

ECOLOGICAL STUDIES AT
NAVAJO NATIONAL MONUMENT

Part II

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Introduction

This report and the data contained therein has been compiled for the southwest region of the National Park Service and for the personnel of Navajo National Monument. The environmental contents of the report evaluate many of the relationships of the plants found growing in the monument as well as the bird fauna found there. The sampling and data collection is the result of three years' effort.

The reports contained herein comprise an updated data base and in many cases a primary data set. Each report is treated as an independent unit and results specific to that unit is contained only within that segment.

MICROHABITAT RELATIONSHIPS OF SIX MAJOR SHRUBS IN NAVAJO NATIONAL
MONUMENT, ARIZONA

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Highlight: Six shrub species were studied to determine their micro-habitat relationships as well as their effect on the immediate environment. Analysis of site characteristics and mineral composition of soils in open areas adjacent to shrubs and beneath shrubs allowed for comparison of the different areas before and after shrub establishment. Soil pH differs beneath the various shrubs and all six species tended to create more alkaline soils beneath their canopy. The concentration of total soluble salts in the soil surface beneath the shrubs varied with the species but was highest beneath fourwing saltbush. All species showed increased soil salinity beneath their canopy. Significant increases in the concentration of magnesium and potassium ions beneath shrubs were observed. Nitrogen and phosphorus were also found in greater concentration beneath the shrub canopy. Soil depth differed beneath the shrub species with the deeper more highly developed types being found beneath fourwing saltbush and sagebrush. There was a positive relationship between the presence of shrubs and the depth of the soil profile.

It has long been known that shrubs influence the soil characteristics of beneath their canopy (Fireman and Hayward 1952). Studies done in the last decade show that shrubs influence both the horizontal and vertical patterning of soil chemicals (Charley and West 1975). Sharma and Tongway (1973) studied the effects of two species of saltbush (Atriplex nummularia and Atriplex vesicaria) on soil salinity and related properties. They recognized an accumulation zone beneath the shrubs, a zone of compensation where leaching of minerals replaced those absorbed, and a depletion zone from which mineral absorption exceeded the rate of replacement. Salt accumulation under shrubs, therefore, represents a redistribution of salts from peripheral regions of root activity (Charley and West 1975).

Plants employ several "strategies" for the removal of mineral wastes. Leaching of minerals from leaves is accomplished when the solution of the leaf surface connects with that of the intercellular spaces of the mesophyll and ions are lost by diffusion. Salts are also excreted with the aid of salt glands, as is the case with many Atriplex species. Salts are also concentrated in the extracellular spaces of leaves during the process of transpiration, thus accumulating minerals in leaves. Leaf fall subsequently serves as a mechanism for the elimination of mineral wastes (Epstein 1972).

Charley and West (1975) used the distributional patterns of carbon and nitrogen under and between shrubs as a measure of the soil organic pool. They showed that as precipitation increases, the average depth of soil wetting improves and so does the overall concentration of soil organic matter beneath shrubs. The mineral concentration in the soil

surface layer was found to be the best indicator for the patterns observed.

Harner and Harper (1973) dealt with the increase in mineral concentration of vegetation along a moisture gradient and concluded that soil moisture allows for greater solubility and, therefore, greater absorption of minerals in more productive sites.

A few papers have treated the effect of mineral enrichment beneath shrubs on the productivity of associated grasses. Tiedeman and Klemmedson (1973) reported that beneath mesquite trees (Prosopis juliflora) the nutrient availability was elevated and accounted for significantly increased yields of Arizona cottontop (Trichachne californica) and plains bristlegrass (Setaria macrostachys). Rickard, et al., (1973) showed greasewood (Sarcobatus vermiculatus) and spiny hopsage (Grayia spinosa) induce predictable changes in mineral composition of soil and create more favorable conditions for production of cheatgrass (Bromus tectorum).

The purpose of this study was to compare various microhabitats resulting from the interaction of six species of shrub with their immediate environment.

STUDY AREA

Navajo National Monument is located in northeastern Arizona about 16 kilometers north and west of Black Mesa, Navajo County, Arizona. The monument headquarters are located on the Shonto Plateau near the head of Betatakin Canyon, a small side canyon of the Tsegi Canyon. The principle features of the monument are three large cliff dwellings of the Anasazi culture. Betatakin and Keet Seel are located in the Tsegi

Canyon complex while Inscription House is located in Nitsin Canyon, a branch of Navajo Canyon.

All three units typify a pinyon-juniper slickrock environment. Average annual temperature at Navajo National Monument headquarters is 10 °C. Yearly maximum temperatures range from 32 ° to 38 °C with an average of 36 °C and yearly low temperatures range from -23 ° to -13 °C with an average of -17 °C. The frost-free season ranges from 107 to 213 days with an average of 155 days.

Total annual precipitation at Betatakin has historically ranged from a low of 17 centimeters to a high of 48 centimeters with an average of 29 centimeters. The period of greatest precipitation is late summer and early fall. Most storms are localized and convectional in nature and, therefore, of high intensity and spotty distribution. This reduced and unpredictable rainfall, so characteristic of arid rangelands, has a profound effect on plant production and also mineral cycling (Charley 1977).

Navajo Sandstone is the major geological formation in each of the three units. At Keet Seel and Inscription House the Navajo Sandstone is the only exposed rock formation. At Betatakin, the Kayenta formation outcrops beneath the Navajo Sandstone and can be observed in the lower reaches of the canyon. In all three canyons the Navajo Sandstone forms tall, sheer cliffs up to 225 meters in height. At the base of these cliffs, talus accumulations occur and the canyon bottoms are filled with deep deposits of sandy alluvium.

METHODS

Three shrub-dominated communities were found on the rim of Betatakin Canyon. Big sagebrush (Artemisia tridentata) dominated the mesa above the canyon where the soil was well developed. A mixed-shrub community composed of cliff fendlerbush (Fendlera rupicola), cliffrose (Cowania mexicana), and buffaloberry (Shepherdia rotundifolia) was found occupying primarily the sloping terrain below the mesa and was characterized by rugged, talus-like topography and shallow soils. Needle-leaf mountain mahogany (Cercocarpus intricatus) was restricted to the slickrock areas and appears to function in soil development and the establishment of islands of vegetation. Four-winged saltbush (Atriplex canescens) was found on talus slopes and sandy alluvium above the streambed in Keet Seel Canyon. In order to avoid sampling heavily grazed areas, all plots were established within the fenced boundary of the park.

Line transects were established for each shrub type. The placement of transects were biased in order to sample areas of optimal habitat for a study species. At 15 meter intervals along the transect the nearest individual of the species being sampled was centered in a plot that measured 4 X 4 meters. Each plot was subsampled with ten quadrats ($1/16\text{m}^2$) to determine vegetative cover of associated species. Soil samples were taken with a tubular soil probe to a depth of 15 centimeters underneath the shrub canopy and from adjacent open areas. Plant samples included only current growth and were taken in mid-summer for all the shrubs to determine mineral composition. The following characteristics were recorded for each plot: exposure, percent slope, topographic

position (ridgetop, midslope, or drainage accumulation area), and soil depth under and between the shrubs.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, and mineral composition. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 soil-water paste (Russel 1948) was used to determine pH and total soluble salts. Soils were extracted with 1.0 normal ammonium acetate for the analysis of calcium, magnesium, potassium, and sodium. Zinc, manganese, iron, and copper were extracted from the soils with DPTA (diethylenetriaminepentaacetic acid). Ion concentrations were determined using a Perkin-Elmer Model 290 atomic absorption spectrophotometer. Soil phosphorus was extracted with sodium bicarbonate. Total nitrogen analysis was made using macro-kjeldahl procedures (Jackson 1968).

Plant material was air-dried, ashed, and later analyzed for mineral composition by atomic absorption spectrophotometry.

RESULTS

Measurements of canopy cover were taken for species associated with the different shrubs to determine if modification of the environment by the shrubs resulted in the establishment of distinct associations of plants (Table 1). Perhaps 16 of the 52 species sampled showed some degree of preference for one shrub habitat over the others. Since understory vegetation in pinyon-juniper communities is often sparse, it was expected that tree canopy also greatly influenced composition of the understory.

Cluster analysis (Sneath and Sokal 1973) was used to group shrub types that were similar with respect to the community composition of the various microhabitats (Fig. 1). Cliff fendlerbush and buffaloberry communities were most similar in this respect although they were also similar to sagebrush and cliffrose. The plant understory associated with fourwing saltbush and mahogany were also highly similar. The greatest amount of exposed rock was also found in these two areas.

The flexibility of the various shrub populations to changes in the environment is shown in Table 1. Needle-leaf mountain mahogany was restricted to the slickrock areas. Fourwing saltbush also was apparently limited in its ability to become established in areas best suited for other shrub species. Sagebrush dominated the mesa tops and was the most widely distributed shrub. The shrub species in the mixed-shrub community (cliff fendlerbush, cliffrose, and buffaloberry) occupied similar sites although areas existed where each was most abundant.

Analysis of the site characteristics in open areas adjacent to the shrubs allows for comparison of the different areas prior to shrub establishment (Table 2a). Soil texture did not vary significantly between shrub types. Average percent sand, silt, and clay was 83%, 12%, and 5% respectively. The pH of the soil was lowest in areas near cliff fendlerbush, sagebrush, and mountain mahogany; intermediate for cliffrose and buffaloberry and most alkaline in areas adjacent to fourwing saltbush. Soil development varied significantly between the different sites. The deepest soil was found in fourwing saltbush and sagebrush areas and averaged 32 centimeters in depth. Sagebrush also grew in areas of shallow soils with an average depth of 10 centimeters.

Topographic position (Table 2) of the different species was represented by index values ranging from 1-3. Drainage accumulation areas, midslope, and ridgetop areas correspond to values of 1, 2, and 3 respectively. Optimum habitat for sagebrush was on nearly level terrain while all other shrubs occupied midslope positions.

Slope aspect data were transformed according to Beers, et al., (1966) to allow the use of aspect as an independent variable in statistical analysis of the six shrub habitats. Northeast aspects receive a value of 2.0, the southwest a value of 0.0, and intermediate aspects vary from 2.0-0.0 in both directions. The low index value for sagebrush (0.60) indicates a more southwestern exposure than is the case for the other shrubs. Cliffrose had an intermediate value for aspect (1.21), while the remaining shrubs averaged 1.74.

Discriminate analysis (Klecka 1975) was used to determine if site characteristics of areas adjacent to shrubs had an influence in their distribution and possible establishment. Data on site characteristics from five plots were used to group each shrub habitat type. Based on these characteristics, 73% of the plots were classified correctly. The most important characteristic for grouping the six habitat types was percent slope, followed by soil depth, aspect, topographic position, pH, and soluble salts. All of the fourwing saltbush plots were classified correctly indicating that unique habitats exist for saltbush establishment. Eighty percent of the sagebrush and mountain mahogany plots, and 60% of those for cliff fendlerbush, cliffrose, and buffaloberry were classified correctly. The use of discriminate analysis showed that shrubs of the mixed-brush zone lacked distinct areas for establishment.

Data presented in Table 2b indicate that shrubs exert a varied influence on their immediate surroundings. With respect to soil texture, areas under mountain mahogany had significantly more sand and less clay in the soil than soils under other shrubs. Mountain mahogany pioneers newly established soils of the slickrock areas. When percent fines (clay plus silt) of the different habitat types are compared, it is evident that extent of soil development in mountain mahogany areas was less than in areas occupied by the other shrubs.

Shrubs also seem to affect pH of the soil in a different manner. Average values ranged from 7.3 to 7.8 for sagebrush and fourwing saltbush respectively. Due to the sample variation, it is difficult to observe patterns, although soil pH beneath fourwing saltbush differed significantly from all shrubs except cliffrose. The larger concentration of total soluble salts beneath the canopy of cliff fendlerbush and fourwing saltbush differed significantly from low values found for sagebrush and mountain mahogany dominated soils. The value for cliffrose was similar to that of fourwing saltbush and cliff fendlerbush, whereas buffaloberry was intermediate in salt concentration and not significantly different from any of the shrubs. A comparison of soil depth under the shrubs shows the deepest soil existed beneath fourwing saltbush, sagebrush being intermediate, and the least depth found under the other shrubs.

When site characteristics for the microenvironment beneath shrubs was used to group different shrub types using discriminant analysis (Klecka 1975), 93% of grouped cases were correctly classified. This compared with a 73% correct classification for the same plots using site

characteristics of open areas adjacent to the shrubs. Soil depth was the most important factor used to classify different microhabitats beneath the shrubs. Other characteristics, in descending order of importance, were: percent slope, percent clay, topographic position, aspect, and soil pH. The microenvironments beneath cliff fendlerbush, fourwing saltbush, cliffrose, and sagebrush were very distinct. Eighty percent of the mountain mahogany plots were also correctly classified with one plot being grouped with buffaloberry. Such evidence indicates that the shrubs influence the general soil characteristics beneath the canopy.

Results of analyses of mineral composition of soils from open areas adjacent to shrubs are provided in Table 3a and are intended to show the characteristics of the soil prior to shrub establishment. Of the ten nutrients analyzed from soils sampled between shrubs, the concentration of calcium, potassium, iron, and manganese varied significantly between the six habitats. Calcium was the most concentrated nutrient and was most abundant in the fourwing saltbush and buffaloberry sites. Potassium was also found in greater concentration in these areas. Buffaloberry and sagebrush sites exhibited the greatest concentration of iron. Buffaloberry sites were also high in manganese. Mountain mahogany dominated areas were consistently low in soil minerals. The macro-nutrients magneisum, phosphorus, and nitrogen were uniformly distributed as were the micronutrients zinc and copper. When mineral composition in the soil between the shrubs was used to classify different habitat types, 70% of the plots were correctly classified by discriminant analysis (Klecka 1975). It appears that different habitats open to

shrub establishment vary with respect to both site characteristics and mineral composition. Eighty percent of the cliffrose, sagebrush, and mahogany plots were correctly classified. Soil mineral composition in areas between these shrubs was fairly distinct. Only 60% of cliff fendlerbush, fourwing saltbush, and buffaloberry were classified correctly. The soil mineral composition of these habitats was not as characteristic. Elements most useful in classification of different shrub types were sodium, calcium, iron, copper, nitrogen, and phosphorus.

Mineral composition of the soil beneath the shrubs also varied between different habitats (Table 3b). Calcium was most concentrated under buffaloberry and fourwing saltbush and least concentrated under sagebrush and mahogany. Potassium was highly concentrated beneath the canopy of fourwing saltbush and was lowest beneath mountain mahogany. The concentration of potassium beneath other shrubs was intermediate. Cliff fendlerbush, cliffrose, and mountain mahogany influenced soils were lowest in magnesium and significantly different from the soils influenced by fourwing saltbush. Buffaloberry and sagebrush influenced soils were intermediate in magnesium concentrations. Sodium was most abundant beneath fourwing saltbush and sagebrush and did not differ significantly among the other shrubs. Phosphorus and nitrogen were uniformly distributed underneath the shrubs as were all the micronutrients except sodium.

Seventy-seven percent of the plots were correctly classified when mineral composition beneath shrubs was used as the basis for classification. Soil mineral composition beneath buffaloberry shrubs was highly characteristic and allowed all plots to be correctly classified. Eighty

percent of cliff fenderbush, fourwing saltbush, sagebrush, and mahogany plots were classified correctly, indicating that these shrubs alter the soil mineral composition in unique ways. Soil mineral composition beneath cliffrose was highly variable and resembled that of cliff fenderbush, fourwing saltbush, and sagebrush. Eighty percent of the plots were correctly classified when soils between cliffrose shrubs were classified, but when the soil mineral composition beneath the shrub canopy was used to group the shrubs only 40% of the cliffrose plots were correctly classified. Cliffrose did alter the soil mineral characteristics of its environment, but did so in a manner highly similar to several other shrubs.

The mineral composition of the current year's growth for each shrub is outlined in Table 4. Unfortunately, not enough plant material was collected from each shrub to provide independent samples for analysis. As a result, statistical analysis of the data is not justified, although mean values are important and represent averages of two composite samples derived from the ten plants sampled per shrub species. Information provided in Table 4 further shows that minerals were not absorbed in the same proportion as found in the soil. As expected, the macronutrients nitrogen, potassium, calcium, magnesium, and phosphorus were concentrated in the leaves and twigs to a greater degree than that of the micronutrients sodium, zinc, iron, manganese, and copper. When compared to the concentrations found to be adequate for higher plants, the concentration of nitrogen, potassium, and manganese appeared to be slightly deficient (Epstein 1972).

DISCUSSION

It has been shown that different species of shrubs have a varied influence on the soil chemistry of their environment. If the influence of shrubs on various parameters of the soil surface is compared with the characteristics of the soil prior to shrub establishment, several trends become apparent.

The concentration of total soluble salts under the shrub canopy was significantly greater than that of open areas adjacent to shrubs (Table 2). Sharma and Tongway (1973) and Charley and West (1975) also found this to be the case. Salts are absorbed throughout the rooting volume of the plant and accumulate in the surface layer beneath the shrubs. The understory vegetation was not sampled in order to determine the effect of shrubs on overall productivity. Other studies have shown that shrubs can be very important in maintaining a favorable microhabitat for plant growth (Tiedeman and Klemmedson 1973; Rickards, et al. 1973).

It was possible to rank the six shrubs according to the variation in concentration of calcium, magnesium, potassium and sodium in the soil beneath them. The concentration of a particular mineral was classified as high, intermediate, or low for each shrub and assigned values of 3, 2, and 1 respectively. Theoretically, a species could receive a value of twelve which would signify that the concentration of the four minerals were always among the highest group.

We should note that of the minerals that did differ significantly under the shrubs, the greatest concentrations were consistently found under fourwing saltbush (Table 5). Saltbush grew in the deepest soils

and the greater rooting volume might account for more extensive redistribution of minerals from other zones. The species was also equipped with salt glands to facilitate the removal of excess minerals.

Buffaloberry was ranked second, although the depth of the soil underneath the canopy did not differ from the other shrubs of the mixed-brush zone. It has been postulated that leaf size might account for some of the variation in the soil mineral composition beneath shrubs (Sharma and Tongway 1973). It is interesting to note that buffaloberry had the largest leaf of all the shrubs studied.

Sagebrush, cliffrose, and cliff fendlerbush all had similar sized leaves, although the greater soil depth under sagebrush may account for the difference in mineral accumulation. Mountain mahogany had the smallest leaves of all the shrubs and was found in shallow soils and cracks in the sandstone.

The soil pH under the shrub canopy was significantly greater than that of adjacent open areas (Table 2). Although the margin of difference was not great, little variation was found under and between shrubs. Sharma and Tongway (1973) and Greenwood and Brotherson (1978) have reported an increase in pH under shrubs, whereas Charley and West (1975) found that such differences were not always predictable.

Of special interest was the percent increase in nitrogen, phosphorus, potassium, and magnesium in soils under shrubs compared to soils adjacent to shrubs. Potassium more than doubled in concentration under shrubs and thus appeared to be highly selected for by the shrubs. Magnesium was also highly concentrated under shrubs. Potassium and magnesium were the only macronutrient cations that function as cofactors of plant

enzymes. It is possible that the shrubs recycle more of these cations as a result of their inefficiency in enzyme systems (Epstein 1972).

Nitrogen was also highly concentrated under shrubs. Charley and West (1975) and Garcia-Moya and McKell (1970) reported nitrogen accumulation under shrubs and an associated concentration decline in the surrounding environment. Charley (1977) suggested the possibility of this also being attributed to an increase in nitrogen fixation by free living microorganisms in and under litter mats, animal activity, and canopy capture of wind transported soils.

The concentration of phosphorus was found to be significantly greater in soils under shrubs. Organic matter accumulation under shrubs probably accounted for the increase. Charley and West (1975) found greatest differences in the concentration of organic phosphorus and also found differences in available phosphorus under and between shrubs. Average values of all minerals were shown to be greater under shrubs, but too much variation was found in the samples to prove statistical differences.

Mineral concentration of plant material versus that of the soil serves to show the extent that minerals are concentrated in the plants. Although mineral composition of the soil differed between the six shrubs, the plants were fairly consistent in their ability to accumulate minerals. On the average, shrubs concentrated phosphorus about 110 times that found in the soil. The concentration of phosphorus found in the soil was far below the 200 ppm suggested by Epstein (1972) as being adequate for maintenance of healthy plant tissue.

Potassium was 68 times more concentrated in plant tissue than in the soil surface. According to Epstein (1972), plants have evolved a mechanism for high accumulation of potassium from the soil to allow for the inefficiency of potassium as a cofactor in enzyme systems. Potassium is the only monovalent cation essential for all higher plants. Arid regions are often characterized by having a greater concentration of potassium in the plant (Epstein 1972). In this study, potassium was found in greater concentration than sodium in both the soils and in the plant material.

When compared to soil mineral concentration, calcium and magnesium were the least concentrated nutrients in the tissue of the shrubs. Their relatively high concentration in soils compared to those values determined by Epstein (1972) as being adequate for higher plants may account for the lower values.

Calcium to phosphorus ratios that are close to 2.0 are considered optimum for the nutritional needs of most animals, although there is evidence that suggests that ruminants can tolerate higher ratios (McDonald, et al. 1973). Mule deer (Odocoileus hemionus) are found in the monument and, since they feed almost exclusively on shrubs during the winter, the balance of these minerals in the diet is important. The most satisfactory calcium to phosphorus ratios were found in the leaves and twigs of sagebrush, cliff fendlerbush, and buffaloberry with values of 4.58, 6.05, and 7.90 respectively. Cliffrose had the highest ratio, 14.71, and was followed by fourwing saltbush (12.77) and mountain mahogany (11.84). The concentration of calcium and phosphorus in leaves and stems was negatively correlated with an "r" value of 0.67.

The average potassium to calcium ratio for the plant material from the six shrubs was 1.33 and compared favorably with the value of 1.4 for shrubs in a study by Harner and Harper (1973). In their study, the ratio for shrubs was lower than that for forbs and grasses. They suggested that the low values for shrubs was related to root cation exchange properties. Dicot roots were found to be more negatively charged than monocot roots and were expected to compete more effectively for divalent cations. The variation in potassium to calcium ratios among the shrubs in this study might also be attributed to root cation exchange capacity. Cliff fenderbush, fourwing saltbush, and sagebush had high values and averaged 2.13, whereas cliffrose, buffaloberry and mountain mahogany averaged 0.52.

The mineral composition of shrubs from various studies are compared with the results from this study in Table 6. It is evident that the mineral composition of shrubs varies among species and individuals on rangelands. The large discrepancies found in mineral composition between the shrubs in this study and those from other studies may be due in part to the fact that in arid rangelands, yearly and seasonal variations in mineral cycling is highly dependent upon the amount, kind, and distribution of rainfall. This variation is partly responsible for the heterogeneous patterning of minerals in a rangeland ecosystem since soil mineral composition beneath shrubs is mostly affected by retention of litter fall, shrub age, and specific chemical composition of inorganic residues (Charley 1977).

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Figure 1. Similarity in understory composition
of the six shrubs.



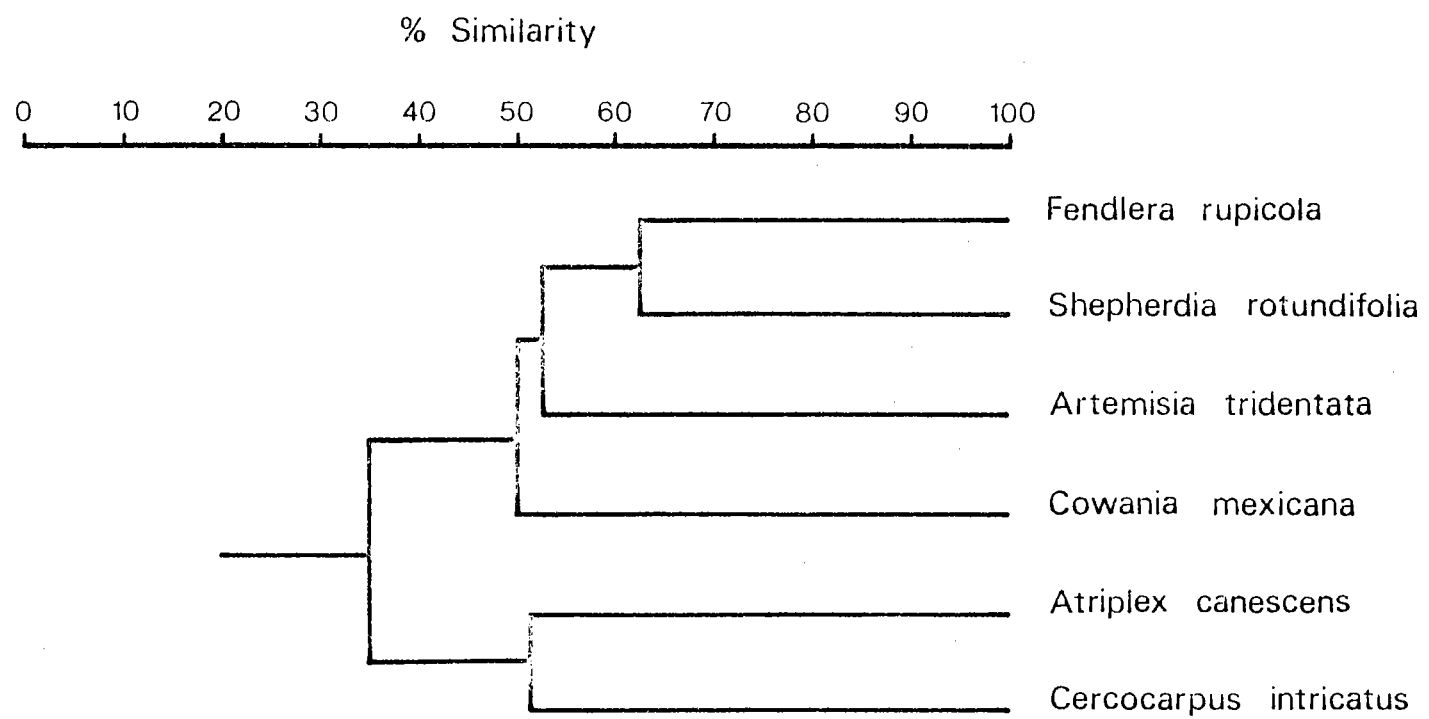


Table 1. Average percent cover for the important plant species of the six microhabitats.

Species	Site #					
	Cliff	Salt	Rose	Buff	Sage	Maho
<i>Amelanchier utahensis</i>				.02		
<i>Arabis perennans</i>	.2					.19*
<i>Artemisia frigida</i>		1.45*				.15
<i>Artemisia ludoviciana</i>		.04		.02		
<i>Artemisia tridentata</i>		.04	.90*	.78	9.24*	
<i>Astragalus mollissimus</i>						.02
<i>Atriplex canescens</i>		10.72*				
<i>Bouteloua gracilis</i>	1.80*	2.64*	2.47*		2.06*	2.39*
<i>Bromus tectorum</i>		1.50*				
<i>Cercocarpus intricatus</i>						27.36*
<i>Chrysothamnus nauseosus</i>		.17*				.18
<i>Cowania mexicana</i>	1.15		17.67*	2.18*		
<i>Cryptantha flava</i>		.15	.15		.05	
<i>Descurainia sophia</i>			.02			
<i>Echinocactus fendleri</i>			.32			.98
<i>Ephedra viridis</i>		.37	.30	1.35		.15
<i>Erigeron concinnus</i>	.06					

Cliff=Cliff fendlerbush, Salt=Saltbush, Rose=Cliffrose, Buff=Buffalo-berry, Sage=Sagebrush, Maho=Mahogany

* Among the most prevalent species for the shrub type.

Table 1. continued.

Species	Site #					
	Cliff	Salt	Rose	Buff	Sage	Maho
<i>Eriogonum microthecum</i>		.30				
<i>Eriogonum umbellatum</i>					.15	
<i>Erysimum asperum</i>	.02		.04		.04	.31*
<i>Fendlera rupicola</i>	16.99*	.02		2.88*		.98
<i>Festuca octaflora</i>	.04	.02	.39*			
<i>Gilia aggregata</i>					.22*	
<i>Gutierrezia sarothrae</i>	.54*	.92*	1.88*			.30
<i>Haplopappus nutalli</i>				.17		.15
<i>Hymenopappus filifolius</i>		.15				
<i>Hymenoxys Richardsoni</i>	.02	.32	.05	.26	.02	
<i>Juniperus osteosperma</i>	.30		.02	6.72*	3.77	
<i>Lappula redowskii</i>		.02	.02			

Cliff=Cliff fendlerbush, Salt=Saltbush, Rose=Cliffrose, Buff=Buffalo-berry, Sage=Sagebrush, Maho=Mahogany

* Among the most prevalent species for the shrub type.

Table 2. Site characteristics in open areas adjacent to shrubs (A) and beneath shrubs (B).

Shrubs	Site Characteristics									
	Sand (%)	Silt (%)	Clay (%)	Fines (%)	pH ⁺	Soluble Salts (ppm)	Soil Depth ⁺ (cm)	Slope (%)	Aspect	Topographic position
A										
Cliff Fendlerbush	82.8a*	12.4a	4.8a	17.2a	7.16a	194.6a	10.40a	22.2ab	1.92a	1.80a
Saltbush	83.0a	12.8a	4.2a	17.0a	7.70b	167.4a	25.80b	70.4c	1.65a	2.00a
Cliffrose	82.8a	12.4a	4.6a	17.0a	7.46ab	160.2a	8.40a	31.8ab	1.21ab	2.20a
Buffaloberry	81.8a	12.8a	5.4a	18.2a	7.42ab	185.6a	10.80a	39.2bc	1.79a	2.00a
Sagebrush	84.8a	10.4a	4.8a	15.2a	7.08a	145.6a	37.80b	16.40a	.60b	2.80b
Mahogany	85.4a	9.8a	4.8a	14.6a	7.18a	136.0a	10.58a	29.90ab	1.63a	2.00a
Average	83.4	11.8	4.8	16.6	7.33	164.9	17.3	35.0	1.47	2.10
B										
Cliff Fendlerbush	81.8a	14.2a	4.0bc	18.2a	7.46ab	269.0ab	26.4a	22.2ab	1.92a	1.80a
Saltbush	82.4a	13.2a	4.4ab	17.6a	7.84c	327.0a	60.0b	70.4c	1.65a	2.00a
Cliffrose	81.6a	13.6a	4.8ab	18.4a	7.70bc	190.8bc	17.8a	31.8ab	1.21ab	2.20a
Buffaloberry	79.4a	14.8a	5.8a	20.6a	7.46ab	216.8abc	23.6a	39.2bc	1.79a	2.00a
Sagebrush	82.4a	12.4a	5.2ab	17.6a	7.34a	126.6c	45.2c	16.4a	.60b	2.80b
Mahogany	88.6b	8.4a	2.8c	11.4b	7.50ab	130.6c	23.0a	29.9ab	1.63a	2.00a
Average	82.7	12.8	4.5	17.3	7.54	210.1	32.7	35.0	1.47	2.10

⁺ Average values for these characteristics differ significantly (0.5 level) under and between shrubs.

*Duncan's multiple range separations (calculated for each microhabitat): within columns for each site characteristic, values without common letters are significantly different at the 5% level.

Table 3. Soil mineral concentrations (ppm) in open areas adjacent to shrubs (A) and beneath shrubs (B).

Shrubs	N ⁺	P ⁺	Ca	Mg ⁺	K ⁺	Na ⁺	Zn	Fe	Mn	Cu
A										
Cliff Fendlerbush	236.6a	5.24a	2008.8a	658.8a	79.8b	9.6a	1.29a	4.27a	3.94bc	0.50a
Saltbush	324.4a	5.70a	3646.2b	368.8a	101.9a	9.6a	1.50a	3.26a	5.22ac	0.40a
Cliffrose	369.8a	7.84a	1700.0a	507.5a	66.8b	6.6a	1.13	3.44a	3.03bc	0.48a
Buffaloberry	492.8a	8.98a	2982.5b	556.2a	103.6a	9.7a	1.50a	6.02ab	6.08a	0.44a
Sagebrush	335.0a	4.60a	1515.0a	608.8a	75.0b	8.4a	1.09a	6.31b	4.22abc	0.46a
Mahogany	327.0a	7.14a	1675.0a	548.8a	52.8b	19.4a	1.18a	3.35a	2.32b	0.38a
Average	347.4	6.58	2254.6	541.5	80.0	10.5	1.28	4.44	4.14	0.44
B										
Cliff Fendlerbush	478.8a	9.10a	2150.0bc	653.8a	142.2a	7.9a	1.24a	5.41a	4.83a	0.50a
Saltbush	545.0a	5.74a	3690.0ac	938.8b	502.5b	9.7b	1.54a	3.71a	7.69a	0.42a
Cliffrose	683.6a	10.50a	2357.5bc	638.8a	115.9a	7.7a	1.63a	4.70a	4.33a	0.46a
Buffaloberry	587.4a	14.28a	4905.0a	783.8ab	153.1a	8.1a	1.63a	7.68a	7.11a	0.55a
Sagebrush	559.6a	6.46a	1740.0b	682.5ab	101.7a	9.7b	1.22a	7.17a	4.16a	0.47a
Mohogany	540.4a	9.16a	1650.0b	530.0a	82.5a	7.9a	1.22a	4.71a	3.38a	0.30a
Average	565.8	9.21	2748.8	704.6	183.0	8.5	1.41	5.56	5.25	0.45

⁺ Average values for these characteristics differ significantly (.05 level) under and between shrubs.

*Duncan's multiple range separations (calculated for each microhabitat): within columns for each mineral, values without common letters are significantly different at the 5% level.

Table 4. Elemental content of current year's growth of six shrubs expressed in micrograms per gram of plant material (ppm).

Shrub	Elements									
	N	P	Ca	Mg	K	Na	Zn	Fe	Mn	Cu
Cliff Fendlerbush	6810	898	5430	1012	9865	312	19.2	147	15.5	6.2
Saltbush	12940	642	8200	2025	16150	350	6.0	115.5	30.0	6.0
Cliffrose	10360	634	9325	1225	3440	250	18.8	75.8	9.0	7.0
Buffaloberry	13125	1018	8040	1188	6915	275	16.8	137.5	24.0	5.5
Sagebrush	8315	975	4465	950	11640	375	26.5	186.0	27.8	8.8
Mahogany	7990	698	8265	962	2830	238	20.5	93.2	22.2	6.7
Average	9923	811	7288	1227	8473	300	17.9	125.8	21.4	6.7

Table 5. Ranking of six shrubs according to extent of mineral enrichment beneath shrub canopy.

Shrub	High	Intermediate	Low	Total
Saltbush	3	1	0	11
Buffaloberry	1	2	1	8
Sagebrush	1	1	2	7
Cliff Fendlerbush	0	2	2	6
Cliffrose	0	1	3	5
Mahogany	0	0	4	4

Table 6. Comparison of the mineral composition of shrubs.

Species	Elemental Concentration (%)					
	H	P	M	Na	Ca	Mg
<i>Atriplex confertifolia</i>	1.66	.07	1.84	5.75	2.69	.77
<i>Atriplex canescens</i>	1.74	1.38	2.88	.16	2.57	1.23
<i>Larrea divaricata</i>	1.86	.15	2.20	.03	.68	.13
<i>Lycium pallidum</i>	1.97	.08	2.41	1.49	2.46	1.05
<i>Grayia spinosa</i>	1.67	.05	4.29	.52	1.67	1.19
<i>Ceratoides lanata</i>		.22	3.24	.05	1.43	.49
<i>Franseria dumosa</i>		.48	4.78	.10	2.49	.59
<i>Artemisia tridentata</i>	1.24	.19	.95	.09	1.02	.40
<i>Atriplex inflata</i>	3.10	.28	3.20	5.90	1.40	2.10
<i>Atriplex vesicaria</i>	2.50	.15	3.90	6.50	1.20	
<i>Kochia sedifolia</i>	2.06	.11	2.80	7.60	1.32	.81
<i>Acacia aneura</i>	2.14	.08	.68	.13	1.47	.51
<i>Coleogyne ramossissima</i>	1.94	.17	1.42	.07	2.23	.41
Average*	1.99	.26	2.66	2.18	1.74	.81
<i>Cercocarpus montanus</i>	.90	.07	.31	.04	.55	.26
<i>Juniperus osteosperma</i>	.77	.05	.35	.03	1.45	.15
Average ⁺	.84	.06	.33	.04	1.00	.21
Average of six shrubs from this study	1.16	.09	.99	.04	.85	1.4

* Charley, J. L., (1977)

⁺ Osayande, S. (Unpublished thesis)

Population Dynamics and Age Relationships of Eight Tree Species in
Navajo National Monument, Arizona¹.

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The presence of three major archeological ruins dating from the 11th to 13th centuries (Woodbury 1963) provided the primary motivation for including Navajo National Monument the National Parks System. Also included in the monument are some unique ecosystems, especially a small relict of "mountain vegetation" found in Betatakin Canyon. As visitor pressures mount annually, proper management of these unique ecosystems becomes highly important. Since trees are the dominant features of these ecosystems, and are central to management considerations, the present work has examined populations of eight major tree species in the monument.

The objectives of this study were, first, to develop age prediction equations for tree species growing in Navajo National Monument, and second, to assess the present age profiles, reproductive recruitment, and density relationships of these tree populations. Variations in the growth-ring widths of trees have been used for many years to date wood (Douglas 1935; Glock 1937) and to garner information on past climates (Fritts 1971; Stockton and Meko 1975; Dean and Robinson 1978; Harper 1979). Additionally, ring width variations have been studied to ascertain differences in the environments of selected habitats (Ferguson and Humphrey 1959; Stockton and Fritts 1973; Fritts 1974) and to assess site quality with reference to timber production (Stage 1966; Brickell 1968; Jones 1969). Although stem diameter measurements have long been used to predict tree age and ascertain population status, it is difficult to use data from one area to extrapolate to conditions in other areas (Dealy 1975, Brotherson et al. 1980). Because of these difficulties and because of the absence of such data on northeastern Arizona plant communities, our studies provide useful baseline information.

