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**Vegetation of the Coniferous-Deciduous Forest Overlap Region
Along the Niobrara River Valley of North-Central Nebraska.**

Carol Sue Crosby

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Vegetation of the Coniferous-Deciduous
Forest Overlap Region Along the Niobrara River
Valley of North-Central Nebraska

A Thesis

Presented to the

Department of Biology

and the

Faculty of the Graduate College

University of Nebraska

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

University of Nebraska at Omaha

by

Carol Sue Crosby

July 1988

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THESIS ACCEPTANCE

Acceptance for the faculty of the Graduate College,
University of Nebraska, in partial fulfillment of the
requirements for the degree Master of Arts, University of
Nebraska at Omaha.

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Introduction

The Niobrara River Valley of north central Nebraska is recognized as an area in which elements of the Rocky Mountain (coniferous), Boreal, and Eastern Deciduous forests meet. These elements occur primarily along river bluffs in an area surrounded by grasslands (Bessey 1887, Pound and Clements 1900, Tolstead 1947, Nixon 1967, Kaul 1975). In this region many species of plants and animals reach their distributional limits (Tolstead 1942). Diverse topography, north/south slope microclimates, soil, hydrology and geologic history have contributed to creating this biological crossroads amidst a chiefly grassland climate.

The co-occurrence of disjunct plant and animal species more typical of forests further to the east, west and north suggests that the Niobrara Valley serves as a glacial and post-glacial refugium in the central plains. Some species may be relicts of cooler glacial and post-glacial times when much of what is now grassland was covered by temperate and boreal forests (Kaul et al. 1988). As the glacial ice retreated and the climate warmed, prairies replaced forests except in suitable habitats, such as the Niobrara River Valley, where some species have persisted. Kaul et al. (1988), suggest that the modern distributional patterns of many species are due to these historical factors rather than to dispersal events.

An area of overlap of the Eastern Deciduous and the Rocky Mountain Forests occurs along the Niobrara River roughly between Ainsworth, Nebraska ($42^{\circ} 35' N$ x $99^{\circ} 59' W$) in the east and Valentine, Nebraska ($42^{\circ} 51' N$ x $100^{\circ} 33' W$) in the west. Rocky Mountain Forest species, particularly ponderosa pine (*Pinus ponderosa*), are found mainly on the fine, sandy loam soils of the Crookston table on the north side of the river. However, pines also occur on the rim of the south bank. There they overlap and intermingle with elements of the Eastern Deciduous Forest which are generally confined to the south side of the river along more protected, spring-fed, north-facing slopes and deep canyons of tributary streams (Harrison 1980). This mixed community is termed an Oak-Pine forest in this study because, while many deciduous species occur in the area, bur oak (*Quercus macrocarpa*) is the recognized dominant in that portion of the south bank that also contains the pines. ✓

This study assumed the occurrence of an east-west vegetation gradient based on the distribution of Eastern Deciduous and Rocky Mountain Forests as indicated by Kaul (1975) and on a known moisture gradient with drier conditions occurring to the west (Lawson et al., 1977). These references suggest Rocky Mountain Forest elements increasing to the west and Eastern Deciduous Forest elements increasing to the east. Elevational gradients, inferred by Harrison (1980), should be reflected in an increase of Eastern Deciduous elements on lower elevations and an

increase in Rocky Mountain Forest elements on upper slope locations.

The focus of this study is the area of overlap of the Eastern Deciduous and Rocky Mountain Forests, specifically along the south bank of the Niobrara River. The objectives of the study are (1) to describe quantitatively the forest community in the region of overlap using classification techniques and (2) to examine the Oak-Pine forest for longitudinal (east-west) and elevational gradients.

Materials and Methods

Study Area

The study was conducted along that portion of the Niobrara River Valley located in Brown and Cherry Counties in north central Nebraska, specifically from 42° 35' N x 99° 59' W to 42° 51' N x 100° 33' W. Included in this region is the Niobrara Valley Preserve, established and maintained by The Nature Conservancy, and the Fort Niobrara National Wildlife Refuge. The climate of the region is highly variable with cold winters and hot summers. Winter temperatures vary from 26° C to -41° C; summer temperatures may reach 40° C. The average annual precipitation is about 57 cm. in the east and 45 cm. in the west, with most precipitation occurring in summer. Periodic droughts and lightning storms subject the area to fires (Lawson et al., 1977). Slopes range from 0-10

degrees on top and bottom elevations and from 30-40 degrees on middle slope elevations.

