CHAPTER IV
ASPEN EXCLOSURES

INTRODUCTION

Exclosures can be used to study the successional status and trend of plant communities, as well as to evaluate the impact of grazing (Barmore 1968a, Laycock 1975). Exclosures can also be used to evaluate climatic effects since the general climate[1] is the same within the exclosures and on adjacent outside plots. I measured aspen communities inside and outside 14 exclosures throughout the Greater Yellowstone Ecosystem (Table 3, Fig. 3). I then analyzed those data to determine (1) whether the aspen stands were seral or climax, (2) whether climatic variation was important in their regeneration, and (3) what impact ungulate grazing has had on those plant communities.

RESULTS AND DISCUSSION

Aspen Stem Heights

Over the years the Park Service and Forest Service collected data on the number of aspen stems and their heights at eight exclosures. They usually did not record DBH of individual stems. The only parameters the agencies calculated from their data were stem density and average stem height. Unfortunately, both of those statistics are of minimal value in evaluating long-term vegetation changes within aspen communities.

If an aspen stand is composed of mature overstory trees and small, recently sprouted suckers, the mean height of those two classes combined tells little about the height distribution of the stems in the stand.

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[1]According to the Random House College Dictionary (1988) climate is defined as "1. the composite or generally previling weather conditions of a region as temperature, barometric pressure, humidity, precipitation, sunshine, cloudiness, and winds, throughout the year, averaged over a series of years."

This is evident for Range Plot 10 (Table 14) where the average height was 152cm in 1939 and only 211cm 26 years later. Yet repeat photographs (Fig. 6) clearly show that stand height distribution over that period was much greater than the average height parameter would indicate.

At the Upper Slide Lake, Mammoth, Junction Butte, and Lamar-West exclosures, the average height of all protected aspen stems increased over time (Tables 14 and 15). Inside the Lamar-East exclosure, the average height increased up to 1981 after which it declined due to the growth of a large number of new suckers (Table 16). If only aspen stems greater than 2m tall are considered, the average height increased inside all exclosures. Aspen outside all exclosures failed to increase in height and all stems which grew after the date of exclosure establishment are < 1m tall (Tables 14 and 15).

Aspen Stem Densities

The number of live aspen stems per m^2 both inside and outside the exclosures (Tables 14-16) varied over the years with little apparent trend. Park Service biologists contend that elk are having little significant impact on aspen because the number of stems has not systematically declined outside the exclosures (Despain et al. 1986:79). However, the number of individual aspen stems taken alone is not an appropriate measure of ecological conditions in the stand (Milner 1977). Density measurements are appropriate only when individual plants are similar. A 20m tall, 20cm DBH tree is not ecologically equivalent to a 1m tall aspen sucker. Many of the density measurements inside the exclosures have actually decreased over time. Hart (1986:16) noted that density-dependent competition for space and other resources can be expected to lower densities inside exclosures as stands develop. Milner (1977) found that shrub and aspen stem densities often were greater outside exclosures and concluded that density measurements provide little meaningful information unless accompanied by size-class data.

Table 14. Aspen stem density and stem height inside and outside Range Plots 10, 16, and 25. Park Service data 1935-1965.

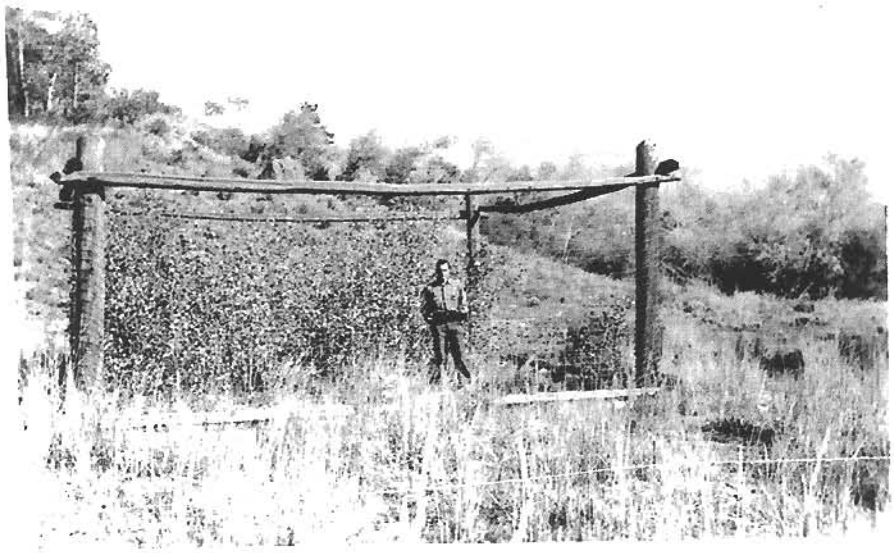
Exclosure	Mean number of live stems per m^2 by year											
	1935	1936	1937	1938	1939	1940	1941	1943	1962	1965	1986	1987
Range Plot 10												
Inside	4.56	5.81	5.93	5.35	5.25	4.93	4.47	4.22	----	2.10	0.98**	----
Outside	2.37	2.10	2.00	0.78	0.29	0.15	0.05	0.00	----	0.12	1.90	----
Range Plot 16												
Inside	2.74	3.79	3.66	2.80	2.23	----	----	----	1.13	----	----	0.86
Outside	3.39	3.42	2.42	3.20	3.44	----	----	----	2.83	----	----	1.05
Range Plot 25												
Inside	----	2.22	3.23	2.51	2.42	2.71	3.45	2.98	----	2.24	2.13	----
Outside	----	3.86	3.59	1.93	1.03	1.48	0.99	0.76	----	5.96	3.74	----
	Mean stem height (cm) by year											
Range Plot 10												
Inside	38	66	104	132	152	175	208	*	--	211	521**	--
Outside	36	36	33	25	38	46	46	*	--	38	43	--
Range Plot 16												
Inside	41	43	56	66	71	--	--	--	99	--	--	419
Outside	33	28	36	41	23	--	--	--	38	--	--	18
Range Plot 25												
Inside	--	*	*	*	*	*	*	*	--	*	844	--
Outside	--	*	*	*	*	*	*	*	--	13	10	--

* Original data are missing from Park Service files (F. Singer, pers. commun. 1986).

** Disease recently killed 28 trees > 10cm DBH (J. Hart, pers. commun. 1987) which are not included.

Fig. 6. Range Plot 10 north of Mammoth on Yellowstone's northern range. (a) Exclosure was built in 1934 the year this photograph was taken. NPS photo 14,082-3. (b) Aspen regeneration after five years protection; mean height 152cm. NPS photo 15,156-2, 9/39. (c) Aspen regeneration after 31 years protection; mean height 211cm. Though the average height only increased 59cm in 26 years, clearly stand development over that period was much greater than the average height parameter would indicate. Wooden posts were replaced with metal posts prior to the 1965 photo. NPS photo 65-582, 8/6/65.

a.



b.

c.

Table 15. Aspen stem density and stem height inside and outside Upper Slide Lake exclosure. Forest Service data 1961-1968 from Thornton (1969).

