REPRODUCTIVE ECOLOGY OF WYOMING BIG SAGEBRUSH
(ARTEMISIA TRIDENTATA SSP. WYOMINGENSIS):
EFFECTS OF HERBIVORY AND COMPETITION

by

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ABSTRACT

Reproductive Ecology of Wyoming Big Sagebrush
(Artemisia tridentata ssp. wyomingensis):
Effects of Herbivory and Competition

by

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Utah State University, 1990

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Herbivory and plant competition affect sexual reproduction of plants in various ways. Exclusion of mule deer (Odocoileus hemionus) and cattle, removal of plant competition (both inter- and intraspecific), and all combinations of the above treatments were used to examine the individual and combined affects on Artemisia tridentata ssp. wyomingensis (Wyoming big sagebrush) reproduction. Reproduction of Artemisia tridentata ssp. wyomingensis was divided into hierarchical levels of the number of: (1) modules per current-year's growth (CYG), (2) nodes per module, (3) inflorescence heads per node, (4) achenes per inflorescence head and (5) percent viable achenes. Counts at hierarchical levels were made to determine the level affected by the treatments.
Deer herbivory significantly reduced reproduction at the reproductive-module-per-CYG-vegetative-biomass hierarchical level, while plant competition (both inter- and intraspecific) significantly reduced reproduction at the nodes-per-reproductive-module level and at the inflorescence-heads-per-node level. Cattle presence had neither a beneficial nor detrimental influence on reproduction during this two-year study. The combined effects of release from deer herbivory and from plant competition on reproduction was more than additive because these biotic interactions affected nested hierarchical levels.
INTRODUCTION

Sustained productivity and long-term survival of plants in grazed systems depends upon successful reproduction in parent generations and upon the subsequent establishment, growth and reproduction of propagules. By mediating plant natality, recruitment and mortality, herbivores can affect the productivity, composition, stability and resilience of plant populations and communities (Archer and Tieszen 1986). Changes in species composition and relative abundance over time in grazed systems inevitably reflect differential reproduction, recruitment, longevity and survival of individuals comprising the community (Jones and Mott 1980).

Reproductive output of a plant is influenced by the hierarchical morphology of the reproductive module. The levels of this morphology, ranging from gross to fine in their hierarchical structure, include: (1) reproductive modules (flowering branches) derived from buds on a vegetative branch, (2) nodes of potential flowering sites along the reproductive module, (3) flowers and fruits at each node, (4) seeds developing within each fruit, (5) seed size and (6) seed viability. Plants with determinate reproduction on primary modules have apical meristems that eventually switch from vegetative to reproductive growth, thus eliminating the potential
for further vegetative growth from that module, whereas plants with indeterminate reproduction may switch from vegetative to reproductive growth or vice versa (Pyke 1989). Plants with indeterminate reproduction may respond to resource limitations such as nutrients and moisture by switching to the least costly state. Plants with determinate reproduction can only respond to limitations by varying the hierarchical components of the previously differentiated bud.

Reproductive output of plants with determinate buds is more susceptible to the combined effects of herbivory and resource limitation than the reproductive output of plants with indeterminate buds. A determinate plant will not compensate for removal of a reproductive bud by switching a remaining vegetative node to a reproductive state. Reproductive compensation for the removed bud can only occur by activating another reproductive module (Pyke 1989).

It is difficult to study effects of herbivores on plant population dynamics under natural conditions without also examining subsequent plant-plant interactions (Harper 1977). Most grazing under natural conditions is selective, which reduces growth of the damaged plant and its competitive ability relative to its ungrazed neighbors (Dirzo 1984).

Although it has been hypothesized that competition is not an important process in stressful environments such as tundra and deserts (Grime 1977, Went 1955, Shreve 1942), experimental evidence indicates otherwise (Archer

