GRADIENT ANALYSIS AND DESCRIPTION OF A TRANSITION ZONE PRAIRIE IN EASTERN SOUTH DAKOTA

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ABSTRACT

Detrended correspondence analysis (DCA) was used to order 23 stands from a prairie in northern Sanborn County, South Dakota. The first ordination axis was correlated with soil-site variables that describe a topographic, soil moisture gradient. Gaussian curves fitted to species frequency of occurrence data resulted in overlapping distributions with separate modal positions along the ordination axis. Upland sites had the highest species diversity and were dominated by *Andropogon gerardi* (big bluestem); lowland sites had the lowest diversity and were dominated by *Spartina pectinata* (prairie cordgrass). Four communities are described on the basis of topographic position.

INTRODUCTION

The natural vegetation of South Dakota is grassland. Most of the western half of the state falls within the northern mixed prairie which consists of a mixture of mid-height and short grasses (Singh *et al.,* 1983), while the eastern edge lies within the true prairie which is dominated by tall grasses (Weaver, 1954). Between these two is a transition zone where dominance is shared among wheatgrass (*Agropyron smithii*), bluestem (*Andropogon gerardi*) and needlegrass (*Stipa spartea*) (Kuchler, 1964). In South Dakota this transition zone extends from the Missouri River eastward to the Coteau des Prairies (Gartner, 1986).

Agricultural practices have eliminated much of the native grasslands in the eastern half of South Dakota. Descriptive studies of that which remains are few (Harvey, 1908; Florell, 1937; Tolstead, 1941; Wilding, 1959; Thiesfeld and Welborne, 1963; Beebe and Hoffman, 1968; Ungar, 1970; Ode *et al.,* 1980). This paper reports the results of an ecological study of a gently rolling, 24 ha prairie in the transition zone. Of particular concern were the species composition and species responses along environmental gradients.

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The study site, called Bonney Prairie, is located in north-central Sanborn County (NW ¼ of Section 17 of T108N, R60W) about 30 km southeast of Huron, South Dakota. Its gently rolling topography has a relief of approximately 5 m between uplands and lowlands. The climate is continental. The mean annual precipitation of 54.48 cm falls mostly during the spring and early summer (Driessen, 1980). Three soil types have been mapped within the study area, all having been derived from glacial drift. On uplands, the soils are deep, well-drained loams of the Ethan-Clarno and Clarno-Ethan series (Driessen, 1980). In lowlands, the soils are poorly drained Tetonka silt loams (Driessen, 1980). According to the owner, the study area has been mowed annually but pastured infrequently.

MATERIALS AND METHODS

During June and July, 1985, the presence of vascular plant species were recorded in 623—0.1 m^2 circular plots that were randomly located in 23 stands on knoll crests (9 stands), knoll slopes (8 stands), meadows (3 stands) and wet meadows (3 stands). Wet meadows held standing water throughout most of the previous year; whereas, meadows had no standing water at that time. At the time of sampling there was no standing water at the study site. Frequency of occurrence was calculated from presence data by dividing the number of plots in which a species had been found by the total number of plots sampled in a stand. Voucher specimens have been deposited in the herbarium at Dakota Wesleyan University. Nomenclature follows that of Van Bruggen (1985).

Six soil cores from each stand were removed to a depth of 15 cm. One core, placed in a stainless steel soil can, was used to gravimetrically determine moisture content after drying for 24 h at 105 C. The remaining five cores were combined in a plastic bag for other analyses. After each composite soil sample had been air-dried and mixed, subsamples were removed for pH, conductivity, and texture determinations. pH was measured with a hydrogen electrode following the methods described by Peech (1965). Conductivity measurements were made on a Hach Model 17250 Mini-conductivity meter following the protocol of Bower and Wilcox (1965). Soil texture was estimated by the Bouvoucos hydrometer method (Day, 1965).

Stand species diversity was determined for richness, heterogeniety and concentration of dominance. Species richness is equal to the mean number of species per 0.1 m^2. Heterogeneity was calculated using the Shannon-Weiner index (Whittaker, 1972) and concentration of dominance using Simpson's index (Whittaker, 1972).

Indirect gradient analysis was performed on the frequency of occurrence data using DCA (Sigma Soft, Placentia, CA 92670). DCA is a detrended correspondence analysis which orders stands on the basis of similarity in vegetational composition. Stand topographic position, soil varables and species diversity values were then correlated with the DCA ordination axis.