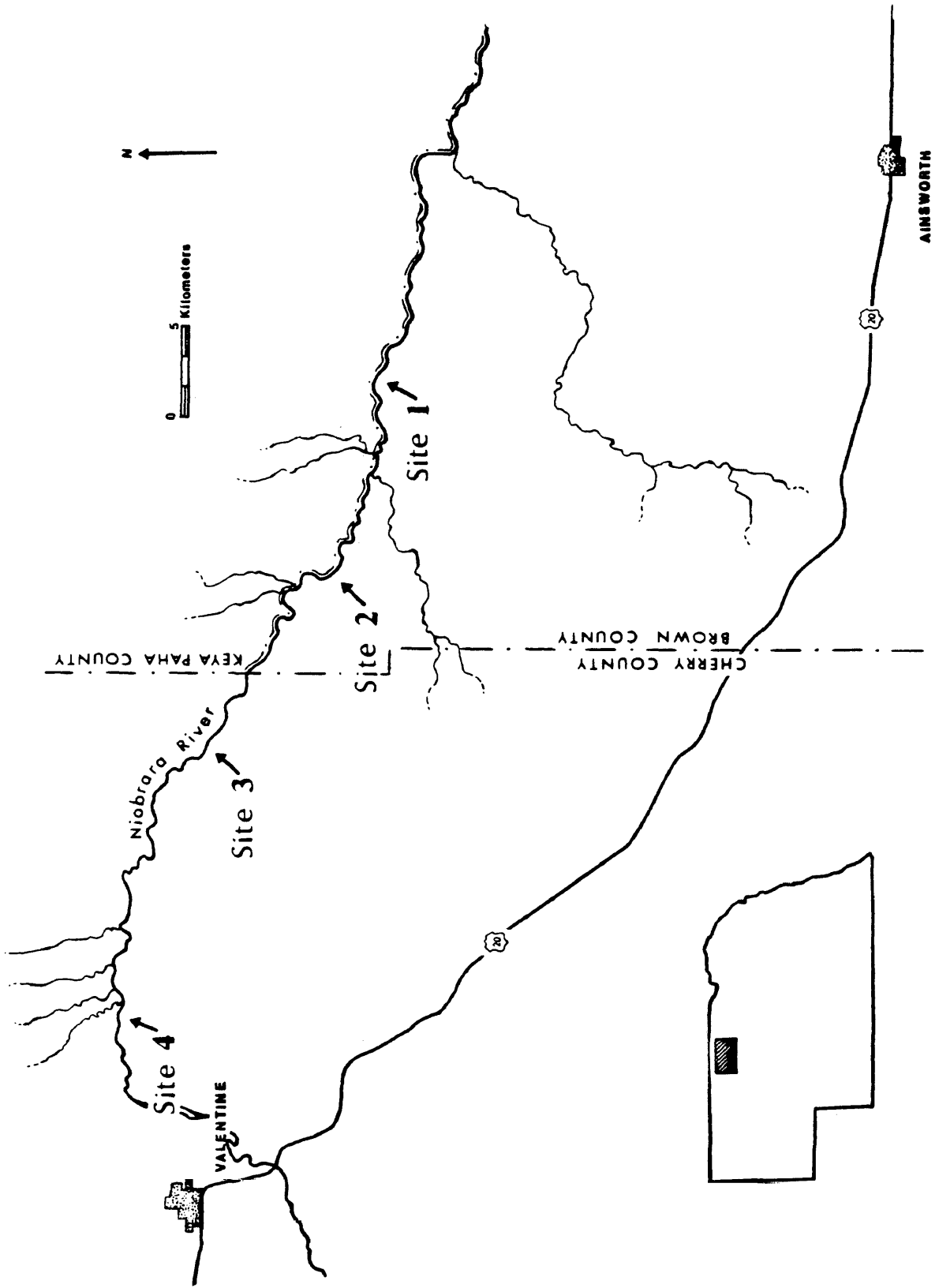
Field Methods

Four sites were identified within the study area based on similar aspect, length of slope, steepness and absence of branch canyons. These sites were approximately 18 km. apart on generally continuous, north-facing slopes. Sites were numbered 1-4 from east to west (Fig.1).

Sites 1-3 were located on the Niobrara Valley Preserve. Site 1 was the driest site with few flowing springs and an abundance of red cedar (Juniperus virginiana). Sites 2 and 3 had several springs intercepting the sample transects. Site 4, situated on the Fort Niobrara National Wildlife Refuge had fewer flowing spring seeps than Sites 2 and 3. It had also been recently disturbed by longhorn cattle grazing and had a dirt road at the base of the bluff which introduced a higher level of disturbance to the lower slope portion of the site.

At each study site, woody vegetation was evaluated using the Line-Intercept Method of measuring canopy cover (Canfield 1941). Line transects 100 meters in length were used to evaluate vegetation at six elevations with each elevation replicated 3 times for a total of 18 transects at each study site. Transects at each elevation were numbered from 1 for hilltop to 6 for lower slope. Transects were

Fig. 1. Location of study sites along the Niobrara River Valley. Nebraska map inset indicates study region.



N

0 5 Kilometers

KEYA PAHA COUNTY

CHERRY COUNTY

Niobrara River

Site 1

Site 2

Site 3

Site 4

VALENTINE

AINSWORTH

20

20

positioned in an east-west direction, parallel to the contour of the slope. This procedure was followed at all 4 study sites for a total of 72 transects. Floodplain forests were excluded. In this study, consistent with ordination terminology, each transect is referred to as a sample. For tree species, the canopy cover for each individual of each species and combined (total) canopy cover of individuals of a species were determined. For shrubs, only total canopy cover was recorded. In addition, inclination and aspect were recorded for each transect.

Data analysis

Mean canopy cover values for all species were calculated for each transect (Appendix Table 1). Dominant tree species, used for ANOVA procedures, were defined as those having the greatest mean canopy cover at a site for each elevation. While many species contribute to the structure of a community, dominance is a common measure of species importance in plant communities. Angular transformation ($\arcsin\sqrt{p}$) of the cover data of dominant species was used to minimize deviations from normality (Zar 1984). With the exception of bur oak, for which this procedure eliminated deviations from normality, transformations did not eliminate the deviations although they did bring the frequency distributions closer to a normal distribution. These

Table 1. List of woody species in the Niobrara River Valley. Four-letter codes given after the scientific name are used for figures and tables throughout the text. Scientific and common names from Great Plains Flora Association (1986).

Trees

Quercus macrocarpa Michx. (Qu ma) bur oak

Pinus ponderosa Laws. (Pi po) ponderosa pine

Juniperus virginiana L. (Ju vi) red cedar

Ostrya virginiana (P. Mill.) K. Koch (Os vi) ironwood

Betula papyrifera Marsh. (Be pa) paper birch

Tilia americana L. (Ti am) American linden

Fraxinus pennsylvanica Marsh. (Fr pe) green ash

Ulmus americana L. (Ul am) American elm

Celtis occidentalis L. (Ce oc) hackberry

Acer negundo L. (Ac ne) box elder

Juglans nigra L. (Ju ni) black walnut

Populus deltoides Marsh. (Po de) cottonwood

Shrubs

Ribes odoratum Wendl. (Ri or) buffalo currant

Prunus pumila L. var. besseyi (Bailey) Gl. (Pr up) sand cherry

Amorpha canescens Pursh (Am ca) lead plant

Table 1. List of species. (continued)

