CHAPTER III

ASPEN ON THE NORTHERN RANGE: INSIDE-OUTSIDE PARK COMPARISONS

INTRODUCTION

The relationship between aspen and elk in Yellowstone National Park has long been a subject of conflicting opinions and intense debate (Barmore 1981; Tyers 1981; Houston 1982; Kay 1985, 1987; Chase 1986; Despain et al. 1986). Prior to 1968, the Park Service believed that an "abnormally" large elk population had severely "damaged" aspen communities on the northern range (Bauer 1939; Barmore 1965, 1967). The deterioration and disappearance of aspen stands first became apparent, or were first mentioned, during the late 1920s. Annual range reports from the late 1930s through 1968 consistently documented the continuing decline of aspen which was attributed to heavy elk browsing (Barmore 1981:371).

With the adoption of "natural regulation," the Park Service changed its interpretation of aspen ecology on the northern range. While agreeing that the distribution of aspen on the northern range may have declined by roughly 50% since the park was established, Houston (1982:127) believed that change was due primarily to suppression of lightning-caused fires, successional replacement of seral aspen communities by conifers or grasslands, and climatic change. Houston (1982:127) concluded "Herbivores doubtless affected the rate of postfire succession but were not the force that determined the direction and timing of events."

However, other researchers have concluded that aspen is not always a seral fire species, and that long-term stable or climax aspen exists throughout the Intermountain West (Coles 1965; Alder 1970; Reed 1971; Beetle 1974; Hoffman and Alexander 1976, 1980, 1983, 1987; Mueggler 1976, 1985, 1988; Severson and Thilenius 1976; Young 1977; Betters and Woods 1981; Youngblood and Mueggler 1981; Mueggler and Campbell 1982, 1986; Hansen et al. 1984; Alexander 1985, 1987; Jones and DeByle 1985b:16; Kay 1985; Kuch et al. 1985; Alexander et al. 1986; Masslich et al. 1988:254). Climax or stable aspen communities can be distinguished from seral stands because they (1) have multi-size or age-class trees (ramets), (2) have characteristic understory plants, and (3) lack substantial conifer invasion (Mueggler 1988). Seral aspen is characterized by (1) single-age-class trees, (2) heavy conifer encroachment, and (3) different understory species. Perhaps as much as one-third of the aspen in the western U.S. is stable or climax (Mueggler 1989). Culwell and Scow (1982) identified stable or climax aspen communities in the Bear Creek drainage north of Yellowstone Park.

I measured a 20% random sample of aspen stands in Eagle Creek and at three sites in the park (Mt. Everts, South Lamar, and North Lamar) to determine their condition and successional trend. Over the years fewer elk have wintered in Eagle Creek than in the park. Since Eagle Creek has the same history of fire suppression and climatic change as the park's northern range, any difference between its aspen communities and those in the park would have to be due primarily to different levels of elk use.

RESULTS

Aspen Size-Class Distribution and Stem Densities

Aspen stands in Eagle Creek had a significantly different size-class stem distribution than stands in Yellowstone Park ($\underline{p} < .001$, Hotelling's T^2 test) (Kendall 1980). In Yellowstone Park, aspen stands had significantly more stems < 2m tall per ha (Table 5) than stands in Eagle Creek (Table 6) ($\underline{t} = 4.79$, $\underline{p} < .001$). However, despite this abundance of suckers, no stems physically available to elk have grown taller than 2m in the park while they have in Eagle Creek. For other size classes, aspen in Eagle Creek had significantly greater stem densities; > 2m, $\leq$ 5cm DBH ($\underline{t} = 16.56$, $\underline{p} < .001$); 6-10 DBH ($\underline{t} = 14.79$,

Table 5. Size-class distribution of aspen stems in 194 stands on Yellowstone National Park's northern range.

Location	Aspen size classes*				
	< 2m	> 2m, ≤ 5cm	6-10cm	11-20cm	> 20cm
<u>Mt. Everts (n = 39)</u>					
Percent of stands with stems in this size class	100	0	0	5	95
Mean no. stems per ha (SEM)	19,983 (2,820)	0 (0)	0 (0)	9 (6)	235 (21)
<u>South Lamar (n = 82)</u>					
Percent of stands with stems in this size class	100	1**	0	0	93
Mean no. stems per ha (SEM)	16,236 (1,533)	0*** (0)	0 (0)	0 (0)	195 (12)
<u>North Lamar (n = 73)</u>					
Percent of stands with stems in this size class	92	0	0	0	36
Mean no. stems per ha (SEM)	3,371 (571)	0 (0)	0 (0)	0 (0)	68 (12)
<u>Totals (n = 194)</u>					
Percent of stands with stems in this size class	97	0***	0	1	72
Mean no. stems per ha (SEM)	12,472 (1,063)	0*** (0)	0 (0)	2 (1)	156 (9)

* m refers to height and cm to DBH; see text.

** 2 stems > 2m in one aspen stand were protected by the intertwining branches of a large fallen Douglas Fir.

*** Not including the 2 stems > 2m protected by the fallen tree.

Table 6. Size-class and age distribution of aspen stems in 74 stands in Eagle Creek.