Gaussian curves were fitted to the species frequency of occurrence data along the DCA ordination axis using PROGRAM NON-LIN (Whitman, 1982). The percent variance accounted for by each Gaussian curve was determined from the ratio of the sum of squared deviations from the curve and the sum of squared deviations from a straight line at the mean (Gauch and Chase, 1974).

To determine beta diversity, a measure of the half-changes in species composition along an environmental gradient, the DCA ordination axis was divided into four segments representing crests, slopes, meadows and wet meadows. Beta diversity was then estimated using the method of Whittaker (1960).

RESULTS

DCA produced one significant axis (Figure 1), indicating the presence of one major environmental gradient. Inspection of the stand sequence along Axis 1 led to the inference that the axis represented a topographic, soil-moisture gradient. Those soil-site variables that were highly correlated with the ordination axis included percent soil moisture ($r = 0.639$, $p<0.01$) and percent clay ($r = 0.755$, $p<0.001$) which increased along the gradient, and pH ($r = -0.677$, $p<0.001$) and elevation ($r = -0.919$, $p<0.001$) which decreased. A multiple regression was not performed because most of the soil-site variables were intercorrelated.

Significant correlations between the DCA ordination axis and species diversity were also found (Table 1). Species richness ($r = -0.616$, $p<0.01$) and heterogeniety ($r = -0.713$, $p<0.001$) decreased along the axis, while concentration of dominance ($r = 0.743$, $p<0.001$) increased.

Beta diversity was estimated at 2.03. This is low compared to that (7.70) reported by Nelson and Anderson (1983) for a tall grass prairie in northern Illinois, but is within ranges reported for other communities (Whittaker, 1960 and Robertson *et al.*, 1984).

Gaussian curves were fitted to 15 of the more important species (Figure 2). Individual curves accounted for up to 90% of the variance in species abundance along Axis 1. At Bonney Prairie *Andropogon gerardi* was one of the leading dominants, having a modal position near the higher and drier end of the gradient along the ordination axis. *Poa* spp. (mostly *Poa pratensis,* but including *P. compressa* and *P. palustris*) were widely distributed along the