Transect	1961	1962	1963	1964	1965	1966	1967	1968	1987
	Mean number of live stems per m^2 by year								
Inside*									
No. 1	0.47	0.52	0.58	0.65	0.65	0.71	0.73	0.71	0.50
No. 2	1.33	1.46	1.64	1.87	1.96	1.61	1.68	1.72	1.53
Outside									
No. 3	----	----	----	0.17	0.26	----	----	0.52	0.50
No. 4	----	----	----	1.18	1.33	----	----	1.18	2.41
	Mean stem height (cm) by year								
Inside									
No. 1	46	71	92	129	159	185	214	241	276**
No. 2	59	81	100	128	146	176	204	228	153**
Outside									
No. 1	--	--	--	20	33	--	--	21	38
No. 2	--	--	--	21	43	--	--	30	54

* From 1961-1968 all ungulates were excluded. The fence was not repaired after 1968, allowing ungulates into the exclosure for several years prior to the 1987 measurements.

** Many trees > 2m were recently killed by disease, and new sprouts subsequently appeared, both have lowered mean height.

Table 16. Aspen stem density and stem height inside and outside Mammoth, Junction Butte, and Lamar exclosures. Park Service data 1957-1981.

	Mean number of live stems per m^2 by year					
Exclosure	1958	1962	1965	1974	1981	1986
Mammoth						
Inside	1.68	0.80	0.75	0.54	0.41	0.41
Outside	3.04	0.93	1.51	1.59	0.62	1.33
Junction Butte						
Inside	----	0.66	0.63	0.40	0.57	0.63
Outside	----	1.15	1.09	1.23	0.92	0.49
Lamar-East						
Inside	0.86	0.95	0.69	0.54	0.52	1.05
Outside	1.08	1.01	1.16	1.05	0.65	2.65
Lamar-West*						
Inside	----	0.15	0.02	0.19	0.17	0.43
	Mean stem height (cm) by year					
Mammoth						
Inside	58	91	104	211	246	353
Outside	38	25	33	38	28	25
Junction Butte						
Inside	--	25	86	229	318	470
Outside	--	20	38	18	15	13
Lamar-East						
Inside	66	109	208	485	678	389
Outside	41	38	41	25	43	23
Lamar-West*						
Inside	--	28	0**	46	180	297

* There is no permanent outside plot; see Chapter 2 above.

** Excluding one old tree which was present at time the exclosure was established.

Furthermore, at most exclosures, aspen protected from browsing likely produced root suckers outside the exclosures. There were no mature aspen or stems > 1m tall outside several exclosures. If the protected aspen root suckered into outside exclosure plots, as they undoubtedly did at Range Plots 10, 16, 25, and Junction Butte, then the protected aspen may have affected sucker densities on adjacent outside plots.

Aspen-stem Size Classes

The data collected by the Park Service during the 1960s at Range Plots 10, 16, and 25 can be partitioned into size classes and compared with data I collected in 1986-87 (Table 17). When analyzed in this manner, differences due to the exclosures are apparent. Except for the three aspen protected by the fence at Range Plot 25 (see below), all aspen regeneration exposed to ungulates is less than 1m tall (Table 14). Protected aspen have grown into mature trees, and all size classes are represented.

My measurements of aspen size-class stem densities and estimated conifer canopy cover inside and outside all exclosures are presented in Table 18. Aspen stands inside exclosures had a significantly different size-class stem distribution than aspen outside exclosures ($\underline{p} < .001$, Hotelling's T^2 test)(Kendall 1980). At all but one, East Elk Refuge, there were more stems < 2m tall per unit area outside than inside. This was not unexpected since larger aspen often suppress new suckers (Schier et al. 1985). All stands protected from ungulate browsing produced stems > 2m tall, and most developed multiple size classes characteristic of stable or climax aspen. In only two instances, Goosewing and Soda Lake, did aspen outside exclosures produce ramets > 2m tall. Even in those cases, there were significantly greater stem densities (> 2m tall but < 20 cm DBH) inside the exclosures.

The Goosewing exclosure is located approximately 100m south of the

Table 17. Aspen size-class distribution inside and outside Range Plots 10, 16, and 25. Park Service data 1962 and 1965 compared with data collected in 1986.

	Percent of total stems			
	1965		1986	
Exclosure	Outside	Inside	Outside	Inside
Range Plot 10				
Aspen size classes				
< 2m	100	19	100	0
> 2m, ≤ 5cm DBH	0	29	0	36*
6-10cm DBH	0	27	0	12*
11-20cm DBH	0	25	0	52*
> 20cm DBH	0	0	0	0
Range Plot 25				
Aspen size classes				
< 2m	98	49	96	33
> 2m, ≤ 5cm DBH	0	11	0	17
6-10cm DBH	2**	18	0	17
11-20cm DBH	0	20	4**	16
> 20cm DBH	0	2	0	18

	1962		1987	
	Outside	Inside	Outside	Inside
Range Plot 16				
Aspen size classes				
< 2m	100	94	100	19
> 2m, ≤ 5cm DBH	0	3	0	41
6-10cm DBH	0	3	0	34
11-20cm DBH	0	0	0	6
> 20cm DBH	0	0	0	0

* Excluding 28 trees > 10cm DBH recently killed by disease.

** Stems are in physical contact with the exclosure fence which has prevented elk from killing them; see text.

Table 18. Aspen stem densities and estimated conifer canopy cover inside and outside 14 Yellowstone exclosures.

Exclosure*	Area sampled (m^2)	Mean number of live stems per m^2 by size classes					Estimated percent conifer canopy cover
		< 2m	> 2m, ≤ 5cm DBH	6-10cm DBH	11-20cm DBH	> 20cm DBH	
1. Mammoth							
Inside	106	0.15	0.16	0.35	0.02	0.00	< 5%
Outside	106	3.40	0.00	0.00	0.00	0.07	> 5%
2. Junction Butte							
Inside	95	0.11	0.26	0.49	0.15	0.00	None
Outside	95	0.49	0.00	0.00	0.00	0.00	None
3. Lamar-East							
Inside	106	0.63	0.37	0.27	0.06	0.00	< 1%
Outside	106	1.91	0.00	0.00	0.01	0.04	None
4. Lamar-West							
Inside	106	0.12	0.29	0.09	0.00	0.00	None
Outside	60	1.63	0.00	0.00	0.00	0.03	None
7. Range Plot 10							
Inside	41	0.00	0.51	0.12	0.34	0.00	None
Outside	41	1.90	0.00	0.00	0.00	0.00	None
16. Range Plot 16							
Inside	37	0.16	0.35	0.30	0.05	0.00	> 15%
Outside	37	1.05	0.00	0.00	0.00	0.00	None
8. Range Plot 25							
Inside	45	0.70	0.36	0.36	0.34	0.38	None
Outside	22	3.00	0.00	0.00	0.13	0.00	None

Table 18. (cont.)

