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Topographic control of vegetation in a mountain big sagebrush steppe

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Abstract

Mountain big sagebrush steppes in Wyoming have strong spatial patterning associated with topography. We describe the spatial variability of vegetation in a sagebrush steppe, and test the relationship between topography and vegetation using canonical correlation. Results of the analysis suggest that the main control over vegetation distribution in this system is wind exposure. Exposed sites are characterized by cushion plant communities and *Artemisia nova*, and less exposed sites by the taller sagebrush species *Artemisia tridentata* ssp. *vaseyana*. Topographic depressions and leeward slopes are characterized by aspen stands and nivation hollows. Measurements of soil microclimate suggest that a major influence of topographic position on vegetation is snow redistribution and its effect on soil moisture and temperature.

Abbreviations: ARNO = *Artemisia nova*; ARTRW = *Artemisia tridentata* ssp. *wyomingensis*; ARTRV = *Artemisia tridentata* ssp. *vaseyana*; PUTR = *Purshia tridentata*; RIP = riparian community; POTR = *Populus tremuloides*; NIV = nivation hollow community

Nomenclature: Hitchcock, C. L. & Cronquist, A. 1973. Flora of the pacific Northwest, Seattle, in general, and Beetle, A. A. & Young, A. 1965, Rhodora 67: 405–406, for sagebrush species and subspecies.

Introduction

Vegetation patterns in semi-arid shrublands have been shown to be controlled by water availability (Billings 1949; Beatley 1975; West 1979; many others). Thus, shrubland vegetation patterns frequently show strong correlation with slope position, parent material, erosional characteristics, or soil texture patterns (Hironaka *et al.* 1983; Nettleton *et al.* 1986; Lentz & Simonson 1987a, b). The mountain big sagebrush steppes in Wyoming have strong spatial patterning associated with topography. In these systems, snow is redistributed across the landscape by winter winds averaging 3–8 m s^{-1}, (Sturges 1979), creating annually repeated spatial patterns of water availability. Over the long term, these repeated patterns of snow accumulation and available moisture across the landscape have led to corresponding species distributions and primary productivity patterns.

The purpose of this paper is twofold. First, we will describe the vegetation of a study site located in south-central Wyoming. Second, we will statistically test the relationship of vegetation pattern to our hypothesized ultimate cause, topographic variation. Studies of topographic control over vegetation in this system are directly applicable to a large region in Wyoming, and are valuable to understanding patterns in the extensive Intermountain Sagebrush Steppe, covering 44.8 million ha. in the western USA (West 1983).

Methods

Site description

Our area of study was the Stratton Sagebrush Hydrology Study Area (SSHA, Sturges 1977, 1980), located at 107° 10′ W, 41° 25′ N (Fig. 1). The site is on Tertiary basin-fill sediments, at an average elevation of 2400 m (Sturges 1980). Most of the drainages have been downcut in a west-east direction, with an average relief of 75 m. Parent material is the Brown's Park sandstone (Love & Christianson 1985), weathering to soils of a loamy sand to sandy texture (Burke 1989). Soils are classified as Argic Cryoborolls, with A horizon depths varying in response to topography by snow deposition patterns (Sturges 1986; Burke *et al.* 1987; Evans 1987).

Sampling procedure

We conducted our study of vegetation at two different spatial scales. Most of the area at SSHSA is covered by sagebrush-dominated communities, but these are set in a context of other vegetation types that occupy more extreme topographic positions. To characterize this larger context, we selected an area ca 1.7 km^2 featuring relatively strong relief (Fig. 1, extensive area). By