STUDY SITE

Navajo National Monument is located in Navajo County, northeastern Arizona. The monument supports a tree flora of 14 species (Brotherson et al. 1978). Betatakin Canyon, the largest of the three segments of the monument, hosts the greatest variety of tree species. Populus tremuloides (quaking aspen), Quercus gambelii (Gambel oak), Pseudotsuga menziesii (Douglas fir) and Acer negundo (boxelder) are of major importance in the communities of the canyon bottom (Woodbury 1963). Growing with these as understory species are Prunus virginiana (chokecherry) and Betula occidentalis (waterbirch). The plant communities of the canyon bottom represent a small relict of "mountain vegetation" and thus are unique in this predominantly desert region.

Juniperus osteosperma (Utah juniper) and Pinus edulis (pinyon pine) grow abundantly as part of the pigmy woodland (Pinyon-Juniper community) on the upper slopes of the canyon, the adjacent slickrock areas and the plateau behind the canyon rim (Brotherson et al. 1978). The pigmy woodland community covers more area than any other type in northeastern Arizona.

Gambel oak is the most extensive type in the Monument aside from the pinyon-juniper community. It is found in all three segments of the monument but reaches its greatest development at Keet Seel and Betatakin. Prunus emarginata (bittercherry) also grows at Keet Seel but is uncommon.

The streamside community of the Inscription House segment of the monument contains Populus fremontii (Fremont poplar), Populus angustifolia (narrowleaf cottonwood), Salix goodingii (Gooding willow), Tamarix

ramosissima (salt cedar), and Elaeagnus angustifolia (Russian olive). Fremont poplar is the dominant tree within this community with salt cedar attaining local importance. All other species are encountered only infrequently.

METHODS

Density data for all species were obtained using the quarter method (Phillips 1959). A total of 40 points were taken for all trees where populations exceeded 160 individuals. Fremont poplar and salt cedar populations numbered less than 160 individuals, so density measurements in these two species are based on fewer sample points.

Tree diameter measurements were taken on all 160 individuals sampled or on all individuals of the population if less than 160. The diameters were measured at breast height in all species except pinyon pine, Utah juniper and salt cedar. In these species, diameters were taken one foot above the ground. All diameters were measured with a standard diameter tape.

Individual stems were sampled for age determinations using an increment borer in all species except pinyon pine and Utah juniper. The wood of these species was impossible to bore, making it necessary to obtain cross-sections using a chain saw.

Stem cross-sections and/or increment borer corings were selected from each population to provide samples for all size classes. The cross-sections and borings were returned to the laboratory, polished with fine sandpaper and ring-counted twice (independently) with the aid

of a binocular microscope (Ferguson 1970). Age determinations were made on the assumption that one ring equals one year.

Linear regression and regression of log-log transformed data (i.e. log age vs. long stem-diameter) were used to analyze all stem-diameter-age relationships. Age prediction equations were then constructed from these relationships (Brotherson et al. 1980). Taxonomy follows McDougall (1973).

RESULTS

Of the 14 tree species found in the monument only 8 were abundant enough for thorough study. Table 1 includes a list of these species together with their densities, general growth rates and sample sizes. This table shows that the evergreen species grew slower than the deciduous species. This is especially true for Utah juniper and pinyon pine. Densities varied from 49 to 50 individuals per acre in Utah juniper and Douglas fir to 856 individuals per acre in salt cedar. Six of the species demonstrated highly clumped distribution patterns with each population occupying discrete habitats. Only Utah juniper and pinyon pine showed dispersion in their distribution patterns.

Population profiles were constructed by size class for all 8 species (Table 2; Fig. 1). Five of the species, Utah juniper, pinyon pine, quaking aspen, Douglas fir and Gambel oak showed stable to expanding populations, while the populations of boxelder, Fremont poplar and salt cedar are all declining as indicated by low numbers of young trees in their profiles. The decline in the boxelder population is likely due to

successional patterns occurring in the bottom of Betatakin Canyon. Boxelder generally occupies rather open sites with abundant sunlight. However, since the establishment of the Monument there appears to have been a thickening of the canopy causing seedlings of this species to experience difficulty in becoming established. Consistent with this interpretation is the fact that nearly all observed boxelder seedlings were found in the upper end of the canyon where canopy development is least. Conversely, older trees were over-represented where the forest canopy was much more dense. Under-recruitment of seedlings in the Fremont poplar and salt cedar populations is likely due to the fact that both populations are located in the Inscription House segment of the Monument along a small stream where domestic sheep and cattle activity is extremely high. The animals concentrate in the area along the stream for both feeding and shading purposes. The result is that little or no understory vegetation is found in the area. When seedlings of these two species become established, they are eliminated by grazing.

A total of 964 stems of the 8 species studied were sampled for diameter. Eighty percent of the stems were less than 14 inches in diameter. Eighty-eight (9%) of the stems were aged using the dissecting microscope and their stem diameters (inches) were plotted against stem age (Figures 2 and 3). Regression equations for age prediction were then generated (Table 3). Both linear and log-log transformed functions were used to generate age prediction equations. All correlation coefficients (r values) but one were improved through the use of the log-log transformation. All prediction equations were significant ($p < 0.05$) except those for Fremont poplar.

Estimated ages showed mean deviations from real ages of from 18 to 67 percent with the use of linear regression equations and from 14 to 52 percent with the use of the log-log transformed equations (Table 4). In the cases of boxelder, Utah juniper, pinyon pine, Fremont poplar and salt cedar, the use of the log-log transformation improved predictive value only slightly over the linear equations. In quaking aspen, Douglas fir and Gambel oak age predictions were much improved by the log-log transformation. The high degree of variation in predicted ages from real ages in Douglas fir comes from the fact that this species grows in a variety of microhabitats which are scattered across a wide spectrum of moisture conditions in Betatakin Canyon. Thus, growth rates are widely different.

Since the predictive value of the equations varied greatly (Table 4), their value as age-predicting tools depends largely upon the species involved and on the level of precision required for the aging of individual trees. If the need for absolute ages is high, then each tree should be individually aged. However, if general trends and/or patterns are sufficient, so that a certain amount of variability in absolute ages is acceptable, then the equations become much more useful tools.

In order to gain insight into the age profiles of the different tree species in the Monument, the ages of all 964 individuals sampled were estimated for each diameter class (Table 5). The predicted ages of the several species varied widely, with the oldest trees in the monument being conifers reaching ages of 700 to 900 years. Conversely, the deciduous trees due at much earlier ages, with the oldest trees predicted to be about 125 years.

Upon examination of the population profile data from Utah juniper and pinyon pine (Table 2), it was noted that in 5 of the first 7 diameter classes the ratio of pinyon pine to Utah juniper was near 2. That is, twice as many pinyons were present as junipers. However, in the 2 inch to 6 inch diameter range (2 diameter classes) the ratio dropped to 1. Since the ratio had been near 2 for 300 of the past 400 years and since the trees grow at approximately the same rate in the area (Table 1), this change in ratio may represent a shift in the past environment of the region toward a drier climate which favored Utah juniper over pinyon pine (West et al. 1979; Wright et al. 1979; Erdman 1970). In an attempt to determine if such a climatic shift had occurred and if it could be correlated to the changes in relative populations of the age classes of the two species, data were obtained from the Laboratory of Tree-Ring Research in Arizona (Dean and Robison 1978). The number of years of below-average moisture (as indicated by the tree-ring indices) was determined in 50 year increments. These values are plotted against the pinyon pine to Utah juniper ratios and against the percent relative densities of pinyon pine and Utah juniper in each age class (Figure 4). The graphs in Figure 5 represent approximately a 600-year period. There is clearly a peak of years of below average moisture associated with the intervals of low pinyon pine to Utah juniper ratio (low relative density of pinyon pine by age class and high relative density of Utah juniper by age class). Although these data are only inferential, the relationships suggested are clear enough to merit further study and offer another possibility for research on past climates.

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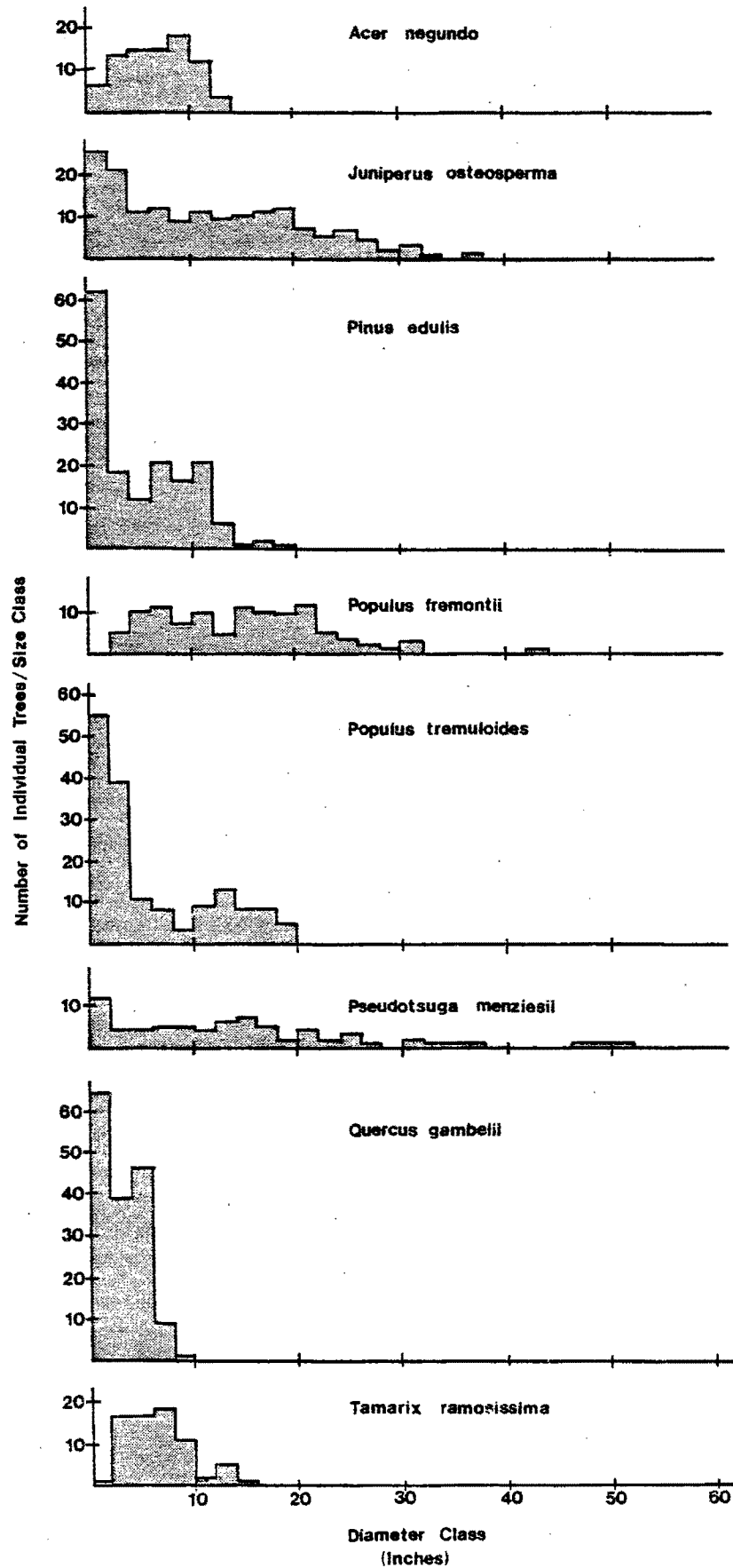
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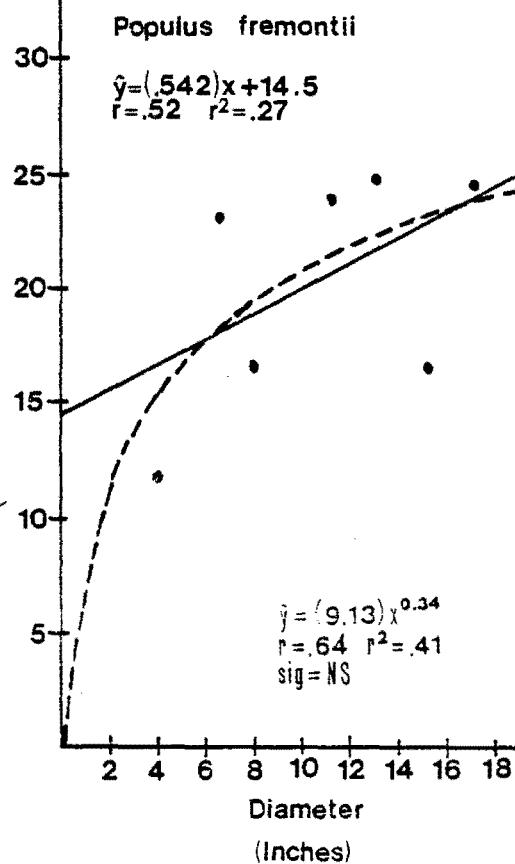
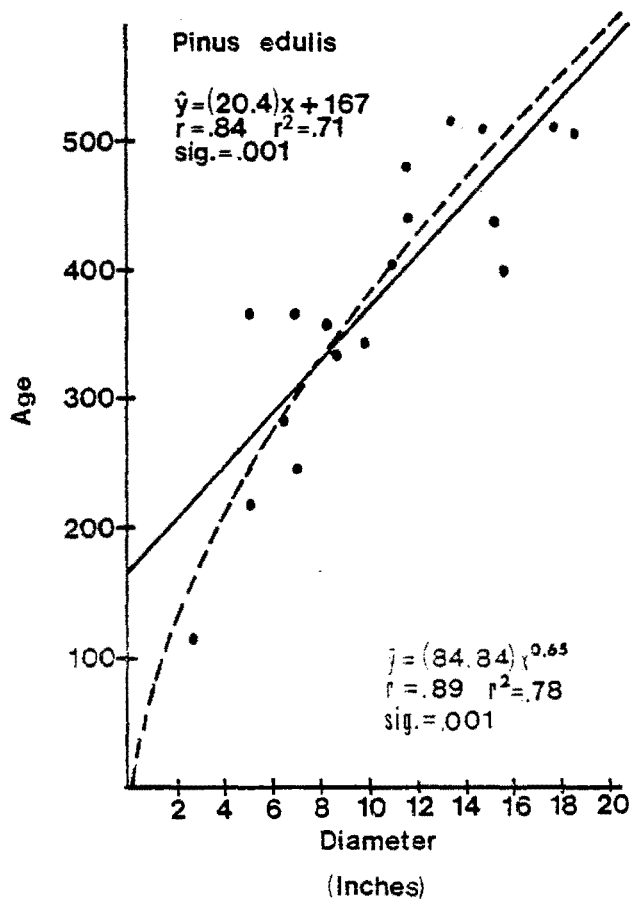
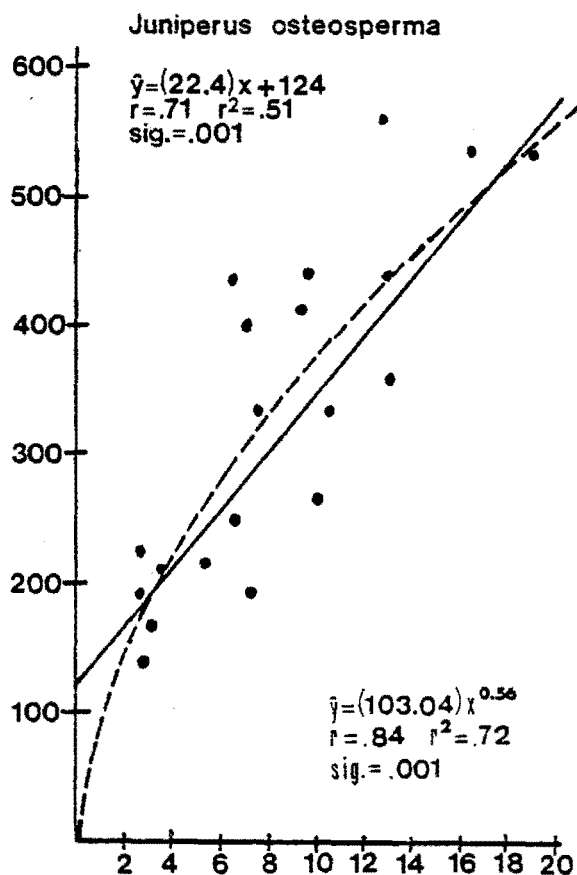
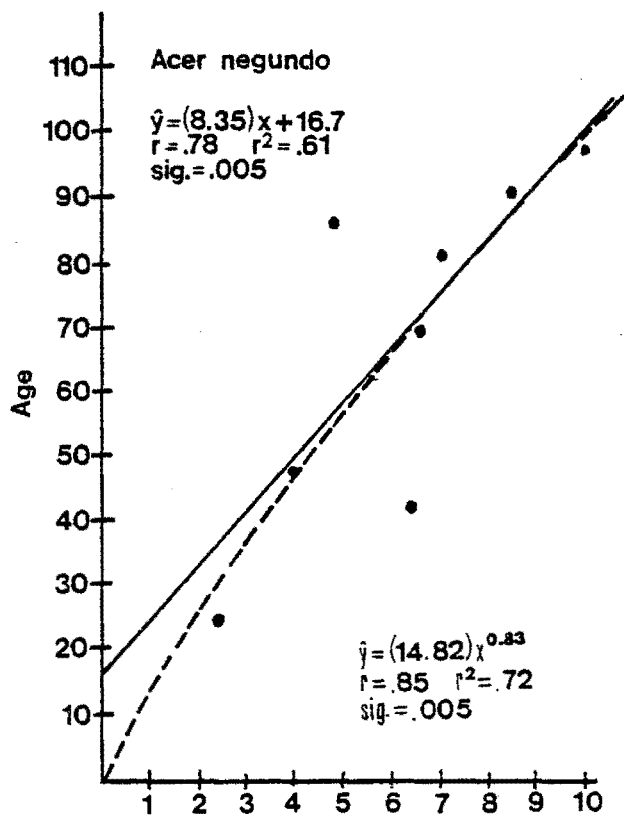
Figure 1. Population profiles by stem diameter class for eight tree species.

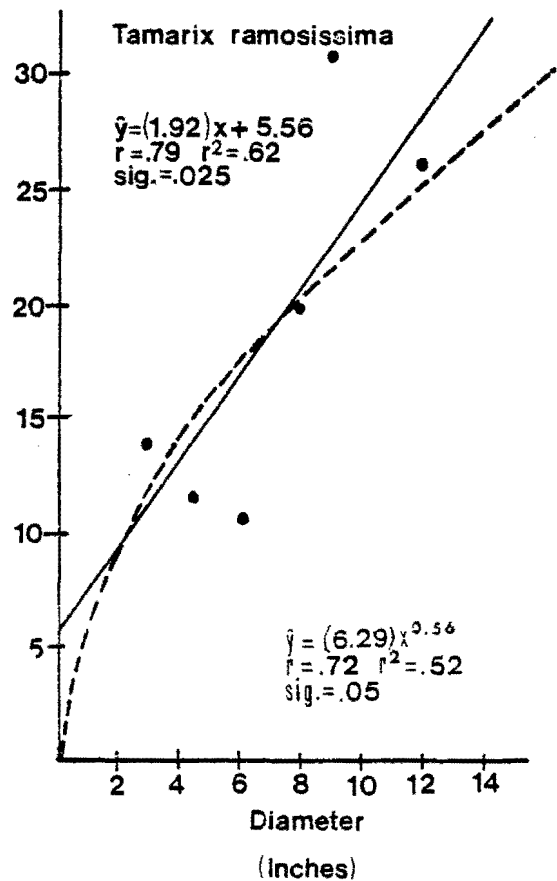
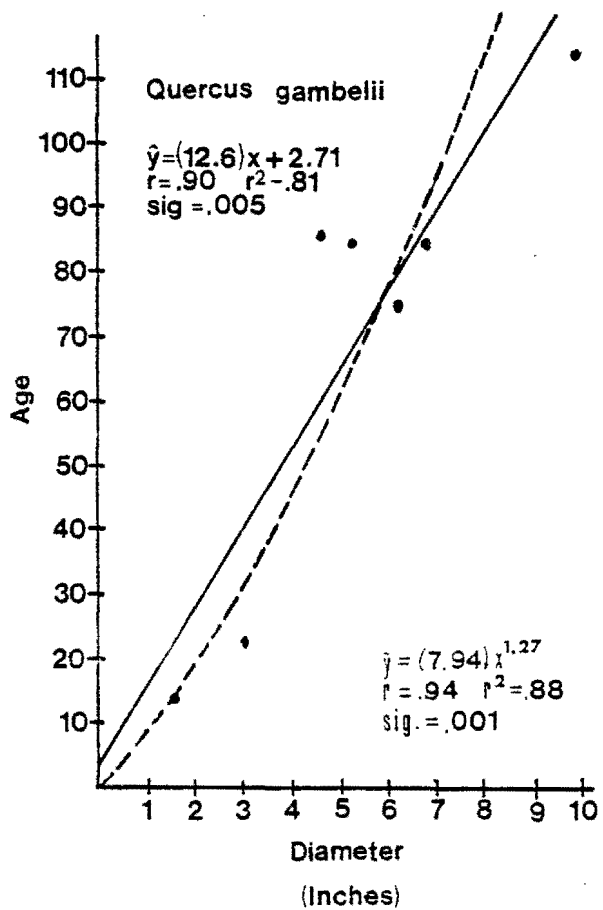
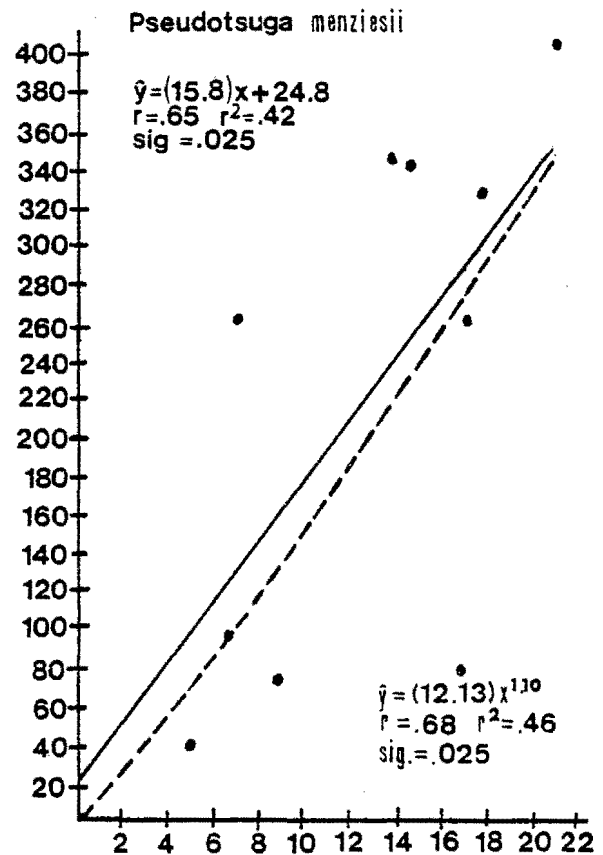
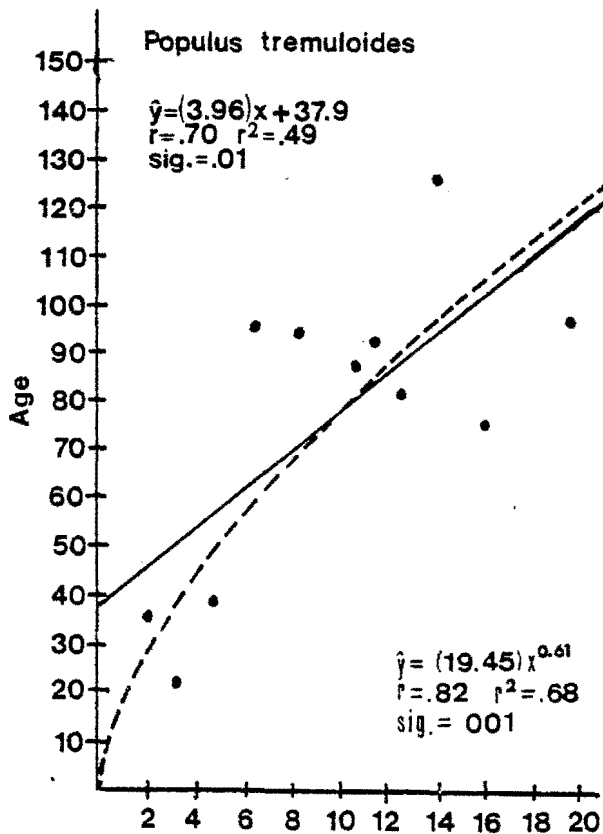
Figure 2. Stem diameter (inches) and age (one ring equals one year) relationships of four tree species.

Figure 3. Stem diameter (inches) and age (one ring equals one year) relationships of four tree species.

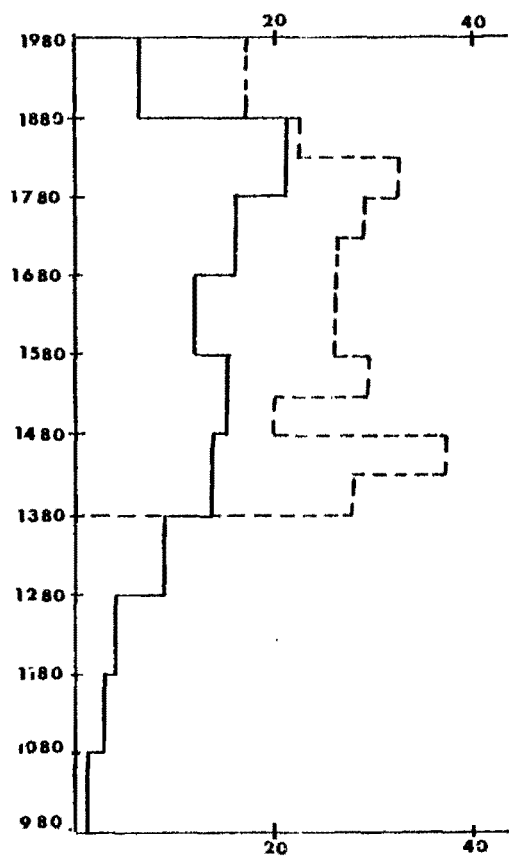
Figure 4. The relationship of years of below average moisture as indicated by tree ring indices to the ratio of pinyon to juniper and percent relative densities of pinyon and juniper by age class for the past 600 years.





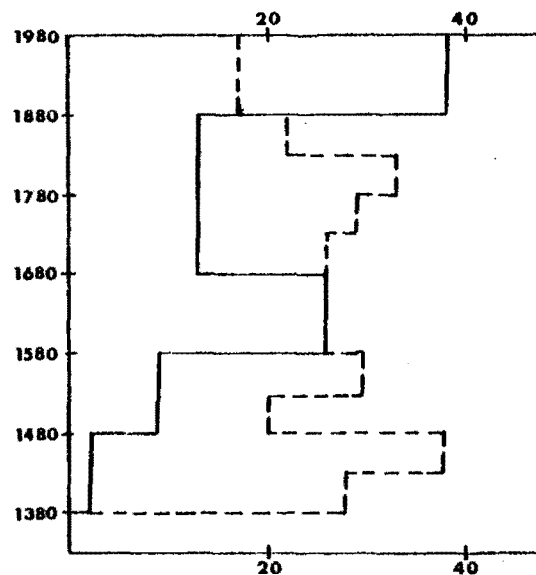


**% RELATIVE DENSITY OF JUNIPER
BY AGE CLASS (SOLID LINE)**



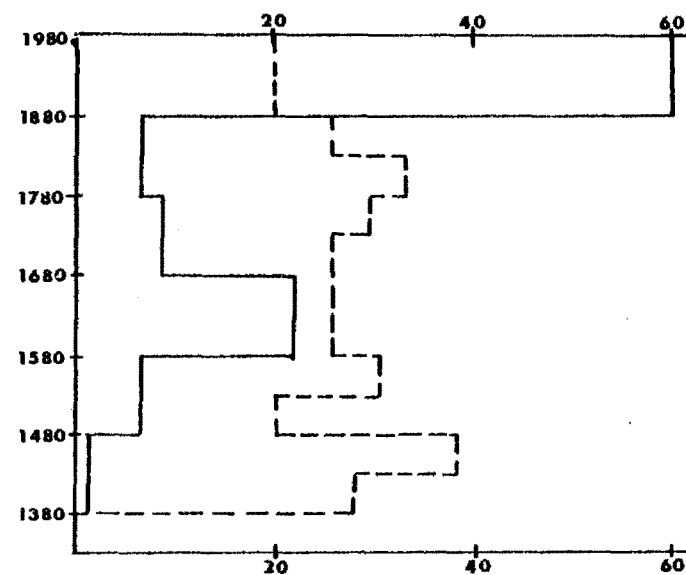
Years of below average moisture as
indicated by tree ring indices.
(dashed line)

**% RELATIVE DENSITY OF PINYON
BY AGE CLASS (SOLID LINE)**



Years of below average moisture as
indicated by tree ring indices.
(dashed line)

**RATIO OF PINYON TO JUNIPER
IN EACH AGE CLASS (SOLID LINE)**



Years below average moisture as
indicated by tree ring indices.
(dashed line)

Table 1. Sample size, density in trees/acre, growth rings/inch and relative growth rates with respect to Juniperus osteosperma.

<u>Species</u>	<u>Sample Size</u>	<u>Density (trees/acre)</u>	<u>Growth rings/inch</u>	<u>Relative growth rate*</u>
<u>Acer negundo</u>	80	163	22.7	4.1
<u>Juniperus osteosperma</u>	160	49	93.6	1.0
<u>Pinus edulis</u>	160	247	79.3	1.2
<u>Populus fremontii</u>	103	425	4.4	21.3
<u>Populus tremuloides</u>	160	502	18.5	5.1
<u>Pseudotsuga taxifolia</u>	72	50	35.9	2.6
<u>Quercus gambelii</u>	160	604	25.2	3.7
<u>Tamarex ramosissima</u>	72	856	6.0	15.6

* Relative growth rate of Juniperus osteosperma is taken to be one. All other species grow faster (the larger the number the larger the growth).

Table 2. Population profiles represented by the number of individuals sampled in each diameter class for each of the eight tree species. Diameter classes are designated by their maximum diameter in inches.

	Diameter Class																									
	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52
<u>Acer negundo</u>	6	13	14	14	18	12	3																			
<u>Juniperus osteosperma</u>	26	21	11	12	8	11	9	10	11	12	7	5	6	4	2	3	1		1							
<u>Pinus edulis</u>	62	18	12	21	16	21	6	1	2	1																
<u>Populus fremontii</u>	0	5	10	11	7	10	4	11	10	9	12	5	3	2	1	2							1			
<u>Populus tremuloides</u>	55	39	11	8	3	9	13	8	8	5																
<u>Pseudotsuga taxifolia</u>	12	4	4	5	5	4	6	7	5	2	4	2	3	1		2	1	1	1					1	1	1
<u>Quercus gambelii</u>	64	38	46	9	1																					
<u>Tamarix ramosissima</u>	1	17	17	18	11	2	5	1																		

Table 3. Age prediction equations for the eight tree species along with their correlation coefficients, coefficients of determination and significance levels. The first equation in each set is from linear regression and the second is from the log-log transformation.

Species	Common Name	Age Prediction Equation	r	R ²	Significance
					level
<u>Acer negundo</u>	Box Elder	Age=(8.35)(Diam)+16.7	.78	.61	.005
		Age = (14.82)(Diam) ^{0.83}	.85	.72	.005
<u>Juniperus osteosperma</u>	Utah juniper	Age=(22.4)(Diam)+124	.71	.51	.001
		Age=(103.04)(Diam) ^{0.56}	.84	.71	.001
<u>Pinus edulis</u>	Pinyon pine	Age=(20.4)(Diam)+167	.84	.71	.001
		Age=(84.84)(Diam) ^{0.65}	.89	.78	.001
<u>Populus fremontii</u>	Fremont poplar	Age=(.542)(Diam)+14.5	.52	.27	NS
		Age=(9.13)(Diam) ^{0.34}	.64	.41	NS
<u>Populus tremuloides</u>	Quaking aspen	Age=(3.96)(Diam)+37.9	.70	.49	.01
		Age=(19.45)(Diam) ^{0.61}	.82	.68	.001
<u>Pseudotsuga taxifolia</u>	Douglas fir	Age=(15.8)(Diam)+24.8	.65	.42	.025
		Age=(12.13)(Diam) ^{1.10}	.68	.46	.025
<u>Quercus gambelii</u>	Gambel oak	Age=(12.6)(Diam)+2.71	.90	.81	.005
		Age=(7.94)(Diam) ^{1.27}	.94	.88	.001
<u>Tamarix ramosissima</u>	Salt Cedar	Age=(1.92)(Diam)+5.56	.79	.62	.025
		Age=(6.29)(Diam) ^{0.56}	.72	.52	.05

Table 4. Average percent absolute deviation in years of predicted age from counted age for eight tree species.

Average Percent Absolute Deviation			
Species	Mean	Standard Deviation	Coef. of Variation
<u>Acer negundo</u>	18 ^a	24 ^a	1.33 ^a
	16 ^b	21 ^b	1.31 ^b
<u>Juniperus osteosperma</u>	19	13	.68
	19	14	.74
<u>Pinus edulis</u>	17	20	1.18
	14	10	.71
<u>Populus fremontii</u>	20	14	.70
	17	11	.65
<u>Populus tremuloides</u>	38	36	.94
	26	19	.71
<u>Pseudotsuga taxifolia</u>	67	73	1.10
	52	61	1.17
<u>Quercus gambelii</u>	34	31	.91
	26	23	.88
<u>Tamarix ramosissima</u>	22	18	.82
	21	20	.94

a % Deviation derived from linear age prediction equation.

b % Deviation derived from log-log transformed age prediction equation.

Table 5. Mean ages of trees found by diameter class. Ages were determined by the linear prediction equations found in Table 3.

	Diameter Class																									
	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52
<u>Acer negundo</u>	27	42	61	77	91	112	125																			
<u>Juniperus osteosperma</u>	148	193	242	281	329	366	419	462	502	547	594	647	679	730	770	820	869		941							
<u>Pinus edulis</u>	194	237	265	310	343	394	429	485	515	536																
<u>Populus fremontii</u>		16	17	18	19	20	22	23	24	25	26	27	28	29	31	31						37				
<u>Populus tremuloides</u>	44	49	57	66	74	83	90	97	105	111																
<u>Pseudotsuga taxifolia</u>	38	79	104	139	173	198	235	262	298	326	366	384	429	458		515	548	570	627					760	805	847
<u>Quercus gambelii</u>	19	40	64	89	122																					
<u>Tamarix ramosissima</u>	94	12	16	19	23	28	30	34																		

SPATIAL PATTERNS OF PLANT COMMUNITIES IN NAVAJO NATIONAL MONUMENT, ARIZONA¹

by J. D. Brotherson, W. E. Evenson, S. R. Rushforth, J. Fairchild, and J. Johansen²

¹Study completed as part of Contract No. PX7029-9-0570 from the Southwest Region of the National Park Service.

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Patterns in vegetative cover across the landscape have been reported in the literature since the time of Darwin and before (Weaver and Clements 1938). Such patterns are generally considered to be the result of a long process of development under the influence of environmental factors, both past and present (Walter 1973). A wide variety of theories have been proposed to explain these patterns. These theories include the monoclimate ideas of Clements (1936), the individualistic and continuum approaches of Gleason (1939) and Curtis (1955), the vegetational mosaic and environmental pattern concepts of Billings (1952) and Whittaker (1953) and the functional factorial approach described by Major (1951).

In floristically homogeneous areas the vegetation structure is determined primarily by uniformity in the climate and soil. On the other hand, high habitat diversity leads to vegetation patterns which are also highly diverse. Environmental patterns are characteristically understood to be due to climatic, orographic or edaphic (soil) differences (Walter 1973). Such broad generalizations are, however, of little help from an ecological point of view when applied to localized areas. Local differences in vegetation, then, can best be explained on the basis of physical conditions at work on the microhabitat level.

Differential weathering is a potent force in altering conditions at the microhabitat level. (Foster 1971; Birkeland 1974). Traditionally two main types of weathering are recognized. Mechanical weathering breaks up a preexisting rock into smaller fragments and chemical weathering, acting on these smaller fragments, rearranges the mineralogical composition of the original rock. A third process which takes place in the presence of living plants (biological weathering) has also been shown to be

important (Foster 1971; Jenney 1958; Wilding and Drees 1969; and Zinke 1962). Our studies have indicated that weathering processes are the primary determinants of habitat alteration and vegetation patterns in Navajo National Monument.

STUDY SITE

Navajo National Monument is in northeastern Arizona. The park headquarters are located on the Shonto Plateau near the head of Betatakin Canyon. The park is made up of three separate units, each of which contains a large "cliff dwelling" of the Anasazi culture (Brotherson et al. 1978). The three units are in pinyon-juniper slickrock country where there are many deep-cut canyons with high-walled sandstone cliffs which often reach 1000 feet above the streambeds. Each unit is in a separate canyon. Betatakin and Keet Seel are two of these canyons and belong to the major Tsegi Canyon complex while Nitzin Canyon (Inscription House) is situated 32 kilometers (20 miles) west and is a branch of Navajo Canyon.

Climatically the area is in the cold temperature desert region of the Great Basin. The total annual precipitation ranges from a low of 17 cm (6.8 in) to a high of 48 cm (18.8 in) with an average of 29 cm (11.4 in) (Brotherson et al. 1978). The period of greatest precipitation is late summer and early fall. Rainfall in the area is often spotty and localized, with cloudbursts occurring more often than general rains. The temperature regimes of the area fluctuate greatly during the seasons with lows of -23°C in winter and highs of 39°C in summer. The frost-free season ranges from 107 to 213 days with an average of 155 days.

The geology of the area is simple. Navajo Sandstone is the major geological formation in all three segments of the monument and is the only exposed rock formation at Keet Seel and Nitzin Canyons. At Betatakin the Kayenta formation is periodically exposed in the canyon's lower reaches. In all three canyons, the Navajo sandstone cliffs form sheer walls which extend above the creek beds 200 to 250 m (700-800 ft.). At the base of these cliffs in each canyon, talus accumulations can be found, while the canyon bottoms are filled with deep deposits of alluvium (quaternary fill). In Keet Seel and Nitzin these alluvial deposits are deeply eroded. In Betatakin canyon the alluvial deposits are less extensive and not nearly so thick. They are underlain by the Kayenta formation in the lower parts of the canyon and are also deeply eroded. The predominance of such erosion (wind, water, etc.) is a major feature of the Monument and of the surrounding country.