14. Porcupine							
Inside	180	0.44	1.12	0.58	0.07	0.03	< 1%
Outside	180	1.80	0.00	0.00	0.00	0.02	None
15. Crown Butte							
Inside	180	0.07	0.47	0.19	0.13	0.03	< 1%
Outside	300	0.93	0.00	0.00	0.00	0.03	< 5%
12. Uhl Hill							
Inside	218	0.06	0.09	0.09	0.00	0.00	< 1%
Outside	180	0.09	0.00	0.00	0.00	0.00	None
9. East Elk Refuge							
Inside	1100	2.30	0.05	0.03	0.03	0.01	None
Outside	60	1.28	0.00	0.00	0.10	0.00	None
10. Upper Slide Lake							
Inside	93	0.40	0.20	0.09	0.00	0.01	> 50%
Outside	93	1.45	0.00	0.00	0.00	0.00	None
11. Goosewing							
Northwest corner							
Inside	120	0.34	0.95	0.12	0.03	0.07	< 1%
Outside	120	0.21	0.25	0.00	0.03	0.01	< 1%
South side							
Inside	120	0.58	0.78	0.53	0.22	0.06	< 1%
Outside	120	2.49	0.20	0.00	0.03	0.03	< 1%
Northeast corner							
Inside	120	1.05	1.09	0.46	0.06	0.03	< 5%
Outside	120	1.84	0.87	0.00	0.00	0.08	< 5%

Table 18. (cont.)

Entire exclosure							
Inside	360	0.66	0.94	0.37	0.10	0.05	< 2%
Outside	360	1.51	0.44	0.00	0.02	0.04	< 2%
18. Soda Lake							
Inside	180	0.02	0.52	0.27	0.05	0.02	None
Outside	300	0.89	0.03	0.03	0.04	0.01	None
	n						
Total							
Inside	14	0.48	0.41	0.26	0.10	0.04	
Outside	14	1.52	0.03	0.002	0.02	0.02	
t		4.52	4.22	6.45	2.45	0.70	
p		< .01	< .01	< .01	< .05	NS	
Total-(11+18)							
Inside	12	0.43	0.35	0.25	0.10	0.04	
Outside	12	1.58	0.00	0.00	0.02	0.02	
t		3.37	4.17	4.63	2.10	0.59	
p		< .01	< .01	< .01	< .10	NS	
	n			Constancy			
Total							
Inside	14	93	100	100	79	50	
Outside	14	100	14	7	36	50	
Total-(11+18)							
Inside	12	92	100	100	75	42	
Outside	12	100	0	0	25	42	

* Exclosure numbers correspond to those given in Table 3 and Fig. 3.

main Gros Ventre road (USFS 015). The Gros Ventre road is not plowed during winter, but is open to snow machine use. In recent years, snowmobile travel over this road increased approximately 300-400% (G. Roby, pers. commun. 1987). Aspen regeneration > 2m tall outside the Goosewing exclosure is a relatively recent phenomenon. Outside, ramets have had insufficient time to attain the next larger size class (6-10cm DBH) while those inside have grown into larger size classes (Table 18). Apparently, human disturbance limits elk use close to roads which allows nearby aspen stands to produce stems > 2m tall. Gruell and Loope (1974:21) reported a similar pattern of aspen regeneration near roads in Jackson Hole. Other studies have shown elk avoid areas of human disturbance and especially open roads (Ward 1973; Ward et al. 1976; Lyon 1979a, 1979b, 1980, 1983, 1984a, 1984b; Leege 1984; Lyon et al. 1985; Witmer and De Calesta 1985).

Conifer Invasion

As noted in Chapter 3, the presence of a limited number of conifers is insufficient evidence on which to classify an aspen stand as seral (Hoffman and Alexander 1980:25). Conifers must be prominent, not merely present (Mueggler 1985). Occasional conifers can be found in basically stable aspen communities. "An uneven-aged conifer understory generally is reliable evidence of a seral aspen site" (Mueggler 1985:46).

Aspen stands must have 5 to 10% conifer canopy cover before they are considered fast-seral (Mueggler 1988). Based on this criterion, aspen inside and outside the Mammoth exclosure are probably seral (Table 18). Aspen inside the Upper Slide Lake exclosure is definitely seral. The other exclosures contained only a few conifers, which suggests that those stands are probably stable. Range Plot 16 contained approximately 15% conifer canopy cover, but 8 of 10 trees were 5-needle white pines. Mueggler (1988:79) identified an aspen-limber pine community type, but doubted that limber pine would ever become dense enough to suppress aspen. Clark's nutcrackers (Nucifraga columbiana) disseminate seeds of limber and white-bark pine (Lanner and VanderWall 1980, Hutchings and Lanner 1982, Arno and Hoff 1989) and probably are responsible for "planting" then in aspen stands throughout this region. This makes it questionable to denote aspen within Range Plot 16 as seral. Except at Mammoth, none of the aspen stands outside the exclosures are fast-seral. Most appear to be potentially stable or climax based on the absence of significant conifer encroachment.

Understory Canopy-Coverage

Data on understory canopy-coverage inside and outside all exclosures are presented in Tables 63-76 (Appendix B). At all exclosures, there were major differences in understory species composition between inside and outside plots. This difference was especially pronounced at exclosures where the inside and outside plots were located within the same aspen clone. This included Range Plots 10, 16, and 25, Junction Butte, Porcupine, Uhl Hill, Soda Lake, and Goosewing. The vegetation inside and outside these exclosures were often designated as different aspen community types according to the dichotomus keys of Youngblood and Mueggler (1981) and Mueggler (1988).

On average, shrubs predominate in the understory inside exclosures, though forbs and a few grasses were present. In areas exposed to elk and other ungulates, there were substantially fewer shrubs and those sites were dominated by grasses (Table 19). A large proportion of those grasses were non-native species, such as timothy or Kentucky bluegrass, which tend to increase under grazing pressure (Mueggler 1988). In the Yellowstone Park sampling plots, timothy and Kentucky bluegrass had an average canopy-coverage of 56.1% outside exclosures and 18.6% inside ($\underline{t}$ = 3.47, $\underline{p}$ < .01, arcsine transformed data).

Table 19. Mean canopy-coverage of understory plants found inside and outside 14 aspen exclosures in the Greater Yellowstone Ecosystem.

	Mean (SEM) percent canopy-coverage			
Vegetation class	Inside	Outside	*t**	*p*
Shrubs	68 (9)	22 (5)	3.78	< .01
Forbs	25 (4)	29 (4)	0.50	NS
Grasses	15 (3)	48 (6)	4.06	< .01

*Arcsine transformed data.

While the difference between average percentage of forbs in understories inside and outside exclosures was not statistically significant (Table 19), there were major differences in species composition. Forbs which tend to decrease under grazing or trampling such as Epilobium augustifolium, Thalictrum fendleri, and Smilacina stellata averaged 14.9% canopy-coverage inside exclosures and 3.0% outside (t = 2.70, p < .02, arcsine transformed data). Forbs more resistant to grazing like Geranium spp. and Fragaria virginiana averaged 8.2% canopy-coverage inside exclosures and 17.2% outside (t = 2.50, p < .02, arcsine transformed data).