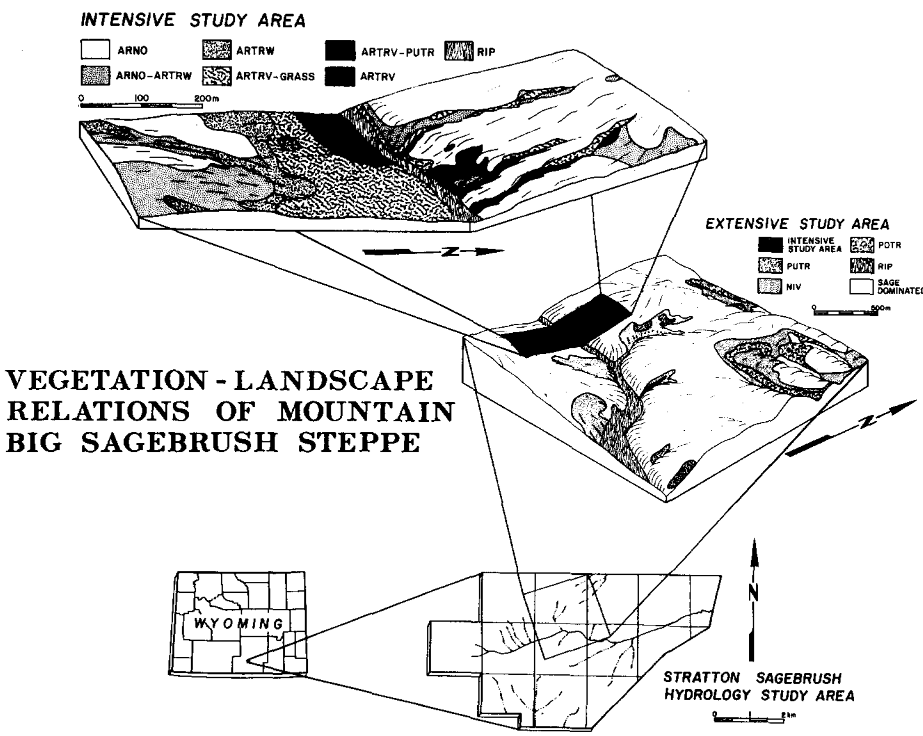

Fig. 1. Maps locating the intensive area studies on the Stratton Sagebrush Hydrology Study Area, and block diagram-maps of both extensive and intensive study areas. ARNO = *Artemisia nova*; ARTRW = *Artemisia tridentata* ssp. *wyomingensis*; ARTRV = *Artemisia tridentata* ssp. *vaseyana*; PUTR = *Purshia tridentata*; RIP = riparian community; POTR = *Populus tremuloides*; NIV = nivation hollow community.

means of ground reconnaissance and aerial photography, we identified and mapped four community types in this area besides sagebrush-dominated types: aspen stands, riparian areas, nivation hollows, and pure stands of *Purshia tridentata*. In order to describe these non-sagebrush vegetation types more intensively, we randomly selected three stands representing each of these community types. In each stand, we described vegetation characteristics in the field, and estimated topographic data from 1:24000 United States Geological Survey topographic maps.

For a relatively fine scale study of sagebrush dominated communities, we chose a subsection of the extensive area crossing the watershed (Fig. 1, intensive study area). We located 6, evenly spaced (60 m apart), 900 m long transects each running north-south across the watershed (long axis). Each transect was divided into 15, 60 m segments. Within each segment, we randomly located a sampling center-plot stake to mark each of the 89 nondisturbed sample locations. Around each center-stake, we laid out 4 parallel 4 m transects, a random distance apart. Each transect was sampled using the line-intercept method of measuring species canopy and bare ground cover.

The entire intensive grid area was surveyed to produce a topographic map with a 0.61 m (2 foot) contour interval. Grid points and plot positions were also individually surveyed to obtain elevations. From the contour map, we determined slope aspect and slope angle for each of the 89 plots. In the field, we estimated windward fetch, or the distance in the windward direction (235 degrees) to the nearest horizon, and fetch angle, the angle from horizontal to that horizon.

We measured soil moisture and temperature in all vegetation plots of the extensive area and representative plots in the upland shrub types once a week during the growing season of 1986. Soil moisture was measured gravimetrically on 0–10 cm samples, and soil temperature was measured at a 10 cm depth.

Statistical procedures

We used a hierarchical cluster analysis (BMDP 1985) using centroid linkage to objectively form vegetation types from plot vegetation data. We condensed species cover data for each plot into individual shrub species cover, bare ground, and cover of cushion plants, forbs and grasses, all having generally low aggregate covers (see Table 1 for list of variables used in analysis). Using the dendrogram from the cluster analysis, we established major groupings or vegetation types. The appropriate number of groups was determined by subjective analysis of a scree diagram (Alden-

Table 1. Average percent cover data for the six sagebrush dominated vegetation types at the Stratton Sagebrush Hydrology Study Area. Standard deviations are shown in parentheses. See text for description of vegetation types.

