markers. Transect lines were extended directly from the reference point, following cardinal directions, or otherwise arranged systematically within the different treatment areas of each site. Plots were established at regular intervals along the transect lines, with 4 plots per treatment at each site. A rebar was placed to mark each plot at tape-measured intervals of 50 m (Twin, Gilson, Dog Slopes, and Railroad sites), or 60 m (Jericho and Paul Bunyan sites). This rebar served as the center of a circular plot of radius 5.6 m (100 m<sup>2</sup>) and also served as the southwest corner of a square-shaped, 1 m<sup>2</sup> plot (McArthur and Sanderson 1996). The larger plot allowed greater scope, while the smaller plot allowed greater precision of data collected. Data were collected each year for 3 consecutive years (July–August 1997, June–early July 1998, and late June–early August 1999).

We used the ocular relevé methods of Shimwell (1971) and McArthur and Sanderson (1996) to estimate cover of vascular plants, bare soil, litter, rock (> 2 cm diameter), and cryptogams (biological soil crusts and non-vascular plants) in both large (100 m<sup>2</sup>) and small (1 m<sup>2</sup>) plots.

**Table 2. Aerial applied seed mixtures and seeding rates for 1996–1997 rehabilitation at sites that burned in the summer of 1996 in west-central Utah (Information supplied by the Fillmore Field Office, USDI BLM).**

Plant Material <sup>1</sup>	Seeding Rate (kg/ha <sup>-1</sup> )
<b>Dog Slopes Site</b>	
Crested wheatgrass ('Hycrest')	5.0
Pubescent wheatgrass <sup>2</sup>	3.4
Russian wildrye ('Bozoisky')	2.4
Tall wheatgrass <sup>2</sup>	1.7
Crested wheatgrass ('Fairway')	0.4
Total	12.9
<b>Gilson Site</b>	
Crested wheatgrass ('Hycrest')	3.4
Smooth brome ('Lincoln')	2.2
Russian wildrye ('Bozoisky')	2.2
Tall wheatgrass <sup>2</sup>	2.2
Fourwing saltbush <sup>2</sup>	1.1
Total	11.2
<b>Jericho Site</b>	
Crested wheatgrass ('Hycrest')	3.5-4.5 <sup>3</sup>
Russian wildrye ('Bozoisky')	2.4-3.4
Tall wheatgrass <sup>2</sup>	2.2
Smooth brome (Lincoln)	0-2.0
Great Basin wildrye <sup>2</sup>	0-1.1
Fourwing saltbush <sup>2</sup>	1.1
Total	11.2-12.3
<b>Paul Bunyan Site</b>	
Crested wheatgrass ('Hycrest')	4.5
Russian wildrye ('Bozoisky')	3.4
Tall wheatgrass <sup>2</sup>	2.2
Fourwing saltbush <sup>2</sup>	1.1
Total	11.2
<b>Railroad Site</b>	
Crested wheatgrass ('Hycrest')	3.5
Russian wildrye ('Bozoisky')	2.4
Tall wheatgrass <sup>2</sup>	2.2
Smooth brome ('Lincoln')	2.0
Great Basin wildrye <sup>2</sup>	1.1
Fourwing saltbush <sup>2</sup>	1.1
Total	12.3
<b>Twin Site</b>	
Crested wheatgrass ('Hycrest')	6.7
Russian wildrye ('Bozoisky')	4.1
Pubescent wheatgrass ('Luna')	3.2
Crested wheatgrass ('Nordan')	2.8
Alfalfa ('Ladak')	0.3
Total	17.3

<sup>1</sup>For scientific names see Table 3.

<sup>2</sup>Cultivar information not available.

<sup>3</sup>The Jericho study site included two seed mixes on opposite sides of U.S. Highway 6, the same mixes as applied to the Paul Bunyan and Railroad sites.

Foliar vascular plant cover percent was estimated first, and the remaining plot area was then assigned to the other categories so that the total of these 5 categories always equaled 100%. Litter was defined as any herbaceous material from a previous growing season, and any dead woody material in contact with the surface of the ground, including fallen branches and bases of dead trees.

Foliar cover was estimated for each vascular plant species having canopy within

**Table 3. Frequency of species by treatment and year in 2 plot sizes at sites burned in the summer of 1996 in west-central Utah. Only species with frequency of 4 or greater in any given year across both treatments are shown [See Ott (2001) for additional detail].**

Species <sup>2</sup>	No. Sites	All Sites						Railroad Site	
		Chained			Non-chained			Late-chained <sup>1</sup>	1999
		1997	1998	1999	1997	1998	1999		
<b>Seeded Shrubs and Forbs</b>									
<i>Atriplex canescens</i> (Pursh) Nutt. (fourwing saltbush)	4 <sup>3</sup>	13 (1) <sup>4</sup>	13 (1)	13 (1)	4	1	2	0	0
<i>Medicago sativa</i> L. (alfalfa)	4	3	5	2	1	3	6	0	4
<b>Seeded Grasses</b>									
<i>Agropyron cristatum</i> (L.) Gaertn. (crested wheatgrass) <sup>2</sup>	6	23 (18)	23 (18)	23 (20)	20 (7)	20 (8)	21 (12)	4	4 (2)
<i>Bromus inermis</i> Leyse (smooth brome)	4	15 (8)	15 (7)	15 (8)	11 (3)	12 (5)	16 (8)	4 (1)	4 (4)
<i>Elymus hispidus</i> (Opiz) Meld. (intermediate wheatgrass) <sup>2,5</sup>	6	23 (17)	22 (15)	23 (17)	17 (4)	16 (5)	22 (8)	4 (1)	4 (3)
<i>Elymus junceus</i> Fisch. (Russian wildrye)	6	8	22 (8)	19 (4)	6	14 (3)	13 (3)	2	2
<b>Exotic Grasses</b>									
<i>Bromus japonicus</i> Thunb. ex Murray (Japanese brome)	5	11	5 (1)	6 (1)	2	6 (1)	3	0	1
<i>Bromus tectorum</i> L. (cheatgrass)	6	23 (16)	23 (20)	24 (20)	24 (17)	24 (22)	24 (24)	4 (4)	4 (4)
<b>Native Grasses</b>									
<i>Elymus elymoides</i> (Raf.) Swezey (bottlebrush squirreltail)	6	16 (4)	15 (3)	13 (5)	18 (3)	19 (4)	20 (4)	4 (2)	4 (2)
<i>Elymus smithii</i> (Rydb.) Gould (western wheatgrass)	2	4 (1)	4 (2)	4 (2)	2	1	1	0	0
<i>Elymus spicatus</i> (Pursh) Gould (bluebunch wheatgrass)	4	10 (5)	11 (5)	10 (4)	13 (9)	14 (8)	13 (9)	0	0
<i>Poa fendleriana</i> (Steudel) Vasey (muttongrass)	5	7 (3)	7 (4)	9 (3)	10 (6)	12 (5)	8 (4)	3	0
<i>Poa secunda</i> Presl (Sandberg bluegrass)	1	4 (2)	4 (2)	4 (1)	4 (4)	4 (1)	3 (1)	0	0
<i>Stipa hymenoides</i> R. & S. (Indian ricegrass)	6	17 (3)	16 (3)	15 (3)	17 (4)	18 (5)	17 (3)	3	3
<b>Exotic Forbs</b>									
<i>Alyssum desertorum</i> Stapf (desert alyssum)	6	14 (1)	16 (7)	18 (7)	17 (6)	18 (14)	20 (15)	2 (2)	2 (1)
<i>Camelina microcarpa</i> Andr. ex DC. (falseflax)	3	4	6 (2)	8 (3)	3 (2)	6 (2)	8 (4)	0	0
<i>Chenopodium album</i> L. (lambsquarter)	4	4	0	0	1	0	0	0	0
<i>Descurainia sophia</i> (L.) Webb ex Prantl (tansymustard)	3	0	0	2	0	3	4	0	0
<i>Erodium cicutarium</i> (L.) L'Her (storksbill)	2	1	2	1	2	3 (2)	3 (2)	0	0
<i>Lactuca serriola</i> L. (prickly lettuce)	6	11 (1)	20 (9)	13 (3)	22 (2)	21 (13)	24 (12)	1	4 (4)
<i>Malcolmia africana</i> R. Br. in Ait. (African mustard)	3	5	3	0	5 (1)	4 (2)	1 (1)	0	0
<i>Ranunculus testiculatus</i> Crantz (bur buttercup)	3	5 (3)	1 (1)	2 (1)	9 (7)	2 (1)	4 (3)	0	0
<i>Salsola pestifer</i> A. Nels. (Russian thistle)	5	4	2	2	1	4 (1)	3 (1)	0	0
<i>Sisymbrium altissimum</i> L. (tumblemustard)	5	7 (1)	18 (10)	16 (6)	6 (1)	18 (12)	18 (10)	4 (2)	4 (4)
<i>Tragopogon dubius</i> Scop. (yellow salsify)	6	7	7	8	8	9 (2)	20 (3)	0	3
<b>Native Annual Forbs</b>									
<i>Camissonia boothii</i> (Dougl.) Raven (Booth's camissonia)	3	1	1	0	7 (2)	2	0	0	0
<i>Descurainia pinnata</i> (Walter) Britt. (pinnate tansymustard)	6	14 (3)	20 (10)	2 (1)	19 (6)	18 (5)	0	3 (1)	0
<i>Eriogonum deflexum</i> Torr. in Ives (skeleton buckwheat)	5	4	1	0	9 (3)	3 (1)	2	0	0
<i>Eriogonum maculatum</i> Heller (spotted buckwheat)	2	1	0	0	6	0	0	0	0
<i>Gilia giliodes</i> (Benth.) Greene (collomia gilia)	1	1	0	0	3 (3)	0	0	0	0
<i>Gilia inconspicua</i> (J.E. Sm.) Sweet (floccose gilia)	6	19 (9)	11 (7)	4	24 (16)	11 (6)	7 (1)	1	3
<i>Helianthus annuus</i> L. (common sunflower)	5	12 (1)	5	3	3	3	4 (1)	0	2 (1)
<i>Lappula occidentalis</i> (Wats.) Greene (western stickseed)	3	1	2	0	9 (1)	1	0	0	0
<i>Mentzelia albicaulis</i> (Hook.) T. & G. (whitestem blazingstar)	4	8	0	0	9 (3)	0	0	0	0
<i>Microsteris gracilis</i> (Hook.) Greene (little polecat)	2	2 (1)	0	0	4 (1)	1 (1)	0	0	0
<i>Nicotiana attenuata</i> Torr. ex Wats. (coyote tobacco)	5	12 (1)	0	0	14 (1)	3	1	0	0
<i>Phacelia ivesiana</i> Torr. in Ives (Ives' phacelia)	4	6	0	0	8	0	0	0	0
<b>Native Perennial Forbs and Shrubs</b>									
<i>Arenaria fendleri</i> Gray (Fendler's sandwort)	1	3 (1)	3 (1)	4 (2)	3 (3)	3 (3)	3 (3)	0	0
<i>Argemone munita</i> Dur. & Hilg. (prickly-poppy)	4	4	4	4	6 (1)	6 (1)	5	0	0
<i>Artemisia tridentata</i> Nutt. (big sagebrush)	4	0	0	0	5	2	2	1	0
<i>Astragalus calycosus</i> Torr. ex Wats. (Torrey's milkvetch)	4	3	4	3	6 (1)	7	4 (1)	1	0
<i>Astragalus eurekaensis</i> Jones (Eureka milkvetch)	4	6 (2)	7 (1)	5 (1)	9 (2)	8 (4)	6 (3)	0	0
<i>Astragalus lentiginosus</i> Dougl. ex Hook (freckled milkvetch)	4	7	6	2	9 (1)	11	4	2	1
<i>Calochortus nuttallii</i> T. & G. in Beckwith (sego lily)	4	16 (1)	11 (1)	7 (4)	14 (3)	11 (2)	7 (1)	2	0
<i>Caulanthus crassicaulis</i> (Torr.) Wats. (spindlestem)	1	2	2	1	2 (1)	3 (1)	2	0	0
<i>Chaenactis douglasii</i> (Hook.) H. & A. (Douglas' dustymaiden)	6	9 (1)	10 (1)	1	12 (1)	10 (1)	3	1	0
<i>Crepis acuminata</i> Nutt. (mountain hawksbeard)	2	2	1	1	3	2	3	0	0
<i>Crepis occidentalis</i> Nutt. (western hawksbeard)	2	4 (1)	5 (1)	4 (1)	4 (2)	4 (2)	4 (2)	0	0
<i>Cryptantha humilis</i> (Greene) Payson (dwarf cryptanth)	3	2	3	2	4	6	5	0	0

(Continued on page 85)

Table 3. Continued.

