

# Impacts of ungulate herbivores on a rare willow at the southern edge of its range

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Received 14 March 2000; received in revised form 6 November 2000; accepted 25 November 2000

## Abstract

In northeastern Arizona, USA, ungulate herbivory was identified as a potential threat to the continued existence of Arizona willow, *Salix arizonica*. In a series of multi-year experiments, I examined the impact of domestic and wild ungulates on growth and reproduction of the protected species in a natural and artificial habitat. Both wild and domestic ungulates significantly reduced above-ground biomass, height, survival, and sexual reproduction. The degree of impact of wild vs. domestic ungulates was related to the amount of time plants were exposed to herbivory, the amount of herbivore-free recovery time, and the numbers and kinds of herbivores present. Because experimental plants did not fully compensate or replace the amount of tissue lost or the reproductive capacity lost to herbivory within 1 year, I predict *S. arizonica* will require years to recover fully from herbivory. Herbivore impacts appear to be more pronounced at the southern edge of the species' range than in more northern sites, and are probably exacerbated by the historically heavy domestic grazing and enhancement of wild ungulate populations. These studies support ongoing conservation actions by land managers to protect *S. arizonica* from ungulate herbivores: (1) fencing, (2) augmenting natural populations, and (3) reducing wild ungulate herds and domestic cattle grazing in the species' habitat. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** Plant–herbivore interactions; Compensation; Cattle herbivory; Elk herbivory; Conservation of rare plant species

## 1. Introduction

Grazing has been recognized as a worldwide conservation concern. Because it is often under human control, actions can be taken to reverse its negative impacts if there is strong supporting evidence to outweigh political and economic concerns. However, the “strong supporting evidence” about the impacts of domestic and wild ungulates is not unequivocal and is little understood for rare species. Many researchers agree that heavy grazing or “improper livestock use” can increase erosion, reduce plant vigor, decrease diversity, and reduce plant stature (Knopf and Cannon, 1982; Kauffman et al., 1983a, b; Kauffman and Krueger, 1984; Platts and Raleigh, 1984; Schulz and Leininger, 1990; Patel and Rapport, 2000), but others contest this view (e.g. Phillips et al., 1999). Similarly, some researchers have shown that wild ungulates reduce plant size and reproduction (Murie, 1951; Kay, 1990,

1997; Case and Kauffman, 1997; Ruhren and Handel, 2000; Opperman and Merenlender, 2000), while others disagree suggesting that factors such as fire suppression, climatic change, and changes in plant chemistry play a more important role than ungulates in vegetation changes observed (Singer et al., 1994; Sharrow and Kuntz, 1999; see Shafer, 2000 for review).

For those wishing to conserve rare plant species, understanding how biotic interactions impact the potential for rare plant persistence or expansion at a site is critical. In one of the few studies that have been done on the impacts of herbivores on rare species, Beville et al. (1999) demonstrated that protecting *Cirsium pitcheri* from insect herbivores with cages and insecticide significantly improved individual plant reproduction, growth, and opportunities for expanding the population. And recent studies by Opperman and Merlender (2000) have shown that restoration efforts in riparian areas must exclude herbivores if they are to succeed.

In a series of experiments, I studied the impact of wild and domestic ungulates on growth, compensatory regrowth and reproduction of the rare Arizona willow,

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*Salix arizonica*, to determine short- and long-term effects of mammalian herbivory on the species' persistence at the southern edge of its range. *S. arizonica* was first recognized as distinct by Granfelt in 1969 (Galeano-Popp, 1988). First described by Dorn (1975) and later by Argus (1995), *S. arizonica* is a small shrub willow up to 2.6 m tall, but more typically is less than 80 cm tall. Although branches may develop adventitious roots if they are buried, *S. arizonica* does not produce subterranean clonal rhizomes. Plants usually grow along streams or in open or partially shaded wet meadows. It often occurs in saturated soils but attains its greatest stature on moist soils that are not entirely saturated. Plants found in drier locations occur in areas where subsurface stream channels exist suggesting that plants had established along flowing streams (Galeano-Popp, 1988; AWITT, 1995). Prior to its formal description, there were few records of its distribution, but historical photographs circa 1913 from locations where *S. arizonica* is present today indicate that willows in the riparian areas have diminished in size and number. Before 1993, the species was only known from 29 high elevation (2600–3290 m) streams and wet meadows in the White Mountains of northeastern Arizona, USA, where it co-occurs with six other willow species (*Salix monticola*, *Salix geyeriana*, *Salix bebbiana*, *Salix planifolia*, *Salix boothii* and *Salix irrorata*). All of the other species except *S. boothii* have larger populations in Arizona than *S. arizonica*.

In Arizona, herbivory was believed to be a major threat to the existence of *S. arizonica* (AWITT, 1995). The species had greater stature and greater population numbers when growing in relatively protected sites that were either fenced, sheltered by larger willow species, or growing on exposed rocks along streams (Galeano-Popp, 1988; AWITT, 1995). In 1992, approximately 37% of the known *S. arizonica* populations in Arizona had individuals less than 30 cm in height, 41% of the populations had less than 12 individuals, few plants flowered and no young plants or seedlings had been observed in years. The habitats showed signs of ungulate impacts such as stream siltation, bank erosion, stream trenching and braiding (e.g. Platts and Raleigh, 1984). Although all willow species in the habitats showed signs of herbivory, the two species that had the greatest amounts of herbivory were *S. arizonica* and *S. planifolia*. Where *S. planifolia* grew intermingled with *S. arizonica*, there was no preferential selection by herbivores of one species over the other. Plants growing at sites where both cattle and wild ungulates were present showed greatest indications of herbivory.

Conditions of the populations and habitat were so dire that the US Fish and Wildlife Service proposed that the species be listed as endangered in 1992. The rediscovery of the species in 1993 in Utah curtailed the listing and led to the development of a conservation agreement

between managers of lands where the species occurs (AWITT, 1995; Prendusi et al., 1996). Recently, more populations have been found in northern New Mexico (Dorn, 1997; Fig. 1). The Utah and New Mexico populations provide a basis for comparison with the Arizona populations to examine factors that may affect overall vigor of the populations.

## 2. Methods

To determine how herbivory impacts *S. arizonica* individuals in Arizona, I conducted a series of parallel experiments in native and ex-situ habitats over several years. The experiments involved a plant establishment phase followed by trials of exposure to wild and/or domestic ungulates.