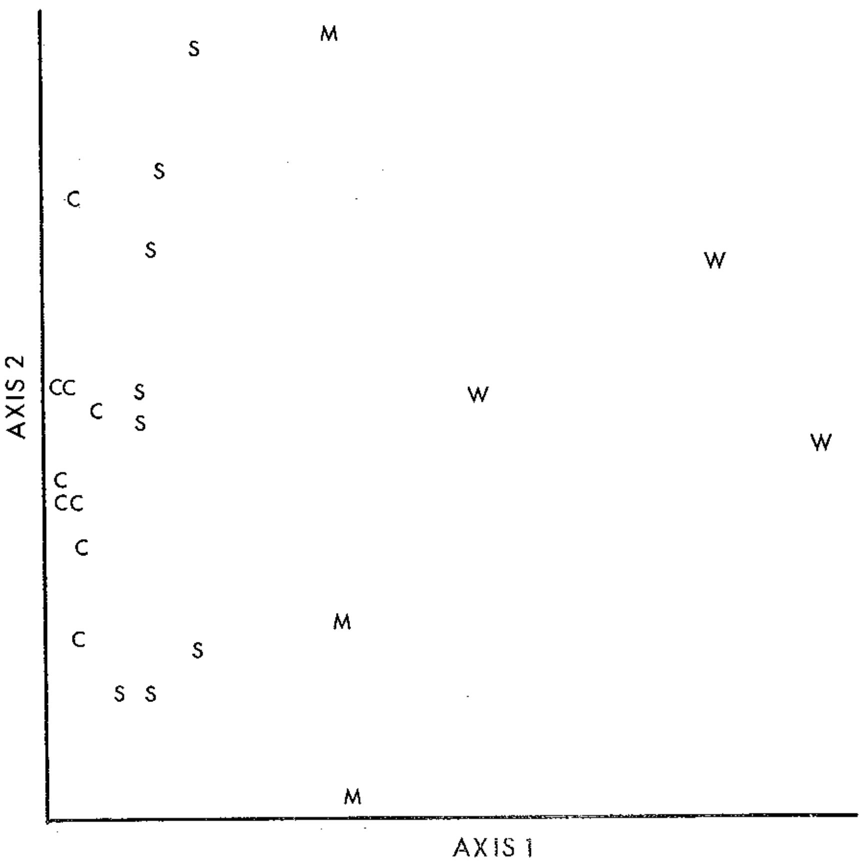

Figure 1. DCA ordination of 23 stands from Bonney Prairie. The letters identify topographic positions: C = crest, S = slope, M = meadow, W = wet meadow. Of the two axes shown, only Axis 1 is meaningful (eigenvalue = 0.680). Axis 2 (eigenvalue = 0.115) is shown only to separate closely associated stands.

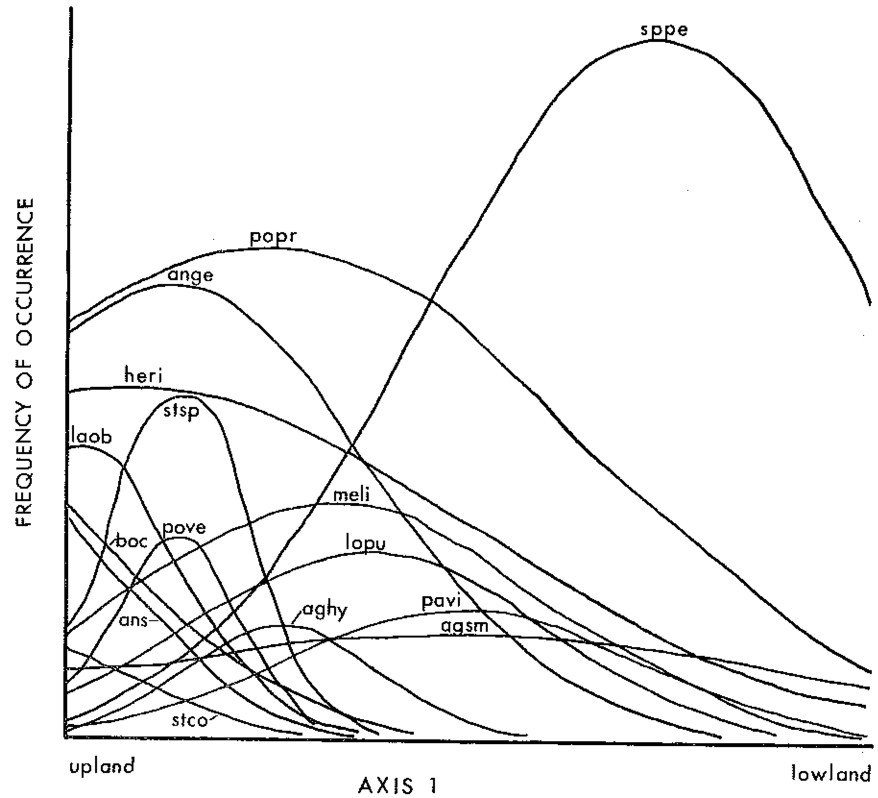

Figure 2. Gaussian curves for 15 species along a topographic, soil moisture gradient at Bonney Prairie. aghy = **Agrostis hyemalis**, agsm = **Agropyron smithii**, ange = **Andropogon gerardi**, ans = **Andropogon scoparius**, boc = **Bouteloua curtipendula**, heri = **Helianthus rigidus**, laob = **Lactuca oblongifolia**, lopu = **Lotus purshianus**, meli = **Melilotus alba** and **M. officinalis**, pavi = **Panicum virgatum**, popr = **Poa pratensis**, pove = **Polygala verticillata**, sppe = **Spartina pectinata**, stco = **Stipa comata**, stsp = **Stipa spartea**.

