The Parker Transects Revisited—Long-term Herbaceous Vegetation Trends on Yellowstone's Northern Winter Range

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Abstract. A method to rapidly assess range condition and trend from line transect measurements of basal area and species composition was first applied in Yellowstone in 1958 in association with 2-ha grazing exclosures established on the northern winter range. Transects in and out of the exclosures were resampled in 1962, 1967, 1974, 1981, 1986 and 1989. Total live plant frequencies increased significantly both in and out of exclosures between 1967 and 1981 and decreased from 1981 to 1986. Changes in plant frequencies between 1958 and 1989 were much more significant than changes because of exclosure from grazing. Precipitation variability was the most probable cause of these temporal changes, as suggested by correlations between precipitation and plant frequencies. Exclosure had no effect on total live plant frequencies. The increase in total plant frequency until 1981 implied a converse decrease in bare ground. The decrease in plant frequency after 1981 was climatically driven, as evidenced by parallel changes outside and within exclosures. Dominant perennial grasses either maintained their relative abundance or increased until 1986. Forbs decreased in relative abundance until 1986 and increased after 1986 in response to drought. On the basis of these trends obtained by application of Parker transects, we conclude that elk winter grazing has not degraded the herbaceous component of the Yellowstone northern winter range. We recommend, however, that the Parker data be converted to basal area using a recent algorithm and that the technique be dropped in favor of less problematic methodologies.

Yellowstone National Park's (YNP) management of ungulates requires reliable long-term monitoring of trends in vegetation cover and plant species diversity (Beetle 1974; Cayot et al. 1976; Houston 1982; Coughenour and Singer 1991). Rangeland measurements date back to the 1930's on the northern range (W. H. Gammill, Range studies of 1939–41, Yellowstone National Park, unpublished data; R. L. Grimm, Range studies of 1935–38 and 1943–47, Yellowstone National Park, unpublished data). The park's current range monitoring program was initiated in 1958–62 (Denton 1958; Bergstrom 1962; Barmore 1980). Eight 2-ha exclosures were constructed in 1958 and 1962 along with a series of permanently marked Parker transects (Parker 1954; Francis et al. 1972). Vegetation intercepts within 1.9-cm loops were measured along the transects. These transects have constituted the principal long-term sampling program of herbaceous vegetation on the Yellowstone northern winter range.

The Parker transect methodology may be outdated and may be inadequate for detecting vegetation change. Parker transect data are obfuscated by differing effects of plant density, shape, size, and size class distribution of plants. As a result, Parker transects are difficult to interpret (Francis et al. 1972; Houston 1982). The data cannot be analyzed in a straightforward, mechanical manner (Francis et al. 1972; Risser 1984). Computer algorithms have only recently been developed to convert Parker frequencies to basal area (Brady et al. 1991; Cook et al. 1992). Parker transect frequencies often overestimate the most common plant species (Cook and Box 1961). A positive bias towards higher frequency in comparison to cover of smaller plants has been reported (Francis et al. 1972). Therefore, Parker frequencies should not be expected to be correlated with estimates of plant cover (Risser 1984). Parker frequencies showed poor relations with plant cover, herbaceous weight, and plant density (Francis et al. 1972). As a result, the

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northern regions of the U. S. Forest Service dropped Parker transect readings in 1982 (D. Tyers, U.S. Forest Service, Gardiner, Montana, personal correspondence). Small sample sizes limit the power of statistical tests, particular for tests of individual species abundances. Species data have necessarily been pooled together to conduct statistical tests (Barmore 1980; Houston 1982). Yet, comments on YNP's ungulate management program have expressed concern over possible species increases or decreases because of possible excessive grazing of the range (Beetle 1974; Chase 1986).

The purpose of this investigation is to reexamine the Parker transect results. We report on more recent trends on Parker transects during 1981–89 which have not been reported following Houston's (1982) report. We attempt to correlate the plant frequency to weather and ungulate population trends. We also compare Parker frequencies to measures of plant cover and biomass from the same sites, and evaluate the Parker transect method.

Methods

Study Sites

The lower winter range study site was located below Mammoth and near the park boundary at Gardiner, Montana. Elevations of the lower winter range are 1,500–2,000 m. The growing conditions are relatively xeric. Precipitation averages 20 cm/year. Less snowfall, faster melting and wind removal of snow from the slopes relative to the upper winter range result in easy access to forage and high use by wintering elk.

The higher elevation (2,000–2,400 m) grassland study sites on the upper winter range were located near Mammoth, Blacktail Creek, Junction Butte, and the Lamar Valley. The upper winter range grasslands tend to be more mesic and more productive than those of the lower winter range; precipitation ranges from 30 cm/year at Mammoth to 55 cm/year at the Lamar ranger station.

Weather Data

Monthly precipitation data were obtained for Mammoth (YNP), Tower Ranger Station, Lamar Ranger Station, Gardiner, and Cooke City. Precipitation data were summarized by site and season. Fall included September–October. Winter precipitation included that in November–March. Spring included April–May. Summer included June–August. Precipitation from September of the preceding year through August of a given year was summed to yield water year precipitation because fall and winter precipitation are manifested in plant growth measurements the following summer. Precipitation for Gardiner was used for the lower winter range site whereas precipitation data for Mammoth, Tower, and Lamar were averaged for correlations with plant growth measurements made on the upper winter range.

Vegetation Sampling

Parker transects were established in 1957 and 1962 in conjunction with 2-ha grazing exclosures on the northern winter range (Barmore 1980; Houston 1982). Six exclosures were established on the four sites of the upper winter range and two exclosures were established on the lower winter range site. Transects were sampled in 1958, 1962, 1967, 1974 (Barmore 1980; Houston 1982), 1981, 1986, and 1989. The original intent of the method was to monitor trends in range condition, primarily by detecting changes in relative species abundances and changes in total vegetated soil surface relative to nonvegetated soil surface. The transects were part of the Parker three-step method: step one—establish transects and record data; step two—analyze the data; step three—establish permanent photopoints (camera location and azimuth) on the range. Permanent line transects 32.8 m (100 feet) in length were established. A 1.9-cm (3/4-inch) loop was lowered to the ground at 30.5-cm (1-foot) intervals, and contacts with plant tissues were recorded. Contacts were classified by species, litter, or type of abiotic material. Data comprised total contact counts for each species and material. Perennial grasses and forbs must have had their root crown within the loop to have been recorded. Transects were organized in paired clusters of one to three—but normally two, with one cluster inside and one cluster outside an exclosure. Thus, 2–6 transects were present per site with about half inside and half outside exclosures. Each cluster pair was selected to represent similar topography and soil. Fourteen clusters containing 29 transects were established inside and 9 clusters containing 18 transects were established outside exclosures. Transects within each pair were located on similar soils and topography. Overstory shrub data were also collected (i.e., shrubs with canopies well above the herbaceous vegetation layer) but these data were not used here because few shrubs were located on any of the transects. Results from a parallel belt transect survey (a better methodology for measuring large shrub abundance) are reported elsewhere (Houston 1982). Dwarf shrubs, however,

were included in the analyses because their shoots were contained within the herbaceous stratum. Our conclusions are thus restricted to the responses of the predominantly herbaceous understory.

A repeated-measures two-way analysis of variance was performed with year and exclosure from grazing as main effects. Cluster means rather than transects were replications because transects within a cluster are nonindependent by definition and because the low number of transects per cluster (usually 2) prohibits accurate assessment of within-cluster variance. Repeated measures ANOVA was used because the same clusters were read every year. Thus, the analysis corrects for possible correlations of frequencies within a given cluster over time. A univariate repeated ANOVA used data from all sample years. Multivariate repeated ANOVA's were also calculated, but only the years 1974–89 could be included because of high numbers of missing values for clusters in earlier years. Exclosure effects were also tested with *t*-tests comparing means inside and outside exclosures in individual years. If variances were unequal, a t' statistic was used (Sokal and Rohlf 1981). Proportion data were transformed with the arcsine function before testing. Duncan's multiple range test was used to determine differences among yearly means.