### 2.1. Experiment 1: impact of herbivory on *S. arizonica* in its native habitat

I studied the impact of naturally occurring herbivory on *S. arizonica* in its native habitat at Stinky Creek (2966 m elevation, 33° 50' N, 109° 25' W) on the Apache-Sitgreaves National Forest near Greer, AZ, USA. Cattle and wild ungulates, including mule deer (*Odocoileus hemionus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and pronghorn (*Antilocapra americana*) are present at the site. Elk are the most numerous wild ungulate in this area. In 1993, populations were estimated to be in the thousands and climbing at rates of 27% per year (AGFD, 1993), however hunting permits were increased in 1998 in an effort to stabilize population numbers (AGFD, 1999). The herd sizes I have observed in the White Mountains range from one to 200 individuals. Since 1910, cattle heavily used the area, but present management has initiated rest-rotation cattle use (AWITT, 1995).

Stinky Creek contains an ephemeral creek running through a wide meadow and spruce-fir forest. Dominant meadow species included Kentucky bluegrass (*Poa pratensis*), Rocky Mountain Iris (*Iris missouriensis*), western sneezeweed (*Dugaldia hoopseii*), skunk cabbage (*Veratrum californicum*), cinquefoil (*Potentilla diversifolia*), and *Carex* sp. Yearly mean temperature is 6.6°C and precipitation is 624 mm. Soils are loamy-skeletal, acidic with pH 5.8, cold with temperatures at 50 cm ranging from 11–16°C, and contain small gravel of basaltic and rhyolitic origin (AWITT, 1995). Only three *S. arizonica* plants grew at Stinky Creek, therefore, it was a site targeted for population expansion by the land managers (AWITT, 1995).

To preserve the genetic integrity of the Stinky Creek population, I collected stem cuttings from the two healthiest plants on the Stinky Creek drainage and propagated them in the greenhouse at The Arboretum at

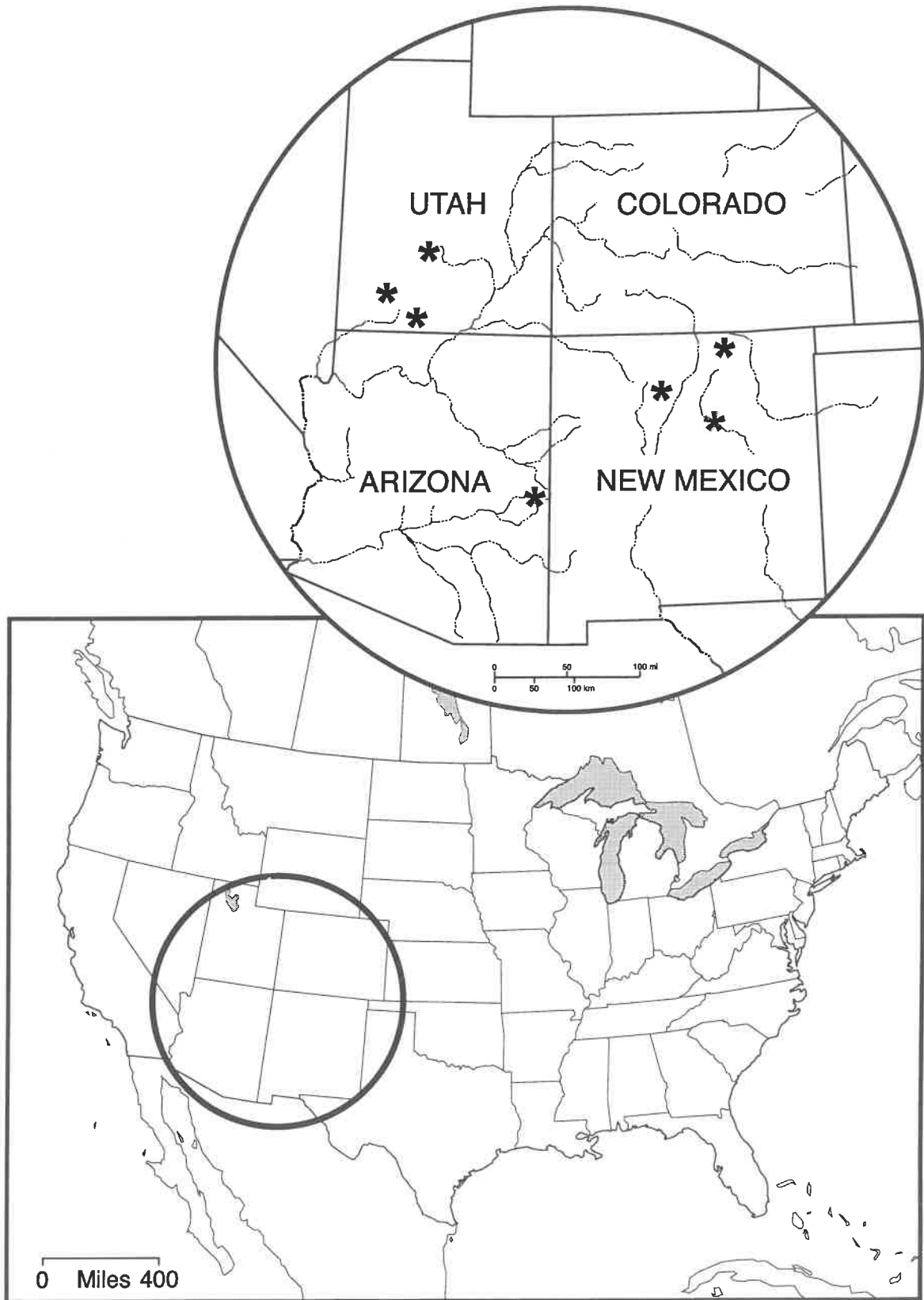


Fig. 1. Distribution of *Salix arizonica*.

Flagstaff by dipping all cuttings into Hormex No. 3 and placing them in perlite, under an automatic mist bench. I transplanted rooted cuttings into standard potting soil and kept them in the greenhouse until they achieved great enough size ( $\geq 8$  cm in height) and root mass to be transplanted to the field. I repeatedly took cuttings from our greenhouse collection to build an experimental population for introduction. I introduced 170 *S. arizonica* along  $\sim 1000$  m of the ephemeral creek at Stinky Creek in June and August of 1995. Mortality of some transplants due to overwintering conditions reduced the number of living experimental plants to 131 by August 1999. At the time of transplanting, I caged all plants with 1.3 m-tall 12 cm<sup>2</sup> mesh fencing to protect them from herbivory by large animals. The caging did not exclude small rodents. For every trial, I randomly assigned only healthy robust plants to control and experimental groups. At the beginning of each trial I attempted to match heights of plants and genotypic representation in both groups. The numbers of plants used in each trial varied with the number of healthy plants available; some plants were repeatedly randomly assigned to groups.