TABLE 1

Correlations of Soil-site Data and Stand Species Diversity Values With DCA Axis 1

Soil-site variables and species diversity values	Correlation coefficients
Moisture content (%)	+0.639 ($p<0.010$)
pH	−0.677 ($p<0.001$)
Conductivity (umhos)	−0.353 ($p<0.100$)
Sand (%)	−0.531 ($p<0.010$)
Silt (%)	+0.272 (not significant)
Clay (%)	+0.755 ($p<0.001$)
Topographic position	−0.919 ($p<0.001$)
Richness (species/0.1 m^2)	−0.616 ($p<0.010$)
Heterogeneity (Shannon-Weiner)	−0.713 ($p<0.001$)
Concentration of dominance (Simpson's Index)	+0.743 ($p<0.001$)

gradient with a mode near the dry end, albiet at a position that is lower and more mesic than that for *Andropogon gerardi.* The leading dominant forb, *Helianthus rigidus,* was found throughout the gradient and had a mode at the higher and more xeric end, near that of *Andropogon gerardi.* Those species with modes at the driest sites included *Andropogon scoparius, Bouteloua curtipendula, Stipa comata* and *Lactuca oblongifolia.* At slightly lower elevations and more mesic positions were modes for *Stipa spartea* and *Polygala verticillata.* Modal positions for *Lotus purshianus, Agrostis hyemalis* and *Agropyron smithii* were at still lower and more mesic sites. *Spartina pectinata* was the leading dominant at the moist end of the gradient.

After the ordination axis had been divided into segments representing topographic positions, it was possible to describe the four integrating communities at Bonney Prairie (Table 2). These communities were located on the major topographical features—knoll crests and slopes, meadows and wet meadows—of the prairie.

Knoll crests are the highest, driest (soil moisture = 28.25%) sites. Soils are slightly acidic (pH = 6.63), low in clay (8.89%) and highest in salts (82.78 umhos) when compared to other sites. Dominance is share by *Andropogon gerardi, Poa pratensis, Carex eleocharis* and *Lactuca oblongifolia,* with *Bouteloua curtipendula* and

Table 2

Frequency of Occurrence of Major Species, Means and Standard Deviations of Soil Variables and Species Diversity Values in Stands Segregated by Topographic Position

	Frequency of occurrence			
	Crests	Slopes	Meadows	Wet meadows
Agropyron caninum	0.0311	0.0737	0.1047	....
A. smithii	0.0973	0.0526	0.2448	0.1444
Agrostis hyemalis	0.0039	0.0473	0.1163	....
Andropogon gerardi	0.7471	0.8158	0.2674	....
A. scoparius	0.3074	0.0526	0.0348	....
Anemone canadensis	....	....	0.1395	....
Artemisia ludoviciana	0.1012	0.0842	0.1512	0.0111
Aster ericoides	0.2685	0.1368	0.1512	0.0614
A. simplex	....	....	0.0930	0.1222
Bouteloua curtipendula	0.3268	0.1737	0.0930	....
Calamagrostis canadensis	....	....	0.0233	0.1111
Carex spp.	0.5252	0.5157	0.7907	0.4778
Cirsium flodmani	0.0623	0.1053	0.0465	....
Dichanthelium wilcoxianum	0.2179	0.1526	....	....
Helianthus rigidus	0.5992	0.6421	0.5465	0.1111
Koeleria pyramidata	0.1012	0.1005	0.0465	....
Lactuca oblongifolia	0.5157	0.1895	0.0465	....
Lotus purshianus	0.0467	0.1421	0.3605	0.0556

Table 2 (Continued)

	Frequency of occurrence			
	Crests	Slopes	Meadows	Wet meadows
Melilotus spp.	0.0895	0.2895	0.3605	0.1444
Oxalis stricta	....	....	0.2209	0.1444
Oxytropis lambertii	0.1206	0.0105	....	....
Panicum virgatum	....	0.0211	0.1860	0.0889
Phalaris arundinacea	....	....	....	0.1333
Poa spp.	0.6809	0.8578	0.8023	0.2111
Polygala verticillata	0.1051	0.3474	0.1279	0.0111
Polygonum amphibium var. emersum	....	....	0.0116	0.1333
Psoralea argophylla	0.1245	0.1158	....	....
Spartina pectinata	....	....	0.2442	0.8556
Stipa comata	0.1323	0.0316	....	....
S. spartea	0.1128	0.5789	0.0116	....
Soil moisture (%)	28.25± 2.11	28.38± 6.86	32.30±4.80	42.19± 4.45
pH	6.63± 0.61	5.57± 1.06	5.86±0.31	5.43± 0.15
Conductivity (umhos)	82.78±54.40	31.88±16.62	25.66±4.04	34.33±14.29
Clay (%)	8.89± 1.36	8.50± 1.60	18.67±3.79	19.83± 5.97
Richness	6.02± 1.08	6.08± 2.32	5.12±3.99	3.08± 1.75
Heterogeneity	1.26± 0.10	1.18± 0.11	1.28±0.08	0.68± 0.56
Conc. of dominance	0.07± 0.02	0.09± 0.03	0.07±0.01	0.21± 0.12

Andropogon scoparius forming subordinate populations. Crests have the greatest species richness (6.02 spp./0.1 m^2) and heterogeneity; dominance is widely shared.