*Artemisia tridentata* is often associated with and can compete with species that are spring forage for livestock (Robertson 1947). However, *A. tridentata* is also an important winter forage for mule deer (*Odocoileus hemionus* [Rafinesque]). Herbivory may directly impact *A. tridentata* reproduction or indirectly affect reproduction by altering its competitive relationship with other species. This study investigated the role of (1) deer and cattle herbivory, (2) inter- and intraspecific plant competition and (3) the combination of herbivory and plant competition on the reproduction of *Artemisia tridentata* ssp. *wyomingensis* Beetle & A. Young (Wyoming big sagebrush; henceforth referred to as *Artemisia*). Each level of the hierarchical morphology of *Artemisia* reproduction was examined separately to determine the impact of herbivory and plant competition.
Brown's Park (40° 53' N lat., 109° 08' W long.) is located along the Green River, Daggett County, Utah, U.S.A. It is a high-elevation valley (approximately 1700 m above mean sea level) of about 21,500 ha that is surrounded by mountains on three sides. Annual precipitation varies from 122 mm to 330 mm, with a 26-year average of 228 mm (NOAA 1988(a)). Precipitation for years immediately before and during the experiment were as follows: 1985, 200 mm; 1986, 328 mm; 1987, 177 mm; and 1988, 122 mm (NOAA 1988(b)). Precipitation for 1986 (the year immediately before the first experimental year) was the second greatest amount recorded, while precipitation for 1988 (the second year of the experiment) was Brown's Park's lowest amount in 26 years of recorded precipitation.

Brown's Park is the winter range for about 7,500 mule deer (Tate 1989) because of a mild winter climate relative to the surrounding mountains and of available forage in the form of palatable shrubs. Mule deer use generally occurs from late-October through late-April. The valley is also grazed by cattle between mid-April and late-June.

Four sites were chosen in winter 1986-87 to be representative of the vegetation and of the overall utilization by animals of the majority of Brown's Park. Exclosures at each site were used to control animal...
access to the study plots. Two exclosures were located
(40° 51' 52" N lat., 109° 9' 46" W long.; 40° 52' 55" N
lat., 109° 9' 46" W long.) on the south side of the
Green River at Taylor Flat. Two exclosures were located
(40° 51' 50" N lat., 109° 6' 32" W long.; 40° 51' 55" N
lat., 109° 6' 18" W long.) on the north side of the
Green River on Kings Point.

The soil at both sites is deep (150 cm or more) and
well drained. The surface varies from brown loam to
pale brown fine sandy loam from 8 to 28 cm thick. The
subsoil varies from brown loam to light yellowish brown
sandy loam from 46 to 120 cm thick. Sites at Taylor
Flat had a more shallow surface layer, but the subsoil
was more than twice as thick as sites on Kings Point
(personal communication, Dwain Nelson, BLM, Vernal, UT,
USA).

Brown's Park is managed by the U.S. Department of
Interior, Bureau of Land Management and by the State of
Utah, Division of Wildlife Resources for improved range
condition. Due to the predominance of *Artemisia* and its
utilization by mule deer as winter forage, management
for sustained or increased production of *Artemisia* is an
important component in maintaining range condition.

The vegetation is dominated by *Artemisia*, with other
shrubs such as *Atriplex confertifolia* (Torr. & Frem.)
Wats. (shadscale), *Atriplex canescens* (Pursh) Nutt.
(four-wing saltbush), *Artemisia spinescens* D. C. Eaton
in Wats. (budsage), *Tetradymia canescens* DC. (gray horsebrush), and *Chrysothamnus viscidiflorus* (Hook.) Nutt. (green rabbitbrush) found in localized areas. Interspaces between shrubs support a variety of grasses including *Stipa comata* Trin. & Rupr. (needle and thread), *Oryzopsis hymenoides* (R. & S.) Ricker = *Stipa hymenoides* Roemer & Schultes (indian ricegrass), *Bromus tectorum* L. (cheatgrass), and *Sitanion hystrix* (Nutt.) J. G. Smith = *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail). Also evident are *Juniperus osteosperma* (Torr.) Little (Utah juniper), *Opuntia polycantha* Haw. (prickly pear cactus) and *Phlox hoodii* Richards (Hood’s phlox).

The phenology of *Artemisia* is relatively consistent across subspecies. Apical growth of branches begins in March or April as temperatures increase. Inflorescence development begins in June, with flowers opening in late summer and seed dispersal occurring in autumn (Goodwin 1956; Price 1965; Coyne and Cook 1970; Wright 1970; Fernandez and Caldwell 1975; Miller and Shultz 1987).
A four-way exclosure was constructed of electric fence at each of four sites. These exclosures contained four, 0.6-ha (60 m by 100 m) subexclosures (Fig. 1) that excluded the following: (1) mule deer and cattle year around (no herbivory); (2) mule deer for about 10 months from July through late April or early May, when weather conditions allowed most of the deer to leave Brown's Park—the fence was lowered after the deer left the area to allow cattle grazing during the spring grazing season (no browsing); (3) cattle for about two months when they were present, but the fence was lowered when cattle were removed from the area (no grazing); and (4) no exclusion year around (control, both browsing and grazing allowed). Ad libitum grazing and browsing occurred when areas were open to animals. The fences for the subexclosures that excluded deer were constructed of 12 strands of wire to a height of 2.7 m and for those that excluded only cattle were constructed of three strands of wire to a height of 1 m.