METHODS

One hundred twenty-nine study plots were selected within the twelve plant communities (Brotherson et al. 1968) of Navajo National Monument. Each community type had at least four plots with those of larger area having more. Each study plot measured 10m x 10m (.01 ha) and was randomly located within the community being studied. The plots were subsampled by placement of 20 regularly placed 0.25 m^2 quadrats in a 100 m^2 grid. Cover estimates (Daubenmire 1959) were obtained for all species encountered as well as for total living cover, cryptogam cover, litter, rock and bare ground. Plant composition by life form was obtained by

recording species in six life form categories: trees, shrubs, grasses, forbs, annuals and cryptogams. Percent cover for all categories was subsequently calculated.

Composite soil samples were taken to a depth of 20 cm from the corners and center of each 100 m² plot. This depth was considered adequate because Ludwig (1969) in a study of different foothill communities in Utah showed that the surface decimeter of soil, when sampled with reference to mineral concentration, yields 80% of the information useful in correlations with plant data. Holmgren and Brewster (1972) also showed in a study of desert communities that greater than 60% of the fine roots (those most likely to absorb soil minerals) were found concentrated in the upper 20 cm of the soil profile. The following characteristics were also recorded for each plot: exposure (aspect), percent slope, and soil depth. Soil depth was determined with the use of a 1-m penetrometer.

Soil samples were analyzed for texture (Bouyoucoz 1951), pH, soluble salts, organic matter, and mineral composition. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 soil-water paste (Russell 1948) was used to determine pH and total soluble salts. Organic matter was determined by weight loss after 24 hours at 450°C in a muffle furnace. Soils were extracted with 1.0 normal ammonium acetate for the analysis of calcium, magnesium, potassium, and sodium (Jones, 1973). Zinc, manganese, iron, and copper were extracted from the soils with DTPA (diethylenetriaminepenta-acetic acid) (Lindsay and Norvell 1969). Soil phosphorus was extracted with sodium bicarbonate (Olsen et al.

1954). Total nitrogen analysis was made using macrokjeldahl procedures (Jackson 1958). Ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971).

Plant nomenclature follows McDougall (1973). Prevalent species (those most frequently encountered during sampling) of the various plant communities are reported as equal to the average number of species per 0.01 ha sampling area examined (Warner and Harper 1972). Diversity values were computed using the formula: $B = 1 / \sum p_i^2$ where B is the diversity index and p_i is a measure of the relative abundance of a species in a given habitat (Levins 1966, MacArthur 1972).

Cluster analysis techniques (Sneath and Sokal 1973) were applied to similarity index values (Ruzicka 1958) using unweighted pair-group clustering (UPGMA). The UPGMA method computes the average similarity of each unit to the cluster, using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972).

Linear regression analysis (Cochran and Snedecor 1976) was applied to the different biotic and abiotic factors measured to determine the degree to which they are associated. Aspect data was transformed according to Beers et al. (1966) to allow its use as an independent variable in the statistical analysis. Northeast aspects receive a value of 2.0, the southwest a value of 0.0, and intermediate aspects vary from 2.0 to 0.0 in both directions.

RESULTS AND DISCUSSION

Along with the unique geological and habitat features of Navajo National Monument, the plant communities within its boundaries are also

varied and in some cases unique. Twelve community types are encountered in the monument (Table 1). Two of these, pinyon-juniper-mixed shrub and oak, are found in all segments of the Monument. Six of the remaining 10 community types are found in 2 of the Monument areas while 4 of the types are restricted to a single Monument segment. Betatakin canyon and its surrounding areas are the most variable and distinct. This is partially due to the favorable moisture regimes created by the canyon geology and Navajo Sandstone hydrology.

Community Descriptions

The talus slope community is located in the monument at the base of the large Navajo Sandstone cliffs. Because of the differential weathering patterns of the sandstone, it is often found above the canyon bottoms in pockets. It is characterized by having many large and small rocks in its soil which varies in depth from a few inches to several feet. Floristically it is highly diverse and contain all lifeforms but is dominated by shrubs and grasses (Table 2).

The Atriplex-grass community is found in two segments of the Monument but is most highly developed at Inscription House on the deep deposits of alluvial fill in the canyon bottom. Vegetatively it is closely aligned with the talus slope type (Table 2), but it is less diverse and shows only half as many prevalent species. At present it shows a great deal of erosion (wind and water) which is due in part to heavy overgrazing.

The pinyon-juniper-grass community is found only in the bottom of Betatakin Canyon. It is found at the base of the sandstone cliffs on both northern and southern exposures in places generally occupied by the

talus slope community. It differ from the talus slope type in that the soils are fine textured and lack a rocky component. It is floristically quite diverse and also shows a high degree of cryptogam development.

The slickrock-scattered shrub community is well developed in two of the Monument's segments (Table 1). It is characteristically associated with the Navajo Sandstone in much of southern Utah and northern Arizona and often exhibits large areas of exposed rocks. The vegetation is found growing in pockets in the sandstone created by differential weathering where some of the fine textured material from the breaking up of the parent rocks has collected. The pockets vary in size from a few feet to several hundred feet across and sport a variety of vegetative forms. Diversity in this community is the highest in the Monument. The type shows little or no grazing influence.

The pinyon-juniper mixed shrub type is found in all segments of the Monument and is the type which occupies the greatest percent of the land base. It occupies a position somewhat between the slickrock and pinyon-juniper-sage communities: It exhibits fairly large areas of exposed sandstone though not to the extent found in the slickrock type. Soil development in the type is also more extensive than in the slickrock. Vegetatively, a major distinguishing factor is the presence of several major shrub species in the understory (Table 2) that do not occur, or occur only rarely, in the other pinyon-juniper related communities.

The pinyon-juniper-sage type is represented in the Monument only at Betatakin, where it is found adjacent to the pinyon-juniper-mixed shrub type on the plateau back from the canyon rim. It contains the oldest and largest trees of the pinyon and juniper species. The soils of the

surrounded in both cases by the oak community and together with it makes up the major portion of the riparian canopy of the canyon bottoms. Floristically it is of average diversity and dominated in the understory by shrubs and forbs (Table 2).

The mixed weed community is found only in Keet Seel Canyon where it occupies a considerable portion of the canyon bottom. It consists of a mixture of introduced and native weeds and is dominated almost exclusively by annuals (Table 2). It grows on deep deposits of alluvial fill and appears to be a remnant of heavy overgrazing in the past.

Hanging gardens, an unusual community type occurring in much of the Navajo Sandstone region, are present in Betatakin and Keet Seel. The garden at Betatakin is in the cliff dwellings and is associated with two seepage areas where water slowly emerges from the rocks. The seepage is slow and no runoff water is present. The hanging garden at Keet Seel is more mesic. Here the vascular plants grow attached to a seepage wall at the base of the northern part of the cliff dwellings. At the wettest portion of the garden a small seep emerges to form a puddle at the base of the hanging garden. With the exception of poison ivy, the gardens are dominated exclusively by forbs.

The streamside tree community is found at Inscription House in Nitzin Canyon. It is dominated by Fremont poplar and grows along the stream bank at the cliff base below the ruin. Understory plants are almost non-existent due to the high activity in the area of domestic sheep and cattle. The animals concentrate in the area along the stream for both feeding and shading purposes. The soil base of the community is the deep deposits of alluvial fill. Erosion is widespread in the area.

Similarity indices.

Indices of similarity (Ruzicka 1958) were computed for each community in relation to all other communities (Table 3). The similarity indices were low, ranging from 0 to 31%, with an average of 4.3%. In 52% of the comparisons the percent similarity was zero, while only 13 of a possible 66 comparisons showed similarities exceeding 10%. Figures of this nature indicate little similarity between communities and thus high community integrity.

Cluster Analyses.

Cluster analyses were performed by clustering the similarity indices to produce a graphical representation of the relationships between the different community types (Fig. 1). Cluster patterns provide insight into community relationships within the Monument since those communities most closely related share floristic and environmental elements. As can be seen from the figure, groups did develop even though the patterns are weak.

Environmental Factors

Information was taken on the biotic and abiotic factors of the different plant communities found within the Monument. Data sets (one per study plot) were lumped by community and summarized (Table 3). There is a great deal of variation in the data, both within and between communities. In an attempt to see relationships more clearly, each measured variable was treated as a gradient. Mean values and standard deviations for each community were graphed in a linear relationship to the gradients (Fig. 2A to 2DD). There is clearly greater variability along some gradients than along others.

If we assume approximate uniformity in the chemical and physical properties of the Navajo Sandstone parent material, then any alterations in these properties should indicate some influence of the weathering process. In assessing this hypothesis, mineral concentrations in the soils of the plant communities under study were compared to mineral concentrations in the sandstone. The results are shown in Table 4. Those minerals exhibiting downward trends indicate mobility and loss of the mineral through leaching, etc. while those minerals showing upward trends indicate buildup of the mineral element in the upper levels of the soil profile.

Attempts were made to assess how the plant communities in the Monument tended to influence or be influenced by the general weathering process. This was done by selecting thirteen of the measured abiotic parameters (i.e. pH, soluble salts, organic matter, calcium, magnesium, potassium, sodium, zinc, iron, copper, manganese, phosphorus, and nitrogen) and treating them as gradients. The gradients were divided into five equal segments and then each plant community was positioned along each gradient according to its mean. The communities were then rated according to their position on the gradient. For example, if a community fell in segment two of a gradient it was rated as two, etc. All twelve communities were rated relative to each of the gradients. Following this the community ratings were summed across all gradients to yield an index which indicates an overall position with respect to all thirteen gradients (Table 5, Fig. 3).

Several patterns emerge. The soil of the slickrock community appears the least changed from the parent material. This is to be

expected since it occurs on sites with large areas of exposed sandstone. The soils of the pinyon-juniper-grass and talus slope communities also tend to show minor change. These types are found at the base of the sandstone cliffs and would receive constant input of generally unweathered material as the cliffs continue to break up and disintegrate. The oak community, on the other hand, is at the extreme weathered end of the composite gradient (Fig. 3). Its soils are very different from the original parent material. This community exhibited the highest levels of litter cover of any of the communities studied. Its soils were also the lowest in percent sand, the highest in percent fines and organic matter and the most acid (Table 3). If we examine the relationship between pH and percent organic matter in the soil (Fig. 4) it becomes apparent that as organic matter incorporation increases, the soil becomes more acid. The relationship is highly significant ($p < 0.001$). Our data are consistent with the findings of Zinke (1962), who found pH's more acid in soils influenced by the canopy. Traditional thinking has generally subscribed to the idea that the increased acidity from organic matter breakdown increases the weathering process considerably (Birkeland 1974). However, recent laboratory and field work have demonstrated that chelating agents (products formed from biological processes in the soil), when in contact with mineral soil, can also bring about significant amounts of weathering (Schalascha et al. 1967). In fact, in some places the amount of weathering by this process is suggested to exceed that brought about by hydrolysis alone (Birkeland 1974; Schatz 1963; Jackson and Keller 1970). All indications are then that the oak communities are contributing a great deal to the weathering process in their habitats. All other communities in the Monument show

positions relative to the composite weathering gradient somewhere in between the cases described above (Fig. 3). In all cases the weathering process appears to be a combination of the major types (physical, chemical, and biological) with those toward the slickrock end being more physical and showing less biotic influence.

Correlation analysis

In an attempt to assess the interrelationships of the different environmental factors measured, correlation analysis was performed. The data are summarized in Table 7 which shows the significant positive and negative relationships. Again, patterns significant to the weathering process emerge. Percent sand in the soil for example, is negatively correlated with percent silt, percent fines, percent litter cover, percent organic matter, nitrogen, iron, manganese and copper while positively correlated with pH. Each case suggests that as sand is broken down, the soil that is derived takes on characteristics of a weathered condition. Percent fines and/or percent silt correlate positively with organic matter, nitrogen, manganese, iron and copper, again indicating the weathering process in action. In fact, careful consideration of the many other relationships displayed the table and discussed in the paper support the assumption differential weathering processes in the Monument and adjacent areas are a potent force in altering conditions at the habitat level, thus creating the variety of environmental conditions seen in the plant communities growing there.

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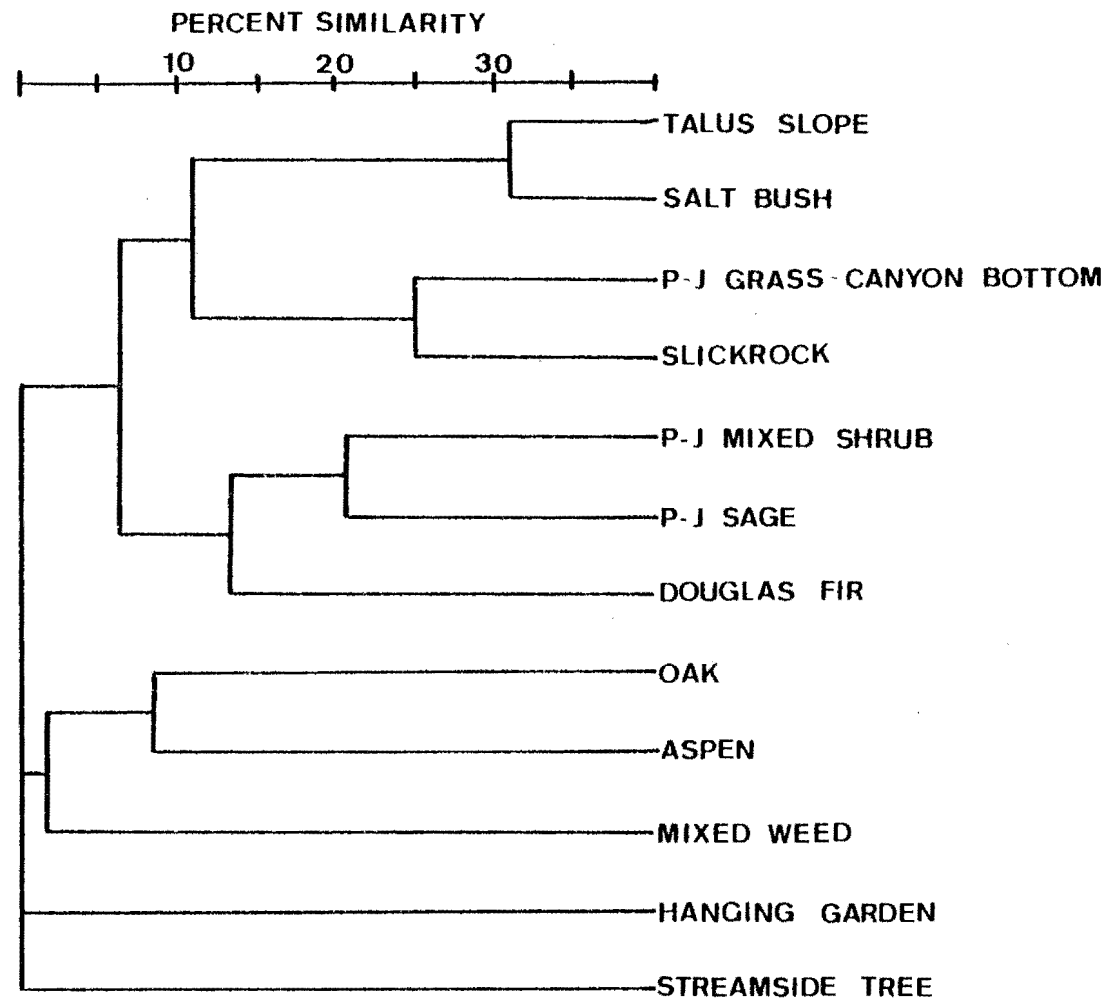
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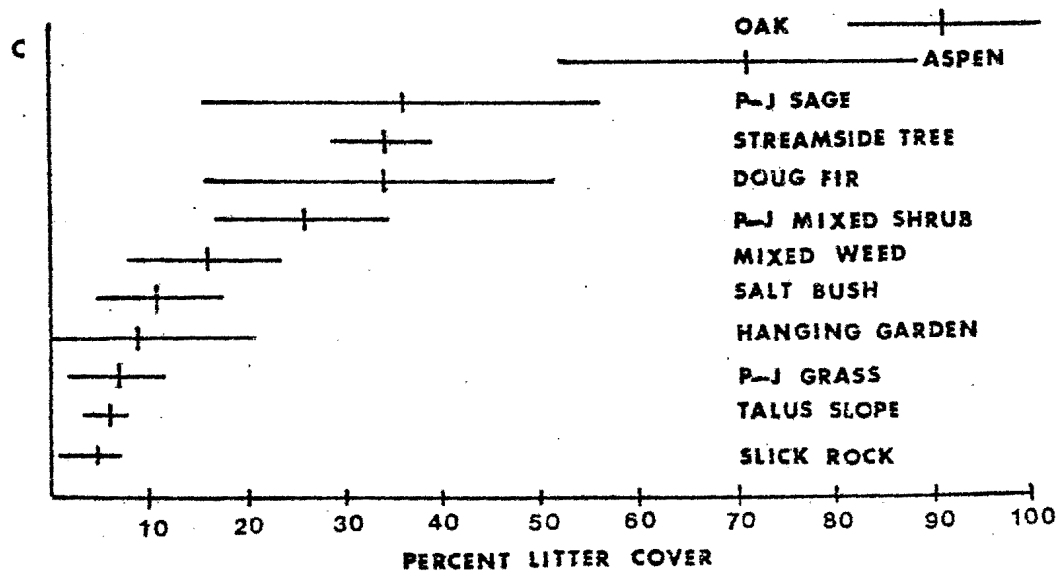
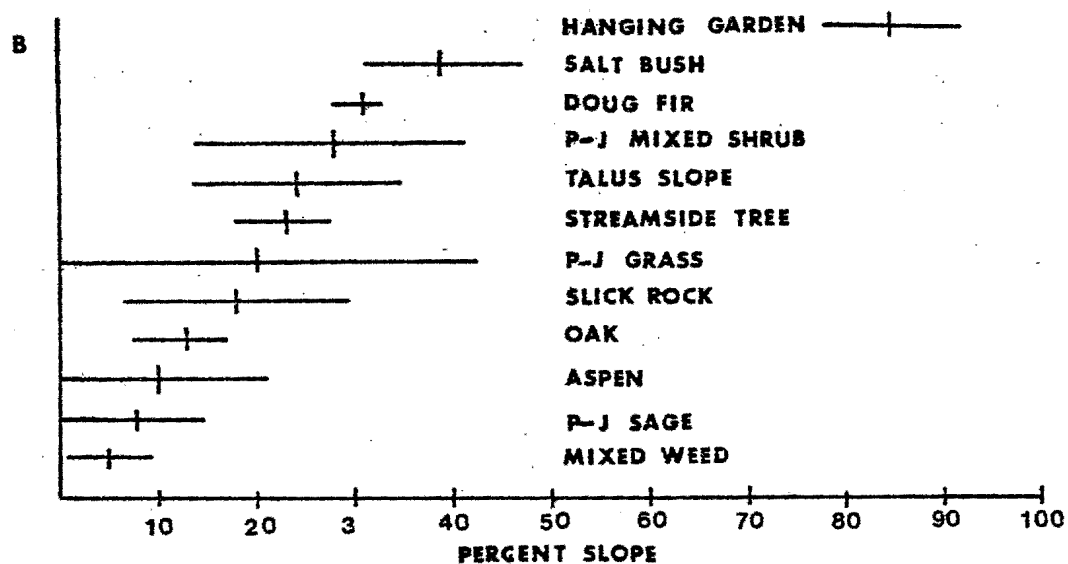
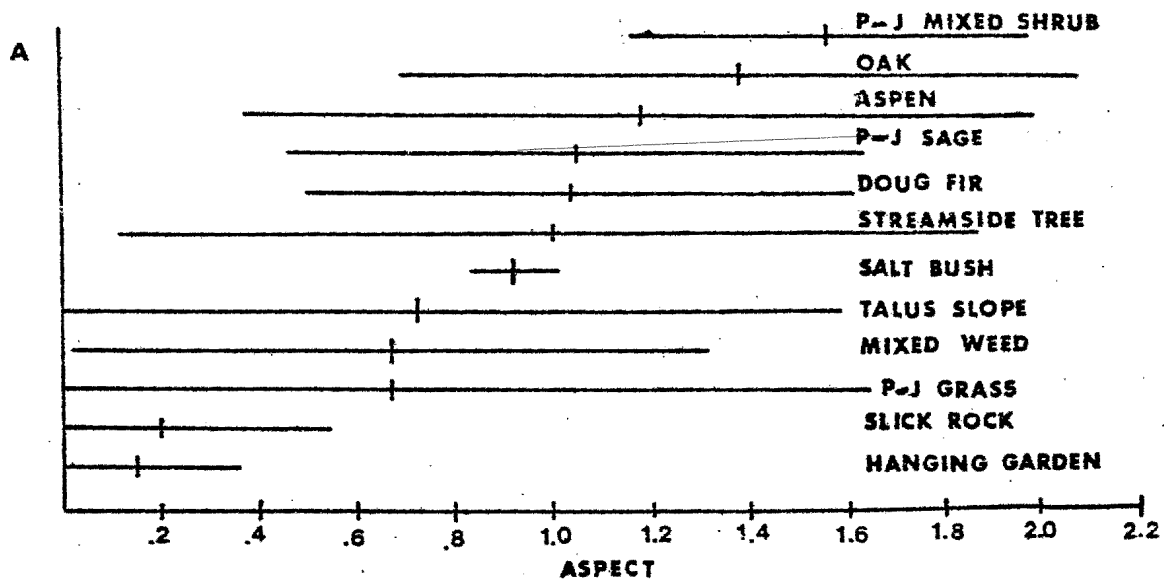
Figure 1. Cluster dendrogram showing similarities of plant communities found within the boundaries of Navajo National Monument.

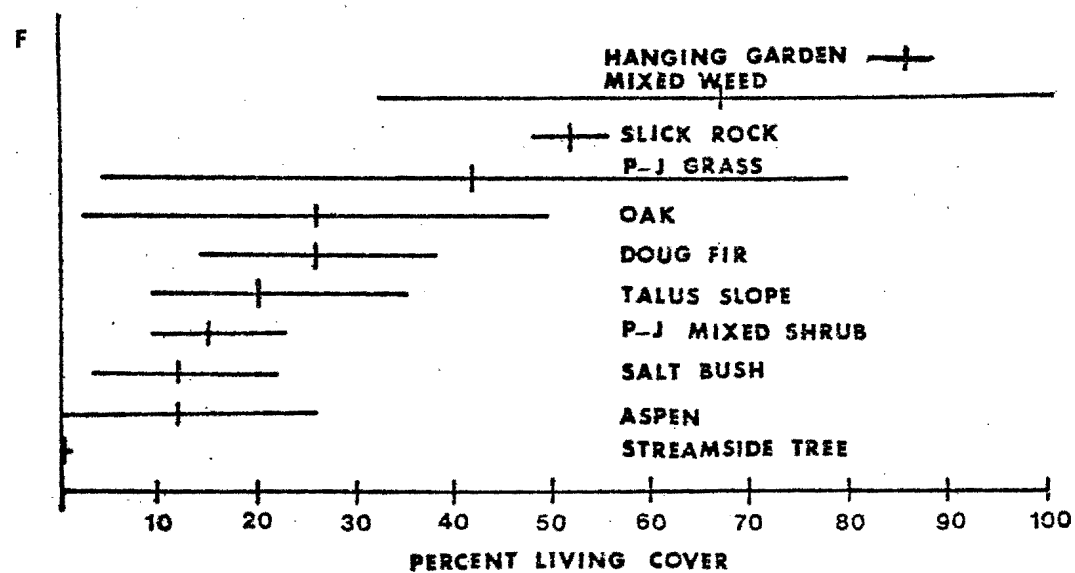
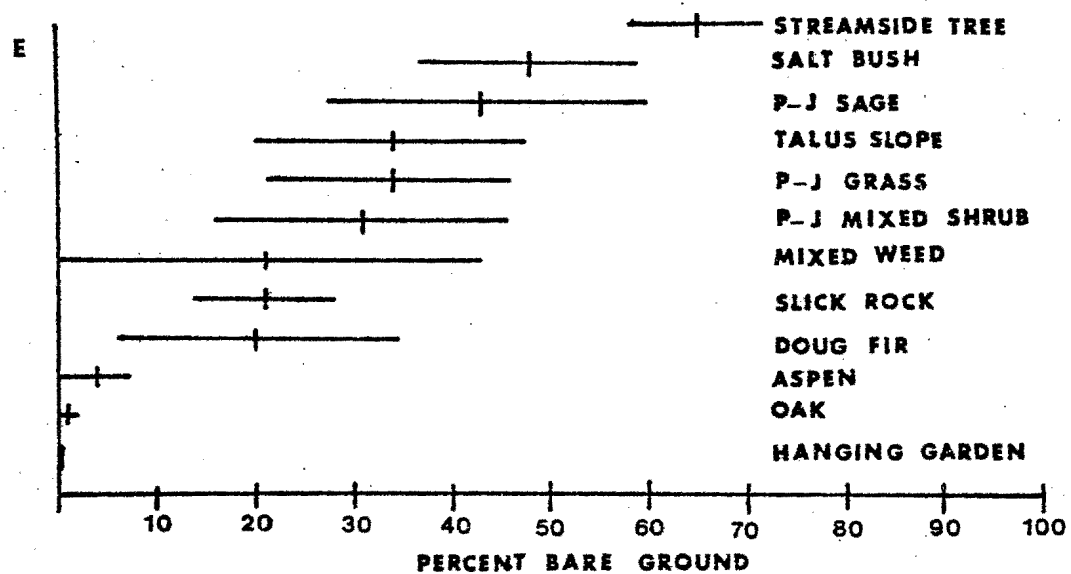
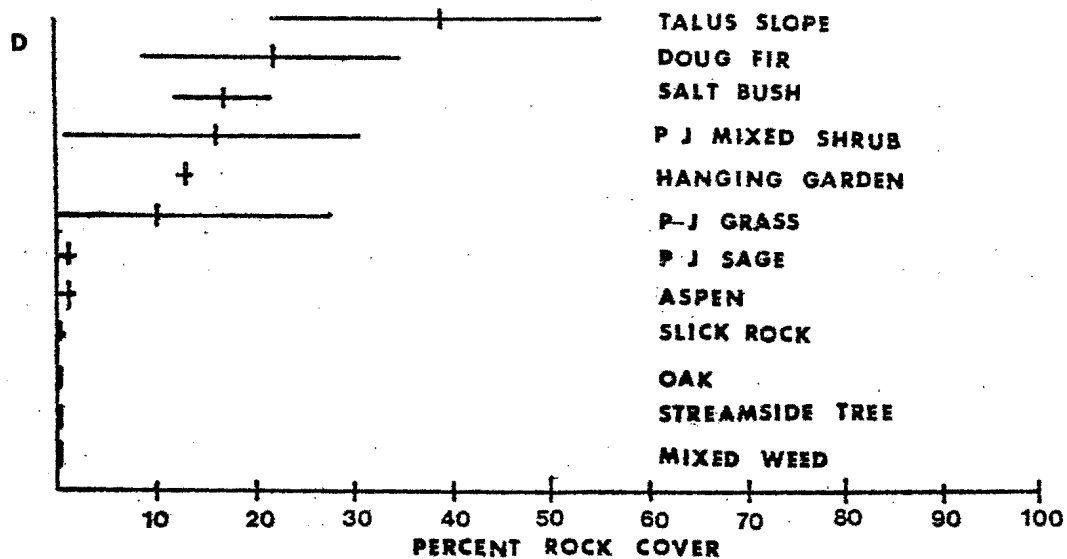
Figure 2A to 2DD. Environmental variables treated as gradients for display of means and standard deviations for the 12 communities found within the Monument.

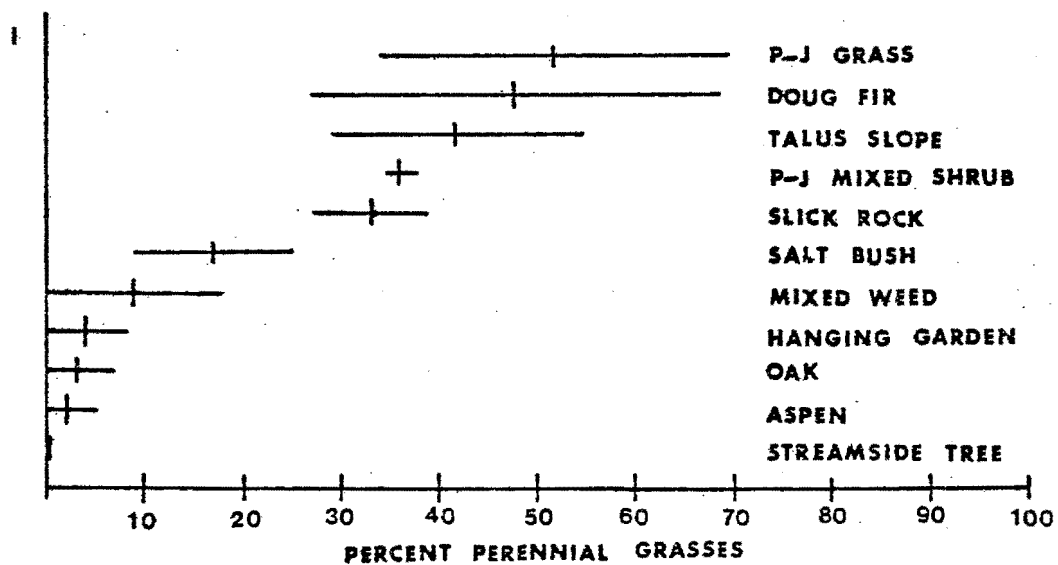
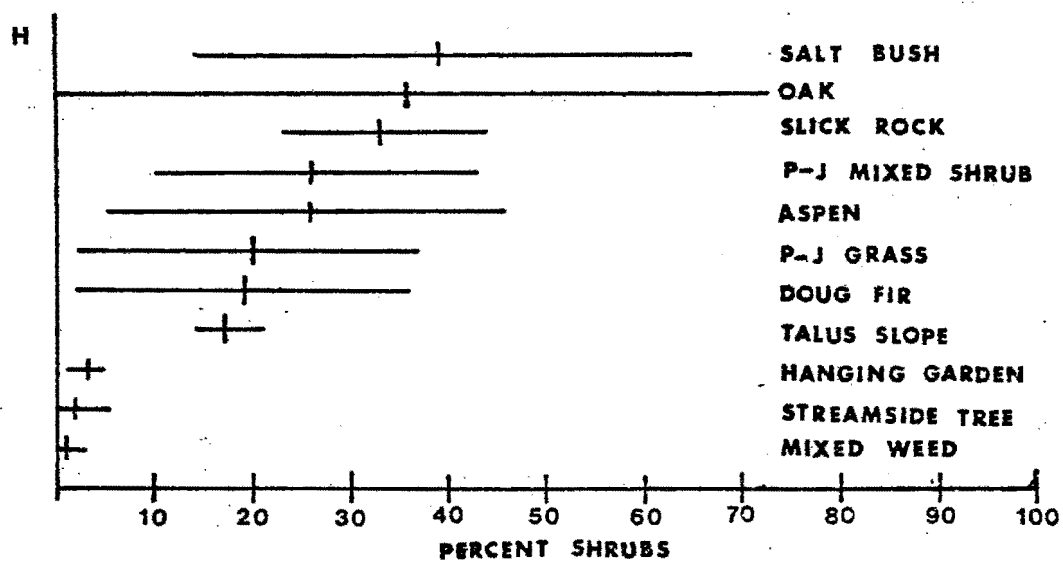
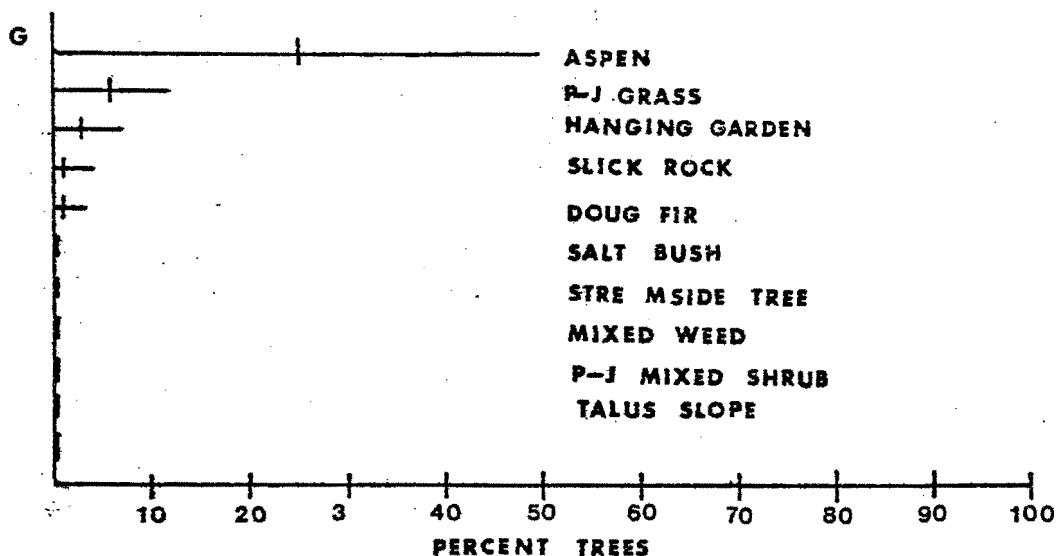
Figure 3. Community positions via gradient summary index (Table 5) relative to each other and with respect to all thirteen gradients.

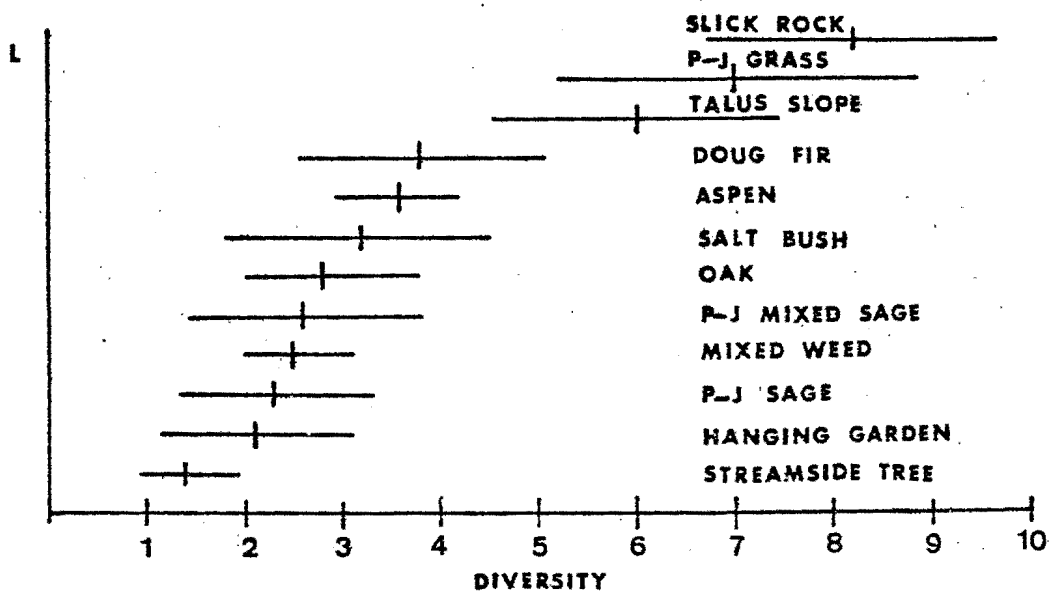
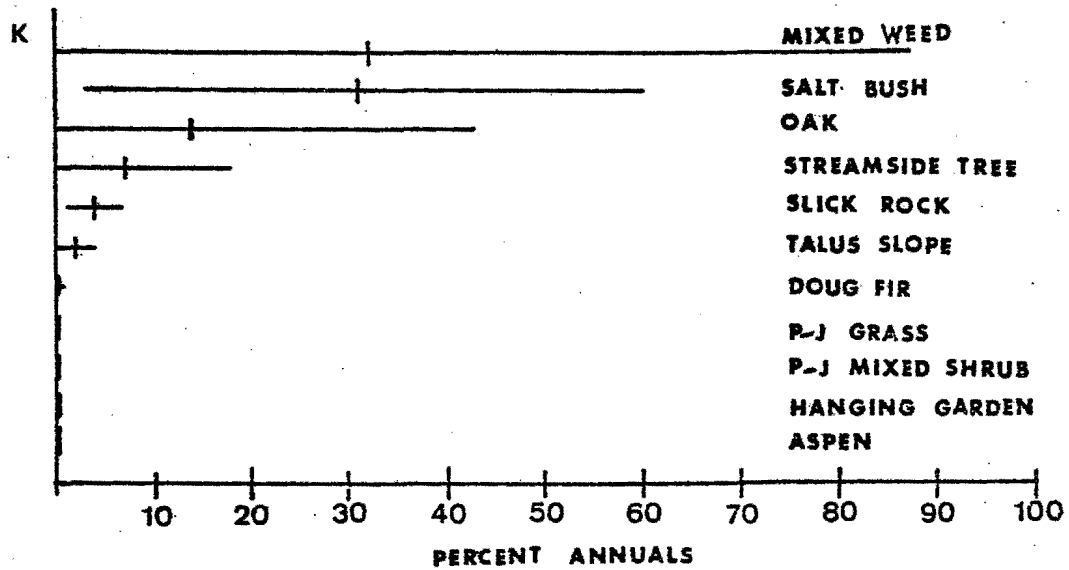
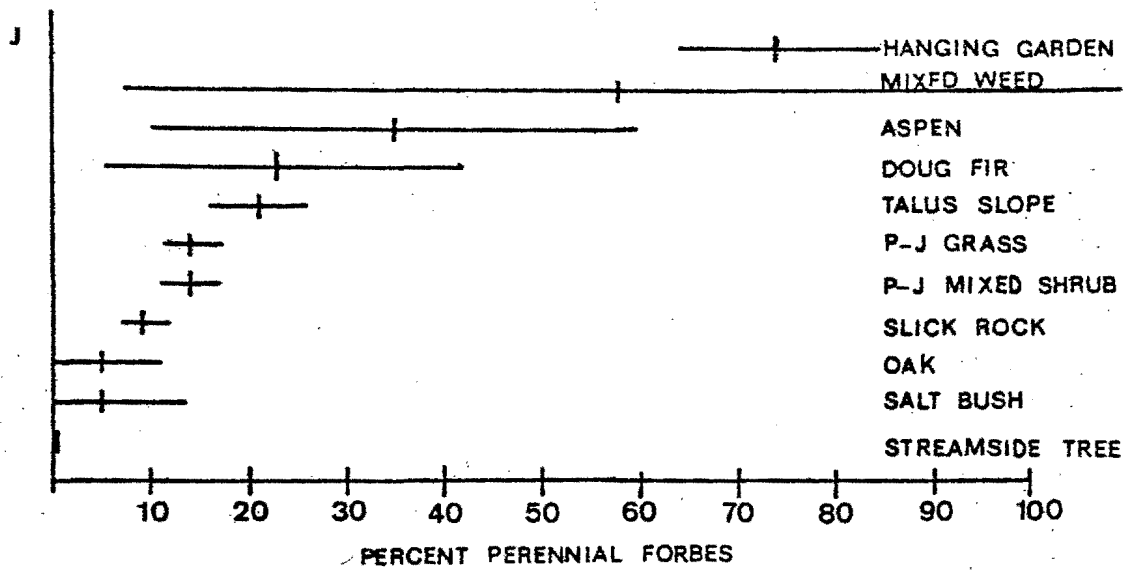
Figure 4. The relationships existent between pH and percent organic matter in the soils of the plant communities of Navajo National Monument.

