Occurrence of Four Major Perennial Grasses in Relation to Edaphic Factors in a Pristine Community

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Highlight: The ecology and phytosociology of a virgin grassland community (Virginia Park, Canyonlands National Park, Utah) have been investigated. Based on the use of C × F index, *Hilaria jamesii* and *Stipa comata* are the most abundant of the four major perennial grasses. *Oryzopsis hymenoides* and *Sporobolus cryptandrus* are less abundant in decreasing order. The sites dominated by *Hilaria* are characterized by soils with finer texture, slightly warmer average temperature and higher surface K+ and organic matter compared to sites dominated by *Stipa comata*. In addition, frequency of both vascular and cryptogamic species is greater on sites dominated by *Hilaria*.

The purpose of this study was to investigate the occurrence and edaphic factors of four major perennial grasses in a pristine grassland area of Canyonlands National Park, Utah. Although the names of the perennial grasses are common in literature of the western range, little seems to be known about specific aspects of their ecology, or, for that matter, about natural grassland ecosystems under undisturbed conditions. Harrahan (1975) refers to the sensitive rangelands of the Southwest as, ". . . a delicately balanced arrangement of thin soils, sparse vegetation, and limited precipitation. Grazing must be carefully regulated to protect the delicate ecosystem. . . ." Analysis of an undisturbed site such as this could suggest possibilities for improved future land use practices.

Site for the investigation is Virginia Park, an ungrazed natural enclosure in the "Needles" area of Canyonlands. Because of its pristine condition, Virginia Park represents an ideal situation in which to examine the comparative ecology of major species under natural conditions in the absence of domestic grazing disturbance. Preservation of such rare, pristine areas is desirable in order to provide control sites for land management and to serve as natural outdoor laboratories for ecological investigations. Such isolated, undisturbed sites are becoming rare in the face of our increasing population, greater mobility, and expanding land use.

The four most prevalent perennial grasses selected for comparison in this study were galleta (*Hilaria jamesii*), needleandthread (*Stipa comata*), sand dropseed (*Sporobolus cryptandrus*), and Indian ricegrass (*Oryzopsis hymenoides*).

Virginia Park comprises an area of approximately 97 ha (240 acres) and is largely enclosed by high rock walls. The park floor consists of lightly dissected alluvial fans sloping from the rock walls. Access is through a rock tunnel leading from a drainage channel below the park. The access tunnel is impassable for cattle and horses and for this reason Virginia Park has not been disturbed by domestic grazers.

Climate is semiarid to arid. Minimum and maximum temperatures recorded since June 1965, when a weather station was installed, were −14 and 39°C, respectively. Annual precipitation is about 25 cm. Warm season rainfall constitutes from 55%–75% of the total annual precipitation. Soils are nonskeletal argids, classified as sandy loams (U.S. Dep. Agr. 1951). Soils are also deep, samples having been obtained readily from the 91 cm depth except in one site.

Methods

Forty circular study plots, each .005 ha (50.58 m^2) in size, were established in Virginia Park. Stands were selected subjectively; the criteria used were homogeneity of vegetation and environment, including elevation and percentage of slope and exposure. An attempt was made to distribute stands uniformly throughout the park. Within each of the stands, 25 small quadrats (0.125 m^2) and 100 point samples were uniformly distributed. Plant species (both vascular and cryptogamic) in each quadrat were noted, and hits on individual species and litter or soil were recorded for each point sample. A presence list was prepared for each stand. All sampling except soil temperature was completed during June and July 1967. Three soil-temperature readings were taken in each stand on September 20, 1967, with a dial-type thermometer having a 61-cm steel stem, which was forced into the soil to the desired depth (38 cm) and allowed to come to equilibrium. Distance and inaccessibility of the study area precluded additional soil temperature readings or continuous monitoring for an extended period.

Soil texture was analyzed by the hydrometer method as described by Bouyoucos (1928). Bulk density was obtained by weighing a known volume of each soil saple. The pH was determined by preparation of a slurry consisting of a soil-water mixture in a ratio of 1:1 and measurement with a glass electrode pH meter.

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Calcium and potassium analyses were performed by flame photometry, organic matter by the $K_2Cr_2O_7$ method, and total nitrogen by micro-Kjeldahl digestion and a modified nesslerization procedure (Jackson 1958). Soil phosphorus ($PO_4^{\equiv}$) was analyzed according to a method developed by Goldenberg and Fernandez (1966).