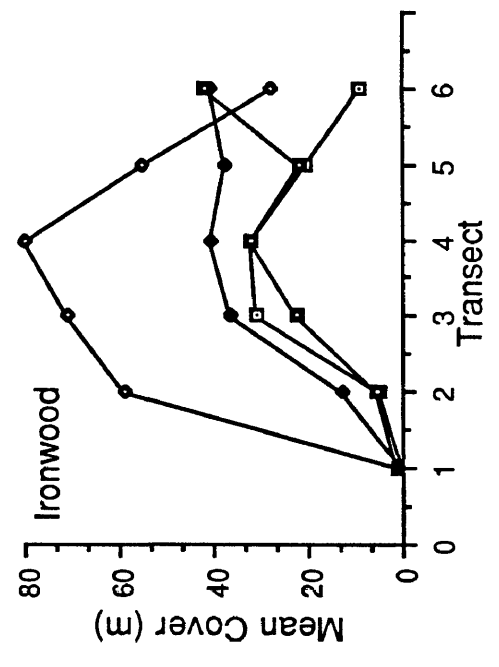
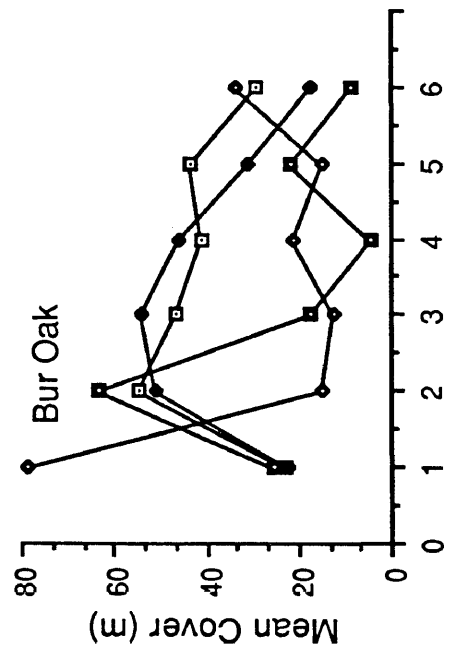
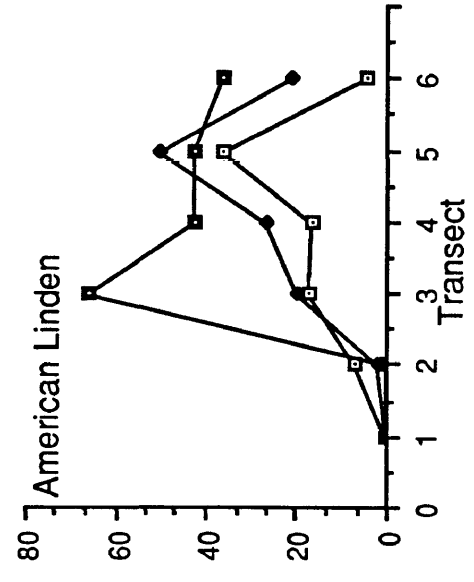
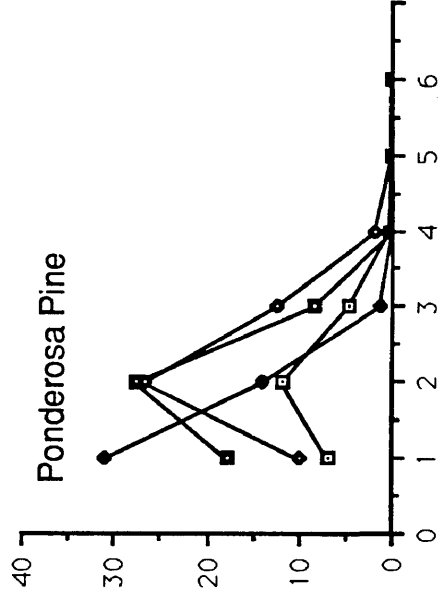
 Shrubs (continued)

- Rosa arkansana Porter (Ro ar) prairie rose
Prunus americana Marsh. (Pr am) wild plum
Amelanchier alnifolia Nutt. (Am al) Saskatoon service berry
Rhus aromatica Ait. (Rh ar) fragrant sumac
Zanthoxylum americanum P. Mill (Za am) prickly ash
Ribes missouriense Nutt. (Ri mi) Missouri gooseberry
Rhus glabra L. (Rh gl) smooth sumac
Prunus virginiana L. (Pr vi) chokecherry
Symphoricarpos occidentalis Hook. (Sy oc) western snowberry
Viburnum opulus L. var. americanum Ait. (Vi op) highbush
 cranberry

Table 2. Two-way ANOVA of canopy cover for selected dominant species. *=significant differences ($P \leq 0.05$).

Source	DF	SS	F	PR>F
<u>Bur Oak</u>				
SITE	3	0.414	1.99	0.1278
ELEVATION	5	0.657	1.88	0.1152
SITE-ELEVATION	15	2.730	2.63	0.0057*
<u>Ponderosa Pine</u>				
SITE	3	0.045	0.39	0.7626
ELEVATION	5	1.830	9.45	0.0001*
SITE-ELEVATION	15	0.390	0.67	0.7982
<u>American Linden</u>				
SITE	3	2.446	19.44	0.0001*
ELEVATION	5	2.632	12.55	0.0001*
SITE-ELEVATION	15	1.814	2.88	0.0027*
<u>Ironwood</u>				
SITE	3	1.762	11.15	0.0001*
ELEVATION	5	3.911	14.85	0.0001*
SITE-ELEVATION	15	1.104	1.40	0.1873

Fig. 2. Mean cover by site and slope location for selected dominant species. Transect 1=hilltop, Transect 6=lower slope; □=Site 1, ◆=Site 2, ■=Site 3, ◇=Site 4.



deviations from normality are probably due to the high frequency of zero values in the data set when species were absent from a particular elevation. Because improvements were made in the frequency distributions, the main effects were tested on dominant species as well as on bur oak using ANOVA procedures. These statistical tests are felt to be sufficiently robust to provide information useful to this study. Transformed data were analyzed using a Two-way Analysis of Variance to test for differences among sites and elevations and site-elevation interactions. For dominant species that showed significant differences using ANOVA procedures, Duncan's Multiple Comparison test was used to determine where differences occur along the slope and between sites. Red cedar, a dominant tree species, was excluded from Analysis of Variance tests because it is considered an invasive species and not of principal importance to the distributional aspect of the study. This species, however, was included in the remainder of the analyses.

