CHAPTER II

STUDY AREAS AND METHODS

STUDY AREAS

The study areas reported in this dissertation are located within the Greater Yellowstone Ecosystem (Tixier 1986, Clark and Zaunbrecher 1987, Clark and Harvey 1988). Study sites were located on the winter ranges of the northern Yellowstone, Jackson Hole, and Gallatin elk herds. Houston (1982) provided a description of the climate, physiography, and vegetation of the northern range while Anderson (1958) and Boyce (1989) provided similar information for Jackson Hole. Historically the Gallatin has had an elk situation similar to that on the northern range (Packer 1963; Patten 1963, 1968, 1969; Streeter 1965; Peek et al. 1967; Lovaas 1970). The winter ranges of these and other elk herds in the Greater Yellowstone Ecosystem are shown in Houston's (1982:33) Fig. 4.2.

Jackson Hole also has had an elk situation similar to Yellowstone's (Anderson 1958; Beetle 1974, 1979; Boyce 1989). At first, it was thought (1) Jackson Hole was not a historic elk winter range; (2) European settlement forced elk to winter in the valley; and (3) supplemental feeding permitted the growth of an abnormally large elk herd, which (4) caused substantial "damage" to the winter range and a marked decline of aspen, (Preble 1911; Murie 1951; Anderson 1958; Krebill 1972; Beetle 1974, 1979; Basile 1979; DeByle 1979; Weinstein 1979; Youngblood and Mueggler 1981; Hart 1986).

However, federal and state agency biologists now believe (1) large numbers of elk have wintered in Jackson Hole for the last several thousand years; (2) feedlots have only replaced winter range lost to human developments; (3) therefore, today's elk population is not unnaturally high, though the distribution of wintering animals may have changed; (4) serious elk-induced "range damage" has not occurred (Cole

1969a; Gruell 1979, 1980a, 1980b; Boyce 1989); and (5) the elk herd would "naturally regulate" if sport hunting were terminated (National Park Service 1986, Boyce 1989). Under this interpretation, aspen is thought to be a seral species maintained by fire and human suppression of lightning fires is believed to be primarily responsible for the observed decline in aspen, not ungulate browsing (Loope and Gruell 1973; Gruell and Loope 1974; Gruell 1979, 1980a, 1980b).

I used study sites in the Gallatin and Jackson Hole both to increase experimental sample size and to take advantage of management situations which served as manipulative experiments (Diamond 1986). By using additional aspen exclosures built in the Gallatin and Jackson Hole, I was able to increase my sample size to 14 and avoid pseudo-replication problems (Hurlbert 1984). Similarly, I measured burned aspen stands in Jackson Hole to determine whether they had successfully regenerated despite elk use because various federal agencies burned extensive areas of aspen there during the early to mid 1970s. By using sites in Jackson Hole, I was able to increase my sample of burned aspen stands from 6 to 473. Moreover the locations of those burns allowed me to evaluate their regenerative response under varying levels of ungulate use, which created a more robust study design (Hurlbert 1984).

Exclosures

The locations, dates of establishment, and sizes of the exclosures discussed in this study are presented in Table 3 and Fig. 3. Barmore (1968b, 1981:453-459), Houston (1982:415-420), and Chadde and Kay (1988) provided additional information for exclosures on Yellowstone's northern range. Beetle (1974:14), Gruell and Loope (1974:23-24, 29), and Hart (1986) described exclosures in Jackson Hole while Thornton (1969) provided additional information on the Upper Slide Lake exclosure.

Range Plots 10, 16, and 25 are small (7x8m) exclosures which contain only aspen. The Goosewing and Soda Lake exclosures are also

Table 3. Location and description of exclosures studied in the Greater Yellowstone Ecosystem.

Winter range Exclosure	Area[1]	Location[2] T	R	S	Date established	Size (ha)	Elevation (m)	Main aspect	Vegetation type[3]	Herbivore use inside exclosure	Other
Northern Yellowstone											
1. Mammoth	YNP	--	--	--	1957	2.116	1902	N	A,W,BS	None	---
2. Junction Butte	YNP	--	--	--	1962	2.116	1890	NW	A,W	None	---
3. Lamar-East	YNP	--	--	--	1957	2.116	2027	S	A,W	Some Elk	---
4. Lamar-West	YNP	--	--	--	1962	2.116	2027	S	A,W,BS	Some moose	---
5. Tower Junction	YNP	--	--	--	1957	2.116	1902	N	W	Fence removed early 1970's	
6. Slough Creek	GNF	9S	13E	18	1961	0.041	2073	S	W	Beaver	---
7. Range Plot 10	YNP	--	--	--	1934	0.004	1881	E	A	None	---
8. Range Plot 25	YNP	--	--	--	1936	0.004	1951	NW	A	None	Burned 1988
Jackson Hole											
9. East Elk Refuge	BTNF	41N	114W	3	1952	0.110	2057	SW	A	None	---
10. Upper Slide Lake	BTNF	42N	112W	20	1960	152.376	2317	S	A	Heavy Elk	Fence down
11. Goosewing	BTNF	41N	112W	3	1942	0.819	2271	N	A	Elk/moose	Fence down
12. Uhl Hill	GTNP	44N	114W	1	1963	0.364	2112	S	A,BS	Some moose	---
13. Camp Creek	BTNF	39N	115W	32	1938	0.281	1920	S	BS	Some deer	---
Gallatin											
14. Porcupine	GNF	7S	4E	16	1945	1.866	1920	SE	A,W	Some elk	---
15. Crown Butte	GNF	9S	5E	7/8	1945	2.066	2210	S	A,W	None	---
16. Range Plot 16	YNP	--	--	--	1935	0.004	2195	W	A	None	---
17. Snowflake Springs	GNF	9S	4E	12	1948	0.100	2027	N	W	Beaver	---
Pinedale											
18. Soda Lake[4]	BTNF	34N	109W	23	1964	0.431	2332	S	A	None	---