The most prevalent species were selected on the basis of a constancy-times-frequency (C × F) index (Curtis 1959). Utilizing both the species average frequency and percent occurrence among stands (constancy), the Curtis method has been widely used as an index of species prevalence. The index value has a possible range of 0 to 10,000 and in this study C × F values range from 0 to 9,710. Species are arranged according to decreasing magnitude of the C×F index and a number of species equal to the species density (average number of species per stand) is counted off from the top of the list. According to this procedure 26 prevalent species were recognized.

All stands were arbitrarily assigned to one of three groups, *Hilaria* (H), *Stipa* (S), or intermediate (I), depending on whether the quadrat frequency of H or S was twice or more greater than that of the other species. All stands that were not classified as H or S by the foregoing criteria were placed in the intermediate class. The H, S, or I designations will be used hereafter to characterize individual stands.

Utilizing percent frequency values of individual species in the stands, the degree of association among all possible species pairs was tested by means of simple correlation. The significant positive correlations between species were used to constuct a species-association diagram. The interstand correlation coefficients form the basis of a cluster analysis which is used to group stands graphically according to similarity of composition.

All data concerning vegetational and environmental factors were placed on punch cards and subjected to the desired statistical tests on a Univac 1108 electronic computer utilizing Fortan V. Species nomenclature follows Hitchcock (1950) for grasses and Holmgren and Reveal (1966) for other vascular plants. Cryptogamic nomenclature follows Fink (1935).

Table 2. Prevalent species of Virginia Park which show significant frequency differences between H and S stands.

Species	Mean frequency of species (%) H group	S group	Significance of *t* value[1]
Hilaria jamesii	91.7	12.0	***
Stipa comata	9.1	62.8	***
Lecidea rubiformis	24.5	5.9	**
Plantago purshii	67.5	28.0	**
Eriogonum cernuum	2.7	13.5	*
Fulgensia bracteata	79.2	48.0	*
Gilia sinuata	18.4	4.3	*
Machaeranthera pulverulenta	2.9	8.0	*
Oryzopsis hymenoides	7.7	17.2	*
Toninia caeruleonigricans	29.3	12.6	*
Aster lucelene	0	4.3	(1)
Calochortus nuttallii	1.3	0	(1)
Descurainia obtusa	14.1	5.9	(1)
Lappula redowskii	22.7	7.7	(1)
Lecidea decipiens	41.1	20.0	(1)
Sporobolus cryptandrus	5.6	12.0	(1)

[1] *** = significant at the .001 level of probability; ** = significant at the .01 level of probability; * = significant at the .05 level of probability; (1) = significant at the .1 level of probability.

Table 1. C × F values, frequency, and cover of prevalent species in Virginia Park for H, S, and I stands.[1]

Species	C × F index	Frequency (%) H	S	I	Cover (%) H	S	I
*Collema tenax**	9710	96.8	98.2	95.7	19.5	17.9	19.5
*Tortula ruralis**	9130	94.7	93.5	84.3	21.1	19.2	12.3
*Buellia papillata**	6540	70.9	64.6	62.0	.9	.2	.3
Hilaria jamesii	5206	91.7	12.0	57.3	18.3	1.0	3.9
*Fulgensia bracteata**	4533	79.2	48.0	24.7	.1	.1	.1
Stipa comata	3626	9.1	62.8	54.7	2.9	12.4	11.0
Plantago purshii	3304	67.5	28.0	23.0	1.3	.3	.2
*Lecidea decipiens**	2040	41.1	20.0	12.0	.3	.4	.1
Festuca octoflora	1876	20.8	28.3	19.7	0	.2	0
*Toninia caeruleonigricans**	1544	29.3	12.6	6.7	0	0	.1
Opuntia aurea	1368	13.6	14.5	15.3	.6	1.9	.8
Oryzopsis hymenoides	1141	7.7	17.2	12.7	1.2	2.8	1.4
*Lecidea rubiformis**	806	24.5	5.9	4.3	.1	.1	0
Sporobolus cryptandrus	663	5.6	12.0	6.0	.5	.5	.5
Descurainia obtusa	588	14.1	5.9	4.0	.1	0	0
Gilia sinuata	538	18.4	4.3	1.0	.1	0	0
Lappula redowskii	476	22.7	7.7	3.0	.5	.2	.2
Machaeranthera pulverulenta	465	2.9	8.0	7.3	0	0	0
Eriogonum cernuum	312	2.7	13.5	8.0	0	0	0
Bromus tectorum	183	9.3	1.5	1.0	.4	0	0
Lepidium densiflorum	163	5.6	1.9	1.3	.1	0	0
Aster lucelene	36	0	4.3	5.3	0	0	0
Stephanomeria exigua	36	1.3	.6	.3	.1	0	0
Cryptantha crassisepala	27	2.4	.6	.3	.1	0	0
Calochortus nuttallii	18	1.3	0	.7	0	0	0
Chaenactis stevioides	17	2.9	0	0	0	0	0