Within each subexclosure, a 10-m buffer was established along each fence to eliminate fence or edge effects on measurements. Within the 0.32-ha (40 m by 80 m) measurement area, 32, 10-m by 10-m plots were delineated (Fig. 2). A 1-m buffer in which no treatments were established and no measurements were made was located along the outer edge of each plot. Two
Fig. 1. Diagram of a four-way exclosure (240 m by 100 m) with four subexclosures (60 m by 100 m) and the animals they excluded.
**Fig. 2.** Diagram of a subexclosure (60 m by 100 m) with delineated plots for plant removal treatments (10 m by 10 m). NR-no removal (control), GR-interspecific competitors removed (intraspecific competition), SR-intraspecific competitors removed (interspecific competition), AR-all competitors removed (no competition).
plants of Artemisia (target plants) were randomly selected for treatments within the remaining 0.8- x 0.8-m area. Each plot was randomly assigned one of four plant removal treatments and was located so that no two treatment plots shared a common side (Fig. 2). Four plant removal treatments were replicated twice in each subexclosure. These treatments were (1) no vegetation removed around the target plant (control), (2) removal of all vegetation within a 1-m radius of the target plant (no competition), (3) removal of all non-Artemisia plants within a 1-m radius of the target plant (intraspecific competition), and (4) removal of all Artemisia plants within a 1-m radius of the target plant (interspecific competition).

Plant removal treatments were conducted in April 1987. Non-Artemisia plants were removed by spot spraying with a nonselective, contact herbicide (ROUNDUP, Monsanto). Artemisia were removed by severing the plant flush to the soil surface since Artemisia is incapable of resprouting. Additional seedlings were removed as they emerged.

Target plants were tagged and measured for reproductive output. A total of 256 plants were used in this experiment. Current-year's growth (CYG) of each target plant was estimated ($r^2 = .89$, based on actual weight of 30 plants outside of the exclosures) using the reference unit method (Andrew et al. 1979). Reproduction per plant was represented relative to the
plant’s CYG since a general correlation between plant size and total flower or fruit production exists for many plants (Waller 1988).

The "neighborhood area" for each target plant was estimated by measuring the distance to the closest intraspecific and interspecific competitor within every 30° angle. These measurements were converted to Thiessen polygon diagrams for each target plant (after Mithen et al. 1984) using the Voronoi tessellation algorithm (Wilkinson 1988). The resulting "neighborhood area" was digitized to calculate the area in m².

The experimental design was a split-split plot with four factors: (1) year (1987, 1988), (2) site (Taylor Flat, Kings Point), (3) animal exclusion (cattle and deer, deer only, cattle only, no exclusion), and (4) plant competition (interspecific, intraspecific, no plant competition). Animal exclusion treatments were split within each site block and were replicated twice. The plant competition treatments were split within each animal exclusion block and were replicated twice.

Reproductive output of *Artemisia* was determined by counting inflorescence heads and by estimating achenes per head for the four target plants of each treatment. Inflorescence heads were counted in situ as inflorescences opened (late September/early October). The average number of achenes per inflorescence head was estimated from a random sample of 25 inflorescence heads
per shrub (or all inflorescence heads on shrubs with less than 25 heads). All measured reproductive parameters (reproductive modules per biomass of vegetative CYG, nodes per reproductive module, inflorescence heads per node, achenes per inflorescence head, and achene viability) were tested for significant differences among treatments using analysis of variance.

Although higher-order interactions were investigated, interactions of three or more factors may be difficult to interpret. Statistical interpretation in this study is limited to main effects and two-way interactions. The statistical testing between all possible factors yielded the greatest information possible from which conclusions could be drawn (see Appendix A).