An ordination program, Detrended Correspondence Analysis (DCA or DECORANA) (Hill 1979a, Hill and Gausch 1980, Gausch 1982) was used to assess vegetation-environment relationships at the community level. DCA orders both samples and species according to their similarity based on species abundance. This ordering occurs along several axes with the first axis accounting for the most variation within the sample and subsequent axes containing less information

as indicated by decreasing eigenvalues.

Two Way Indicator Species Analysis (TWINSpan) (Hill 1979b, Gausch 1982) was used to classify both samples (100 meter transects) and species into broad groups based on species composition and abundance. The TWINSpan program begins with all samples together in a single cluster and successively divides the samples into a hierarchy of smaller and smaller clusters until the final cluster contains either one sample or some previously specified number of samples (Gausch 1982). In this study, the program default of five samples per cluster was used. This level was achieved after six divisions. In addition, this classification of samples was used to produce a corresponding classification of species. These two classifications (samples and species) were used together to obtain an ordered, two-way, samples-by-species table from which corresponding dendrograms, one by sample and one by species can be drawn. Similar samples or species are placed closer together in a dendrogram sequence. Both the sample placement order along the dendrogram sequence and the clustering of samples are important considerations in interpreting the dendrogram. The dendrogram for samples was only interpreted to three divisions because beyond this point vegetation patterns were not distinguishable.

Results

Twenty-five species of woody plants were identified in the study, 11 trees and 14 shrubs (Table 1). Four dominant tree species: bur oak, ponderosa pine, American linden, (Tilia americana) and ironwood (Ostrya virginiana) were analyzed for elevational and longitudinal (east-west) differences. One shrub, highbush cranberry (Viburnum opulus v. americanum), was considered to have escaped from cultivation and thus was not considered in community or species evaluations. Mean canopy cover for all species is listed in Appendix Table 1.

Species-Level Distribution

There were no significant differences in the distribution of bur oak among sites or elevations but significant site- elevation interactions were detected (Table 2). Sites 1 and 2 were similar in their mean cover of bur oak (Fig.2, Appendix Table 1). The interactions arise because Site 2 exhibited an increase in bur oak at mid-slope locations whereas Site 1 showed a decrease. The greatest difference in bur oak cover occurred at the upper elevations where Site 3 exhibited a greater cover while the abundance at Site 4 was lower (Fig. 2). These interactions show that the distribution of bur oak from lower to upper

slopes will vary according to site location.

Ponderosa pine showed significant elevational differences (Table 2, Fig. 2). The Duncan's Test indicates that upper elevations (Transects 1-3) had significantly higher mean cover values than lower elevations ($P \leq 0.05$).

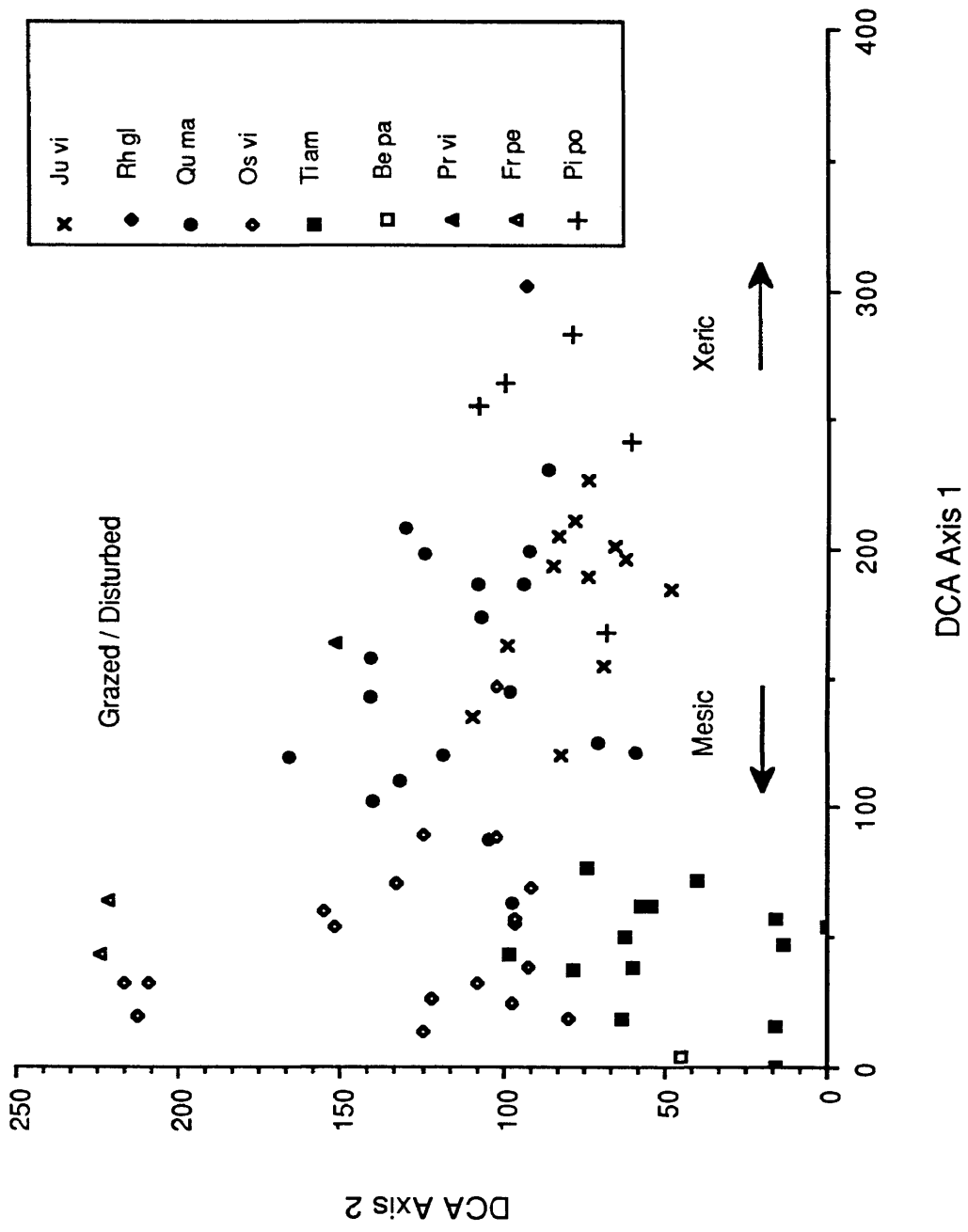
American linden showed significant site and elevation differences and site-elevation interactions (Table 2). Site differences were most evident at mid-slope and lower slope locations (Transects 3-6), where American linden exhibited an increase in abundance from east to west except in Site 4 where it was absent. Elevational differences were shown, for example, at Site 3 where the abundance of American linden was relatively low at upper-slope and considerably higher at mid-slope elevations (Fig. 2, Appendix Table 1).