To test the impact of cattle and wild ungulate herbivory on *S. arizonica*, I exposed subsets of experimental plants to either one or both ungulates in 4 years for different lengths of time (Table 1). The duration of the trials varied with cattle presence in the pasture. The unpredictable presence of trespass cattle in 1996 prohibited a “wild” only trial that year. The lack of cattle in 1997 and 1999 prohibited a “cattle” only trial that year. I observed elk droppings and tracks, but saw no sign of other ungulates at Stinky Creek during the experimental periods.

Prior to and after each exposure period, I measured plant height and the length of all branches of *S. arizonica*. Total branch length was positively and significantly related to biomass (biomass =  $8.876 + 8.76 \times$  total branch length,  $r^2 = 0.72$ ,  $P < 0.0001$ ); the equation was derived from measures of 34 branches dried for 24 h at 100°C. I analyzed differences between experimental and control groups in each year using repeated measures analysis of variance (ANOVA). Data were normally distributed. To adjust for uneven sample sizes, I used a weighted means model (Yates, 1934; Kuehl, 1994). To account for multiple measures on the same

experimental plants, all alpha levels reported herein reflect Bonferroni adjustment (Snedecor and Cochran, 1980).

## 2.2. Experiment 2: controlled ex-situ herbivory study

Approximately 420 km from the native field site at Stinky Creek is The Arboretum at Flagstaff, Flagstaff, Arizona (2380 m elevation, 35° 10' N, 111° 42' W), where controlled ungulate herbivory studies occurred. Climatic conditions at The Arboretum were generally warmer and drier than at Stinky Creek. During the course of this experiment May through Oct (the active growing season) temperatures fluctuated from  $-12$  to 33°C. Yearly-mean temperature was 7°C and precipitation was 506, 662, 462 and 675 mm in 1994 through 1997, respectively. Soils are silty-clay loam of basalt origin with pH 6.6–7 and have a high capacity to hold water.

The Arboretum at Flagstaff incorporates 0.06 ha of native deergrass-Arizona fescue (*Muhlenbergia wrightii* and *Muhlenbergia rigens*-*Festuca arizonica*) meadow through which the ephemeral Sinclair Wash runs and herds of Rocky Mountain elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), and antelope (*Antilocapra americana*) freely graze (personal observation). The herd sizes of the ungulates I have observed vary from four to 40 animals. In addition, there is a 3-m fence that excludes large wild ungulates from 0.02 ha of grassland, ponderosa pine forest, and a stretch of Sinclair Wash. Inside the deer-elk enclosure, an 11,245-m<sup>2</sup> fenced area with ample amounts of shade from ponderosa pine trees, a trough to provide adequate water, and ample vegetation for browse served as the “cattle only” pasture. The cattle pasture was dominated by smooth brome (*Bromus inermis*), Arizona fescue (*Festuca arizonica*), deergrass (*Muhlenbergia rigens* and *Muhlenbergia wrightii*), ponderosa pine (*Pinus ponderosa*), *Carex* sp., wand penstemon (*Penstemon virgatus*), cinquefoil (*Potentilla hippiana*), and sweet clover (*Melilotus officinalis*).

Conditions in the “wild” and “cattle” pastures exceeded forage supply thresholds previously described for adequate cattle growth. Hobbs et al. (1996) reported that  $> 45$  g/m<sup>2</sup> live and dead biomass was required forage to sustain cattle growth. In May 1997, mean green standing crop measured in the Arboretum “cattle” pasture

Table 1  
Summary of experimental treatments conducted at Stinky Creek (Exp, experimental group)

Trial	Year	Herbivore type (No. of animals)	Days of exposure (month)	Sample size	
				Control	Exp
1	1995	CATTLE (530) + WILD (unknown)	30 Days (September–October)	60	21
2	1996	CATTLE (12) + WILD (unknown)	10 Days (June)	36	36
3	1997	WILD (unknown)	10 Days (June)	17	17
4	1999	WILD (unknown)	10 Days (August)	22	22

was 71.71 g/m<sup>2</sup> and was 66.09 g/m<sup>2</sup> in the “wild” meadow indicating that there was abundant herbaceous forage for wild and domestic ungulates in the area where the *S. arizonica* experiment was installed.

To establish experimental plants, I propagated 160 *S. arizonica* plants from cuttings taken from several wild Arizona White Mountain populations in the same manner described for experiment 1. I randomly assigned plants to one of three treatments: (1) year-round exposure to wild ungulates (WILD), but no cattle; (2) 10-day exposure to two cattle (CATTLE), but no wild ungulates; and (3) control plants caged to exclude both wild and domestic ungulates, but not small rodents (CONTROL). Along ~120 m of Sinclair Wash, I transplanted the WILD plants outside of the deer/elk fence enclosure and CATTLE plants within the cattle pasture in July 1994. I caged control plants inside and outside the pasture with 1.3 m-tall rabbit-deer fencing. All plants received supplemental water throughout the growing seasons of the experimental period. I included only healthy plants in the experiments and included only plants that survived from 1994 through 1997 in the analysis.

To simulate the exposure to the two types of herbivores that *S. arizonica* experiences in its natural habitat, I conducted two experiments (Table 2). In the WILD experiment, plants had year-round exposure to wild ungulates. After 3 months of caged protection to allow adequate root establishment, experimental plants were exposed to wild ungulates from 1 November 1994 throughout the 3 years of the experiment. I measured WILD plants each year for height and total lengths of all branches. I related total branch length to total aboveground biomass (g) as previously stated. In addition, I noted the presence or absence of flowers on experimental plants in the spring of 1996 and 1997 to document the occurrence of sexual reproduction.

I analyzed the influence of wild ungulate herbivory on Arizona willow plant growth using a repeated measures ANOVA. Data were normally distributed. Repeated measure alpha levels reflect Bonferroni adjustment for multiple measures on the same experimental plants (Snedecor and Cochran, 1980).