The Parker transect data were correlated against seasonal, annual, and multiannual precipitation data. Data from inside and outside exclosures were pooled at each site for correlations on precipitation because of lack of significant exclosure effects (Barmore 1980; Houston 1982; this study).

Results

Total live plant frequencies (Fig. 1a) increased from 1967 to 1981 (Houston 1982) and decreased from 1981 to 1986, both inside and outside exclosures. Whereas the decrease from 1981 to 1986 reduced lower winter range frequencies to pre-1974 levels, upper winter range frequencies were greater in 1986 than in 1958–67. Lower winter range frequencies were consistently less than those on the upper winter range, probably as a result of a warmer, drier climate near Gardiner. Significant temporal changes occurred only between 1967–74 and 1981–86 (Fig. 1a). In comparison, elk numbers declined from 1956 to 1968, then generally increased from 1968 to 1988 (Fig. 1b).

ANOVA indicated *Koeleria macrantha* and *Poa* spp. were more abundant outside than inside exclosures (Table 1), however, an interaction existed between exclosure and year effects on *Poa* spp. However, *t*-tests indicated significant differences between inside and outside exclosure frequencies for *K. macrantha* in 1974 only ($P < 0.05$), with marginally significant differences ($0.05 < P < 0.01$) in 1986 and 1989 (Table 2). The exclosure effect on *Poa* spp. was limited to 1989, with a marginally significant effect in 1974. There were no significant differences in plant frequencies inside versus outside lower winter range exclosures (Tables 1 and 2), despite notable changes in elk population numbers (Fig. 1b). Data for means of plant frequencies in each cluster are provided in Appendix Tables 1 and 2 in this report to facilitate potential uses by others in the future.

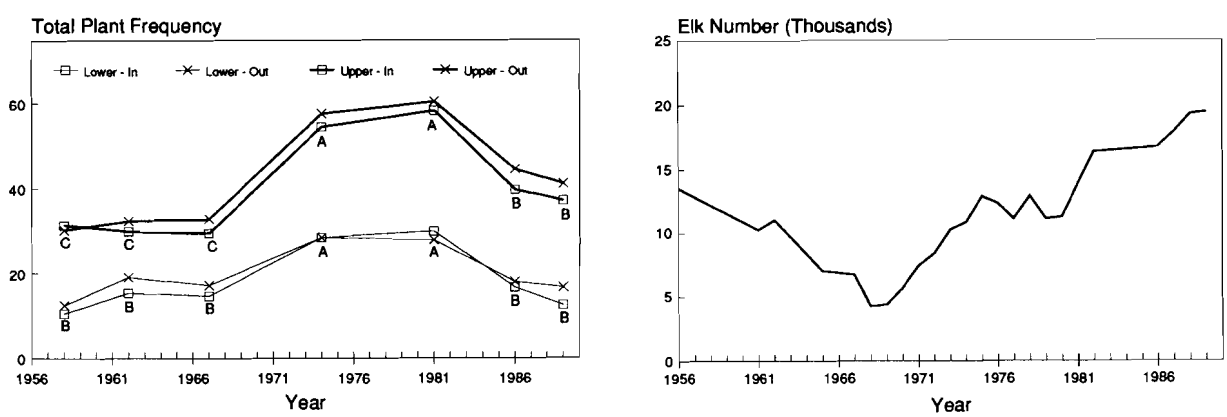

Fig. 1. (*a—left*) Total plant frequency on upper and lower winter range, inside and outside exclosures. There were no significant differences between frequencies in and out of exclosures. Means for years (upper or lower winter range) having the same letter are not statistically different ($P < 0.05$). (*b—right*) Elk numbers on Yellowstone's northern winter range.

Table 1. Significance testing using repeated measures ANOVA (univariate approach) for effects of year and exclosure.[a]

	Upper winter range			Lower winter range
Variable	Year	Exclosure	Year × exclosure	Year
Grass	***[b]			*[b]
Forb		***		m[b]
Dwarf shrub				**[b]
Agropyron spicatum				
Festuca idahoensis	***			
Koeleria macrantha	***	*		***
Poa spp.	***	*	*	**
Total	***			***
Grass (%)	**			
Forb (%)	**			***
Dwarf shrub (%)				m
A. spicatum (%)	m			
F. idahoensis (%)	***			
K. macrantha (%)		**		**
Poa spp. (%)	***	*	**	*

[a]No significant exclosure main effects or year × exclosure interactions on the low elevation winter range were evident.
[b]* = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$; and m = marginal, $0.05 < P < 0.10$.

Proportions of species and plant functional groups changed over time (Fig. 2). Grass proportion declined during 1958–62, then increased during 1974–81 and declined again during 1986–89. These changes were mirrored by an increase in the proportion of forbs 1958–62, a decrease in 1974–86, and an increase again in 1986–89. Dwarf shrub fraction did not change significantly with time. *Agropyron spicatum* fraction declined in 1958–62. *Festuca idahoensis* fraction increased in 1962–67 and 1981–86, but declined in 1986–89. *K. macrantha* fraction declined in 1958–67, increased in 1974–81,

Table 2. Total grass, forb, and dwarf shrub frequencies.[a]

	Grass		Forb		Dwarf shrub	
Year	In	Out	In	Out	In	Out
			Upper winter range			
1958	25.5(15.0)3	24.2(11.1)3	5.4(4.4)2	5.8(3.1)3	0.6(0.52)3	0.17(0.29)3
1962	19.6(5.7)8	22.4(8.9)5	9.8(4.5)8	9.9(4.5)5	0.69(0.88)8	0.0(0)5
1967	17.3(5.2)8	21.6(10.6)5	11.7(8.6)8	10.9(7.3)5	0.48(0.47)8	0.40(0.55)5
1974	34.1(5.9)10	41.3(10.4)7	19.4(6.3)10	16.1(4.4)7	0.96(1.6)10	0.21(0.29)7
1981	41.5(13.2)10	46.3(10.0)7	16.4(7.1)10	13.2(4.9)7	0.46(1.0)10	1.0(1.2)7
1986	30.9(9.5)10	35.0(8.0)7	8.8(4.0)10	9.4(3.6)7	0.02(0.06)10	0.18(0.24)7
1989	23.7(7.8)10	27.9(6.5)7	13.2(4.9)10	12.8(4.5)7	0.26(0.44)10	0.41(0.72)7
			Lower winter range			
1958	6.8(3.2)2	7.7(3.9)2	2.7(0.35)2	4.7(3.2)2	1.0(0.71)2	0.0(0)2
1962	9.2(4.6)3	11.2(6.1)2	3.8(2.7)3	5.5(0.49)2	2.6(1.8)3	2.5(1.9)2
1967	5.2(1.5)3	9.0(4.9)2	6.2(3.7)	36.7(0.35)2	3.3(2.5)3	1.5(2.1)2
1974	16.8(9.8)4	13.9(8.3)2	3.4(2.5)4	2.3(2.6)2	8.3(3.5)4	11.9(15.4)2
1981	17.8(6.2)4	18.5(17.7)2	3.6(3.6)4	1.6(1.2)2	8.5(1.9)4	7.9(10.4)2
1986	11.5(4.8)4	10.3(2.6)2	0.70(0.77)4	1.6(2.3)2	4.5(2.5)4	6.1(7.2)2
1989	6.0(4.0)4	5.9(2.9)2	5.2(5.5)4	8.5(4.6)	21.3(1.1)4	2.5(1.4)2

[a]Mean(standard deviation)*n*. Here, *n* is the number of clusters sampled each year. For these aggregate plant groups there were no significant differences between inside and outside exclosures (*t*-tests, each year). Units are hits/transect.