Species <sup>2</sup>	No. Sites	All Sites						Railroad Site	
		Chained			Non-chained			Late-chained <sup>1</sup>	
		1997	1998	1999	1997	1998	1999	1998	1999
<i>Erigeron aphanactis</i> (Gray) Greene (hairy daisy)	1	2	1	1	4	4	4	0	0
<i>Erigeron engelmannii</i> A. Nels. (Engelmann's daisy)	3	0	3	1	0	2	2	1	1
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby (broom snakeweed)	3	5	4	5	6 (1)	6	7 (1)	0	0
<i>Machaeranthera canescens</i> (Pursh) Gray (Hoary aster)	4	4	4	2	7	8	6	0	0
<i>Opuntia polyacantha</i> Haw (central pricklypear)	3	4 (1)	3 (1)	4	0	0	1 (1)	0	0
<i>Phlox austromontana</i> Cov. (desert phlox)	3	8 (2)	7 (1)	7 (1)	6 (3)	6 (4)	6 (4)	0	0
<i>Phlox longifolia</i> Nutt. (longleaf phlox)	5	12 (8)	9 (8)	7 (6)	12 (5)	8 (3)	4 (2)	1	2
<i>Physaria chambersii</i> Rollins (Chamber's twinpod)	3	4	3	3	2	2	1	0	0
<i>Senecio multilobatus</i> T. & G. (Uinta groundsel)	5	3	2	2	2	3	2	1	1
<i>Sphaeralcea coccinea</i> (Nutt.) Rydb. (common globemallow)	1	4 (1)	4	4	4 (2)	4 (3)	4 (3)	0	0
<i>Sphaeralcea grossulariifolia</i> (H. & A.) Rydb. (gooseberry-leaf globemallow)	3	10 (1)	10 (1)	11 (1)	8	8	8	4	4
<i>Streptanthus cordatus</i> Nutt. ex T. & G. (twistflower)	4	9 (1)	6	2	12	6	2	2	2

<sup>1</sup>Late-chained refers to the Railroad site non-chained treatment that was reseeded and chained between 1998 and 1999. Note that the frequency values in these columns are also part of the total frequency values shown in the 1998 and 1999 columns of the non-chained treatment for all sites.

<sup>2</sup>Scientific nomenclature follows Welsh et al. (1993). In that treatment, *Agropyron desertorum* (Link) Schultes is synonymized with *A. cristatum* and both *A. intermedium* (Host) Beauv. and *A. trichophorum* (Link) Richter are treated as *Elymus hispidus*.

<sup>3</sup>Number of sites where species was recorded, of 6 sites total.

<sup>4</sup>Value on left is frequency in 100 m<sup>2</sup> plots; value in parentheses is frequency in 1 m<sup>2</sup> plots, shown if greater than zero. Maximum frequency value is 24 for all sites, 4 for the Railroad site.

<sup>5</sup>Includes tall wheatgrass [*Elymus elongatus* (Host) Runem.] because we could not distinguish it from *E. hispidus* at the time of data collection.

plot boundaries. Species nomenclature followed Welsh et al. (1993). We did not attempt to distinguish varieties of seeded species; all varieties of crested and desert wheatgrass were placed together and referred to as crested wheatgrass, and all varieties of intermediate, pubescent, and tall wheatgrass were combined and referred to as intermediate wheatgrass. For the large plots, each species was assigned a cover class, following Daubenmire (1959) with an additional class for less than 1% cover (McArthur and Sanderson 1996). For the small plots, percent cover of each species was estimated to the nearest whole number. We combined individual species into 7 groups of interest, based on growth form, longevity, and origin (Table 3). "Exotic" species, principally cheatgrass, were neither native to the region nor derived from the fire rehabilitation seed mixes but were present in the seed bank. Cover values of species in the same group within the same plot were added together to create total cover values for these groups. For the large plots, total cover values were calculated using the midpoints of cover classes. The total number of species (species richness) and the number of native species were tabulated for each large plot, as were total and native species diversity using the Shannon-Wiener Index (Krebs 1999). Cover was used as a measure of species abundance in diversity calculations.

We compared chained and non-chained treatments using SAS PROC MIXED in a mixed model, first order autoregressive

repeated measures analysis (SAS 1990). This statistical approach adjusts standard errors so that comparisons can be made across factors (Littell et al. 1996). Large and small plot sizes were analyzed separately. All combinations of these 2 treatments, 6 sites, and 3 years were included in this analysis, except the 1999 Railroad site non-chained treatment (which had lost its non-chained status by 1999, as described above). The variables analyzed were species richness, species diversity, and percent cover of selected species and categories. Percent cover values were transformed by taking the arcsine of the square root (Steel and Torrie 1960). Site and the interaction of site with treatment and year were treated as random effects, while treatment, year, and their interaction were treated as fixed effects. Tukey's HSD procedure (Steel and Torrie 1960) was used to test differences among treatment, year, and treatment by year means. We chose the value of  $P < 0.05$  as the level of significant differences.

With site as a random factor in the mixed model, statistical inferences can be made for the larger set of sites from which the sites of this study were drawn. Differences between sites and their interaction with treatment and year are incorporated into the error terms of the mixed model (Littell et al. 1996). Thus site differences were not analyzed explicitly, although site means were examined visually for each treatment and year.

## Results

### Species Frequencies, Richness, and Diversity

A total of 117 species were recorded in 48 plots over the course of 3 years, not including unidentified species or species within taxa that were lumped. Groups with the most recorded species were native perennial forbs and shrubs (49 species), native annual forbs (27 species), exotic forbs (mostly annual, 16 species), and native grasses (mostly perennial, 8 species). Species recorded more than 4 times in large plots during the course of the study are shown in Table 3. Species frequencies in both large plots and small plots are shown in Table 3, allowing for visual assessment of species importance and trends at 2 different scales. In the text that follows we use common names; we refer readers to Table 3 for scientific names and authorities.

The most frequently recorded species in 1997 (recorded in 40 or more of 48 large plots) were cheatgrass, crested wheatgrass, intermediate wheatgrass, and floccose gilia (Table 3). Frequency of seeded species was greater with chaining in 1997, but most other species were unaffected by chaining. Annual forbs had higher frequency in the non-chained treatment in 1997. Over the 3-year study seeded grasses increased in frequency in both large and small plots in the non-chained treatment. Low frequency of Russian wildrye in 1997 reflects our failure to properly identify this



**Table 4. Mean species richness and species diversity of 100 m<sup>2</sup> plots, by treatment and year at sites burned in the summer of 1996 in west-central Utah.**

	Chained			Non-chained		
	1997	1998	1999	1997	1998	1999 <sup>1</sup>
Species richness (all spp.)	20 <sup>AB2</sup>	18 <sup>ABC</sup>	15 <sup>C</sup>	22 <sup>A</sup>	19 <sup>ABC</sup>	17 <sup>B</sup>
Species richness (native spp.)	12 <sup>AB</sup>	10 <sup>CD</sup>	7 <sup>D</sup>	15 <sup>A</sup>	11 <sup>BC</sup>	8 <sup>D</sup>
Shannon-Wiener index (all spp.)	0.91 <sup>AB</sup>	0.77 <sup>ABC</sup>	0.69 <sup>C</sup>	0.87 <sup>A</sup>	0.62 <sup>ABC</sup>	0.62 <sup>B</sup>
Shannon-Wiener index (native spp.)	0.82 <sup>AB</sup>	0.73 <sup>CD</sup>	0.61 <sup>D</sup>	0.92 <sup>A</sup>	0.75 <sup>BC</sup>	0.55 <sup>D</sup>

<sup>1</sup>Means were based on 6 sites, except for the 1999 non-chained treatment that was based on 5 sites (Railroad site excluded).  
<sup>2</sup>Means within rows followed by the same letter were not significantly different at  $P < 0.05$  as determined by Tukey's HSD in a mixed-model, first-order autoregressive repeated measures analysis.

species before flowering. Cheatgrass occurred in nearly all large plots from the beginning of the study, but increased in the small plots over time, indicating a spatial expansion of cheatgrass within the large plots. Two exotic forbs (lambquarters and African mustard) decreased in both treatments, whereas 4 others (desert alyssum, falseflax, tansymustard, and yellow salsify) increased in both treatments. Frequency of prickly lettuce and tumble-mustard peaked in 1998, while frequency of bur buttercup was lowest in 1998. Frequency of native grass species fluctuated among years without clear trends. Most native annual forbs decreased in frequency over time in both treatments. The native perennial forb/shrub group also included some species that decreased in both treatments over time; for example, sego lily, freckled milkvetch, longleaf phlox, and twistflower. Big sagebrush, which occurred as seedlings, was not present in the chained treatment and was lost from 3 non-chained plots between 1997 and 1998 (Table 3).

Total species richness was highest in 1997, when 94 species occurred in the chained plots and 93 in the non-chained plots (Table 4). Within each treatment, species richness was significantly lower in 1999 than 1997. Within years, treatment did not significantly affect species richness, except that in 1999 the mean species richness of the non-chained was slightly higher than the chained treatment. When only native species were considered, mean species richness did not differ between treatments for a given year, although native species richness decreased significantly in both treatments between 1997 and 1999. Responses for species diversity (Shannon-Wiener index) were identical to those of species richness, for native species as well as total species (Table 4).

## Percent Cover of Categories and Species

In general, mean cover values were similar for small and large plots and patterns of

statistical significance were similar. The most noticeable variation between plot sizes was for vascular plants and bare soil, where the difference in mean percent cover between large and small plots was as high as 12–14% (Table 5). In the text that follows, mean values are written as a range from the mean of one plot size to the mean of another, unless otherwise specified.

Mean values for total vascular plant cover did not differ significantly between treatments within years, but increased significantly in both treatments between 1997 and 1998 (Table 5). The increase in vascular plant cover between 1997 and 1998 in the chained treatment was due primarily to seeded grasses, while the increase in the non-chained treatment was due primarily to exotic grasses (Table 6). In 1997, total cover of seeded grasses was 10–12% in the chained and 2% in the non-chained treatment, a difference that was significant in the large plots ( $P = 0.01$ ) but not the small plots ( $P = 0.16$ ). Total cover of seeded grasses in the chained treatment increased significantly to 27–30% in 1998, and maintained that high cover (31–33%) in 1999 in contrast to the non-chained treatment cover values, 4–7% in 1998 and 8–11% in 1999. Cover of exotic grasses (almost exclusively cheatgrass) increased significantly between 1997 (18–22%) and 1998 (42–48%) in the non-chained but not

the chained treatment. Exotic grass cover was significantly higher in the non-chained large plots in 1998 and 1999.

Of the seeded grasses, crested wheatgrass and intermediate wheatgrass were dominant with about equal amounts of cover within treatments and years. In the chained treatment, cover of each of these 2 species was 4–6% in 1997, rising to 12–14% in 1999 (Table 6). This increase was significant for crested but not intermediate wheatgrass. In the non-chained treatment, mean cover of each of these 2 species remained between ca. 1–4% and was not significantly different among years. Cover of smooth brome, seeded at only 4 of the 6 study sites, increased significantly in the large plots of the chained treatment between 1997 (1%) and 1998 (5%). At individual sites where smooth brome had been seeded, cover was as high as 9–10% in the chained treatment. Russian wildrye was present at all sites but was not accurately recorded until 1998. Lower cover of Russian wildrye in 1999 resulted from preferential grazing by livestock. In 1998, cover of Russian wildrye was slightly greater in the chained treatment (4% in large plots) than the non-chained treatment (<1% in large plots) (Table 6). Considering the high seeding rates of Russian wildrye at some sites (Table 2), establishment of this species was poor. Basin wildrye, which was seeded at 2 sites, was not conclusively identified at any of the plots or sites.