The CATTLE experiment also mimicked the exposure experienced by Arizona willow in its native habitat, i.e. short, intense exposure to cattle herbivory with seasonal rotation timing across years. I transplanted CATTLE group plants in July 1994. Each year following, CATTLE plants received 10 days of exposure to two cattle (Table 2). Before and after the 10-day experimental introduction of cattle, I measured plant height and total branch lengths. As in the WILD experiment, I related total branch length to total aboveground biomass and noted the presence or absence of flowers on experimental plants in the spring of 1996 and 1997 to document the occurrence of sexual reproduction.

I analyzed the influence of cattle herbivory on plant growth using a repeated measures ANOVA. Data were normally distributed. Repeated measure alpha levels reflect Bonferroni adjustment for multiple measures on the same experimental plants (Snedecor and Cochran, 1980).

### 3. Results

#### 3.1. Impact of herbivory on *S. arizonica* in its native habitat

Exposure of Arizona willow to both wild and domestic ungulates significantly reduced plant height and total branch length. Plants exposed to cattle and wild ungulates were significantly shorter by 30% in 1995 and by 35% in 1996 (REPEATED MEASURES, ANOVA, Group×Time,  $95F_{1,79}=21.85$ ,  $P=0.005$ ,  $96F_{1,70}=16.95$ ,  $P<0.005$ , Fig. 2). Mean total branch length significantly decreased after exposure to cattle and wild herbivores by 26% in 1995 and by 34% in 1996 (REPEATED MEASURES, ANOVA, Group×Time,  $95F_{1,79}=18.98$ ,  $P<0.005$ ,  $96F_{1,70}=22.62$ ,  $P<0.005$ , Fig. 3). Mean biomass of the control groups increased from 180.65 g to 200 g in 1995, whereas the group exposed to cattle and wild ungulates decreased from 174.09 g to 131 g in 1995. In 1996, mean biomass of the control group increased from 501.3 g to 519 g, whereas

Table 2  
Summary of Experiments conducted at The Arboretum at Flagstaff<sup>a</sup>

Trial	Year	Herbivore type (No. of animals)	Days of exposure	Sample size	
				Control	Exp
1	1995	CATTLE (2)	10 Days	16	16
2	1996	CATTLE (2)	10 Days	16	16
3	1997	CATTLE (2)	10 Days	16	16
4	1994–1995	WILD (unknown)	8 Months	22	22
5	1995–1996	WILD (unknown)	12 Months	22	22
6	1996–1997	WILD (unknown)	14 Months	22	22

<sup>a</sup> Exp, experimental group. Specific dates of exposure to CATTLE were from 28 July 1995 to 8 August 1995, from 24 June 1996 to 4 July 1996, and from 10 September 1997 to 19 September 1997 to mimic mid, early, and late season pasture-rotation, respectively.

the experimental group decreased from 480 g to and 320 g in 1996.

Exposure to wild and domestic ungulates also resulted in plant mortality. In 1995, 33% of experimental plants died after 30 days of exposure and in 1996, 25% of the experimental plants died after 10 days of exposure. No controls died in either trial.

During the experimental period, the presence of fresh elk and cow manure in close proximity to plants indicated that both animals were potential herbivores of *S. arizonica*. I observed no deer or antelope scat or tracks in the vicinity.

Exposure to wild ungulates in 1997 and 1999 significantly decreased total branch length in both years, but did not significantly affect plant height in either year ( $97F_{1,31} = 0.16, P > 0.05, 99F_{1,42} = 1.85, P > 0.05$ , Fig. 4). In 1997, control plants significantly increased total branch length by 24%, while WILD plants had 12% reduction in total branch length (REPEATED MEASURES, ANOVA, Group $\times$ Time,  $F_{1,34} = 5.8, P < 0.05$ , Fig. 5). This translates to a gain of 496 g of above-ground biomass in control plants and a loss of 126 g in WILD plants. A single experimental plant died, whereas all controls lived. In 1999, mean total branch length of wild exposed plants, which did not significantly vary from controls before the experiment, significantly decreased by 9%, while controls significantly increased by 7% (REPEATED MEASURES, ANOVA, Group $\times$ Time,  $F_{1,42} = 5.75, P < 0.05$ , Fig. 5). Neither experimental nor control plants died in 1999. Overall control plants gained 158 g biomass, while experimental plants exposed to wild ungulates lost branch length and 237 g

biomass, but not to as great an extent as when both cattle and wild ungulates were present.

### 3.2. Controlled ex-situ herbivory study

The two ex-situ experiments indicated that exposure to wild and domestic ungulates significantly decreased total branch length and plant height. Branch length was a more sensitive measure of change in plant status than

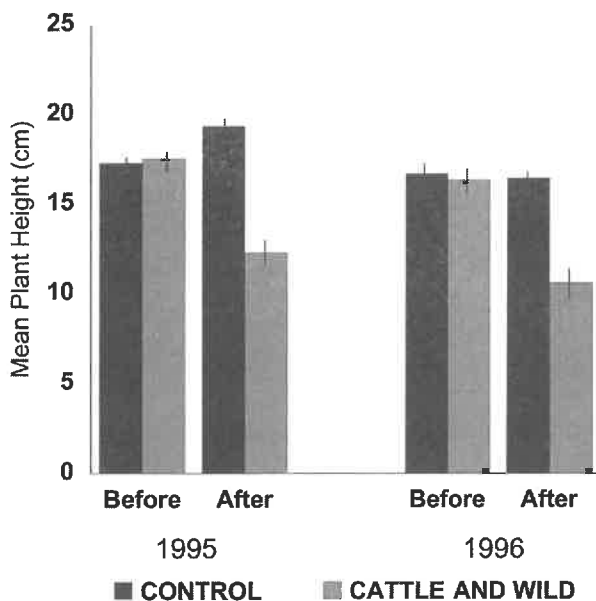


Fig. 2. Comparison of mean plant height (cm) of *Salix arizonica* plants in control and cattle/wild groups at Stinky Creek in 1995 and 1996.  $\bar{X} \pm 1$  S.E. are indicated. Note that duration of trials differed between years.