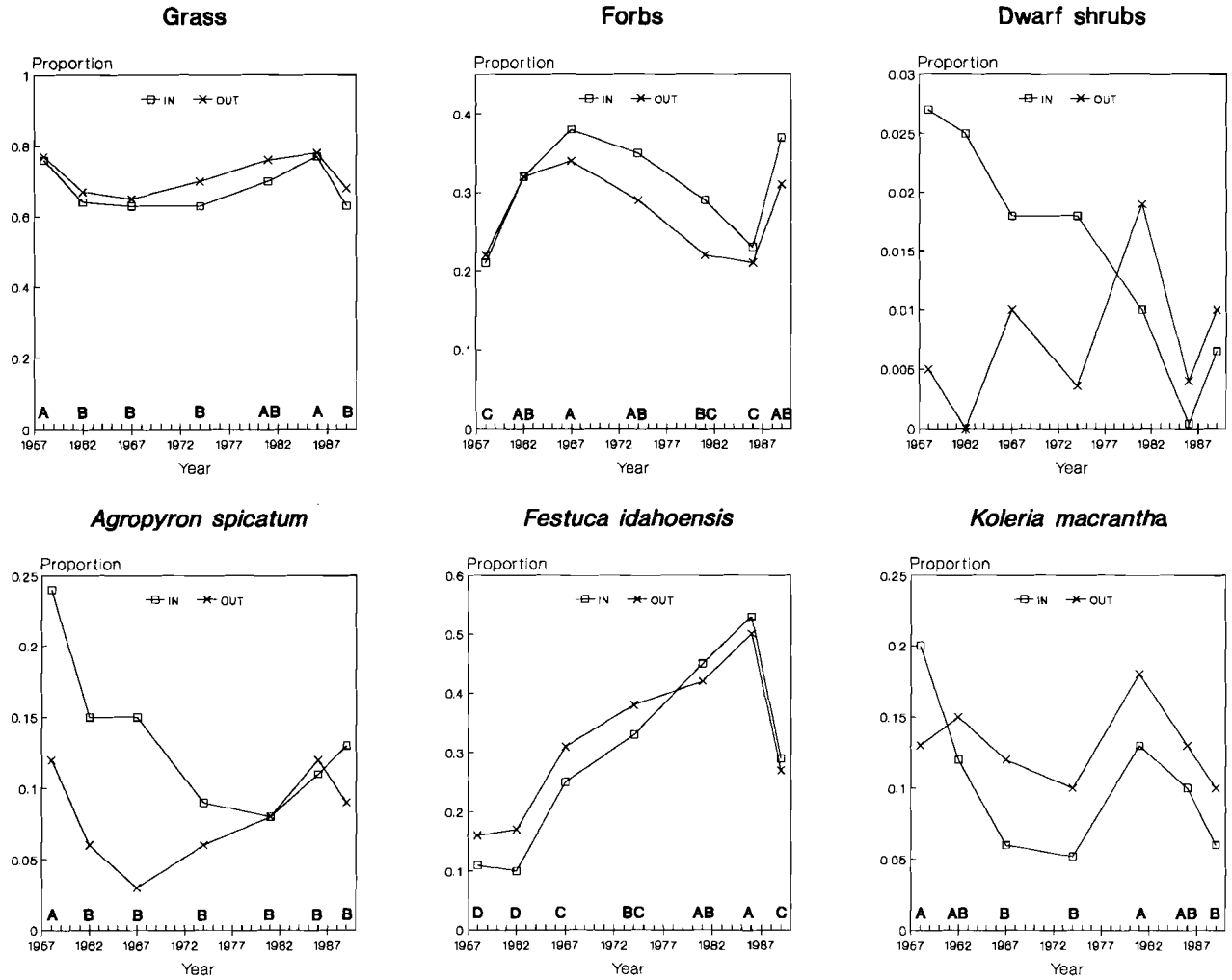

Fig. 2. Proportions of plant groups and major species in the Parker transect data from the upper winter range. Means for years with the same letter above the *X*-axis are not significantly different ($P < 0.05$). The single significant difference between exclosed and nonexclosed proportions in a given year was *Koeleria macrantha* in 1974.

and decreased in 1986–89. *Poa* spp. fraction declined 1974–81, but increased again in 1986–89.

Proportions changed in similar patterns over time on the lower winter range (Fig. 3). No significant changes in the proportion of grass over the years were detectable. Forb proportion declined significantly, however, from 1968 to 1972, and increased from 1986 to 1989. Dwarf shrub fraction increased significantly between 1958 and 1976. The fraction of *A. spicatum* did not change significantly as sample sizes were small relative to variance. *K. macrantha* increased from 1962 to 1976, from 1976 to 1981, then decreased from 1986 to 1989. *Poa* spp. decreased from 1976 to 1981, and increased from 1986 to 1989.

On the upper range, however, the fraction of *Poa* spp. was relatively more abundant outside exclosures in 1989. The fraction of *K. macrantha* was significantly greater outside the exclosure in 1974 only (*t*-test, $P < 0.001$). On the lower range it appeared that *A. spicatum* relative abundance had declined outside exclosures by 1989, however the difference was not significant in any test ($P < 0.1$). In 1989, *A. spicatum* was 0, 12, 24, and 45% of total plant hits in the four clusters inside and 0 and 7% of the two clusters outside the lower range exclosures (refer also to Appendix Tables 1 and 2 for individual cluster data).

The multivariate repeated measures MANOVA for 1974–89 yielded only slightly different results from Table 1. On the upper winter range MANOVA indicated significant year × exclosure effects on *A. spicatum* ($0.01 < P < 0.05$) and percent *A. spicatum* ($0.05 < P < 0.1$). The year × exclosure effects on *Poa* and percent *Poa* were marginal in MANOVA ($0.05 < P < 0.1$). On the lower range, MANOVA indicated no year effects on forb, dwarf shrub, percent forb, or percent dwarf shrub. A significant year × exclosure