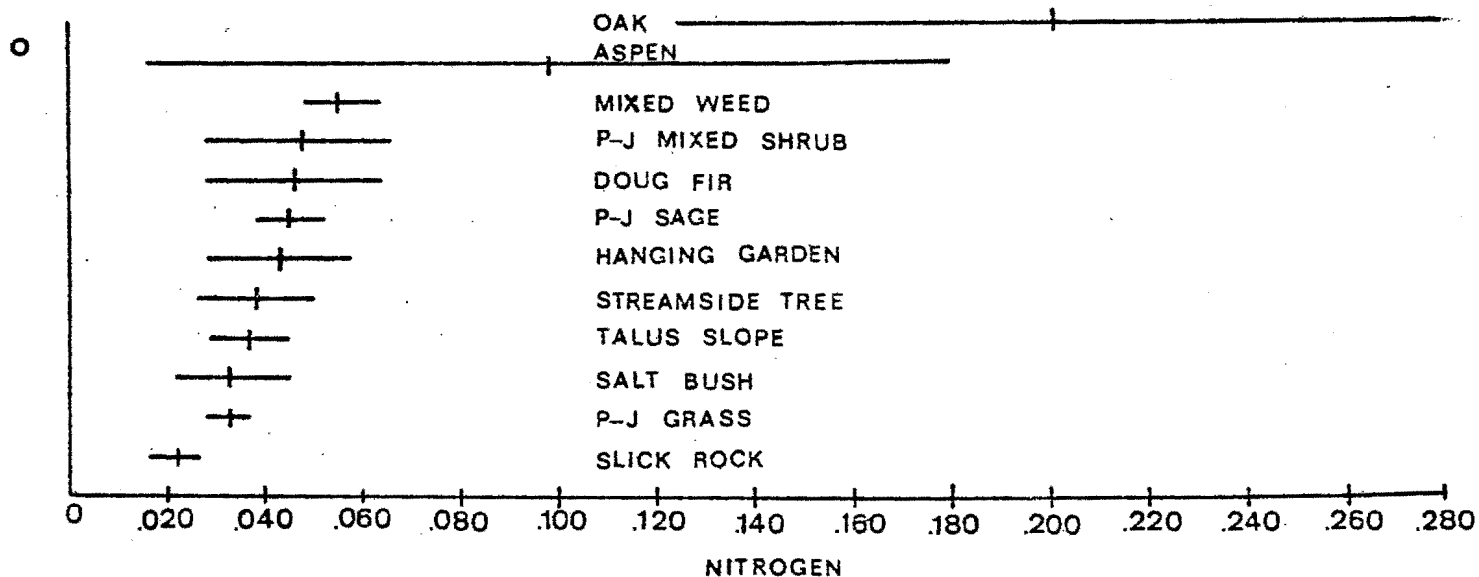
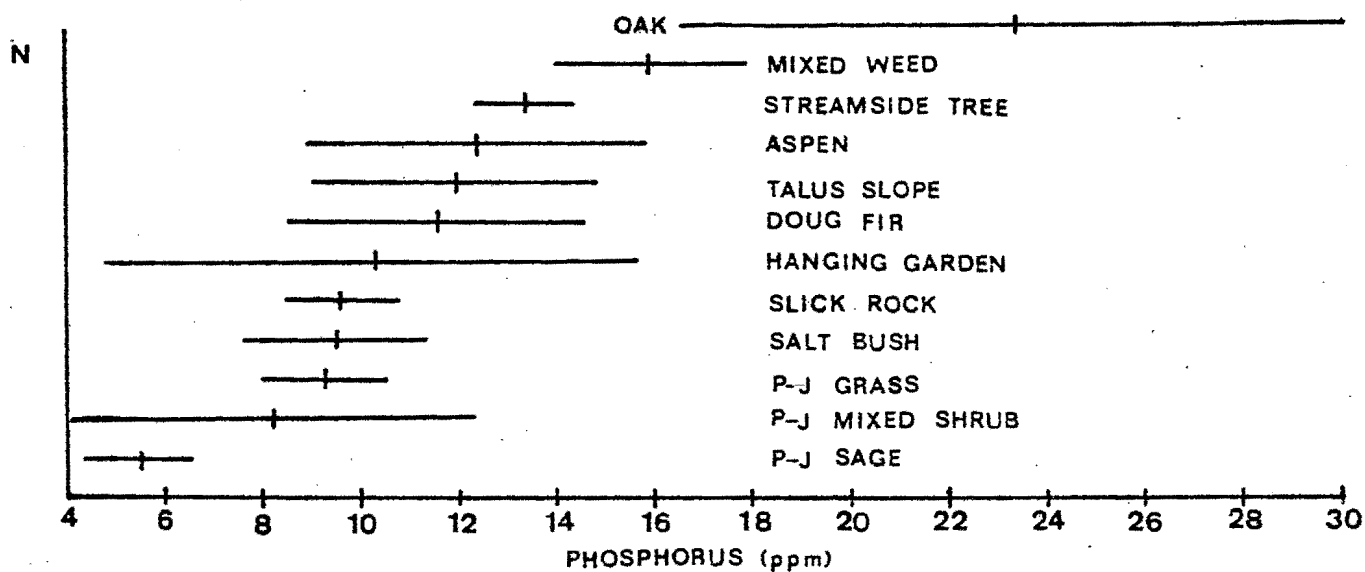
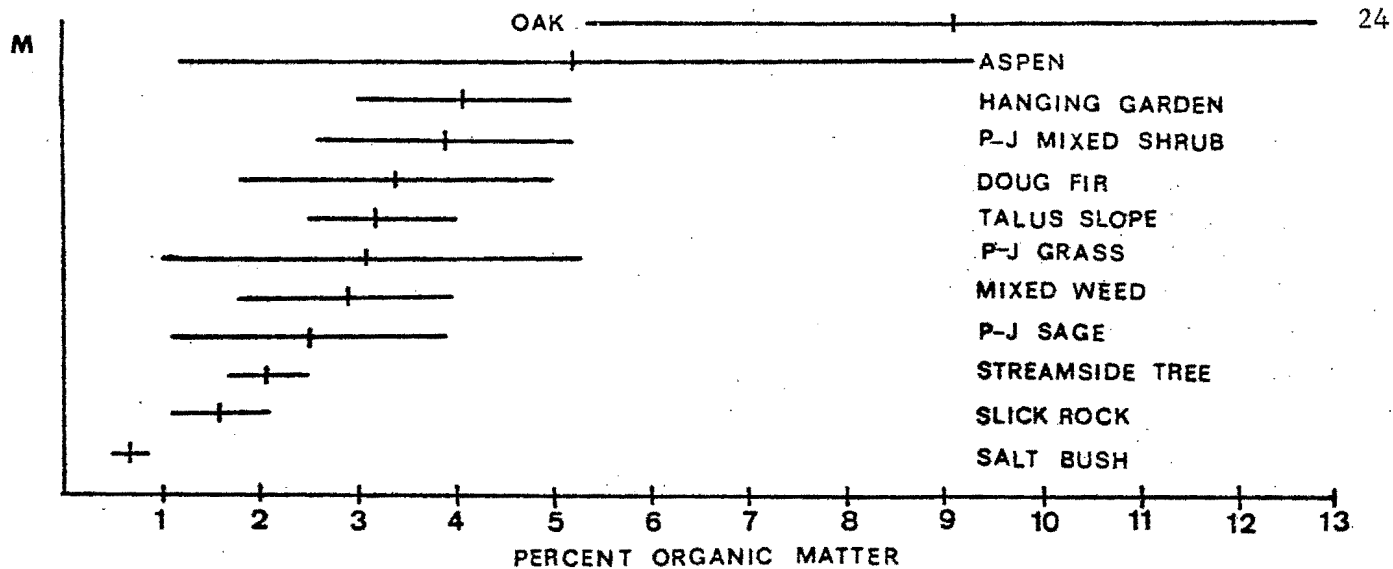


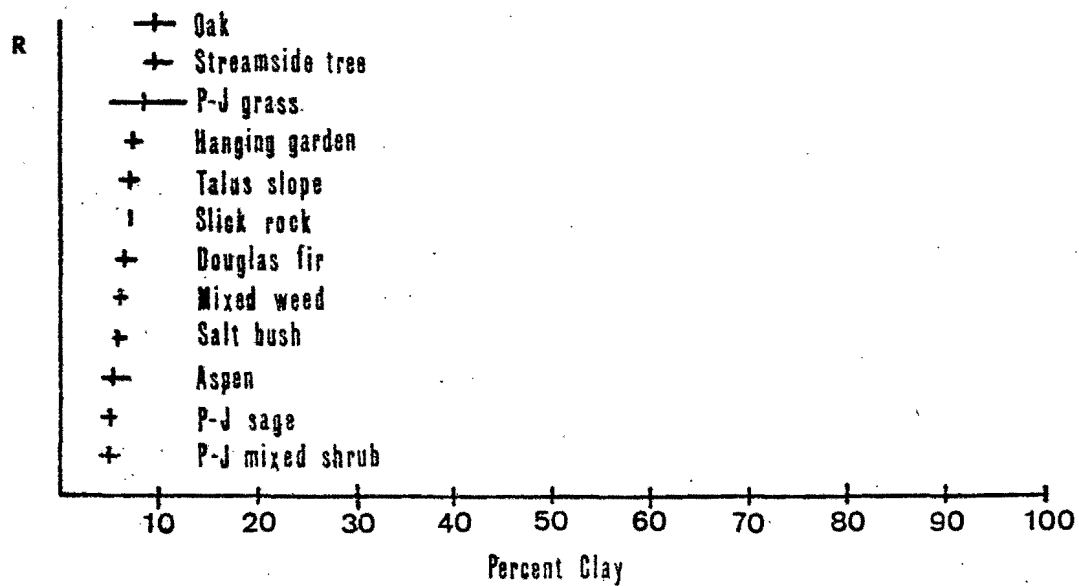
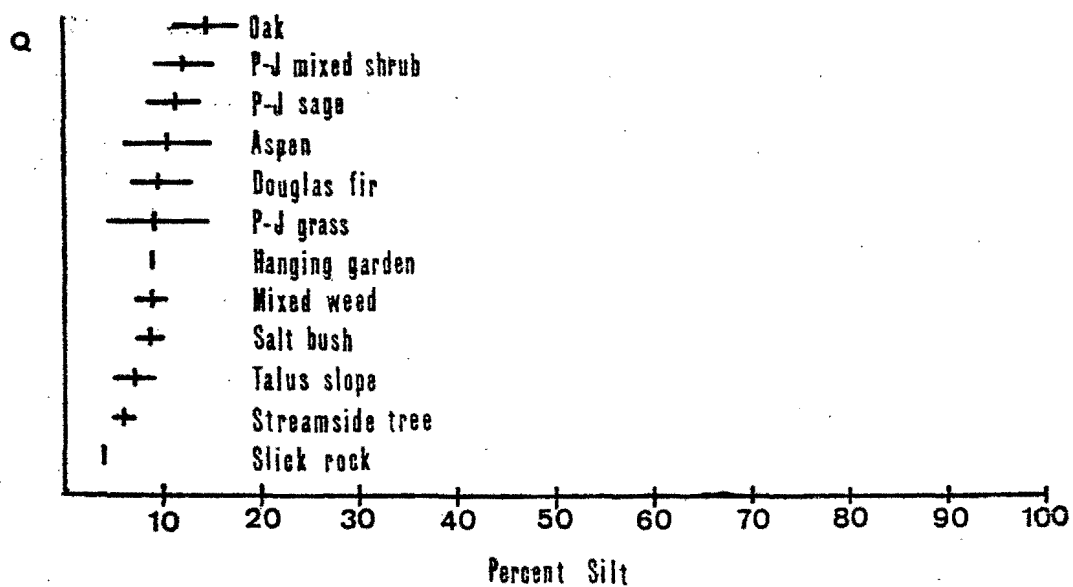
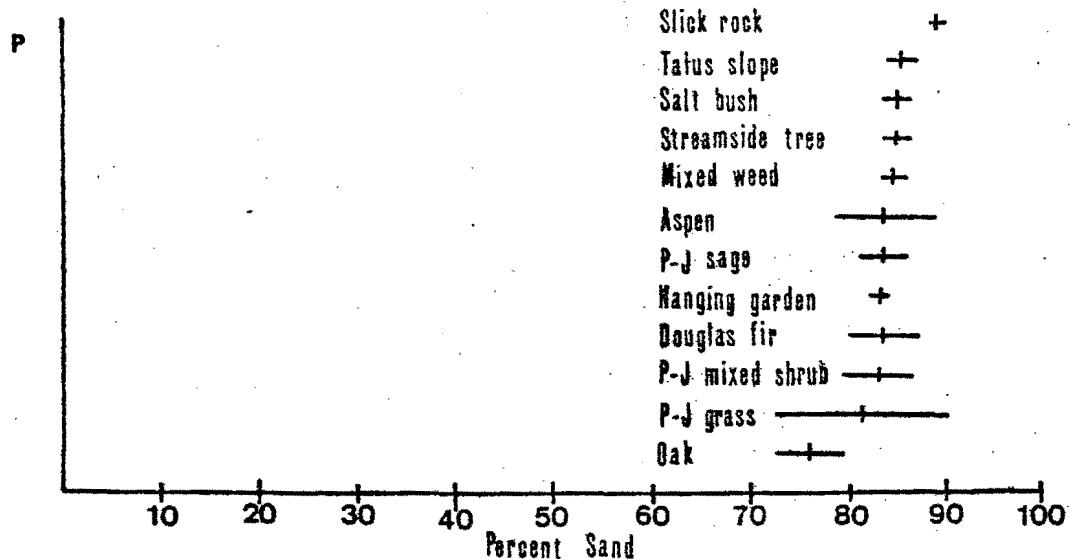


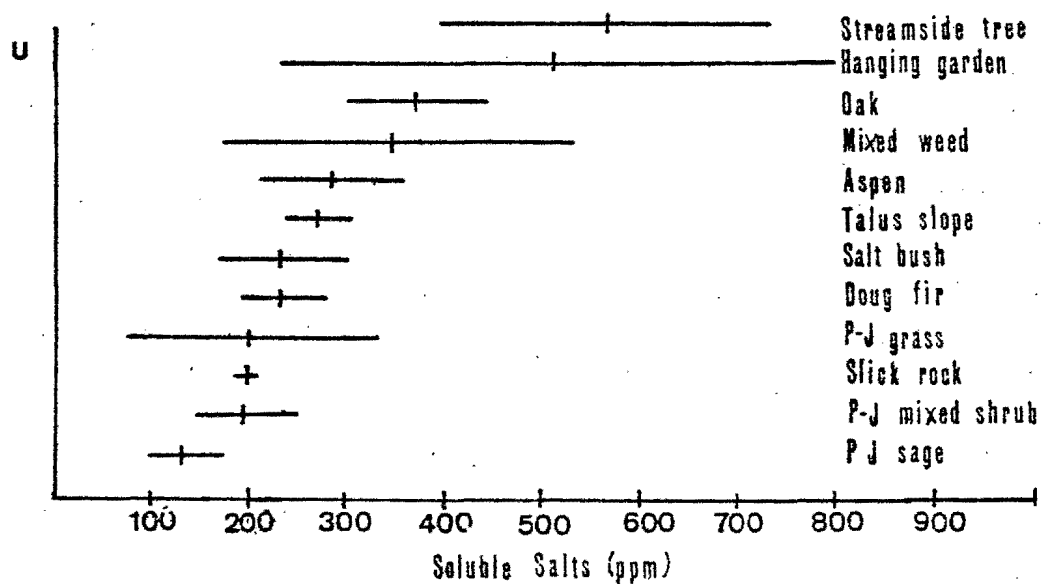
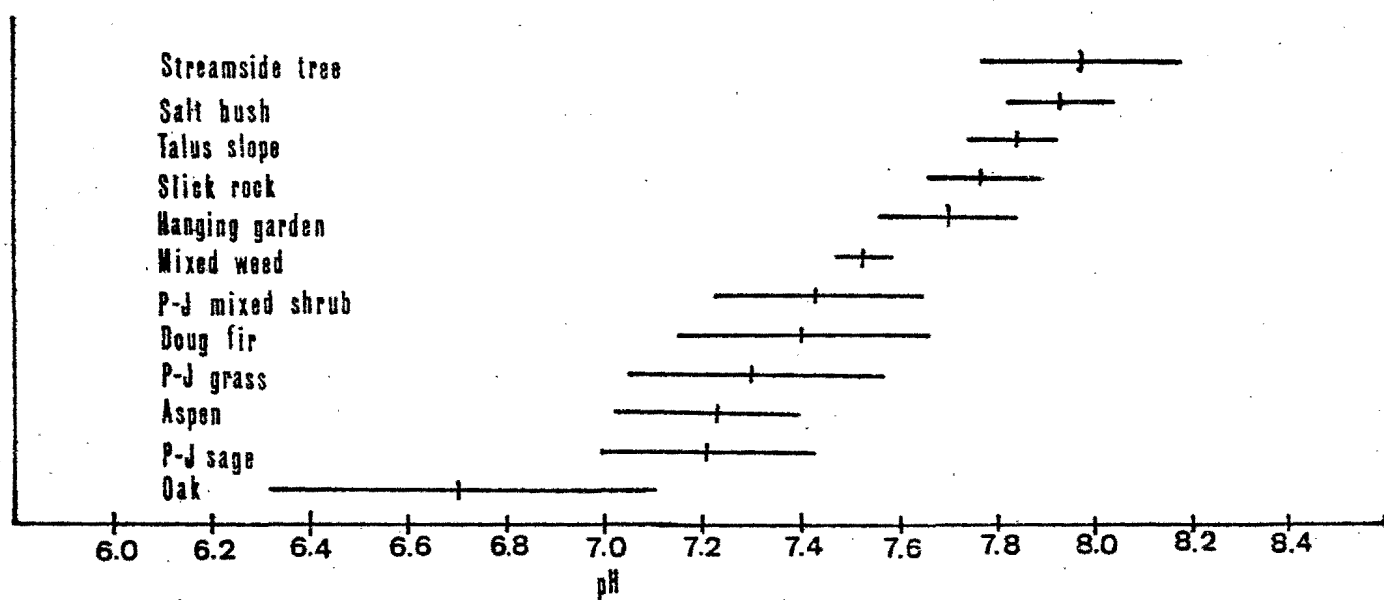
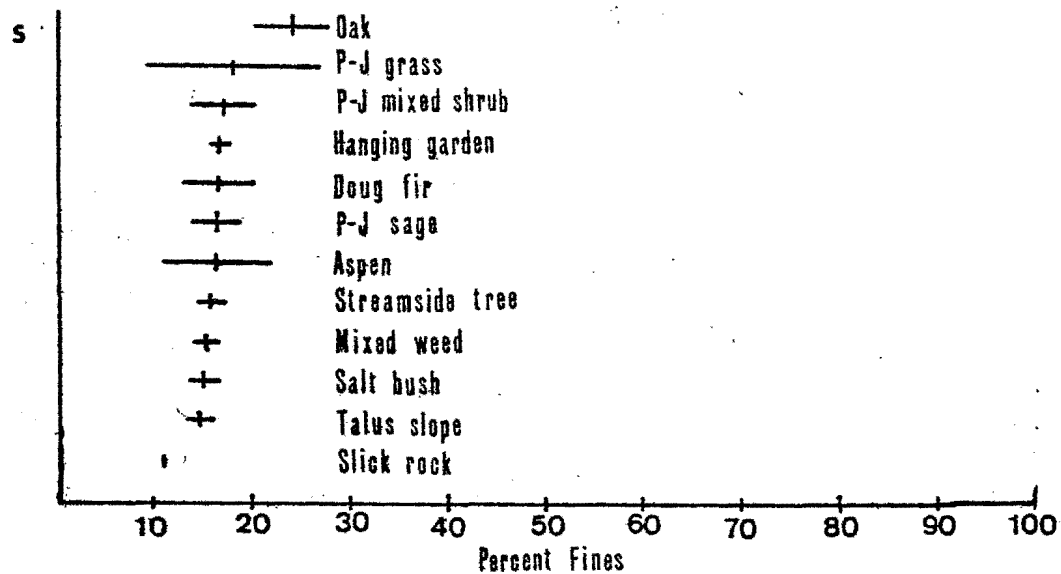


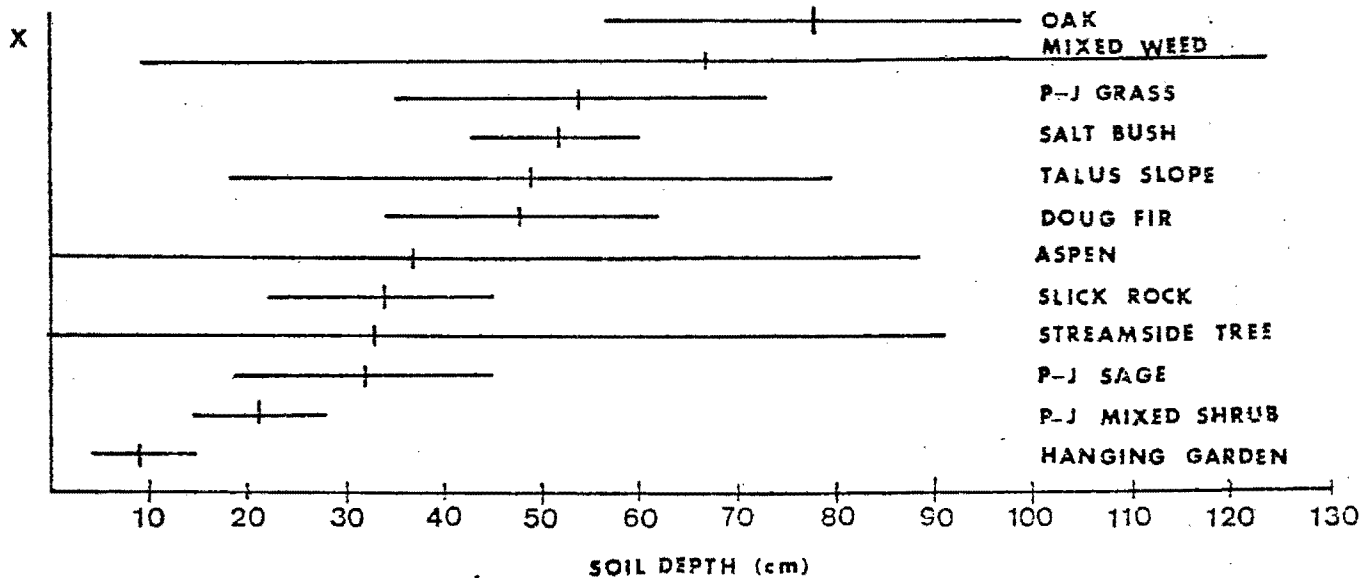
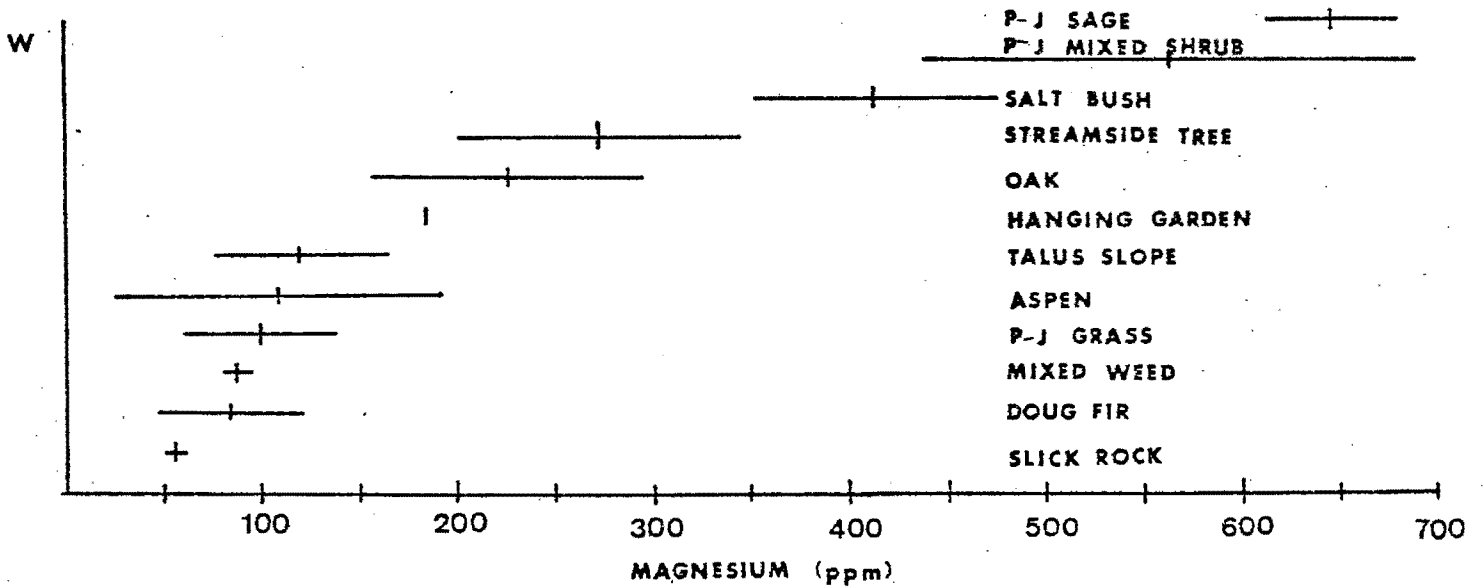
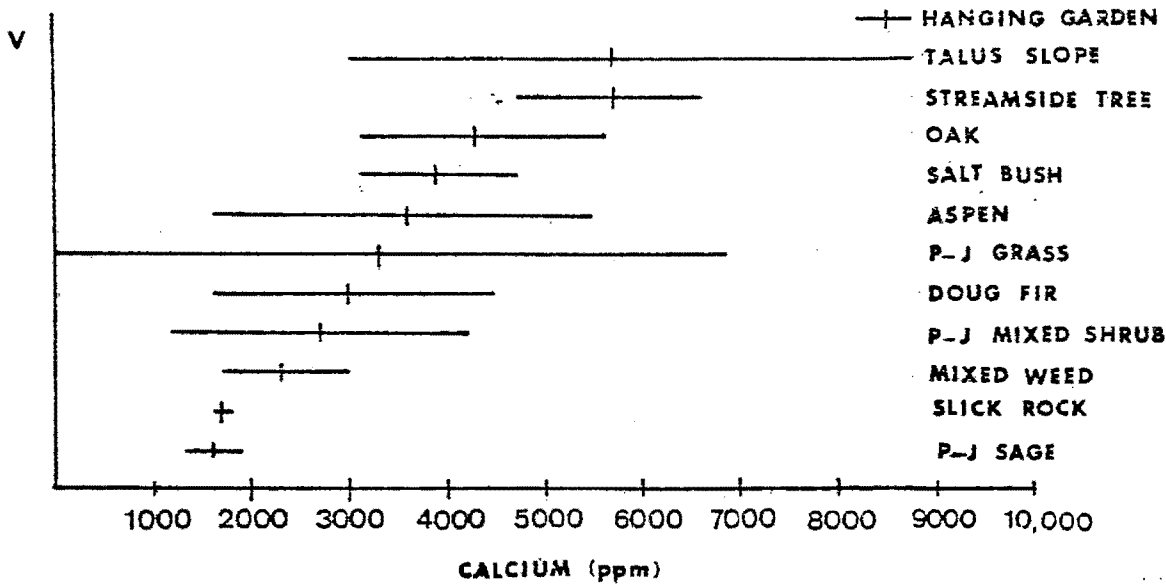


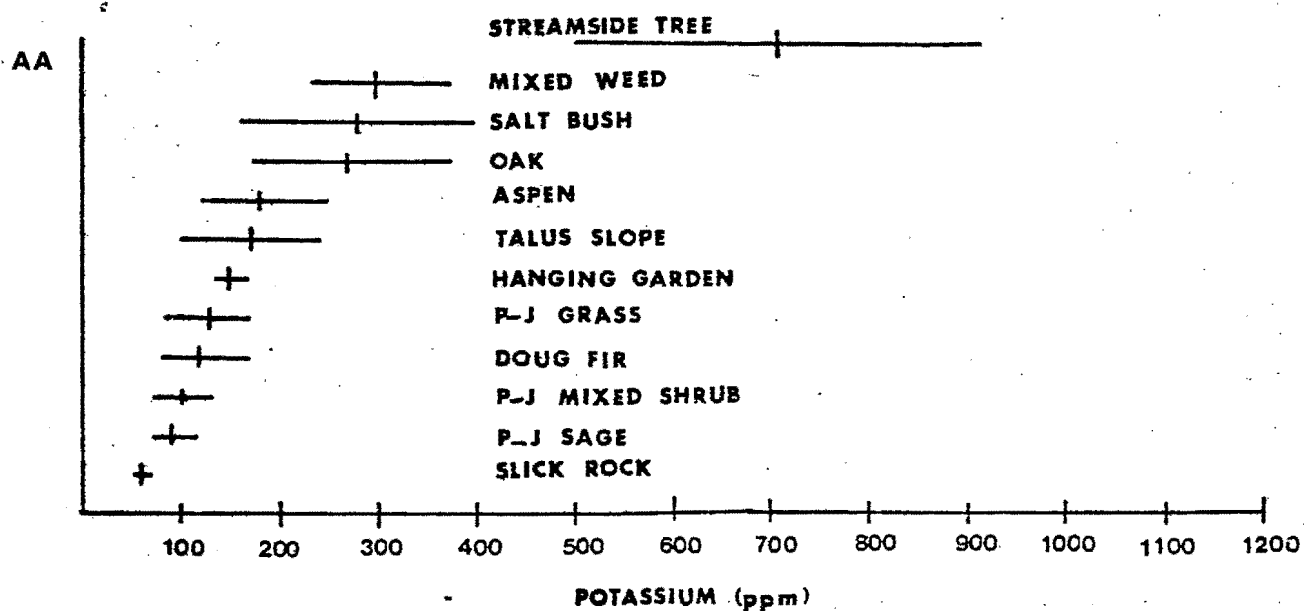
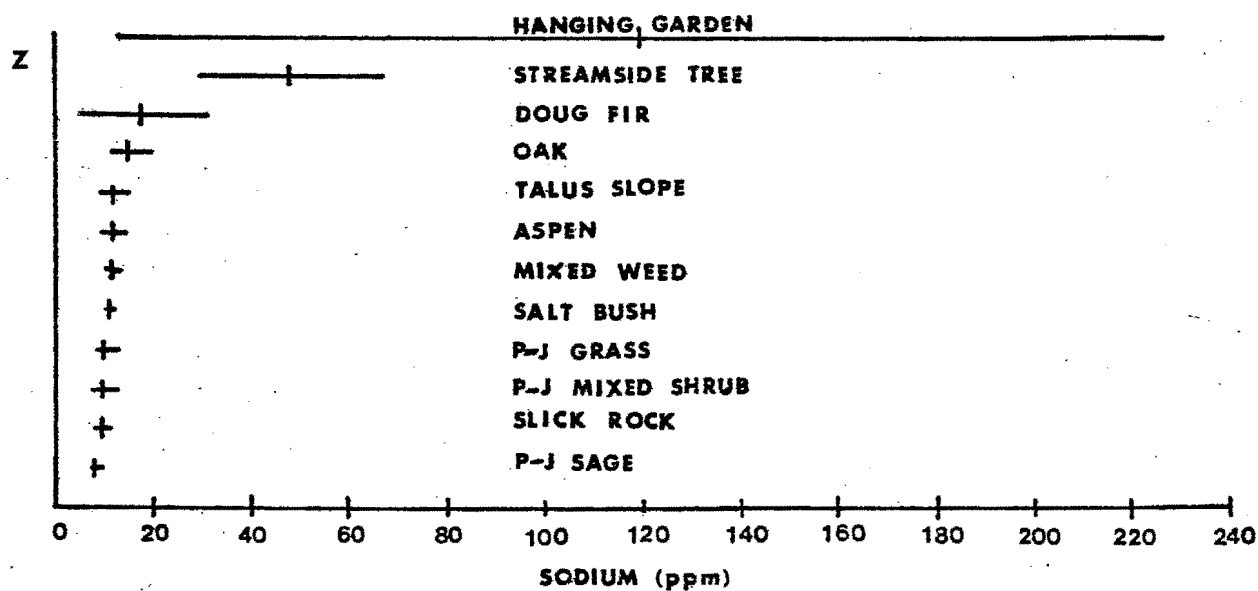
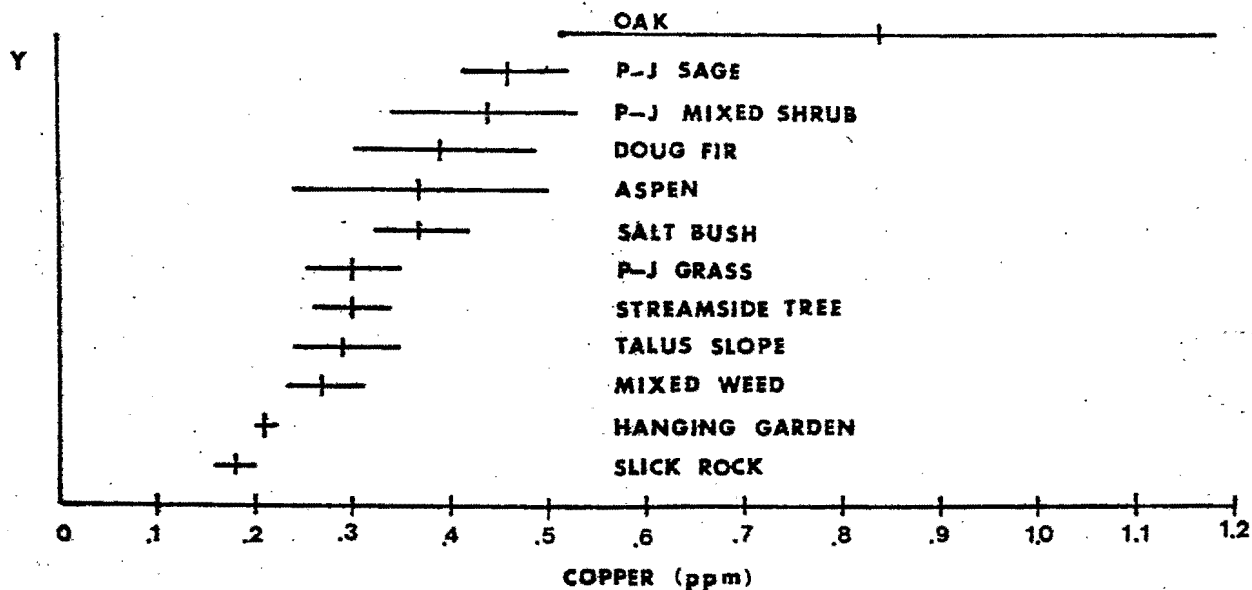