At only one exclosure, East Elk Refuge, had agency personnel established a permanent system to measure understory species over time. Those data (Table 20) indicate that inside the exclosure shrubs increased and forbs and grasses declined. Highly palatable species such as serviceberry and chokecherry increased from 0.5% to 39.5% average canopy-coverage.

Unfortunately, the Forest Service did not establish outside plots for comparison. However, I sampled the entire exclosure and comparable areas immediately adjacent on the south and north. I recorded 91% shrub canopy-coverage inside and 27% outside (Table 21). Repeat photographs (Kay unpub. data) support the conclusion that shrubs increased inside this exclosure while remaining relatively static outside. Based on photographic evidence, grasses dominated outside when the exclosure was established as they do today.

Ungulate-induced reductions in shrub canopy-coverage and growth have been reported over a wide range of habitat types (Graham 1958, Beals et al. 1960, Gysel 1960, Klein 1965, Pimlott 1965, Ross et al. 1970, Mueller-Dombois and Spatz 1975, Janke 1976, Milner 1977, Anderson and Loucks 1979, Bobek et al. 1979, Trottier and Fehr 1982, Allen et al. 1984, Pojar and Banner 1984, Frelich and Lorimer 1985, Brandner 1986, Kroll et al. 1986, Hanley 1987, Risenhoover and Maass 1987, Stewart et

Table 20. Shrub canopy-coverage inside the East Elk Refuge exclosure 1952-1987. Forest Service data 1952-1967 Parker three-step method. 1987 measurements by line intercept.

Transect and species	Percent canopy-coverage by year			
	1952	1959	1967	1987
G-09				
<u>Artemisia</u> <u>tripartita</u>	2	4	2	0
<u>Symphoricarpos</u> <u>oreophilus</u>	9	7	6	5
<u>Rosa</u> <u>woodsii</u>	8	10	17	43
<u>Chrysothamus</u> <u>nauseosus</u>	3	2	0	1
<u>Chrysothamus</u> <u>viscidiflorus</u>	0	0	4	0
<u>Prunus</u> <u>virginiana</u>	1	3	8	35
<u>Ribes</u> spp.	0	3	8	22
<u>Amelanchier</u> <u>alnifolia</u>	0	0	2	16
Subtotals	23	29	47	122
G-010				
<u>Artemisia</u> <u>tripartita</u>	0	0	3	2
<u>Symphoricarpos</u> <u>oreophilus</u>	18	19	20	22
<u>Rosa</u> <u>woodsii</u>	6	8	16	49
<u>Chrysothamus</u> <u>nauseosus</u>	11	5	0	10
<u>Chrysothamus</u> <u>viscidiflorus</u>	0	2	15	0
<u>Prunus</u> <u>virginiana</u>	0	0	2	11
<u>Tetradymia</u> <u>canescens</u>	1	1	1	0
<u>Amelanchier</u> <u>alnifolia</u>	0	2	2	17
Subtotals	36	37	64	111

Table 21. Shrub canopy-coverage inside and outside the East Elk Refuge exclosure as measured by line-intercept. 244m outside, 288m inside.

Species	Mean (SD) percent canopy-coverage	
	Inside (n=9)	Outside (n=8)
Prunus virginiana	11.9 (14.2)	0.9 (1.5)
Symphoricarpos oreophilus	16.2 (11.7)	1.4 (2.3)
Artermisia tripartita	5.1 (6.1)	4.2 (3.4)
Rosa woodsii	31.9 (12.1)	10.0 (9.4)
Chrysothamus nauseosus	6.8 (5.2)	8.1 (4.9)
Chrysothamus viscidiflorus	0.6 (1.2)	1.1 (1.4)
Amelanchier alnifolia	13.0 (13.9)	0.4 (1.1)
Tetradymia canescens	0 (0)	0.5 (1.1)
Ribes spp.	3.5 (7.0)	0.4 (0.7)
Lonicera involucrata	1.6 (3.8)	0 (0)
Artermisia tridentata	0.1 (0.4)	0.2 (0.7)
Totals	90.8 (34.9)	27.2 (10.7)

al. 1987, Takatsuki 1987, Alverson et al. 1988, Pastor et al. 1988, Putman et al. 1989, Tilghman 1989, Veblen et al. 1989). Others have concluded that grazing by elk limits shrubs and favors grasses (Tiedemann and Berndt 1972, Hanley and Taber 1980, Edgerton 1987).

Repeat Photographs

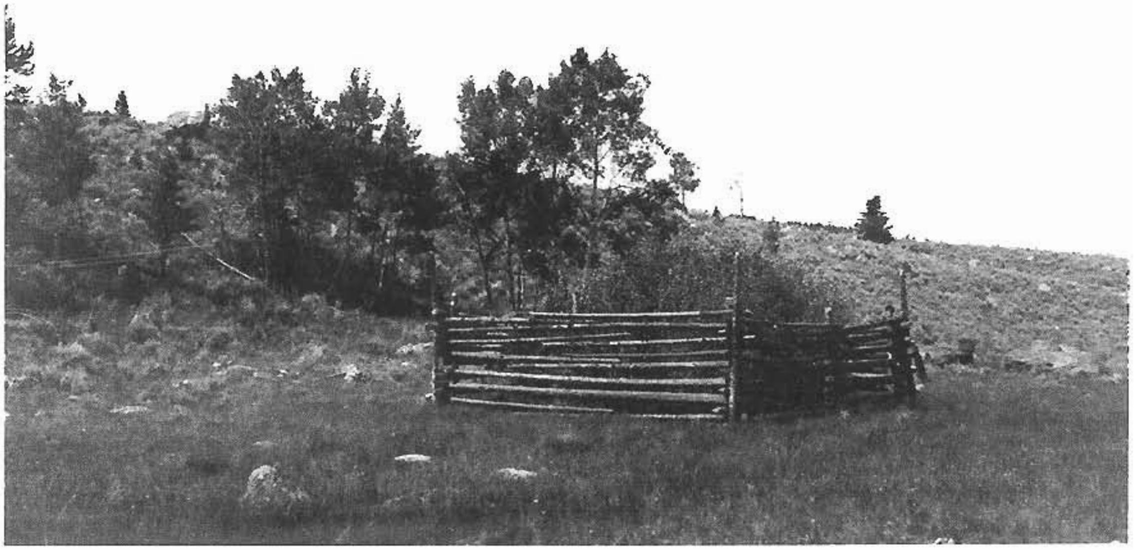
I located old photos for all but the Uhl Hill exclosure. I found photos of outside permanent plots or adjacent aspen stands for all exclosures in Yellowstone plus Porcupine, Upper Slide Lake, and Crown Butte. I rephotographed all of those sites.

During the late 1800s and early 1900s, hay was cut and stored in Yancy's Hole on Yellowstone's northern range to feed draft animals. With the advent of motorized transportation, those storage facilities fell into disuse. During the late 1920s, a stand of young aspen grew up inside an abandoned hay corral where entry by elk and other ungulates was prevented (Fig. 7a). As an experiment, the Park Service removed the protective corral and exposed half the aspen to browsing in 1936. The other half was protected by an exclosure called Range Plot 25 (Fig. 7b). That stand was approximately 12 years old in 1936 (Barmore 1965:5).