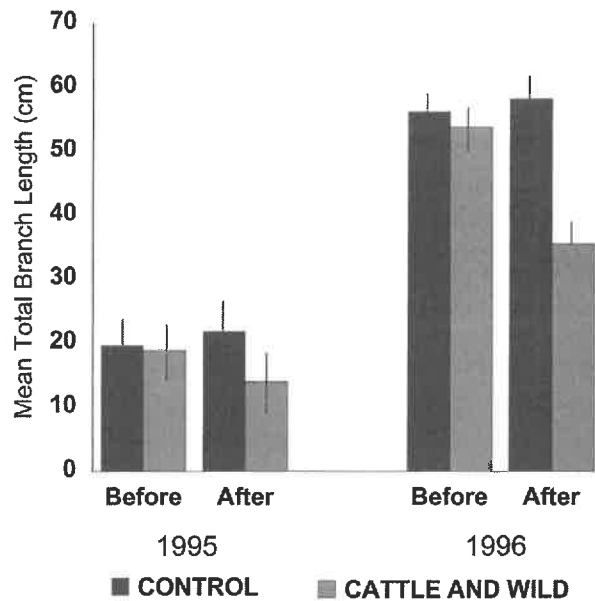


Fig. 3. Comparison of mean total branch length (cm) of *Salix arizonica* plants in control and cattle/wild groups at Stinky Creek in 1995 and 1996.  $\bar{X} \pm 1$  S.E. are indicated. Note that duration of trials differed between years.

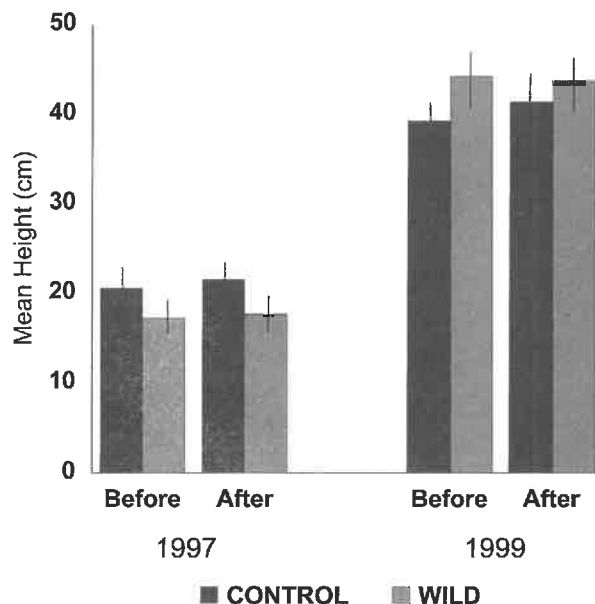


Fig. 4. Comparison of mean plant height of *Salix arizonica* plants in control and wild groups at Stinky Creek in 1997 and 1999.  $\bar{X} \pm 1$  S.E. are indicated.

was plant height. Before any experimental treatment was imposed in 1994, all Arizona willow plants established at The Arboretum at Flagstaff had similar size; i.e. total branch length and plant height did not significantly differ across treatment groups. While CONTROLS gained branch length and biomass, WILD plants significantly declined over the 3 years of the study

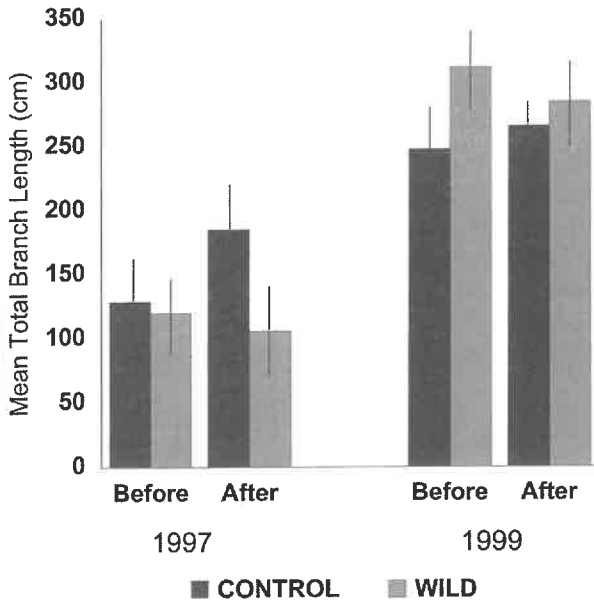


Fig. 5. Comparison of mean total branch length (cm) of *Salix arizonica* plants in control and wild groups at Stinky Creek in 1997 and 1999.  $\bar{X} \pm 1$  S.E. are indicated.

following exposure to wild ungulates ( $F_{3,126} = 11.12$ ,  $P = 0.005$ , Fig. 6). Both CONTROL and WILD plants decreased in stature over the 3 years, however WILD plants were significantly shorter than CONTROLS ( $F_{1,42} = 34.16$ ,  $P = 0.001$ , Fig. 7). In 1995, the WILD group experienced a 70% reduction in total branch length and this loss was never compensated for in 1996 or 1997 (Fig. 6). Similarly, mean plant height of the WILD group was significantly reduced by 36% (Fig. 7). By the end of 1997, WILD plants had 74% less above-ground biomass (from 2006 g in 1994 to 537 g in 1997) and 80% less height than they had at the beginning of the experiment. In contrast, CONTROLS increased aboveground biomass by 23% (from 1717 g in 1994 to 2225 g in 1997) and decreased in height by 48% over the 3 years, but maintained significantly greater stature than the WILD plants. Three CONTROL plants produced flowers, whereas no WILD plants produced flowers. Because WILD group plant height did not vary between 1996 and 1997 and total branch length has not varied since 1995, no recovery or compensation has been sustained.

Similarly, the CATTLE experiment indicated that exposure to cattle significantly reduced total branch length and height ( $F_{1,30} = 8.5$ ,  $P = 0.007$ , Fig. 8;  $F_{1,30} = 8.5$ ,  $P = 0.007$ , Fig. 9). Prior to the first exposure to cattle CONTROL and CATTLE groups did not significantly differ in total branch length or height (See 94 and 95b Figs. 8 and 9). However, after 10-days exposure to cattle in 1995, CATTLE plants lost 44% of total branch length or aboveground biomass (95f, Fig. 8) and