	Aspen size classes*				
	< 2m	> 2m, ≤ 5cm	6-10cm	11-20cm	> 20cm
Percent of stands with stems in this size class	89	84	73	84	64
Number of stems per ha					
mean	3,947	2,749	1,122	692	357
SEM	692	268	122	68	43
Age - years					
mean	**	16.0	23.4	55.9	86.4
standard deviation	**	4.0	7.7	11.3	17.7
DBH (cm)					
mean	**	3.91	8.07	16.50	28.41
standard deviation	**	0.96	0.86	1.39	4.72

* m refers to height and cm to DBH; see text.

** Data not recorded.

$p < .001$); 11-20 cm DBH ($t = 16.50$, $p < .001$); and > 20cm DBH ($t = 6.59$, $p < .001$).

In Eagle Creek, 42% of the stands contained all four size classes of aspen > 2m tall, 32% contained three out of four while 15% had two of four. Thus, 74% contained at least three of four size classes > 2m tall while 89% had at least two. The majority of aspen stands in Eagle Creek were multi-sized, and 89% of the stands had successfully regenerated without disturbance. In Yellowstone Park, only 1% of the stands had more than one size class of aspen > 2m tall, and no stands had successfully regenerated in the last 80 or so years (Table 5). Aspen stands in the park were also smaller than those in Eagle Creek (mean 4,171m^2 vs. 5,131m^2), but that difference was not statistically significant ($t = 1.27$, $p > .10$).

Aspen Age

In Eagle Creek, I determined the age of 895 aspen stems. Age is positively correlated with DBH [age in years = 2.89 (DBH in cm) + 4.86, $r^2 = 0.84$]. Other researchers reported similar correlations between aspen age and diameter (Alder 1970:15-17, Masslich et al. 1988:258). Thus, the multi-sized aspen stands in Eagle Creek are also multi-aged (Tables 6 and 7). I cored over 400 aspen in Yellowstone Park, but less than 1% could be aged because of various forms of heart rot (Hinds 1985). Hence, age data were not obtained for aspen in the park. Based on the regression equation for Eagle Creek, all aspen > 20cm DBH in the park are 80 to 100 years old or older.

Conifer Encroachment

Data on visually estimated conifer canopy cover in entire aspen stands and the mean number of conifers recorded on 2x30 aspen belt transects is presented in Table 8. Both in Eagle Creek and the park, estimated percent conifer canopy cover was positively correlated with

Table 7. Regeneration dates and age distribution of aspen trees within 74 stands in Eagle Creek.

10-year periods	Age (yrs)	Percent of aspen stands in regeneration period and age class. Largest size class in stand	All size classes in stand
1977-1986	1- 10	0	8
1967-1976	11- 20	0	77
1957-1966	21- 30	0	63
1947-1956	31- 40	5	11
1937-1946	41- 50	0	11
1927-1936	51- 60	23	40
1917-1926	61- 70	16	29
1907-1916	71- 80	11	13
1897-1906	81- 90	21	23
1887-1896	91-100	10	10
1877-1886	101-110	11	11
1867-1876	111-120	2	2
1857-1866	121-130	2	2

Table 8. Assessment of visually estimated conifer canopy cover by comparing such estimates with measured conifer constancy and density on aspen belt transects.

Estimated conifer canopy cover by area	Percent of aspen belt transects with one or more conifers	Mean number of all conifers per ha (SD)
Eagle Creek (n = 32 of 74)		
< 1%	27	45 (78)
1-5%	18	30 (67)
6-10%	66	278 (254)
> 10%	100	691 (150)
Yellowstone Park		
Mt. Everts (n = 29 of 39)		
< 1%	12	21 (59)
1-5%	12	83 (236)
6-10%	100	250 (118)
> 10%	91	485 (398)
South Lamar (n = 32 of 82)		
< 1%	0	0 (0)
1-5%	11	19 (56)
6-10%	33	222 (255)
> 10%	100	429 (242)
North Lamar (n = 32 of 73)		
< 1%	0	0 (0)
1-5%	10	17 (53)
6-10%	0	0 (0)
> 10%	88	488 (378)
Subtotals (n = 98 of 194)		
< 1%	4	7 (35)
1-5%	11	37 (133)
6-10%	43	167 (192)
> 10%	93	443 (341)

increasing conifer densities on the sampled transects. This suggests that the estimated conifer canopy coverages are an appropriate measure of actual conifer encroachment rates. Aspen stands estimated to have < 5% conifer canopy cover, on average, contained fewer than 50 conifers per ha (Table 8). Aspen stands estimated to have > 10% conifer canopy cover averaged 400-700 conifers per ha (Table 8).

Of sampled aspen stands, 43% in Eagle Creek and 51% of those in the park had at least one conifer present (Table 9). In Eagle Creek, 9% of the stands had more than 10% conifer canopy cover while that was true for 21% of those in the park (Table 8), a significantly higher rate of conifer invasion ($x^2 = 58.74$, $df = 3$, $p < .001$). In both locations, the majority of aspen stands present today are not being readily invaded by conifers.