[1] H—stands dominated by galleta; S, by needleandthread; I—all other stands.
* Cryptogams.

Results

Of a total of 59 species (vascular and cryptogamic) observed in Virginia Park, 26 with a C × F value of 15 or higher are shown in Table 1. Cryptogams constitute seven of these species, three of which, black lichen (*Collema tenax*), moss (*Tortula ruralis*), and white lichen (*Buellia papillata*) are the most prevalent species in the park. Galleta and needleandthread are much more abundant than Indian ricegrass or sand dropseed. Percent frequency and cover of each species for the groups of stands designated H, S, and I are also included in Table 1. Fifteen of the 40 stands (38%) are dominated by galleta and 13 (33%) by needleandthread.

Sixteen of the 26 prevalent species which reflect significant frequency differences between H- and S-dominated sites are shown in Table 2, as well as the significance of comparison by *t*. Nine of these species, exclusive of galleta and needleandthread, exhibit higher frequency in H stands than in the S group. Indian ricegrass and sand dropseed show significantly higher frequencies on the sites dominated by needleandthread. Four of the 16 species are lichens, all of which show a markedly lower (average 22% less) frequency on S than on H stands.

Physical and chemical characteristics of the soils dominated by galleta and needleandthread are shown in

Table 3. Investigations reveal that the soils of the sites dominated by galleta have slightly warmer temperatures, finer texture, (less sandy, lower bulk densities, higher percent silt), higher organic matter (lower pH), and higher K^+ (0–5 cm) and $PO_4^{\equiv}$ (15–91 cm) than the needleandthread sites. Of these factors, percent sand (0–30 cm), temperature, and K^+ (0–5 cm) are highly significantly different between the two groups of stands. The relationships among these three factors and the two groups (H and S) are shown three-dimensionally in Figure 1. In this diagram, site preference of the galleta and needleandthread subcommunities may be seen at a glance.

A table showing all-species floristic and vegetational characteristics, the association diagram depicting degree of positive association among prevalent species, summary of this interspecific association data and a dendrogram prepared from cluster analysis for the stands of Virginia Park appear elsewhere (Kleiner and Harper 1972).

Table 3. Maximum, minimum, mean values and significance of comparison by *t* for 19 phisical-chemical variables associated with sites dominated by *Hilaria* or *Stipa*.

	Site dominant[1]						
	H group			S group			Significance
Variable	Min.	Max.	Mean	Min.	Max.	Mean	of *t* value[2]
Sand (0–30 cm) (%)	41	72	59.7	58	81	66.5	**
Sand (31–91 cm) (%)	38	87	57.1	44	91	67.2	*
Silt (0–30 cm) (%)	12	39	29	11	33	23.92	*
Silt (31–91 cm) (%)	7	56	27.3	2	38	19.53	*
Clay (0–30 cm) (%)	4	22	10.5	4	15	9.59	NS
Clay (31–91 cm) (%)	5	24	15.6	7	21	13.27	NS
Bulk density (0–5 cm) (g/cc)	1.27	1.33	1.3	1.28	1.36	1.32	**
Bulk density (15–91 cm) (g/cc)	1.13	1.29	1.22	1.19	1.3	1.25	(1)
Soil temperature (38 cm) (°C)	19.4	20.6	20.1	19.1	20.3	19.6	**
pH (0–5 cm)	7.35	8.34	7.95	7.98	8.3	8.13	*
pH (15–91 cm)	8.33	8.96	8.49	8.28	8.65	8.42	NS
Calcium (0–5 cm) (mg/g soil)	2.4	24.2	4.72	2	18.3	4.84	NS
Calcium (15–91 cm) (mg/g soil)	5.5	30.9	17.88	6	28	16.2	NS
Nitrogen (0–5 cm) (mg/g soil)	.28	.63	.43	.26	.74	.4	NS
Phosphorus (0–5 cm) (mg/g soil)	.006	.15	.09	.003	.15	.09	NS
Phosphorus (15–91 cm) (mg/g soil)	.004	.14	.02	.003	.03	.01	*
Potassium (0–5 cm) (mg/g soil)	.018	.301	.15	.014	.692	.09	**
Potassium (15–91 cm) (mg/g soil)	.012	.411	.07	.012	.383	.08	NS
Organic matter (0–5 cm) (%)	.85	1.96	1.54	.18	2.04	1.23	*