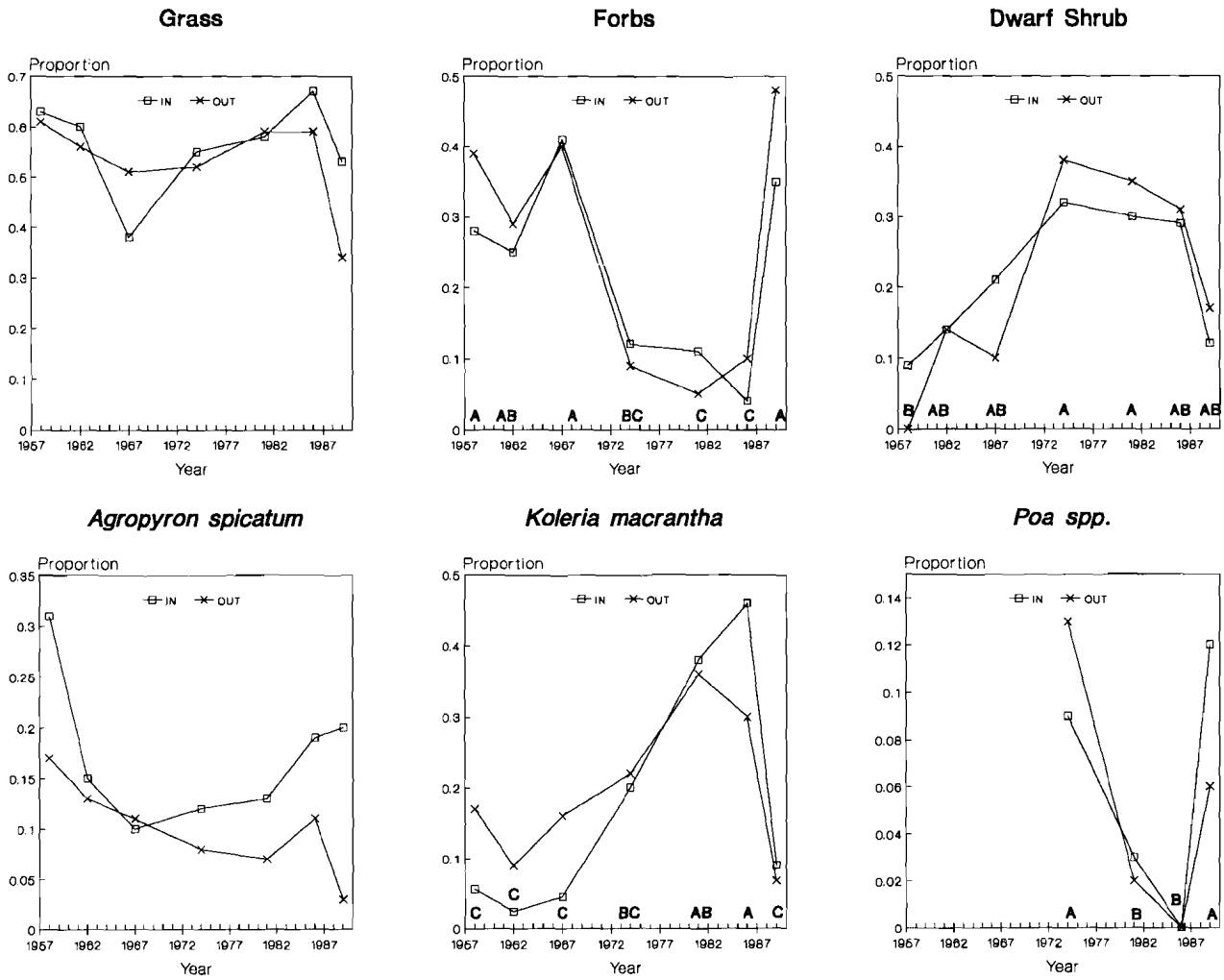

Fig. 3. Proportions of plant groups and major species in the Parker transect data from the lower winter range. Means for years with the same letter above the *X*-axis are not significantly different ($P < 0.05$). There were no significant differences between frequencies inside and outside exclosures in any given year.

effect on percent *K. macrantha* ($0.01 < P < 0.05$) was present.

Climatic causes of changes in total plant frequencies among years were explored with correlation (Table 3). Correlations were attempted between all vegetation variables and seasonal precipitation in the current year, the previous year, and the mean of all years since the previous Parker sample date. Only correlations that were significant at $P < 0.1$ are displayed in Table 3. On the upper winter range, *K. macrantha* was highly correlated with summer precipitation in the current year. The composition of percent grass versus forb was highly correlated with precipitation in the previous winter; wet winters favored grass over forbs. *F. idahoensis* was highly correlated with summer rainfall over the period since last sampling. Weaker correlations were observed between previous winter precipitation and *A. spicatum* and *K. macrantha*, previous summer rainfall and total grass, and period winter precipitation and dwarf shrub.

On the lower winter range, a significant correlation was observed between period spring rainfall and forb and dwarf shrub abundances (Table 3). Forbs were favored by wet springs whereas dwarf shrubs were disfavored. The percentage of forbs tended to be greater in years with wet springs; *A. spicatum* percentage was greater in years with wet winters in the previous year; grass percentage was greater if previous year's summer was wet and dwarf shrub was greater when fall of the previous year was wet.

Seasonal precipitation data for each year were examined to seek a finer resolution explanation for the rise in Parker frequencies between 1967 and 1974 (Fig. 4). There were no runs of unusually wet falls,

Table 3. Significant correlations with seasonal and total precipitation in the current year, the previous year, and the period between the previous sample date and the current sample date (3–8 years).[a]

Variable	Correlation coefficient (r)
Upper winter range	
Current year—summer	
Koeleria macrantha	0.82[b]
K. macrantha (%)	0.70[b]
Previous year—winter	
Agropyron spicatum	0.66[c]
K. macrantha	0.72[c]
Grass (%)	0.82[b]
Forb (%)	–0.81[b]
Period—summer	
Grass	0.69[c]
Festuca idahoensis	0.87[b]
F. idahoensis (%)	0.95[b]
Period—winter	
Dwarf shrub (%)	0.67[c]
Lower winter range	
Current year—spring	
Forb (%)	0.78[c]
Previous year—winter	
A. spicatum (%)	0.79[c]
Previous year—summer	
Grass (%)	0.65[c]
Period—fall	
Dwarf shrub (%)	0.67[c]
Period—spring	
Forb	0.84[b]
Dwarf shrub	–0.70[c]
K. macrantha	–0.74[b]
Forb (%)	0.90[b]
Dwarf shrub (%)	–0.82[b]

[a]In all cases $n = 7$.
[b]$P < 0.05$.
[c]$0.05 < P < 0.1$.

winters, or springs that would explain the increase. Summer 1968 was exceptionally wet; June and August were both wet and September was moderately wet.

Discussion

Responses to Climate

Changes in plant frequencies between 1958 and 1989 were much more significant than changes because of exclosure (Table 1). Climate, specifically precipitation, was the most probable cause of these temporal changes (Table 3). The marked increases in *F. idahoensis* on the upper winter range and of dwarf shrubs and *K. macrantha* on the lower winter range between 1967 and 1974 (Table 4) were most responsible for the large increases in total plant frequency over that period (Fig. 1).

A plausible explanation for the large increase in total plant frequency on the upper range between 1967 and 1974 was an increase in *F. idahoensis* in response to a favorable year for germination and seedling establishment. This year could have been 1968, when summer rainfall was far above normal (Fig. 4). A single favorable year for germination and establishment would, if not followed by drought, be followed by a steady increase in plant size. The combination of increased plant number and size could explain the increase in Parker frequency. The increase between 1967 and 1974 on the lower range site was in dwarf shrubs and *K. macrantha*. According to the correlations, these plants increase during relatively dry springs. Indeed, there were no wet springs during 1967–74.

Total plant frequency decreased between 1982 and 1986. This roughly paralleled a declining trend in precipitation. In particular, the spring of 1983 was dry, and this was preceded by a relatively dry winter. A dry spring also occurred in 1979, but this was preceded by a wet winter. The dry winter–dry spring pattern could have increased plant mortality in 1983. The dry years of 1987 and 1988 caused an insignificant decrease in frequencies 1986–89, but spring was moist in both years.

Plant community composition proved to be dynamic, rather than static, both inside and outside of the exclosures (Figs. 2 and 3). Changes in relative abundances of species and plant functional groups over time were likely the results of changing weather patterns over the period. Community changes included a decline in the proportion of *A. spicatum* 1958–62 on upper and lower ranges, along with an increase in proportion of forbs on the upper range and in dwarf shrubs on the lower range. The forbs observed here were mostly perennials. As such, their abundances depend on climatic events that affect germination, establishment, and survival. Changes in the abundances of long-lived perennial grasses probably affect the space available for forb and dwarf shrub establishment, as suggested by the inverse relations between forbs or dwarf shrubs and *A. spicatum*.