In both areas, Douglas fir (Pseudotsuga menziesii) is the most common conifer (Table 10). I found a few 5-needle white pines in some stands. These could be either limber pine (Pinus flexilis) or whitebark pine (P. albicaulis); the two species cannot be separated without male or female cones, which were not present. Both species have been identified throughout the Yellowstone area, where small numbers of 5-needle pines commonly occur in aspen stands (Kay unpub. data).

I found lodgepole pine (P. contorta) in aspen stands in the park, but not in Eagle Creek (Table 10). Subalpine fir (Abies lasiocarpa) is rare in aspen stands from both areas while Engelmann spruce (Picea engelmanii) is common. Engelmann spruce dominates most stands which are being heavily invaded by conifers. Many of those are located along streams or other areas of cold-air drainage and high soil moisture where Engelmann spruce is often climax (Cooper 1975).

Understory Vegetation

Shrubs and forbs are significantly more abundant in the understories of aspen stands in Eagle Creek than in the park (Table 11).

Table 9. Percentage of aspen stands with conifers in Eagle Creek and Yellowstone Park.

Area	No. stands	Percent of stands with at least one conifer present	Percent of stands by estimated conifer canopy cover > 1%	> 5%	> 10%
Eagle Creek	74	43	28	14	9
Yellowstone Park					
Mt. Everts	39	74	54	33	28
South Lamar	82	39	32	21	17
North Lamar	73	51	38	25	22
Subtotals	194	51	39	25	21

Table 10. Abundance of conifer species on 2x30m belt transects in aspen stands in Eagle Creek and Yellowstone Park for stands which contained at least one conifer.

	Percent stands containing species by 4 cover classes			
Location and species	< 1%	1-5%	6-10%	> 10%
Eagle Creek (n = 32 of 74)				
Douglas fir	82	100	66	71
Whitebark or limber pine	18	18	0	0
Engelmann spruce	9	18	33	43
Subalpine fir	0	0	33	57
Yellowstone Park				
Mt. Everts (n = 29 of 39)				
Douglas fir	100	100	100	100
Whitebark or limber pine	0	12	0	0
Engelmann spruce	25	12	50	9
Subalpine fir	0	0	0	9
Lodgepole pine	12	25	0	22
South Lamar (n = 32 of 82)				
Douglas fir	17	100	0	71
Engelmann spruce	100	89	100	71
Subalpine fir	0	11	0	7
Lodgepole pine	0	33	0	0
North Lamar (n = 37 of 73)				
Douglas fir	33	60	50	50
Engelmann spruce	56	50	100	81
Subalpine fir	0	0	0	6
Lodgepole pine	11	0	50	6
Subtotals (n = 98 of 194)				
Douglas fir	52	85	43	71
Whitebark or limber pine	0	4	0	0
Engelmann spruce	57	56	86	59
Subalpine fir	0	4	0	7
Lodgepole pine	9	19	14	7

Table 11. Average percent canopy-coverage of shrubs, forbs, and grasses in the understories of aspen stands in Eagle Creek and Yellowstone Park.

		Mean (SEM) percent canopy-coverage		
Area	n	Shrubs	Forbs	Grasses and Sedges
Eagle Creek	74	16.9	63.9	18.1
		(2.3)	(2.2)	(1.8)
Yellowstone Park				
Mt. Everts	39	3.3	41.2	53.5
		(0.8)	(3.0)	(2.8)
South Lamar	82	13.4	27.5	60.3
		(1.6)	(1.4)	(2.0)
North Lamar	73	9.9	32.9	59.7
		(0.9)	(1.8)	(2.0)
Subtotals	194	10.0*	32.5*	58.8*
		(0.8)	(1.2)	(1.3)

*all $p < .001$, t-test on arcsine transformed data.

Stands in the park are dominated by grasses while those in Eagle Creek are forb dominated. Moreover, there are major differences in species composition (Table 12). For instance, forbs such as cow parsnip (Heracleum lanatum) and tall fireweek (Epilobium angustifolium) are more common in Eagle Creek while graminoids like timothy (Phleum pratense) and pine grass (Calamagrostis rubescens) are more abundant in the park.

DISCUSSION

Successional Trend and Status

As mentioned previously, three factors can be used to evaluate the successional trend and status of aspen communities: (1) stem age structure, (2) conifer encroachment, and (3) understory species composition.

Age Structure

The majority of aspen stands in Eagle Creek are multi-aged indicating that they could be stable or climax communities (Mueggler 1988). While most aspen outside the park have been able to regenerate successfully without disturbance, stands in Yellowstone have not been able to produce stems > 2m tall. Stems < 2m tall are more common in the park, so lack of regeneration effort (suckers) cannot be the reason for this difference.

New aspen stems in the park are repeatedly browsed by elk and to a lesser extent mule deer and moose (Houston 1982). Utilization rates of 50-70% or more are common (Barmore 1967, 1981:364-365). Kittams (1948, 1949, 1950, 1952a, 1952b) reported that aspen suckers on the park's northern range experienced an average yearly mortality of 28%, the majority of which he attributed to repeated browsing by elk.