Species or growth form	Vegetation type					
	ARTRV	ARTRV-GRASS	ARTRV-PUTR	ARTRW	ARNO-ARTRW	ARNO
A. tridentata ssp. *vaseyana*	57.7 (14.5)	25.4 (8.5)	30.6 (13.0)	0.0 (0)	0.0 (0)	0.0 (0)
A. tridentata ssp. *wyomingensis*	0.0 (0)	0.0 (0)	0.0 (0)	23.2 (12.1)	12.9 (7.4)	1.1 (2.2)
A. nova	0.0 (0)	0.0 (0)	0.0 (0)	0.5 (0.8)	2.0 (2.5)	15.1 (6.5)
Purshia tridentata	0.0 (0)	0.0 (0)	12.3 (6.4)	0.0 (0)	0.0 (0)	0.0 (0)
Cushion plants	0.1 (0.2)	0.6 (1.1)	0.5 (0.5)	0.3 (0.5)	3.0 (1.7)	5.5 (3.5)
Forbs	0.2 (0.1)	7.9 (4.0)	8.0 (3.2)	6.7 (0.4)	8.0 (7.2)	5.3 (0.4)
Grasses	15.0 (5.8)	27.6 (15.2)	7.3 (4.5)	18.1 (6.2)	8.2 (3.5)	9.0 (3.3)
Bare ground	27.8 (12.0)	38.5 (12.3)	41.3 (7.3)	51.2 (6.9)	65.9 (9.2)	64.0 (6.5)
Number of plots	6	20	4	10	18	35
% of map area	4.0	23.4	5.9	9.5	19.1	38.2

derfer & Blashfield 1984). The characteristics of plots within each major grouping were used to name vegetation types and produce descriptive statistics.

We used two statistical analyses to test for a significant relationship between topographic variables and vegetation features of the plots: 1) Analysis of variance (BMDP 1985) to test for significant differences of topographic variables among intensive site vegetation types identified through cluster analysis; 2) Canonical correlation (BMDP 1985) for evaluating the relationships between the two sets of continuous variables, topographic and vegetation. Canonical correlation is a powerful tool for examining relationships between 2 sets of continuous variables (Gittins 1985). Because we used a minimum number of species variables and life form variables (Table 3) whose distribution is relatively linear, these data could be analyzed using canonical correlation rather than canonical correspondence analysis (ter Braak 1987).

We transformed 2 of the 6 topographic variables (Table 2), aspect and fetch, to obtain the highest quality linear relationship with vegetation. We obtained best relationships with log of fetch, and an aspect scalar defined as below:

$$\text{aspect scalar} = \text{cosine (absolute value (aspect} - 235)^* \; 0.5)$$

This equation produces a maximum effect at 235 degrees, the windward direction (= 1), and a minimum effect at 55 degrees (= 0).

Mapping

A map of the extensive area was based on field reconnaissance and aerial photo analysis (Fig. 1). A more detailed map of the intensive area was produced from the results of the cluster analysis. Cluster analysis defined the vegetation type for each of the sample locations. Polygons were initially mapped around contiguous sample locations in the same type. The borders of these polygons were then adjusted by extensive comparison of vegetation on the ground with characteristics defined by the cluster analysis. These boundaries were then transferred to the detailed map of the area (Fig. 1).

Table 2. Average topographic data for each of the vegetation types at the Stratton Sagebrush Hydrology Study Area. Analysis of variance and Student Neuman Keuls range test results for upland shrub types are shown with small letters; types with the same letter are not significantly different at $p = 0.05$. Values in parentheses are standard deviations.