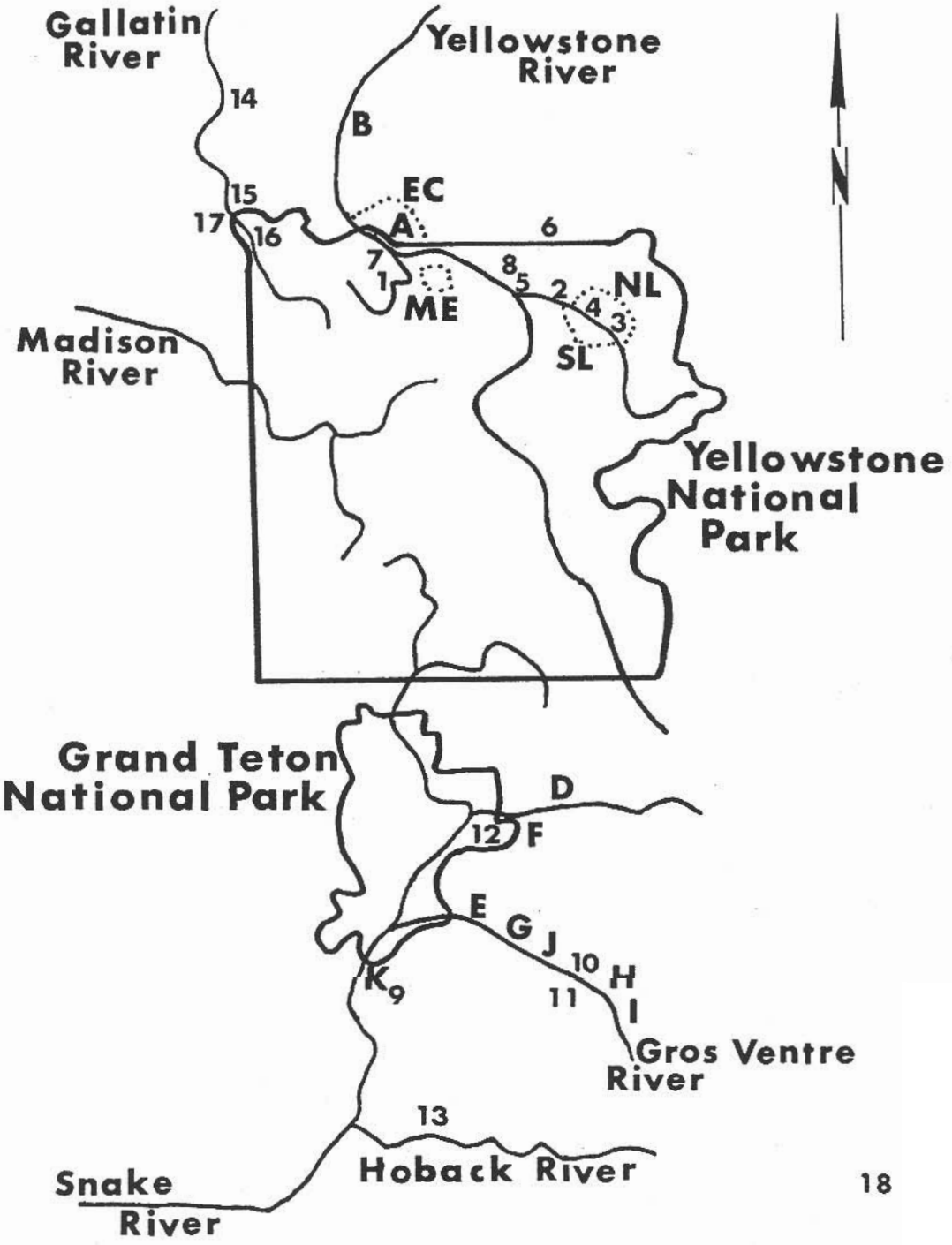
1. YNP = Yellowstone National Park, GNF = Gallatin National Forest, BTNF = Bridger-Teton National Forest, and GTNP = Grand Teton National Park.

2. Yellowstone Park has not been surveyed.

3. Only the vegetation types measured or discussed in this study. Several exclosures also contain areas of grassland/sagebrush. A = aspen, W = willow, and BS = berry producing shrubs.

4. Located in the Green River Drainage to the east of Jackson Hole but within the Greater Yellowstone Ecosystem. Exclosure is behind the Soda Lake elk feedground and was included in this study to maximize sample size.

Fig. 3. Location of exclosures, aspen study sites, and aspen burns studied in the Greater Yellowstone Ecosystem. Exclosures: 1) Mammoth, 2) Junction Butte, 3) Lamar East, 4) Lamar West, 5) Tower Junction, 6) Slough Creek, 7) Range Plot 10, 8) Range Plot 25, 9) East Elk Refuge, 10) Upper Slide Lake, 11) Goosewing, 12) Uhl Hill, 13) Camp Creek, 14) Porcupine, 15) Crown Butte, 16) Range Plot 16, 17) Snowflake Springs, and 18) Soda Lake. Aspen study sites: EC = Eagle Creek, ME = Mt. Everts, NL = North Lamar, and SL = South Lamar. Aspen burns: A) Eagle Creek, B) Yankee Jim Canyon, C) Junction Butte (same as 2 above), D) Burro Hill, E) Russold Hill, F) Coal Mine Draw, G) Lightning Creek, H) Breakneck Ridge, I) Dry Cottonwood, J) Dry Dallas, and K) Elk Refuge.


Gallatin River
Yellowstone River
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B
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EC
17
16
A
6
7
1
8
5
2
4
3
NL
ME
SL
Madison River
Yellowstone National Park
Grand Teton National Park
D
12
F
E
G
J
10
H
K
9
11
I
Gros Ventre River
13
Hoback River
Snake River
18

predominantly aspen while the Tower Junction, Slough Creek, and Snowflake Springs exclosures are mainly willows. The other exclosures contain areas of non-aspen or non-willow habitats, primarily grassland-sagebrush (Artemisia spp.). Most exclosures are located at or near the grassland-forest ecotone.

To the best of my knowledge, I sampled all of the aspen-containing exclosures in the Greater Yellowstone Ecosystem. I also included all major willow-containing exclosures except the Goosewing willow exclosure in Jackson Hole's Gros Ventre River drainage. Other grassland exclosures exist on the northern range, Gallatin, and Jackson Hole, but they were not included in this study.