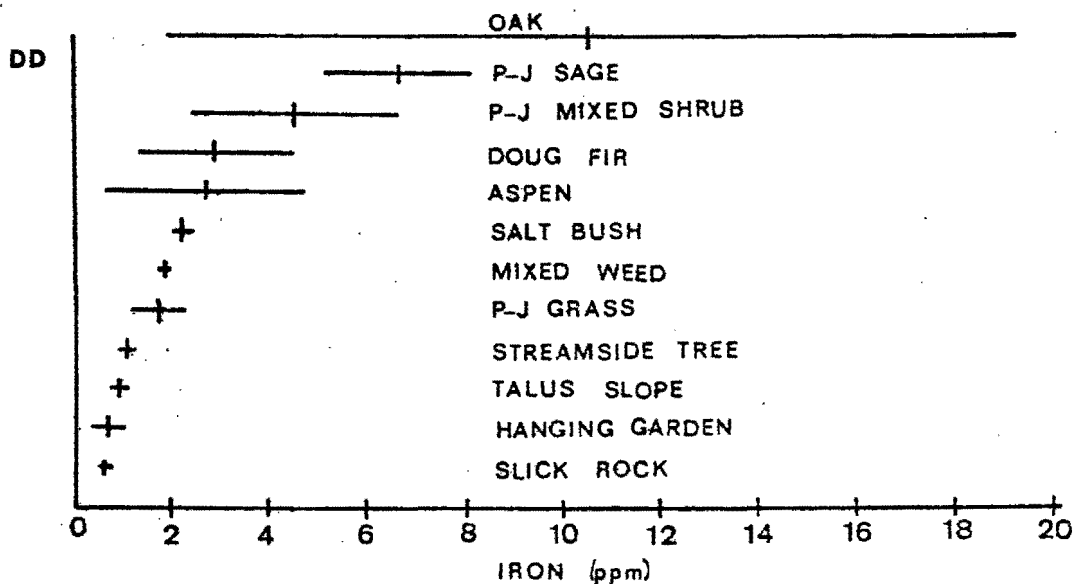
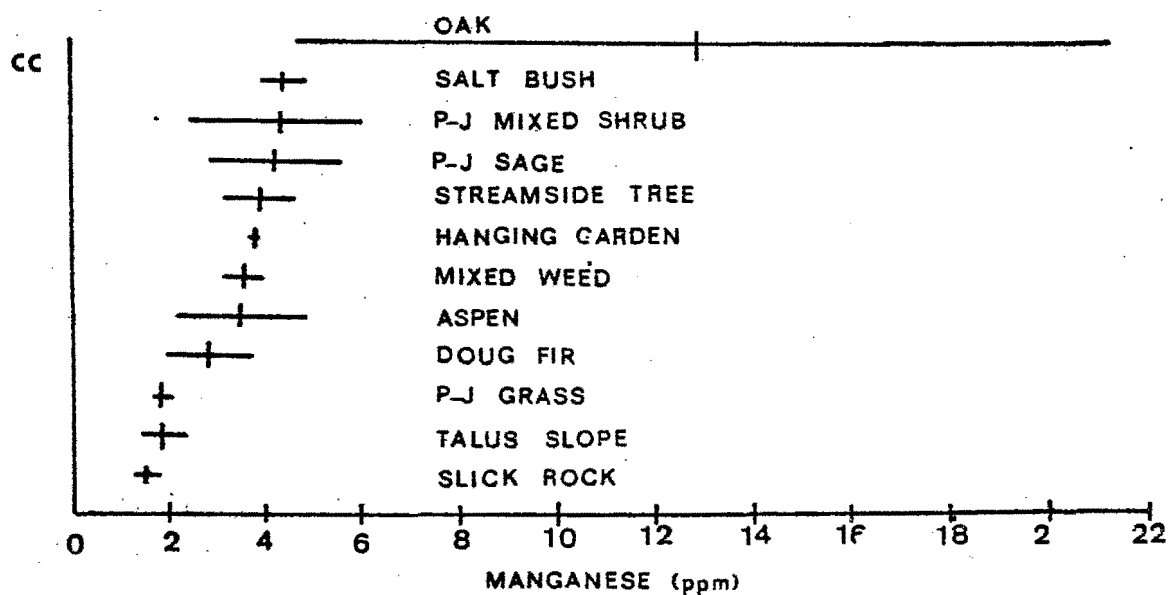
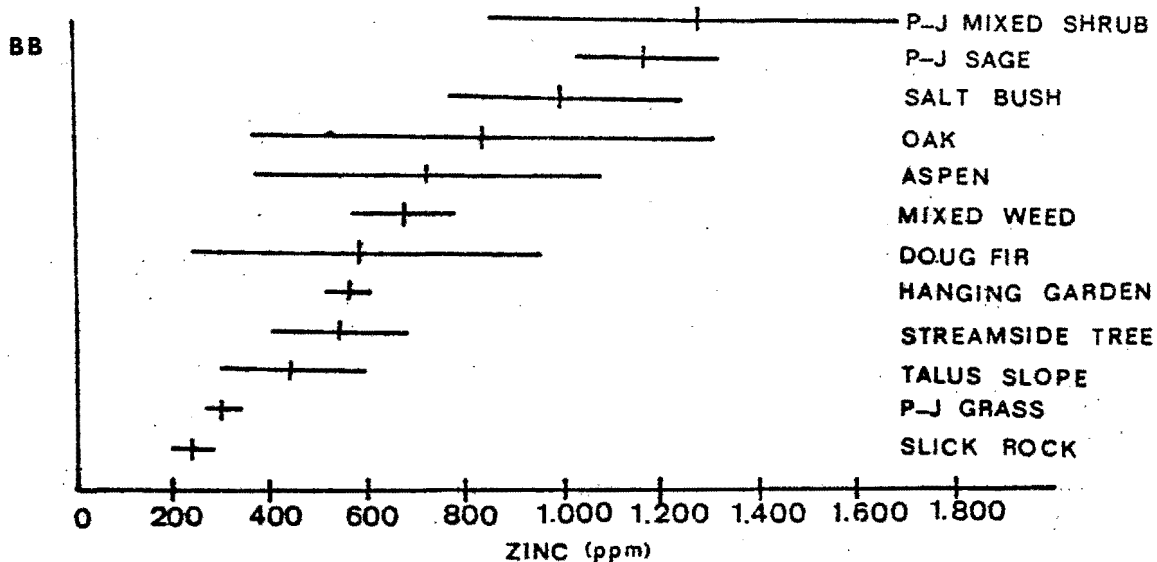


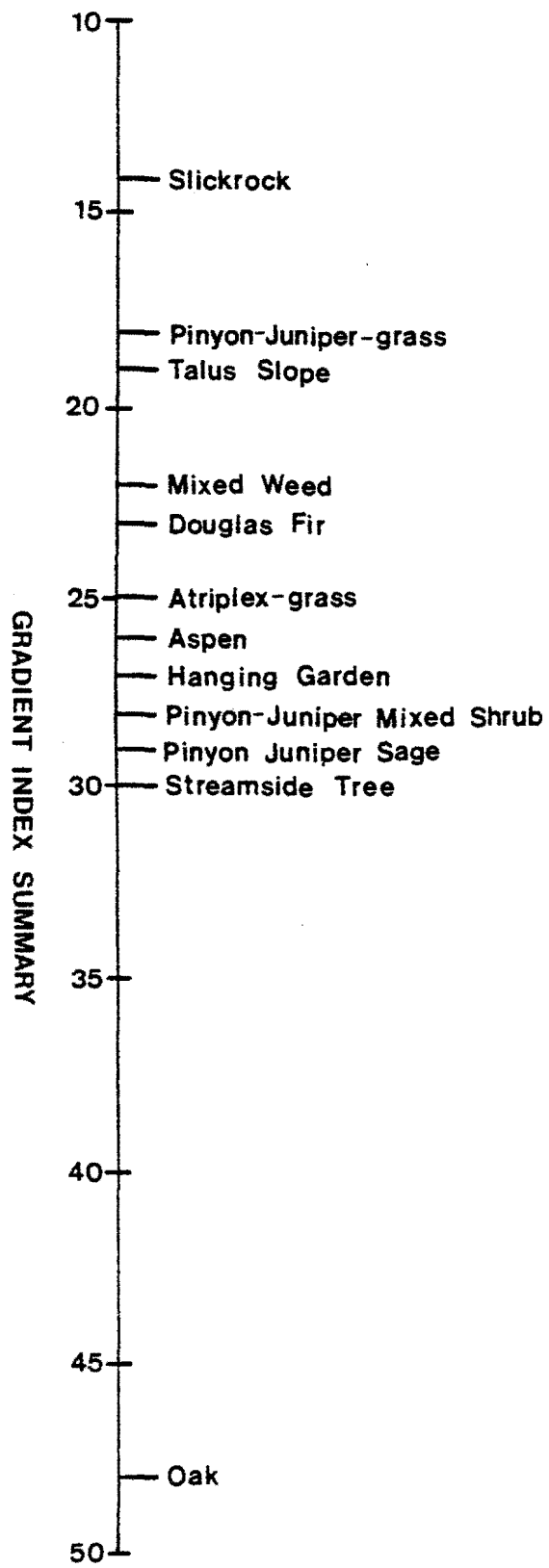












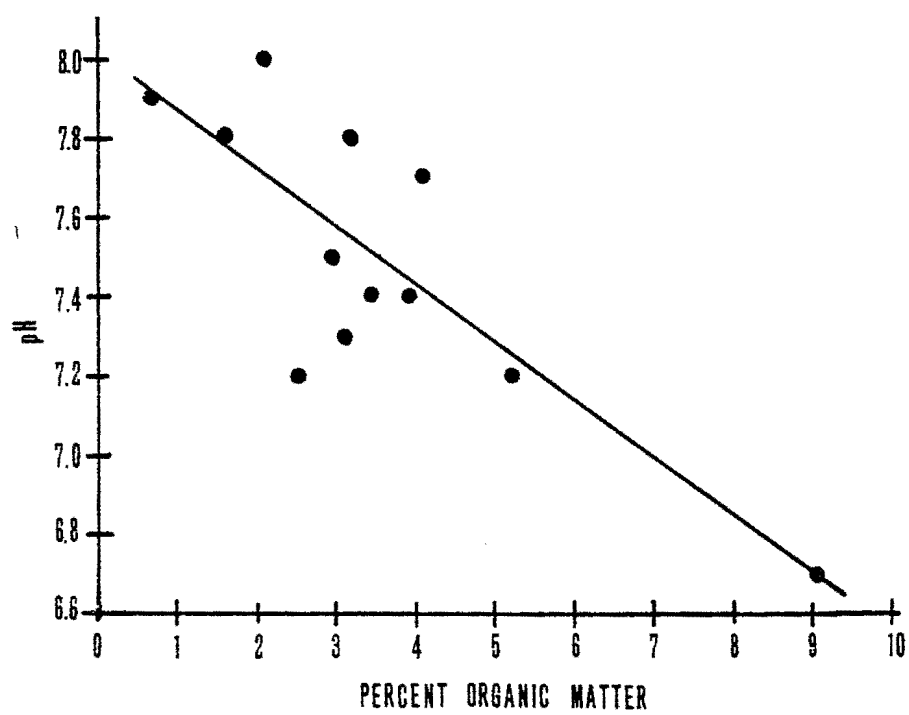


Table 1. Vegetative communities encountered within the boundaries of Navajo National Monument and the segments within which they occur.

Vegetation Type	Monument Segment		
	Betatakin	Keet Seel	Inscription House
Pinyon-Juniper-Sage	X		
Pinyon-Juniper-Grass	X		
Aspen	X	X	
Douglas Fir	X	X	
Hanging Garden	X	X	
Oak	X	X	X
Pinyon-Juniper-Mixed Shrubs	X	X	X
Mixed Weed		X	
Talus Slope		X	X
Atriplex-Grass		X	X
Slickrock-Scattered Shrub		X	X
Streamside Tree			X

Table 2. Prevalent species lists for the twelve vegetative communities of Navajo National Monument. Numbers represent species importance values in average percent cover.

Species	Importance Value
Talus Slope	
<i>Atriplex canescens</i>	4.6
<i>Bouteloua gracilis</i>	2.9
<i>Sporobolus cryptandrus</i>	2.8
<i>Poa longiligula</i>	1.6
<i>Oryzopsis hymenoides</i>	1.6
<i>Psilostrophe sparsiflora</i>	1.4
<i>Artemisia nova</i>	1.4
<i>Opuntia erinacea</i>	1.2
<i>Yucca angustissima</i>	1.0
<i>Pinus edulis</i>	1.0
<i>Bouteloua curtipendula</i>	0.9
<i>Xanthocephalum sarothrae</i>	0.9
<i>Aristida fendleriana</i>	0.8
<i>Bromus tectorum</i>	0.4
<i>Heterotheca villosa</i>	0.4
Atriplex-Grass	
<i>Atriplex canescens</i>	8.8
<i>Oryzopsis hymenoides</i>	2.7
<i>Bouteloua gracilis</i>	1.9

Table 2. Continued

<i>Quercus gambelii</i>	1.8
<i>Chrysothamnus viscidiflorus</i>	1.7
<i>Poa longiligula</i>	1.3
<i>Bromus tectorum</i>	1.1
Pinyon-Juniper-Grass	
<i>Bouteloua gracilis</i>	14.3
<i>Stipa comata</i>	7.5
<i>Artemisia tridentata</i>	7.4
<i>Poa longiligula</i>	6.1
<i>Juniperus utahensis</i>	4.9
<i>Muhlenbergia pungens</i>	2.8
<i>Oryzopsis hymenoides</i>	2.0
<i>Gilia leptomeria</i>	1.9
<i>Artemisia frigida</i>	1.7
<i>Haplopappus nuttallii</i>	1.5
<i>Eriogonum umbellatum</i>	1.5
<i>Atriplex canescens</i>	1.3
<i>Lesquerella rectipes</i>	1.3
<i>Tradescantia occidentalis</i>	1.2
<i>Eriogonum microthecum</i>	1.1
<i>Opuntia polyacantha</i>	1.1
<i>Machaeranthera grindelioides</i>	0.9
<i>Erigeron divergens</i>	0.9
<i>Ephedra viridis</i>	0.7
<i>Penstemon eatoni</i>	0.6

Table 2. Continued

Slickrock	
<i>Bouteloua gracilis</i>	12.8
<i>Oryzopsis hymenoides</i>	9.6
<i>Ephedra viridis</i>	5.8
<i>Cercocarpus intricatus</i>	4.4
<i>Xanthocephalum sarothrae</i>	3.0
<i>Yucca angustissima</i>	2.9
<i>Vulpia octoflora</i>	2.7
<i>Opuntia polyacantha</i>	2.4
<i>Muhlenbergia pungens</i>	2.3
<i>Artemisia frigida</i>	1.9
<i>Streptanthella longirostris</i>	1.7
<i>Artemisia nova</i>	1.3
<i>Sidalcea neomexicana</i>	1.1
<i>Juniperus utahensis</i>	1.0
<i>Stipa comata</i>	1.0
<i>Eriogonum microthecum</i>	0.9
<i>Arenaria eastwoodiae</i>	0.8
<i>Astragalus convallarius</i>	0.8
<i>Psilostrophe sparsiflora</i>	0.7
<i>Townsendia incana</i>	0.3
Pinyon-Juniper-Mixed Shrub	
<i>Cercocarpus intricatus</i>	6.3
<i>Pinus edulis</i>	5.0
<i>Cowania mexicana</i>	4.2

<i>Fendlera rupicola</i>	4.2
<i>Juniperus utahensis</i>	3.1
<i>Poa longiligula</i>	2.9
<i>Bouteloua gracilis</i>	1.9
<i>Shepherdia rotundifolia</i>	1.8
<i>Leptodactylon pungens</i>	0.9
<i>Xanthocephalum sarothrae</i>	0.6
<i>Ephedra viridis</i>	0.4
<i>Artemisia tridentata</i>	0.3
<i>Arenaria eastwoodiae</i>	0.3
<i>Echinocereus fendleri</i>	0.3
<i>Oryzopsis hymenoides</i>	0.3
Pinyon-Juniper-Sage	
<i>Pinus edulis</i>	14.3
<i>Artemisia tridentata</i>	7.3
<i>Juniperus utahensis</i>	3.6
<i>Bouteloua gracilis</i>	2.1
<i>Poa longiligula</i>	0.8
<i>Artemisia nova</i>	0.8
<i>Oryzopsis hymenoides</i>	0.5
<i>Fendlera rupicola</i>	0.4
<i>Sporobolus cryptandrus</i>	0.4
<i>Gilia aggregata</i>	0.2
Douglas Fir	
<i>Pseudotsuga menziesii</i>	17.8
<i>Poa longiligula</i>	12.3

<i>Pinus edulis</i>	5.0
<i>Quercus gambelii</i>	4.9
Moss	3.0
<i>Symphoricarpos vaccinioides</i>	2.8
<i>Arenosus</i>	2.7
<i>Juniperus utahensis</i>	1.9
<i>Artemisia ludoviciana</i>	1.4
<i>Fendlera rupicola</i>	1.3
<i>Oryzopsis hymenoides</i>	1.1
<i>Shepherdia rotundifolia</i>	1.1
<i>Ribes viscosissimum</i>	1.0
<i>Astragalus sesquiflorus</i>	0.7
Oak	
<i>Quercus gambelii</i>	43.3
<i>Symphoricarpos vaccinioides</i>	12.6
<i>Bromus tectorum</i>	5.7
<i>Mahonia repens</i>	4.2
<i>Smilacina stellata</i>	3.2
<i>Thalictrum fendleri</i>	3.1
<i>Clematis ligusticifolia</i>	2.7
<i>Oryzopsis micrantha</i>	1.6
<i>Silene menziesii</i>	1.4
<i>Ribes viscosissimum</i>	0.9
Aspen	
<i>Populus tremuloides</i>	44.5
<i>Betula occidentalis</i>	26.0

Table 2. Continued

<i>Cornus stolonifera</i>	24.2
<i>Equisetum hyemale</i>	19.7
<i>Acer negundo</i>	6.6
<i>Symphoricarpos vaccinioides</i>	5.3
<i>Clematis ligusticifolia</i>	3.5
<i>Smilacina stellata</i>	2.7
<i>Thalictrum fendleri</i>	2.2
<i>Mahonia repens</i>	1.7
<i>Rosa woodsii</i>	1.1
Mixed Weed	
<i>Salsola iberica</i>	48.7
<i>Bromus tectorum</i>	13.1
<i>Sisymbrium altissimum</i>	12.3
<i>Cleome serrulata</i>	5.2
<i>Epilobium hornemani</i>	3.5
<i>Lappula redowskii</i>	1.4
<i>Ribes viscosissimum</i>	0.6
<i>Chenopodium fremontii</i>	0.6
Hanging Garden	
<i>Mimulus eastwoodiae</i>	47.8
<i>Aquilegia micrantha</i>	25.3
<i>Mentzelia albicaulis</i>	7.9
<i>Galium aparine</i>	3.9
<i>Smilacina racemosa</i>	2.5
<i>Toxicodendron radicans</i>	2.5
<i>Habenaria sparsiflora</i>	1.2

Table 3. Indices of similarity as computed for each community relative to all other communities. Values were computed from average cover of species found in each community.

Community Type	Talus Slope	Atriplex Grass	P-J-Grass	Slickrock	P-J-Mixed Shrub	P-J-Sage	Douglas Fir	Oak	Aspen	Mixed Weed	Hanging Garden	Streamside Tree
Talus Slope	100											
Atriplex-grass	31	100										
P-J-Grass	12	11	100									
Slickrock	13	12	25	100								
P-J-Mixed Shrub	13	8	10	10	100							
P-J-Sage	11	6	17	5	22	100						
Douglas Fir	5	5	8	2	16	10	100					
Oak	0	3	0	0	0	0	7	100				
Aspen	0	0	0	0	0	0	2	8	100			
Mixed Weed	0	1	0	1	0	0	1	4	0	100		
Hanging Garden	0	1	0	0	0	0	1	1	0	0	100	
Streamside Tree	0	0	0	0	0	0	0	0	0	0	0	100

Table 4. Community characteristics (biotic and abiotic) of each vegetation type: means and standard deviations.

Community Type	Talus Slope	Atriplex Grass	P-J-Grass	Slickrock	P-J-Mixed Shrub	P-J-Sage	Douglas Fir	Oak	Aspen	Mixed Weed	Hanging Garden	Streamside Tree
<u>Biotic Factors</u>												
Percent living cover	19.8 +10.8	12.4 + 9.9	42.1 +38.1	51.6 + 4.0	15.4 +6.2	57.4 +16.7	25.8 +11.9	26.2 +24.0	11.7 +13.9	66.8 +34.6	86.0 + 4.1	0.5 +0.8
Percent tree cover	0.0 +0.0	0.0 +0.0	5.7 +6.2	1.3 + 2.3	0.0 +0.0	64.3 +18.1	1.0 + 1.9	0.0 + 0.0	24.9 +24.8	0.0 + 0.0	2.9 + 4.1	0.0 +0.0
Percent shrub cover	17.4 +3.3	39.1 +25.5	19.7 +17.4	33.3 +10.4	26.3 +16.6	22.3 + 8.3	18.8 +17.1	36.1 +36.7	25.7 +20.6	1.0 + 1.7	2.8 + 2.1	1.8 +2.9
Percent grass cover	41.9 +12.8	16.9 +8.2	52.1 +18.9	33.0 +6.0	36.5 +1.5	13.3 +11.9	47.8 +20.8	3.2 + 4.0	1.7 + 3.2	8.5 + 9.3	3.5 + 4.9	0.0 +0.0
Percent forb cover	21.2 + 4.9	4.5 +8.8	13.8 + 2.7	9.4 +2.5	13.7 +2.2	1.2 + 1.3	23.5 +18.1	5.4 + 6.1	34.8 +25.0	58.2 +50.7	74.1 + 9.9	0.0 +0.0
Percent annual cover	1.7 + 2.4	31.5 +28.3	0.0 + 0.0	3.1 +2.4	0.0 +0.0	0.0 + 0.0	0.1 + 0.2	13.8 +29.1	0.0 + 0.0	32.3 +56.0	0.0 + 0.0	6.6 +11.6
Percent cryptogam cover	0.7 +1.0	0.1 +0.2	12.1 +15.3	5.1 +3.2	5.5 +3.3	6.6 + 5.9	0.5 + 0.7	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0	22.1 +13.8	0.0 +0.0
Diversity	6.0 +1.5	3.2 +1.4	7.0 + 1.9	8.2 +1.5	2.6 +1.2	2.3 + 1.0	3.8 + 1.3	2.8 + 0.8	3.6 + 0.7	2.5 + 0.6	2.1 + 1.0	1.4 +0.5
Mean # of species/stand	14.8 +4.9	6.5 +1.9	20.3 + 2.5	19.8 +5.4	14.9 +2.9	8.6 + 3.0	13.3 + 0.7	10.8 + 4.3	11.3 + 2.7	7.7 + 1.5	7.0 + 2.8	3.3 +3.2

Gross Habitat Factors

Soil depth (cm)	49.4 +31.0	51.7 +8.3	54.2 +19.3	33.7 +11.5	20.8 +7.2	32.4 +12.9	47.9 +13.6	77.9 +21.3	37.5 +51.7	66.6 +57.7	9.3 +5.5	33.3 +57.7
Aspect	0.7 +0.9	0.9 +0.1	0.7 + 1.0	0.2 + 0.3	1.6 +0.4	1.1 +0.6	1.0 + 0.5	1.4 + 0.7	1.2 + 0.8	0.7 + 0.7	0.2 +0.2	1.0 + 0.9
Percent slope	24.2 +10.6	39.1 +8.6	20.0 +22.9	18.3 +11.6	28.0 +14.1	7.9 +7.0	30.6 + 2.7	12.6 + 4.7	10.0 +10.8	5.3 + 4.6	85.0 +7.1	23.0 + 5.3
Percent litter cover	6.1 +1.8	11.4 +6.8	7.0 +5.4	4.7 +3.4	25.9 + 8.8	36.1 +20.4	33.6 +17.6	91.3 + 9.4	70.8 +18.3	16.4 +7.6	9.3 +11.8	34.0 +4.9
Percent rock cover	38.1 +16.9	16.9 +5.2	10.1 +17.5	0.3 +0.5	15.7 +14.9	0.9 + 1.2	22.0 +12.6	0.1 + 0.3	0.6 + 1.6	0.0 +0.0	13.1 +0.3	0.0 +0.0
Percent bare ground	34.1 +14.3	47.7 +10.9	33.5 +12.3	21.0 +6.9	30.8 +15.1	43.3 +16.6	20.2 +14.7	0.8 +1.5	3.6 +3.2	21.3 +22.1	0.0 +0.0	64.5 +7.0

Soil Factors

Percent sand	85.6 +1.8	85.3 +1.7	81.7 +8.4	89.3 +0.6	83.0 + 3.6	83.6 +2.5	83.5 +3.8	76.1 +3.8	83.9 +5.3	84.7 +1.5	83.5 +0.7	85.0 +1.7
Percent silt	7.2 +1.9	8.9 +1.1	9.3 +4.9	4.0 +0.0	12.1 + 2.8	11.4 +2.3	9.9 +3.0	14.4 +2.9	10.4 +4.3	9.0 +1.7	9.0 +0.0	6.0 +1.0
Percent clay	7.2 +0.8	6.2 +0.8	8.7 +3.8	7.0 +0.0	4.9 +1.0	5.0 +0.8	6.6 +1.1	9.7 +2.0	5.9 +1.6	6.3 +0.6	7.5 +0.7	9.7 +1.2
Percent fines	14.4 +1.8	15.1 +1.8	18.0 +8.7	11.0 +0.0	17.0 +3.6	16.4 +2.5	16.5 +3.8	24.1 +4.0	16.3 +5.5	15.3 +1.5	16.5 +0.7	15.7 +1.5
pH	7.8 + .1	7.9 +0.1	7.3 +0.3	7.8 +0.1	7.4 +0.2	7.2 +0.2	7.4 +0.3	6.7 +0.4	7.2 +0.2	7.5 +0.1	7.7 +0.1	8.0 +0.2
Soluble salts	274.4 +33.6	236.7 +68.1	205.0 +129.7	201.0 +13.8	197.8 +52.2	136.1 +36.3	233.9 +47.5	376.9 +75.2	286.0 +74.8	349.7 +176.1	517.0 +281.4	568.3 +171.7

Percent organic matter	3.2 <u>+0.7</u>	0.7 <u>+0.2</u>	3.1 <u>+2.2</u>	1.6 <u>+0.5</u>	3.9 <u>+1.3</u>	2.5 <u>+1.4</u>	3.4 <u>+1.6</u>	9.1 <u>+3.8</u>	5.2 <u>+4.1</u>	2.9 <u>+1.1</u>	4.1 <u>+1.1</u>	2.1 <u>+0.4</u>
Nitrogen (ppm)	0.04 <u>+0.01</u>	0.03 <u>+0.01</u>	0.03 <u>+0.01</u>	0.02 <u>+0.01</u>	0.05 <u>+0.02</u>	0.05 <u>+0.01</u>	0.05 <u>+0.02</u>	0.20 <u>+0.08</u>	0.10 <u>+0.08</u>	0.06 <u>+0.01</u>	0.04 <u>+0.02</u>	0.04 <u>+0.01</u>
Phosphorus (ppm)	12.0 <u>+2.9</u>	9.5 <u>+2.0</u>	9.3 <u>+1.2</u>	9.6 <u>+1.2</u>	8.2 <u>+4.1</u>	5.5 <u>+1.1</u>	11.6 <u>+3.0</u>	23.4 <u>+6.7</u>	12.4 <u>+3.5</u>	15.9 <u>+2.0</u>	10.3 <u>+5.5</u>	13.4 <u>+1.0</u>
Calcium (ppm)	5708.6 <u>+2668.0</u>	3911.0 <u>+832.6</u>	3331.3 <u>+3563.5</u>	1729.7 <u>+57.6</u>	2674.9 <u>+1515.3</u>	1627.5 <u>+310.3</u>	3027.8 <u>+1428.2</u>	4334.7 <u>+1245.4</u>	3588.0 <u>+1953.8</u>	2336.3 <u>+615.6</u>	8455.0 <u>+264.5</u>	5650.7 <u>+925.7</u>
Magnesium (ppm)	120.0 <u>+45.5</u>	412.6 <u>+61.3</u>	100.0 <u>+39.9</u>	55.3 <u>+6.4</u>	526.6 <u>+124.4</u>	645.6 <u>+33.5</u>	83.3 <u>+36.6</u>	226.4 <u>+70.3</u>	108.9 <u>+84.1</u>	86.7 <u>+6.7</u>	184.0 <u>+0.0</u>	272.0 <u>+72.0</u>
Potassium (ppm)	170.0 <u>+69.2</u>	280.1 <u>+115.7</u>	128.3 <u>+44.8</u>	63.3 <u>+7.6</u>	102.1 <u>+30.4</u>	88.4 <u>+16.7</u>	121.9 <u>+44.8</u>	272.5 <u>+105.1</u>	181.3 <u>+68.9</u>	303.3 <u>+75.2</u>	152.5 <u>+116.7</u>	710.0 <u>+208.0</u>
Sodium (ppm)	12.1 <u>+3.4</u>	10.8 <u>+0.9</u>	10.3 <u>+2.8</u>	9.7 <u>+1.4</u>	9.8 <u>+3.0</u>	9.1 <u>+0.6</u>	18.0 <u>+13.1</u>	14.7 <u>+4.2</u>	12.1 <u>+2.7</u>	12.0 <u>+1.3</u>	118.8 <u>+107.1</u>	48.0 <u>+19.0</u>
Iron (ppm)	1.0 <u>+0.3</u>	2.3 <u>+0.2</u>	1.8 <u>+0.5</u>	0.7 <u>+0.1</u>	4.6 <u>+2.1</u>	6.7 <u>+1.5</u>	3.0 <u>+1.6</u>	10.6 <u>+8.7</u>	2.8 <u>+2.1</u>	2.0 <u>+0.1</u>	0.8 <u>+0.4</u>	1.2 <u>+0.2</u>
Manganese (ppm)	1.9 <u>+0.5</u>	4.4 <u>+0.5</u>	1.9 <u>+0.2</u>	1.6 <u>+0.2</u>	4.3 <u>+1.8</u>	4.2 <u>+1.3</u>	2.9 <u>+0.9</u>	12.9 <u>+8.4</u>	3.5 <u>+1.4</u>	3.6 <u>+0.4</u>	3.8 <u>+0.1</u>	3.9 <u>+0.7</u>
Zinc (ppm)	0.4 <u>+0.2</u>	1.0 <u>+0.2</u>	0.3 <u>+0.1</u>	0.2 <u>+0.1</u>	1.3 <u>+0.4</u>	1.2 <u>+0.2</u>	0.6 <u>+0.4</u>	0.8 <u>+0.5</u>	0.7 <u>+0.4</u>	0.8 <u>+0.1</u>	0.6 <u>+0.1</u>	0.5 <u>+0.1</u>
Copper (ppm)	0.3 <u>+0.1</u>	0.4 <u>+0.1</u>	0.3 <u>+0.1</u>	0.2 <u>+0.0</u>	0.4 <u>+0.1</u>	0.5 <u>+0.1</u>	0.4 <u>+0.1</u>	0.8 <u>+0.3</u>	0.4 <u>+0.1</u>	0.3 <u>+0.1</u>	0.2 <u>+0.0</u>	0.3 <u>+0.1</u>

Table 5. Mean concentrations of minerals in Navajo Sandstone parent material along with indicated deviations from these concentrations in the plant communities. Soils derived from the parent material.

Mineral	Mean ^a	Number of Communities	
	Concentration in	with Mean Concentration	
	Parent Material	Less than	Greater than
	(ppm)	Parent Material	Parent Material
Zn	1.54	12	0
Na	23.0	10	2
Ca	4631.0	9	3
K	111.0	3	9
Mg	53.0	0	12
Fe	.54	0	12
Cu	.14	0	12
Mn	.69	0	12
P	3.6	0	12
N	Trace	0	12

a. Mean concentrations based on two samples.

Table 6. Plant community ratings relative to specific gradients and index indicating overall position with respect to all gradients.

Community type												Soluble		Index
	Ca	Mg	P	N	Zn	Mn	Fe	Cu	Na	K	pH	Salts	O.M.	
Slickrock	1	1	2	1	1	1	1	1	1	1	1	1	1	14
Pinyon-Juniper-Grass	2	1	2	1	1	1	1	1	1	1	3	1	2	18
Talus Slope	3	1	2	1	2	1	1	1	1	1	1	2	2	19
Mixed Weed	1	1	3	1	3	1	1	1	1	2	2	3	2	22
Douglas Fir	2	1	2	1	2	1	2	2	1	1	3	2	2	23
Atriplex-Grass	2	4	2	1	4	2	1	2	1	2	1	2	1	25
Aspen	2	1	2	3	3	1	2	2	1	1	3	2	3	26
Hanging Garden	5	2	2	1	2	1	1	1	5	1	2	5	3	27
Pinyon-Juniper-Mixed Shrub	1	5	1	1	5	2	2	2	1	1	2	1	2	28
Pinyon-Juniper-Sage	1	5	1	1	5	2	4	3	1	1	3	1	1	29
Streamside Tree	3	2	3	1	2	2	1	1	3	5	1	5	2	30
Oak	2	2	5	5	3	5	5	5	1	2	5	3	5	48

Table 7. Significance levels for correlations of the environmental factors (biotic and abiotic) measured in all stands studied. The number 1 indicates the 0.001 level of significance and the number 2 indicates the 0.01 level of significance.

Factors	Factors																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Percent sand	#																					
2. Percent silt	-1	#																				
3. Percent fines	-1	1	#																			
4. pH	1	-1	-2	#																		
5. Soluble salts					#																	
6. Percent organic matter	-1	2	1	-1		#																
7. Phosphorus					2	2	#															
8. Nitrogen	-1	2	1	-2		1	1	#														
9. Zinc									#													
10. Manganese	-1	2	1			2	2	1		#												
11. Iron	-2	1	2	-1		2		1		1	#											
12. Copper	-1	1	1			2		1		1	1	#										
13. Sodium					2								#									
14. Potassium														1	#							

15. Calcium									2	#
16. Magnesium								1		#
17. Soil depth				2						- #
18. Aspect		2				2		2		2 #
19. Percent litter cover	-2		2	-2		2		1	2	2 1 #
20. Percent total living cover									-1	-2 #
21. Percent grass cover									2	#
22. Diversity										2 #
23. Percent bare ground					-2					#

Bird Species Diversity in Relation to Habitat and Season in Betatakin
Canyon, Navajo National Monument, Arizona¹

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INTRODUCTION

The effect of habitat diversity and seasonal change on bird species diversity have been extensively documented in the ecological literature (MacArthur and MacArthur 1961, Willson 1974, Karr and Roth 1971, Roth 1977). Two of the most commonly investigated components of habitat diversity are foliage height diversity and plant species composition (MacArthur and MacArthur 1961). Willson (1974) demonstrated that as the forest canopy becomes increasingly stratified, additional foraging guilds (bird groups of similar foraging habitat and behavior) are able to invade, thus increasing bird species diversity. The interrelationship between bird species diversity, foliage height, and vegetational complexity has been explored by a number of researchers (Roth 1977, Cody 1974, Johnsgard and Rickard 1957, Johnson 1975, Whitmore 1975 and 1977, Yeaton 1974, Johnston and Odum 1956, Karr 1968 and 1976, Karr and Roth 1971).

There are some habitats, however, where foliage height diversity alone is not a reliable predictor of bird species diversity. MacArthur and MacArthur (1961) suggested that birds living in desert scrub might require more than foliage height differences to partition their environment. This was subsequently confirmed by Tomoff (1974), who found that plant species composition was the best determinant of bird species diversity in desert scrublands. He suggested that the extreme diversity in growth forms of desert plants would provide greater habitat variability than would differences in mature plant height.

STUDY SITE

Navajo National Monument is located in northeastern Arizona about 16 km north and west of Black Mesa and Arizona Highway 160. The principle sites of the Monument are three large Anasazi Indian cliff dwellings located in three separate canyons. Betatakin Canyon belongs to the Tsegi Canyon complex, which has been described by several authors (Gregory 1916 and 1917, Hack 1942 and 1945, Harshbarger et al. 1957, Cooley 1958 and 1962).

The major geological formation within Betatakin Canyon is the Navajo Sandstone, which forms tall, sheer cliffs towering more than 200 m above the canyon floor. The floor itself consists of deep alluvial deposits of sandy Quaternary fill, overlain by talus at the base of the cliffs. The Kayenta Sandstone formation outcrops beneath the Navajo and is occasionally seen in the lower reaches of the canyon.

The annual temperature recorded at Park headquarters within the Monument ranges from -23°C to 38°C with mean of 10°C . The number of frost-free days during the year extends from 107 to 213, with an average of 155 days. Total annual precipitation in Betatakin has historically ranged from 17 cm to 48 cm, with a yearly mean of 29 cm. There is a single wet season, lasting from late summer to early fall. Rainfall within the canyon is variable and spotty, with localized cloudbursts rather than large regional storms.

A mature pinyon-juniper community occurs on the mesa and slopes above the canyon and extends onto the exposed slickrock and walls which slope down to the canyon floor. Although pinyon pine (Pinus edulis) and

Utah juniper (Juniperus osteosperma), are consistently the dominant overstory species, there are 3 distinctive understory communities, dominated by big sagebrush (Artemisia tridentata), littleleaf mountain mahogany (Cercocarpus intricatus), and a mixed shrub zone consisting of cliffrose (Cowania mexicana), antelope bitterbrush (Purshia tridentata), cliff fendlerbush (Fendlera rupicola) and roundleaf buffaloberry (Shepherdia rotundifolia).

A riparian forest and associated trees are found on the canyon floor and along the tallus banks above the intermittently flowing stream. Many of the plant species found here are usually associated with high mountain habitats. The dominant species include quaking aspen (Populus tremuloides), boxelder (Acer negundo), water birch (Betula occidentalis), redozier dogwood (Cornus stolonifera), Gambel oak (Quercus gambelii) and Douglas fir (Pseudotsuga menziesii).

METHODS

Birds were censused during all four seasons of the year by the transect method (Emlen 1971 and 1977). For 1978, the sampling dates were 7-10 May, 8-10 July, 6-7 November and 19-21 February 1979. Sightings were noted as to plant community. During a separate spring and summer census from May through August of 1977, the perching site of each bird seen was also recorded. During this 1977 census, five rather than three sampling transects were used. Birds observed flying through the area were not included in the analyses, although such sightings are included in the species list for the Monument. Nomenclature follows the A.O.U. guidelines and subsequent revisions.

Distinctions between habitat types were made on the basis of vegetational differences. Standard diversity indices (H' , J') were calculated for the bird assemblages seasonally and within the different habitats (Pielou 1975). The diversity of a community depends on two things: the number of species present and the evenness with which the individuals of the species are scattered throughout the community (Kircher 1972). To describe a community's diversity only in terms of its diversity index (H') is to confound these two factors. A community with a few, evenly represented species can have the same diversity index as one with many, unevenly represented species. Therefore, we also calculated the equitability index, (J') which is designed to measure this evenness component (Lloyd and Ghelardi 1964).

Niche width and niche overlap values (Colwell and Futuyma 1971) were also calculated. Niche width is a measure of the breadth of utilization of the available resources (in this study, habitat types and seasons). Niche overlap measures the amount of mutual utilization of resources by two species.

Birds were clustered on niche overlap (Sneath and Sokal 1963) using as resource bases habitat type, individual perch site and seasonal occurrence. Additional cluster analyses were run to check the effects of seasonality and habitat using Ruzicka's (1958) similarity index, without respect to niche overlap.