The increase in the proportion of *F. idahoensis* on the upper winter range over the years 1962–74 was accompanied by decreases in *A. spicatum* and *K. macrantha*, suggesting possible competition between dominant perennial grasses. Correlations suggested that competitive interactions between plant groups are altered by precipitation (Table 3). The percentage of grass was positively correlated and the

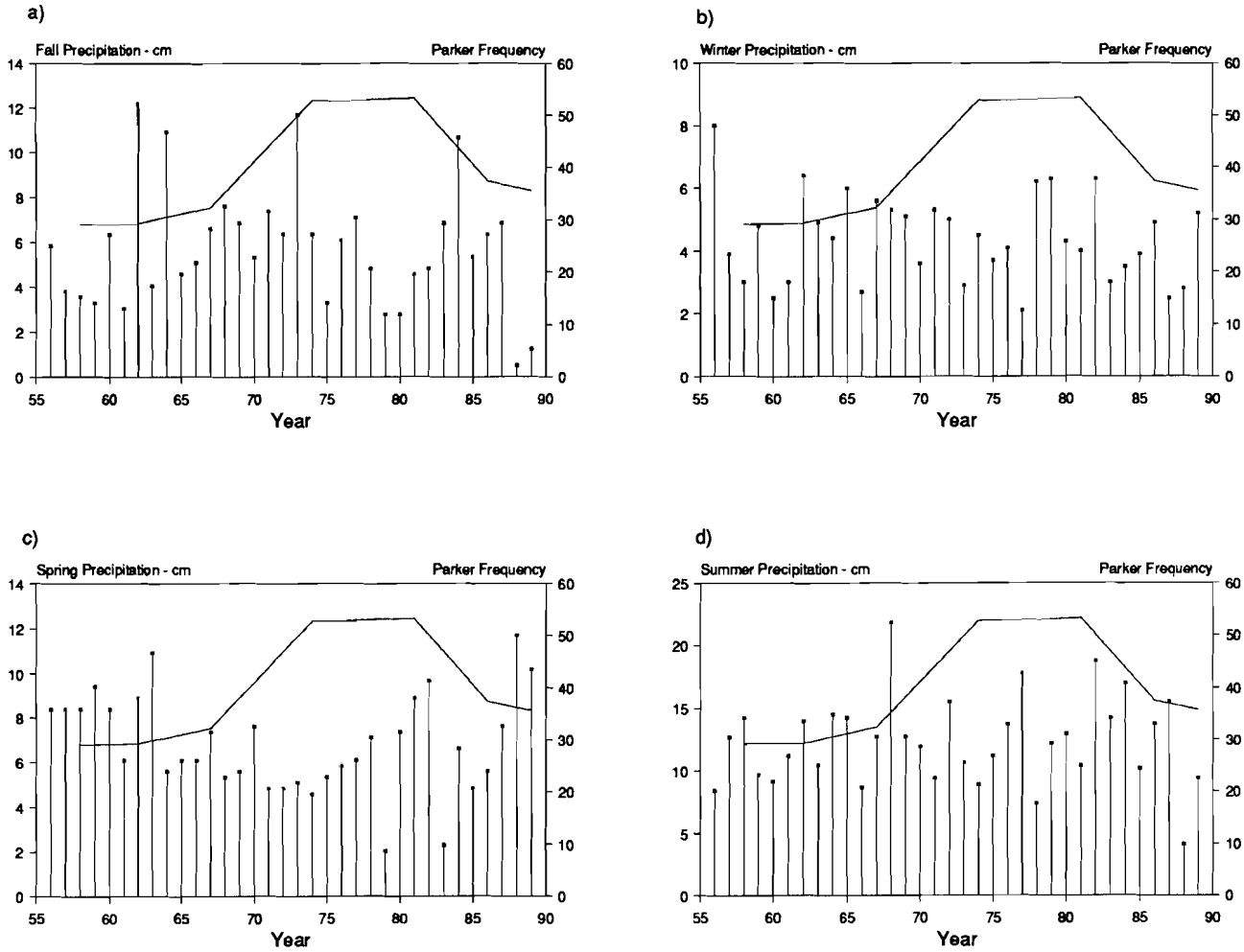

Fig. 4. Seasonal precipitation over the period in comparison to total plant frequency: (*a*) fall; (*b*) winter; (*c*) spring; (*d*) summer. Precipitation is displayed as bars, Parker frequency is displayed as a line.

percentage forb was negatively correlated with winter precipitation on the upper range, suggesting that wet winters shift the competitive balance towards grass. On the lower winter range, *K. macrantha* and dwarf shrubs generally decreased whereas forbs increased, and their correlations with spring precipitation were also opposite. The latter relations suggested that forbs may respond favorably to spring rainfall, and when they do, they become increasingly competitive with perennial grasses.

If climatic events are stochastic, and if plant community composition responds to these fluctuations, then the concept of a singular climax community composition becomes untenable. Rangeland plant community compositions may change in response to weather events and patterns, irrespective of grazing (Westoby et al. 1989; Coughenour and Singer 1991; Friedel 1991; Laycock 1991). Differences among species in their responses to climatic events inevitably cause changes in plant community composition. Temporal changes in composition may simply arise from secondary competitive interactions among plants. For example, a dry year may cause mortality of one perennial grass species, which provides an opportunity for establishment of another species given another climatic event.

Changes are sometimes momentous as environmental thresholds for various plant population events are crossed (Westoby 1991; Friedel 1991; Laycock 1991). Movements across thresholds may or may not be irreversible. There was no evidence for such shifts here. The changes that were observed here, however, point out that the long prevailing, steady-state climatic climax plant community of Clements (1916) should be thought of as dynamic, with responses to short term climatic fluctuations, as Clements originally discussed. Fortunately, an experimental control for the grazing treatment (inside exclosures) showed that plant

Table 4. Major grass species frequencies.[a]

Year	*Agropyron spicatum* In	*Agropyron spicatum* Out	*Festuca idahoensis* In	*Festuca idahoensis* Out	*Koeleria macrantha* In	*Koeleria macrantha* Out	*Poa* spp. In	*Poa* spp. Out
				Upper winter range				
1958	6.8(2.4)3[b]	3.3(.85)3[b]	4.1(6.8)2	5.1(4.5)3	5.4(3.8)3	3.8(1.2)3		
1962	4.9(3.5)8[b]	1.8(1.2)5[b]	3.3(3.8)8	5.8(5.3)5	3.4(3.5)8	4.5(2.6)5		
1967	4.4(6.4)8	1.0(.35)5	6.8(4.4)8	10.6(5.8)5	1.6(2.1)8	3.2(1.6)5		
1974	5.0(3.4)10	3.2(1.8)7	18.6(10.1)10	22.4(7.2)10	2.7(2.1)10[c]	5.9(2.2)7[c]	3.6(1.7)10[b]	5.9(3.2)7[b]
1981	4.1(3.9)10	4.8(2.3)7	28.6(18.8)10	25.3(9.0)7	6.7(4.8)10	11.8(8.0)7	0.62(1.1)10	0.0(0.0)7
1986	4.2(4.4)10	5.3(3.2)7	21.8(11.9)10	22.3(6.4)7	3.1(2.7)10[b]	5.9(3.4)7[b]	0.18(0.33)10	0.0(0.0)7
1989	4.9(3.9)10	3.6(2.4)7	12.1(9.4)10	11.0(3.7)7	2.3(1.9)10[b]	4.4(3.0)7[b]	0.65(1.3)10[c]	4.6(5.2)7[c]
				Lower winter range				
1958	4.0(5.6)2	2.2(3.2)2			0.75(1.1)2	2.2(3.2)2		
1962	1.8(1.6)3	3.0(4.2)2			0.80(0.87)3	2.0(2.8)2		
1967	1.3(1.1)3	2.1(2.9)2			0.67(0.76)3	3.0(4.2)2		
1974	3.8(3.3)4	2.0(2.8)2			5.3(1.8)4	5.6(6.5)2	2.5(0.6)4	3.9(2.9)2
1981	4.5(5.2)4	2.2(3.2)21			1.0(4.7)4	11.2(10.9)2	1.0(0.7)4	0.8(1.0)2
1986	3.6(3.4)4	1.8(2.5)2			7.7(2.0)4	5.5(2.1)2	0.0(0)4	0.0(0)2
1989	2.4(2.7)4	0.8(1.1)2			1.0(0.82)4	1.1(0.14)2	1.6(1.4)4	1.0(0.0)2

[a]Mean(standard deviation)n. Here, n is the number of clusters sampled each year. Significant differences between inside and outside exclosures were tested with t-tests in each year. Units are hits/transect.
[b]$0.01 < P < 0.05$.
[c]Marginal, $0.05 < P < 0.1$.

community changes that otherwise might have been ascribed to grazing were, instead, the result of climate.