[1] 15 stands dominated by *Hilaria;* 13 by *Stipa.*
[2] ** = significant at the .01 level of probability; * = significant at the .05 level of probability; NS = not significant; and (1) = significant at the .1 level of probability.

Discussion

Species which are characteristic of pristine sites may increase or decrease under grazing pressure. In the case of a grazed community, an investigator may never know whether the species now occupy their optimum habitat. It is possible they occupy a larger or smaller niche than would be the case under virgin conditions or they may not occupy the niches compatible with an optimum balance of nature under the given conditions. Because of this uncertainty about niche specificity, distinct environmental requirements

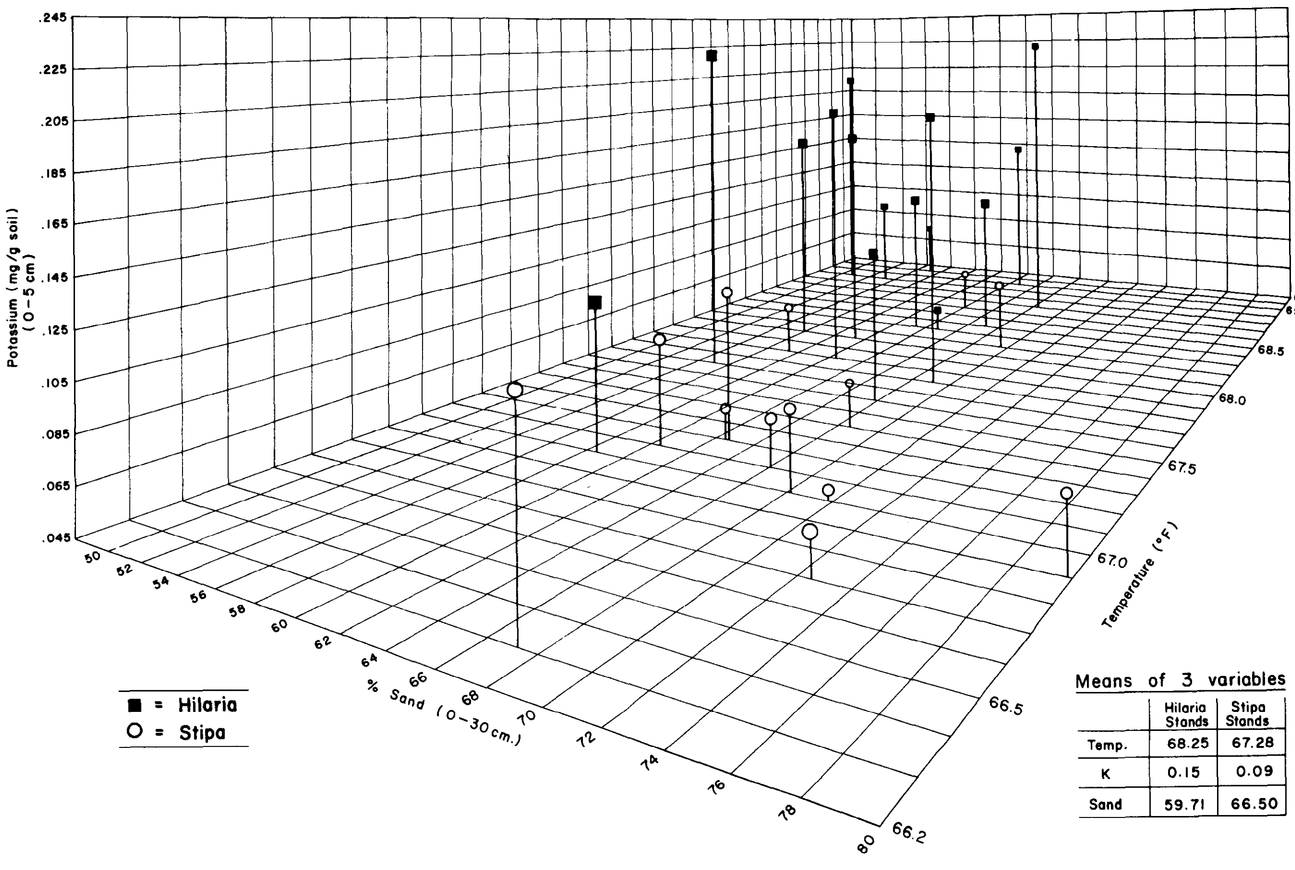

Fig. 1. *Three-dimensional diagram depicting stands dominated by* Hilaria *and* Stipa *with reference to soil temperature, K, and sand.*