Aspen Study Sites

Four aspen study sites were selected for intensive sampling on Yellowstone's northern range, three inside the park and one outside (Fig. 3). The Eagle, Phelps, and Pole Creek drainages, referred to collectively as Eagle Creek, are adjacent to the park's northern boundary and have a history of fire suppression similar to the park's. This area has experienced the same climatic fluctuations as the park (Stockton 1973, Douglas and Stockton 1975), is within the Gallatin National Forest and is managed as big game winter range. Livestock grazing has been excluded for at least 50 years. Yellowstone's northern herd uses this and other areas north of the park during winter. However, Eagle Creek receives less elk use than the park because it is open to public hunting including a special late hunt which continues into February (Erickson 1981, Vore 1990). There also are fewer elk in Eagle Creek during spring due to human disturbances, such as antler gathering (Kesselheim 1983). By early spring, elk have migrated back into the park (Houston 1982). Elk and mule deer are uncommon in Eagle

Creek during May, June, and the summer months.

In Yellowstone Park, I selected the southeast side of Mt. Everts, and areas north and south of the Lamar River for in-depth vegetation analyses after consultations with Park Service biologists. Aspen stands in those areas are believed to be representative of aspen communities throughout the park's northern range. Mt. Everts was selected because it has the same general aspect and elevation as Eagle Creek but is removed from the park's boundary. Houston (1982) suggested that hunting outside the park may have created an abnormal concentration of elk along the park's northern boundary which, in turn, adversely impacted vegetation in that zone. Since Mt. Everts is 6 to 10km from the boundary, it is unlikely that elk concentrated there to avoid hunting outside the park.

The North Lamar study site included all drainages north of the park highway from just above Lamar Canyon to Druid Peak ridge near the junction of Soda Butte Creek and Lamar River. The South Lamar study site included all drainages south of Lamar River or the park road from west of Crystal Creek to Amethyst Creek. I selected these two areas because Cole (1969b) and Houston (1979) postulated that Lamar Valley contained a resident, winter herd segment most likely to be "naturally regulated."

Aspen Burns

To determine whether burning can, in fact, regenerate aspen despite heavy utilization by ungulates, I measured stands burned at 11 different locations within the Greater Yellowstone Ecosystem. Data on the location, timing, and size of those burns are presented in Table 4 and Fig. 3.

Breakneck Ridge was burned as part of a research study conducted by the Intermountain Forest and Range Experimental Station (Bartos and Mueggler 1979, 1981; Basile 1979). The Fish and Wildlife Service

Table 4. Location and description of aspen burns studied in the Greater Yellowstone Ecosystem.

Winter range / Burn	Area[1]	Location T	R	S	Date burned	Approx. area burned (ha)[2]	Aspect	Elevation (m)
Northern Yellowstone								
1. Eagle Creek	GNF	9S	8E	12	Spring 1978 and 1980	120	E - S	2027-2075
2. Yankee Jim Canyon	GNF	7S	7E	4	4/22/77	20	W - NW	1700-1800
3. Junction Butte	YNP	--	--	--	Fall 1986	2	NW	1890
Jackson Hole								
4. Burro Hill	BTNF	45N 45N	113W 112W	25 19,30	8/27/74	178	NE-S-SW	2100-2200
5. Russold Hill	BTNF	42N 43N	114W 114W	1,2 35	5/15/74	188	NE-S-NW	2150-2255
6. Coal Mine Draw	BTNF	44N	113W	3,4,9	5/18/76	121	N-E-S-W	2200-2270
7. Lightning Creek[3]	BTNF	42N 42N	112W 113W	7,18,19 10,11,14 15	4/21-23/1977 Spring 1978 Spring 1980	466 26 24	NE-S-NW	2286-2560
8. Breakneck Ridge	BTNF	42N	112W	25,26,35	8/29/74	366	NE-S-NW	2377-2590
9. Dry Cottonwood[4]	BTNF	42N 42N	112W 111W	23,24,27,30 30	Spring 1978, 1979, and 1980	226	NE-S-NW	2377-2652
10. Dry Dallas[5]	BTNF	42N	112W	15,16,17,20 21,22,23	Spring 1978, 1979, and 1980	340	NE-S-NW	2317-2621
11. Elk Refuge	NER	42N	115W	20	8/73	16	W - N	2134-2164

1. GNF = Gallatin National Forest, YNP = Yellowstone National Park, BTNF = Bridger Teton National Forest, and NER - National Elk Refuge.
2. Total area burned including sagebrush-grasslands.
3. Includes the area between Lightning and Dry Dallas Creeks.
4. Includes the area between Dry Cottonwood and Cottonwood Creeks.
5. Includes the area between Dry Dallas and Dry Cottonwood Creeks.

experimentally burned aspen on the National Elk Refuge. Management burns were conducted by the Bridger-Teton National Forest primarily to reduce sagebrush and increase forage production. However, those fires did burn a number of aspen stands (Bartos 1979, 1981) which experience various levels of ungulate use, and thus, are suited to address this question. U.S. Forest Service researchers established permanent plots on Breakneck Ridge, Coal Mine Draw, Russold Hill, and Burro Hill aspen burns (Bartos 1979, 1981).

While burning sagebrush/grasslands in Eagle Creek (see Aspen Study Sites), the Gallatin National Forest inadvertently burned four aspen stands. They specifically burned the Yankee Jim Canyon site to regenerate aspen. Houston (1982:111, 115) and Kay (1985:143) provided additional information on the Yankee Jim Canyon Burn, which is located approximately 20km north of the park's Gardiner entrance. That site is situated near the limit of the northern herd's winter range as defined by Houston (1982).

When the Park Service constructed the Junction Butte exclosure in 1962 (Table 3), one side of that exclosure was built through an aspen clone. Both portions of that clone were experimentally burned by the Park Service in fall 1986.