Slopes, leading from knoll crests, exhibited similar mean soil moisture (28.38%) as the crests, but are much more variable in their soil moisture content. This condition was influenced by aspect, south-facing sites being drier than north-facing sites. The soils are considerably more acidic (pH = 5.57) than those of the crests, but are less saline (31.88 umhos). Clay content on slopes is low (8.50%). Species diversity, in terms of richness (6.08 spp/0.1 m^2) and heterogeneity, remains high. The most frequently encountered species were *Andropogon gerardi, Poa pratensis, Helianthus rigidus, Stipa spartea* and *Carex eleocharis.* Less frequently encountered was *Polygala verticillata,* one of the few annuals of native grasslands.

Meadows are low areas at the bases of slopes. While the soil is moist (soil moisture = 32.30%), water seldom stands for long periods of time. Meadow soils contain about twice as much clay (18.67%) as those on the uplands. The species richness (5.12 spp./0.1 m^2) is slightly less than that for crests and slopes. Dominant species of the meadows are *Poa* spp. (mostly *P. pratensis,* but also *P. compressa* and *P. palustris), Carex,* spp. *(C. brevior, C. praegracilis* and *C. tetanica* were not separated because of difficulty in identifying specimens that lacked inflorescences), and *Helianthus rigidus.* Important, but less frequently encountered, species included *Lotus purshianus, Melilotus* spp. *(M. alba* and *M. officinalis), Agropyron smithii, Andropogon gerardi* and *Spartina pectinata.*

The lowest and wettest (42.19%) areas at Bonney Prairie are the wet meadows. During wet years, these areas maintain standing water for at least a part of the growing season. Soils are more acidic (pH = 5.43) and contain more clay (19.83% clay) than those in the rest of the study area. Species richness is the lowest (3.08 spp./0.1 m^2), with dominance concentrated in one species, *Spartina pectinata.* Common species of the wet meadows are *Carex* spp. *(C. atherodes, C. brevior, C. praegracilis* and *C. tetanica), Poa* spp. *(P. compressa, P. palustris* and *P. pratensis), Agrostis hyemalis* and *Oxalis stricta.*

DISCUSSION

The DCA ordination first axis depicted Bonney Prairie as a series of communities responding to a topographic, soil moisture gradient, with a continuous change in species composition from one end to the other. The gradient, however, is a complex one, additionally involving soil texture and pH. Three of these soil-site variables—topographic position, soil moisture and clay content—

are interrelated. The drier sites are on crests where runoff of water received as precipitation is the greatest. This runoff, carrying with it the clay-sized soil particles, accumulates in the lowlands. Thus, the meadows are wetter and retain soil moisture longer because of slow percolation through a heavier soil.

Species diversity decreased from higher, drier sites to lower, wetter sites, wet meadows having the lowest diversity. This lower diversity in the wet meadows is due probably to low environmental stability. The soils, being very heavy, do not permit rapid infiltration of water but cause the accumulation of standing water above them during wet seasons. For the same reason, these areas become very dry during droughts. The low species diversity indicates that few native species are adapted to such extremes.

Although 135 species have been collected from Bonney Prairie (unpublished species list available from author) with approximately 100 occurring in sample plots, the between stand (beta) diversity was not high. This low beta diversity probably results from the existence of a shallow environmental gradient (elevational differences between knoll crests and wet meadows were 5 m or less), which seemed to be determined to a large extent by topography. Soil moisture differences (ca. 25%) and percent clay differences (17%) between gradient ends also were not great. Consequently, a high rate of turnover in species composition would not be expected.