RESULTS

One hundred thirty-five species of birds are known from Navajo National Monument (Appendix I). Sixty-six species were noted in Betatakin

Canyon during the 1978-1979 census, and 43 during the spring census of 1977. Of these 43, 10 were eliminated from our analyses due to insufficient habitat data.

The avifauna assemblages demonstrate definite habitat selection. Data from the spring and summer census of 1977 (Figure 1) show a clear separation of the bird fauna associated with the riparian and pinyon-juniper communities (2% similarity). Subzones of the riparian communities are distinguished as streambank habitats (aspen, boxelder, and some Gambel oak) and tallus slope habitats above the stream (aspen, gambel oak, and Douglas fir). The subzones of the pinyon-juniper communities are distinguished by their principle understory species (sagebrush, mountain mahogany and mixed shrubs). Later analyses lumped the subzones of the riparian community into one and those of the pinyon-juniper community into two by combining the P-J mahogany subzone with the P-J mixed shrub subzone.

The riparian and pinyon-juniper communities support highly distinct avifauna. From Table 1 we see that the riparian habitat supports nearly a third more species than the pinyon-juniper habitat. The total density of individuals in the riparian communities is about 60% greater than the mixed shrub zone. The number of species seems to be the major factor determining diversity in the avian community rather than the relative abundances of the species present.

Avian niche widths are similar during the spring and summer. Figure 2 is a graph of average niche overlaps against absolute niche width. Only those birds found exclusively in either the pinyon-juniper or riparian habitats were included in the figure. If we exclude the two outlying points (turkey vulture and Swainson's thrush, which were

observed only in the Douglas fir and on the ground), we find that habitat use, as deduced from the niche metrics, is similar in the two communities.

If we examine habitat use throughout the year, the pattern changes (Figure 3). The pinyon-juniper-sage and mixed-shrub zones remain similar, as expected, but riparian habitat use becomes much broader. Early spring migrants arriving before the riparian forest has greened out face limited resources and are therefore forced to forage widely. The deciduous nature of the forest also precludes specialization during the winter months when food resources become scarce.

Habitat Selection by Perch Site

The spring-summer census of 1977, which recorded specific perch sites, permits examination of tree use within and between habitats. We identified the nine most frequently chosen perches (those plant species with less than three sightings were excluded from analysis), and calculated diversity indices (Table 2) as described above. Excluding the Ground category, which is common to both communities, we see that the riparian habitat has 26% more bird species than the pinyon-juniper, the largest numbers of birds being found in pinyon pine and oak. The use of pinyon pine and oak by birds is not a factor of availability, as cover of mature pinyon pines and junipers is approximately equal in the P-J community, and cover of gambel oak and aspen is approximately equal in the riparian community. Furthermore, boxelder also makes a substantial contribution to the cover. The disproportionate use of pinyon and oak

is reflected in the high H' values and the lower J' values, suggesting that these tree species are used preferentially by many species throughout the spring and summer. This unequal use of pinyon pine and oak is likely due to greater availability of insects associated with these trees (Balda 1969) than with neighboring juniper or aspen (S. L. Wood, personal communication). In addition, greater foliage density in oak than in aspen may attract some birds.

Cluster analysis applied to the perching data taken in the 1977 census (Figure 4) exhibits general patterns similar to those shown in Figure 1 and confirms the distinction between bird communities in the riparian and pinyon-juniper habitats. It also permits separation of the subzones within these communities. Figure 5 shows a cluster by niche overlap of 33 bird species associated with the recorded perch sites. The cluster identified 9 major groups (for species identification relative to each group, see Table 3).

Seasonality

Numbers of both species and individuals increase during the spring and summer, with correspondingly high diversity values (Table 4). The avifaunal similarities also split according to spring-summer and fall-winter residents (13% similarity, Figure 6).

When examined seasonally by habitat type, the riparian fauna is also clearly distinct from the pinyon-juniper-sage and pinyon-juniper-mixed shrub fauna in both the spring-summer and fall-winter seasons (Figure 7). The two pinyon-juniper subzones are clearly distinguished only during the fall and winter months, becoming less so in spring, and showing high degrees of similarity (56%) during the summer.

Figure 8 shows a cluster of all sixty-six bird species according to season. The clustering identifies 6 major groups. For species identification relative to each group see Table 5.

Habitat Preference and Niche Overlap

Figure 9 is a cluster diagram of the niche overlaps of all sixty-six species, clustered according to both season and habitat. The clustering identifies 13 major groups. (For species identification relative to each group see Table 6). Birds restricted to the pinyon-juniper-sage and pinyon-juniper-mixed shrub habitats (habitats with the least apparent floristic diversity), and birds found in the canyon during the harsh winter months show the narrowest niches and the least overlap with other species. Those found in the riparian forest or during the spring and summer months have broader niches and show considerably greater niche overlaps (Figures 2, 3, and 10). Our data do not permit us to differentiate between birds that are better adapted to harsher, resource-poor habitats and those which are competitively excluded from other areas and subsisting on the extreme edge of their habitat tolerance.

Discussion

The avifauna of Betatakin Canyon, Navajo National Monument, constitute a highly diverse system, well adapted to the climate and vegetation of the canyon. Bird species diversity in Betatakin is regulated by plant species diversity, with unique avifaunal assemblages occurring in the deciduous riparian and evergreen scrub communities.

The birds of Betatakin are not randomly distributed throughout the canyon, but are specific to habitat and season. Habitat selectivity has long been known to occur between successional stages of forests, with entire suites of fauna replacing one another as a forest succeeds towards the climax stage (Johnston and Odum, 1956).

Tomoff (1974) demonstrated that plant species diversity and lifeform were the best predictors of bird species diversity in desert scrubland. Our data support this hypothesis. The data also suggest that the full range of plant species diversity in Betatakin is required to maintain the high diversity of bird species found there.

There are some theoretical anomalies worth considering, as they point out factors unique to the canyon. Figure 10 shows the average niche widths and the average niche overlaps of the birds, broken down into seasonal components. If we assume resource variability to peak in the spring and summer, and if abundant resources permit extensive resource partitioning, then both niche width and niche overlap should be smallest in the spring and summer.

Obviously, the exact opposite is occurring. Several factors may help to explain this. First of all, during the late fall and winter, the available food resources become localized in the dried fruits and seeds of the riparian forest, and in the limited remaining evergreen community. Regardless of actual abundance, this narrow resource spectrum would automatically generate mathematically small niche widths, although one might expect niche overlap to be greater than observed. The small niche overlap values obtained may be a result of the species pool dropping from 45 in the summer to 12 in the winter, a loss of over 75%. The low number of species present may allow resource partitioning despite the narrow resource spectrum.

Secondly, while the bird species pool is rapidly increasing in the early spring (up to 48), not all the vegetation has emerged by May, nor are insects yet very abundant. The strain upon available food resources should encourage broad niche widths and considerable niche overlap. As the summer fruits and leaves appear, resources increase, but so do the numbers of newly fledged young, and the niche widths drop only slightly. By the time of our fall census in November, the species pool is drastically reduced, and seeds are abundant, thus permitting resource partitioning to begin again. Thus, consideration of the biology of the system harmonizes the results of this study with general niche theory.

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- Figure 2 Graph of average niche overlap values against absolute niche width values from data taken in summer. Depicts only riparian species and pinyon-juniper species restricted to those zones.
- Figure 3 Graph of average niche overlap values against absolute niche width values from data taken throughout the year. Depicts values for birds restricted to any one of the three habitat types sampled: riparian, pinyon-juniper, and pinyon-juniper-mixed shrub.
- Figure 4 Dendrogram of the cluster analysis of perch site choice of bird species (Summer, 1977 data only).
- Figure 5 Dendrogram of the cluster analysis of 33 bird species by niche overlap from perch site data. For identification of bird species found in each group see Table 3.
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- Figure 9 Dendrogram of cluster analysis of 66 bird species by niche overlap habitat and seasonal data. For identification of bird species found in each group see Table 6.
- Figure 10 Histograms comparing average niche breadths and average niche overlaps of birds species by season.

Fig. 1

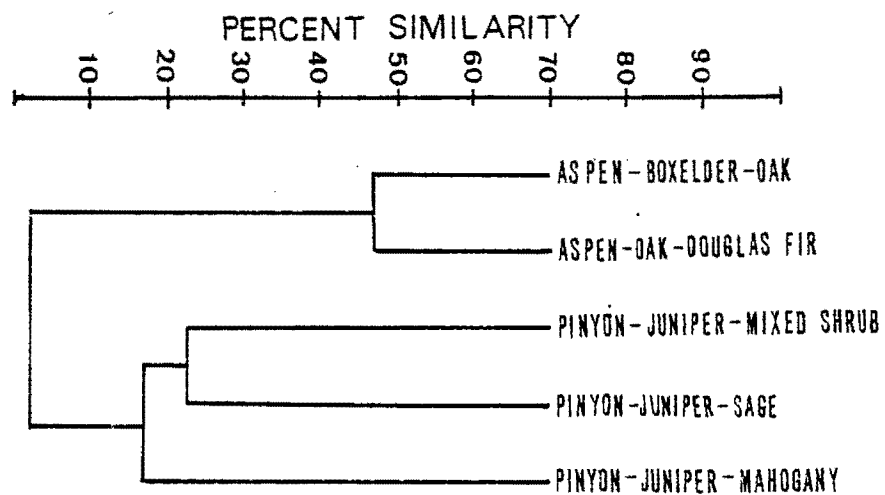
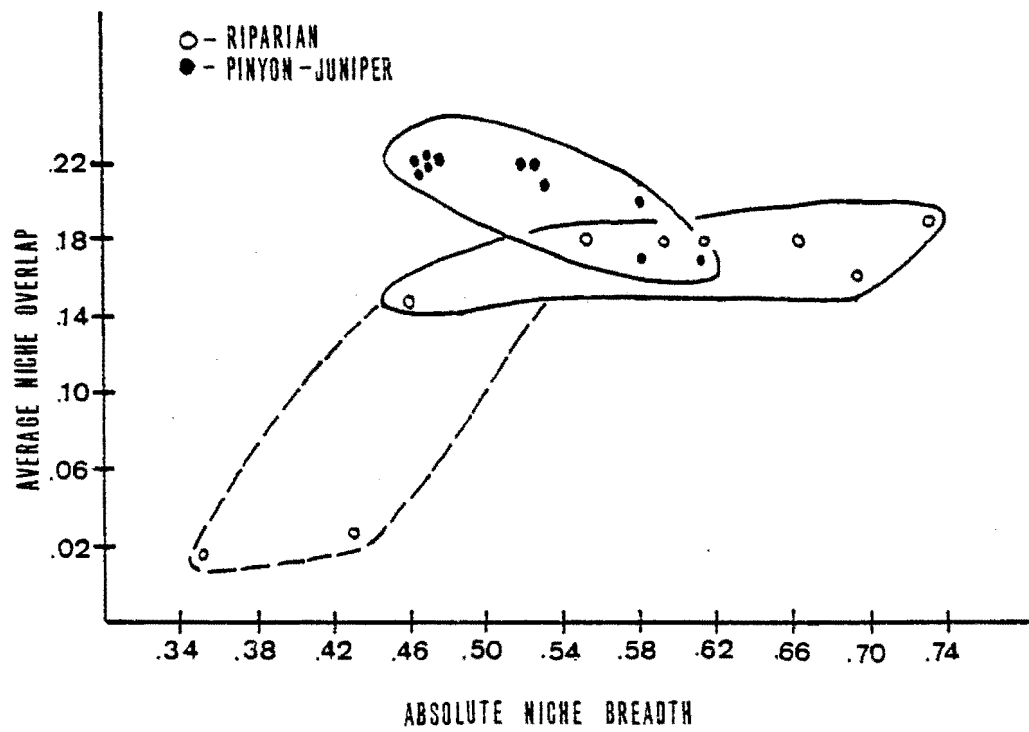


Fig. 2



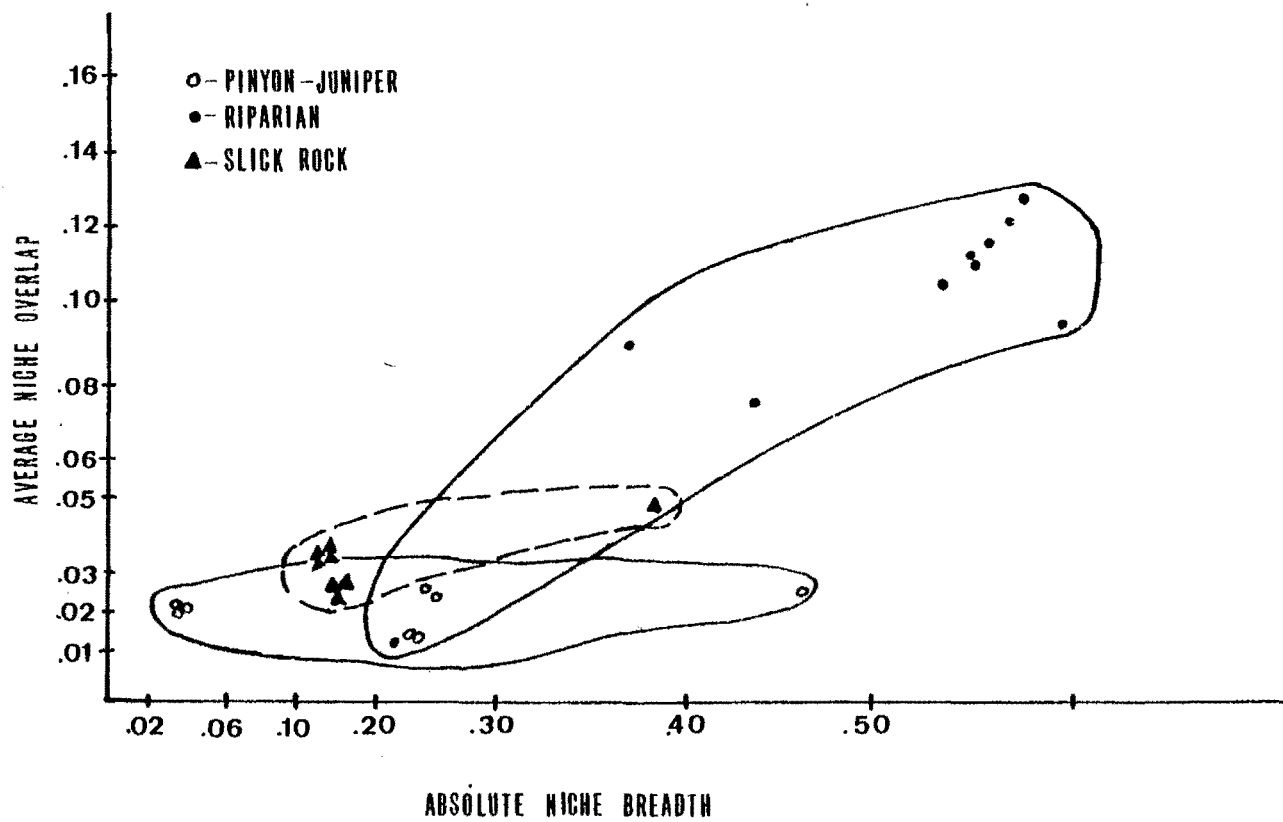
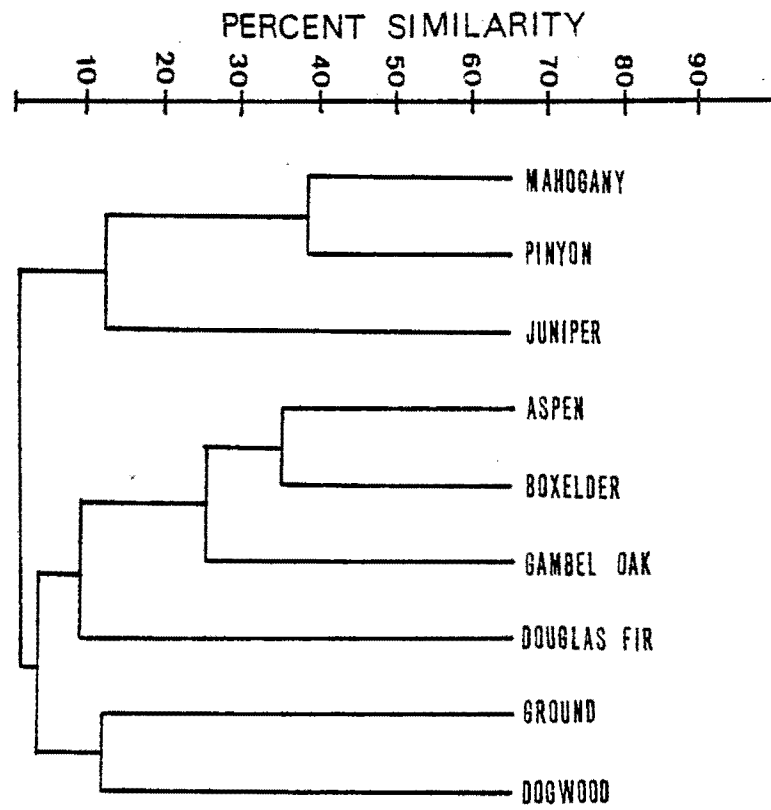


Fig. 3



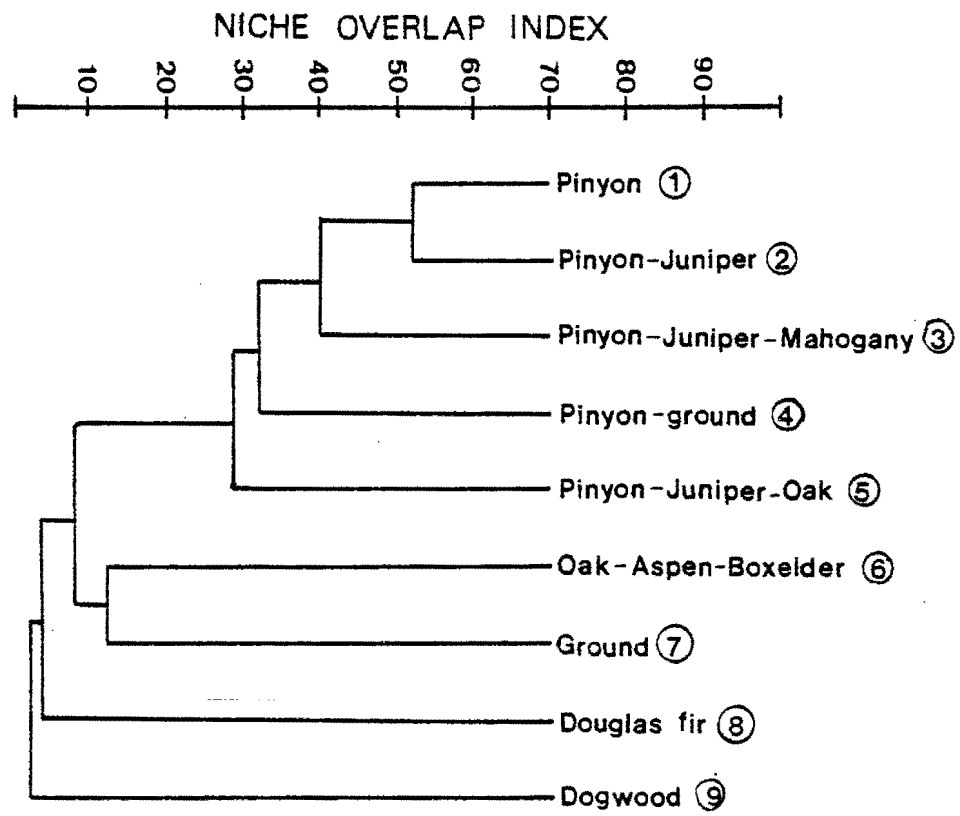


Fig. 6

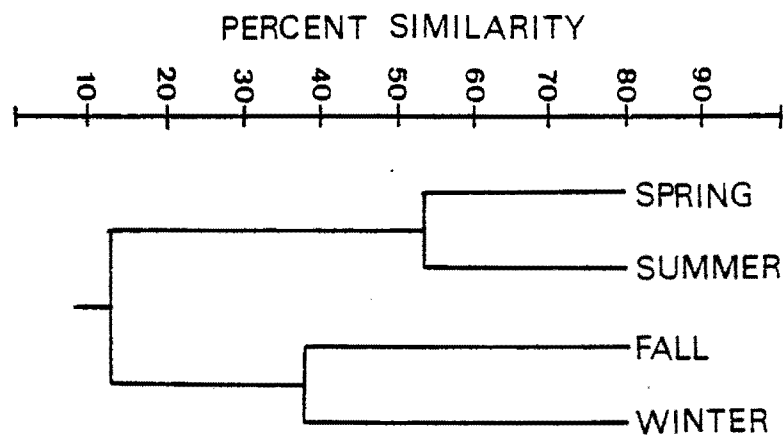
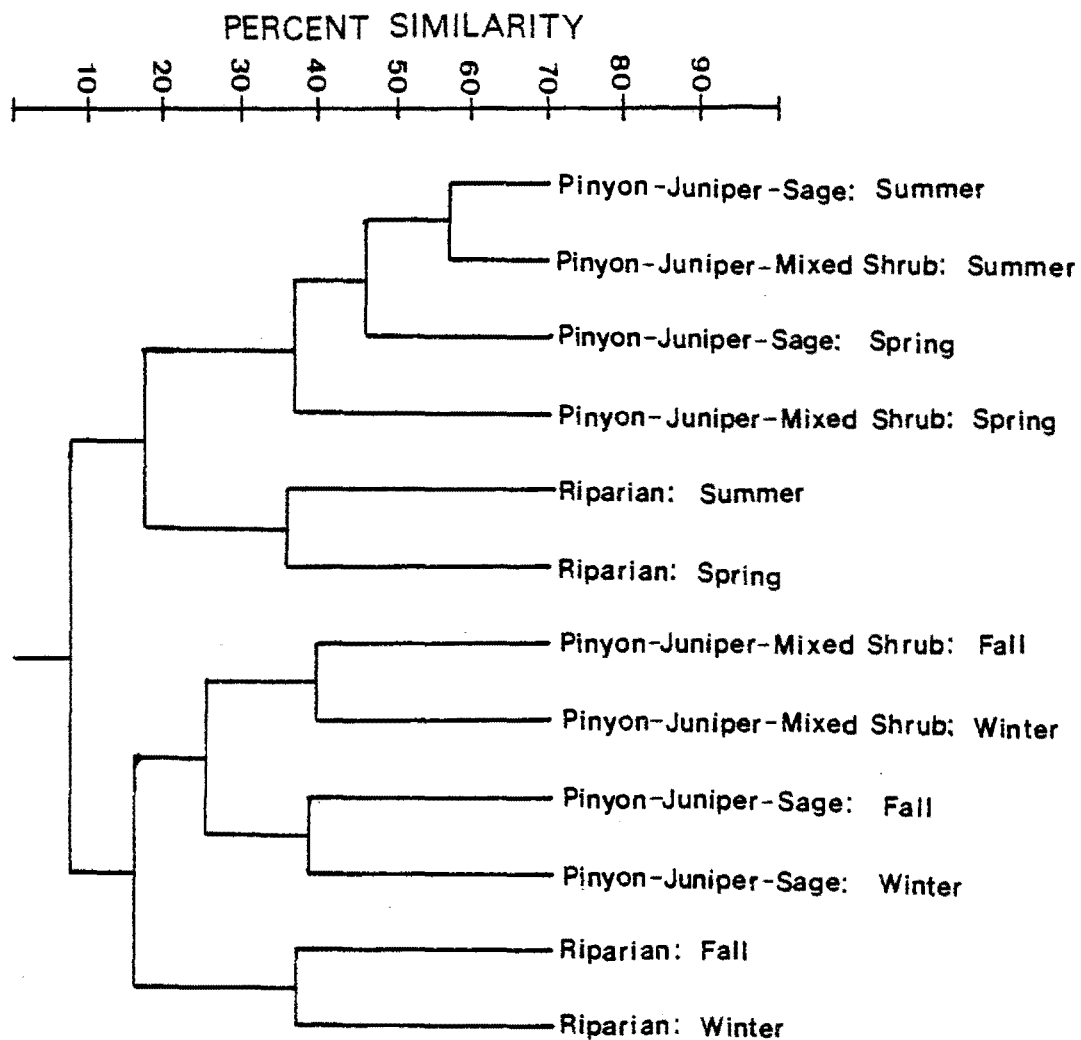
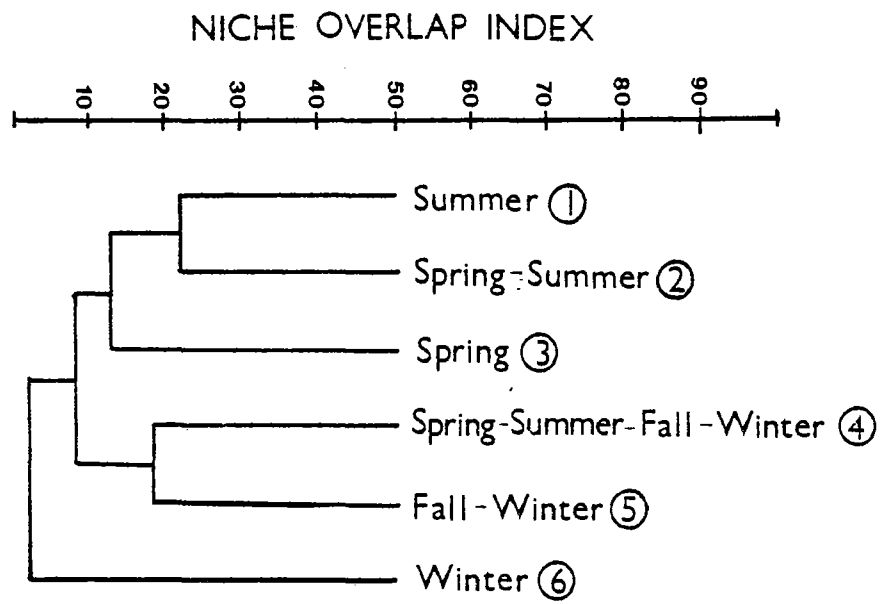
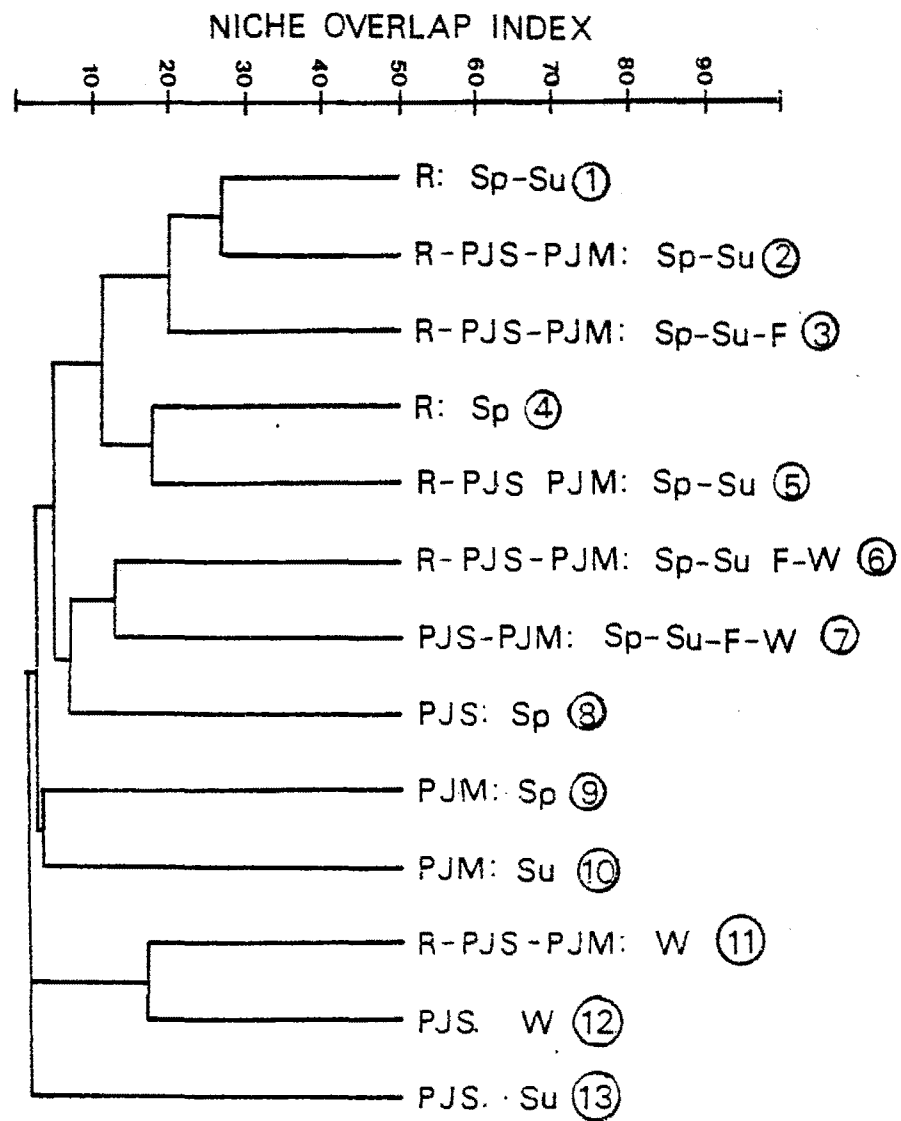


Fig. 7







R = RIPARIAN

PJS = PINYON-JUNIPER-SAGE

PJM = PINYON-JUNIPER-MIXED SHRUB

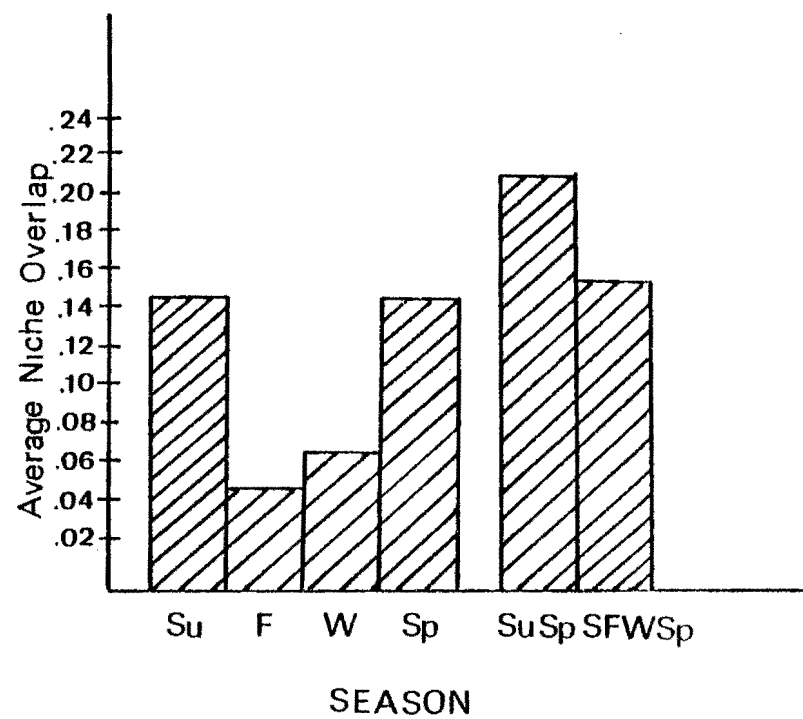
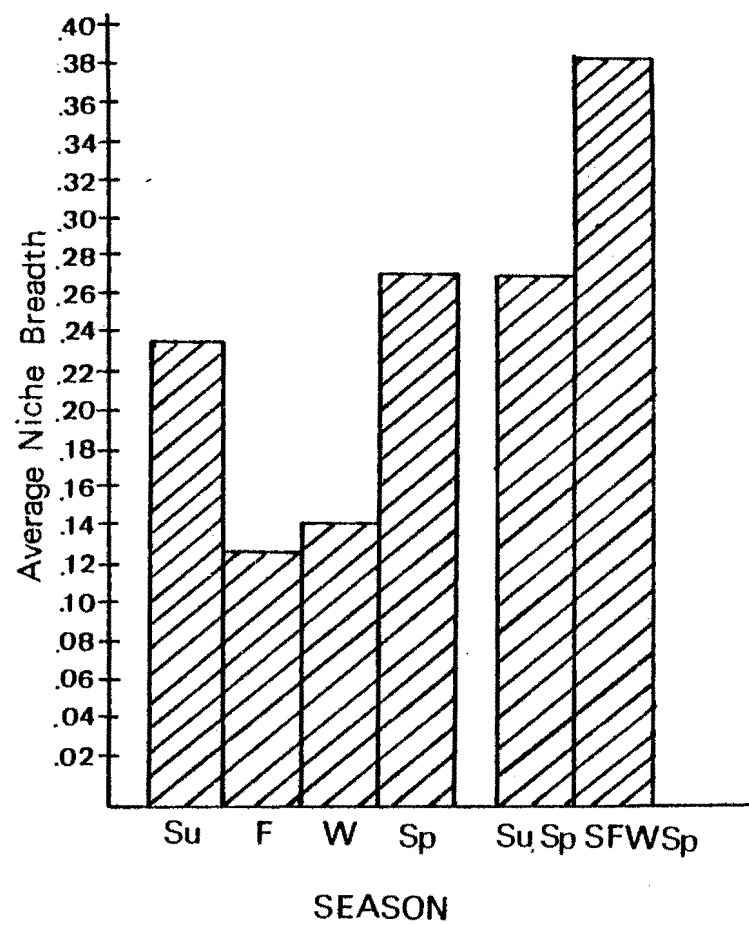


Fig. 10

Table 1. Major habitat types along with their total number of bird species, total densities (D) and diversities (H', J').

Community type	No. of Avian Species	D	H'	J'
Riparian	46	17.4	1.455	.380
Pinyon-Juniper-Sage	34	15.4	1.301	.389
Pinyon-Juniper-Mixed Shrub	36	10.8	1.307	.305

D = Total densities of all individuals present per ha

H' = Shannon-Weaver Diversity index = $-\sum p_i \log p_i$ where p_i equals the proportion of a species in the whole community.

J' = Equitability index = $H'/\log S$ where S = total number of species present in habitat.

Table 2. Perching sites of birds from the spring-summer census of 1977.
 N = total number of individuals, H' = Shannon-Weaver diversity index,
 J' = equitability (see Table 1).

Perching Sites	No. of Species	N	H'	J'
Aspen*	11	42	.910	.379
Boxelder*	9	43	.855	.389
Gambel Oak*	19	137	1.037	.352
Douglas Fir*	10	49	.555	.241
Dogwood*	4	6	.578	.417
Pinyon	23	149	1.025	.327
Juniper	12	24	.994	.400
Mahogany	7	58	.366	.188
Ground	5	28	.513	.319

* R = Riparian community

P-J = Pinyon-juniper community

Table 3. Bird species grouped by cluster analysis of niche overlaps (date from perch site information). Table corresponds to Figure 4.

Group	Species	Group	Species
1	Mourning Dove Violet-green Swallow Brown-headed Cowbird Bluebird Bushtit	6	Virginia's Warbler Sharp-shinned Hawk Audubon's Warbler Black-headed Grosbeak Hairy Woodpecker Dusky Flycatcher
2	Black-throated Gray Warbler Rock Wren Gray Flycatcher Plain Titmouse		Warbling Vireo Downy Woodpecker Ruby-crowned Kinglet White-breasted Nuthatch Hermit Thrush Flicker
3	Chipping Sparrow Common Bushtit	7	Rufous-sided Towhee Swainson's Thrush
4	Gray-headed Junco	8	Black-capped Chickadee Turkey Vulture
5	Black-chinned Hummingbird Scrub Jay Blue-gray Gnatcatcher Mountain Chickadee	9	Wilson's Warbler

Table 4. Summary of population data collected on census in the Betatakin Canyon area of Navajo National Monument.

Habitat Type	Number of Species				Mean Density*				Shannon-Weaver (H')			
	Sp	S	F	W	Sp	S	F	W	Sp	S	F	W
Riparian	34	26	7	5	5.7	7.0	1.9	1.6	1.71	1.19	0.83	0.34
Pinyon-Juniper mixed shrub	24	27	5	7	3.8	4.9	1.5	0.7	0.87	1.38	0.56	0.57
Pinyon-Juniper-Sage	22	24	9	9	5.4	3.6	3.7	2.7	1.14	1.23	0.68	0.82

Sp = Spring. Census period: May 7-10

S = Summer. Census period: July 8-11.

F = fall. Census period: November 6-7.

W = winter. Census period: February 19-21.

*Individual birds per ha.

Table 5. Bird species grouped by cluster analysis of niche overlaps (Data from seasonal information). Table corresponds to Figure 8.

Group	Species	Group	Species
1	Audubon's Warbler Black-capped Chickadee Black-headed Grosbeak Western Bluebird Black-chinned Hummingbird Cassin's Kingbird Gray Flycatcher Lesser Goldfinch Red Crossbill Virginia's Warbler Western Tanager	3	Band-tailed Pigeon Brown-headed Cowbird Gray-headed Junco Common Grosbeak Mountain Bluebird Vesper Sparrow Yellow Warbler Yellow-rumped Warbler Orange-crowned Warbler Red-breasted Nuthatch Ruby-crowned Kinglet Swainson's Thrush Wilson's Warbler Yellow-bellied Sapsucker
2	Rufous-sided Towhee Say's Phoebe Common Bushtit Cooper's Hawk Violet-green Swallow Hermit Thrush Blue-gray Gnatcatcher Solitary Vireo Green-tailed Towhee White-throated Swift Bewick's Wren Western Flycatcher MacGillivray's Warbler Warbling Vireo Downy Woodpecker Traill's Flycatcher Black-throated Gray Warbler Mourning Dove House Wren Chipping Sparrow Ash-throated Flycatcher Broad-tailed Hummingbird Canyon Wren Rock Wren	4	Scrub Jay White-breasted Nuthatch Common Flicker Hairy Woodpecker Plain Titmouse Raven House Finch Robin Mountain Chickadee
		5	Black-billed Magpie Sharp-shinned Hawk Dark-eyed Junco Stellar's Jay
		6	Cassin's Finch Golden-crowned Kinglet Brown Creeper Pinyon Jay

Table 6. Bird species grouped by cluster analysis of niche overlaps (data from season and habitat information). Table corresponds to Figure 9.