Houston (1982:414-415) evaluated 175 aspen stands in the park and 28 stands outside, mostly in Eagle Creek. He found that outside the park "in the virtual absence of elk, moose, and fire, some stands could reproduce successfully." He noted that 7% of the aspen stands in the

Table 12. Average percent canopy-coverage and (constancy) of understory plants in aspen stands in Eagle Creek and Yellowstone National Park.

Species	Mean percent canopy-coverage and (constancy)				
		Yellowstone National Park			
	Eagle Creek (n=74)	Mt. Everts (n=39)	South Lamar (n=82)	North Lamar (n=73)	Subtotal (n=194)
Shrubs					
Amelanchier alnifolia	0.4 (18)	--- --**	0.6 (23)	0.2 (5)	0.3 (12)
Symphoricarpos albus	6.6 (65)	0.5 (31)	2.4 (60)	2.4 (62)	2.0 (55)
Rosa woodsii	3.5 (32)	0.6 (31)	5.2 (91)	2.2 (77)	3.2 (60)
Spirea spp.	0.7 (11)	--- --	0.1 (6)	0.1 (3)	0.1 (4)
Ribes spp.	0.5 (20)	--- --	0.3 (26)	0.3 (21)	0.2 (19)
Artemisia tridentata	0.5 (34)	2.0 (38)	0.7 (18)	2.8 (55)	1.8 (25)
Salix spp.	2.3 (16)	T (3)	0.8 (15)	0.8 (25)	0.6 (16)
Alnus incana	1.0 (12)	--- --	--- --	0.5 (16)	0.2 (6)
Symphoricarpos oreophilus	0.5 (5)	--- --	--- --	--- --	---
Prunus virginiana	0.9 (12)	--- --	0.6 (15)	0.1 (7)	0.3 (9)
Shepherdia canadensis	T* (1)	T (3)	1.5 (33)	0.1 (5)	0.7 (16)
Potentilla fruticosa	--- --	0.1 (5)	0.7 (20)	0.1 (8)	0.3 (12)
Berberis repens	--- --	0.1 (5)	0.1 (4)	0.1 (5)	0.1 (4)
Lonicera involucrata	--- --	--- --	0.2 (13)	0.2 (22)	0.2 (14)
Arctostaphylos uva-ursi	--- --	--- --	0.1 (4)	--- --	T (2)
Juniperus spp.	--- --	--- --	0.1 (7)	--- --	T (3)
Cornus stolonifera	--- --	--- --	--- --	T (1)	T (1)
Forbs					
Heracleum lanatum	12.3 (73)	0.2 (21)	0.3 (18)	0.9 (32)	0.5 (24)
Epilobium angustifolium	23.5 (66)	0.4 (38)	7.6 (67)	0.7 (36)	3.6 (50)
Geranium viscosissimum	2.3 (46)	2.2 (69)	3.8 (70)	6.0 (77)	4.3 (72)
Geranium richardsonii	0.4 (8)	1.1 (13)	0.6 (10)	0.3 (1)	0.6 (7)
Fragaria virginiana	1.0 (8)	9.2 (82)	5.9 (67)	4.8 (66)	6.2 (70)
Helianthus lanifolia	3.9 (19)	11.4 (54)	0.4 (5)	1.4 (18)	3.0 (20)

Table 12. (cont.)

Balsamorhiza sagittata	4.8 (30)	0.3 (3)	0.1 (2)	0.4 (11)	0.2 (6)
Thalictrum fendleri	0.5 (12)	1.2 (15)	0.3 (10)	0.4 (8)	0.5 (10)
Lupinus spp.	0.7 (12)	3.6 (59)	2.6 (34)	1.4 (30)	2.4 (38)
Achillea millefolium	--- --	1.5 (41)	0.1 (2)	0.1 (1)	0.4 (10)
Perideridia garirdneri	--- --	7.9 (64)	1.2 (24)	0.8 (19)	2.4 (30)
Smilacina stellata	--- --	--- --	0.7 (21)	T (1)	0.3 (9)
Senecio spp.	--- --	0. (18)	1.0 (20)	2.5 (58)	1.5 (34)
Aster spp.	--- --	T (3)	0.5 (6)	3.6 (51)	1.6 (22)
Others	14.5 (58)	1.7 (36)	2.4 (37)	9.6 (86)	5.0 (55)
Grasses and sedges					
Phleum pratense	2.6 (36)	7.8 (41)	42.4 (88)	36.5 (77)	33.4(74)
Poa pratensis	5.6 (49)	7.8 (46)	2.2 (30)	5.3 (32)	4.5 (34)
Calamagrostis rubescens	2.4 (19)	19.3 (59)	6.5 (32)	5.5 (33)	8.7 (38)
Bromus inermis	1.8 (7)	--- --	0.2 (4)	T (1)	0.1 (2)
Agropyron spicatum	0.1 (1)	0.9 (10)	0.7 (10)	0.4 (7)	0.6 (9)
Festuca idahoensis	0.3 (7)	2.3 (26)	1.8 (18)	1.8 (22)	1.9 (21)
Elymus cinereus	0.1 (3)	0.5 (5)	0.9 (15)	0.4 (14)	0.6 (13)
Carex spp.	0.9 (8)	0.5 (5)	0.8 (9)	1.7 (18)	1.1 (12)
Stipa richardsonii	--- --	0.9 (5)	0.8 (7)	0.2 (3)	0.6 (5)
Calamagrostis canadensis	--- --	0.8 (5)	0.6 (4)	0.1 (1)	0.4 (3)
Poa secunda	--- --	1.8 (15)	T (1)	--- --	0.4 (4)
Elymus glaucus	--- --	4.0 (21)	0.2 (5)	0.3 (10)	1.0 (10)
Bromus anomalus	--- --	4.4 (38)	T (1)	1.0 (12)	1.3 (13)
Agropyron trachycaulum	--- --	0.9 (15)	0.1 (2)	--- --	0.2 (4)
Stipa nelsoni	--- --	0.5 (8)	--- --	--- --	0.1 (2)
Danthonia intermedia	--- --	--- --	0.7 (2)	0.1 (3)	0.3 (2)
Poa palustris	--- --	--- --	0.4 (6)	0.1 (3)	0.2 (4)
Others	4.3 (30)	1.1 (23)	2.0 (32)	6.3 (82)	3.4 (49)