METHODS

Repeat Photography

I searched archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, the Museum of the Rockies, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological Survey's Denver Photographic Library for historical photos of the northern range. I reviewed nearly 50,000 images taken in the park. Only a small portion of these were taken on the northern range, and a still smaller number

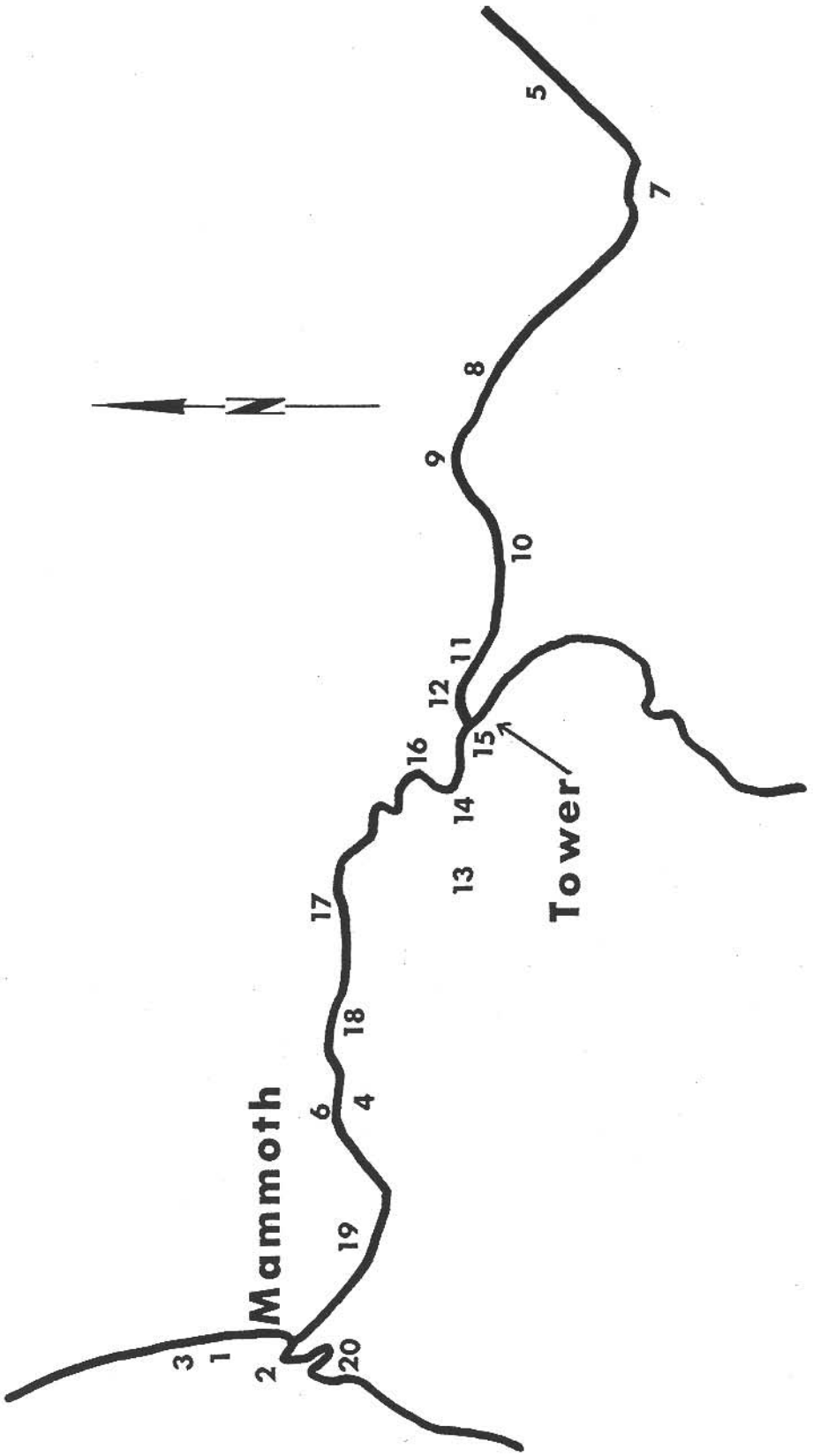
contained views of willow or aspen communities. I also obtained historic photographs from Warren (1926) and Jonas (1955), and I examined several drawings made by Seton (1909) of willow communities and beaver dams near Tower Junction in 1897.

During 1986-89, I rephotographed the locations in the historic pictures to form sets of comparative photos, a process called repeat photography (Rogers et al. 1984). Under magnification, I visually evaluated the photosets to determine changes in the abundance and distribution of aspen and tall willow communities (Garry Rogers, pers. commun. 1987). Where possible, aspen trees were counted on the photosets to obtain estimates of rates of change for tree numbers.

On other photos, I estimated the extent of individual aspen stands or clones using methods developed by Dr. Garry Rogers (pers. commun. 1987). Since the pictures in my photosets were not exact duplicates, I could not use a dot matrix to measure the area covered by aspen. Instead, I divided the photographs into comparable subunits based on topographic or landform features. I then visually estimated the area occupied by aspen within those subunits on my paired photos. On some closeup photosets, it was possible to obtain estimates for more than one clearly defined aspen stand. For distant views of aspen, where individual stands could not be identified, I summed my estimates for the entire photo.

In 1947, Park Service biologist Walter Kittams (1948, 1949, 1950, 1952a, 1952b) established 20 aspen study plots throughout Yellowstone's northern range (Fig. 4). His study was designed to measure aspen regeneration and sucker survival, but he also took black and white photos of his plots in 1947 and 1952. Yellowstone biologist Barmore rephotographed those plots in 1964 (Barmore 1965, Houston 1982:413-414). Because Yellowstone's Research Office did not have any record of Kittams' aspen study (F. Singer, pers. commun. 1987), I obtained copies of Kittams' 1947 and 1952 photos from Yellowstone's archives and then

Fig. 4. Locations of Park Service biologist Kittams' aspen photo-plots on Yellowstone's northern range in relation to park roads. Locations were personally provided by Kittams and then verified in the field.


Mammoth
Tower
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contacted Mr. Kittams. Mr. Kittams has copies of all his Park Service reports, as well as his field notes. Thus, he was able to delineate his aspen study plots on current topographic maps. With this information, I was able to relocate and rephotograph all of Kittams' aspen plots during August 1988.