Vegetation type	Aspect (degrees)	Aspect scalar (dimensionless)	Log of fetch (m)	Relative elevation (m)	Fetch angle (degrees)	Slope angle (degrees)
ARTRV	298.5 b (90.7)	0.57 b (0.03)	1.68 a (1.26)	38.5 a (35.2)	2.3 a (1.6)	5.0 a (1.3)
ARTRV-GRASS	283.7 b (91.8)	0.60 b (0.14)	1.91 a (0.8)	41.5 a (30.0)	1.8 a (1.1)	5.9 a (1.8)
ARTRV-PUTR	109.7 a (62.4)	0.70 a (0.09)	2.01 a (1.30)	41.5 a (46.3)	1.5 a (1.7)	8.4 a (1.4)
ARTRW	307.2 b (61.4)	0.64 b (0.10)	2.23 a (0.80)	74.5 b (19.6)	0.6 b (1.2)	4.9 a (1.9)
ARNO-ARTRW	196.8 a (107.4)	0.67 b (0.19)	2.79 b (0.92)	102.1 c (46.2)	0.7 b (1.0)	6.1 a (3.0)
ARNO	181.7 a (66.2)	0.78 a (0.08)	3.43 c (0.47)	95.2 b (35.3)	0.2 b (0.4)	5.7 a (2.8)
Extensive sites						
POTR	64 (32.0)	0.18 (0.25)	2.7 (2.1)	42.0 (86.2)	0.6 (0.1)	7.6 (4.1)
RIP	103 (45.9)	0.45 (0.33)	2.02 (1.7)	−48 (35.1)	2.6 (0.9)	7.1 (0.8)
NIV	134 (76.9)	0.61 (0.50)	2.4 (2.2)	25 (65.5)	0.5 (0.3)	5.6 (1.4)
PUTR	105 (49.2)	0.47 (0.37)	3.1 (2.9)	−48 (40.4)	0.4 (0.2)	4.2 (3.0)

Results and discussion

Extensive area vegetation description

Six vegetation types were mapped in the extensive area. The majority of this area is covered by sagebrush-dominated vegetation, described in detail for the intensive study area (see below). The other types are easily differentiated by their bold contrasts in physiognomy, topographic position, or species dominance.

Nivation hollows (NIV)
Extreme, leeward slopes accumulate deep drifts of snow, forming conspicuous nivation hollows in the landscape (Fig. 1). These hollows may accumulate as much as 10 m of snow by early spring (Sturges unpubl. data), often not melting until mid-June. Dense stands of *Stipa comata* occur, as well as many forbs and sub-shrubs such as *Artemisia ludoviciana*, *Achillea millefolium*, and *Cirsium pulcherrimum*. Sagebrush growth is apparently limited in these hollows by a curtailed growing season and the presence of a snowmold disease under the heavy snowpack (Nelson & Sturges 1986). While extremely wet early in the season, they become very dry in the late growing season, and so are the most xeric of the extensive study area vegetation types.

Purshia tridentata vegetation type (PUTR)
Pure stands of *Purshia tridentata* occur in relatively high snow accumulation areas, sometimes within NIV areas, or else in rills where soils are relatively stony. These stands have very little if any grass or forb cover, as the shrub canopies are almost continuous. Grass and subshrub species that may be present are *Stipa comata*, *S. columbiana*, and *Eriogonum subalpinum*.

Aspen stands (POTR)
Stands of aspen (*Populus tremuloides*) are distributed on extreme, leeward slopes that accumulate large amounts of snow, or are downslope of large snowbanks (NIV) (Fig. 1). These aspen stands have been described by Knight *et al.* (1976) as 'atolls', or concentric arcs of aspen. These atolls are apparently formed by a snow-barrier effect of aspen, causing increased snow distributions upwind and downwind of the aspen, eliminating aspen growth in the centers and downwind of stands. Dominant shrubs are *Symphoricarpus oreophilus*, *Amelanchier utahensis*, *Rosa* spp., *Salix scouleriana*, *Berberis nervosa*, and *Artemisia tridentata* ssp. *vaseyana*. The more common forbs are *Frasera radiata*, *Cirsium* sp., *Antennaria microphylla*, *Eriogonum umbellatum*, *Geranium caespitosum*, and *Galium boreale*. Graminoids include *Stipa comata*, *Stipa nelsonii*, *Sitanion hystrix*, and *Carex geyeri*. These stands are very heavily grazed and browsed by cattle and deer.