Group	Species	Group	Species
1	Black-headed Grosbeak Western Tanager Cooper's Hawk MacGillivray's Warbler Warbling Vireo Western Flycatcher Virginia's Warbler Traill's Flycatcher		Rufous-sided Towhee Broad-tailed Hummingbird Violet-green Swallow White-throated Swift
2	Brown-headed Cowbird Yellow-rumped Warbler House Wren Rock Wren Ash-throated Flycatcher Black-throated Gray Warbler Blue-gray Gnatcatcher Canyon Wren	6	Hairy Woodpecker Plain Titmouse House Finch Raven White-breasted Nuthatch Mountain Chickadee Dark-eyed Junco Pinyon Jay
3	Bewick's Wren Downy Woodpecker Common Bushtit Mourning Dove Black-billed Magpie Sharp-shinned Hawk Stellar's Jay Common Flicker Robin	7	Chipping Sparrow Scrub Jay
		8	Gray-headed Junco Red-breasted Nuthatch
		9	Ruby-crowned Kinglet Vesper Sparrow Mountain Bluebird
4	Band-tailed Pigeon Common Grosbeak Orange-crowned Warbler Swainson's Thrush Yellow Warbler Yellow-bellied Sapsucker Wilson's Warbler	10	Black-capped Chickadee Cassin's Kingbird Red Crossbill Lesser Goldfinch
		11	Brown Creeper
		12	Cassin's Finch Golden-crowned Kinglet
5	Black-chinned Hummingbird Green-tailed Towhee Solitary Vireo	13	Gray Flycatcher Western Bluebird Audubon's Warbler

APPENDIX I

Navaho National Monument

Field Bird Check List*

STATUS

HABITAT TYPE

S-Spring

Su-Summer

F-Fall

W-Winter

H-General Habitat Preferences

PJ-Pinyon-Juniper and sagebrush

SI-Slickrock and canyon escarpment creek bottom,

R-Riparian (aspen-oaks along creek bottom)

G-General distribution throughout the park

ABUNDANCE

c=common; easily found in proper habitat in the right season.

f=fairly; may be found in low numbers scattered through the proper habitat in the right season.

u=uncommon; present but not easily found.

o=occasional; unpredictable occurrence, seen only a few times during a season.

r=rare; seen at intervals of 2 to 5 years.

*This checklist includes the 72 species listed on "Checklist of Birds, Navajo National Monument, Arizona" as well as 63 additional species observed in the present study.

	S	Su	F	W	H
Turkey Vulture	c	c			G
Cooper's Hawk	u	u	u		R
Sharp-shinned Hawk	u	u	u		R
Red-tailed Hawk	u	u	u	u	G
Swainson's Hawk	o	o	o		G
Golden Eagle	o	o	o	o	G
Prairie Falcon	r	r	o	r	G
Merlin	r		r		R
American Kestrel	f	f	u	o	G
Gambel's Quail	o	o	o	o	R
Killdeer	r	r	r		R
Solitary Sandpiper	r		r		R
Spotted Sandpiper	r	r	r		R
Ring-billed Gull	r		r		G
Band-tailed Pigeon	u	u			R
Rock Dove	o	o	o	r	S
Mourning Dove	c	c	c	o	G
Yellow-billed Cuckoo		u			G
Screech Owl	u	u	u	u	G
Great Horned Owl	f	f	f	f	G
Long-eared Owl	O	o	c	o	G
Spotted Owl	o	o	o	o	G
Saw-whet Owl	r		r	r	G
Flammulated Owl	u	u	u		G
Pygmy Owl	o	o	o	o	G
Poor-will		f			G
Common Nighthawk		f			G
Lesser Nighthawk		u			G
White-throated Swift	f	f	u		G
Broad-tailed Hummingbird	c	c	u		G
Calliope Hummingbird	o		o		G
Black-chinned Hummingbird	u	f	u		G
Rufous Hummingbird	r		r		G
Common Flicker	c	c	f	r	G
Lewis' Woodpecker	r	o	r		R
Yellow-bellied Sapsucker	u		u	r	R
Williamson's Sapsucker	o	o	o	r	G
Hairy Woodpecker	c	c	c	c	G
Downy Woodpecker	c	c	c	c	G
Western Kingbird		f			G
Cassin's Kingbird		f			G
Ask-throated Flycatcher	c	c	f		G
Black Phoebe		o			R
Say's Phoebe		o			R
Willow Flycatcher	f	f	u		G
Hammond's Flycatcher	u	u	u		PJ
Dusky Flycatcher	u	f	u		PJ
Western Flycatcher	u	f	u		R
Olive-sided Flycatcher	u	u	u		R
Barn Swallow		o			SI
Cliff Swallow		o			SI
Violet-green Swallow	c	c	c		G

Stellar's Jay	u	u	f	r	G
Scrub Jay	c	c	c	f	G
Pinyon Jay	u	u	u	f	PJ
Black-billed Magpie	o	o	o	o	G
Clark's Nutcracker	r	r	r	r	G
Common Raven	c	c	c	c	G
Common Crow	u	o	u	o	G
Black-capped Chickadee	o	o	o	o	G
Mountain Chickadee	c	c	c	c	G
Plain Titmouse	c	c	c	c	PJ
Common Bushtit	c	c	u	o	PJ
White-breasted Nuthatch	f	f	f	f	PJ
Red-breasted Nuthatch	u	u	u	u	G
Pygmy Nuthatch	o	o	o	o	PJ
Brown Creeper	o	r	u	f	G
House Wren	f	f	u		R
Bewick's Wren	f	f	u	r	G
Canyon Wren	f	f	u	u	SI
Rock Wren	f	f	u	u	SI
Mockingbird		o			PJ
Sage Thrasher	o		o		PJ
Robin	f	f	f		R
Townsend's Solitaire	o	o	o	o	G
Hermit Thrush	c	c	u		R
Swainson's Thrush	u		u		R
Western Bluebird	u	u	o		PJ
Mountain Bluebird	u	u	u	r	PJ
Blue-gray Gnatcatcher	f	c	u		G
Golden-crowned Kinglet	o		o	u	PJ
Ruby-crowned Kinglet	f	o	f		G
Bohemian Waxwing				r	PJ
Cedar Waxwing	o		o	o	PJ
Northern Shrike				r	G
Loggerhead Shrike	u	u	u	o	G
Starling	o	o	o	o	Ca
Solitary Vireo	c	c	u		R
Warbling Vireo	u	f			R
Orange-crowned Warbler	u	r	u		R
Virginia's Warbler	f	c	u		R
Yellow Warbler	f	c	u		R
Yellow-rumped Warbler	c	f	c		G
Black-throated Gray Warbler	f	c	u		PJ
Yellowthroat	f	f	u		R
Yellow-breasted Chat	u	f	o		R
MacGillivray's Warbler	f	f	f		R
Wilson's Warbler	f		f		R
House Sparrow	u	u	u	u	G
Western Meadowlark	u	u	u	u	G
Red-winged Blackbird	u	u	u		G
Brewer's Blackbird	u	u	u		G
Brownheaded Cowbird	f	f	u		G
Bullock's Oriole	u	f	u		R

Western Tanager	u	f	u		G
Black-headed Grosbeak	u	f	u		R
Evening Grosbeak	o	o	o	u	G
Blue Grosbeak		r			R
Lazuli Bunting	o	o	o		R
Purple Finch			r		R
Cassin's Finch	u	o	u	f	G
House Finch	f	f	f	f	G
Pine Grosbeak				r	
Pine Siskin	u		u	u	G
American Goldfinch	u	o	u	u	G
Lesser Goldfinch	u	f	u		SI
Red Crossbill	r	r	r	r	PJ
Green-tailed Towhee	f	f	f		R
Rufous-sided Towhee	c	c	c	o	R
Brown Towhee	o	o			G
Savannah Sparrow	o	o	o		R
Vesper Sparrow	o	o	o		G
Lark Sparrow	u	u	u		PJ
Black-throated Sparrow	o	o	o		PJ
Sage Sparrow	o	o	o		PJ
Dark-eyed Junco	f	f	c	c	G
Gray-headed Junco	u	u	u	u	PJ
Chipping Sparrow	c	c	c	o	PJ
Brewer's Sparrow	o	u	o		PJ
White-crowned Sparrow	f		f	u	G
Fox Sparrow	u		u	o	G
Lincoln's Sparrow	o	u	o		R
Song Sparrow	o		o	o	R

APPENDIX II

NAVAJO NATIONAL MONUMENT

Seasonal bird census - 1978-79

S = Summer

F = Fall

W = Winter

Sp = Spring

Table 1. Population data collected on census at Betatakin Canyon area, Navajo National Monument. Numbers equal bird/acre.

Bird Species	SEASON			
	S	F	W	SP
Turkey Vulture				
Cooper's Hawk	1.2			0.7
Sharp-shinned Hawk		0.3		
Sparrow Hawk				
Band-tailed Pigeon				1.4
Mourning Dove	5.1			8.0
White-throated Swift	3.7			3.8
Broad-tailed Hummingbird	4.6		10.2	
Black-chinned Hummingbird	4.3			
Common Flicker	2.3	3.1		2.5
Hairy Woodpecker	1.1	0.9	0.4	0.7
Downy Woodpecker	4.9		0.2	1.1
Yellow-bellied Sapsucker				0.4
Traill's Flycatcher	4.6			1.1
Western Flycatcher	1.4			0.6
Ash-throated Flycatcher	2.3			5.4
Dusky Flycatcher				
Gray Flycatcher	0.3			
Western Kingbird				
Cassin's Kingbird	0.6			
Say's Phoebe	0.8			0.6
Violet-green Swallow	8.3			4.8
Black-billed Magpie		3.0		
Common Raven	1.8	1.0	0.6	1.7
Pinyon Jay		1.4	2.4	
Scrub Jay	5.4	6.4	0.3	6.2
Stellar's Jay		2.1	0.7	
Crow				
Black-capped Chickadee	0.8			
Mountain Chickadee	17.5	20.3	30.7	20.5
Plain Titmouse	13.9	15.7	5.7	10.1
Common Bushtit	20.3			15.6
Red-breasted Nuthatch				1.3
White-breasted Nuthatch	3.8	3.7	1.6	3.8

Table 1. Continued

Bird Species	SEASON			
	S	F	W	SP
Brown Creeper			5.8	
Bewick's Wren	5.4			2.3
House Wren	3.7			6.1
Canyon Wren	1.1			2.3
Rock Wren	0.9			2.6
Robin	0.9	2.6		0.8
Hermit Thrush	7.3			4.1
Swainson's Thrush				0.4
Western Bluebird	0.3			
Mountain Bluebird				0.6
Blue-grey Gnatcatcher	12.1			14.2
Ruby-crowned Kinglet				1.0
Golden-crowned Kinglet			1.6	
Warbling Vireo	4.1			1.4
Solitary Vireo	7.6			9.3
MacGillivray's Warbler	6.1			2.3
Virginia's Warbler	13.4			
Audubon's Warbler	0.4			
Black-throated Gray Warbler	5.6			9.0
Wilson's Warbler				1.8
Orange-crowned Warbler				1.8
Yellow Warbler				1.1
Yellow-rumped Warbler				13.2
Brown-headed Cowbird				1.3
Western Tanager	2.4			
Common Grosbeak				1.2
Black-headed Grosbeak	3.0			
Green-tailed Towhee	2.0			1.8
Rufous-sided Towhee	9.1			6.8
Gray-headed Junco				2.0
Dark-eyed Junco		32.1	14.1	1.3
Cassin's Finch			2.5	
House Finch	1.2	2.7		1.8
Lesser Goldfinch	1.5			
Vesper Sparrow				2.1
Lark Sparrow				
Black-throated Sparrow				
Chipping Sparrow	10.7			19.8
Red Crossbill	0.6			

APENDIX III

NAVAJO NATIONAL MONUMENT

Perch Site Census - 1977

AP = Aspen

B = Boxelder

D = Douglas Fir

G = Ground

J = Juniper

M = Mahogany

O = Oak

P = Pinyon

W = Dogwood

Figures equal numbers of sightings during sampling periods

PERCH SITE

[illegible]

Perch Site (cont'd).

Blackbird						4	
Brown-headed Cowbird						5	
Black-headed Grosbeak	2	1			7		
Green-tailed Towhee					1		
Rufous-sided Towhee	1		17	1	1	7	2
Gray-headed Junco			3				2
Black-throated Sparrow					1		
Chipping Sparrow				5	44	45	

The Algal Flora of Navajo National Monument, Arizona¹.

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Abstract

Navajo National Monument is located in northern Arizona, U.S.A. in massive Navajo Sandstone cliff-canyon topography. Most habitats in the park are dry and desertic. However, a few moist to wet microenvironments exist locally. The algal floras of both xeric and moist habitats were studied through 1977-78. A total of 136 algal taxa were observed during this study and their distribution and abundance noted.

Introduction

Navajo National Monument is located in northeastern Arizona about 16 km north and west of Black Mesa and Arizona Highway 160. The principal sites of the monument are three large Indian cliff dwellings of the Anasazi culture. These cliff dwellings are located in separate canyons. Betatakin and Keet Seel Canyons are part of the Tsegi Canyon complex while Inscription House is located about 32 km west of Betatakin in Nitsin Canyon. All lie in country dominated by pinyon-juniper communities (Pinus edulis, Juniperus osteosperma) growing in soil pockets associated with sandstone slickrock. Many deep-cut canyons with high-walled sandstone cliffs exist within the region often reaching heights of 300 m above the streambeds. Springs and seeps are often encountered in these canyons, creating unique habitats which develop plant and animal communities foreign to the overall pinyon-juniper type. Aspen (Populus tremuloides), Gambel oak (Quercus gambelii), and Douglas-fir (Psuedotsuga menziesii) communities are present in Betatakin Canyon; oak and mixed weed communities are present in Keet Seel; and a large, heavily grazed, annual weed community exists in the Inscription House segment (Brotherson et al., 1978; Brotherson et al., in review).

A variety of algal habitats are found within the boundaries of the monument. Hanging gardens, which are currently receiving attention in other parts of western America for their unusual floras, are present in Betatakin and Keet Seel. Plant communities in these gardens are similar to those found in Utah in Glen Canyon and in Zion National Park, but are of particular interest since they are more xeric than those previously studied (Rushforth, et al., 1976; Rushforth, et al., in review; Clark and Rushforth, in press).

The most xeric hanging garden community occurs on a drip wall at the bottom of the trail into Betatakin ruins (Fig. 1). A few mosses and algae grow on the rock face at this site, though the wall is dry most of the year. A second hanging garden in the cliff dwellings at Betatakin is xeric but contains a better developed plant community (Fig. 2). Vascular plants, mosses, and algae mark two seepage areas where water slowly emerges from the rock. However, the seepage is so slow that the soil is only slightly dampened, and no runoff or standing water is present. The hanging garden at Keet Seel ruin contains a more mesic community (Fig. 3). Here a thick growth of vascular plants and mosses grow attached to a long seepage wall at the base of the northern part of the cliff dwellings. Large colonies of Nostoc are evident in the wettest portion of the garden surrounding a small seep which emerges from the wall and forms a puddle at the base of the hanging garden. A lichen-covered moist wall occurs in the cliff dwellings at Inscription House ruin.

A spring emerges below the cliff dwellings at Betatakin (Fig. 4) and has a greater flow than the seep at Keet Seel. However, it does not puddle and the water is absorbed almost directly into the ground.

The land surrounding Navajo National Monument is heavily overgrazed. However, Betatakin has been protected from grazing for many years and Keet Seel has been protected for a short time. Inscription House is still heavily grazed. Because of these differences, the soils of the monument show a varying amount of cryptogam development with the best developed cryptogamic soil communities occurring in Betatakin.

The two streams in the monument also reflect different grazing pressure. Betatakin Creek is an ephemeral stream which runs through Betatakin Canyon (Fig. 5). This stream is free of animal induced organic enrichment although it is also warm and stagnant. Inscription House Creek is organically enriched by the cattle and sheep which water and excrete there. Often manure can be seen in the small stream which flows through a badly eroded wash (Fig. 6).

The wide variety of habitats encountered makes the monument a good place for comparative taxonomic studies of algae. The algal habitats discussed above were sampled from June 1977 to March 1978. Included in this paper are descriptions of algae found, and general conclusions and observations which were made.

Methods

Collecting sites were established within the boundaries of the three monuments collectively called Navajo National Monument in June, 1977. Betatakin Creek, Inscription House Creek, and the springs and hanging gardens of Betatakin and Keet Seel were sampled four times through the following year in June, August, November, and March. The soils were sampled only once. Likewise, the two very xeric drip walls, one at the base of the trail into Betatakin and the other in the cliff dwellings at Inscription House, were sampled only once.

Samples were returned to the laboratory for analysis. The non-diatom algae of the soils were examined as fresh material after culturing three days in distilled water. All other non-diatom algae were mounted in a semi-permanent glycerin based mounting medium consisting of 10% glycerin, 3% ethyl alcohol, 1% phenol, and 80% distilled water.

After non-diatom algae were mounted, the remainder of each sample was subsequently used to make permanent diatom slides. Standard acid oxidation techniques were used and cleaned diatoms were mounted in Naphrax mountant (St. Clair and Rushforth, 1976). All algae were studied and identified using Zeiss RA research microscopes equipped with Nomarski interference phase contrast accessories. Specimens were photographed using Nikon

AFM photomicrographic equipment. Drawings of non-diatom algae were prepared from these photographs and from direct microscopical examination.

Systematic Part

Division CYANOPHYTA

Family CHROOCOCCACEAE

Genus CHROOCOCCUS

Chroococcus rufescens (Kuetz.) Naegeli (Fig. 7)

Cology globose to ovate, 10-25 μ m in diameter, may be aggregated with other colonies; gelatinous matrix usually lamellose, scarcely evident in some plants; cells globose, compactly arranged, nongranular, pale blue-green, yellowish, or rarely dark blackish-brown, 3-11 μ m in diameter.

C. rufescens was common in xeric habitats such as soils and drip walls, though it did occur once in Betatakin Creek. The hanging gardens of Betatakin and Inscription House, as well as the more well developed cryptogamic crusts of these localities, hosted this species.

Chroococcus turgidus (Kuetz.) Naegeli (Fig. 8)

Colony oblong to spherical, 18-20 μ m wide, 20-25 μ m long, containing 2-4 cells; gelatinous matrix lamellose, colorless; cells compressed, nongranular, blue-green, 6-13 μ m in diameter.

C. turgidus was found in slightly more mesic conditions than C. rufescens, occurring in the hanging gardens of Keet Seel and Betatakin and the soils of Inscription House. Our specimens were smaller than normal for this taxon, probably due to water stress.

Chroococcus varius A. Braun in Rabenhorst (Fig. 9)

Colony irregular in shape, containing 2-8 cells; gelatinous envelope not evident; cells globose, nongranular, blue-green, 2-3 μ m in diameter.

C. varius was seen in the June collection from Inscription House Creek.

Genus CHLOROGLOEA

Chlorogloea fritschii Mitra (Fig. 10)

Colony pseudofilamentous, or a small aggregation of cells; gelatinous matrix absent; cells spherical, nongranular, pale blue-green, 4-6 μ m in diameter.

C. fritschii was seen in the hanging gardens of Keet Seel and Betatakin, the soils of Inscription House, and the spring at Betatakin. The small aggregates resemble Chroococcus dispersus, but lack the mucilaginous envelope and have cells which are too large for that taxon.

Genus GLEOCAPSA

Gleocapsa aeruginosa (Carm.) Kuetzing (Fig. 11)

Colony ovate or irregularly shaped; cells spherical to ovate, nongranular, blue-green, 2-4 μ m in diameter; individual sheaths distinct, homogenous, colorless to ochrous.

G. aeruginosa was found in the November and March collections from the hanging garden and spring at Betatakin, and the hanging garden at Keet Seel.

Gleocapsa decorticans (A. Braun) Richter (Fig. 12)

Colony spherical to ovate, 22-35 μ m in diameter; cells spherical to ovate, nongranular, grey-green, 5-10 μ m in diameter; individual sheaths distinct, lamellated, colorless.

G. decorticans was abundant in the hanging garden in Betatakin and common in the hanging garden in Keet Seel.

Gleocapsa magma (Breb.) Kuetzing (Fig. 13, 14)

Colony spherical to irregular; cells spherical, grey-green becoming bright orange-red, 4-7 μ m in diameter; individual sheaths distinct, homogenous to slightly lamellose, colorless to reddish.

G. magma was seen in a collection from Inscription House Creek. It is distinguished by its bright red color.

Gleocapsa punctata Naegeli (Fig. 15)

Colony irregular in shape, consisting of small aggregates of 4-8 cells; colonial envelope distinct, homogenous, colorless; cells spherical, dark blue-green, up to 1 μ m in diameter; individual sheaths indistinct.

G. punctata was found year-round in Keet Seel and in the springtime in Betatakin and Inscription House. It was chiefly a hanging garden species, though it also occurred in the creek at Inscription House. It formed blue-green patches under sandstone scales at Keet Seel and was the only taxa in such collections.

Genus APHANOCAPSA

Aphanocapsa grevillei (Hass.) Rabenhorst (Fig. 16)

Colonies ovate, 30-40 μ m in diameter; gelatinous envelope colorless; cells spherical, usually solitary, evenly dispersed in the mucilage, 4-5 μ m in diameter.

A. grevillei was rare in samples collected from the Betatakin hanging garden and Inscription House Creek.

Genus MICROCYSTIS

Microcystis aeruginosa Kuetzing (Fig. 17, 18)

Colony small and spherical when young, becoming ovate or irregularly lobed and clathrate when mature; colonial mucilage

homogenous, colorless; cells spherical, very crowded in young plants, becoming less so in older colonies, granular, blue-green, 3-4.5 μ m in diameter.

M. aeruginosa was common in the seep at Keet Seel and the creeks of Betatakin and Inscription House. The small colonies are often very similar to compact colonies of Nostoc, Chroococcus, or Aphanocapsa, but were distinguished by their compactness, homogenous mucilage, and lack of heterocysts.

Microcystis incerta Lemmermann (Fig. 19)

Colony irregularly shaped, often small; colonial mucilage homogenous, colorless; cells spherical, very crowded, blue-green, 1.5-2.5 μ m in diameter.

M. incerta was collected in low numbers from the hanging gardens of Betatakin and Keet Seel, though at Keet Seel it was present year-round.

Genus MERISMOPEDIA

Merismopedia glauca (Ehr.) Naegeli (Fig. 20)

Colony a flat rectangular plate, 20 μ m wide, 25 μ m long; gelatinous matrix colorless; cells ovate, nongranular, blue-green, 3-5 μ m in diameter.

M. glauca was rare in a single collection from Inscription House Creek.

Genus GOMPHOSPHAERIA

Gomphosphaeria aponina var. cordiformis Wolle (Fig. 21)

Colony spherical or ovate, 60-70 um in diameter; colonial mucilage difficult to discern, colorless; cells cordate, compact, regularly arranged, blue-green to purple, 6-8 um in diameter, 12-15 um long; individual sheaths indistinct.

G. aponina var cordiformis was found in a November collection from the seep at Keet Seel. Our specimens were very regular in their arrangement.

Family OSCILLATORIACEAE

Genus OSCILLATORIA

Oscillatoria angusta Koppe (Fig. 22)

Trichomes usually solitary, nongranular, pale gray-green, 1-1.5 um in diameter; crosswalls not discernable; ends bluntly rounded.

O. angusta was rare in collections from the hanging gardens of Betatakin and Inscription House.

Oscillatoria angustissima West and West (Fig. 23)

Trichomes usually solitary, nongranular, glue-green, .6-.8 um in diameter; crosswalls not discernable; ends rounded.

O. angustissima was rare in June collections from the hanging garden and spring in Betatakin.

Oscillatoria geminata Meneghini (Fig. 24)

Trichomes straight, solitary, constricted at the crosswalls which appear as clear spaces between cells; cells nongranular, dark blue-green, 2-2.5 μm in diameter, 3-5 μm long; apical cell rounded.

O. geminata was collected from the hanging garden and creek in Betatakin and from Inscription House Creek.

Oscillatoria obscura Bruhl and Biswas (Fig. 25)

Trichomes straight, solitary, not constricted at the crosswalls, slightly attenuated in mature trichomes, not attenuated in hormogonia; cells granular at the crosswalls, blue-green, 3.5-4 μm in diameter, .6 μm long.

O. obscura was collected from the aquatic sites in Betatakin and Inscription House.

Oscillatoria subbrevis Schmidle (Fig. 26)

Trichomes straight, solitary, not constricted at the crosswalls, not attenuate; cells nongranular, light blue-green, 5 μm in diameter, 2 μm long; apical cell rounded.

O. subbrevis was collected from the hanging garden in Keet Seel, the creek in Inscription House, and all communities in Betatakin.

Oscillatoria tenuis C. A. Agardh (Fig. 27)

Trichomes straight, solitary, not constricted at the crosswalls, not attenuate; cells granular at the crosswalls, light blue-green, 4-5 μ m in diameter, 2.5-3 μ m long; apical cell rounded.

O. tenuis was collected from the hanging garden and spring in Betatakin, the hanging garden in Keet Seel, and Inscription House Creek. Our specimens were unusual in that they were not constricted at the crosswalls as is often the case with this taxon. They were separated from O. subbrevis on the basis of the granular crosswalls. It is very possible that either or both of what we are calling O. subbrevis and O. tenuis are actually growth forms of Microcoleus vaginatus, a highly variable species common in the soils and hanging gardens of the study.

Genus PHORMIDIUM

Phormidium angustissimum West and West (Fig. 28)

Plant mass a thick mat; trichomes nongranular, blue-green, 1 μ m in diameter; crosswalls not discernable; individual sheaths not clearly evident.

P. angustissimum was collected from Inscription House Creek.

Phormidium tenue (Menegh.) Gomont (Fig. 29)

Plant mass in mats or large filaments, pale grey-green or reddish; trichomes constricted at the crosswalls, often attenuate at apices; cells nongranular, .7-2.5 μm in diameter, 2-3 μm long; individual sheaths occasionally discernable.

P. tenue was collected from the hanging garden, spring, and creek in Betatakin and from the slickrock soils of Inscription House. Some of our specimens resembled Lyngbya purpurea because of their reddish color.

Genus LYNGBYA

Lyngbya limnetica Lemmermann (Fig. 30, 31)

Trichomes straight, solitary, not to slightly constricted at the crosswalls, not attenuate; cells nongranular, dark blue-green, blue-green, or olivaceous, 1-3 μm in diameter, 1.6-6 μm long; individual sheaths often present, usually thin and colorless.

L. limnetica was widespread, occurring in nearly all communities throughout the year. It was highly variable and took several forms, two of which are illustrated. Drouet (1968) places this taxa under Schizothrix calcicola.

Genus MICROCOLEUS

Microcoleus vaginatus (Vauch.) Gomont (Fig. 32-35)

Colony a filament composed of several to many trichomes in a common, colorless sheath, about 20-32 μm in diameter, or a

lime incrustated mat, or solitary trichomes having distinct individual sheaths; trichomes straight, not constricted at the crosswalls, sometimes tapering at the apices; cells granular, blue-green, grey-green, or olivaceous, 2.5-8 μm in diameter, 2-9 μm long; apical cell rounded; calyptra absent; individual sheaths thin and colorless when present, or occasionally incrustated with lime.

M. vaginatus was widespread in the study. It occurred in the hanging gardens and springs of Betatakin and Keet Seel and in the creek at Inscription House. However, its most important role is as a soil alga. Nearly all cryptogamic crusts throughout the Intermountain West contain this taxon, and those in the monument are no exception. It plays a major role in holding together the soil, production of cryptogamic soil hummocks, and prevention of soil erosion. Though highly variable, the colonial filament form is the most common form found in the soils of this study.

Family NOSTACACEAE

Genus ANABAENA

Anabaena variabilis Kuetzing (Fig. 36)

Trichomes solitary or entangled in other algae, constricted at the crosswalls; cells compressed globose, nongranular, pale grey-green, 4 μm in diameter, 2-4 μm long; heterocysts ovate, 7 μm in diameter, 6 μm long; gonidia unobserved.

A. variabilis occurred in well developed soil crusts throughout the monument, though it was always in low quantities.

Genus NOSTOC

Nostoc commune Vaucher (Fig. 37, 38)

Colony microscopic when young or in soils, becoming larger when older, 3-7 mm in diameter; trichomes compact and entangled in young colonies, becoming looser in older colonies, constricted at the crosswalls; cells globose, nongranular, olivaceous, 4-5 μ m in diameter, 4-6 μ m long; heterocysts spherical, usually terminal, but can be intercalary, 6-8 μ m in diameter; gonidia rare, 6 μ m in diameter, 8 μ m long.

N. commune was one of the most abundant taxa in the hanging garden communities of Keet Seel and Betatakin, forming thick, dense clusters in Keet Seel. It also occurred in soils and in Betatakin Creek.

Nostoc muscorum C. A. Agardh (Fig. 39)

Colony microscopic to 1 mm in diameter; colonial mucilage homogenous, yellowish brown; trichomes closely arranged and entangled, constricted at the crosswalls; cells globose, nongranular, olivaceous, 2.5-4 μ m in diameter; heterocysts spherical, 6 μ m in diameter; gonidia unobserved.

N. muscorum occupied the same communities as N. commune, but was not as abundant. It was found in samples collected in November and March. It closely resembles N. commune, but has smaller cells.

Nostoc paludosum Kuetzing (Fig. 40)

Colony microscopic; colonial mucilage homogenous, colorless to olivaceous, contain one to a few trichomes; trichomes constricted at the crosswalls; cells spherical, olivaceous, 3 μ m in diameter; heterocysts spherical, 4 μ m in diameter; gonidia unobserved.

N. paludosum was rare, occurring in the spring at Betatakin, and in the seep and hanging garden of Keet Seel.

Family SCYTONEMATACEAE

Genus SCYTONEMA

Scytonema myochrous (Dillw.) C. A. Agardh (Fig. 41, 42)

Filaments entangled, rarely branching, 12-15 μ m in diameter; sheath clear, becoming yellowish brown, occasionally lamellated; trichomes occasionally constricted at the crosswalls; cells granular, olivaceous, 6-12 μ m in diameter, 3-12 μ m long; heterocysts compressed-quadrangle, 10-12 μ m in diameter, 7.5-10 μ m long.

S. myochrous was found in collections from the hanging garden and spring in Betatakin and from Inscription House Creek. It was also important in the soils. The sheaths of our specimens were thinner than normal for this taxon.

Family RIVULARIACEAE

Genus CALOTHRIX

Calothrix marchica Lemmermann (Fig. 43, 44)

Colony a dense tuft adherent to a grain of sand; filaments up to 7 μ m in diameter; trichomes nonbranching, not constricted at the crosswalls, 4-6 μ m in diameter at the base, tapering to 1-2 μ m at the ends, about 50-75 μ m long; sheaths difficult to detect, colorless and usually thin, though occasionally up to 7 μ m wide; cells nongranular, blue-green, 2.5-3 μ m long; heterocysts hemispherical, basal, 5-6 μ m in diameter.

C. marchica was found in the March collection from Betatakin Creek.

Calothrix parietina (Naeg.) Thuret (Fig. 45)

Colony a small tuft; filaments 10-15 μ m in diameter at the base; trichomes rarely branching, not to slightly constricted at the crosswalls, which often appear as clear spaces, 6-7.5 μ m in diameter at the base, tapering to 2 μ m at the ends; sheaths yellow-brown and persistent, often devoid of cells; cells nongranular, olivaceous, 4-7 μ m long; heterocysts hemispherical, basal, 5-6 μ m in diameter.

C. parietina was collected infrequently from the spring at Betatakin.

Division CHLOROPHYTA

Family CHLOROCOCCACEAE

Genus CHLOROCOCCUM

Chlorococcum humicola (Naeg.) Rabenhorst (Fig. 46)

Cells spherical or rarely ellipsoidal, solitary or in small aggregates, granular, bright green, 6-15 μm in diameter; chloroplast covering most of the periplast.

C. humicola was common in the soils and hanging garden in Betatakin. It was abundant in Inscription House Creek in August. Several unusual ellipsoidal forms were seen in collections from this site.

Family OOCYSTACEAE

Genus OOCYSTIS

Oocystis species (Fig. 47)

Colony consisting of 1-8 cells inclosed by the old mother cell wall; cells elipsoid or ovate, broadly at the poles, 10-27 μm wide, 17-42 μm long; chloroplasts numerous, not parietal.

This taxon was abundant in the March collections from the seep and hanging garden in Keet Seel. It resembles O. borgei and O. gigas, but has a different size range. The chloroplasts

did not appear to be parietal, which is unusual, but the central position observed may be a result of the preparation they underwent before examination.

Division EUGLENOPHYTA

Family EUGLENACEAE

Genus EUGLENA

Euglena fusca (Klebs) Lemmermann (Fig. 48)

Cells metabolic, subcylindric, twisted, 20-22 um wide, 85-90 um long; posterior end narrowed and extended into a tail piece; periplast striated with rows of shining granules; cell contents bright green, masked by the striated periplast.

E. fusca was infrequent in the June collection from Betatakin Creek.

Euglena oxyuris var. minor Prescott (Fig. 49)

Cells slightly metabolic, elongate-cylindric, twisted, narrowing posteriorly, 12-17 um wide, 50-75 um long; chloroplasts numerous, disclike; paramylon grains large flattened rings, usually only one of the two being detectable.

E. oxyuris var. minor was abundant in the March collection from Inscription House Creek. A single specimen was seen in the

hanging garden at Betatakin. Our specimens were much smaller than normal, but were identified on the basis of their paramylon grains.

Genus TRACHELOMONAS

Trachelomonas abrupta (Swir.) Deflandre (Fig. 50)

Test oval to subcylindric, coarsely punctate, 18-19 um in diameter, 30 um long; anterior end truncate; flagellum aperture wide.

T. abrupta was rare in the June collection from Betatakin Creek.

Division CHRYSOPHYTA

Family TRIBONEMATACEAE

Genus TRIBONEMA

Tribonema bombycinum (C. A. Agardh) Derbes and Solier (Fig. 51)

Trichomes entangled, not to slightly constricted at the crosswalls; cells 6-10 um in diameter, 20-40 um long; cell walls thin; chloroplasts small, bright green, often aggregated to give the appearance of 1 or 2 large plates; aplanospores spherical, common, 4-6 um in diameter.

T. bombycinum was common to abundant in collections from the creek and spring in Betatakin.

Division BACILLARIOPHYTA

Family COSCINODISCACEAE

Genus MELOSIRA

Melosira roeseana Rabenhorst (Fig. 52, 53)

Diameter 12-70 μ m; length 16-33 μ m; valve striae 7-9 in 10 μ m; longitudinal striae 16-20 in 10 μ m; punctae 16-18 in 10 μ m (Hustedt, 1930a, p. 266).

M. roeseana was rare to infrequent in collections from Keet Seel and the hanging garden and creek in Betatakin. It also occurred in the soils.

Genus CYCLOTELLA

Cyclotella bodanica Eulenstein (Fig. 55)

Diameter 30 μ m; striae 10 in 10 μ m (Hustedt, 1930a, p. 354).

C. bodanica was identified from two specimens seen in the soils of Betatakin. The striae were coarser than normal. Though this taxon, described as C. compta, has been found in playa soils of southwestern Utah (Anderson and Rushforth, 1976), it was unusual that it should occur in Betatakin in soils that never have standing water such as that that is present in the playas.

Cyclotella meneghiniana Kuetzing

Diameter 11 um; striae 8 in 10 um (Hustedt, 1930a, p. 341).

C. meneghiniana was seen once in a collection from the drip wall at the bottom of the trail into Betatakin.

Genus STEPHANODISCUS

Stephanodiscus astraea var. minutula (Kuetz.) Grunow (Fig. 54)

Diameter 18 um; striae 12 in 10 um (Hustedt, 1930a, 369).

S. astraea var. minutula was rare in collections from the slickrock soils of Inscription House.

Family FRAGILARIACEAE

Genus DIATOMA

Diatoma vulgare var. breve Grunow (Fig. 56)

Length 29-45 um; width 12 um; costae 7 in 10 um; striae unresolved (Patrick and Reimer, 1966, p. 109).

D. vulgare var. breve was rare in the hanging garden and soils of Betatakin.

Genus FRAGILARIA

Fragilaria lapponica Grunow (Fig. 59)

Length 14-24 um; width 6-8 um; striae 8 in 10 um (Patrick and Reimer, 1966, p. 130).

F. lapponica was infrequent in samples from Keet Seel and Inscription House Creek.

Fragilaria vaucheriae (Kuetz.) Petersen (Fig. 57, 58)

Length 14-30 um; width 4-5 um; striae 14 in 10 um (Patrick and Reimer, 1966, p. 120).

F. vaucheriae was rare to infrequent in samples collected from the spring and hanging garden in Betatakin. Some of our specimens were unusual in that they had capitate ends.

Fragilaria species 1 (Fig. 60, 61)

Valve lanceolate, swollen in the middle portion, tapering to rostrate or subcapitate ends; axial area narrow; central area absent or a slight widening of the axial area; striae parallel, 10-11 in 10 um; length 15-22 um; width 5.5-7 um.

This Fragilaria was rare to infrequent in collections from the seep at Keet Seel. It resembles F. construens, F. leptostauron, F. pinnata var. lancetula, and Synedra parasitica, but does not fit well into any of those taxa.

Genus HANNAEA

Hannaea arcus (Ehr.) Patrick

Width 6 um; striae 12 in 10 um (Patrick and Reimer, 1966, p. 132).

H. arcus was identified from two broken specimens in lichen collections from the oaks in Keet Seel.

Family ACHNANTHACEAE

Genus COCCONEIS

Cocconeis placentula var. euglypta (Ehr.) Cleve (Fig. 62, 63)

Length 17-35; width 8-18 um; striae on raphe valve 16 in 10 um; striae on non-raphe valve 13-16 in 10 um (Patrick and Reimer, 1966, p. 241).

C. placentula var. euglypta was infrequent in the March collection from Betatakin spring. Our specimens had much coarser striae than normal. They would have fit C. fluviatilis except that the raphe value was too coarsely striated for that taxon.

Cocconeis placentula var. lineata (Ehr.) Van Heurck (Fig. 62, 64, 65).