Seed viability was tested by dividing 100 randomly selected achenes per shrub into four lots of 25 achenes each and by imbibing the achenes with a 1% solution of 2,3,5-triphenyltetrazolium chloride (Woodstock 1973). Reduction to the red (pink)-colored formazan by the dehydrogenase enzymes indicates living tissue and correlates with seed respiration and seedling vigor (Bewley and Black 1982). Those achenes stained red were considered to contain a viable seed. Significance among treatments was tested using the G-test of homogeneity (Sokal and Rohlf 1981).

Nutrient availability, both total nutrient pool and nutrient concentration, were suspected to be potential factors of competition that affect the quantity and quality of reproduction. Nutrient analysis (N,P,K) for
total nutrient pool and nutrient concentration (Allen et al. 1986) was conducted on destructively sampled CYG collected in 1988 from 16 control (exposed to animal use and plant competition) plants and 16 no-animal utilization, no-plant competition treatment plants. This allowed the two extremes of animal use and plant competition to be compared for nutrient analysis of the vegetation. The analysis was conducted by the Soil, Plant, and Water Analysis Laboratory, Utah State University, Logan, Utah. Nitrogen was determined using standard Kehjdahl nitrogen analysis. Phosphorus and potassium were determined using standard acid digestion analysis. Significance between treatments was tested with analysis of variance.
RESULTS

Browsing of Artemisia by mule deer caused on average a 37% reduction in the number of reproductive modules per biomass of vegetative CYG (Fig. 3). However, this varied from a 55% reduction in 1987 to no significant effect in 1988 (Fig. 4).

Deer herbivory also affected the number of nodes per reproductive module, an intermediate-hierarchical level of reproduction, in the second experimental year. The number of nodes per reproductive module was not affected by deer herbivory in 1987, but it was increased by 14% in 1988 (Fig. 5). Neither the presence nor absence of cattle significantly affected any level of reproduction during the two years of this study.

Herbivory and plant competition significantly reduced the reproductive output of Artemisia but at different hierarchical levels of reproduction. Plant removal treatments were effective in increasing the “neighborhood area” of each target plant. The following were the “neighborhood area” measurements of the four plant competition removal treatments: (1) no removal (control) - .205 m², (2) all competitors removed (no competition) - .885 m², (3) interspecific competitors removed (intraspecific competition) - .416 m², and (4) intraspecific competitors removed (interspecific competition) - .181 m². The “neighborhood area” of the
Fig. 3. Mean number of reproductive modules per gram of biomass of vegetative current-year’s growth of *Artemisia tridentata* ssp. *wyomingensis* when mule deer (*Odocoileus hemionus*) are present or absent in Brown’s Park, UT (1987-8). Bar indicates one standard error.
Fig. 4. Mean number of reproductive modules per gram of biomass of vegetative current-year’s growth of *Artemisia tridentata* ssp. *wyomingensis* when mule deer (*Odocoileus hemionus*) are present or absent in Brown’s Park, UT (1987-8). Bar indicates one standard error.
Fig. 5. Mean number of nodes per reproductive module of *Artemisia tridentata* ssp. *wyomingensis* when mule deer (*Odocoileus hemionus*) are present or absent in Brown's Park, UT (1987-8). Bar indicates one standard error.
control treatment (1) and of the interspecific competition treatment (4) did not differ significantly.

The plant removal treatments could make nutrients available for the target plant which in turn could affect the quantity and quality of reproductive output. However, no significant difference in total nutrient pool or nutrient concentration in CYG was detected between treatments (Fig. 6).

Although no significant difference in nutrient content was detected, plant removal affected Artemisia reproduction at finer hierarchical levels than did herbivory. Intra- and interspecific plant competition reduced the number of nodes per reproductive module by 12% and 8% (Fig. 7), and reduced the number of inflorescence heads per node by 43% and 29% (Fig. 8(a)), respectively. Interspecific plant competition had no significant effect on the number of nodes per reproductive module in 1987, but reduced the number of nodes per reproductive module by 13% in 1988 (Fig. 9). The percent viability for Artemisia achenes increased 179% with interspecific plant competition yet viability remained less than 4% (Fig. 10(a)).