* T = trace
** To reduce confusion, dashes are used instead of zeros for absent species.

park escaped browsing, while outside 28% had regenerated successfully. Although Houston did not note a significant difference, statistical analysis of his data indicates that more aspen stands successfully regenerated outside the park ($x^2 = 12.82$, $p < .001$). I found that 89% of the aspen stands outside the park had successfully regenerated. This figure is similar to that reported by Kay (1985).

In an earlier paper (Kay 1985), I noted that 4% of the aspen stands in the park had been able to produce stems > 2m tall. Houston (1982:414) reported 7%. During this study I found none, except for two stems in one stand protected by the intertwining branches of a large, fallen Douglas fir (Table 5). Like Houston, my previous aspen research in the park was conducted primarily along roads and trails where steep road cuts and human disturbance can limit elk use. Some stands in those locations have been able to regenerate successfully.

Few of the aspen stands which I sampled on Mt. Everts and in the Lamar Valley during the present study are near or adjacent to park roads or heavily used trails. None is located on steep road cuts. This factor most likely accounts for the difference between aspen regeneration rates reported in this study and in earlier work. This conclusion is supported by measurements of two aspen stands located on the north side of Mt. Washburn, where elk access is severely limited by near-vertical rock cuts along the park's highway. Both stands contained multi-aged aspen, were not being readily invaded by conifers, and had understories dominated by tall forbs (Table 13). Those sites more closely resemble aspen communities in Eagle Creek than other stands in the park.

Understory Species Composition

The understories of aspen stands in the park are dominated by plants resistant to grazing or ones which are less palatable, while understories in Eagle Creek are dominated by tall forbs sensitive to grazing and trampling. For example, cow parsnip had an average canopy-

Table 13. Aspen-stand parameters and estimated understory canopy-coverage for two road-cut protected sites, Mt. Washburn, Yellowstone Park. Each stand was measured with a single 2x30m belt transect similar to other aspen stands in the park and Eagle Creek. Road built 1932, stands measured in 1987.

	Stand A	Stand B
Number of stems per ha by size class*		
< 2m	6,501	18,004
> 2m, ≤ 5cm	9,002	17,170
6 - 10cm	4,501	3,334
11 - 20cm	2,667	0
> 20cm	667	0
Mean age of aspen stems by size class		
< 2m	**	**
> 2m, ≤ 5cm	23.4	15.2
6 - 10cm	35.2	32.4
11 - 20cm	55.6	----
> 20cm	67.7	----
Percent conifer canopy cover in entire stand	< 5%	< 1%
Percent canopy-coverage of understory plants		
Shrubs - total	19	26
Symphoricarpos albus	5	2
Artemisia tridentata	6	1
Rubus parviflorus	8	20
Shepherdia canadensis	0	2
Juniperus communis	0	1
Forbs - total	68	69
Epilobium angustifolium	15	15
Thalictrum fendleri	23	20
Geranium viscossissimum	5	5
Aster spp.	20	20
Fragaria virginiana	0	4
Others	5	5
Grasses - total	13	5
Phleum pratense	T***	T
Calamagrostis rubescens	8	0
Others	5	5

* m refers to height and cm to DBH; see text.
** Data not recorded.
*** T = trace

coverage of 12.3% in Eagle Creek aspen communities and only 0.5% in park stands ($p < .001$, t-test on arcsine transformed data)(Table 12) I sampled. Cow parsnip had a constancy (the percentage of total measured stands containing the species) of 73% in Eagle Creek and 24% in the park. When only those stands with parsnip are considered, it averaged 16.6% canopy-coverage in Eagle Creek and 2.2% in the park ($p < .001$, t-test on arcsine transformed data). Cow parsnip is also rarely found in wetland plant communities on the park's northern range (Chadde et al. 1988).