Ironwood, an understory tree, also showed significant site and elevation differences (Table 2). The highest mean value for this species was recorded in Site 4 (Fig. 2), the most disturbed site.

Community Patterns

The first two DCA axes suggest that two environmental factors, moisture and disturbance, are important in explaining the distribution of vegetation (Fig. 3). These axes represent a large component of the variation (eigenvalues=0.427, and 0.223). The interpretation of

Fig. 3. Ordination of all 72 samples on the first two DCA axes. Symbols represent the dominant species of each sample. Environmental characteristics of selected regions of the ordination field are labeled. See Table 1 for species codes.



moisture as an important factor is based on the occurrence of samples dominated by xeric species at the high end of Axis 1 while samples dominated by mesic species are grouped at the lower end. Thus, Axis 1 is interpreted to represent a moisture gradient. Along Axis 2, the samples that are dominated by species considered to be adapted to disturbance or that are from Site 4, a disturbance site, are grouped together at the upper end of the axis. The remaining samples are distributed lower along the axis. This distribution suggests that Axis 2 represents a disturbance gradient.

The distribution of all 72 sample points along DCA Axes 1 and 2 form a wedge-shape with the point of the wedge in the xeric end of the ordination field (Fig. 3). A distribution of this type suggests that environmental conditions at the upper, xeric end of Axis 1 are more limiting or restrictive than conditions at the lower end. These less restrictive conditions are reflected in the greater number of samples plotted in the low end of the ordination field. It is at the low end of the ordination field where factors, such as disturbance, may play an important role in determining the distribution of vegetation in more mesic settings.

Ordination of species, which groups together ecologically similar species, gave results similar to the sample ordination. Axis 1 corresponds to a distribution

along a moisture gradient and Axis 2 suggests a disturbance gradient (Fig. 4).

The results of TWINSpan generally clustered samples into mesic and xeric groups (Fig. 5). Xeric samples included ponderosa pine, woody prairie species, and a mixed oak-juniper-pine forest. These samples are located mainly on hilltop or prairie-forest edge locations. Within the more mesic samples, three categories can be distinguished; 1) undisturbed, linden-paper birch stands, 2) disturbed, ash-ironwood-elm stands and 3) oak-linden stands, which were found mainly in eastern sites at mid-slope locations. Disturbed, mesic samples were grouped together even though they were separated at the third division. This grouping was made (1) because the samples found in these clusters were similar in their location and in the dominant species found in the samples and (2) the samples were next to each other in the dendrogram sequence indicating that they were similar.

The TWINSpan analysis also arranged species into two broad groups consistent with the moisture and disturbance gradients shown by DCA and by TWINSpan classification of samples (Fig. 6). Two distinct clusters are (1) the more xeric, prairie/savanna species and (2) the more mesic moist woodland species. Bur oak, red cedar, plum (Prunus virginiana.) and service berry (Amelanchier alnifolia), however, occupy intermediate positions on the xeric side which cannot be easily categorized.

Fig. 4. Ordination of species on the first two DCA axes. Environmental characteristics of selected regions of the ordination field are labeled. See Table 1 for species codes.