Riparian areas (RIP)
Perennial and annual streambeds are characterized by dense stands of grasses and sedges (Fig. 1). The wettest sections of the riparian meadows typically contain many sedges and rushes, such as *Carex limniphila*, *C. nebrascensis*, *Juncus saximontus*. With increasing dryness and distance away from the stream, other graminoids, forbs and subshrubs increase, such as *Poa interior*, *Hordeum brachyantherum*, *Agrostis stolonifera*, *Artemisia ludoviciana* and *Astragalus sericoleucus*.

Intensive area vegetation description

The hierarchical cluster analysis indicated that there were 6 sagebrush dominated vegetation types at SSHSA (Table 1). The following descriptions present both the composition of plots that fall within these clusters or vegetation types, and subjective descriptions of their distributions upon the landscape (Fig. 1).

Artemisia nova vegetation type (ARNO)
Over 30% of the plots fell into a vegetation type dominated by *Artemisia nova*, a prostrate shrub. This type generally has over 50% bare ground and a sparse cover of cushion plants and grasses. The most common cushion plants are *Happlopappus acaulis*, *Arenaria hookeri*, *Phlox hoodii*, *P. multiflora*, and *Leptodactylon pungens*. Grasses in this

vegetation type include *Agropyron smithii* and *Koeleria cristata*. The *A. nova* vegetation type occurs on dry, windswept ridges that are often blown free of snow, but may accumulate up to 0.25 m (Sturges 1977).

Artemisia nova – Artemisia tridentata ssp. wyomingensis vegetation type (ARNO-ARTRW)
Plots falling into this cluster may have significant cover by *Artemisia nova* and *Artemisia tridentata* ssp. *wyomingensis*. Bare ground cover and floristic composition are similar to the *A. nova* vegetation type, the primary difference between these vegetation types being the presence of *A. tridentata* ssp. *wyomingensis*. This vegetation type also occurs on exposed windward areas, but those that are slightly more protected than the *A. nova* vegetation type (Fig. 1).

Artemisia tridentata ssp. wyomingensis vegetation type (ARTRW)
A third vegetation type is dominated by *Artemisia tridentata* ssp. *wyomingensis*. A consistent constituent of this vegetation type is *Festuca idahoensis*, with some intermixing of other grasses such as *Stipa comata* and *Agropyron smithii*. The *A. tridentata* ssp. *wyomingensis* vegetation type has an average of 51% bare ground cover, and a more apparent production than the two former vegetation types. This vegetation is found on gentle slopes that accumulate moderate amounts of snow (0.9 m) (Sturges 1977) (Fig. 1).

Artemisia tridentata ssp. vaseyana – grass ssp. vegetation type (ARTRV-GRASS)
The plots falling into this vegetation type are dominated by *A. tridentata* ssp. *vaseyana* with a continuous cover of grasses among the shrubs. The grasses most commonly occurring are *Leucopoa kingii*, *Stipa comata*, and *S. columbiana*, and *Poa* sp. The subshrubs *Lupinus argenteus* and *Eriogonum subalpinum* are also common constituents. This vegetation type occurs in moderate to high snow accumulation areas, with generally 1 or more meters of snow in late spring (Fig. 1) (Sturges 1977).

Artemisia tridentata ssp. vaseyana vegetation type (ARTRV)
In high snow accumulation areas, with more than 1 m but less than 2 m of snow accumulating by early spring (Sturges 1977), a community with a continuous cover of *A. tridentata* ssp. *vaseyana* occurs (Fig. 1). This vegetation type has relatively high vegetation cover, and more apparent production than any of the other upland shrub vegetation types.

Artemisia tridentata ssp. vaseyana – Purshia tridentata vegetation type (ARTRV-PUTR)
Finally, one upland shrub vegetation type is codominated by *Purshia tridentata* and *A. tridentata* ssp. *vaseyana*, with some grasses and forbs intermixed. Typical grasses include *Stipa comata*, *Leucopoa kingii*, and forbs and subshrubs include *Cordylanthus ramosus* and *Eriogonum subalpinum*. In many cases, the ARTRV-PUTR type is found where heavy snow is deposited on stony substrates, as in the rill zones of the south-facing slopes of the intensive area in Fig. 1.