Responses to Elk Grazing

The ANOVA indicated that there was more *K. macrantha* and *Poa* spp., outside exclosures in certain years. Similarly, the only grazing related differences detected by Barmore (1980) were slightly, but significantly higher graminoid frequencies outside exclosures and this was interpreted as spurious. There were no significant exclosure effects on frequencies on the lower winter range (Table 1).

The only significant exclosure effects were increases in *K. macrantha* and *Poa* spp. the result of grazing, and consistent parallel changes in frequencies inside and outside exclosures, indicating that elk grazing has not impaired herbaceous plant growth on the northern winter range in spite of fluctuations in elk numbers (Fig. 1b). Houston (1982) also concluded from his analysis of Parker transect data 1958–74 that grazing had no significant effect on perennial grasses, forbs, shrubs, total perennial vegetation, bare ground, or litter. Pavement decreased inside exclosures, probably because of increases in dead plant material. Direct sampling of plant biomass (Coughenour 1991) also revealed no differences in total root biomass inside versus outside exclosures. No differences in aboveground plant biomass inside versus outside were observed in 1987. Grass biomass was reduced outside exclosures in 1988, but elk remained on the winter range longer that spring (D. Vales, University of Idaho, personal communication). Frank (1991) documented increases in plant growth due to grazing.

Two differences in species composition were observed between the inside and outside of the upper winter range exclosures. *K. macrantha* and *Poa* spp. were relatively more abundant outside exclosures, but only in certain years. *K. macrantha* was significantly more abundant (relative and absolute) outside exclosures only in 1974. *Poa* spp. was more abundant outside exclosures only in 1989. These differences in composition are limited but positive responses to grazing (Figs. 1–2).

On the lower winter range there seemed to be progressively decreasing relative abundance of *A. spicatum* outside exclosures, particularly from 1986 to 1989 (Fig. 3). Variances among clusters, however, were high, the number of clusters was small, thus the differences were not significant. The trend of increasing divergence between relative *A. spicatum* abundances in and out of exclosures was most pronounced during the drought year of 1988. Elk used the lower winter range heavily during the severe winter of 1988–89 when much of the herd died. The combined effect of drought and increased elk use could have been particularly stressful, but the response was inconsistent among clusters.

A widespread method for assessing rangeland condition is that derived from Dyksterhuis (1949). The

method evaluates condition with respect to changes in cover of plant species which typically either increase or decrease in response to overgrazing. Most often, overgrazing will cause decreases in dominant perennial grasses, increases in weedy forbs and increases in bare ground. On the Yellowstone winter range, total plant frequency increased until at least 1981. By definition, this was necessarily accompanied by a converse decrease in bare ground. The decrease in plant frequency after 1981 was climatically driven, as evidenced by parallel changes outside and within exclosures. Dominant perennial grasses either maintained relative abundance, or increased. Forbs decreased until 1986, and increased after 1986 in response to declining grass during drought. On the basis of these trends, we cannot conclude that elk grazing has degraded the Yellowstone northern winter range.

Elk use the winter range during a time of year when most plants are dormant and after seasonal production has already occurred. Thus, elk grazing would not be expected to have large effects on the plant community except through responses to trampling, removal of dead leaves, and increased rates of nutrient recycling (see also Coughenour 1991). Although herbaceous plants are largely snow-covered, herbaceous plants comprised 90% of the diet of elk wintering in 1985–99 (Singer and Norland 1991).

The Method

Parker transect data primarily reflect, but overestimates, basal cover rather than aboveground standing crop; the protocol requires that plant bases are within the sampling loop. Basal cover is primarily affected by the number of plants and the size of the perennating root crown of bunch grasses. Frequencies of forbs are more strongly affected by the numbers of plants and their stem diameters. Basal area of perennial bunch grasses changes more slowly than, and is not necessarily correlated with, annual variations in peak aboveground standing crop. For example, a large basal area may have accumulated because of previous wet years, but a subsequent dry year may cause low grass production without reducing basal area. Plant productivity is determined by plant height and leaf length as well as by basal area.

A problem with the technique is that it is influenced by plant size and plant numbers in different ways. The method is biased towards higher frequencies if plants have small basal area (Hutchings and Holmgren 1959; Smith 1962; Francis et al. 1972). Measurements are also affected by the shape of plants and the pattern of their distribution, such that there is positive bias towards plants with noncircular shapes (Hutchings and Holmgren 1959). Even with constant basal area then, changes in plant size and shape influence Parker frequencies. Thus, any changes in plant form because of grazing or climate could confound interpretation. If plants were larger in an exclosure for example, the measured grazing effect would be diminished because the method is biased towards smaller plants.

Insufficient sample size may be the most serious limitation of the method. Each half of a cluster pair in YNP is comprised of one to three transects or 100–300 hits on an exclosed/nonexclosed treatment at a site. The number of 100-ft transects required to measure dominant grasses at 95% confidence within 10% of the mean can vary from 2 to 68 (Johnston 1957). Smith (1962) concluded that 200–3,400 hits (loops) are required to establish 95% confidence intervals that are within 10% of the mean, depending on plant abundance. Everson et al. (1990) reached a similar conclusion for plant frequency hits. They estimated that 1,200 hits of a Tidmarsh wheel (Everson et al. 1990) were required to detect changes of plant species comprising 5% or more of the community within 90% confidence intervals that are +20% of the mean. Pooling of species improves accuracy statistically (Smith 1962). Because of limited sample sizes, Barmore (1980) and Houston (1982) were forced to pool plant species frequencies for YNP to conduct statistical tests. Unfortunately, pooling of plant species represents a loss of information.

Plant frequencies measured with the Parker transect method in Yellowstone had high variances. This problem is partly because of small numbers of transects, but also from landscape heterogeneity. Stratification of samples on the landscape could reduce variance. The organization of transects into clusters that have similar soils and plant communities is a form of stratification; but statistical tests cannot be conducted with 1–2 samples per strata. Here, we were forced to treat clusters as samples because the transects are nonindependent and the number of transects per cluster was too small to assess within-cluster variance. Despite the heterogeneity that was covered by the transects, the transects were located primarily on upland sites (Beetle 1974; Houston 1982). No transects were located in swales or valley bottoms, probably because upland sites seemed to be most intensively grazed (Coughenour and Singer 1991).

Despite these limitations, the method does provide important information. The method was sensitive enough to detect changes that have occurred over the 30-year period, which suggests that it would also be sensitive enough to detect significant changes of comparable magnitude that would result from

grazing. Whereas it is difficult to determine what the Parker transect data are measuring in an absolute sense, the data contain information about relative differences in plant abundance over time and as affected by exclosure from grazing.

A promising set of procedures for converting old Parker data to equivalent basal area has been developed (Cook et al. 1992). This technique accounts for the various effects of plot size, plant size, shape, and density on loop frequency. Once old data are converted they can be compared to data from future studies that use better sampling methods (although it is unclear how the method might account for changes in plant size and shape within a species over time). We concur with Cook et al. (1992) in recommending that old Parker data be converted to basal area, and that future monitoring programs not include the Parker method.