I also searched historical photographs taken on the northern range and throughout Yellowstone Park for evidence of conifer high-lining by ungulates. In some cases, I made repeat photographs to document the presence or absence of conifer high-lining. However, I also used repeat photosets of willow or aspen communities to evaluate high-lining because they often contained some conifers. Houston (1982) and Gruell (1980a, 1980b) used comparative photography to study vegetation changes on the northern winter range and other areas within the Greater Yellowstone Ecosystem.

Aspen Sampling

I partitioned each aspen study site into topographic subunits based on aerial photos and ground reconnaissance. Subunits were delineated such that all aspen stands could be seen on a single trip through the subunit. This was necessary because individual aspen stands could not be identified from available Park Service or Forest Service aerial photos. In all instances, I considered individual aspen clones single stands. For this study, I judged aspen separated by > 30m to be different stands. Large blocks of aspen are rare throughout the northern range, but when encountered, I considered them single stands unless clonal variation (Jones and DeByle 1985a) was evident.

I began sampling each subunit at a location nearest the most convenient access point. At the start of each subunit, I drew a random number to determine which of the first five stands would be measured. This procedure was repeated until one stand from each group of five had been measured in each subunit. This produced a random sample of 20% of the aspen stands on a study area. I also visually evaluated each aspen

stand following previously established procedures (Kay 1985)to see if it had successfully regenerated or was being invaded by conifers.

At each sampled stand, I placed a 2x30m belt transect perpendicular to the slope, beginning at the stand's edge and directed towards its center. To facilitate data recording, I subdivided each 30m transect into 3m segments and recorded the number of aspen stems by five size-classes within each 3m segment. Those five size classes were (1) < 2m tall, (2) > 2m tall but ≤ 5cm DBH (diameter at breast height), (3) 6-10cm DBH, (4) 11-20cm DBH, and (5) > 20cm DBH. Ages of five aspen within each size class were determined by counting annual rings. I obtained ages of large aspen with an increment borer and cross-sectioned small stems. Ages were determined near ground level, and the DBH of each aged tree was recorded.

Within each measured stand, I also recorded the following information: (1) elevation, (2) aspect, and (3) stand size. In order to estimate the abundance of conifers in the measured aspen stands, I recorded the number, size, and species of all conifers in each transect. I recorded conifers by four size classes; < 2m tall, > 2m tall but ≤ 5cm DBH, 6-10cm DBH, and > 11cm DBH. In addition, I visually estimated the percent conifer canopy cover in each stand according to procedures established by Mueggler (1988).

I recorded the canopy-coverage (Daubenmire 1959) of major understory plants in each transect. I measured shrubs by 30m line-intercepts (Hanley 1978) along the transect center lines. This method produced a single percentage for each shrub species. Following Mueggler (1988), I visually estimated understory forb and grass canopy-coverage for the entire stand. I recorded only forbs and grasses with > 3% canopy-coverage since minor species usually have little influence on community dynamics. I grouped those species together as other forbs or other grasses. However, I recorded forbs and grasses which are important in aspen community classification (Youngblood and Mueggler

1981; Mueggler and Campbell 1982, 1986; Mueggler 1988) whenever they occurred. I used Youngblood and Mueggler's (1981) aspen community key to classify each measured stand.

Aspen Exclosures

I first searched agency files to obtain all existing information on each exclosure. Care was taken to locate (1) all prior vegetation data, (2) any written desceiption of permanent vegetation sampling schemes, and (3) any old photographs. Whenever possible, previously established permanent plots were resampled using the methods which had been implemented by the management agency. Unfortunately, only eight exclosures contained permanent aspen measurement plots and only one contained permanent transects to measure understory species composition. I made all exclosure measurements during 1986-87.

When the exclosures were constructed, the Park Service established one permanent aspen belt transect inside and another outside each 2.1 ha exclosure in Yellowstone except at Lamar-West where no outside transect was established (Barmore 1968b, 1981:453-459; Houston 1982:415-420). Instead, the agency used the Lamar-East outside aspen belt as a control for both the Lamar-East and Lamar-West exclosures. Thus, seven permanent aspen belt transects are associated with these exclosures; three outside and four inside. The belt transects at Mammoth, Lamar-East and Lamar-West are all 1.5 x 30.5m (5 x 100ft), while those at Junction Butte are 1.5 x 22.9m (5 x 75ft). Data on aspen height and the number of individual stems (ramets) have been collected by the Park Service at various intervals since these exclosures were built.

At Range Plots 10, 16, and 25, the Park Service recorded the height of all aspen inside each exclosure and on comparable immediately adjacent outside areas at various periods since those exclosures were constructed. The Forest Service established two contiguous 1.5 x 30.5m (5 x 100ft) aspen belt transects both inside and outside the Upper Slide

Lake exclosure when it was erected. The agency collected data on the height of all aspen stems on those transects each year from 1961 through 1968. Inside the East Elk Refuge exclosure, the Forest Service installed two 30.5m (100ft) Parker three-step lines (Parker 1954, Reppert and Francis 1973) to measure understory species. Those plots were read in 1952, 1959, and 1967.

Except at Range Plots 10, 16, and 25, I used one or more 2x30m belt transects to measure aspen communities inside and outside the exclosures in addition to any permanent plots which may have existed. Based on visual inspection (Mueggler 1988), I placed all belt transects so that they would be representative of inside and outside conditions. I measured each belt transect and recorded data using the methods previously described under Aspen Sampling. However, I made complete counts of all aspen stems inside the East Elk Refuge and Elk Ranch Reservoir exclosures.

When injured, aspen are more susceptible to attack by pathogens, many of which are quite virulent (Hinds 1985, Hart 1986). Aspen inside Range Plot 10, East Elk Refuge, and Upper Slide Lake exclosures were under pathogen attack when they were sampled (Hart 1986; J. Hart, pers. commun. 1987). Since some exclosures contain relatively few aspen, any mortality could affect the subsequent development of those communities. To prevent human-induced mortality and to preserve the scientific value of these exclosures, I did not core the aspen or otherwise disturb them to determine their ages.