Relationship between topographic position and vegetation

Extensive site
The PUTR (*Purshia tridentata*) stands are located in areas with lower aspect scaler than the upland shrub types dominated by *Artemisia* (Table 2, Fig. 1). PUTR stands tend to be at low elevation, have a SSW aspect, relatively high fetch values and low fetch angles compared with ARTRV. Thus, using aspect and elevation as indicators of exposure, PUTR occurs in nonexposed sites, but using fetch and fetch angle, PUTR occurs in highly exposed areas. Distribution of PUTR may be related to intermediate levels of snow distribution in combination with soil rockiness. PUTR sites may be equivalent to ARTRV-PUTR sites except for rockiness associated with some PUTR sites.

Riparian vegetation (RIV) is clearly located in drainages, having low elevation and low wind exposure as indexed by fetch angle, log of fetch, and aspect scaler (Table 2, Fig. 1).

POTR (aspen) stands are located in landscape positions with steep slope angles, and those that we sampled were generally east-facing, thus having low aspect scalers. Surprisingly, exposure as indexed by fetch and fetch angle is fairly high compared to other vegetation types. Nivation hollows have similar fetch and fetch angle to aspen stands, but tend to be on slightly less steep slopes. Our field observations suggest that POTR occurs on longer lee slopes, often when below or surrounded by NIV.

Intensive site

The average topographic data for all of the vegetation types illustrate that ARNO and ARNO-ARTRW vegetation types are generally located on more exposed sites (high aspect scaler, lower fetch angle, high fetch), and at higher elevations than the vegetation types dominated by *A. tridentata* ssp. *vaseyana* (Table 2). ARTRV, ARTRV-GRASS and ARTRV-PUTR vegetation are not significantly different from one another for most topographic variables, however, exposure (fetch, fetch angle, aspect scaler) and elevation generally increase from ARTRV to ARTRV-GRASS to ARTRV-PUTR.

The continuous relationship of shrub cover to elevation and fetch in the intensive sites are shown in Fig. 2. Shrub cover decreases dramatically in response to both increasing log fetch and elevation. At high values of log fetch, elevation does not affect total shrub cover, and similarly, at high elevations, log fetch does not affect shrub cover.

We performed a canonical correlation to examine the multiple continuous relationships between the sets of vegetation and topographic variables in the intensive study site. Canonical correlation forms the maximum relationship between two sets of variables by extracting new axes (the canonical variables) that are linear combinations of the original variables. Our results indicated that only one canonical equation was necessary to explain the interdependence of the two data sets; vegetation and topography share 66.6% of their variance through this correlation. These results indicate that there is only one significant (p = 0.04) relationship between the two data sets (Fig. 3). A graph of the study plots in two-dimensional space (Fig. 3) shows the strength of the relationship, and indicates that one axis for vegetation and one for topography separate the plots sufficiently.

The structured coefficients, or correlations between the original variables and the canonical variables (Table 3), suggest that fetch and fetch

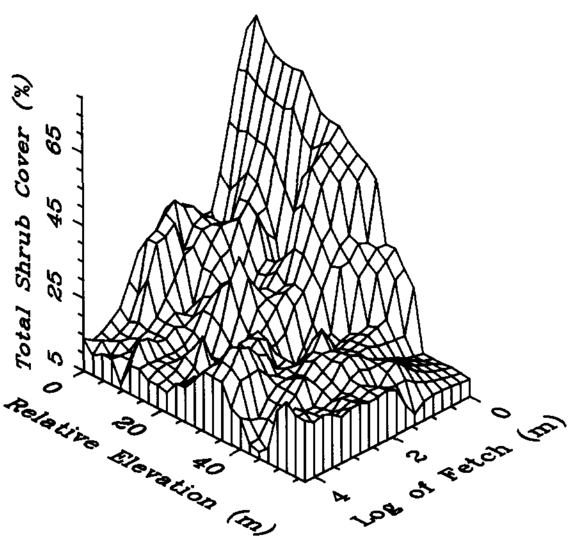

Fig. 2. Response surface of total shrub cover vs log of fetch and relative elevation in the upland shrub communities of the Stratton Sagebrush Hydrology Study Area. Fetch was surveyed as the distance in the windward direction to the nearest horizon.