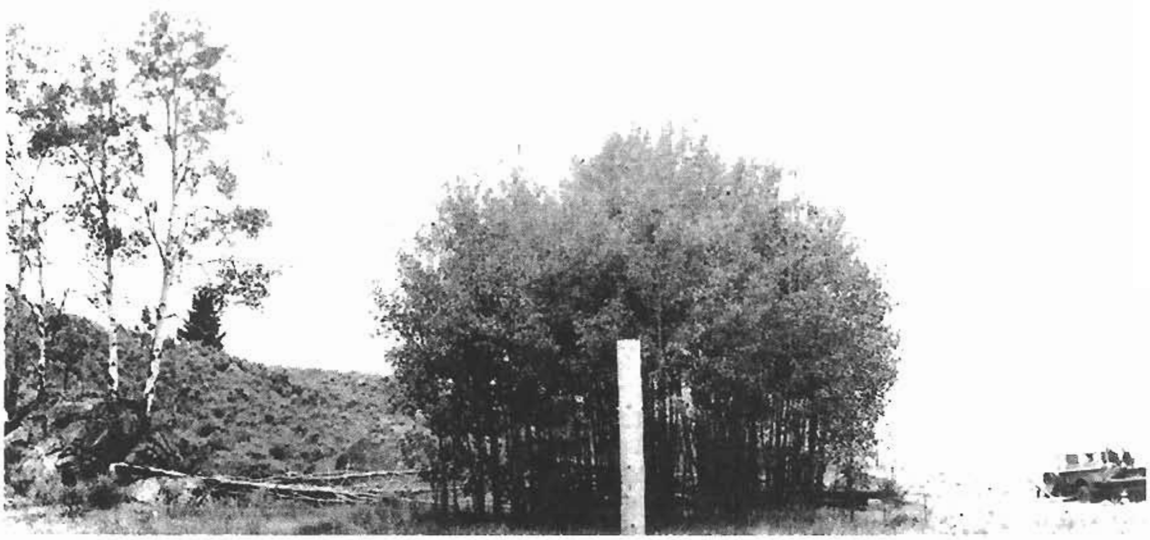
Within 1 year, all aspen exposed to ungulates had been high-lined (Fig. 7c). Of the original 86 stems exposed to browsing, all but five were dead by 1941 despite the fact their terminal leaders were beyond the reach of elk (Barmore 1965:5)(Fig. 7d). The elk killed the aspen by bark wounding and stripping (Krebill 1972, DeByle 1985a, Hart 1986). The three original stems which were alive outside Range Plot 25 in 1986 all had one side of their trunks in contact with the exclosure wire. This prevented elk from eating the bark on that portion of the trunk (Barmore 1965:5). Over the years, aspen inside Range Plot 25 expanded to fill the entire exclosure while individual stems increased in height. By 1986, many trees were taller than 20m and over 20cm DBH (Fig. 7e).

The following conclusions are based on visual evaluation of these

Fig. 7. Range Plot 25 near Yancy's Hole on Yellowstone's northern range from 1932 to 1986. (a) Aspen regeneration which volunteered inside an old, unused hay corral. NPS photo 51,048, 7/32. (b) As an experiment, the Park Service took down that hay corral and built Range Plot 25 in its place with one-half the aspen stand exposed to elk browsing and the other half protected. This photo was taken during construction of Range Plot 25 and is a view north down what became the west side of the exclosure. The aspen to the right of the post were protected by the exclosure while the stems to the left were open to elk. NPS photo 52,386, 1936.

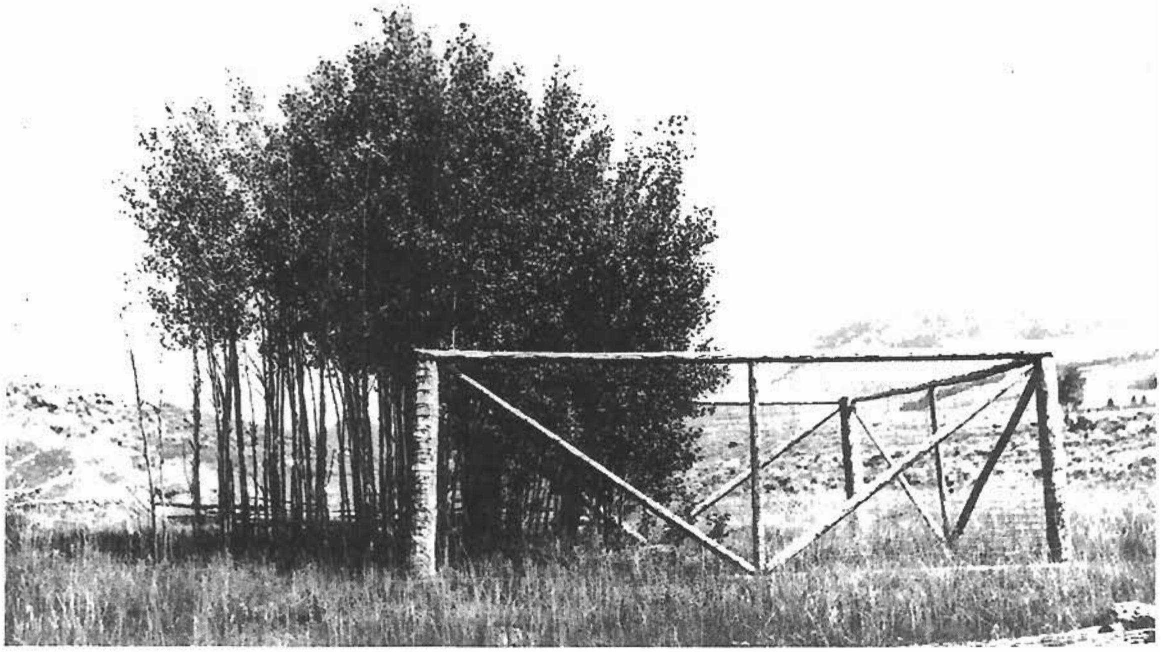


a.



b.