Although native perennial grasses were subordinate to seeded grasses and cheatgrass over the study area as a whole, they dominated certain sites and plots. Cover of western wheatgrass, a rhizomatous species, appeared to be higher in the chained (1–5%) than the non-chained treatment (<1%) (Table 6), but only because more chained plots fell within its patches. At 1 chained plot at the Gilson site, cover of western wheatgrass was in

**Table 5. Mean percent cover of cover categories, by treatment and year, in 2 plot sizes at sites burned in the summer of 1996 in west-central Utah.**

	Chained			Non-chained		
	1997	1998	1999	1997	1998	1999 <sup>1</sup>
Vascular Plants	38 <sup>B</sup> (27 <sup>b</sup> ) <sup>2</sup>	65 <sup>A</sup> (51 <sup>ac</sup> )	59 <sup>A</sup> (52 <sup>ac</sup> )	41 <sup>B</sup> (34 <sup>bc</sup> )	71 <sup>A</sup> (61 <sup>a</sup> )	62 <sup>A</sup> (53 <sup>a</sup> )
Bare Soil	40 <sup>A</sup> (52 <sup>a</sup> )	22 <sup>B</sup> (34 <sup>bc</sup> )	20 <sup>B</sup> (26 <sup>bcd</sup> )	37 <sup>A</sup> (41 <sup>ac</sup> )	16 <sup>B</sup> (21 <sup>bc</sup> )	14 <sup>B</sup> (15 <sup>de</sup> )
Litter	11 (10)	7 (8)	15 (16)	8 (9)	5 (7)	15 (20)
Rock (>1 cm)	11 (11)	6 (7)	6 (6)	14 (17)	9 (11)	9 (12)
Cryptogams	+	+	+	+	+	+

<sup>1</sup>Means were based on 6 sites, except for the 1999 non-chained treatment that was based on 5 sites (Railroad site excluded).

<sup>2</sup>Value on left is mean percent cover for 100 m<sup>2</sup> plots; value in parentheses is mean percent cover for 1 m<sup>2</sup> plots. Means within rows followed by the same letter of the same case were not significantly different at  $P < 0.05$  as determined by Tukey's HSD in a mixed-model, first-order autoregressive repeated measures analysis.

+ indicates mean values less than 0.5; other values are rounded to the nearest whole number.

the 26–51% class in 1997 and 1999, and the 51–75% class in 1998. Bluebunch wheatgrass cover remained between 2–4% in the chained treatment, but increased annually in the non-chained treatment. In the small plots, the change in bluebunch wheatgrass cover from 4% in 1997 to 14% in 1999 was significant. The Dog Slopes site had the highest cover of bluebunch wheatgrass and accounted for most of this trend. Mean percent cover of bottlebrush squirreltail, Sandberg bluegrass, muttongrass, and Indian ricegrass was about 1% or less in both treatments during the study. Total cover of native grasses ranged from 8–10% in the large plots and 4–15% in the small plots, but was not significantly different between treatments or among years.

Cover for most forbs and shrubs mirrored average frequency; only a few forbs consistently occurred with greater than 1% cover. Total cover of exotic forbs was significantly greater in the non-chained treatment in 1998 (ca. 8%) than the chained treatment in 1997 and 1999 (ca. 0–4%; Table 6). The most important species in this category was tumbled mustard, which did not differ significantly in cover between treatments within years, but increased significantly in the non-chained treatment between 1997 (< 0.5%) and 1998 (5%). Native annual forbs cover was 4–8% in 1997, decreasing significantly in both treatments to 1% or less in 1998 and 1999. Floccose gilia accounted for about half of the cover of native annual forbs in the 1997 non-chained treatment. Total cover of native perennial forbs and shrubs was not significantly different between treatments within years and did not change significantly over time except in the large plots of the non-chained treatment, where a significant decrease occurred from 6% in 1997 to 4% in 1999. Cover of seeded shrubs and forbs was low and was not significantly different between treatments or among years. Mean cover of fourwing saltbush in the chained treatment averaged about 1% across 3 years (Table 6). Fourwing saltbush was present in fewer plots in the non-chained than in the chained treatment, and cover never exceeded 1% in any plot. Alfalfa was a component of the seed mix of the Twin site (Table 2), but cover never exceeded 1% in any plot.

## Discussion

### Seeded Plant Establishment

The enhancement of establishment through chaining is a consequence of seed

burial, the modification of soil physical properties, and development of safe sites. Crested wheatgrass, intermediate wheatgrass, smooth brome and other grasses with seeds of medium to large size tend to germinate and establish successfully when buried at depths of 1–3 cm (Hull 1966, Keller 1979, Vallentine 1989). Germination of uncovered seed and establishment of seedlings may be poor because of inadequate soil contact, dessication, or rooting difficulty (Vallentine 1989, Winkel et al. 1991). Exposed seed may also be lost through predation (Nelson et al. 1970). In contrast, deep burial can inhibit seedling emergence and survival (Vallentine 1989, Lawrence et al. 1991). Chaining results in irregular seed burial, which can be considered a disadvantage of this technique compared to drilling (BLM 1999b).

Alternatively, the multiple microsites and seed burial depths generated by chaining can be advantageous for the establishment of mixes containing seeds with different depth requirements (Stevens 1999). Loosening soil surfaces by chaining may also increase aeration, porosity, and water infiltration, which are beneficial soil properties of plowed soils (Wood et al. 1982, Cluff et al. 1983).

The greatest response of seeded grasses to chaining occurred at the Twin Peaks site, on soils derived from basalt cobbles and loess. Chaining at this site resulted in cobbles being overturned and scattered, which initially appeared to be detrimental in terms of soil protection, yet resulted in near 50% foliar cover of seeded grass by 1998.

Where aerial seeding was not followed

**Table 6. Mean percent cover of species groups and selected species, by treatment and year, in 2 plot sizes at sites burned in the summer of 1996 in west-central Utah.**

	Chained			Non-chained		
	1997	1998	1999	1997	1998	1999 <sup>1</sup>
<b>Total seeded shrubs and forbs</b>	<b>1 (1)<sup>2</sup></b>	<b>1 (1)</b>	<b>1 (1)</b>	<b>+ (0)</b>	<b>+ (0)</b>	<b>+ (0)</b>
Alfalfa <sup>3</sup>	+ (0)	+ (0)	+ (0)	+ (0)	+ (0)	+ (0)
Fourwing saltbush	1 (1)	1 (1)	1 (1)	+ (0)	+ (0)	+ (0)
<b>Total seeded grasses</b>	<b>12<sup>B</sup> (10<sup>b</sup>)<sup>4</sup></b>	<b>30<sup>A</sup> (27<sup>a</sup>)</b>	<b>31<sup>A</sup> (33<sup>a</sup>)</b>	<b>2<sup>C</sup> (2<sup>b</sup>)</b>	<b>4<sup>BC</sup> (7<sup>b</sup>)</b>	<b>8<sup>BC</sup> (11<sup>b</sup>)</b>
Crested wheatgrass	4 <sup>C</sup> (4 <sup>c</sup> )	8 <sup>B</sup> (8 <sup>b</sup> )	12 <sup>A</sup> (14 <sup>a</sup> )	1 <sup>D</sup> (1 <sup>c</sup> )	1 <sup>CD</sup> (2 <sup>c</sup> )	4 <sup>CD</sup> (4 <sup>c</sup> )
Intermediate and tall wheatgrass	6 <sup>AB</sup> (6 <sup>ab</sup> )	10 <sup>AB</sup> (13 <sup>ac</sup> )	13 <sup>A</sup> (14 <sup>a</sup> )	1 <sup>B</sup> (1 <sup>b</sup> )	1 <sup>B</sup> (1 <sup>b</sup> )	2 <sup>B</sup> (3 <sup>b</sup> )
Russian wildrye	+ <sup>B</sup> (0 <sup>b</sup> )	4 <sup>A</sup> (2 <sup>a</sup> )	1 <sup>B</sup> (1 <sup>ab</sup> )	+ <sup>B</sup> (0 <sup>ab</sup> )	+ <sup>B</sup> (1 <sup>ab</sup> )	+ <sup>B</sup> (1 <sup>ab</sup> )
Smooth brome	1 <sup>B</sup> (1 <sup>a</sup> )	5 <sup>A</sup> (2 <sup>a</sup> )	4 <sup>AB</sup> (4 <sup>a</sup> )	+ <sup>B</sup> (1 <sup>a</sup> )	1 <sup>AB</sup> (2 <sup>a</sup> )	2 <sup>AB</sup> (2 <sup>a</sup> )
<b>Total exotic grasses</b>	<b>10<sup>B</sup> (8<sup>b</sup>)</b>	<b>18<sup>B</sup> (17<sup>bc</sup>)</b>	<b>14<sup>B</sup> (16<sup>bd</sup>)</b>	<b>22<sup>B</sup> (18<sup>b</sup>)</b>	<b>48<sup>A</sup> (42<sup>ac</sup>)</b>	<b>35<sup>A</sup> (27<sup>acd</sup>)</b>
Cheatgrass	9 (8)	18 (17)	14 (16)	22 (18)	48 (42)	35 (27)
<b>Total native grasses</b>	<b>8<sup>A</sup> (4<sup>a</sup>)</b>	<b>8<sup>A</sup> (7<sup>a</sup>)</b>	<b>10<sup>A</sup> (6<sup>a</sup>)</b>	<b>7<sup>A</sup> (5<sup>a</sup>)</b>	<b>10<sup>A</sup> (10<sup>b</sup>)</b>	<b>14<sup>A</sup> (15<sup>a</sup>)</b>
Bluebunch wheatgrass	2 <sup>A</sup> (2 <sup>ab</sup> )	4 <sup>A</sup> (2 <sup>ab</sup> )	3 <sup>A</sup> (3 <sup>ab</sup> )	4 <sup>A</sup> (4 <sup>b</sup> )	6 <sup>A</sup> (8 <sup>ab</sup> )	10 <sup>A</sup> (14 <sup>a</sup> )
Bottlebrush squirreltail	1 (1)	1 (1)	+ (1)	1 (1)	1 (1)	1 (1)
Indian ricegrass	1 (+)	1 (+)	1 (+)	1 (1)	2 (1)	2 (1)
Bluegrass spp.	+ (+)	+ (1)	+ (+)	1 (1)	1 (1)	+ (+)
Western wheatgrass	3 (2)	2 (2)	4 (2)	+ (0)	+ (0)	+ (0)
<b>Total exotic forbs</b>	<b>2<sup>B</sup> (+<sup>c</sup>)</b>	<b>5<sup>AB</sup> (6<sup>ab</sup>)</b>	<b>2<sup>BC</sup> (4<sup>bc</sup>)</b>	<b>5<sup>AB</sup> (5<sup>abc</sup>)</b>	<b>8<sup>A</sup> (8<sup>a</sup>)</b>	<b>7<sup>AC</sup> (4<sup>abc</sup>)</b>
Desert alyssum	+ (+)	1 (+)	+ (+)	1 (1)	+ (2)	2 (1)
Falseflax	+ (0)	+ (+)	+ (+)	1 (1)	+ (+)	+ (+)
Prickly lettuce	1 (+)	1 (2)	+ (+)	1 (3)	1 (1)	1 (+)
Tumbled mustard	+ <sup>B</sup> (+ <sup>ab</sup> )	2 <sup>AB</sup> (3 <sup>ab</sup> )	1 <sup>AB</sup> (3 <sup>ab</sup> )	+ <sup>B</sup> (+ <sup>b</sup> )	5 <sup>A</sup> (5 <sup>a</sup> )	2 <sup>AB</sup> (1 <sup>ab</sup> )
<b>Total native annual forbs</b>	<b>5<sup>A</sup> (4<sup>ab</sup>)</b>	<b>1<sup>B</sup> (1<sup>bc</sup>)</b>	<b>+B (+<sup>c</sup>)</b>	<b>8<sup>A</sup> (6<sup>a</sup>)</b>	<b>1<sup>B</sup> (1<sup>bc</sup>)</b>	<b>+<sup>B</sup> (+<sup>c</sup>)</b>
Common sunflower	1 (+)	+ (0)	+ (0)	+ (0)	+ (0)	+ (0)
Coyote tobacco	2 (+)	0 (0)	0 (0)	1 (+)	+ (0)	+ (0)
Floccose gilia	1 (4)	+ (+)	+ (0)	4 (3)	+ (+)	+ (+)
<b>Total native perennial forbs and shrubs</b>	<b>4<sup>ABC</sup> (1<sup>a</sup>)</b>	<b>3<sup>ABC</sup> (1<sup>a</sup>)</b>	<b>2<sup>BC</sup> (1<sup>a</sup>)</b>	<b>6<sup>A</sup> (3<sup>a</sup>)</b>	<b>5<sup>AB</sup> (4<sup>a</sup>)</b>	<b>4<sup>C</sup> (3<sup>a</sup>)</b>
Milkvetch spp.	+ (+)	+ (+)	+ (+)	1 (+)	1 (+)	+ (+)
Phlox spp.	1 (+)	1 (+)	+ (+)	1 (1)	+ (1)	+ (1)
Globemallow spp.	1 (+)	1 (+)	+ (+)	1 (1)	1 (1)	1 (+)

<sup>1</sup>Means are based on 6 sites, except for the 1999 non-chained treatment which is based on 5 sites (Railroad site excluded).