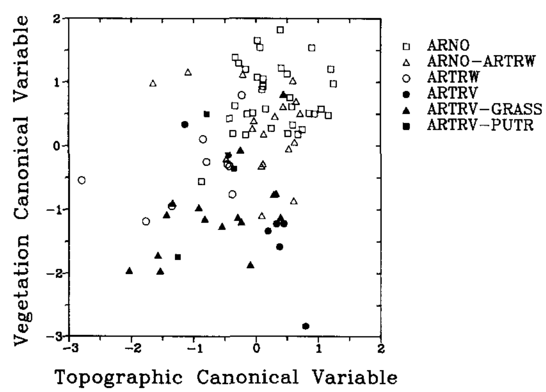

Fig. 3. Study plots in 2-dimensional space formed by a topographic canonical variable and a vegetation canonical variable. R^2 = 66.7.

Table 3. Structured coefficients from a canonical correlation of topographic variables and vegetation composition in a mountain big sagebrush steppe in Wyoming. The structured coefficients are correlations of the canonical variables with the original variables.

	Structured coefficient
Topographic variable	Topographic canonical variable
Aspect scaler	.736
Relative elevation	.684
Log of fetch	.836
Fetch angle	−.822
Slope angle	.134
Vegetation variables	Vegetation canonical variable
Artemisia tridentata ssp. *vaseyana*	−.844
A. tridentata ssp. *wyomingensis*	−.025
A. nova	.644
Total grass	−.693
Total cushion plant	.703

angle are the most important topographic variables controlling vegetation composition at Stratton. The aspect scaler and relative elevation are also closely related to the topographic canonical variable; the composite of variables suggests that this axis represents wind exposure. Exposure increases with fetch, elevation, and aspect scaler, and decreases with fetch angle. Slope angle is not related to this axis; apparently processes related to slope angle, such as alluvial transport, are not important to vegetation composition in this system.

The vegetation canonical axis (Table 3) is most closely related to *A. tridentata* ssp. *vaseyana* and cushion plant cover. This axis is strongly positively correlated with *A. nova* and cushion plant cover, and negatively correlated with *A. tridentata* ssp. *vaseyana* and grass cover. *A. tridentata* ssp. *wyomingensis* is unrelated to this axis, perhaps because it is a fairly plastic species that occurs across the range of wind exposures.

Our interpretation of the canonical correlation is that landscape variation in vegetation is strongly related to topographic features that determine wind exposure. Wind gradients in the sagebrush landscape are likely to correspond with repeated snow distribution, soil moisture, and soil temperature patterns across the landscape, all of which control species composition and primary productivity. Snow depth and growing season soil moisture increase with decreasing fetch and increasing fetch angle. Once vegetation is established, there are feedbacks between topography and vegetation that reinforce these trends.

Relationship between vegetation and soil microclimate

Fig. 4 illustrates weekly soil moisture and temperature data we collected during the 1986 growing season. The extensive sites had markedly different soil microclimatic regimes than the upland shrub types. Aspen stands, with greater snowpacks, had high soil moistures, and low soil temperatures during the early part of the growing season, but by mid-summer had dried and warmed considerably. Nivation hollows, the most extreme example of a snow accumulation area, began the growing season in late June with cold and wet soils, but because of their steep slope angles, warmed and dried to the opposite extreme by late summer. Riparian communities maintained wet and cold soil conditions throughout the growing season.

ARNO upland shrub vegetation had relatively low soil moistures throughout the growing season, and relatively high soil temperatures. ARTRV vegetation, with the greatest snow accumulation of the sagebrush-dominated types, had greater soil moistures and lower temperatures than ARNO for the early part of the growing season, due to snowmelt, and much greater seasonal amplitude in soil microclimate. Similar trends to ARTRV were observed in the PUTR stands.

The strong differences among vegetation types suggest that soil microclimate may be one of the major vectors through which topographic variation controls vegetation distribution. In addition, soil microclimate in semiarid sagebrush steppe influences nutrient availability (Burke 1989), which can further control plant species assemblages and productivity.