Modal positions of species along the ordination axis (Figure 2) are generally consistent with reports on other prairies. At Bonney Prairie, *Andropogon gerardi* reached its greatest frequency on high, dry sites. While three other studies (Curtis and Greene, 1949; Dix and Butler, 1960; Nelson and Anderson, 1983) concur, the majority of reports (Albertson, 1937; Beebe and Hoffman, 1968; Curtis, 1955; Good and Good, 1971; Hopkins, 1951; Partch, 1962; Steiger, 1930) indicated that *Andropogon gerardi* is a more mesic species. Its presence at high frequencies on upland sites may be due to its spread immediately after the drought of the 1930's as a result of decreased competition from other upland species that had succumbed to the drought (Weaver, 1954).

In most studies *Poa pratensis* reached its greatest importance in mesic prairies (Archer, 1984; Dix and Butler, 1960; Dix and Smeins, 1967; Good and Good, 1971; Hopkins, 1951; Steiger, 1930); however, Beebe and Hoffman (1968) reported it to be abundant on upper slopes in parts of southeastern South Dakota. Upper slopes are where it reached its peak abundance at Bonney Prairie. Its broad curve (Figure 2) indicates not only its ubiquity within the study area but also my inability to separate it in the vegetative state from related species, especially when it was found in meadows

and wet meadows. Nevertheless, its presence throughout the study site may have been due to its promotion by annual mowing (Weaver, 1954).

The most abundant forb at Bonney Prairie, *Helianthus rigidus*, was found on most sites, but reached its abundance mode on higher, drier sites. This is consistent with its position in other prairies (Beebe and Hoffman, 1968; Curtis and Greene, 1949; Redmann, 1972). Curtis (1955), however, claimed it to be an indicator of mesic prairies in Wisconsin.

Andropogon scoparius and *Bouteloua curtipendula* reach their greatest abundance on highest, driest sites, which is where they were placed in the studies previously cited.

The two species of *Stipa* which occur at Bonney Prairie do not reach maxima at the same positions along the ordination axis (Figure 2). *Stipa comata* occupies higher and drier sites than *S. spartea*, a condition also found by Coupland (1950), Dix and Smeins (1967) and Good and Good (1971).

Spartina pectinata was the dominant grass of the lowest, most mesic sites. This position is consistent with reports on other prairies.

Generalizations about the optimal habitats for species exhibiting broad distributions are tenuous. First, both obvious and subtle differences exist between one location and another. These differences interact in complex ways to give rise to species patterning on the landscape, making precise comparisons from one place to another difficult. Secondly, because species are made up of populations which may show phenotypic differences related to ploidy (Lewis, 1980) and result in ecotypic variation (McMillan, 1959), such species are not expected to behave in precisely the same manner in all locations. Finally, differential competition may displace a species from what are usually considered its normal habitats (Cody, 1978).

At Bonney Prairie, species populations sort out along a complex topographic, soil-moisture gradient. While species distributions overlap producing a continuum of communities that gradually grade into each other, species modal positions are separate as would be predicted by the competitive exclusion principle (Hardin, 1960).

Although Bonney Prairie is located in the transition zone where the dominant species should include *Agropyron smithii*, *Andropogon gerardi*, and *Stipa spartea* (Kuchler, 1964), a quantitative sampling of this prairie has shown otherwise. *Poa pratensis*, on the basis of frequency of occurrence, is either the leading dominant (in meadows) or shares dominance with *Andropogon gerardi* and *Stipa* *spartea* (on uplands). *Agropyron smithii* is one of the lower ranking dominant grasses, but only in the meadows. These shifts in ranks of dominance are probably due to the past history of the study site, which includes annual mowing and fire suppression, both of which have been shown to markedly effect the species composition of a prairie. Curtis and Partch (1948) have shown that annual burning significantly decreases the abundance of *Poa pratensis* in tallgrass prairie. More recently, Engle and Bultsma (1984) reported that burning, in addition to decreasing *Poa pratensis*, increases *Agropyron smithii* in mixed grass prairie depending on when the burn occurs. Mowing can also alter the species composition of a prairie, increasing the abundance of some species, while decreasing the abundance of others (Weaver and Hougen, 1939).

Finally, the local environment (i.e., topography, soil texture, etc.) can affect species composition as I have shown for Bonney Prairie. While classifications of vegetation, like that of Kuchler (1964), are valuable in portraying what types of vegetation should be expected under pristine circumstances, their broad brush strokes obscure detail. Thus, studies of what vegetation actually exists are needed to fill in the detail and to depict the landscape as it currently exists.

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