The Parker transects have provided data over a long period utilizing a consistent methodology. Nevertheless, the value of this longevity is reduced because the data are difficult to interpret, biologically and statistically. We therefore recommend that YNP institute a program that includes more extensive sampling of other plant–soil associations. It should be designed to reduce variance through stratification, with adequate random sampling within strata. More frequent sampling, at least annually, is recommended to enable clearer interpretation of responses to annual and seasonal climatic variation. The attribute or attributes to be measured (frequency versus cover versus biomass) need to be carefully considered. Biomass has the most direct effect on ungulate forage abundance and it is the most direct and incontestable measure of plant abundance; it measures the amount of energy, carbon and mineral elements that are incorporated by the plant. Unfortunately, it is very laborious and costly to obtain biomass data at the species level. Plant community composition may be best sampled with a quadrat-based cover technique. If Parker transects are continued, we recommend their sample sizes be increased severalfold.

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Appendix

Table A1. Frequencies for plants at each cluster of the high winter range sites.[a] There were 2 transects per cluster except at J-62-2 where $n = 1$ and B-57-1 and B-62-1 where $n = 3$. Each value is mean over the transects in a cluster; units are hits per transect.

In/ Out	Year	Cluster[b]	Rep	Grass	Forb	Dwsh[c]	**Total**	Agsp[c]	Feid[c]	Kocr[c]	Posp[c]	Posa[c]
						Inside						
1	58	B-57-1	4	8.2	5.3	0.8	14.3	4.8	0.3	4.8	[d]	
1	58	B-57-2	5	36	1	1	38	6	12	2		
1	58	L-57-1	8	32	10	0	42	9.5	0	9.5		
1	62	J-62-11	13.5	14.5	0	28	2	2	1.8			
1	62	J-62-22	22.5	8.50	31	4	4	2				
1	62	B-57-14	10.5	12.3	2.5	25.3	1.7	1.3	5.5			
1	62	B-57-25	202	1	23	1	7	0				
1	62	B-62-16	18.7	8.70	27.4	5.8	0	11				
1	62	B-62-27	29.2	7.71	37.95	10.8	1					
1	62	L-57-1	8	22.5	16.5	1	40	11	1	2		
1	62	L-62-1	9	20	8	0	28	8.5	0	4		
1	67	J-62-11	15.2	26.8	0.5	42.5	0.75	8	1.5			
1	67	J-62-2	2	14.5	16.5	0	31	0	8.5	0		
1	67	B-57-1	4	8	20	0.3	28.3	1.2	2	3.2		
1	67	B-57-2	5	17	1	1	19	0	13	0		
1	67	B-62-1	6	18	8	0	21	3.5	0.5	6		
1	67	B-62-2	7	18	7	1	26	0.5	11.5	0.5		
1	67	L-57-1	8	25	6	1	32	15.5	7.5	0		
1	67	L-62-1	9	23	8	0	31	13.5	3.5	2		
1	74	J-62-1	1	35.5	31.8	0.5	67.8	1.5	25	0.75	5	0
1	74	J-62-2	2	40.5	23	0	63.5	0	32.5	2	1.5	0
1	74	J-62-3	3	25.8	27.7	2.2	55.7	4.5	11.2	3.5	2	2
1	74	B-57-1	4	29.5	19.3	0.8	49.6	6.7	9.2	5.3	5.6	2.5
1	74	B-57-2	5	37.5	15.5	0	53	3.8	27.2	0.5	5	0
1	74	B-62-1	6	28.8	18	5.1	51.9	12.2	1.7	0.5	5.2	0
1	74	B-62-2	7	43.8	17.2	0.5	61.5	3.5	27.8	3	1	0
1	74	L-57-1	8	36	15	0	51	7	17	6.8	2.8	0
1	74	L-62-1	9	27.5	11.5	0.5	39.5	6.5	10.2	3.5	4.2	0
1	74	M-57-1	10	36.2	15.2	0	51.4	4.2	24	1.2	4.2	0
1	81	J-62-1	1	34	28.5	0	62.5	0	28.7	4.7	0	0
1	81	J-62-2	2	57.5	10.5	0	68	0	51	4.5	0	0
1	81	J-62-3	3	25.2	27.2	0.5	52.9	2.5	12.5	7.2	0	0
1	81	B-57-1	4	29.7	22.2	0.3	52.2	7.7	15.2	6.3	0.5	0
1	81	B-57-2	5	45.7	13.8	0	59.5	3.7	38.2	3.2	0	0
1	81	B-62-1	6	29.3	13.3	3.3	45.9	10	1	17.7	0	0
1	81	B-62-2	7	61.7	13.2	0	74.9	0	52	1.5	0.25	0
1	81	L-57-1	8	44	12	0	56	6.2	26.5	8.7	2.5	0
1	81	L-62-1	9	32.8	8	0.5	41.3	9.2	9.8	10.5	3	0
1	81	M-57-1	10	55.5	15.5	0	71	2.25	50.7	2.5	0	0
1	86	J-62-1	1	28.8	12.8	0	41.6	0.5	25.8	2.5	0	0
1	86	J-62-2	2	35	4	0	39	0	34	0	0	0
1	86	J-62-3	3	17	7	0	24	2.5	9.5	4.5	0	0
1	86	B-57-1	4	18.8	10.5	0	29.3	1.7	13.7	3.5	0	0
1	86	B-57-2	5	37.2	8.2	0	45.4	2	35.2	2	0	0
1	86	B-62-1	6	24.6	15.3	0.2	40.1	12.8	3.5	7.5	0.3	0.3
1	86	B-62-2	7	43	11.2	0	54.2	3	24.5	0.25	0.5	0
1	86	L-57-1	8	38.5	11.2	0	49.7	11	22.5	4	1	0
1	86	L-62-1	9	24	5	0	29	6	11	7	0	0
1	86	M-57-1	10	42	3	0	45	2.5	38	0	0	0