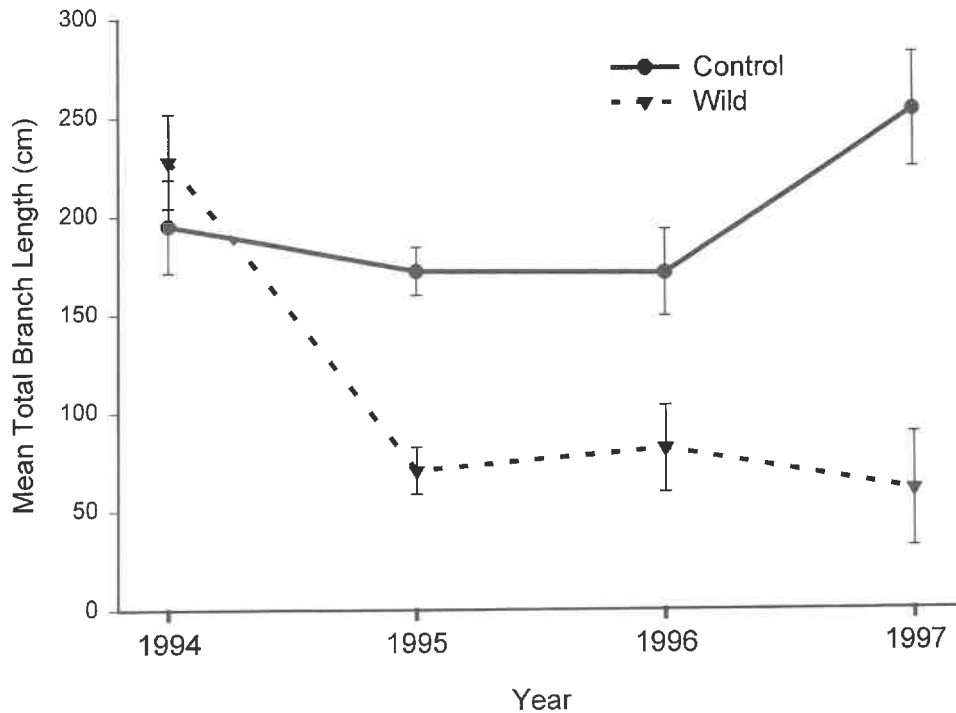


Fig. 6. Comparison of the mean total branch length of *Salix arizonica* plants in control and wild groups established at The Arboretum at Flagstaff measured from 1994 through 1997.  $\bar{X} \pm 1$  S.E. are indicated.

mean plant height was reduced by 23% (95f, Fig. 9), while CONTROLS remained the same.

By June 1996, the second year of the study, all plants experienced significant declines in height and no plants

produced flowers. The winter of 1995/1996 was dry with 75% less winter precipitation than the previous winter. I observed many branches with tip death, presumably caused by freezing and/or drought. Consequently the

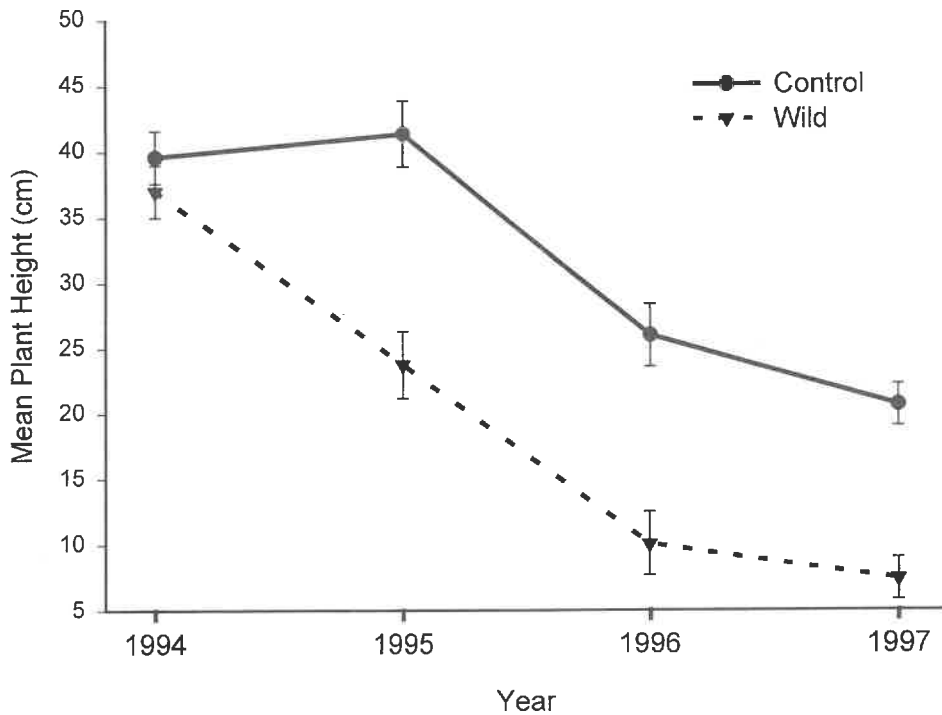


Fig. 7. Comparison of the mean plant height of *Salix arizonica* plants in control and wild groups established at The Arboretum at Flagstaff measured from 1994 through 1997.  $\bar{X} \pm 1$  S.E. are indicated.