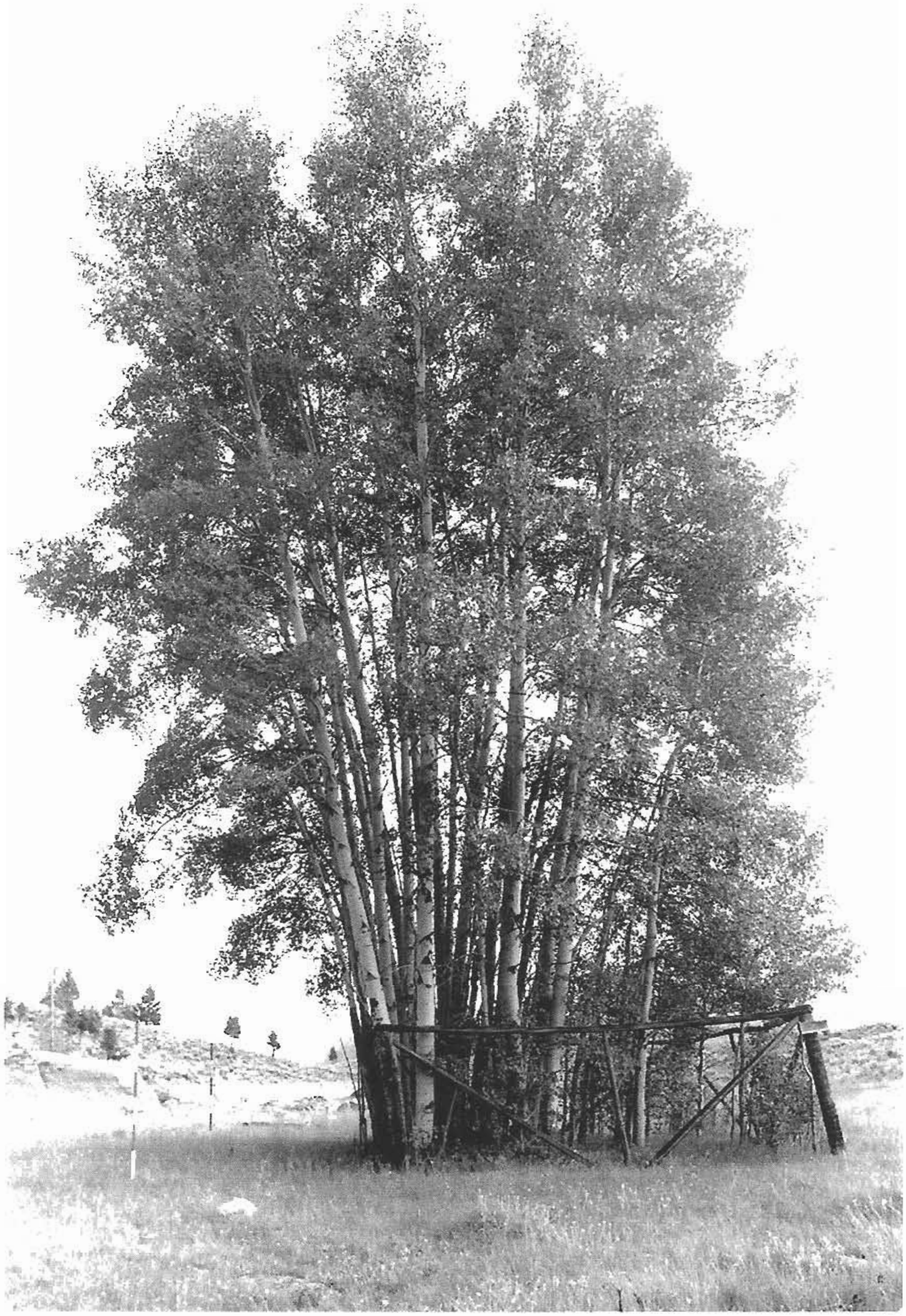
Fig. 7. (cont.)(c). One year after the exclosure was built, the aspen exposed to browsing had already been high-lined by elk. NPS photo 15,128-3, 1937. (d) Within five years, nearly all the aspen exposed to browsing had been killed by elk even though their terminal leaders were beyond the reach of those ungulates. The elk killed the aspen by bark wounding and stripping. NPS photo 41-326, 10/15/41.



c.

d.

Fig. 7. (cont.) (e). Range Plot 25 in 1986. The largest aspen were approximately 20m tall and 20cm DBH. For scale, the two survey poles which mark the outside plot to the left of the exclosure are 2m tall.



comparative photosets (Figs. 6, 7, 8, and 9). (1) All enclosed aspen successfully regenerated into multi-size-class stands. (2) Aspen did not produce regenerated stems > 2m tall in any of the unprotected stands except at Goosewing and Soda Lake. (3) Aspen outside the exclosures experienced continued mortality and all of the mature trees outside several exclosures died, including Range Plot 10, Junction Butte, and Lamar-East. Based on the presence of dead, standing trees, all mature aspen outside the Uhl Hill exclosure had also recently died. (4) Aspen clones within all exclosures increased in area and many expanded into and replaced sagebrush-grasslands within the exclosures. (5) Within most exclosures, there was a substantial increase in understory shrubs. (6) Conifers had not encroached upon most of the inside or outside aspen communities.

Based on all of the photosets I have examined, it appears to take 10-15 years or longer for aspen to show a visible response to protection from ungulates. I suspect that the aspen communities inside the exclosures have not returned to pre-grazing conditions even after 40 or 50 years of protection. This could conceivably take 100-150 years or longer, judging by the rates of change observed in these photographs and current stand age structures (Tables 17 and 18).

Other Aspen Exclosure Studies

Mueggler and Bartos (1977) reported that shrubs increased inside two, three-part aspen exclosures in southern Utah where mule deer and cattle were the primary ungulate herbivores. They concluded that

> . . . the most striking difference in understory attributable to animal use was the great reduction in total shrubs . . . After 41 years, the ungrazed area at Grindstone Flat produced almost 10 times more shrubs than the area grazed by both cattle and deer and over three times more than that grazed just by deer. The graminoids increased under grazing at Grindstone Flat . . . (p. 13)

Aspen protected from all grazing developed multi-size-class stands while those outside did not. Conifers readily established in both inside and

Fig. 8. Aspen belt transect (1.5x22.9m) outside Junction Butte exclosure in 1962 and 1986. The two steel posts mark the north end of the belt transect. Exclosure fence is on right. Four mature aspen were alive outside the exclosure in 1962, but had all died by 1986. Shrub evident in 1962 and to a lesser degree in 1986 is shrubby cinquefoil which is usually considered to be unpalatable and to increase with livestock grazing. Here it apparently decreased outside the exclosure while increasing inside, probably a result of elk browsing. NPS photo 62-548, 9/18/62. Charles Kay photo 58,982-12, 7/25/86.

1962

1986

Fig. 9. Aspen belt transect (1.5x22.9m) inside Junction Butte exclosure in 1962 and 1986. Exclosure fence is in top of 1962 photo and the two steep posts mark the west end of the belt transect. The plant in foreground of 1986 photo is shrubby cinquefoil which has increased to form a nearly closed canopy. Where aspen have grown up, shrubby cinquefoil has been replaced by mesic forbs which apparently are more shade tolerant. NPS photo 62-547, 9/20/62. Charles Kay photo 58,982-17, 7/25/86.

1962

1986

outside plots.

Coles (1965:38-41) measured the age structure of aspen communities inside and outside a three-part exclosure in central Utah. Where all ungulates were excluded, aspen were multi-aged. Where cattle were excluded but mule deer were not, few new stems had grown taller than 2m. However, "Damage to aspen reproduction was even greater on the open plot grazed by both deer and cattle" (Coles 1965:40). Not only did cattle consume some of the aspen, but "an indirect effect of cattle grazing appeared to be the destruction of desirable game forage which forced game to utilize aspen" more heavily (Coles 1965:56).