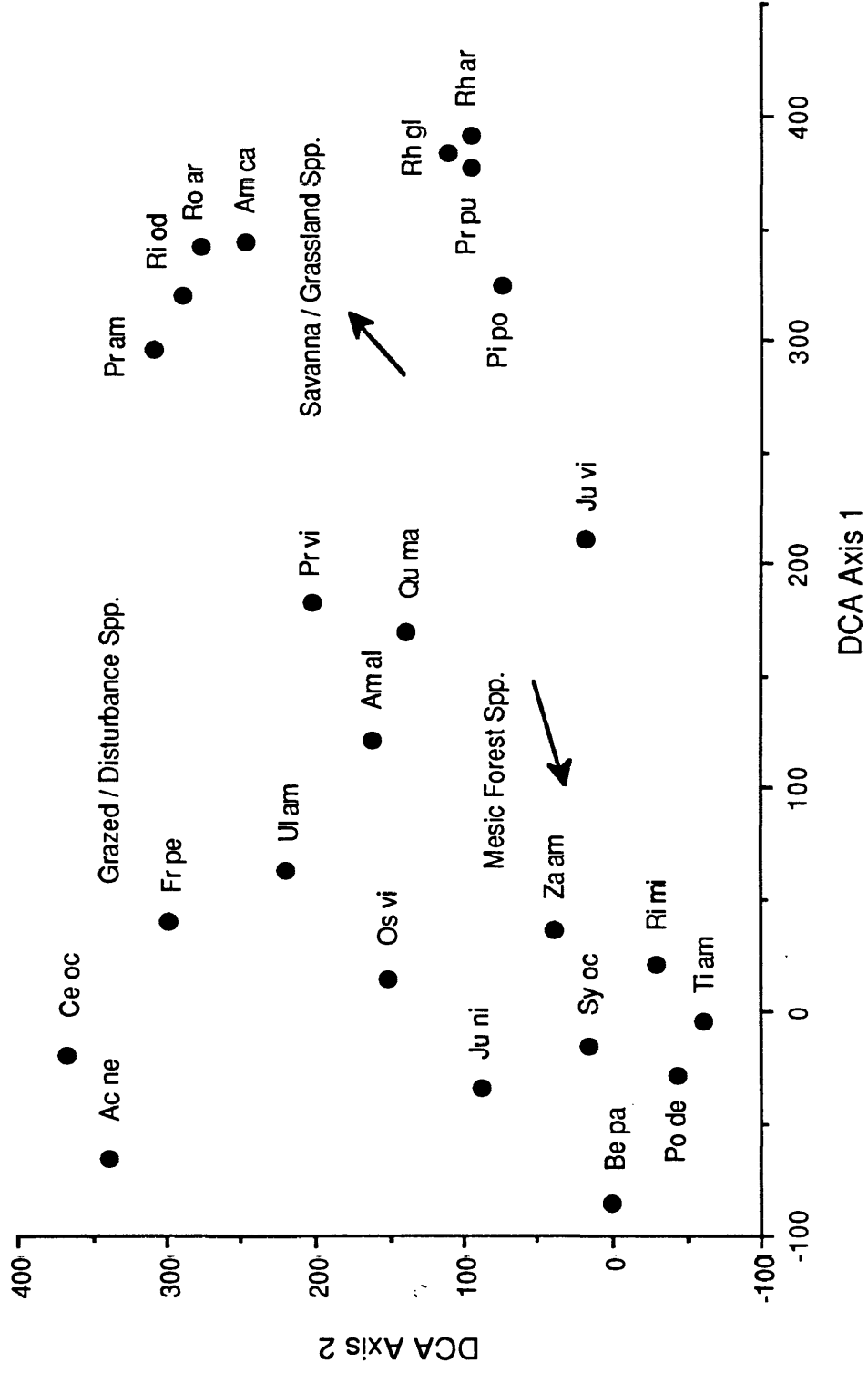


Fig. 5. Dendrogram illustrating the classification of samples using TWINSpan. Numbers indicate the number of samples per cluster.