<sup>2</sup>Value on left is mean percent cover for 100 m<sup>2</sup> plots; value in parentheses is mean percent cover for 1 m<sup>2</sup> plots.

<sup>3</sup>Scientific names are given in Table 3.

<sup>4</sup>Means within rows followed by the same letter of the same case were not significantly different at alpha = 0.05 as determined by Tukey's HSD in a mixed-model, first-order autoregressive repeated measures analysis. + indicates mean values less than 0.5; other values are rounded to the nearest whole number.

by chaining, seeded plants established primarily in washes, soil cracks, and beneath burned juniper or pinyon trees. The soil surfaces beneath these trees were typically blackened, devoid of litter and plants, and probably hydrophobic (Blank et al. 1995). Nevertheless, some seeded plants established in this soil, perhaps because soil movement due to uneven topography or low organic cover enhanced seed burial. The highest measured cover of seeded grasses in a non-chained treatment occurred at the Dog Slopes site, where establishment may have been enhanced by soil movement downslope and by favorable water relations on the mostly north-east-facing slopes. Koniak (1983) reported that establishment of aerially-seeded intermediate wheatgrass following fire on pinyon-juniper sites was greater on north-facing slopes than on other aspects. The experience of the BLM in the region of this study suggests that aerial seeding without chaining can be successful in higher-elevation areas where soil water tends to be greater, specifically above 1,830 m elevation, on sloping topography where seed can be broadcast onto a winter snowpack (BLM personal communication, MacDonald 1999). The relatively high cover of seeded grass observed at the Dog Slopes site suggests that aerial seeding may be successful at elevations below 1,830 m on cooler exposures.

Seed burial can increase the chances of successful plant establishment, but climatic factors ultimately determine the outcome of wildfire rehabilitation and other rangeland revegetation projects (Call and Roundy 1991). Low precipitation was implicated as the primary reason for the limited success of wildfire rehabilitation treatments studied by Ratzlaff and Anderson (1995) in southeastern Idaho. In contrast, precipitation events in west-central Utah following the 1996 fires were initially highly favorable for plant establishment and growth. Several peaks of above-average precipitation occurred in 1997 and 1998 during spring and early summer (Fig. 2), the period of growth for seeded grasses. These were exceptional conditions associated with an El Niño event, and would not be expected during most years in this region.

Results of this study indicate that aerial seeding of agronomic cultivars of introduced grasses (see Table 2) followed by chaining will provide perennial plant cover and soil stability. Chaining is a more efficient means of rehabilitation than drill seeding when a large acreage is involved (BLM 1999b). Agronomic cultivars of

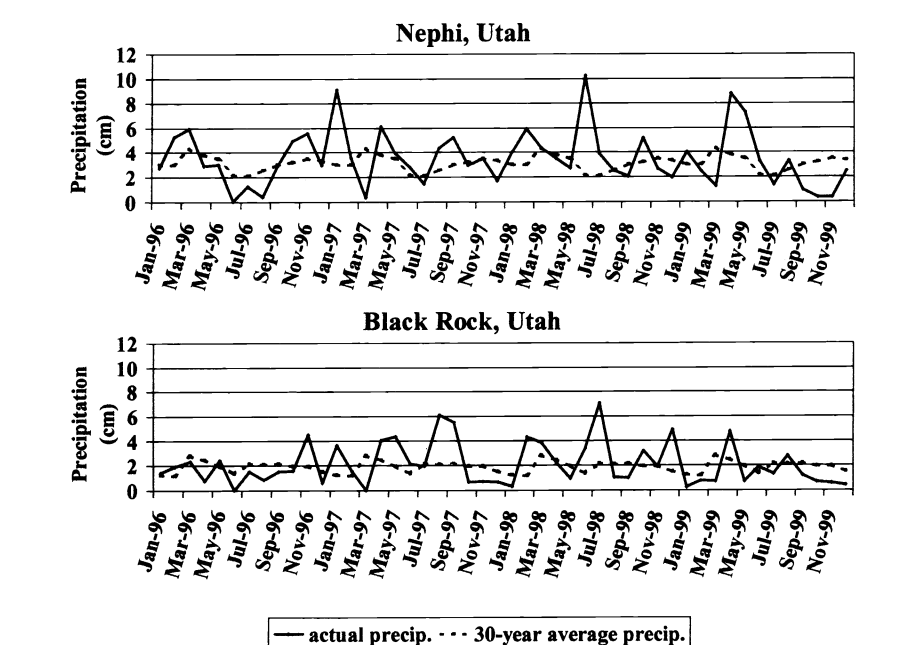


Fig. 2. Monthly precipitation from 1996 to 1999 at 2 weather stations in west-central Utah (NOAA 1996–1999).

introduced grasses are often preferred over native grasses by managers because of their availability, adaptability, responsiveness to standard seeding methods, and utility (Richards et al. 1998, Asay et al. 2001).

### Cheatgrass Dynamics

Cheatgrass suppression is a common management goal in consequence of the increased fire risks, decreased resource values, and loss of ecological diversity that arise when cheatgrass becomes dominant (Whisenant 1990, Monsen 1994, Roberts 1999). The ability to compete with cheatgrass is an important requirement for rehabilitation plant materials, given the near-ubiquitous occurrence of cheatgrass in the semiarid zones of the Intermountain West (Monsen 1994).

Although the fires likely reduced the amount of viable cheatgrass seed present at our study sites, especially in subcanopy zones of shrubs and trees, an adequate seed bank and favorable climatic conditions following fires allowed cheatgrass population explosions (Young and Evans 1978, Ott et al. 2001). Cheatgrass benefited from high precipitation events of autumn 1997 and early spring 1998 (Fig. 2), and above-average temperatures of the intervening winter (NOAA 1997, 1998).

Chaining could have initially inhibited cheatgrass establishment by burying cheatgrass seed too deeply for successful

germination or affecting seedling emergence (Wicks 1997). However, a chained surface could subsequently promote cheatgrass invasion because of its rough surface microtopography (Evans and Young 1972). The presence of seeded grasses appears to have been the principal factor that kept cheatgrass cover lower in the chained treatment.

Successful competitiveness against cheatgrass has been demonstrated for commonly seeded plants including 'Hycres' crested wheatgrass, 'Luna' intermediate wheatgrass, 'Bozoisky' Russian wildrye, and smooth brome (Aguirre and Johnson 1991, Francis and Pyke 1996, Wicks 1997, Whitson and Koch 1998). Nevertheless, at certain sites such as the Railroad site, large amounts of cheatgrass were found in the interspaces among seeded grasses. The extent of cheatgrass invasion may be influenced by the density and composition of seeded grasses, or by other site-specific environmental variables such as elevation, soils, slope, and aspect. In our study, cheatgrass was most abundant on sites at lower elevations in central valley areas, especially the Railroad and Jericho sites. The least cheatgrass occurred on the Dog Slopes site, located on a northeast-facing exposure that also had the highest native perennial grass cover. The native perennial grasses bluebunch wheatgrass and bottlebrush squirreltail can also have a competitive impact

on cheatgrass growth and reproduction as mature plants (Harris 1967, Monsen 1994, Stevens 1997). Suppression of cheatgrass invasion following fire has been observed in areas where these grasses or other fire-tolerant native plants were abundant in the pre-burn plant community and readily recovered following fire (West and Hassan 1985, Ratzlaff and Anderson 1995).

### Impacts on Native Plants and Diversity

Responses of native species were not as statistically conclusive in our study as were seeded species and cheatgrass, but they offer rough insights concerning native plant performance after aerial seeding and chaining following wildfire. Species with approximately equal frequency and cover in chained and non-chained treatments during the first year of this study are assumed to have been unaffected by chaining and to have been approximately equal in frequency before the fires. Chaining may have directly influenced species that differed in first-year frequency and cover between treatments. Seed burial at depths inhibiting germination or emergence may account for lower frequencies of many annual species in the chained treatment, with the exception of common sunflower, which has large seeds whose germination may have been enhanced by burial.

Chaining reportedly minimally affects post-fire recovery of native perennial grasses and forbs (Monsen, personal communication). This was true for most native perennial species in our study, although frequency and cover of bluebunch wheatgrass and muttongrass were slightly lower in the chained treatment. The potential for uprooting established perennials by chaining in certain soil types, with varying soil water and larger chain size should be investigated further.

Changes in abundance of native species over the 3-year course of the study may have been due to a combination of succession, climatic factors, and competition. High native species diversity in 1997 could be attributed to the presence of surviving components of the pre-burn community, combined with a seed bank of species that respond to burns, e.g., flocose gilia, common sunflower, whitemstem blazingstar, coyote tobacco—see Table 3. Annual forbs such as flocose gilia and coyote tobacco are common following fire in the pinyon-juniper zone of the Great Basin, but decline as succession proceeds (Everett and Ward 1984). Successional changes may have been accelerated by the rapid expansion of grasses during favor-

able climatic conditions in 1998. If this were the case, our results suggest that seeded grasses and cheatgrass had similar competitive impacts, because native species declined in both the areas dominated by seeded grasses and those dominated by cheatgrass. Climatic conditions may have interacted with competition to cause these declines. Established native grasses appeared to withstand competition from seeded grasses and cheatgrass for the duration of this study, although their growth and recruitment would have probably been greater in the absence of such competition (Harris 1967, Reichenberger and Pyke 1990). The long-term outcome of competitive interactions among species was not revealed by our short-term study.

Based on our results we suggest that the influence of seeded plants on native plants may be minimal in the short term, or perhaps no worse than the alternative influence of cheatgrass proliferation. If the reestablishment of native vegetation is desired, the long-term affects of introduced plants are of more concern. Several authors have expressed concern over the competitive, persistent nature of crested wheatgrass, intermediate wheatgrass, and smooth brome on seeded sites (Anderson and Marlette 1986, Lesica and DeLuca 1996, Walker 1999). Much emphasis has recently been placed on using native plant materials for wildfire rehabilitation on public lands of the Intermountain West, for the purpose of maintaining site biodiversity and ecosystem function (Richards et al. 1998, Brown and Amacher 1999, McArthur and Young 1999). We support this ideal while recognizing some yet-unresolved practical limitations, such as the difficulty of establishing native grasses on drier sites (Asay et al. 2001).

### Additional Management Implications

A relationship between perennial grass establishment and soil protection was not clearly indicated by this study, because soil cover provided by seeded grasses was low during the first season following the fire, and cheatgrass rapidly covered the soil in areas where seeded grasses were not present. Dense cheatgrass stands offer soil protection (Young and Allen 1997). But because of low cheatgrass cover during drought years (Hosten and West 1994) and repeated soil denudation following burning of cheatgrass stands, soil loss may be high in cheatgrass stands in the long term. Managers should realize that ground cover is not the only factor influencing soil erosion, and that revegetation treatment will not affect erosion rates in the

same manner at all sites. Differences in background site erosion potential, which is related to soil characteristics, geomorphology, and climate, may cause some sites to be inherently more erodible than others (Davenport et al. 1998).