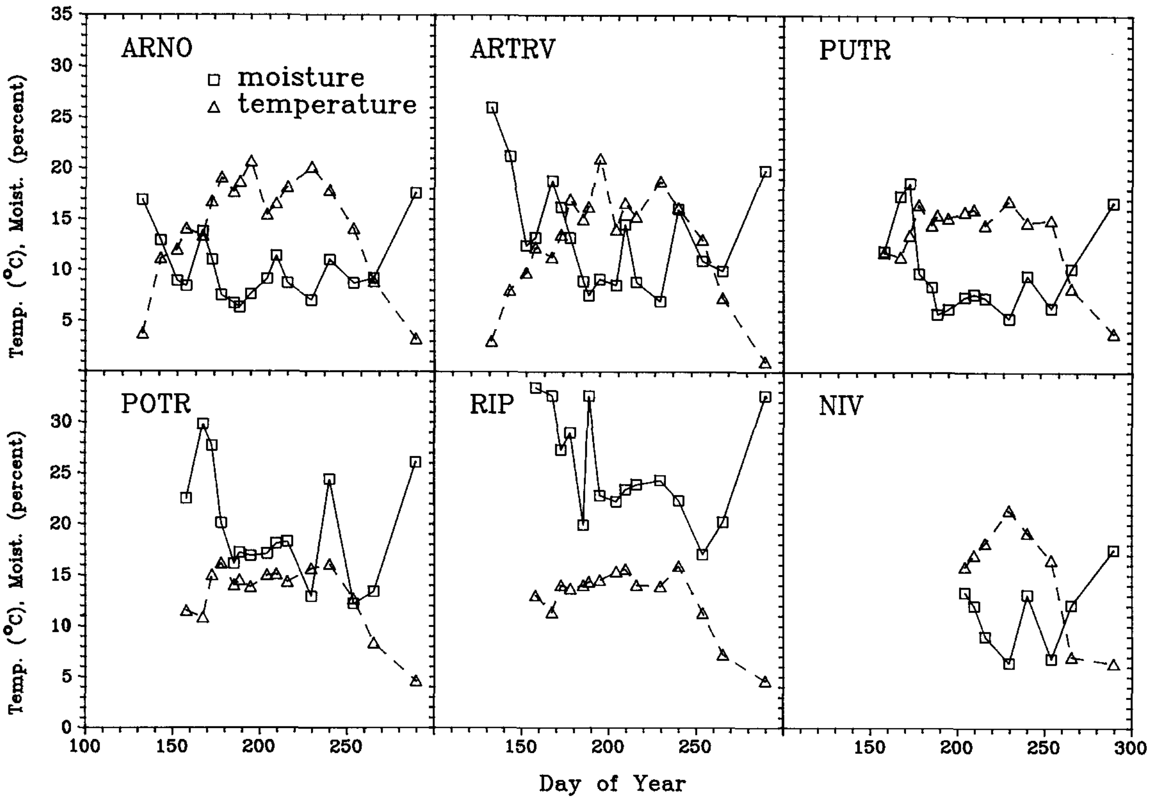

Fig. 4a–f. Soil moisture at 0–5 cm and soil temperature at 10 cm during the 1986 growing season in 6 of the vegetation types at the Stratton Sagebrush Hydrology Study Area. ARNO = *Artemisia nova* vegetation type, ARTRV = *Artemisia tridentata* ssp. *vaseyana* vegetation, PUTR = *Purshia tridentata*, POTR = *Populus tremuloides*, RIP = riparian grassland communities, NIV = nivation hollow vegetation types.

Conclusion

In summary, we have used spatial variation present in a sagebrush steppe landscape to test hypotheses about controls over vegetation distribution in this system. We established quantitative relationships between vegetation and its ultimate control, topography. In addition, we sampled variation in soil microclimate, and were able to relate patterns in vegetation type to temporal and spatial patterns in soil microclimate. Furthering our understanding of direct and indirect controls over vegetation in this system will allow us to make predictions about vegetation distribution outside of the realm of the field measurements, for instance, over larger spatial scales, or under changing climatic regimes.

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