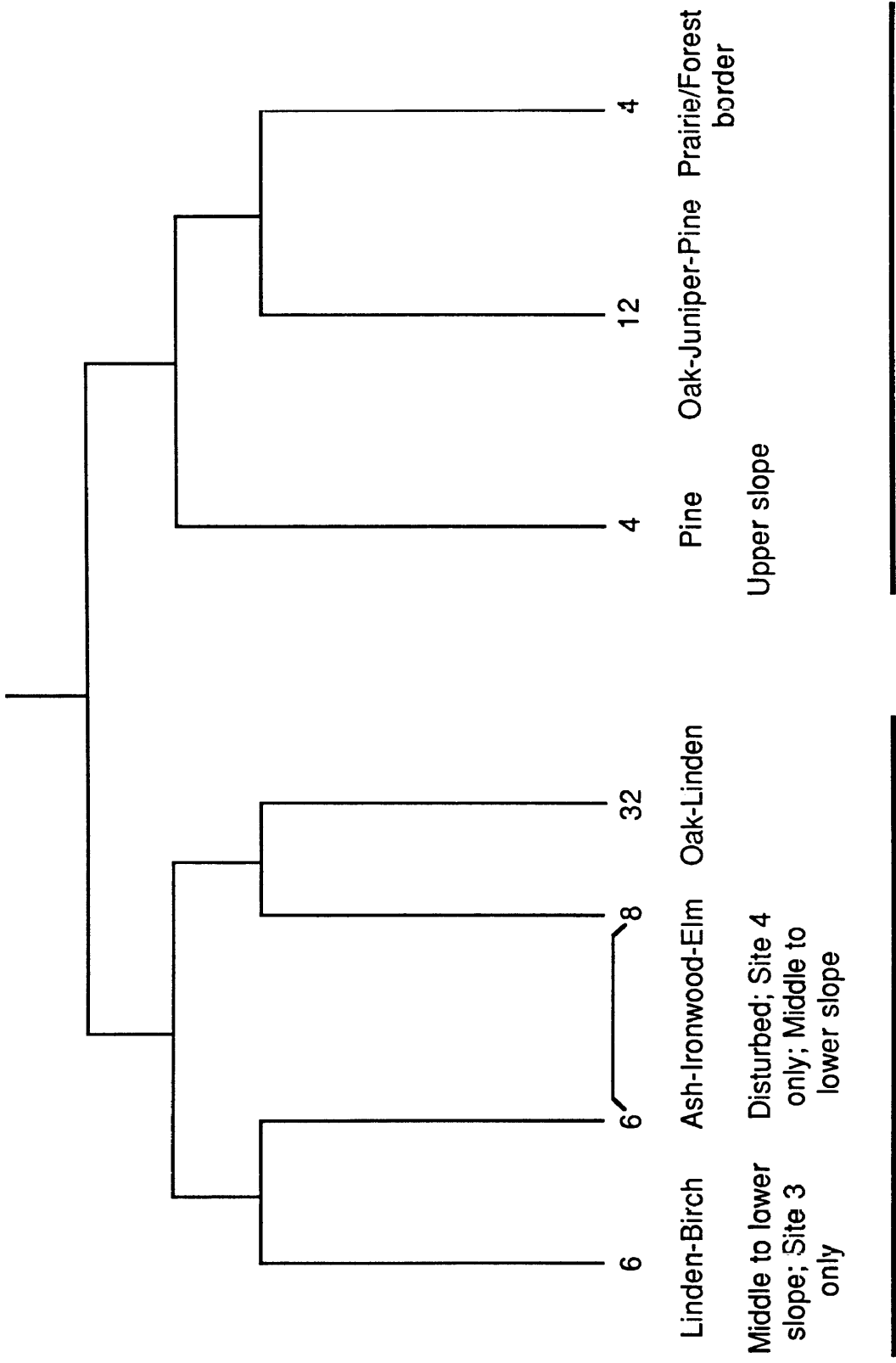
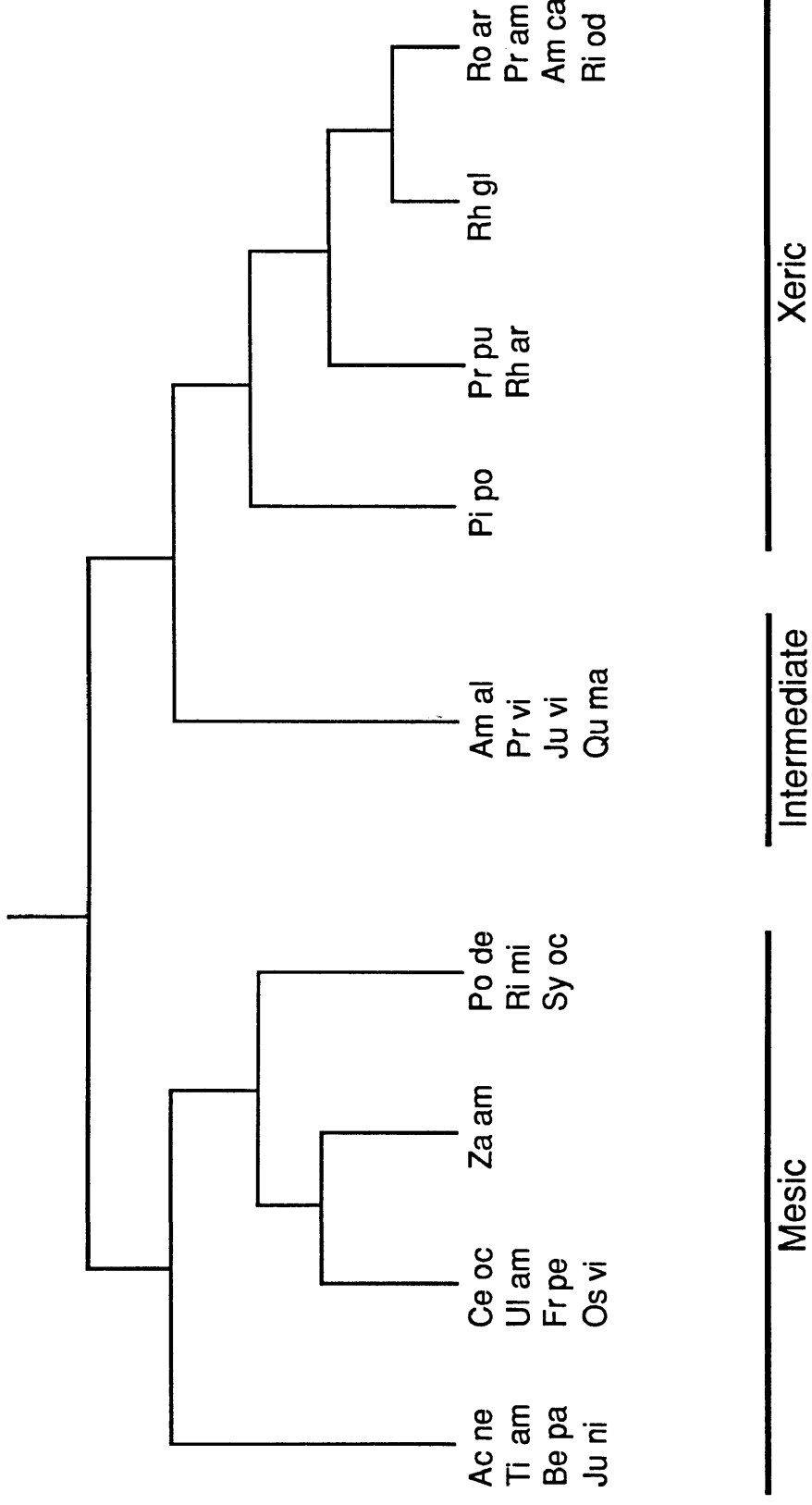


Fig. 6. Dendrogram illustrating the classification of species by TWINSpan. See Table 1 for species codes.



Discussion

The vegetation patterns of the Oak-Pine region along the Niobrara River are complex and probably are influenced by many factors. This study assumed the occurrence of an east-west vegetation gradient. Based on data from the sites used in this study, a clear vegetation gradient from east to west was not apparent. Future studies may need to use more sites in order to test for such a gradient.

As expected, elevation was one factor affecting species distribution patterns. The largest difference was between the upper most slope and the middle and lower slopes (Fig.1). These upper transects were located in the prairie/forest ecotone which was highly variable and patchy, probably due to recent expansion of woody plants into the surrounding prairie. The expansion of forest into the prairie appears to take place with fingers of forest extending into the prairie in suitable habitats, such as small draws, resulting in pockets of prairie interspersed with forests. Steinauer and Bragg (1987) documented the invasion of ponderosa pine into the surrounding prairie. In addition, recent invasion of uplands is supported by preliminary soil $\delta^{13}\text{C}$ analysis conducted at selected sites, some of which were included in this study. These analyses show that the soils along the bluff rim are prairie-type soils even though they are presently wooded (personal communication, A.S. Steuter, 1987).