Following the 1996 fires, an overriding concern for soil protection and weed suppression, plus the logistical dilemma of rehabilitating a huge burned acreage, led the BLM Fillmore Field Office to rely on standard rehabilitation techniques and plant materials. Rehabilitation was planned even for locations where it might not have been necessary to maximize the probability for soil protection and weed suppression. Consideration of a different set of risks (impact of chaining treatments on archeological sites and on the integrity of wilderness resources and native vegetation) led others to conclude that the application of rehabilitation should be minimized. Ideally, open communication of objectives and concerns in a public participatory process can lead to compromises in public lands management issues, but when fundamental differences are involved, consensus is difficult (SUWA 1994, Moote and McClaran 1997).

Because of issues such as the chaining controversy which followed the 1996 fires, the BLM has recently revised certain aspects of their approach to wildfire rehabilitation. One such revision was the introduction of Normal Fire Rehabilitation Plans, which entail environmental assessments and public participation in advance of potential wildfires (BLM 1999a). Such measures have the potential to streamline the rehabilitation process and reduce controversy in the event of an actual wildfire. Planning for the future is prudent, in view of the likelihood of continued wildfire impacts on public lands of the Intermountain West. Foresight, clear management objectives, public support, appropriate technology, and ecological understanding will contribute to the success of wildfire rehabilitation programs.

The results of this study support chaining as a method to better establish aerially seeded species over the alternative of no seedbed preparation or seed coverage in wildfire rehabilitation plantings. The establishment of seeded species also reduces the incidence of cheatgrass in the post-fire communities.

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U.S. Geological Survey (USGS) 7.5 minute digital elevation model, which is relatively imprecise in the vertical direction. The root mean square error (RMSE) is used to describe the digital elevation model accuracy and is defined as:

$$RMSE = \sqrt{\frac{\sum (Z_i - Z_t)^2}{n}}$$

where

$Z_i$  = interpolated DEM elevation of a test point

$Z_t$  = true elevation of a test point

$n$  = number of test points

For 7.5-minute digital elevation models derived from a photogrammetric source, 90% of control points on the ground have a vertical accuracy of 7-m root mean square error or better and 10% are in the 8 to 15 m range. For 7.5 and 15-minute digital elevation models derived from vector or digital line graph hypsographic and hydrographic source data, a root mean square error of one-half contour interval or better is required (National Mapping Division, U.S. Geological Survey 1998). This level of resolution is inappropriate for many ecological studies and for precision agriculture.

Coarse-acquisition code differential corrected global positioning system (C/A code DGPS) technology has revolution-

ized field mapping and is widely used in natural resources because X (longitude) and Y (latitude) position can be ascertained with a root mean square error of 50 to 100 cm (Trimble Navigation Ltd. 2001a). However, vertical errors of 100 to 200 cm are common with coarse-acquisition code differential global positioning systems (Clark and Lee 1998, Trimble Navigation Ltd. 1996). Real-time stop-and-go and real-time kinematic carrier-phase differential global positioning systems mounted on vehicles have been used to map boundaries (Sumpter and Asher 1994) and elevation with vertical root mean square errors reported to be from 2 to 9 cm (Clark and Lee 1998, Johansen et al. 2001, Trimble Navigation Ltd. 2001b, Leica Geosystems AG 1999). Carrier-phase differential global positioning system units cost from \$20,000 to \$100,000 (Johansen et al. 2001). Because of the cost, carrier-phase differential global positioning systems are not as widely available as coarse-acquisition code differential global positioning systems.

Our research required a digital elevation model with vertical accuracy (root mean square error) of approximately 10 cm and neither a real-time stop-and-go nor real-time kinematic carrier-phase differential global positioning system was available. Therefore, we developed a method to efficiently generate highly accurate elevation

models for open, relatively level land using a coarse-acquisition code differential global positioning system (<\$8000) and a low-cost laser level (<\$1000).

## Materials and Methods

The procedure we have developed includes both data collection in the field and computer processing in the office (Table 1).

### Field Setup

We collected topographic information via 2 technologies: coarse-acquisition (C/A) code differential global positioning system for the latitude (Y) and longitude (X) position and laser level with metric leveling rod for elevation (Z) (Fig. 1). We used a Trimble Navigation Pathfinder Pro XR<sup>®</sup>, 12-channel, L1/CA-code differential global positioning system. With this system we can obtain an X, Y coordinate with a root mean square error of 50 to 100 cm in approximately 25 seconds. The laser level system was a Laser Reference Inc. Proshot L4<sup>®</sup> with a R4<sup>®</sup> laser receiver and a Crain Enterprises, Inc. CR-5.0M<sup>®</sup> metric leveling rod. This laser level has a working radius of 230 m, with a leveling accuracy of better than 2 cm. Laser levels of this type are readily available from

**Table 1. Field and office (computer) procedures for developing a digital elevation model (DEM).**

Location	Procedures
Field	<p><u>Step 1: Identify a reference position</u></p> <ol style="list-style-type: none"> <li>Locate a National Geodetic Survey Ground Control Point, or</li> <li>Create a Temporary Bench Mark <ol style="list-style-type: none"> <li>Phase processing RTSG<sup>1</sup> DGPS<sup>1</sup>, or</li> <li>Occupy static location for an extended time</li> </ol> </li> </ol> <p><u>Step 2: Establish the Laser Level in the Area to be Surveyed</u></p> <ol style="list-style-type: none"> <li>Determine the height of the laser beam above GCP<sup>1</sup> using leveling rod and receiver</li> <li>Record the X Y<sup>1</sup> locations of the laser lever and laser height identification code (LHID)<sup>1</sup> using the GPS<sup>1</sup> data Logger</li> <li>Enter height of the laser above the GCP<sup>1</sup> or TBM<sup>1</sup> as a comment in the GPS<sup>1</sup> data logger</li> </ol> <p><u>Step 3: Start Grid Sampling</u></p> <ol style="list-style-type: none"> <li>Record location X Y<sup>1</sup> using GPS<sup>1</sup> unit and data logger</li> <li>Record height of the laser beam above the ground as a comment</li> </ol>
Office	<p><u>Step 4: Create Spreadsheet with XYZ<sup>1</sup> Locations</u></p> <ol style="list-style-type: none"> <li>Differentially correct GPS<sup>1</sup> data to give XY<sup>1</sup> locations within 1m</li> <li>Subtract the height above the ground (comment) from the laser beam height to obtain the Z<sup>1</sup>-value</li> </ol> <p><u>Step 5: GIS<sup>1</sup> Applications</u></p> <ol style="list-style-type: none"> <li>Import data into GIS<sup>1</sup> software</li> <li>Interpolate between points using a weighted-averaging, spline, or kriging technique, or a triangulated irregular network (TIN)<sup>1</sup> model</li> </ol> <p><u>Step 6: Produce Digital Elevation Models</u></p> <ol style="list-style-type: none"> <li>Contour maps</li> <li>3-D<sup>1</sup> maps</li> </ol>

<sup>1</sup> Abbreviations used are DGPS (differential global positioning system); GCP (Ground Control Point); GIS (Geographical Information System); GPS (Global Positioning System); LHID (Laser Height Identification); NGS (National Geodetic Survey); RTSG (real-time stop-and-go); TBM (temporary bench mark); TIN (Triangulated Irregular Network); XYZ are longitude, latitude, and elevation.



**Fig. 1.** Equipment used to generate highly accurate digital elevation models include a laser level and a sliding laser receiver attached to a leveling rod. In the horizontal mode, the laser level self levels via a wire-hung, air-damped compensator. The Pro Shot® L4 (Laser Reference, Inc.) laser level we used has a working radius of 230 m, with a leveling accuracy of 1.6 mm per 30 m.

equipment rental stores for approximately \$40 per day. Necessary components are described in Table 2.

If it is important to determine the true elevation of the laser for reasons other than creating a relative digital elevation model, it is necessary to either find an existing National Geodetic Survey (NGS) ground control point or establish a temporary bench mark. The National Geodetic Survey maintains ground control points represented by survey monuments. Locations of these can be obtained from

National Geodetic Survey (1996) on CD-ROM or found on the web at: <http://www.ngs.noaa.gov/datasheet.html> (accessed April 2002). In most cases a National Geodetic Survey ground control point marker will not exist in the vicinity and a temporary bench mark must be established by marking the point with a surveyor's stake and using differential global positioning system or traditional survey techniques to determine its location. Since all elevations collected using the laser level are referenced to this single

point, it is advantageous to locate the temporary bench mark at a location where vehicles or vandals will not damage it and it can be used in the future. It should be placed so it is close to and visible from the area to be surveyed. For most of our work, we are interested in vertical position relative to the elevation of the temporary bench mark. In this case, we position the temporary bench mark by collecting numerous coarse-acquisition code differential global positioning system fixes with the global positioning system antenna in a static position on a tripod at a set height above the point. Our coarse-acquisition code differential global positioning system records a position every second and we normally record data for an hour or more to achieve accuracy within 60 cm. If we want to define absolute elevations of the area being surveyed, we will position the temporary bench mark using either traditional survey techniques or carrier-phase differential global positioning system. Carrier-phase differential global positioning system requires 2 global positioning system units, a rover, and a local base station. Accuracies within 10 cm (Trimble Navigation 1996) are attainable with carrier-phase differential global positioning system processing by occupying a location for 30 minutes.

Once the temporary bench mark has been positioned, the laser level (source) is set in the area to be surveyed and the height of the laser above the reference point is measured with a leveling rod and laser receiver (Fig. 1). Our laser level has a working radius of 230 m. We record the X, Y location of the laser level with the differential global positioning system, and 2 additional pieces of information as comments in the data file: (1) the laser height identification code, which includes the date and sequence number of each particular setup of the laser level, and (2) the elevation of the laser beam. The elevation of the rotating laser is determined by measuring its height above the temporary bench mark with a laser receiver attached to a leveling rod then adding the elevation of the temporary bench mark. This information will be used to determine the elevation of each point and helps us organize data during office processing.

### Grid Sampling

Once the laser level has been set up on a ground-control position, it rotates 360° automatically and the 2-person crew moves across the area to be surveyed, stopping to record differential global positioning system points across the terrain. At

**Table 2.** Equipment used to collect topographic data in the field.

Equipment	Specification	Accuracy
Differential Global Positioning System (DGPS) with Data Logger	12-channel, L1/CA <sup>1</sup> code Differential Global Positioning System	Normally 50 to 100 cm with open sky conditions
Laser Level System		
Laser Level	Self-leveling compensated laser level	2 cm across 230-m radius
Laser Receiver	Laser receiver with rod clamp	
Tripod	Aluminum tripod with 1.6-m maximum height	
Leveling Rod	5.0-m fiberglass leveling rod	0.5 cm
Stakes		

<sup>1</sup>Global Positioning System satellites transmit ranging signals on 2 D-band frequencies: Link 1 (L1) and Link 2 (L2). Two different ranging codes are transmitted, a coarse-acquisition (C/A) code on L1 frequency and a precision (P) code on both L1 and L2 frequencies.

each sample location the person carrying the differential global positioning system records a northing (latitude or Y) and easting (longitude or X) coordinate. The second person adjusts the height of the electronic laser receiver on the calibrated leveling rod to capture the rotating laser beam and measures the height of the laser beam above the ground. This height is entered into the differential global positioning system data logger as a comment. A 2-person crew can record a location in approximately 25 seconds plus walking time. The crew would typically pace across the landscape in a grid pattern to systematically sample the field. It is important that they also sample other features of interest, such as hilltops and low spots as well as 'break lines' along drainage ways and ridges. To ensure that areas are adequately sampled, each point is marked with foam that persists long enough to finish a job. The quality of the digital elevation model will be a function of: (1) how many points are obtained; and (2) how the points are positioned (Clark and Lee 1998). As Clark and Lee (1998) point out "the procedure requires good judgment on the part of the surveyor, and is essential to obtaining a good topographic map."