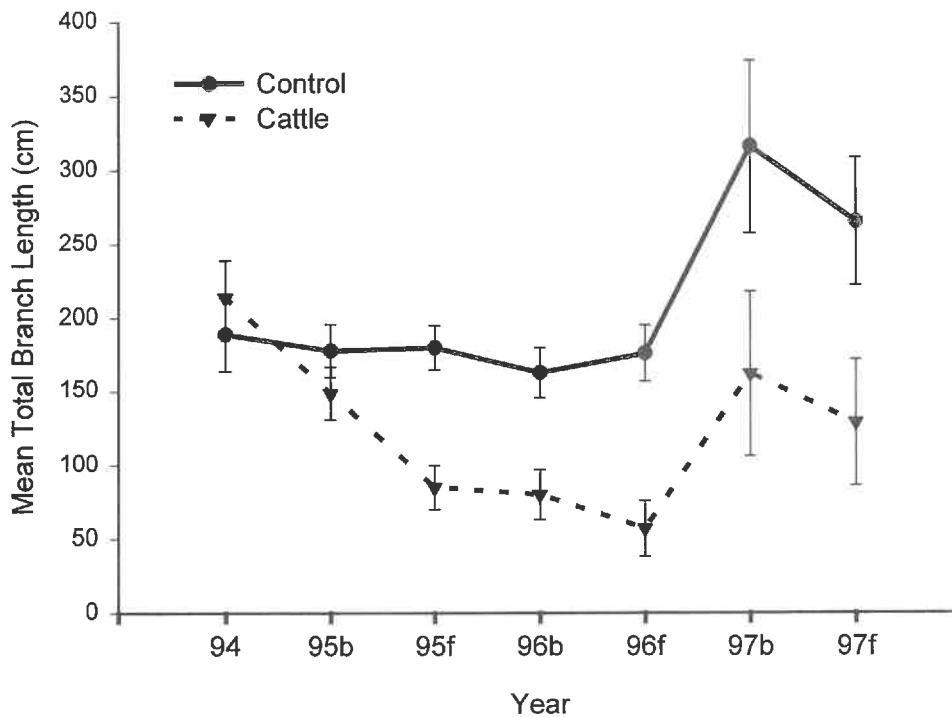


Fig. 8. Comparison of the mean total branch length of *Salix arizonica* plants in control and cattle groups established at The Arboretum at Flagstaff measured from 1994 through 1997.  $\bar{X} \pm 1$  S.E. are indicated. Numbers along the x-axis indicate the year the measurement was taken. Notation b indicates the measurement taken before 10-day exposure to cattle, while f indicates the measurement taken after 10-day exposure to cattle.

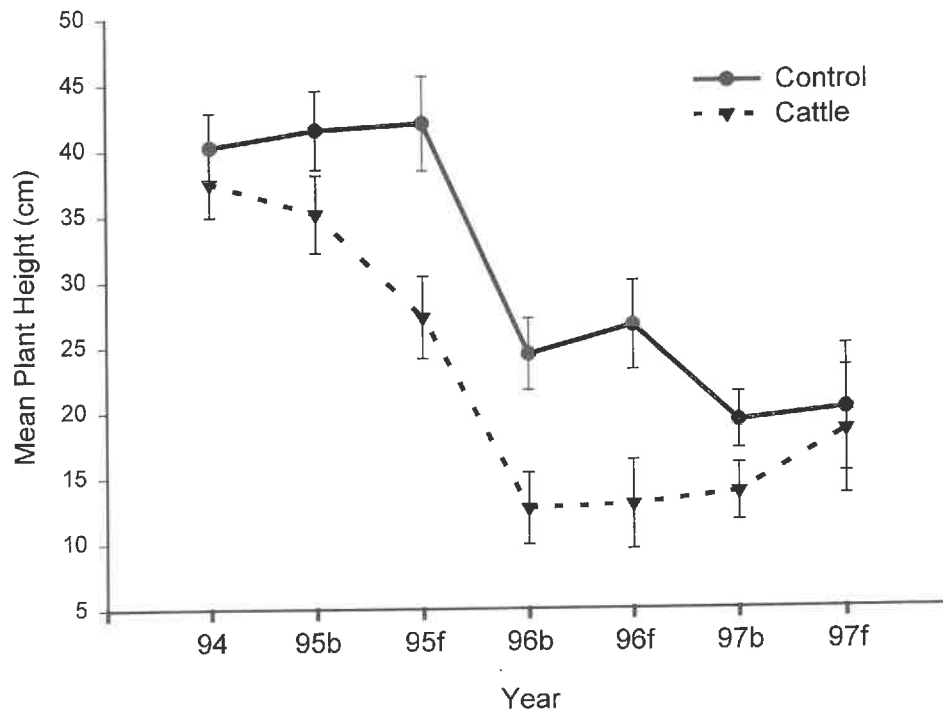


Fig. 9. Comparison of the mean plant height of *Salix arizonica* plants in control and cattle groups established at The Arboretum at Flagstaff measured from 1994 through 1997.  $\bar{x} \pm 1$  S.E. are indicated. Numbers along the x-axis indicate the year the measurement was taken. Notation b indicates the measurement taken before 10-day exposure to cattle, while f indicates the measurement taken after 10-day exposure to cattle.

heights of both experimental and control plants were less than those measured in 1995. At the beginning of the experimental exposure to cattle, the CATTLE group had 51% less branch length (Fig. 8) and was 48% shorter than CONTROLS (Fig. 9). These results indicate that the experimental plants did not compensate for tissue lost in the first year of the study.

The 10-day experimental period in 1996 did not significantly impact any plant character. CONTROL plants had slight, but insignificant, increases in total branch length, while CATTLE plants slightly decreased (96f, Fig. 8). Plant height slightly increased in CONTROL plants, but did not change in CATTLE plants (96f, Fig. 9).

By 1997, the third year of the study, plants in both groups had significantly grown. Mean total branch length of CONTROL and CATTLE plants increased, but both groups had significantly shorter stature in comparison to the previous year (Figs. 8 and 9). Four CONTROL plants produced flowers and a single CATTLE plant produced flowers in the spring. After the 10-day experimental period, CATTLE group lost 20% of total branch length, but recovered height equal to controls (Figs. 8 and 9). This indicates that cattle grazed branches, but did not necessarily graze the tallest terminal branches.

Over the entire duration of the experiment, the CONTROL group significantly increased total branch length and maintained relatively and significantly greater

above-ground biomass than the CATTLE group (Fig. 8). From 1994 to 1997, the above-ground biomass of the CONTROL group increased by 665 g, whereas the CATTLE group lost 744 g of above-ground biomass. This indicates that the CATTLE group never completely compensated for tissue lost in 1995.

#### 4. Discussion

The herbivory experiments clearly demonstrated that *S. arizonica* is eaten by both wild and domestic ungulates in native habitat and controlled ex-situ settings. The degree of impact of wild vs. domestic ungulates was related to the amount of time plants were exposed to herbivory, the amount of herbivore-free recovery time, and the numbers and kinds of herbivores present.

At Stinky Creek, the greatest reduction of *S. arizonica* total branch length and greatest mortality occurred in 1995 and 1996 when both types of wild and domestic ungulates were present. Experimental plants had significantly reduced plant height and total branch length, and 33 and 25% of plants died in 1995 and 1996, respectively. Numbers of cattle were especially high in 1995 and impacts were significantly greater that year. In contrast, when plants were exposed only to wild ungulates, experimental plants lost 11 and 8% of total branch length in 1997 and 1999, respectively, and one plant died.