Cow parsnip is a palatable umbellifer readily eaten by elk. Elk in Yellowstone select cow parsnip despite an abundance of other forage (Skinner 1928, Kay unpub. data). Within the park, cow parsnip often grows only where it is physically protected from ungulates by dead or dying woody vegetation (Kay unpub. photos). Moreover, cow parsnip is very susceptible to trampling damage. Simulated elk trampling research has shown that tall forbs are the class of plants most severely impacted by trampling (Bradley 1982). Since cow parsnip is very sensitive to herbivory (Youngblood and Mueggler 1981:12, Stivers 1988), and there have been substantially fewer elk outside the park (Kay 1985, 1987) where cow parsnip is more abundant, it appears reasonable to attribute the observed differences to elk grazing.

Most aspen communities in the park have understories dominated by non-native grasses such as timothy or Kentucky bluegrass (Poa pratensis). On average, timothy had a canopy-coverage of 33.4% in park aspen stands, but only 2.6% in Eagle Creek ($p < .001$, t-test on arcsine transformed data)(Table 12). A similar trend was reported by Chadde et al. (1988) in their study of riparian communities on the park's northern range.

In the North and South Lamar study areas, timothy had an average canopy-coverage of 42.4% and 36.5% respectively with constancies of 88% and 77% (Table 12). Only park aspen stands on Mt. Everts were not dominated by timothy; but there, timothy and Kentucky bluegrass still had a combined average canopy-coverage of 15.6% (Table 12). Houston (1982:415) indicated that timothy dominated "about 17%" of the stands he measured but provided no other data. Of the aspen stands on Mt. Everts and in the Lamar Valley, 59% had $\geq$ 25% timothy canopy-coverage while 35% of those stands had $\geq$ 50% timothy in their understories.

Timothy is resistent to grazing and tends to increase with grazing pressure or disturbance (Chadde et al. 1988). Elsewhere, aspen stands with understories dominated by non-native grasses have been classified as grazing disclimaxes (Mueggler 1988). Based on this criterion, the majority of the aspen stands in the park represent ungulate-induced retrogressive plant succession. On the other hand, aspen communities in Eagle Creek are dominated by understories composed of cow parsnip and other tall forbs which are associated with climax conditions (Youngblood and Mueggler 1981; Mueggler and Campbell 1982, 1986; Mueggler 1988).

Conifer Encroachment

The presence of a limited number of conifers is insufficient evidence on which to classify any aspen stand as seral (Hoffman and Alexander 1980:25). Conifers must be prominent, not merely present (Mueggler 1985:46). Occasional conifers can be found in basically stable aspen communities (Mueggler 1976). "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), a term foresters asign to aspen stands which will be replaced by conifers within 100 years or less.

Using this criterion, I found only 14% of the present aspen communities in Eagle Creek and 25% of those in Yellowstone Park (Table 9) to be fast-seral. Since 57% of the present stands in Eagle Creek and 49% of those in the park contain no conifers, one-half to two-thirds of those stands are potentially stable or climax as judged by this indicator.

Houston (1982:414-415) sampled 203 aspen stands inside and outside the park and reported that 70% "showed substantial invasion by conifers (mostly Douglas-fir) and in the absence of fire were clearly seral." Houston measured aspen stands as he encountered them during other range studies and he made no attempt to sample all stands randomly in entire drainages. His figures are not representative of the aspen stands in Eagle Creek, on Mt. Everts, in the Lamar Valley, or most other areas throughout the Greater Yellowstone Ecosystem which I have sampled (Kay 1985, unpub. data).

If aspen stands had been entirely replaced by conifers, they would not have been surveyed during the present study. Thus, a larger proportion of the aspen present on the northern range in 1872 may be seral to conifers than indicated by these measurements (see Chapter 8 below). Nonetheless much of the aspen present in Eagle Creek and the park today, is not being significantly invaded by conifers.

Moreover, aspen stands in the park have a higher rate of conifer encroachment than aspen communities in Eagle Creek. While this may be due to site differences, it may also be due to grazing influences. Young (1977:50) and Cooper (1975:80-81) suggested that lush, herbaceous understories in aspen stands may prevent conifer establishment. Dense cover affords few sites for conifer seedling establishment and also provides heavy competition for light and moisture. In Jackson Hole where a similar elk-aspen situation exists, Wyoming state range specialist Weinstein (pers. commun. 1987) concluded that ungulate grazing-induced deterioration of aspen communities was a prerequisite for conifer invasion.

Understories of aspen stands in Eagle Creek are dominated by shrubs and tall forbs which form a dense, lush growth 1m or more in height. Many aspen understories in the park are dominated by non-native grasses and short forbs which often do not form a dense growth especially in stands with high rates of conifer establishment. Since these understory differences are most likely due to ungulate grazing, aspen in Eagle Creek may have experienced a lower rate of conifer encroachment than stands in the park due to the higher level of ungulate grazing which has occurred in the park.