On level, open terrain without brush or other obstructions, 16 ha can be measured from a single, central, laser location. For larger areas, we back-shoot from a new instrument location to the original temporary bench mark reference point. Since the elevation data is referenced to the temporary bench mark or ground control points, data can be collected over an extended time, as long as the temporary bench mark remains in place. Because the rotating laser beam sweeps 360°, more than 1 team can collect data at the same time. We have sampled agronomic fields, wetlands, and research plots using this technique. We collected the data necessary to map a 35-ha grass seed field on a 20-m grid pattern (1204 sample points) with 1 team in 24 hours.

### Office Processing

In the office we differentially correct the global positioning system data with data from a local base station. We then export data to a spreadsheet program with each worksheet containing all data collected while the laser was at 1 location and height. Ground elevation is calculated for each sample point by subtracting the laser beam-to-ground distance (comment value in the global positioning system data logger) from the elevation of the laser beam that was determined from the temporary

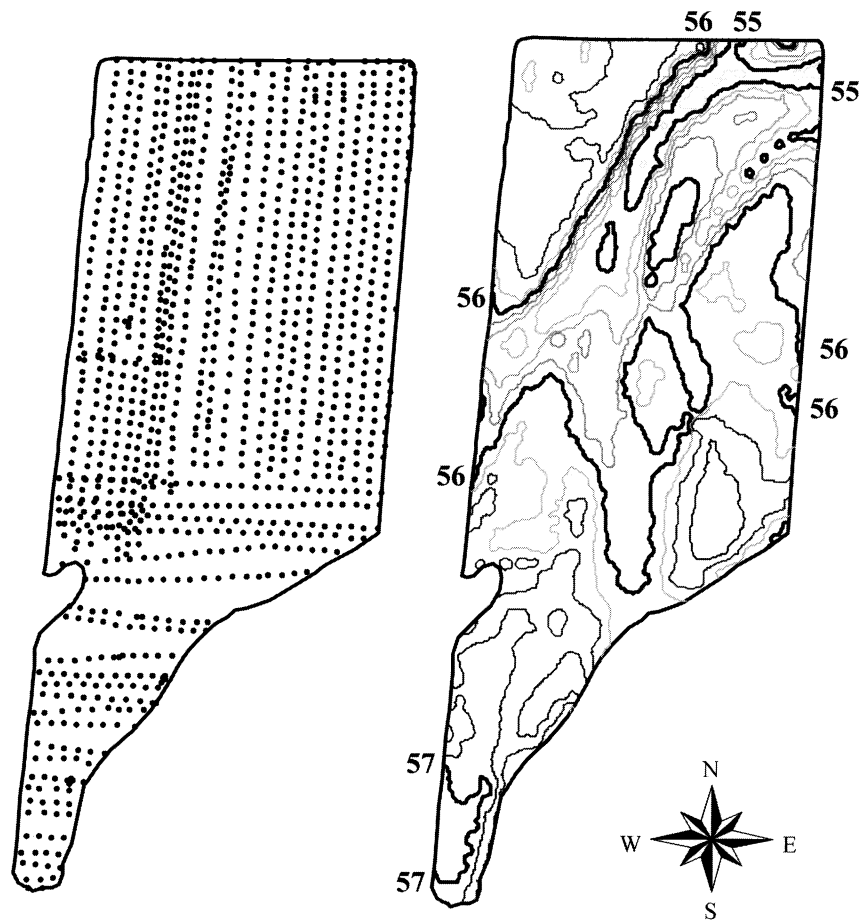


Fig. 2. Sample locations are depicted by the dots on the image of the field on the left. A contour map of the field, which was created by interpolation between sample locations, is shown on the right. Numbers are meters above ellipsoid (approximately above sea level). Note both within field variability and a general increase in elevation from north to south.

bench mark. Interpolation of a digital elevation model from point data is accomplished with any of the numerous commercial geographic information system software packages (ERDAS®, IDRISI®, Rockworks®, ArcView®, ArcGIS®, etc.). The sampling pattern and resulting contour map of a 76-ha field, sampled with 2181 points, is shown in Figure 2.

### Limitations

This technique was developed for measuring land with gently rolling topography, such as found in agronomic fields, wetlands, and research plots. Since X, Y coordinates may have a root mean square error of 50 to 100 cm, it is not appropriate for short, deep cut-banks or short, steep escarpments where the cut face must be precisely positioned. Because the leveling rod and receiver unit has a working height from near ground level to 5 m, rugged land can require frequent repositioning of the laser level, which reduces efficiency

and increases costs. Shrubs and trees that block either the laser beam or reception of NAVSTAR satellite signals limit application of our technique as do weather conditions such as fog, rain, or excessive dust that absorb the laser beam and reduce the working radius of the laser level. For large fields or extensive areas, the labor cost of our technique can be high and using carrier-phase differential global positioning system technology becomes more attractive.

This procedure is intended to generate topographic models for agricultural and ecological interpretation. It is not appropriate for legal definition of floodplains, property boundaries, etc., which would require professional surveyors.

### Cost

Assuming possession of a differential global positioning system and geographical information system/Image processing software, the cost of acquiring the field

data and producing a topographic map are salary for 2 technicians and rental of the laser level. Spring 2002 cost of traditional surveying methods for the 35-ha field described above was \$2000 to \$2500 (professional surveyors bids). Our cost, assuming \$15 per hour labor cost, was \$720 for field time plus \$120 laser rental, plus 6 hours computer processing time for a total of \$930.

## Conclusion

The technique described above allows researchers and others to create high-resolution digital elevation models in a cost-effective fashion. This method is suitable for research fields, wetlands, and experimental plots. The digital elevation model can be used to help explain patterns of vegetation, yield, and soils; and to help elucidate the role of topography on ecological processes.

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## Comment: "Perspectives on water flow and the interpretations of FLIR images" J. Range Manage. 55:106-111 2002

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Science is increasingly being called upon as a fundamental element in managing the nation's natural resources for the public good. Thus, we were quite surprised to see a recent feature article in the *Journal of Range Management* by Larson et al. (2002) which provided several scientifically unsubstantiated and potentially controversial conclusions. Their conclusions not only misrepresent current understandings of thermal remote sensing but generally disregard a wealth of peer-reviewed research. Given that range managers and researchers unfamiliar with the capabilities of thermal remote sensing and heat transfer processes in streams might simply accept the conclusions of Larson et al. (2002) without question, we feel that additional discussion is needed.

Before addressing issues of concern, we are encouraged that Larson et al. (2002) recognize that salmon recovery in the Pacific Northwest is an important natural resources management issue and a major concern in watersheds where high summertime stream temperatures occur. Improving instream habitat in general and reducing abnormally high stream temperatures specifically are important regional issues that need to be addressed to help insure the recovery and sustainability of depressed salmonid populations (Beschta 1997). A broad base of literature indicates that where high summertime temperatures are common, a number of adverse effects to salmonids and other aquatic organisms are possible (for an extensive review of the literature see McCullough et al. 2001).

In the discussion that follows, we address five major concerns raised by the Larson et al. (2002) article:

### (1) The scientific credibility of thermal remote sensing for stream temperature assessment

Thermal infrared remote sensing is a well-established method for measuring water temperature, particularly in ocean and lake environments (Lillesand and Kiefer 1994). There is also an increasing body of literature that provides the background necessary to apply remote sensing techniques for mapping temperature patterns in streams (Atwell et al. 1971, Belknap and Naiman 1998, Kay et al. 2001).

Researchers at Oregon State University, in cooperation with the Oregon Environmental Protection Agency and the U.S. Army Corps of Engineers, have been investigating the application of

FLIR imagery for stream temperature assessment since 1994 (Norton et al. 1996). In an accuracy assessment, 67 ground-truth measurements were compared with concurrently sensed FLIR temperatures. Data from five different streams and four different years indicated a near perfect linear relationship ( $r^2 = 0.99$ ) and an average difference of 0.3° C (Torgersen et al. 2001). The analysis demonstrated that FLIR technology provides accurate measurements of stream temperature in a variety of geographic and environmental conditions.

Torgersen et al. (2001) also confirmed that FLIR surveys were effective for mapping spatial patterns of water temperature by comparing longitudinal temperature profiles produced from the analysis of FLIR imagery to that measured by instream sensors. The authors concluded that thermal stratification has a negligible effect on the accuracy of remote measurements under most stream conditions due to turbulent mixing in the water column. However, they also recognized that thermal stratification may develop in side channels, backwaters, floodplain ponds, and other low-velocity habitats, thus complicating image interpretation of unmixed aquatic habitats.

Larson et al. (2002) base much of their criticism over the use of FLIR imagery on the interpretation of a very small portion of a single FLIR image in a draft agency report (Fig. 1 [Larson et al. 2002]). The image in question was collected in the late afternoon (16:40) on 22 August 1995 along a reach of the Grande Ronde River in eastern Oregon (45° 24.916' N, 117° 55.576' W). Close inspection of the FLIR image and the associated aerial photograph indicate that the relatively cool pixels of concern to Larson et al. (2002) occur near the edge of the stream and represent a microhabitat that might best be described as a small local backwater. Given this situation, it would be reasonable to expect that water in this location is relatively shallow, slow-moving, and not well-mixed relative to that of the mainstream flow. Thus, its temperature regime is likely to behave differently to changing environmental conditions than that of the mainstream.

### (2) The use of FLIR imagery by the scientific community

Traditional methods of measuring stream temperatures using instream data loggers provide data that are temporally continuous but spatially limited. However, spatially continuous data along stream and river reaches are increasingly needed to map thermal conditions at the scale of watersheds to provide better understanding of non-point sources of thermal pollution and mechanisms of human-caused thermal degradation (Poole and Berman 2001). Torgersen et al. (1999 and 2001) and Faux et al. (2001) have found that thermal infrared imagery can be an effective tool for quantifying watershed and reach-scale temperature patterns in

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medium- to large-sized streams and rivers (2nd-order or higher). Integrating spatial imagery (e.g., FLIR imagery) with temporal thermal data from instream data loggers can provide a more spatially and temporally continuous perspective on water temperature patterns within and among stream systems. Contrary to the assertions of Larson et al. (2002), the research community and the Oregon Department of Environmental Quality (ODEQ) are not using FLIR imagery to evaluate microhabitat effects of streamside vegetation on water temperatures.

### (3) An energy balance approach to assessing stream cooling

In an attempt to support their contention that shaded water near the edge of a stream cannot be ~2° C cooler than the mainstream water, Larson et al. (2002) provide a mathematical development of how energy loss by conduction might be evaluated. However, understanding changes in water temperature requires consideration of multiple energy transfer processes. An energy balance approach (Sellers 1969) to predicting stream temperature dynamics involves a delineation of the various heat sources and sinks, such as net solar radiation (sr), net longwave radiation (lr), evaporation (ev), convection (co), advection (ad), and bed conduction (bc). Algebraically, the energy balance can be represented as:

$$Q = +sr \pm lr \pm ev \pm co \pm ad \pm bc$$

where  $Q$  represents the total heat energy that is absorbed (+) or released (-) by a stream.

Larson et al. (2002) undertake an extensive mathematical development focused on bed conduction (typically a relatively minor component of the energy balance) to explain why water along the edge of a channel cannot be cooler than the mainstream flow, which is exposed to full sunlight. In the process, they ignore the potential role of other heat transfer components such as absorbed solar radiation (sr), net longwave radiation (lr), and evaporation (ev) that are often of much greater importance.

### (4) A field experiment

Larson et al. (2002) provide the results of a field experiment that was ostensibly designed to prove that stream temperatures cannot differ by ~1-2° C over a channel distance of 12 m. Unfortunately, their experiment was not undertaken along the reach of concern (i.e., Fig. 1). Instead, another unspecified stream was selected in

the general region of eastern Oregon. Stream temperature measurements were made along an exceptionally short (12-m long) section of channel during several clear days in late summer when the solar angle was ~54° at noon. The velocity of flow was 0.3 m/s. Temperature sensors, with a reported accuracy of +0.2° C, were placed at a depth of 25 cm, however the depth of water, a critical variable in stream temperature dynamics, was not indicated.