A positive correlation between aspen diameter growth and age has been reported by other researchers (Alder 1970, Jones and Schier 1985, Masslich et al. 1988:258). For the purposes of this study, it was sufficient to know that multi-sized aspen were of varying ages without knowing their exact ages. Moreover, since the dates of exclosure establishment were known, new ramets must postdate that event. Aspen enclosed at the time of construction exhibited extensive bark scarring

due to previous wounding by elk (Krebill 1972; Olmsted 1977, 1979; DeByle 1985a; Hart 1986) while younger stems were all unscarred.

I obtained old photos of the exclosures, as well as any inside and outside plots, from the files of the National Park Service, Forest Service, or Montana Department of Fish, Wildlife, and Parks. I rephotographed the locations in those pictures during 1986-88 to form sets of comparative photos. I used the resulting, multiple-image photosets to evaluate changes inside and outside the exclosures over time. They were also used to evaluate changes in other aspen repeat photosets (see Repeat Photography above) because in several cases, visual estimates from the exclosure photographs could be compared with actual plant measurements. This served to calibrate the visual estimation technique used in the repeat-photography portion of this study.

Aspen Burns

I first searched agency files to obtain all existing information for each burn. Within each burn, I visually evaluated every aspen stand to determine whether or not it had regenerated. A burned stand was recorded as regenerating if at least one aspen stem had grown taller than 2m after the fire. Even if only a small portion of the original stand had regenerating stems > 2m tall, those stands were still considered to have regenerated successfully for this study. Thus, visual evaluation of the proportion of aspen stands which regenerated following fire is biased in favor of successful regeneration. I also visually evaluated unburned aspen stands immediately adjacent to each burn to determine if they had regenerated. An unburned stand was recorded as having regeneration if and only if the number of aspen stems > 2m tall but $\leq$ 5cm DBH were equal to or greater than the number of trees in the largest DBH size class (Kay 1985). I used the same criteria as described under Aspen Sampling to distinguish individual

stands. However, at Junction Butte, I considered aspen inside and outside the exclosure to be separate stands even though they are part of the same clone.

I placed a 2x30m belt transect perpendicular to the slope to measure characteristics of burned and unburned stands. Each belt transect was measured and data were recorded using the methods previously described under Aspen Sampling. In addition, I both estimated the proportion of aspen trees killed by fire and recorded the number of live aspen trees within each burned aspen stand. All of the burned aspen stands at Russold Hill, Elk Refuge, Yankee Jim Canyon, Eagle Creek, and Junction Butte were measured. In areas where more stands had been burned, I randomly selected a 20% sample utilizing the procedures described under Aspen Sampling. I also measured 20% of unburned aspen stands at Burro Hill, Russold Hill, and Coal Mine Draw.

At Junction Butte, the Park Service established one permanent aspen belt transect inside and another outside when that exclosure was constructed (Barmore 1981:453-459, Houston 1982:415-420). Both transects are 1.5 x 22.9m (5 x 75ft). Data on plant height and number of aspen stems have been collected by the agency at intervals since the exclosure was constructed. I measured plant height and counted stems on those transects in 1986 prior to burning and after the fire in 1987, 1988, and 1989. I measured the burns in Jackson Hole in 1987, and those in Eagle Creek during 1986. I measured the Yankee Jim Canyon Burn in 1989, although I visited and photographed it each year from 1983 to 1988.

Files of the Wyoming Game and Fish Department in Jackson yielded estimates of long-term winter and summer elk use on the burned areas in Jackson Hole. I also consulted department biologists among whom Garvice Roby was especially helpful. I contacted Yellowstone National Park, Gallatin National Forest, and Montana Department of Fish, Wildlife and Parks for information on ungulate use at Yankee Jim Canyon, Eagle Creek,

and Junction Butte. Since none of the agencies had actual use data on any of the burned areas, I could only rank elk utilization as none, low, moderate, or high.

I obtained data on lightning strikes in Yellowstone and Jackson Hole from the Bureau of Land Management's Interagency Fire Center in Boise, Idaho. That agency's Automatic Lightning Strike Detection System (ALDS) records cloud-to-ground strikes throughout the western U.S. as part of their Initial Attack Management System (IAMS). Archival data on date and location of lightning strikes were available for 1985, 1986, 1987, and 1988. For this portion of the study, Yellowstone's northern range was defined as Long. 110°50′ to Long. 110° by Lat. 45°2′ to Lat. 44°50′. Jackson Hole was delineated by the following coordinates: Long. 110°52′ to 110° by Lat. 43°55′ to Lat. 43°10′.

Willow Exclosures

When the 2.1 ha exclosures were constructed on Yellowstone Park's northern range, the Park Service established one permanent willow belt transect inside and another outside each exclosure except at Lamar-West where no outside transect was established (Barmore 1981:453-459, Houston 1982:415-420, Singer 1987). Instead, the agency used the Lamar-East outside willow belt as a control for both the Lamar-East and Lamar-West exclosures. Thus, seven permanent willow belt-transect measurements are associated with these exclosures: three outside and four inside. The belt transects at Mammoth, Lamar-East and Lamar-West are all 1.5 x 30.5m (5 x 100ft), while those at Junction Butte are 1.5 x 22.9m (5 x 75ft).

Data on willow canopy-coverage, plant height, and number of individual plants have been collected by the Park Service at intervals since the exclosures were constructed (Singer 1987). The agency plotted each willow clump within the transect onto graph paper and then determined canopy-coverage by a grid method. These belt transect measurements have inherent inadequacies which limit their usefulness in

long-term willow trend studies. First, the single canopy-coverage value inside and outside each exclosure precludes statistical testing of mean differences. Second, the plotting technique is subject to a wide degree of observer variability and error. Third, each belt transect includes significant portions of non-willow communities. Fourth, rare species and other undergrowth shrubs are underestimated or not recorded. Park Service counts of individual willow plants also have been highly variable.

For this study, I established a series of line-intercepts (Hanley 1978) within the existing belt transects so that willow canopy-coverage within and outside each exclosure could be statistically compared. I subdivided each belt transect into six 30.5m line-intercepts, except at Junction Butte where there were six 22.9m line-intercepts. The length of each line intercepted by various willow species, as well as other shrub species, was recorded to the nearest cm, and the maximum height of each plant recorded, all in August 1988.