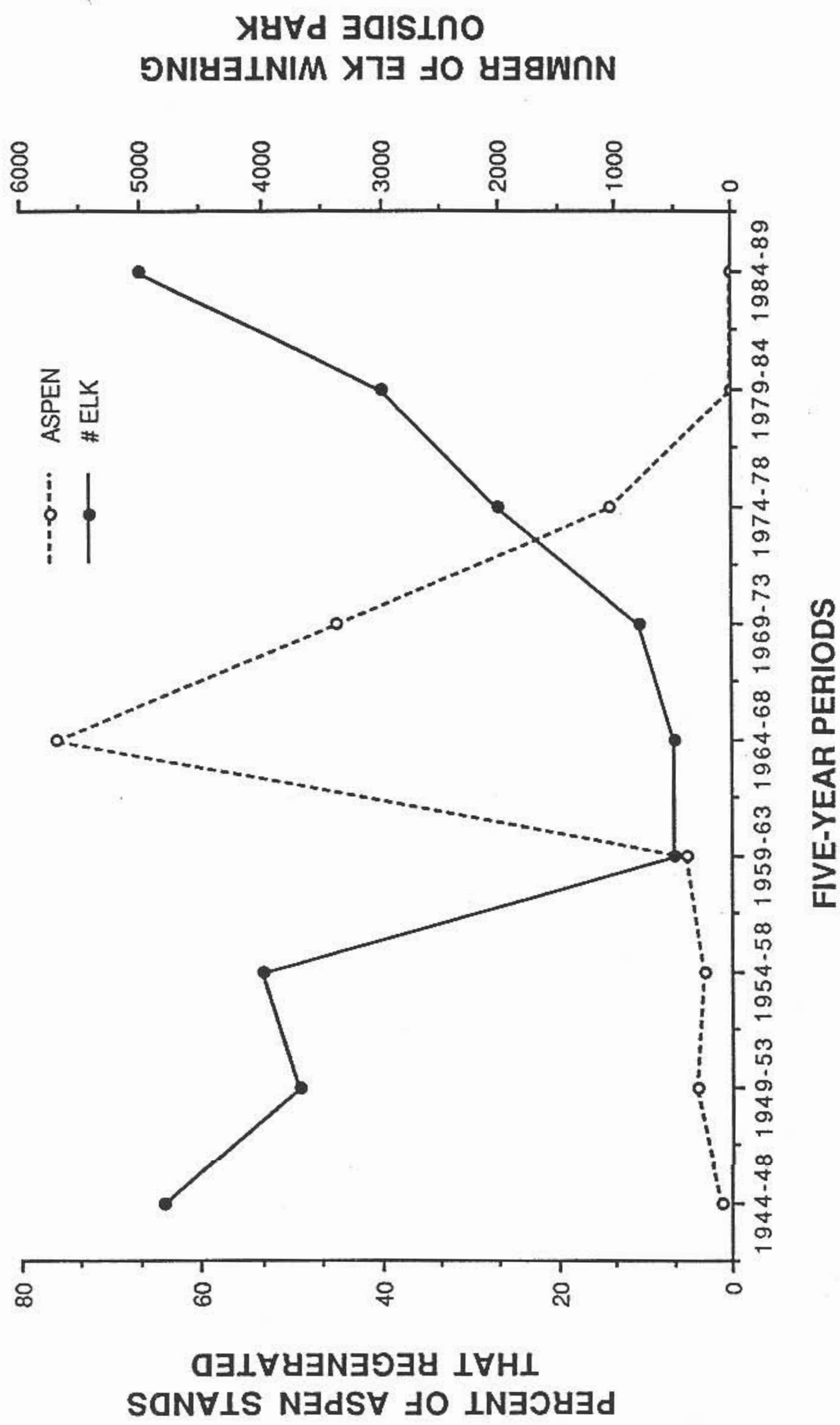
In ponderosa pine (P. ponderosa) communities, recent increases in pine have commonly been attributed to fire suppression. However, Madany and West (1983, 1984) demonstrated that ponderosa pine in southern Utah will not increase in the absence of fire unless the sites were first disturbed by heavy grazing. Sindelar (1971) reported that conifer invasion of grasslands in western Montana was most closely associated with "overgrazing," not climatic change or fire suppression. He has (B. Sindelar, pers. commun. 1988) suggested that much of the conifer invasion on Yellowstone's northern range may have been triggered by "excessive" ungulate grazing. Once conifers became established, the lack of fires then allowed them to dominate those sites.

Correlation Between Elk Numbers and Aspen Regeneration

Since fires have been suppressed in Eagle Creek and the park, and both have experienced the same general climatic trends, those factors cannot be responsible for the differences between aspen communities which I have documented. That those differences can be attributed primarily to different histories of ungulate use is illustrated in Fig. 5. When the Park Service believed there were too many elk on Yellowstone's northern range, the agency removed animals from the herd by live-trapping or killing elk in the park (see Chapter 1 above).