The ex-situ studies demonstrated how long-term cumulative impacts of exposure to wild ungulates and periodic repeated exposure to cattle influenced *S. arizonica* plant growth, reproduction and ability to recover or compensate from herbivory. Although all plants significantly reduced height over the 3 years, plants in the WILD group maintained the lowest values and plants in the CATTLE group had intermediate values, and CONTROL plants had highest values. The CONTROL group lost height, but gained total branch length. Factors such as overwinter branch tip death contributed to the loss of *S. arizonica* height in addition to herbivory. The CATTLE group received periodic rest > 11 months between bouts of herbivory and recovered some branch growth and most height by the end of the experiment. In contrast, wild ungulates apparently browsed new growth repeatedly throughout the growing season, eliminating sexual reproduction and maintaining plant heights below 10 cm and plant biomass below 500 g. Elk are known to browse willows at all times of the year favoring young shoots (Murie, 1951; Despain, 1989) continually tracking above-ground production (Frank and McNaughton, 1992). Heavy summer browsing by caribou suppressed growth of dwarf birch even after release from herbivory (Crete and Doucet, 1998). Repeated browsing of *S. arizonica* new growth maintains plants in a stunted condition in the wild Arizona populations (AWITT, 1995). In areas of high elk concentrations, plant heights are < 10 cm (Maschinski, personal observation).

None of the experimental plants compensated or replaced the amount of tissue lost or the reproductive capacity lost to herbivory. As is true of wild populations, the overall stature, above-ground biomass as measured by branch length, and sexual reproduction were significantly reduced in the experimental plants in comparison to controls. These results contrast to other studies that have shown compensation in response to browsing (Danell et al., 1985; Danell and Huss-Danell, 1985; Bergstrom and Danell, 1987; Du Toit et al., 1990; Damhoureyeh and Hartnett, 1997).

Because Arizona willow did not fully compensate from herbivory any year, it implies that once *S. arizonica* is browsed, a single year of rest will not be enough to replace lost tissue. The amount of time required for recovery may be much longer. Platts and Nelson (1985) indicated that 11 years of protection dramatically improved riparian vegetation, while Knopf and Cannon (1982) have suggested that removing cattle for 10–12 years from a riparian habitat may not be sufficient time for a riparian willow community to recover from excessive grazing.

Herbivores have been shown to limit the distribution of plants in other systems (Weltzin et al., 1997; Gomez, 1996; Cantor and Whitham, 1989). In Arizona, herbivore pressure threatens the continued existence of *S.*

*arizonica*. The ex-situ experiments demonstrated that year-round exposure to herbivores maintained plants in a stunted, non-reproductive condition, which corroborates the observations that Arizona wild populations are stunted in stature, low in number, and not reproducing sexually. Except for one caged population, New Mexico populations also experience high levels of herbivory by livestock and elk and are classified as being in poor health (Dorn, 1997). In comparison, Utah populations have greater stature (>91cm) and experience lower levels of mammalian herbivory than either the Arizona or New Mexico populations (Dorn, 1997; Harper and Van Buren, 1997). Insect herbivory is much more prevalent in Utah than either Arizona or New Mexico, but does not seem to influence overall plant vigor (Harper and Van Buren, 1997). Many factors may contribute to the differences observed between the populations in the different states. Utah populations generally receive more precipitation than either Arizona or New Mexico populations (AWITT, 1995), which may influence the healthier conditions of more northern populations. Utah and Arizona populations have low genetic similarity ~37% (Tolman et al., 1997). There is a possibility that there is a genetic basis to the great susceptibility to herbivory of *S. arizonica* populations in Arizona, but this hypothesis has not been tested. New Mexico population genetics have not been studied.

The findings of these experiments support several ongoing conservation actions by land managers. Since 1995, the US Forest Service caged *S. arizonica* to protect plants from ungulate herbivory in an attempt to restore Arizona populations and protect Utah populations (AWITT, 1995). However, caging individuals will not address the problem of regeneration in the degraded habitats. Prolonged release from herbivory will be necessary for plants to recover tissue and reproductive health, and it may be necessary to protect large sections of drainage from both wild and domestic herbivores to restore healthy, naturally regenerating *S. arizonica* populations in Arizona (i.e. Rickard and Cushing, 1982). Whether or not *S. arizonica* could ever achieve height and biomass that could sustain reproduction in the presence of grazing is unknown. In the meantime, reproduction can be aided by hand-propagation and transplanting of seedlings in addition to protection.

Also uncertain is whether cages can ever be removed from plants at some future time. One may ask, "Didn't these plants evolve with herbivores?" As has been seen in other systems where grazing pressure increased dramatically (Fuller and Gough, 1999), the current pressures from herbivores in Arizona far exceed any the plants would have encountered in evolutionary time. In the western United States, there has been considerable concern about the damaging impact of overstocking domestic livestock on public lands (GAO, 1988; Fleischner, 1994). In the past 20 years, cattle use in

White Mountain pastures where *S. arizonica* grows ranged from 1755 and 583 head for 5–9 months. In the past 5 years, great efforts have been made to reduce the numbers of cattle and length of time they used pastures (John Moore, personal communication). The native Merriam Elk (*Cervus elaphus merriamii*) was extirpated shortly after 1900. In 1913, Rocky Mountain elk (*Cervus elaphus nelsoni*) from Yellowstone National Park were translocated into the state. With supplemental water and food, elk populations increased significantly until the late 1990's (AGFD, 1999). It is reasonable to assume that human-enhanced resources increased populations of the introduced Rocky Mountain elk far above the numbers of native Merriam elk, and that these subsidized wild ungulate populations are not in equilibrium with the natural vegetation that is available (e.g. van de Koppel and Reitkerk, 2000). The persistence of Arizona willow under pressure of high numbers of cattle and elk is doubtful; therefore, the current management trend of reducing wild ungulate herds and removing of cattle from *S. arizonica* habitats will aid the conservation of the species.

### Acknowledgements

I am grateful to George Fischer, John and Sharon Winniki for loaning cattle for the Arboretum studies, to Scott Strohmeier, Jeff Hines, Kenric Kesler, Cheryl Casey, Jeff Berg, Joanne Baggs, Jackie Campbell, Karen Hueston, Hugh Murray, Shawn Bensey, Kai and Mira Petersen, Kristen Widmer, and Monica Mahoney for field assistance, and to Bruce Palmer for his undying confidence and support. Tom Subirge and John Moore provided logistic support for the studies on the Apache-Sitgreaves National Forest. These studies were funded by Section 6 Cost-Share Contracts from the Arizona Department of Agriculture through the efforts of Bruce Palmer, Jim McGinnis, and Angie Brooks. Ron Redsteer kindly drew the figures. This manuscript benefited from critique by three anonymous reviewers and Carl-Eric Granfelt.

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