In addition to the measurements taken by the Park Service over the years, the agency also took pictures of the willow belt transects each time they were sampled. I repeated these photographs in 1987-88. I used the resulting, multiple-image photosets to evaluate changes inside and outside the exclosures over time. I also used these comparative photos to evaluate changes in willow communities observed in other repeat photosets because visual estimates from the exclosure photographs could be compared with actual plant measurements. This served to calibrate the visual estimation technique used in the Repeat Photography portion of this study.

Willow communities and their environments were sampled and classified as part of a recent study of wetlands on the northern range by Chadde et al. (1988). Their sample plots were located within relatively homogeneous stands of willows, based on species composition and dominance within the stand. They estimated canopy-coverage

(Daubenmire 1959) and height of all species occurring within $50m^2$ sample plots. Chadde et al. (1988) and Brichta (1987) sampled and described soils on their plots using standard pedon description methods and terms (Soil Survey Staff 1975), describing soils associated with willow communities to the family level. They monitored water levels associated with representative willow stands from May to September of 1986 and 1987 using 1m-long PVC tubes and a portable ceramic-tipped tensiometer. Chadde et al. (1988) recorded other soil-water characteristics (conductivity, pH, dissolved-oxygen content) and physical features (elevation, aspect, topographic position) for each willow plot.

To develop a classification, Chadde et al. (1988) grouped sample plots into sets based on floristic similarities in both overstory and undergrowth layers. Information on soil and site characteristics allowed them to place community groupings along environmental and successional gradients. They also defined associations or stable communities in equilibrium with environmental conditions, as well as seral community types. They inferred grazing relationships for each community from field observations of browsing levels and from previously published studies on palatability and browsing response. I used the data collected by Chadde et al. (1988) and Brichta (1987) to evaluate the condition, trend, and successional status of willow communities inside and outside exclosures, as well as throughout Yellowstone's northern range.

Deciduous Shrubs and Berry Production

At selected exclosures, I made additional line-intercept measurements to obtain more precise canopy-coverage estimates for deciduous shrubs. In addition, I recorded the height, crown length, crown width, and number of berries on individual serviceberry and chokecherry plants inside and outside selected exclosures. All shrubs within the Camp Creek, Uhl Hill, and East Elk Refuge exclosures were

measured in this manner. Outside those exclosures, I delineated an adjacent comparable area and measured all shrubs. Because the Mammoth exclosure contained a great many buffaloberry plants, I measured 60 randomly selected shrubs inside and 60 outside. At the Lamar-West exclosure, I measured a random sample of serviceberry and chokecherry plants inside and all individuals of those species on an adjacent outside area.

For plants which appeared to have less than 400 berries, I counted all berries. I divided plants which appeared to have greater than 400 berries but less than 2,000 into quarters and randomly selected a quarter on each. All berries within that quarter were counted and that number multiplied by four to estimate total berries on each plant. Plants appearing to have more than 2,000 berries were divided into eighths and an eighth randomly selected on each. All the berries on that eighth were counted and that count was multiplied by eight to estimate total berries. I counted berries while green to minimize removals by birds (Schopmeyer 1974, Stiles 1980, Robinson 1986, Willson 1986) or bears. Except for the Camp Creek, Lamar-West, and Mammoth exclosures, I only measured shrubs in the understories of aspen stands. I sampled the Lamar-West exclosure in 1989, the others during 1987.

A few chokecherry plants on Yellowstone's northern range are beyond the reach of elk. On those plants, a few tall central stems are typically surrounded by a larger number of lower, repeatedly browsed stems. To measure the effect of browsing on berry production of individual plants, I recorded the number of berries for all stems above and below the browse height (2.5 m) on each plant. I measured plants near the park highway east of Slough Creek in this manner during 1989.

Willow Seed Production

During spring 1989, I recorded the number of willow aments (catkins) on permanent willow belt transects outside the Mammoth,

Junction Butte, Lamar-East, and Lamar-West exclosures (see Willow Exclosures). Large areas of potential willow habitat (Chadde et al. 1988) adjacent to these exclosures were also searched for willow aments and those numbers recorded. Inside the exclosures, male and female aments were counted using m^2 plots and a 2.5m step-ladder.

Whenever possible, I sampled willows on the inside belt transects, but in most instances I also measured some plants adjacent to the permanent belt transects to obtain an adequate sample. Most willows inside the exclosures produced aments, but it was easier to count aments on plants which were in full flower at the time they were sampled. Furthermore, my equipment did not allow the sampling of plants taller than 3.5m. I recorded the sex of all willows on and adjacent to the permanent belt transects.

I sampled only major willow species (Chadde et al. 1988) inside the exclosures, including Salix bebbiana, S. boothii, S. lutea, and S. geyeriana. For those species, I counted the number of mature fruits on 60 female aments which I collected from each exclosure. I then air-dried those aments in the laboratory and counted the number of seeds in 10 fruits from each species-exclosure. I had planned to make comparable measurements on female aments collected outside exclosures, but ament production outside was nonexistent.

As part of another study, Chadde et al. (1988), constructed two small exclosures (2x4m) in 1986 adjacent to each of the exclosures at Mammoth and Junction Butte so that the older exclosures and the mini-exclosures had one side in common. A trench 0.5m deep was dug along that side and a plastic barrier installed to sever all root connections with plants in the older exclosure. Willow stems < 30cm tall were present inside each mini-exclosure when they were erected (S. Chadde, pers. commun. 1989). I counted all the aments inside the mini-exclosures in 1989 after three seasons of protection.

A few willows and other shrubs on the northern range are beyond

the reach of elk. On those plants, a few tall central stems are usually surrounded by a larger number of lower, repeatedly browsed stems. Several of these "mushroom" willows exist near Geode Creek. To measure the effect of browsing on ament production of individual plants, I recorded the number of male or female aments on all stems above and below the browse height (2.5m) on each willow. I also gathered similar data on river birch near the Mammoth exclosure. These measurements were taken in 1989.

Balsamroot

In 1988, I counted the number of flowers on balsamroot (Balsamorhiza sagittata) plants in Yellowstone Park at 9 different locations along the old Mammoth to Gardiner road and outside the park at 9 separate sites in Eagle Creek (see Aspen Study Areas above) near Forest Service Road 3243. I counted the number of flowers on 150 plants with crown diameters > 30cm at each of the 18 sites. Elk, mule deer, and pronghorn antelope were common in this portion of the park prior to and during sampling, but were rare in Eagle Creek.