Under clear-sky meteorological conditions typical of eastern Oregon in late summer and with no shading from streamside vegetation or topography, a net solar radiation of approximately 1.27 cal/cm<sup>2</sup>/min would be available to the stream (assuming a solar angle of 54° at noon, a latitude of 45°, an elevation of 1000 m, no clouds, and an atmospheric relative humidity of 10%) Beschta and Weathered 1984). These solar inputs during the 40 seconds required for water to flow through the 12-m long reach (assuming an average stream velocity of 0.3 m/s) and a water depth of 25 cm (the depth of the sensors) indicate that the maximum expected temperature increase would only be 0.03° C, a value that is nearly an order of magnitude smaller than the accuracy of the employed sensors. Even if the sun were at its zenith in late summer, there were no clouds, and the stream section were totally devoid of canopy cover, it would not be possible for solar radiation (the dominant term in the energy balance for an unshaded stream) to sufficiently increase water temperature so that the downstream sensors could detect a change. Thus, the field experiment presented by Larson et al. (2002) and the tabular data presented in their Table 2 have no relevance regarding the issue of whether unshaded vs. shaded water can warm over this short reach. The experiment certainly has no relevance to the importance of conduction, which is the focus of their mathematical development (e.g., see their section on "The Effect of Water Flow on Temperature Profiles" and Appendix A).

### (5) Vegetation shade and water temperature

In their abstract, Larson et al. (2002) conclude that the "temperature data taken from a stream channel are used to show that the water flowing in the channel is essentially unaffected by the patterns of vegetation shade on the surface of the channel." Because no measured change in temperature occurred in their experiment, Larson et al. (2002) conclude that vegeta-

tion shade has no role in affecting stream temperatures. As indicated in the previous discussion, the experiment was apparently designed, intentionally or unintentionally, so that it was not possible for any change to be measured. Had a longer reach been studied, they would have come to the opposite conclusion.

The conclusion that shade from riparian vegetation does not influence stream temperature is contrary to an abundant body of stream temperature research (e.g., see Beschta et al. 1987, Sullivan and Adams 1990). A wide range of studies have consistently shown, by both field experiments and energy balance modeling, that reductions of shading vegetation along a channel result in increased summertime maximum temperatures during clear-sky conditions. Since energy losses from streams are often of a smaller magnitude, it would appear that the best management strategy to minimize the potential for high stream temperatures would be to maintain fully functional riparian plant communities.

Two experiments conducted by researchers at Oregon State University specifically addressed the role of shade and stream temperature. One of these involved the use of a shaded and unshaded tank whereby Moore et al. (1999) concluded that "shade is a very important factor in influencing the rate of heating and cooling of water bodies". Shaded tanks had lower maximum and minimum temperatures, with experimental location and air temperature having no significant influence on the rates of heating and cooling. The second study involved the application of shade treatments to an irrigation channel; the channel was chosen to provide the researchers with control over flow, water column depths, and to minimize potential groundwater inputs. From this second study, Peterson et al. (1999) concluded that "results substantiate the hypothesis that stream shade can be an important factor in decreasing water heating".

The erroneous conclusion of Larson et al. (2002) regarding the effects of shade is an extremely important concern. If such a conclusion were accepted by rangeland professionals, it would give pseudo-credibility to assertions that management practices which continue to maintain relatively low levels of riparian vegetation have little effect on stream temperature. We would suggest that the recovery of degraded riparian plant communities (i.e., a recovery of shade and the other important ecological functions associated with healthy streamside vegetation) is a major ecological and environmental concern along



many rangeland streams throughout the American West. This is particularly the case where high stream temperatures threaten native salmonids or where stream temperatures are out of compliance with water quality standards. The conclusions by Larson et al. (2002) appear to represent a major obstruction to the proper management of rangeland riparian systems.

### Final comments

Larson et al. (2002) focus on a small portion of a single thermal image along the edge of a stream in a draft agency report. From this, they make sweeping generalizations about the inaccuracies of FLIR methodology and conclude that thermal remote sensing is inappropriate for obtaining stream temperature measurements for scientific or management purposes. Such conclusions are very disconcerting. In our review of the literature on thermal remote sensing, we find that the body of published research would disagree with their conclusions.

Larson et al. (2002) used thermodynamic principles to indicate that conduction is likely to be a relatively small portion of a stream's energy balance. We agree that bed conduction is an inefficient energy transfer process and is often of minor significance with regard to stream temperatures. However, in assessing conduction alone they ignore other more important processes that determine temperature patterns along a stream reach. Had Larson et al. (2002) considered a simple energy balance that included the other major energy sources and sinks, their conclusions would have been much different.

The field experiment that Larson et al. (2002) present is inconsequential for assessing the role of shade on stream temperatures. In spite of unconvincing results, they conclude that stream temperature is essentially unaffected by shade. The level of rigor and logic associated with this experiment is disheartening.

Larson et al. (2002) developed their controversial conclusions with little reference to the current literature. For example, they provide only 4 citations from which a reader might evaluate the status of the science—2 are introductory physics texts, and the other 2 are reports by the ODEQ that address basin-wide stream temperatures. With regard to the ODEQ reports, we suggest that Larson et al. (2002) grossly misinterpreted how that agency uses FLIR data. Furthermore, they have chosen to ignore a rich body of published research and energy balance models that would have provided an important guide for

assessing the influences of riparian shade and stream temperature. Had the authors sampled this literature, they would have found that it did not support their conclusions.

In recent years, Larson et al. (2002) have produced other reports and articles on stream temperature and have played active roles in criticizing the need for stream temperature management along aridland streams in Oregon and elsewhere in the Pacific Northwest. While the authors obviously have a right to express their views on streamside management and stream temperatures, we urge readers to carefully assess and evaluate the science presented in Larson et al. (2002).

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## Rebuttal: "Perspectives on water flow and the interpretations of FLIR images" J. Range Manage. 55:106–111 2002

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Larson et al (2002) examined an application of FLIR technology that related image exposures to stream temperature. The FLIR image presented in the paper (see Fig. 1 in Larson et al. (2002)) delineated a 2° C difference between a shaded portion and unshaded portion of the river. The photo interpretation and descriptions authored by ODEQ cited personal communications with B. McIntosh (1999) for the photo interpretations (Oregon Department of Environmental Quality 1999). They explicitly noted that temperature in shaded portions of the river were different than unshaded portions, and made no references to the image as unmixed, shallow, slow moving water (Oregon Department of Environmental Quality 1999).

Recent TMDLs in Oregon have gathered mainstem and tributary data using FLIR technology and contain figures describing thermal habitat fragmentation of warmed reaches separated by isolated cool-water refugia and/or thermal microclimate. In the Grande Ronde system alone 600+ river miles of paired aerial photographs were developed and examined. In one example (Oregon Department of Environmental Quality 1999) ODEQ stated that 8 thermisters were utilized to ground truth 95 river miles of mainstem photographs. In this particular application camera images were taken at a distance that yielded 'digital images that cover approximately 100 x 150 m'. The indirect nature of this application places limitations on the quantity and quality of information that can be gleaned from a sample. The purpose of Larson et al. (2002) was to consider the implications of well established and understood laws of basic thermodynamics and relate it to FLIR photo interpretations that suggested correlation between white light shadows, changes in infrared signature, and stream temperature.

The Larson et al. (2002) analysis suggests that care must be taken in the interpretation of FLIR imagery on a case by case basis, especially in the absence of direct ground truthing of the imaged area. The Larson et al. (2002) analysis also suggests that more robust methods need to be applied if FLIR technology is used to monitor thermal qualities of water, and that extreme changes in FLIR signatures must be accurately correlated with water temperature ground truthing in a wide spectrum of stream profiles before this method can be trusted as a reliable estimator of instantaneous water temperature profiles.

An example of direct measurements from shaded and unshaded sensors were provided in the paper. Had a series of FLIR images been taken of the experimental area in coincidence with sensor measurements, the ODEQ interpretation methods would have identified shaded sensors as being in cooler water than the unshaded sensors. The sensor data did not indicate differences

between the 2 situations. If the ODEQ description of the FLIR image was correct, the Larson et al. (2002) study should have been able to measure changes in temperature between the shaded and unshaded portions of the stream. Furthermore, the use of many sensors across a wide area of the sampled stream, and the collection of time-resolved data in which many of the sensors are alternately illuminated by the sun or sheltered by vegetative shade throughout the course of an entire day (not just at a single instant in time, as a FLIR image might capture), should provide an adequate sample of data to guide intuition about interpreting imagery in the absence of direct ground truthing. It is understandable that proponents of FLIR monitoring will be skeptical of the implications of this study; this skepticism clearly demonstrates that this type of *spatially* and *temporally* resolved data should be acquired and studied in many more cases to conclusively illuminate the thermal physics of a stream system.

The Larson et al. (2002) study exploited the traditional symbiosis between theory and experiment in the physical sciences to probe the secrets which Nature endeavors to hide from us. To provide motivation for the experimental investigation that was conducted, Larson et al.(2002) provided a mathematical derivation for the distance river water traverses given certain physical stream properties for a 1° C cooling event. The calculations do not agree with the FLIR image depiction of a 2° C water temperature change identified by the white line oval in the published image. Bestcha et al. (2003) provide a heat budget formula to calculate heat, but calculations for the change in heat are needed to examine whether the FLIR interpretations are accurate. It is worth noting that the supposition of a dominant thermal sink for heat transfer is irrelevant on the scale of individual tree shadows. Water cannot cool or heat over short time scales as the power (*i.e.*, the rate of energy transfer) would be extraordinarily high.

Individuals who interpret and draw inference from FLIR imagery need to craft statements that accurately reflect the data. The Larson et al. (2002) analysis is a caution about photo interpretations that indicate 'mixed water columns' will change temperature abruptly and over short distances. Such interpretations are likely in error and cannot be supported by field data. Larson et al. concluded from spatially and temporally resolved field data that the stream temperatures were not affected by the shade as suggested in the ODEQ TMDL assessment. Rather than being an obstruction to proper management of rangeland riparian systems, this effort offers new insights about the limitations of FLIR interpretations. The study did not offer a definitive conclusion with bias toward low or high levels of riparian vegetation. Quite to the contrary, several possible explanations for the apparent discrepancy with FLIR interpretation were suggested, and should be pursued in future research. The ultimate goal of any such investiga-

tion is to understand how physical laws and photo interpretation within the watershed environment can be correlated with direct temperature sensor data.

Science is a crucible containing our cherished beliefs, theoretical expectations and observations of Nature. In it, we burn away irrelevancies and misconceptions until left with a product—the truth—no matter how disturbing. The strength and credibility of rangeland professionals rests in their willingness to examine new ideas before lockstep acceptance, their expectation for ubiquitous theories applicable to the science and art of range management, and a commitment to engage in discussions that improve their understanding and effectiveness as rangeland managers.

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# Book Review

**Agricultural Extension and Rural Development.** Breaking Out of Traditions. Edited By Ray Ison and David Russell. 2000. Cambridge University Press, 40 West 20<sup>th</sup> Street, New York. 239 p. US\$59.95 hardback. ISBN 0-521-64201-9.

Based on 8 years of active collaboration and 3 years of intensive research, Ison and Russell have attempted to develop alternative modes of conducting research and development with graziers on semiarid rangelands in New South Wales (NSW), Australia. Their book concentrates on some key questions: Can traditional extension methods become blind spots? Are extension practices so ingrained that they no longer foster ongoing review? Research and development (R&D) in extension has evolved into what the editors term a *blind practice*, because of a loss of connection i.e., context, meaning, and relevance (Part I, Breaking Out of Traditions). From these concepts that scrutinize present day extension, Ison and Russell introduce a *systematic action* research project to illustrate how the relationship between the rural community and acknowledged experts might be differently and more fruitfully managed.

Extension has repackaged itself multiple times since the concept was first specified in the U.S. by the Smith-Lever Act of 1914. Most recently in Australia, greater emphasis has been placed on field days with farmer groups and the involvement of farmers on decision-making bodies, with little or no increase in technology implementation or improved educational level. The authors term these efforts as 'more of the same extension' and the approach adapted to the social and ecological milieu of North American rangelands as *first-order change* (Part I, Chapter 1: The research-development relationship).