As the elk herd was reduced, fewer and fewer elk migrated to wintering areas north of the park such as Eagle Creek (Fig. 5). Thus, elk removals and number of out-migrating elk are inversely correlated (Table 1), and based on the age distribution of aspen stems, when few elk moved out of the park during the late 1960s and early 1970s, aspen

Fig. 5. Percent of aspen stands ($n = 74$) which regenerated during five year intervals in Eagle Creek plotted with the estimated number of elk wintering outside Yellowstone Park. From 1944 to 1966, the number of elk wintering north of the park was estimated from hunter harvest records provided by Erickson (1981) while 1967 to 1985 data are adapted from Chrest and Herbert (1985:88). The Montana Department of Fish, Wildlife, and Parks (pers. commun. 1990) provided data for 1986-89. See Table 1 for the number of elk killed and live-trapped inside Yellowstone Park from 1944 to 1989.


NUMBER OF ELK WINTERING OUTSIDE PARK
6000
5000
4000
3000
2000
1000
0
ASPEN
ELK
PERCENT OF ASPEN STANDS THAT REGENERATED
80
60
40
20
0
1944-48
1949-53
1954-58
1959-63
1964-68
1969-73
1974-78
1979-84
1984-89
FIVE-YEAR PERIODS

in Eagle Creek were able to regenerate successfully. When elk numbers were high, few stands in Eagle Creek were able to produce stems > 2m tall (Fig. 5). Olmsted (1977, 1979) reported a similar correlation between reduced mule deer and elk populations and increased aspen regeneration in Rocky Mountain National Park. In Canada's Jasper National Park, Dekker (1985a, 1985b) reported that increased wolf predation caused a decline in the elk population which, in turn, resulted in the growth of dense stands of aspen saplings for the first time in recent history.

When elk numbers were being reduced in Yellowstone, agency biologists monitored the response of aspen suckers on the northern range. Barmore (1967:7) reported "although a consistent downward trend in average percent twig [aspen sucker] use has occurred . . . browsing is apparently still too high to permit significant gain in sprout height." Houston (1982:127) concluded "there was no measurable feedback with elk density." My data show that this was not true in Eagle Creek.

Ecological Importance of Aspen

Based on other studies (Young 1973, 1977; Balda 1975; Flack 1976; Page et al. 1978; Casey and Hein 1983; Oakleaf et al. 1983; Taylor 1986; Loft et al. 1987; Putman et al. 1989), I suggest that the decline of aspen communities also may have adversely affected birds, small mammals, beaver (see Chapter 8 below), and even grizzly bears (Kay 1989). Entire plant and animal communities, not just aspen, may have been altered by ungulate use on Yellowstone's northern range. Park Service biologists have declared that the decline of aspen in Yellowstone "means relatively little to the ecological functions" of the park (Despain et al. 1986:104). In my opinion, the opposite is true. The plight of grizzly bears in Yellowstone has garnered considerable attention (Knight and Eberhardt 1984, 1985, 1987; Chase 1986). Based on what is presently known about ecosystem control and function, aspen are more important to the integrity of ecosystem function than grizzlies.

Furthermore, mature aspen trees or aspen clones do not develop from seed in the Intermountain West and have not done so for thousands of years (McDonough 1979, 1985; Schier et al. 1985). Aspen produces vast numbers of viable seeds, but conditions in this area seldom are right for germination and establishment (but see Kay 1990). It is thought that conditions may not have been favorable for clonal establishment since shortly after the glaciers receded (McDonough 1985, Schier et al. 1985). Hence, aspen clones seen today may have occupied their respective sites for 7,000 to 10,000 years through vegetative regeneration. During those thousands of years, aspen survived climatic variation and other natural phenomena. Yet normal aspen communities will be virtually extinct over much of the Yellowstone area within 50 years under present conditions (Kay 1985, 1987; Ekey 1987).

SUMMARY OF INSIDE-OUTSIDE DIFFERENCES

1. Outside the park in Eagle Creek, 89% of aspen stands have successfully produced new aspen stems > 2m tall without fire or other disturbance while those in the park have not.

2. For stems taller than 2m, most aspen stands in Eagle Creek exhibit a multi-age structure characteristic of climax aspen while those in the park do not.

3. The understories of aspen stands in Eagle Creek are dominated by shrubs and forbs characteristic of climax aspen while stands in the park are dominated by exotic grasses and forbs which increase under grazing.

4. Few aspen stands present in Eagle Creek or in the park today are being heavily invaded by conifers.

5. As judged by these indicators, most present aspen stands in Eagle Creek are long-term stable or climax. Many stands in the park exhibit this same potential but have been unable to develop multi-age

structures because of repeated ungulate browsing.

6. These inside-outside park differences are due primarily to different histories of ungulate use, not climatic change or fire suppression.

7. Aspen stands in the park are ungulate-induced grazing disclimaxes.

8. While not measured in this study, it seems probable that, given the marked differences in vegetation, there are also marked differences in faunal diversity between Eagle Creek and park aspen stands: invertebrates, small mammals, and birds. Hence, the measured vegetation differences may be indices of differences in the entire biotic communities. Repeated ungulate browsing may have impacted entire communities, not just aspen.