Combined effects of deer herbivory and interspecific plant competition were also found at the level of nodes per reproductive module. Interspecific plant competition significantly reduced the number of nodes per reproductive module by 13% when deer herbivory was present, but deer herbivory increased the number of nodes per reproductive module by 9% when interspecific
Fig. 6. Percent nutrient concentration a) and percent total nutrient pool for nitrogen (N), phosphorus (P) and potassium (K) in current-year's growth of Artemisia tridentata ssp. wyomingensis with and without herbivores and plant competitors in Brown’s Park, UT (1988). Bar indicates one standard error.
Fig. 7. Mean number of nodes per reproductive module of *Artemisia tridentata* ssp. *wyomingensis* with interspecific and intraspecific competitors present or absent in Brown’s Park, UT (1987-8). Bar indicates one standard error.
Fig. 8. Mean number of inflorescence heads per node on a reproductive module of _Artemisia tridentata_ ssp. _wyomingensis_ for (a) interspecific and intraspecific competitors, and (b) year of treatment in Brown’s Park, UT (1987-8). Bar indicates one standard error.
Fig. 9. Mean number of nodes per reproductive module of *Artemisia tridentata* ssp. *wyomingensis* when interspecific competitors are present or absent during the two treatment years in Brown's Park, UT (1987-8). Bar indicates one standard error.
Fig. 10. Mean percent viability of *Artemisia tridentata* ssp. *wyomingensis* for main effects of (a) interspecific competitors, and (b) year of treatment in Brown’s Park, UT (1987-8). Bar indicates one standard error.
plant competition was absent (Fig. 11).

Year was the only other significant main effect at any reproductive level. The number of inflorescence heads per node in 1987 was 30% less than in 1988 (Fig. 8(b)). Viability in 1987 was 72% less than in 1988 (Fig. 10(b)).

The combined effects of treatment year and of interspecific plant competition were found at an intermediate hierarchical level. In the absence of interspecific plant competition the number of inflorescence heads per node increased by 82% from 1987 to 1988 (Fig. 12). The absence of interspecific plant competition in 1988 increased the number of inflorescence heads per node by 78% (Fig. 12).

The number of achenes per inflorescence head (fine-hierarchical level) did not significantly change as a result of herbivory or plant competition ($x=2.189$, SE=.076).

The number of inflorescence heads is calculated using average values for the significant main effects of deer herbivory, of plant competition, and for the interaction of deer herbivory and plant competition, at three hierarchical levels and four treatments (deer herbivory, no deer herbivory, plant competition, no plant competition) (Fig. 13). The effect of plant removal increased inflorescence head production by 82% while restricted deer access only increased inflorescence head production by 60% (Fig. 13). The combined effect of plant removal and restricted deer access increased
Fig. 11. Mean number of nodes per reproductive module of *Artemisia tridentata* ssp. *wyomingensis* when mule deer (*Odocoileus hemionus*) and interspecific competitors are present or absent in Brown's Park, UT (1987-8). Bar indicates one standard error.
Fig. 12. Mean number of inflorescence heads per node on a reproductive module of *Artemisia tridentata* ssp. *wyomingensis* when interspecific competitors are present or absent during the two treatment years in Brown’s Park, UT (1987-8). Bar indicates one standard error.
Fig. 13. Average number for the reproductive components of *Artemisia tridentata* spp. *wyomingensis* multiplied to show the effects of mule deer (*Odocoileus hemionus*) herbivory and of plant competition on the production of inflorescence heads in Brown's Park, UT (1987-8). The number of inflorescence heads is standardized to the control treatment.
inflorescence head production by 165% (Fig. 13). When standardized to control, the combined effect of restricted deer access and of plant removal was found to be more than additive with respect to inflorescence head production in *Artemisia* (Fig. 13).
DISCUSSION

While plant mortality is the most dramatic means by which herbivores affect plant fitness, decreases in growth and subsequent reproduction are more likely impacts of herbivore damage than plant death (Hendrix 1988). Both deer herbivory and plant competition (inter- and intraspecific) had a major impact on reproductive output at differing hierarchical levels of reproduction of *A. tridentata* ssp. *wyomingensis*. Deer herbivory during the winter mainly affected gross hierarchical levels by removing buds that differentiate into reproductive modules in the following summer. Plant competition (inter- and intraspecific) mainly affected levels of reproduction that were nested within the reproductive module by reducing the number of nodes per reproductive module and the number of inflorescence heads per node.