Historical Evidence

Murie (1940), Gruell (1973), and Houston (1982) used accounts left by early explorers to estimate the relative abundance of elk throughout the Greater Yellowstone Ecosystem prior to 1872. Those authors quoted from historic journals but did not make a detailed analysis of first-person journals on a continuous basis.

To avoid problems of bias and obtain an accurate reflection of the observations contained in early historic journals, I completed a continuous-time analysis of all first-person accounts for the Greater Yellowstone area for the years 1835-1876. This included the following journals (1) Osborne Russell (1965) for the years 1835-39; (2) William Raynolds (1868) -- 1860; (3) Walter Delacy (1876) -- 1863; (4) Bart

Henderson (1867) -- 1867; (5) Cook-Folsom-Peterson Expedition (Cook et al. 1965) -- 1869; (6) Bart Henderson (1870) -- 1870; (7) Washburn Expedition (Gillette 1870, Doane 1875, Langford 1972) -- 1870; (8) Barlow-Heap Expedition (Barlow and Heap 1872) -- 1871; (9) Hayden survey (1872) -- 1871; (10) Frank Bradley (Bradley 1873) -- 1872; (11) Sidford Hamp (Brayer 1942) -- 1872; (12) William Blackmore (1872) -- 1872; (13) Jones Expedition (Jones 1875) -- 1873; (14) Earl of Dunraven (Dunraven 1967) -- 1874; (15) William Ludlow (Ludlow 1876) -- 1875; (16) General Strong (Strong 1968) -- 1875; and (17) Doane Expedition (Doane 1876, Server 1876-77) -- 1876. I systematically recorded all observations on ungulates, vegetation, beaver, predators, or other factors bearing on the "natural regulation" paradigm.

Beaver

During the early 1920s, Warren (1926) conducted a detailed study of beaver around Tower Junction on Yellowstone's northern range. His report contained extensive photographs, as well as scale drawings of all of the beaver workings which he studied. Jonas (1955) repeated Warren's study in the early 1950s. Because of the detail in Warren's report, I was able to relocate all his beaver study sites and to repeat his photographs during 1986-88.

I located Warren's original negatives in the archives of the College of Environmental Science and Forestry, State University of New York at Syracuse and Robert Jonas permitted me to use his original negatives. This enabled me to complete several sets of multi-image repeat photographs which contained images from the 1920s, 1950s, and 1986-88. Furthermore, early governmental reports and historic journals were searched to obtain information on the abundance of beaver in and around Yellowstone Park from 1835 to 1876.

Archaeological Evidence

Houston (1982) and Boyce (1989) cited archaeological evidence to support their contention that thousands of elk always wintered on Yellowstone's northern range and in Jackson Hole. To determine the relative abundance of ungulate species in pre-Columbian times, I reviewed published archaeological reports for sites in and adjacent to Yellowstone Park, for sites in Jackson Hole and, to achieve maximum sample size, for sites throughout the Intermountain West including Montana, Wyoming, Idaho, Washington, Utah, Nevada, and Oregon. In all, I reviewed more than 500 studies. I also conducted an extensive review of the archaeological literature on site formation processes so that I could make informed interpretations from the available archaeological record. Taphonomic and transportation questions were given major consideration. Moreover, I reviewed all ethnographic material for Shoshone and other Intermountain tribes, with particular reference to whether or not Native Americans could or would choose to kill elk.

Many recent archaeological excavations have been salvage projects mandated under Federal antiquities laws. Unfortunately, most of those studies have only appeared in the "grey literature," if at all (Frison 1984). To ensure that my evaluation of archaeological evidence was as complete and up-to-date as possible, I interviewed, in person, the following leading archaeologists from the Intermountain West (1) Mark Bammer, Montana State Archaeologist; (2) Dee Taylor, University of Montana; (3) Thomas Green, Idaho State Archaeologist; (4) Jerry Galm, Eastern Washington University; (5) Frank Leonhardy, University of Idaho; (6) Carl Gustafson, Washington State University; (7) Alston Thoms, Center for Northwest Anthropology; (8) Greg Cleveland, Yakima Indian Nation; (9) Morris Uebecacker, Yakima Indian Nation; (10) Ken Reid, Washington State University; (11) Max Pavesic, Boise State University; (12) Susan Miller, Idaho State University; (13) Rich Holmer, Idaho State University; (14) James O'Connell, University of Utah; (15) Duncan

Metcalfe, University of Utah; (16) David Madson, Utah State Archaeologist; (17) Dan Walker, Assistant Wyoming State Archaeologist; (18) George Frison, University of Wyoming; (19) Charles Reher, University of Wyoming; (20) Steve Craesman, Western Wyoming College; (21) Anthony Swenson, Wyoming State Cultural Records Office; and (22) Tom Roll, Montana State University.

In addition, I contacted by letter or telephone the following archaeologists whom I could not interview in person: (1) Lee Lyman, University of Missouri-Columbia; (2) Leslie Davis, Montana State University; (3) Gary Wright, State University of New York at Albany; and (4) Donald Grayson, University of Washington.

I obtained approximately 20,000 pages of archaeological reports from all of these experts.

Statistical Tests

According to Hurlbert (1984), comparison of the vegetation inside and outside of a single exclosure can constitute pseudo-replication. The transects and the individual plants are not homogeneous and some measure of variance is necessary to evaluate the adequacy of sampling procedures. Statistical tests on data collected inside and outside one exclosure only indicate that the vegetation is different at that site. Statistical tests using each exclosure as a sample point are true replicates and those results are more conclusive. My statistical results should be viewed with these concepts in mind. Where appropriate, I compared sample means using student's t-test and reported the p values (Sokal and Rohlf 1981). Data expressed as percent (mainly canopy-coverage) were transformed using arc sine transformation prior to the computation of statistical tests (Sohal and Rohlf 1981). The chi-square test for goodness of fit was used to compare expected and observed values (Sokal and Rohlf 1981).