The woodland-into-prairie invasion appears to originate from the Rocky Mountain Forest community, primarily by ponderosa pine. On the south side of the river valley, this species occurs along a relatively narrow band on the ridge tops although a few individual pines occur further down-slope in xeric sites. The Eastern Deciduous element, however, occupies a broader portion of the slope along protected middle to lower slope locations. Ordination suggests that species composition at these slope locations is influenced primarily by moisture.

A precipitation gradient does exist from east to west with western sites receiving less annual precipitation than eastern sites (Lawson et al., 1977). However, a more important moisture factor in determining vegetation distribution appears to be the occurrence of spring seeps along the north-facing slopes of the Niobrara River Valley. In the study area, spring seeps are common and scattered along the slopes. The occurrence of these seeps may, for example, account for the unanticipated increase in American linden from east to west yet its absence from Site 4, the western-most site. American linden, considered an eastern species, would be expected to decrease gradually to the west if its distribution were due to dispersal from its eastern origin. This anomalous distribution appears to be consistent with the refugium theory suggested by Kaul et al. (1988) suggesting that relict stands of American linden, once a more wide-spread species, became restricted to

suitable sites found in the Niobrara River Valley. These sites appear to be characterized by spring seeps. The occurrence and location of spring seeps should be more closely examined in any future studies on communities of the region in order to determine their effect on the vegetation.

DCA ordinations also suggest that disturbance plays an important role in determining vegetation patterns in the study area. Sites 1-3, located on the Niobrara Valley Preserve, have not been grazed during the past several years. In contrast, the Fort Niobrara National Refuge site (Site 4) currently experiences periodic disturbance by longhorn cattle grazing and by the location of a road at the base of the bluff. The increase in young ironwood saplings at this site may be a response to these disturbances. Studies of the age structure of the communities would be needed to assess the effect of grazing on the plant community.

Plant communities are inherently complex and difficult to analyze using statistical methods. Ordination and classification techniques used in this study detected elevational gradients, and for some species, east-west gradients. The results of this study suggest that future studies on vegetation patterns in the Oak-Pine overlap region of the Niobrara River Valley should include a consideration of both hydrologic and disturbance factors.

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APPENDIX

Appendix Table 1. Mean species canopy cover (m) by site and elevation. $P < 0.5$ m. See Table 1 for species codes.

Species by elevation	Site			
	1	2	3	4
Hilltop (Transect 1)				
Qu ma	23	22	26	79
Pi po	7	31	18	10
Ju vi	23	5	58	11
Os vi	0	0	1	P
Fr pe	1	0	4	2
Ul am	0	0	0	4
Ce oc	0	0	0	P
Sy oc	0	P	P	P
Pr vi	0	1	0	0
Rh gl	17	10	0	0
Ri mi	0	0	0	P
Rh ar	3	0	0	0
Ro ar	0	P	0	0
Am ca	0	2	0	0
Pr up	P	P	0	0
Lower Hilltop (Transect 2)				
Qu ma	54	51	64	15
Pi po	12	14	28	27
Ju vi	64	4	54	25
Os vi	5	13	5	59
Be pa	0	0	0	7
Ti am	7	2	0	0
Fr pe	2	1	2	1
Ul am	1	P	1	5
Ce oc	0	P	2	P
Sy oc	P	1	0	2
Pr vi	5	29	5	P
Rh gl	0	1	0	0
Ri mi	0	0	0	P
Za am	0	2	1	0
Am al	0	3	0	0
Pr am	0	P	0	0
Ro ar	0	P	0	0
Am ca	0	2	P	0
Po de	0	0	1	0
Pr up	0	P	0	0

Appendix Table 1. Mean Species Canopy Cover (continued).

Upper Middle Slope (Transect 3)	Site			
	1	2	3	4
Qu ma	47	54	17	12
Pi po	5	1	8	13
Ju vi	51	2	33	13
Os vi	31	37	22	71
Be pa	0	0	12	15
Ti am	17	20	66	0
Fr pe	P	8	P	9
Ul am	2	4	1	4
Ce oc	1	1	P	P
Ju ni	0	P	0	0
Sy oc	1	1	5	9
Pr vi	1	17	3	0
Rh gl	0	1	0	0
Ri mi	0	0	1	P
Za am	0	1	1	0
Rh ar	0	0	0	P
Am al	0	9	0	0
<hr/>				
Lower Middle Slope (Transect 4)				
Qu ma	41	46	4	21
Pi po	P	0	0	2
Ju vi	45	P	22	8
Os vi	32	41	32	80
Be pa	0	0	31	28
Ti am	17	27	42	0
Fr pe	3	6	6	9
Ul am	4	3	3	6
Ce oc	0	2	P	3
Ju ni	0	8	0	0
Sy oc	P	9	9	1
Pr vi	2	10	1	P
Ri mi	0	0	0	P
Za am	1	1	1	0
Po de	0	0	3	0
Vi am	0	0	P	0

Appendix Table 1. Mean Species Canopy Cover (continued).

Upper Lower Slope	Site			
	1	2	3	4
(Transect 5)				
Qu ma	43	31	22	15
Ju vi	43	2	16	8
Os vi	20	37	22	55
Be pa	0	2	11	4
Ti am	36	50	43	0
Fr pe	2	5	7	20
Ul am	1	2	2	6
Ce oc	3	8	P	22
Ac ne	0	1	P	5
Ju ni	0	7	0	0
Sy oc	0	P	12	P
Pr vi	1	P	0	0
Ri mi	0	0	1	P
Za am	0	P	3	0
Lower Slope (Transect 6)				
Qu ma	29	18	9	34
Ju vi	82	3	17	0
Os vi	9	41	42	28
Be pa	0	0	2	0
Ti am	5	21	36	0
Fr pe	13	4	8	31
Ul am	8	0	2	7
Ce oc	0	1	P	4
Ac ne	0	5	0	2
Ju ni	0	17	0	0
Sy oc	0	1	14	2
Pr vi	1	0	0	P
Rh gl	P	4	0	0
Za am	0	1	8	0
Po de	0	2	3	0