Table A1. *Continued.*

In/ Out	Year	Cluster[b]	Rep	Grass	Forb	Dwsh[c]	**Total**	Agsp[c]	Feid[c]	Kocr[c]	Posp[c]	Posa[c]
1	89	J-62-1	1	22.2	21.5	0	43.7	1	16.7	1	0	0
1	89	J-62-2	2	32.5	13.5	1	47	1.5	30	1	0	0
1	89	J-62-3	3	22	21.5	0	43.5	4.2	8.2	5	0	0
1	89	B-57-1	4	22	11	0	33	8.5	8.1	2.7	0	0
1	89	B-57-2	5	6	10.7	0	16.7	0.5	1	0	1	0
1	89	B-62-1	6	22.2	10.8	1.1	34.1	12.7	3.7	5.8	0	0
1	89	B-62-2	7	24	6	0	30	2.5	7.8	0.5	1.5	0
1	89	L-57-1	8	29.5	13.5	0.5	43.5	4.2	12.5	2.5	4	0
1	89	L-62-1	9	22.5	10.5	0	33	8.5	7	3.5	0	0
1	89	M-57-1	10	34.5	13	0	47.5	5	25.8	1.5	0	0
						Outside						
2	58	B-57-1	4	11.8	8.8	0	20.6	4.2	1	4	[d]	
2	58	B-57-2	5	28	2.5	0.5	31	2.5	10	2.5		
2	58	L-57-1	6	33.0	6	0	39	3.3	4.2	5		
2	62	J-62-1	1	16.5	13	0	29.5	1.5	6.5	3		
2	62	J-62-2	2	18.5	15.5	0	34	3	4	6		
2	62	B-57-1	4	13.5	10.5	0	24	2.8	0.5	8.2		
2	62	B-57-2	5	29.7	4.8	0	34.5	0	14.5	2		
2	62	L-57-1	6	34	6	0	40	1.8	3.5	3.2		
2	67	J-57-1	1	19.2	19.7	0	38.9	1.5	12	3		
2	67	J-57-2	2	17	17	1	35	1	11	2		
2	67	B-57-1	4	9.5	7.50	17	1	1	6			
2	67	B-57-2	5	24.5	1.81	27.3	0.5	17	2			
2	67	L-57-1	6	38	8.5	0	46.5	1	12	3.2		
2	74	J-62-1	1	35.7	19	0.7	55.4	3	19.2	5.8	3	0
2	74	J-62-2	2	34	21.5	0	55.5	1.5	22	4	5.5	0
2	74	J-62-3	3	30.7	19	0	49.7	1.5	16.8	6.2	5	0
2	74	B-57-1	4	32.8	15.8	0.3	48.9	5	13.7	9.7	3.8	0
2	74	B-57-2	5	49.5	9.2	0	58.7	1.5	33	3	3.5	0
2	74	L-57-1	6	49.7	111.2	0	160.9	4.5	21	5.2	10.85	0
2	74	M-57-1	7	56.7	17.2	0.5	74.4	5.5	31.5	7.8	10	1.5
2	81	J-62-1	1	56.7	15	0.8	72.5	5	28.5	18.5	0	0
2	81	J-62-2	2	56.5	16.5	0.5	73.5	2	29.5	24	0	0
2	81	J-62-3	3	37.2	16.8	1	55	2.5	18.5	14.5	0	0
2	81	B-57-1	4	29.8	18.3	3.3	51.4	7.3	15.7	6.8	0	0
2	81	B-57-2	5	49.8	4.2	0	54	3.2	38.5	1.7	0	0
2	81	L-57-1	6	43.8	11.2	1.8	56.8	7.7	15	4.2	0	0
2	81	M-57-1	7	50.2	10.2	0	60.4	6	31.5	12.8	0	0
2	86	J-62-1	1	38.1	9.5	0	47.6	4.8	24.5	6.8	0	0
2	86	J-62-2	2	27.5	11.5	0	39	1	20.56	6	0	0
2	86	J-62-3	3	29.5	14.5	0.5	44.5	2.5	18.5	8.5	0	0
2	86	B-57-1	4	25.8	6.2	0.3	32.3	7.3	15.5	3	0	0
2	86	B-57-2	5	48.8	5.2	0	54	10.2	33.5	0	0	0
2	86	L-57-1	6	37.7	12.7	0.5	50.9	7.5	16.8	10.2	0	0
2	86	M-57-1	7	38.2	6.2	0	44.4	3.8	27.2	7.2	0	0
2	89	J-62-1	1	26.7	13.7	0	40.4	4.8	9.8	4.8	2	0
2	89	J-62-2	2	30.5	16.5	0	47	2	8.5	4	15	0
2	89	J-62-3	3	20	13.5	0	33.5	4.5	7	3	3.2	0
2	89	B-57-1	4	22.5	10.8	1.7	35	8.2	9.2	2.8	1.7	0
2	89	B-57-2	5	24.7	3.7	0	28.4	1.5	12.3	2.2	0	0
2	89	L-57-1	6	32.2	17.5	0	49.7	2	12	3	2.5	0
2	89	M-57-1	7	39	14	1.2	54.2	2	18.2	11	7.8	0

[a]J = Junction Butte; B = Blacktail; L = Lamar.
[b]Year number in the cluster code refers to the year of establishment.
[c]Dwsh = dwarf shrub; Agsp = *Agropyron spicatum*; Feid = *Festuca idahoensis*; Kocr = *Koeleria macrantha*; Posp = *Poa* spp.; Posa = *Poa sandberghii*.
[d]Blanks indicate values not available for this analysis.

Table A2. Frequencies of plants at each cluster at the low elevation site (Gardiner). Mean for each cluster is the mean over two transects; units are hits per transect.

In/ Out	Year	Cluster[a]	Rep	Grass	Forb	Dwsh[b]	**Total**	Agsp[b]	Feid[b]	Kocr[b]	Posp[b]	Posa[b]
						Inside						
1	58	G-57-1	1	4.5	3	0.5	8	0	0	0	[c]	
1	58	G-57-2	2	9	2.5	1.5	13	8	0	1.5		
1	62	G-57-1	1	6	7	4	17	0	0	0		
1	62	G-57-2	2	14.5	2.5	3	20	2.5	0	1.5		
1	62	G-62-1	3	7	2	0.5	9.5	3	0	0	14.5	
1	67	G-57-1	1	3.5	10	5	18.5	0	0	0.5		
1	67	G-57-2	2	6.5	2.5	4.5	13.5	2	0	1.5		
1	67	G-62-1	3	5.5	6	0.5	12	2	0	0		
1	74	G-57-1	1	8	2.5	13.2	23.7	2	0	4.2	1.8	0
1	74	G-57-2	2	29.2	6.2	5	40.4	7	0	3.5	3.2	0
1	74	G-62-1	3	10	4.5	7.2	21.7	0	0	7.3	2.7	0
1	74	G-62-2	4	19.8	0.5	8	28.3	6.2	0	6.2	2.2	0
1	81	G-57-1	1	9	2	10.5	21.5	0	0	7.8	0.5	0
1	81	G-57-2	2	20.8	8.8	7	36.6	8.5	0	8.8	2	0
1	81	G-62-1	3	19	0.75	9.7	29.45	0	0	18	0.5	0
1	81	G-62-2	4	23	2.8	6.8	32.6	9.5	0	9.5	1.2	0
1	86	G-57-1	1	7	0	8151.505.500						
1	86	G-57-2	2	17	1.8	3.8	22.6	6.5	0	10.5	0	0
1	86	G-62-1	3	8	0.5	4	12.5	0	0	7.5	0	0
1	86	G-62-2	4	14.2	0.5	2.2	16.9	6.5	0	7.2	0	0
1	89	G-57-1	1	5.2	1.5	1.8	8.5	1	0	0	1.8	0
1	89	G-57-2	2	11.8	13	1	25.8	6.2	0	2	3.5	0
1	89	G-62-1	3	2.5	5.5	2.5	10.5	0	0	1	0.5	0
1	89	G-62-2	4	4.5	1	0	5.5	2.5	0	1	0.5	0
						Outside						
2	58	G-57-1	1	10.5	2.5	0	13	4.5	0	4.5	[c]	
2	58	G-57-2	2	5	7	0	12	0	0	0		
2	62	G-57-1	1	15.5	5.9	1.1	22.5	6	0	4		
2	62	G-57-2	2	7	5.2	3.8	16	0	0	0		
2	67	G-57-1	1	12.5	6.5	0	19	4.2	0	6		
2	67	G-57-2	2	5.5	7	3	15.5	0	0	0		
2	74	G-57-1	1	8	0.5	22.8	31.3	0	0	1	6	0
2	74	G-57-2	2	19.8	4.2	1	25	4	0	10.2	1.8	0
2	81	G-57-1	1	6	0.75	15.2	21.95	0	0	3.5	0	0
2	81	G-57-2	2	31	2.5	0.5	34	4.5	0	19	1.5	0
2	86	G-57-1	1	8.5	0	11.2	19.7	0	0	7	0	0
2	86	G-57-2	2	12.2	3.2	1	16.4	3.5	0	4	0	0
2	89	G-57-1	1	3.8	5.2	3.5	12.5	0	0	1	1	0
2	89	G-57-2	2	8	11.7	1.5	21.2	1.5	0	1.2	1	0

[a]Year number in the cluster code refers to the year of establishment.
[b]Dwsh = dwarf shrub; Agsp = *Agropyron spicatum*; Feid = *Festuca idahoensis*; Kocr = *Koeleria macrantha*; Posp = *Poa* spp.; Posa = *Poa sandberghii*.
[c]Blanks indicate values not available for this analysis.