Promotion of innovative technology to the rural community under the first-order directive has followed the linear extension model that most North American extension faculty will recognize: Research → knowledge → transfer → adoption → diffusion. This diffusion of innovations model has shaped the practice of agricultural extension in the last thirty years. Ison and Russell outline the limitations of this model by evaluating model effectiveness studies that show only a specific minority of farmers adopted research results, while the majority considered the model neither a viable nor an economic strategy for agricultural improvement, and therefore discarded it almost immediately. The problem is often defined incorrectly as a failure of technology adoption. The grazer is often modeled as a passive obstacle to ecological diversity and sustainable production on rangelands—leading to the contemporary managerial wisdom of simply reducing grazer as well as stock numbers. The authors also assign the term *first-order* to reductionist scientific effort that they consider is problematic on rangelands—in that it assumes that rangelands can be studied in isolated fragments and that an understanding of the whole can be gained by aggregating these fragments. Often, supposedly recent technologies are found to have been in use by graziers for many years, indicating that they are researchers and experimenters in their own right. Some of the most significant examples on Australian rangelands are mechanical approaches to deal with woody weeds.

Stepping out of the existing first-order extension system, abandoning the term *extension* altogether, and revisiting the system with a different rationale—change implemented from the perspective that the complete system is altered, the authors termed *second-order change*. These efforts are an attempt to provide a

contextual science for rural research and development that links with the expressed needs of the day-to-day lives of the people involved. It is, in part, a response to the lack of participation of graziers in the design and implementation of rangeland development projects in the developing world—a persistent criticism espoused in most reviews of project effectiveness. They raise the question of “how much longer do we [as researchers/extension specialists] need to be told that the ‘mainstream view’, the ‘dominant paradigm’, the ‘top-down-approach’, just does not work and is, in fact, detrimental to both the people and the ecosystem of which they are a part?” This *second-order* scientific underpinning accepts that rangeland systems are unknowable and that phenomena are self-referential (mirror-like) and dialectical (e.g., neither graziers nor degraded rangeland is the problem—but these are complementary pairs, distinct but related). It is not objects that command attention but the relations between them. This model of translation is a web that encompasses or enmeshes people, machines and facts.

A new body of biological theory (Fell and Russell 1994, *Cybernetics and Human Knowing* 2:3-15.) promotes the concept that understanding between researchers and graziers does not come from information transfer or from a compelling argument but results from an inseparable circular unity—we only do as we understand. Understanding revolves around the engagement of researchers with graziers and the quality and history of past similar engagements. The flow of our language and our emotions are interwoven into semantic understanding that matches only when the emotion between grazer and researcher matches—we make conversation in the form of a ‘dance.’

Ison and Russell's design for second-order R&D included to: (1) develop and sustain conversation and equal respect among experts, government bodies and the principal producers; (2) attempt to break out of first-order extension; (3) be aware of grazer traditions and attempt to maintain their way of life; (4) create and sustain research enthusiasm as a crucial element in successful technology transfer, e.g., using data-supported maps useful to graziers, discussing imaginative ranch practices. The design was based on an increasingly recognized need for emancipation from dependency, empowerment through collaboration, and collaboration based on a mutual acceptance of different realities (Part III: 133).

To identify and analyze second-order change, a group that included many of the authors, of ‘systematic action researchers’ teamed with a community of sheep graziers in the semiarid rangelands of Australia over a 2-year period. Study areas covered 17,600 km<sup>2</sup> and 45 properties aggregated into 33 holdings averaging 53,500 ha per family unit. Early insights found that new technologies, i.e., computers and other electronic devices were taking away grazer's ability to adapt, innovate and sustain their operation from their workshop. No longer could the landowner “fix” their machines themselves—thereby losing their independence and autonomy (Part I, Chapter 3: Technology transforming grazer experience). By and large the concerns of researchers and those who fund research and development were not the concerns of graziers, and most graziers knew little about the organizations and the people involved.

Part of the analysis (Part II Historical Patterns, Technological Lineages and the Emergence of Institutionalized Research and Development & Chapter 4, From theodolite to satellite: technology and power in the Western Division of NSW) included the identification and understanding of grazer-operated agricultural

enterprises, and how they historically approached innovations and government regulators. The first land survey by the Australian government provided the first lines of contact between government regulators and the ownership boundaries that defined what being a grazier was. Many of the early technological innovations introduced by graziers, e.g., dingo fences and water points, were later taken up by government regulators, shifting power from a focus on proper land occupation and maximum pastoral production to power associated with improvement of degraded rangelands and limits on productivity.

Chapter 5 was based on 2 distinct but related pieces of research: (1) semi-structured interviews conducted with staff from Australia's traditional extension service and (2) developing a second-order approach to the work of a group of research and development staff. Interviews explored the concepts supporting extension in semiarid Australian rangelands and investigated the relationships between the ethos, structures and cultures of extension organizations, and the opportunities and bottlenecks that influenced staff effectiveness. Provocative insights from these exercises included the feeling that rangeland extension folks were often exposed to *induction by deep-ending* or in the U.S. vernacular, thrown out there and allowed to sink or swim. Young or newly recruited extension officers often sought out experienced officers who acted as role models, helping to define priorities and the concept of extension itself, and assisting with extension program direction. Innovation, initiative, and outside collaboration by younger or newly recruited officers often was stifled by other 'old guard' officers as having little relevance for the future. These contrasting activities set up a tension between success within the structure of the department and effectiveness out on the rangelands. Tensions among extension officers exist as remnants of a first-order-only system. For example, the perception of being a credible extension officer to senior officials was associated with each individual's particular calling, e.g., researchers had credibility as researchers, not extension officers. If you merge them too closely, i.e., convert a researcher into an extension officer the credibility of both might be lessened. Tensions also can be manifested as a mismatch between the short-term political demands of the agency and the needs of programs that are by their biophysical, environmental or commercial nature long-term.

Apparently certain fundamentals must be processed if there is to be a relationship between an organization designed to work with farmers and the farmers themselves: (1) acceptance that knowledge and the potential to spark understanding are the bases for any relationship, (2) the need by graziers for knowledge is bound by context and is typically complex, (3) that the farmers are the ones to take control of any relationship, and (4) that the relationship will be inherently hierarchical and creating a dependency culture, thereby reducing the power of the grazier, reducing the relationship to only a part of a wider and more durable network of relationships.

In Chapter 6, simple technological changes were adopted only when graziers were able to embrace them within the cultural dimensions of their lives. With *enthusiasm* for the practice or activity, graziers could deal with complexity, initiate innovation, and accommodate change. Enthusiasm was stimulated by situations where researchers listened respectfully to graziers. Apparently each individual possesses a reservoir of unexpended energy/excitement/enthusiasm available for collective action if organized and directed properly. To identify this energy, graziers were asked: "What do you want to do, why are you a grazier, and what is it you get out of this work that is satisfying (Chapter 6:144)? Enthusiasms were mapped and mirrored back to gra-

ziers—who were then invited to work together on projects supported by their common excitement. First-order-driven service agencies can block the local ability to organize around common enthusiasms meeting institutional, rather than local needs (Chapter 6:158).

Chapter 7 provides a context for their efforts in Australia and a pathway to follow for those researchers contemplating a second-order collaborative research process. Design characteristics included (1) choosing the research area with suggestions for contextual grounding, (2) designing interviews—the roles of narrative, storytelling, semi-structured interviews and reflection on the processes, (3) protocols for conducting the interviews—tips for triggering enthusiasm, evaluating, and relating experiences, (4) interpreting interview data, (5) second-order workshop design and efforts to continue the *conversation*, (6) action co-researching—a cycle of planning, action, observation, and critical reflection with graziers/landowners, and (7) adaptation of the design to a variety of contexts.

Capping the text are 2 chapters (Chapters 8 and 9) that practically, should be read first. Chapter 8 provides the reader with a peek into one grazier's Australian outback experience—the pace of life, sense of community, dealing with isolation, and gender. These issues are fascinating. Grazer insights and bottlenecks into their past involvement in research and with researchers, and why they agreed to become involved with this second-order research effort, are a must read for new extension officers and specialists. Landowner thirst for knowledge and dealing with information gaps, confidence building through recognition of their own importance to the world outside their rangeland environment, visiting and understanding the production infrastructure that determined their survival and provided incentives, and finally understanding their achievements and limitations and possibilities for the future were all excellent lessons. Chapter 9 provides the template to design a researching/learning/action system in a series of detailed stages created to meet the needs of different and often conflicting stakeholders.

According to the authors, the rangelands project successfully accomplished its first-order objectives, second-order goals, and provided the raw material and emotional climate where the research and development process could itself be evaluated and modified. The text is rich with some unique and insightful perceptions that might guide new and experienced extension professionals working in natural resource management. Though identified as a book for practitioners, it was jargon rich, introducing new terminology (to this reviewer) that required clear definitions, application and review, and consistent usage from section to section, criteria that were not always met. Portions of the text read like theoretical sociology, perhaps to emphasize that the concepts are science-based and theoretically grounded. But often important concepts or terms were defined within the text more than once, followed by a simplification with few, if any clear-cut examples. Words or points were emphasized using single quotes, double quotes, or terms in italics, leading to confusion in the search for a hierarchy of emphasis. At times, the profusion of jargon coupled with the different types of emphases resulted in tedious and difficult reading, especially early in the book. Once the reader finally captures the sense of the discussion, coupled with frequent trips to the glossary provided, and with a little faith, weighty concepts are delivered.—James P. Dobrowolski, Washington State University, Pullman, Washington.

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The Associate Editor sends approved manuscripts, with recommendations for publication, to the Editor, who notifies the author of a projected publication date. Manuscripts found inappropriate for the *JRM* are released to the author by the Associate Editor. Manuscripts returned to an author for revision are *returned to the Associate Editor for final acceptability of the revision*. Revisions not returned within 6 months, are considered terminated. Authors who consider that their manuscript has

received an unsatisfactory review may file an appeal with the Editor. The Editor then may select another Associate Editor to review the appeal. The Associate Editor reviewing the appeal will be provided with copies of an correspondence relating to the original review of the manuscript. If the appeal is sustained, a new review of the manuscript may be implemented at the discretion of the Editor.

Authors should feel free to contact the Associate Editor assigned to their manuscript at any stage of the review process: to find out where the paper is in the process; to ask questions about reviewer comments; to ask for clarification or options if a paper has been rejected.

## Page Proofs

Page proofs are provided to give the author a final opportunity to make corrections of errors caused by editing and production. Authors will be charged when extensive revision is required because of author changes, even if page charges are not assessed for the article. One author per paper will receive page proofs. These are to be returned to the **Production Editor, 3059A Hwy 92, Hotchkiss, Colorado 81419-9548**, within 48 hours after being received. If a problem arises that makes this impossible, authors or their designates are asked to contact the Production Editor immediately, or production and publication may proceed without the author's approval of his edited manuscript.

## Page Charges and Reprint Orders

Authors are expected to pay current page charges. Since most research is funded for publication, it will be assumed that the authors are able to pay page charges unless they indicate otherwise in writing, when submitting a manuscript. When funds are unavailable to an author, no page charges will be assessed. Only the Editor will have knowledge of fund status of page charges; the Associate Editors and reviewers will accept or reject a manuscript on content only.

An order form for reprints is sent to one author with the page proofs. Information as to price and procedure are provided at that time. The minimum order is 100; no reprints are provided free of charge. We are also providing electronic reprints for a cost of \$50.00.

## Basic Writing Style

Every paper should be written accurately, clearly, and concisely. It should lead the reader from a clear statement of purpose through materials and methods, results, and to discussion. The data should be reported in coherent sequence, with a sufficient number of tables, drawings, and photographs to clarify the text and to reduce the amount of discussion. Tables, graphs, and narrative should not duplicate each other.

Authors should have manuscripts thoroughly reviewed by colleagues in their own institution and elsewhere before submitting them. Peer review before submission insures that publications will present significant new information or interpretation of previous data and will speed *JRM* review process.

Particular attention should be given to literature cited: names of authors, date of publication, abbreviations or names of journals, titles, volumes, and page numbers.

It is not the task of Associate Editors or *Journal* reviewers to edit poorly prepared papers or to correct readily detectable errors. Papers not properly prepared will be returned to the author.