Most shrubs and forbs regenerate forage removed through grazing. Vegetative and reproductive axes in some plants are produced in characteristic, predictable positions, but in other cases a particular meristem may give rise to either a vegetative shoot or a flower or inflorescence (Waller 1988). Bilbrough (1990) showed that greater than 95% of all reproductive modules in *A. tridentata* ssp. *vaseyana* arise from the distal one-third on the previous year's vegetative growth. This is the most susceptible portion of the branch to browsing by
mule deer. The current study showed deer herbivory reduced the number of reproductive modules produced (Fig. 3). Similar results were reported in a five-year study by Rodriguez and Welch (1987) and in one of three years by Cook and Stoddart (1960).

The effects of deer herbivory were particularly evident in 1987 when reproductive modules per biomass of vegetative CYG were reduced by over 50% (Fig. 4). This may have been pronounced due to abundant precipitation in the previous year (see Study Area). The high precipitation may have triggered the production of a greater number of reproductive buds, and of an increase in vegetative growth. Plants that escaped deer herbivory had more reproductive buds to produce reproductive modules than plants subject to deer herbivory.

A one-year lag in response to precipitation may also explain the lack of significance between browsed and unbrowsed plants in 1988. Precipitation in 1987 was about 30% below normal which may have resulted in the production of fewer reproductive buds in the following year, thus the impact of deer herbivory in 1988 did not appear to be as severe (Fig. 4).

Removal of potentially reproductive buds results in a total loss of reproduction for that module. Compensation for this loss would require initiation of additional reproductive modules or increases in other hierarchical levels on remaining reproductive modules similar to recovery options for annual plants that have
experienced temporary resource limitations (Pyke 1989). Since *Artemisia* has determinate growth it is incapable of switching a bud from vegetative to reproductive growth, therefore initiation of additional reproductive modules is not a viable option.

Compensation for removed reproductive buds may be accomplished by allocating greater growth, including more nodes, to reproductive modules that remained after browsing. The current study, however, found that deer herbivory had varied impacts on the number of nodes per reproductive module. In 1987, deer herbivory reduced the number of nodes per reproductive module, while in 1988, it increased the same reproductive level.

Compensatory responses to herbivory may or may not be expressed depending on the competitive regime and on the nutrient availability of the microsite in which the browsed plant is growing (Maschinski and Whitham 1989). *Artemisia* experiencing browsing but no plant competition were capable of producing slightly more inflorescence heads than when deer browsing was eliminated and plant competition was maintained (Fig. 13).

Many reported studies have indicated proper livestock grazing maintains or improves the vegetative habitat for mule deer (Smith 1949, Smith and Doell 1968, Jensen et al. 1972, Longhurst et al. 1979, Smith et al. 1979, Neal 1981, Urness 1982, Reiner and Urness 1982). This current study showed no effect of spring grazing by cattle on the reproduction of *Artemisia*. However, two years of exclusion from cattle grazing may not have been
sufficient time for herbaceous plants to respond and to increase their competitive affect on Artemisia, especially when 1988 was a severe drought. It is likely that spring grazing by cattle in Brown’s Park over many years may reduce the understory competition for Artemisia and thus benefit the reproduction of Artemisia (Fig. 12). Visual observation of a long-term permanent cattle exclosure showed overwhelming grass competition with many Artemisia “skeletons” and few live Artemisia.

The presence of plant competitors does impact Artemisia reproduction. Plant competition (both inter- and intraspecific) had a greater effect on overall achene production than deer herbivory by primarily impacting two rather than one hierarchical level of reproduction, the number of nodes per reproductive module and the number of inflorescence heads per node, reducing each by 10% and 36%, respectively. The overall effect of plant competition on total inflorescence head production was a reduction of 45% (Fig. 13).

Release from plant competitors, particularly intraspecific competitors, should result in increased production (both vegetatively and reproductively) as resources become available. Release from interspecific competitors may result in a lesser increase of production (both vegetatively and reproductively) depending on the degree of niche overlap between species. This study showed that release from inter- or intraspecific plant competition followed a similar pattern of increased nodes per reproductive module and
inflorescence heads per node (Fig. 7 and 8(a)). However, release from interspecific plant competition decreased achene viability (Fig. 10(a)). The release of interspecific competition increased the number of nodes per reproductive module and inflorescence heads per node, causing an associated increase in potential achenes. However, the amount of nutrients available to each achene would be reduced due to limited nutrients, resulting in lower viability.