Trottier and Fehr (1982:28-33) reported on an aspen exclosure in Canada's Banff National Park where elk and moose are the most abundant ungulates. They (p. 28) noted that "Browsing by elk in this area has a tremendous influence on shrub and tree regeneration in the aspen forest." The protected plot had greater shrub density and a more diverse height class distribution than the browsed plot. "About 97% of the shrubs in the browsed plot were less than 100cm high and there were no plants taller than 150cm" (p. 30). These authors (p. 30) concluded that aspen regeneration was limited by ungulate browsing. "Under protection there were plants [aspen] in all height classes indicating that growth to tree stage was proceeding. On the browsed plot all plants were less than 100cm" (p. 30). Yet densities of aspen stems < 1m tall were greater outside, as was total stem density.

Milner (1977) measured aspen communities inside and outside four exclosures in Canada's Elk Island National Park where elk and moose are the major ungulates. Inside each exclosure, aspen "attained a greater basal area, height and DBH class" than on outside plots (p. 52). Moreover, "Regeneration of the tree structure was restricted in unprotected areas . . . [and] shrub height and diameter class were greater in the exclosures" (pp. 52-53). Highly palatable shrubs increased significantly inside the exclosures.

Gysel (1960), Olmsted (1977), Hart (1986), and Stevens (1980) reported on aspen exclosures in Colorado's Rocky Mountain National Park where elk and mule deer are the primary ungulates. In three out of four exclosures, aspen developed into multi-size-class stands while those outside did not. In the fourth, aspen was completely replaced by conifers (Hart 1986), but conifers did not establish in the other exclosures (Olmsted 1977:27, Kay unpub. photos). Inside the three exclosures, aspen spread into and replaced grasslands while outside, grazing changed aspen communities into grasslands (Gysel 1960, Stevens 1980, Hart 1986, Kay unpub. photos). Shrubs were more common inside the exclosures than out (Stevens 1980, Kay unpub. photos). A temporary reduction of elk numbers in that park allowed some aspen stems to escape browsing and to grow into larger size classes (Olmsted 1977, 1979).

Hart (1986) measured aspen communities inside and outside four exclosures I used, East Elk Refuge, Upper Slide Lake, Goosewing, Uhl Hill, and reached conclusions similar to those I have reported. In South Dakota's Custer State Park, aspen expanded into and replaced grassland inside an exclosure within 2 years following exclusion of grazing (Hoffman and Alexander 1987:15). At South Dakota's Wind Cave National Park, aspen inside an exclosure developed into a multi-size class stand while those subject to ungulate grazing did not (R. Klukas, pers. commun. 1989). At one aspen exclosure in Montana and six others in southern Utah, I observed (unpub. photos) similar inside-outside trends.

EXCLOSURES AS A TEST OF THE CLIMATIC CHANGE HYPOTHESIS

Utility of Exclosure Studies

I measured vegetation inside and outside exclosures in the Yellowstone Ecosystem to obtain information on the central issue of the "natural regulation" paradigm, the relationship between elk and vegetation. Indeed the exclosures were established in the pre-"natural regulation" era for that purpose. However, since 1968, Park Service biologists have questioned the utility of exclosures on two grounds. One is that vegetation inside exclosures does not represent "natural" conditions because the fences themselves act to cause "unusual drifting of snow and thereby concentrating moisture near the fences" (Despain et al. 1986:80). This effect is commonly suggested by plant ecologists, although in discussions with them (e.g. Martyn Caldwell, pers. commun. 1990; David Pyke, pers. commun. 1990) they have stated that this is largely conjectural and they are not aware of any measurements which document such an effect.

I question whether the fence effect has been a significant determinant of the inside-outside vegetation difference in the Yellowstone Ecosystem exclosures on three grounds. (1) Many of the exclosures are large, ranging in size from 1.8 to 152 ha (Table 3). The inside vegetation differences extend fully into the interiors, well beyond any fence-induced drifting around the margins. (2) If drifting were an important phenomenon, one would expect aspen and shrubs on the downwind side of exclosures to show an appropriate response. None of the repeat photosets shows any evidence of enhanced vegetation expression on the downwind sides of exclosures. (3) A number of exclosures are on moist sites, with water at or near the surface both inside and outside the fences. Measurements of subsurface water levels throughout the summer inside and outside exclosures in Yellowstone Park failed to show any less water available to the plants outside the exclosures (Brichta 1987, Chadde et al. 1988) yet the marked inside-outside vegetation differences prevail in these situations. In total, I know of no evidence to support the fenceline-drifting hypothesis for Yellowstone's exclosures.

I do not suggest that the microclimates of the exclosure as a whole may not be different inside. The more profuse vegetation itself probably entraps snow and casts shade. But these are incorporated variables caused by the plants' response to elimination of ungulate browsing, not the cause of the vegetation's response. Such microclimatic conditions would prevail in any aspen stands not subject to heavy ungulate use, whether in exclosures or not.

Whether or not, and if so how, the Park Service's microclimate objection is intended to interject some uncertainty about the utility of the exclosures for studying the elk-vegetation interrelationship is not clear. For in other contexts, the role of ungulate browsing in producing the inside-outside differences is implicitly acknowledged. The National Park Service (1971) has stated that "Interpretations from such comparisons require an awareness that protected vegetation represents an artificial 'standard' which increases in artificiality over time...Interpretations that such exclosures illustrate how things should be in a park would more often than not be confusing artificial with natural conditions." Gruell and Loope (1974:29) added that

> Exclosures present a highly atypical picture, since they show response of vegetation when not exposed to heavy ungulate browsing. Removal of the influences of both fire disturbance and ungulate browsing leads to a response of vegetation within exclosures which is undoubtedly unique in the vegetational history of northwestern Wyoming.

These are the second grounds on which agency biologists question the utility of the exclosures. What they seem to be saying is that conditions outside exclosures are "natural" while those inside are not (Despain et al. 1986). In essence they have a priori concluded the validity of the major assumption underlying the "natural regulation" paradigm: that conditions prevailing today outside exclosures are like those which prevailed in prehistory. This circular logic will not help answer the questions which have been posed regarding elk-aspen interactions (Chase 1986, Bonnicksen 1989).

I consider that vegetation inside and outside exclosures represents two ends of a grazing continuum, with the Eagle Creek vegetation falling somewhere near the inside-exclosure end. Other types of evidence must be employed to determine where on the continuum conditions which existed in the park prior to European influence fall. I will examine that evidence in Chapters 8-10 below.

The Climatic-change Hypothesis

The decline of aspen on the northern range has also been attributed in part to climatic change, especially the drought during the 1930s (Houston 1982). More generally, Houston (1982:101-107) noted that since the late 1890s, the mean annual temperature on the northern range at Mammoth increased 0.5-1.0°C while the mean annual precipitation declined 1-2 cm. Since the macroclimate is the same both inside and outside the exclosures, they can be used to test the climate-change hypothesis.

Regarding the 1930s-drought question, aspen inside Range Plots 10, 16, and 25 grew vigorously during and after the 1930s drought while those outside did not (Table 14, Figs. 6 and 7, Barmore 1981:374). Drought alone did not prevent aspen growth during the period if it was protected from elk use.