of a species may not be detectable.

Under the virgin conditions of Virginia Park, one may assume species occupy their most appropriate niches and that their richness and pattern are stabilized in a climax community as a result of permanent isolation. Some sites in Virginia Park are dominated by galleta and others by needleandthread. Separate and distinct communities are thriving side by side. By knowing distribution and pattern characteristics under virgin conditions, range managers are better able to judge the relative condition of disturbed areas.

The greater vegetational richness of galleta sites is evidenced in both frequency and cover. Based on data shown in Table 1, average total species frequency and total living cover on H sites are 30% and 18% higher respectively, than on S sites. This distinctiveness may be related to environmental characteristics, particularly three soil factors which have been shown to be statistically ($p = 0.01$) different between the two sites. Higher potassium content along with finer texture and slightly higher average temperatures are distinct on the galleta sites. It is unlikely that a slight difference in one factor of the environment would account for such distinctive vegetational differences. Morelikely, the vegetational mosaic is the result of a host of interwoven factors, all of which may reveal only slight environmental variations. For example, the mean difference (about .5°C) of soil temperature is small but it is nonetheless highly significant statistically. Whether this factor in itself has a significant relationship to the pattern of vegetational distribution between the two groups of stands is highly questionable. Rather, its significance is probably intertwined with other parameters such as slope, exposure, and soil moisture—factors which have proven to have direct significance for species distribution and community relationships. The variable, bulk density, is also statistically lower ($p = 0.01$) on galleta sites (Table 3) although as a function of texture, this is to be expected. Although only three characteristics prove to be highly significantly different between the two groups of stands, other factors which could be instrumental in determination of vegetational pattern and which are noteworthy on the galleta sites, are lower pH and calcium (0–5 cm), higher nitrogen, higher phosphorus (15–91 cm), and higher organic matter. The higher organic matter and nitrogen may in turn be related to the greater frequency and cover of cryptogams on galleta sites (H, avg 62.4% frequency, 6% cover; S, avg 49% frequency, 5.4% cover). It has been shown that cryptogams are instrumental in the buildup of organic matter and soil nutrients (Shields 1957; Shields, Michell and Drouet 1957). The trend of positive association among finer soil texture, higher cryptogamic frequency and cover, and higher organic matter is consistent with the results of related investigations involving a comparison of this virgin site with a grazed area (Kleiner 1968; Kleiner and Harper 1972).

Both vegetational and environmental characteristics of I stands approach those of S stands much more closely than of H stands.

The increase in frequency of Indian ricegrass and sand dropseed on needleandthread-dominated sites (114% and 123% greater, respectively) has been noted. Even though both species are much less significant (on the basis of percent frequency in Table 1) than a number of other species, the increase is noteworthy. The differential suggests that under natural, undisturbed, climax conditions, these two species are not as good competitors as the two other species on higher quality sites. Interspecific competition is apparently a stronger factor in control of these species in the niche conditions characteristic of H sites.

Sand dropseed is historically a late season, increaser range grass. It would be expected this species would be a better competitor on the more harsh sites (coarser soils, lower nutrients). This hypothesis is supported in this study and elsewhere (Kleiner and Harper 1972) as indicated by the higher frequency on the lower quality S sites. As other species (and all the annuals in this environment) have passed flowering and seed-set stage, sand dropseed is in a more favorable competitive posture than galleta, Indian ricegrass or needleandthread.

Slight differences in variables between the two types of stands have proven to be quite significant in this analysis. With small variations in the data of a parameter within one group of stands, a small difference between groups can be highly significant. It is suggested that some species at least may be surviving in this extreme climate at close to the maximum of their tolerance range for some variables and that a small variation in a factor such as temperature or moisture may have an important influence on distribution and pattern such as that found with regard to these galleta and needleandthread stands.

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