The timing of competitive release appears important in reproduction. The number of nodes per reproductive module showed no change during the first year (Fig. 9), probably because plant removal treatments were not implemented until after snowmelt in spring of 1987; the time of temporary nutrient flush in semiarid soils (Wallace et al. 1978). The time of initial competitive release may not have included this critical period of nutrient uptake. By the second year, target plants experienced the potentially important snowmelt and subsequent period of nutrient flush, and showed a significant difference in the number of nodes per reproductive module (Fig. 9). This difference may also have been enhanced by the low precipitation in 1987.

Although nutrient analysis did not result in significant differences in either nutrient concentration or total nutrient pool (Fig. 6), the long-term cumulative effect of increased nutrient pool for nitrogen and potassium found in this two-year study (Fig. 6(b)) cannot be overlooked. A slight increase
yearly accumulated over a number of years may have a significant effect at any hierarchical level of reproduction.

The effects of herbivory and competition on plants are dependent on the competitive environment of the plant and on the level of herbivory (Fowler and Rausher 1985, Maschinski and Whitham 1989). The joint affect of herbivory (simulated by clipping) and competition on Aristolochia reticulata was best described as additive (Fowler and Rausher 1985). The joint affect of herbivory and competition in the current study was additive with respect to total inflorescence head production of Artemisia, indicating a synergistic interaction between herbivory and plant competition (Fig. 13).

The postherbivory effects caused by competition are likely to reduce growth, survival, and reproduction of individual plants and eventually affect the population dynamics and community plant composition. Herbivory studies are difficult at best to perform in a natural environment due to multiple interactions within the community. Harper (1977) references several studies which indicate herbivores reduced the competitive advantage of otherwise overwhelmingly dominant species resulting in greater species diversity for the community. The interactive effects of herbivory and of plant competition cannot be ignored but may be effectively partitioned into affected levels of a hierarchical reproductive structure.
MANAGEMENT IMPLICATIONS

Brown's Park is an important winter range for mule deer, due to the mild winter climate. Recently the number of wintering mule deer has increased from 3,000 to 7,500 (Tate 1989). This dramatic increase has affected Artemisia which is the primary winter forage and predominant shrub. Brown's Park is also used for spring grazing by cattle which utilize the understory of grasses and forbs. This two-year study showed that cattle had no effect on Artemisia reproduction, yet many years of spring grazing by cattle has apparently kept the understory competition "in check" and should therefore be continued. Visual observation of a long-term permanent cattle and deer exclosure showed overwhelming grass competition with many Artemisia "skeletons", few live Artemisia and no seedling or newly recruited Artemisia.

Artemisia have episodic reproduction (surviving seedlings) on an average of once in seven years due to the apparent specific climatic conditions necessary for Artemisia germination and survival. There is no Artemisia seed bank, therefore the only seeds available for germination are those produced in the current year. Artemisia in Brown's Park during this two-year study produced about 1000 seeds per plant per year. Less than 5% viability was recorded, lowering the potential number of seedlings to 50, of which only 1% will survive the
first year. From this it is calculated that each *Artemisia* is currently producing the potential of only a half (0.5) a plant per year. Under ideal greenhouse conditions, *Artemisia* may become reproductive after 3 years, certainly a much shorter period than in natural conditions. *Artemisia* must produce seed every year on the chance there might be adequate climatological conditions. In order to allow *Artemisia* a reasonable chance to successfully reproduce appropriate management must be implemented.

The principle factor affecting *Artemisia* reproduction is deer herbivory. Plants protected from deer herbivory experienced an average increase of reproductive (flowering) stems by 50% (Fig. 3). With no other treatments the number of inflorescence heads increased by 60% when *Artemisia* was protected from deer (Fig. 13). A significant reduction in the deer population is necessary if *Artemisia* is to reproduce in sufficient numbers to have long-term stable winter forage for mule deer.
LITERATURE CITED


Smith, A. D., and D. D. Doell. 1968. Guides to allocating forage between cattle and big game on big game winter ranges. Utah State Division of Fish and Game Publication 68-11.


Woodstock, L. W. 1973. Physiological and biochemical tests for seed vigor. Seed Science and Technology
Appendix A. Experimental design

Table A.1. Experimental design used to test all possible combinations using analysis of variance.

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Repetitions 128
Total 255