Other studies have shown that conversion of aspen forests to herbaceous vegetation, such as grasses or forbs, increases water yield (Johnston et al. 1969; Hibbert 1979; Harniss 1981; DeByle 1985b, 1985c). Thus, conversion of aspen to grasslands, as has and is occurring in Yellowstone Park and throughout that ecosystem, could reasonably be expected to increase, not decrease, soil moisture for the remaining aspen. Observations at Range Plot 16 and other sites on the northern range lend tentative support to this hypothesis. Early photos show a sagebrush understory inside and outside Range Plot 16. Park Service data collected 27 years after that exclosure was constructed indicate 50 big sagebrush (<u>Artemisia</u> <u>tridentata</u>) plants were present inside and another 39 on the outside plot in 1962. By 1987, no sagebrush plants were left outside (Table 64 in Appendix B). Inside, sagebrush had only

2% canopy-coverage, though several dead plants were present. Comparative photos also show a substantial decline over the years in the number of mature aspen trees outside the exclosure.

In 1987 and 1988, the water table outside Range Plot 16 was at or near the surface. Sagebrush cannot tolerate high soil moisture and is easily killed by rising water levels (Ganskopp 1986, Sturges 1989). The soil outside Range Plot 16 now appears to be too wet to support sagebrush. This sequence of events suggests that as aspen declined outside the exclosure, the water table rose which in turn killed the sagebrush. This influence even extended into Range Plot 16, probably because of the exclosure's small size (7x7m).

At the Lamar-West exclosure, springs which arise inside flow outside through what was once a dense aspen stand. Today, practically no mature trees are left outside the exclosure (Kay unpub. photos), yet water from the exclosure still flows through the outside area. Thus, aspen declined outside these exclosures despite an abundance of soil moisture. This suggests that Houston's (1982:101-107) 1-2cm decline in mean annual precipitation had a negligible impact on aspen-stand dynamics compared to repeated ungulate browsing.

Despain et al. (1986:109) stated that "Yellowstone is not the center of good aspen habitat and even a slight change in climate could have significant effects on aspen here." They (p. 109) added "Aspen . . . may at times find only marginal hospitality in Yellowstone." Park Service biologists have also been quoted as saying Yellowstone's "climate is not optimal for aspen" (Collins 1988). If this were true, it would be logical to predict (1) aspen near creeks, streams and other mesic locations should be more successful at regenerating than stands on more xeric sites, (2) aspen with north exposures should be more successful at regenerating than stands on south-facing hillsides, (3) aspen at high elevations should regenerate more successfully than stands at low elevations, and (4) aspen on south-facing slopes inside exclosures exhibit signs of physiological stress such as stunted growth or twisted trunks.

Based on data presented in Chapter 3 (above) for aspen both inside and outside the park, on exclosure data presented in this chapter, and on my observations and repeat photographs of aspen throughout the park (see Chapter 8 below) the following conclusions are drawn. (1) Aspen outside exclosures near water courses have not been more successful in regenerating than stands on xeric sites. Repeat photographs show that aspen along streams and creeks have experienced a decline (> 90%) similar to other stands. (2) Aspen on the park's northern range has failed to regenerate irrespective of exposure. Repeat photosets do not show any exposure differences. (3) Despite an elevational difference of approximately 900m between the lowest and highest aspen stands on the park's northern range, there is not correlation between elevation and successful regeneration. Again, repeat photographs do not show any elevational difference. Moreover, stands at high elevations, on north slopes, near streams have not been able to regenerate successfully. (4) Aspen inside exclosures show no signs of physiological stress (Kay unpub. photos). Aspen 60 years old inside Range Plot 25 in 1987 were approximately 20m tall, were over 20cm DBH, and had straight trunks (Fig. 7e). Furthermore, aspen stands on south-facing hillsides inside several exclosures (Lamar-East, Crown Butte, Porcupine) have expanded and replaced grass-sagebrush (Kay unpub. photos). (5) Aspen in Eagle Creek, only 2 km from the park's northern range and at similar exposures and elevation, regenerated successfully in years when elk numbers were at low levels.

In total, there is considerable evidence indicating that the decline of aspen on the northern range was strongly associated with heavy ungulate pressure and not any climatic variation. I know of no evidence that a climatic shift of a mean temperature rise of 0.5-1.0° and a mean annual precipitation decline of 1-2cm will have any long-term impact on aspen, especially since many aspen communities appear to be subirrigated (Brichta 1987). Most perennial, woody floras have so much biological or vegetational inertia that major climatic changes of long duration are required before shifts in plant species composition or stature occur (Smith 1965, Cole 1985, Davis and Botkin 1985, Davis 1986, Neilson 1986). Simulations of cool-temperate forest growth in response to a 0.5°C climatic change using the JABOWA computer model have demonstrated that no tree species showed a significant response even after 400 years (Davis and Botkin 1985, Davis 1986). Even with a 2°C change, it took 100-200 years for the species composition of the forest to show a significant response.

In conclusion, I regard the climate-change explanation as a hypothesis without supporting evidence or theoretical rationale in aspen ecophysiology. Whatever climatic change may have occurred in Yellowstone's northern range, it has had a negligible effect on aspen compared with ungulate browsing.

CONCLUSIONS

1. Aspen stands inside all exclosures regenerated successfully (produced stems > 2m tall) without fire or other disturbance.

2. Aspen inside all exclosures developed multi-size-class stands. Because DBH is correlated with age (see Chapter 3 above), aspen inside exclosures are also multi-aged, a characteristic of stable or climax aspen communities.

3. Few aspen stands in Yellowstone, inside or outside exclosures, are being heavily invaded by conifers. Lack of conifer encroachment, is also characteristic of stable or climax aspen communities.

4. Aspen understories inside exclosures are dominated by plant species different from those outside. Understories within Yellowstone exclosures are dominated by tall shrub and tall forb species characteristic of stable or climax aspen communities. Understories

outside the exclosures are dominated by exotic grasses or forbs which tend to increase under grazing pressure.

5. Data from these exclosures support my earlier conclusion (see Chapter 3 above; Kay 1985, 1987) that a significant proportion of aspen stands present in the Greater Yellowstone Ecosystem today are stable or climax.

6. Since the general climate is the same inside and outside the exclosures and since soil moisture is abundant both inside and outside, it seems highly unlikely that the decline of aspen throughout Yellowstone Park (see Chapters 3 and 8 herein) can be attributed to the climatic variation which may have occurred over the years.

7. This, and information from other aspen exclosure studies, suggests that single-age aspen stands common throughout the Greater Yellowstone Ecosystem (Krebill 1972) and the Intermountain West (Mueggler 1989) have been created by livestock and wild ungulate grazing.

In Chapters 8-11 below, I will present evidence which indicates that aspen communities in the West were not subjected to high ungulate populations prior to European influence. For instance, aspen stands photographed in Yellowstone during the late 1800s resemble in physical appearance those found within exclosures today, not outside aspen stands.