Length 12-28 um; width 6-26 um; striae on raphe valve 19 in 10 um; striae on non-raphe valve 16-18 in 10 um (Patrick and Reimer, 1966, p. 242).

C. placentula var. lineata was common in collections from the seep at Keet Seel. It was infrequent in the spring at Betatakin. Our specimens had striae that were coarser than normal for this taxon, and seemed to intergrade with our C. placentula var. euglypta frustules. They were separated by the finer longitudinal striae in the non-raphe valve of var. lineata. Also, transverse striae were coarser in our var. euglypta.

Genus ACHNANTHES

Achnanthes coarctata (Breb. in W. Sm.) Grunow (Fig. 66, 67)

Length 35-38 um; width 8-9 um; striae 12-14 in 10 um; punctae 16 in 10 um (Patrick and Reimer, 1966, p. 277).

A. coarctata was rare in collections from the hanging gardens of Betatakin and Keet Seel, and from Betatakin Creek.

Achnanthes exigua Grunow (Fig. 68, 69)

Length 13-15 um; width 5 um; striae 24 in 10 um (Patrick and Reimer, 1966, p. 257).

A. exigua was rare in collections from Keet Seel and the spring and creek in Betatakin.

Achnanthes lanceolata (Breb.) Grunow (Fig. 70-73)

Length 13-39 um; width 4-11 um; striae 11-14 in 10 um (Patrick and Reimer, 1966, p. 269).

A. lanceolata was common throughout the year in the springs of Keet Seel and the spring and creek of Betatakin.

Achnanthes lewisiana Patrick

Length 15-18 um; width 5-5.5 um; striae 15 in 10 um (Patrick and Reimer, 1966, p. 266).

A. lewisiana was rare in the hanging garden and spring in Betatakin. Some of our specimens were larger than normal for this taxon.

Achnanthes linearis (W. Sm.) Grunow (Fig. 74, 75)

Length 9-13 um; width 2.5-3 um; striae 24 in 10 um, becoming up to 30 in 10 um near the ends (Patrick and Reimer, 1966, p. 251).

A. linearis was abundant in the August collections from Keet Seel hanging garden and Betatakin spring. It was also abundant in March collections from Betatakin Creek. It was rare in the hanging gardens and soils of Betatakin. This taxon is easily confused with A. minutissima, but is distinguished by its coarser striae.

Achnanthes microcephala (Kuetz.) Grunow

Length 18 um; width 3.5 um; striae 24-30 in 10 um, becoming finer near the ends (Patrick and Reimer, 1966, p. 250).

A. microcephala was rare in the soils and hanging gardens of the monument. The capitate ends separate it from A. minutissima.

Achnanthes minutissima Kuetzing (Fig. 76)

Length 5.5-20 um; width 2.5-4 um; striae unresolved (Patrick and Reimer, 1966, p. 253).

A. minutissima was found in low numbers in collections from all sites.

Family NAVICULACEAE

Genus STAURONEIS

Stauroneis anceps Ehrenberg (Fig. 77)

Length 42-60 um; width 11-13 um; striae 17-18 in 10 um (Patrick and Reimer, 1966, p. 361).

S. anceps was rare in the June collection from Betatakin Creek. Our specimens had coarser striae than normal, though Cleve-Euler (1953) reported seeing specimens with striae as coarse as 16 in 10 um.

Stauroneis phoenicenteron (Nitz.) Ehrenberg (Fig. 80)

Length 140-190 um; width 30-37 um; striae 11-12 in 10 um (Patrick and Reimer, 1966, p. 359).

S. phoenicenteron was rare in the June collection from the creek in Betatakin Canyon.

Stauroneis wislouchii Poretzky and Anisimowa (Fig. 78, 79)

Length 23-28 um; width 5.5-8.5 um; striae 20-24 in 10 um in the center to 28 in 10 um near the ends (Hustedt, 1959, p. 792).

S. wislouchii was infrequent in the Keet Seel hanging garden and rare in the creek in Betatakin Canyon.

Genus ANOMOEONEIS

Anomoeoneis sphaerophora (Ehr.) Pfitzer (Fig. 81)

Length 59 um; width 18 um; striae 15 in 10 um (Patrick and Reimer, 1966, p. 374).

A. sphaerophora was identified from a single specimen seen in the August collection from Inscription House Creek.

Anomoeoneis zellensis (Grun.) Cleve (Fig. 82)

Length 13-14 um; width 3-4 um; striae 20-21 in 10 um (Hustedt, 1930b, p. 243).

A. zellensis was rare in collections from Betatakin Creek and Keet Seel seep. Our specimens were at the lower size limit for this taxon.

Genus NEIDIUM

Neidium affine var. amphirhynchus (Ehr.) Cleve (Fig. 83)

Length 55-60 um; width 14-16 um; striae 20-21 in 10 um
(Hustedt, 1930b, p. 243).

N. affine var. amphirhynchus was rare in the June collection from the creek in Betatakin. Our specimens were larger than those normally observed in this country.

Genus NAVICULA

Navicula abiskoensis Hustedt (Fig. 84)

Length 40-45 um; width 11-12 um; striae 8-11 in 10 um
(Hustedt, 1961, p. 806).

N. abiskoensis was rare in collections from the seep at Keet Seel and both creeks.

Navicula accomoda Hustedt (Fig. 84)

Length 15-23 um; width 5-7 um; striae 20-24 in 10 um, becoming finer near the ends (Patrick and Reimer, 1966, p. 468).

N. accomoda was infrequent in collections from Inscription House Creek and rare in samples from the hanging garden and creek in Betatakin. Some of our specimens were smaller than normal for this taxon.

Navicula arvensis Hustedt (Fig. 86)

Length 8-11 um; width 3-4 um; striae unresolved (Patrick and Reimer, 1966, p. 483).

N. arvensis was infrequent to common in collections from the creek and hanging gardens in Betatakin. It was rare in Inscription House Creek.

Navicula capitata var. hungarica (Grun.) Ross (Fig. 88)

Length 17 um; width 5 um; striae 8-9 in 10 um (Patrick and Reimer, 1966, p. 537).

N. capitata var. hungarica was rare in the August collection from Inscription House Creek.

Navicula cincta (Ehr.) Ralfs (Fig. 89)

Length 25 um; width 5 um; striae 11-12 in 10 um (Patrick and Reimer, 1966, p. 515).

N. cincta was rare in Betatakin Creek.

Navicula contenta f. biceps (Arnott) Grunow (Fig. 87)

Length 10.5-13 um; width 2.5-3 um; striae unresolved (Hustedt, 1961-66, p. 209).

N. contenta f. biceps was rare to common in collections from Keet Seel, and rare in Betatakin Creek.

Navicula cryptocephala var. veneta (Kuetz.) Rabenhorst (Fig. 90)

Length 15-27 um; width 5-5.5 um; striae 12-16 in 10 um (Patrick and Reimer, 1966, p. 504).

N. cryptocephala var. veneta was found in collections from all sites, though it was particularly common in the creek at Betatakin and the seep at Keet Seel. Some of our specimens had striae which were coarser than normal for this taxon.

Navicula cuspidata (Kuetz.) Kuetzing (Fig. 99)

Length 44-55 um; width 13-17 um; striae 16-20 in 10 um (Patrick and Reimer, 1966, p. 464).

N. cuspidata was rare in collections from Inscription House Creek and the hanging garden in Betatakin.

Navicula excelsa Krasske (Fig. 93)

Length 9-9.5 um; width 4.5-5 um; striae 12 in 10 um, becoming 20-24 in 10 um near the ends (Hustedt, 1961-66, p. 164).

N. excelsa was rare to infrequent in the hanging gardens and spring at Betatakin. It was seen once at Keet Seel. Our specimens were all smaller than normal for this taxon.

Navicula gallica (W. Sm.) Van Heurck (Fig. 94)

Length 8-18 um; width 3-4 um; striae 28 in 10 um; marginal thickenings about 12 in 10 um (Hustedt, 1961-66, p. 207).

N. gallica was abundant in the June and November collection from the Keet Seel hanging garden. It was infrequent in the seep at Keet Seel at those times.

Navicula heufleri Grunow (Fig. 92)

Length 22-25 um; width 4.5-5 um; striae 9-12 in 10 um
(Patrick and Reimer, 1966, p. 515).

N. heufleri was rare in the hanging garden at Betatakin and
in both creeks.

Navicula longicephala Hustedt (Fig. 91)

Length 16-20 um; width 3.5-4 um; striae 19 in 10 um (Hustedt,
1944, p. 277).

N. longicephala was found in collections from all sites,
but was most common in the hanging gardens.

Navicula luzonensis Hustedt (Fig. 95)

Length 10-12 um; width 4 um; striae 20 in 10 um (Patrick
and Reimer, 1966, p. 492).

N. luzonensis was rare to infrequent in collections from
the creek in Betatakin Canyon.

Navicula minima Grunow (Fig. 96)

Length 5-10 um; width 3-4 um; striae 26 in 10 um or finer
(Patrick and Reimer, 1966, p. 488).

N. minima was common to abundant in the hanging gardens,
infrequent to common in the spring and seep and rare to infrequent
in Betatakin Creek.

Navicula mutica Kuetzing (Fig. 100-101)

Length 14-29 um; width 6-9 um; striae 18-20 in 10 um (Patrick and Reimer, 1966, p. 454).

N. mutica was common in collections from the hanging garden in Betatakin, and rare in collections from the hanging garden in Keet Seel. It was also an important soil diatom.

Navicula mutica var. cohnii (Hilse) (Fig. 103)

Length 11-21 um; width 6-8 um; striae 18-20 in 10 um (Patrick and Reimer, 1966, p. 454).

N. mutica var. cohnii was common to abundant in the hanging garden and creek in Betatakin, and was rare at Keet Seel. It was also common to abundant in nearly every soil sample.

Navicula mutica var. nivalis (Ehr.) Hustedt (Fig. 102)

Length 20-22 um; width 6-7 um; striae 16-18 in 10 um (Hustedt, 1930b, p. 275).

N. mutica var. nivalis was rare in the drip wall at the bottom of the trail in Betatakin.

Navicula mutica var. undulata (Hilse) Grunow (Fig. 104)

Length 13-19 um; width 6 um; striae 16-20 in 10 um (Patrick and Reimer, 1966, p. 456).

N. mutica var. undulata was rare in the drip wall and hanging garden at Betatakin and in the slickrock soils of Inscription House.

Navicula notha Wallace

Length 18 μ m; width 3.5-4 μ m; striae 16 in 10 μ m, becoming 19-20 in 10 μ m near the ends (Patrick and Reimer, 1966 p. 528).

N. notha was rare in the November collection from Betatakin Creek. Our specimens have finer striae than normal for this taxon.

Navicula pupula Kuetzing (Fig. 105-107)

Length 17-31 μ m; width 7-9 μ m; striae 17 in 10 μ m, becoming 20-24 in 10 μ m near the ends (Patrick and Reimer, p. 495).

N. pupula was abundant in collections from Inscription House Creek. It was infrequent in the August collections from the hanging garden and creek in Betatakin.

Navicula pupula var. rectangularis (Greg.) Grunow (Fig. 109)

Length 23-51 μ m; width 7-10 μ m; striae 14 in 10 μ m, becoming 21 in 10 μ m near the ends (Patrick and Reimer, 1966, p. 497).

N. pupula var. rectangularis was infrequent in the June collection from the creek in Betatakin Canyon.

Navicula radiosa Kuetzing (Fig. 110)

Length 94-98 μ m; width 13-14 μ m; striae 9-11 in 10 μ m (Patrick and Reimer, 1966, p. 509).

N. radiosa was infrequent in the November collection from the creek in Betatakin.

Navicula secreta var. apiculata Patrick (Fig. 108)

Length 12 um; width 5.5 um; striae 16 in 10 um (Patrick and Reimer, 1966, p. 463).

N. secreta var. apiculata was rare in the November collections from both creeks. Our specimens were shorter than normal for this taxon.

Navicula seminuloides Hustedt

Length 7-8 um; width 3-3.5um; striae 20 in 10 um (Hustedt, 1961-66, p. 244).

N. seminuloides was common in Betatakin Creek and infrequent in the hanging gardens. This species closely resembles Navicula minima, but has coarser striation than that taxon.

Navicula seminulum Grunow (Fig. 97)

Length 7-8 um; width 3-4 um; striae 20 in 10 um (Patrick and Reimer, 1966, p. 489).

N. seminulum was found throughout the year in Betatakin Creek.

Navicula seminulum var. hustedtii Patrick

Length 12 um; width 4 um; striae 20-22 in 10 um (Patrick and Reimer, 1966, p. 489).

N. seminulum var hustedtii was rare in collections from the Keet Seel hanging garden. This taxon differs from the nominate variety in that it is more linear and not swollen around the central area.

Navicula tantula Hustedt (Fig. 98)

Length 8-12.5 μ m; width 3-3.5; striae 28-30 in 10 μ m, except at the center, where there are as few as 24 in 10 μ m (Hustedt, 1961-66, p. 250).

N. tantula was common in collections from the seep at Keet Seel. It was also seen in both hanging gardens. This taxon resembles N. minima, and because our specimens are coarser in the center than normal, the resemblance is heightened. The wider, larger central area of N. tantula separates this species from N. minima.

Navicula tripunctata (O. F. Muell.) Bory (Fig. 111)

Length 31 μ m; width 7 μ m; striae 12-14 in 10 μ m (Patrick and Reimer, 1966, p. 513).

N. tripunctata was rare in soil samples from Inscription House.

Navicula tripunctata var. schizonemoides (V. H.) Patrick (Fig. 112, 113).

Length 27-40 μ m; width 7-8 μ m; striae 11-12 in 10 μ m (Patrick and Reimer, 1966, p. 514).

Navicula tripunctata var. schizonemoides was common in both creeks and rare to infrequent in the hanging gardens. It was also rare in the soils. Our specimens were variable, and more than one taxon may be represented by what we have chosen to place under this name.

Navicula viridula var. rostellata (Kuetz.) Cleve (Fig. 114)

Length 42-45 um; width 9-11 um; striae 9-11 in 10 um (Patrick and Reimer, 1966, p. 507).

N. viridula var. rostellata was rare in the August collection from Inscription House Creek.

Navicula species 1 (Fig. 115)

Valve linear-lanceolate with rostrate ends; axial area linear, narrow; central area small, marked by only a slight widening of the axial area; striae radiate, 20-22 in 10 um at the center, unresolved near the ends; length 15-18 um; width 3-4 um.

This Navicula was common to abundant in the hanging gardens and rare in the spring at Betatakin. It was also important in the soils. This diatom is very similar to Achnanthes linearis, but raphes could be clearly seen on both valves.

Navicula species 2 (Plate VII, Fig. 19)

Valve elliptical-lanceolate with rounded ends; axial area linear, narrow, more heavily silicified than the rest of the valve; central area orbicular, caused by regularly shortened striae on both sides of the raphe; striae radiate, 18-22 in 10 um; length 31-33 um; width 11-12 um.

This Navicula was rare in the August collection from Inscription House Creek.

Genus CALONEIS

Caloneis bacillum (Grun.) Cleve (Fig. 117)

Length 14-37 μm ; width 3.5-5 μm ; striae 20-22 in 10 μm
(Patrick and Reimer, 1966, p. 586).

C. bacillum was common in many collections from the springs and hanging gardens of Betatakin and Keet Seel. It was also important in the soils of the monument. It was rare in the November collection from Betatakin Creek. Our specimens, like others seen in xeric habitats of the Intermountain West, had coarser striae than normal for this taxon.

Caloneis lewisii Patrick (Fig. 118)

Length 38-47 μm ; width 8-9 μm ; striae 16-18 in 10 μm (Patrick and Reimer, 1966, p. 588).

C. lewisii was common in the November collection from Betatakin Creek. Our specimens were larger and had coarser striae than normal for this taxon.

Caloneis ventricosa var. truncatula (Grun.) Meister (Fig. 119)

Length 31-53 μm ; width 7-11 μm ; striae 16-20 in 10 μm
(Patrick and Reimer, 1966, p. 585).

C. ventricosa var. truncatula was rare to infrequent in collections from the creek and hanging garden in Betatakin, and from Keet Seel. Our specimens had coarser striae than normal for this taxon.

Genus PINNULARIA

Pinnularia appendiculata (C. A. Ag.) Cleve (Fig. 120)

Length 21-32 μm ; width 4.5-6 μm ; striae 16-19 in 10 μm
(Patrick and Reimer, 1966, p. 593).

P. appendiculata was rare to common in the hanging gardens and soils. It was rare in the spring and creek in Betatakin. Our specimens did not have the wedge-shaped apices described by Patrick and Reimer (1966).

Pinnularia borealis Ehrenberg (Fig. 121)

Length 29-45 μm ; width 7-8 μm ; striae 4-5 in 10 μm (Patrick and Reimer, 1966, p. 618).

P. borealis was rare to infrequent in the hanging gardens. It was an important soil diatom.

Pinnularia borealis var. rectangularis Carlson (Fig. 122)

Length 19-45 μm ; width 7-8 μm ; striae 7 in 10 μm (Patrick and Reimer, 1966, p. 619).

P. borealis var. rectangularis was infrequent in the Keet Seel hanging garden and the creek in Betatakin.

Pinnularia brebissonii (Kuetz.) Rabenhorst (Fig. 123)

Length 38-45 μm ; width 11-12 μm ; striae 13-14 in 10 μm
(Patrick and Reimer, 1966, p. 614).

P. brebissonii was observed in the June collections from Inscription House Creek.

Pinnularia microstauron (Ehr.) Cleve

Length 54 μ m; width 11 μ m; striae 11 in 10 μ m (Patrick and Reimer, 1966, p. 597).

P. microstauron was rare in collections from the slickrock in Inscription House.

Pinnularia sudetica var. commutata (Grun.) Cleve-Euler (Fig. 139)

Length 60-110 μ m; width 13-15 μ m; striae 8 in 10 μ m (Cleve-Euler, 1955, p. 75).

P. sudetica var. commutata was rare to infrequent in collections from the creek in Betatakin Canyon. Some of our specimens were longer than originally reported by Cleve-Euler (1955). They appear similar to the specimen illustrated by Foged (1971) under the epithet P. brevicostata, but do not fit the description given in Hustedt (1930b) for that taxon. This species also closely resembles P. viridis var. commutata but has a filamentous raphe and striae which are radiate in the center and convergent at the ends. Cleve-Euler (1955) placed Navicula commutata Grun. as illustrated in A. Schmidt's Atlas der Diatomaceen-Kunde (1876) in P. sudetica var. commutata, but also considered P. viridis var. commutata a synonym. Patrick and Reimer (1966) in their discussion of P. sudetica state that N. commutata does not seem to be P. sudetica. Further examinations of these taxa are warranted.

Genus CYMBELLA

Cymbella cymbiformis var. nonpunctata Fontell (Fig. 131)

Length 40 um; width 11 um; dorsal striae 8-9 in 10 um; ventral striae 10-11 in 10 um (Patrick and Reimer, 1975, p. 55).

C. cymbiformis var. nonpunctata was rare in the August collection from Inscription House.

Cymbella incerta var. naviculacea Grunow (Fig. 124)

Length 35-48 um; width 9-10 um; dorsal striae 13-14 in 10 um, becoming 19-20 near the ends; ventral striae 16 in 10 um, becoming 19-20 near the ends (Cleve-Euler, 1953, p. 140).

C. incerta var. naviculacea was rare in the hanging gardens and Betatakin Creek. This species is a common constituent of hanging gardens throughout the Intermountain West.

Cymbella mexicana var. janischii (A. S.) Reimer (Fig. 133)

Length 147-250 um; width 40-62 um; striae 6-9 in 10 um (Patrick and Reimer, 1975, p. 60).

C. mexicana var. janischii was rare in both the spring and seep in the study. Our specimens did not have an isolated stigma in the central area.

Cymbella microcephala Grunow (Fig. 127, 128)

Length 15-16 um; width 3 um; striae 24 in 10 um, becoming finer near the ends (Patrick and Reimer, 1975, p. 33).

C. microcephala was rare to infrequent in collections from both hanging gardens. It was common to abundant in collections from the seep at Keet Seel. Our specimens, like others we have seen in hanging gardens, are not as rostrate at the ends as usual.

Cymbella minuta var. silesiaca (Bleisch in Rabh.) Reimer (Fig. 129, 130)

Length 15-30 μm ; width 6-10 μm ; striae 10-12 in 10 μm , becoming 14-16 in 10 μm near the ends (Patrick and Reimer, 1975, p. 49).

C. minuta var. silesiaca was rare to common in collections from the hanging gardens, springs, and Inscription House Creek. Some of our specimens were small for this taxon.

Cymbella naviculiformis Auerswald in Rabenhorst (Fig. 126)

Length 40-42 μm ; width 10-12 μm ; striae 10-15 in 10 μm (Patrick and Reimer, 1975, p. 31).

C. naviculiformis was seen in samples from Betatakin Creek.

Cymbella norvegica Grunow (Fig. 125)

Length 46 μm ; width 9 μm ; dorsal striae 12 in 10 μm , becoming 18 in 10 μm near the ends; ventral striae 11 in 10 μm , becoming 16 in 10 μm near the ends (Patrick and Reimer, 1975, p. 25).

C. norvegica was rare in collections from the seep at Keet Seel. Our specimens had striae which were coarser in the center and finer at the ends than normal.

Cymbella turgida (Gregory) Cleve

Length 33-40 μm ; width 10-12 μm ; striae 8-9 in 10 μm (Hustedt, 1930b, p. 358).

C. turgida was rare in Inscription House Creek. A single specimen was seen in the soils.

Cymbella species 1 (Fig. 132)

Valve linear-lanceolate with rostrate to capitate ends; axial area narrow, linear, more heavily silicified than the rest of the valve; central area small, orbicular; striae slightly radiate, 20-22 in 10 μm ; length 16-25 μm ; width 4-4.5 μm .

This Cymbella was infrequent to common in collections from Keet Seel and the Betatakin hanging garden. It resembles C. microcephala, but it differs in shape from what we normally consider that taxon.

Genus AMPHORA

Amphora coffeiformis (C. A. Ag.) Kuetzing (Fig. 134, 135)

Length 15-23 μm ; valve width 3.5-4 μm ; girdle width 10 μm ; striae 20-22 in 10 μm (Patrick and Reimer, 1975, p. 78).

A. coffeiformis occurred only in the more mesic sites, and usually in low frequencies. It was most common in Betatakin Creek, but was also found in the spring and the seep in the study. The striae were finer than normal for this taxon.

Amphora perpusilla (Grun.) Grunow (Fig. 144)

Length 11 μ m; girdle width 6 μ m; striae 18 in 10 μ m (Patrick and Reimer, 1975, p. 70).

A. perpusilla was rare in collections from Keet Seel seep and Betatakin spring.

Amphora veneta Kuetzing (Fig. 136, 137)

Length 19-27 μ m; valve width 4-5 μ m; girdle width 10 μ m; striae 20 in 10 μ m, becoming finer at the ends (Patrick and Reimer, 1975, p. 72).

A. veneta was found in low numbers in collections from the creeks and hanging gardens in the monument.

Family GOMPHONEMACEAE

Genus GOMPHONEMA

Gomphonema parvulum Kuetzing (Fig. 138)

Length 23-27 μ m; width 5.5-7 μ m; striae 11-13 in 10 μ m (Patrick and Reimer, 1975, p. 122).

G. parvulum was rare to infrequent in both creeks and in the spring at Betatakin.

Family EPITHEMIACEAE

Genus DENTICULA

Denticula elegans Kuetzing (Fig. 140)

Length 20-35 μm ; valve width 5-7 μm ; girdle width 12-15 μm ; costae 3 in 10 μm ; striae 16-18 in 10 μm (Patrick and Reimer, 1975, p. 170).

D. elegans was rare to common in the seep at Keet Seel. It was rare in the hanging gardens.

Denticula elegans f. valida Pedicino (Fig. 141, 142)

Length 24-30 μm ; width 4-8 μm ; costae 3-4 in 10 μm ; striae 20 in 10 μm (Patrick and Reimer, 1975, p. 171).

D. elegans f. valida was common in the hanging gardens and rare in the springs. It was also important in the soils. This taxon is very close to the nominate variety, but differs by having finer striae. Though reported chiefly from hot springs, we have seen this species in other hanging gardens in the Intermountain West.

Genus EPITHEMIA

Epithemia adnata (Kuetz.) Brebisson (Fig. 147-150)

Length 24-78 μm ; width 9.5-12 μm ; costae 2-4 in 10 μm ; alveoli 10-14 in 10 μm (Patrick and Reimer, 1975, p. 179).

E. adnata was common in the hanging gardens and Betatakin Creek, and rare in the springs. Our specimens showed a great deal of variety, but because all of the forms intergraded they were kept in this taxon.

Epithemia adnata var. minor (Perag. & Herib.) Patrick (Fig. 145, 146)

Length 35-38 um; width 7-9 um; costae 2-3 in 10 um; alveoli 13-14 in 10 um (Patrick and Reimer, 1975, p. 180).

E. adnata var. minor was common in Betatakin Creek and rare at Keet Seel. It is distinguished from the nominate variety by its rostrate ends.

Genus RHOPALODIA

Rhopalodia gibba (Ehr.) O. Mueller (Fig. 152)

Length 65-80 um; girdle width 16-18 um; valve views unobserved; costae 6 in 10 um; alveoli unresolved (Patrick and Reimer, 1975, p. 189).

R. gibba was rare in the August collections from Betatakin. Our specimens are shorter than normal for this taxon and therefore resemble R. parallela. However, they do not have the striae composed of double rows of punctate peculiar to that taxon. The size range fits R. gibba var. ventricosa, but the frustules are not swollen enough to be placed in that taxon.

Rhopalodia gibba var. ventricosa (Kuetz.) H. & M. Peragallo (Fig. 151)

Length 64-75 um; girdle width 23-25 um; valve width 6-7 um; costae 6-8 in 10 um; alveoli 12-14 in 10 um (Patrick and Reimer, 1975, p. 190).

R. gibba var. ventricosa was common in collections from the creek in Betatakin Canyon.

Rhopalodia gibberula (Ehr.) O. Mueller (Fig. 143)

Length 26-28 um; width 6-7 um; costae 4 in 10 um; alveoli 13-15 in 10 um (Patrick and Reimer, 1975, p. 191).

R. gibberula was rare in collections from the creek in Betatakin Canyon.

Family NITZSCHIACEAE

Genus HANTZSCHIA

Hantzschia amphioxys (Ehr.) Grunow (Fig. 153, 154)

Length 29-45 (65-75) um; width 6-9 um; fibulae 6-9 in 10 um; striae 18-25 in 10 um (Hustedt, 1930b, p. 394).

H. amphioxys was the most important soil diatom, and was common in the Betatakin hanging garden. It was also rare to infrequent at all other sites. Most of our specimens were 29-45 um long, but in the June collection from Betatakin Creek specimens ranging from 65-75 um were seen. Many of our specimens had finer striae than normal.

Hantzschia amphioxys f. capitata O. Mueller (Fig. 155)

Length 27-40 um; width 5-7 um; fibulae 7-9 in 10 um; striae 20-25 in 10 um (Hustedt, 1930b, p. 394).

H. amphioxys f. capitata was infrequent to common in the hanging gardens. It was rare in Betatakin Creek. Like the nominate variety, our specimens had finer striae than normal.

Genus NITZSCHIA

Nitzschia communis Rabenhorst (Fig. 156-158)

Length 27-32 μm ; width 5-5.5 μm ; fibulae 9-11 in 10 μm ; striae 30 in 10 μm , or unresolved (Hustedt, 1930b, p. 417).

N. communis was collected from all sites in Betatakin and from Inscription House Creek. It was common to abundant in the spring, infrequent to common in the creeks; and rare to infrequent in the hanging garden.

Nitzschia hantzschiana Rabenhorst (Fig. 159-163)

Length 16-35 μm ; width 2.5-4 μm ; keel punctae 8-14 in 10 μm ; striae 22-24 in 10 μm (Hustedt, 1930b, p. 415).

N. hantzschiana was abundant throughout the year in the spring at Betatakin. It was common in Betatakin Creek, and rare to infrequent in all other sites in the study.

Nitzschia linearis W. Smith (Fig. 166)

Length 107-122 μm ; width 5-6 μm ; fibulae 9-11 in 10 μm ; striae 28-30 in 10 μm (Hustedt, 1930b, p. 409).

N. linearis was rare in collections from both springs, the hanging garden at Keet Seel, and Inscription House Creek.

Nitzschia minutula Grunow in Van Heurck

Length 21-36 μm ; width 4-5 μm ; keel punctae 11-14 in 10 μm ; striae 28 in 10 μm (Lange-Bertalot, 1976, p. 264).

N. minutula was rare to infrequent in collections from both creeks and the hanging garden in Betatakin.

Nitzschia palea (Kuetz.) W. Smith (Fig. 167, 168, 176)

Length 27-35 μm ; width 3-5 μm ; fibulae 12-14 in 10 μm ; striae unresolved (Hustedt, 1930b, p. 416).

N. palea was common to abundant in collections from Inscription House Creek. It was rare to common in collections from all sites in Betatakin.

Nitzschia paleacea Grunow (Fig. 173, 174)

Length 23-38 μm ; width 1.5-4 μm ; fibulae 12-17 in 10 μm ; striae unresolved (Hustedt, 1930b, p. 416).

N. paleacea was rare to common in both creeks, infrequent in the hanging garden at Betatakin, and rare in both the spring and the seep. Some of our specimens fit the description of N. holsatica, but this taxon has recently been placed under N. paleacea (Lange-Bertalot, 1976).

Nitzschia pusilla (Kuetz.) Grunow emend. Lange-Bertalot (Fig. 165)

Length 20-26 μm ; width 4-5 μm ; fibulae 13-14 in 10 μm ; striae unresolved (Lange-Bertalot, 1976, p. 273).

N. pusilla was common in the November collection from Betatakin Creek.

Nitzschia romana Grunow (Fig. 164)

Length 15-20 um; width 4.5-5 um; fibulae 12 in 10 um;
striae 24-25 in 10 um (Hustedt, 1930b, p. 415).

N. romana was rare to infrequent in collections from the
seep at Keet Seel and rare in collections from both creeks.

Nitzschia tryblionella var. debilis (Arnott) A. Mayer (Fig. 175)

Length 20-21 um; width 10 um; costae 14-16 in 10 um (Hustedt,
1930b, p. 400).

N. tryblionella var. debilis was rare to infrequent in
collections from the creek in Betatakin Canyon.

Nitzschia valdestriata Aleem & Hustedt (Fig. 170)

Length 8-14 um; width 2-3 um; fibulae 8 in 10 um; striae
11-14 in 10 um (Lange-Bertalot & Simonsen, 1978, p. 58).

N. valdestriata was infrequent in collections from Betatakin
Creek. Our specimens had coarser striae than normal for this
taxon.

Family SURIRELLACEAE

Genus SURIRELLA

Surirella angusta Kuetzing (Fig. 169)

Length 27 um; width 8 um; costae 5-7 in 10 um; striae 26 in 10 um
(Hustedt, 1930b, p. 435).

S. angusta was identified from a single frustule seen in the June
collection from Inscription House Creek.

Surirella ovalis Brebisson (Fig. 171)

Length 45-55 um; width 26-28 um; costae 3-4 in 10 um;
striae 14-15 in 10 um (Hustedt, 1930 b, p. 441).

S. ovalis was rare in collections from both creeks.

Surirella spiralis Kuetzing (Fig. 172)

Length 103-122 um; width 57-73 um; costae 1-2 in 10 um;
punctae scattered through valve (Hustedt, 1930b, p. 445).

S. spiralis was rare to infrequent in collections from Keet
Seel seep and Betatakin spring.

Conclusions

A total of 138 algal taxa were observed in this study. Of these, 30 were blue-green algae (Cyanophyta); 2 were green algae (Chlorophyta); 3 were Euglenophyta; 1 was a chrysophyte; and 102 were diatoms (Bacillariophyta). Achnanthes linearis, Achnanthes minutissima, Caloneis bacillum, Hantzschia amphioxys, Lyngbya limnetica, Microcoleus vaginatus, Navicula cryptocephala var. veneta, Navicula mutica var. cohnii, and Nitzschia hantzschiana were the most common and widespread species, each occurring in all three segments of the monument in most study sites. Betatakin Canyon had the greatest diversity with 113 algal taxa. Keet Seel and Inscription House both had 69 taxa.

Algal distribution by division is summarized in Table 1. The creeks had the highest number of taxa with 93 species. The

two creeks were fairly dissimilar in their floras, most likely due to the differences in organic enrichment. Betatakin Creek had 70 algal taxa, while Inscription House Creek had only 49 taxa. The dominant algae in Betatakin Creek were Epithemia adnata, Epithemia adnata var. minor, Navicula cryptocephala var. veneta, Nitzschia hantzschiana, Oscillatoria subbrevis, Rhopalodia gibba var. ventricosa, and Tribonema bombycinum. The dominant algae in Inscription House Creek were Chlorococcum humicola, Navicula pupula, Nitzschia palea, and Nitzschia paleacea. Many of the species of this creek are indicative of organically enriched water of high mineral content.

The springs were also fairly different from each other, perhaps due to the differences in flow. A total of 73 algal taxa were seen in the two habitats with 53 taxa in Keet Seel and 44 taxa in Betatakin. The dominant species in the spring at Keet Seel was Microcystis aeruginosa. Also present were many of the species important in the hanging garden, particularly Nostoc species. Diatoms in the seep varied with the seasons, but the most common were Caloneis bacillum, Cymbella minuta var. silesiaca, Navicula minima, and Navicula tantula. The dominant species in the spring at Betatakin were Achnanthes lanceolata, Calothrix parietina, Nitzschia communis, Nitzschia hantzschiana, and Tribonema bombycinum.

Floras of the two hanging gardens were quite similar. Of the 80 algal taxa in the hanging gardens, 40 were common to both sites, with 63 taxa in Betatakin and 53 taxa in Keet Seel. The dominant algae were filamentous Cyanophyta, particularly Lyngbya limnetica, Microcoleus vaginatus, Nostoc commune, and Nostoc

muscorum. The diatom flora of the Betatakin hanging garden was similar to a soil flora. Hantzschia amphioxys, Navicula mutica, Navicula mutica var. cohnii, and Pinnularia appendiculata were the dominant species. The Keet Seel drip wall was more mesic, with Achnanthes linearis, Denticula elegans f. valida, and Navicula gallica being dominant, and also demonstrated more seasonality than Betatakin. The lichen-covered wall in Inscription House had a sparse flora. Only 7 taxa were observed and all of these were found in the other hanging gardens.

The algal flora of the hanging gardens is very similar to the floras of gardens we have studied elsewhere. Filamentous Cyanophyta make up the bulk of the biomass and several diatoms have been present in all gardens we have observed. These include Achnanthes coarctata, Achnanthes lanceolata, Caloneis bacillum, Cymbella incerta var. naviculacea, Cymbella minuta var. silesiaca, Cymbella norvegica, Denticula elegans, Denticula elegans f. valida, Hantzschia amphioxys, Navicula cryptocephala var. veneta, Navicula mutica, and Pinnularia appendiculata. Hanging gardens in the monument did not have the extensive Cymbella and Gomphonema floras that are common in the more mesic gardens of other localities.

The soils were floristically uniform. Microcoleus vaginatus, Nostoc muscorum, and Scytonema myochrous comprised the bulk of the biomass. The diatom flora was dominated by Hantzschia amphioxys and Navicula mutica var. cohnii, with Caloneis bacillum, Navicula mutica, and Pinnularia borealis also being important.

Algal distribution in the monument by species is summarized in Table 2. The seasonal distribution of the algae is given in Table 3. The soils and Betatakin hanging garden showed little seasonality, having much the same floras year-round. The creek in Betatakin also showed little variation through the year. The diatom flora in the hanging garden and seep at Keet Seel demonstrated seasonal changes, though the non-diatom flora was fairly constant.

The present study in Navajo National Monument has been important for at least three reasons. First, it has increased our knowledge of the algal flora of hanging garden habitats. Second, it has contributed to knowledge of arid land algal floras in general. And third, it has aided in our understanding of the ecological distribution of algal species in microhabitats. Similar studies are planned, both to refine our knowledge of the cryptogam floras of Navajo National Monument and to provide further information on other arid land sites.

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Table 1. Algal Distribution in Habitats by Division.

Division	Total	Hanging Garden	Spring	Creek	Soil
<u>Cyanophyta</u>	30	20	19	18	10
<u>Chlorophyta</u>	2	2	1	1	1
<u>Euglenophyta</u>	3	1	0	3	0
<u>Chrysophyta</u>	1	0	1	1	0
<u>Bacillariophyta</u>	100	58	51	70	20
Total species	136	81	72	93	31
Restricted species		6	7	33	4

Table 2. Algal Distribution in Navajo National Monument.*

Species	Betatakin	Keet Seel	Inscription House
<u>Cyanophyta</u>			
Anabaena variabilis	So		So
Aphanocapsa grevillei	H		C
Calothrix marchica	C		
Calothrix parietina	S		
Chlorogloea fritschii	HS	H	So
Chroococcus rufescens	HCSO		HSO
Chroococcus turgidus	H	HS	So
Chroococcus varius			C
Gleocapsa aeruginosa	HS	H	
Gleocapsa decorticans	H	H	
Gleocapsa magma			C
Gleocapsa punctata	H	HS	HC
Gomphosphaeria aponina var. cordiformis		S	
Lyngbya limnetica	HSCSo	HS	HC
Merismopedia glauca			C
Microcoleus vaginatus	HSSO	HS	CSO
Microcystis aeruginosa	C	S	C
Microcystis incerta	H	HS	
Nostoc commune	HCSO	HS	

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree lichens.

Table 2. Continued*

Species	Betatakin	Keet Seel	Inscription House
<i>Nostoc muscorum</i>	HSo	HS	So
<i>Nostoc paludosum</i>	S	HS	
<i>Oscillatoria angusta</i>	H		H
<i>Oscillatoria angustissima</i>	HS		
<i>Oscillatoria geminata</i>	HC		C
<i>Oscillatoria obscura</i>	SC		C
<i>Oscillatoria subbrevis</i>	HSC	H	C
<i>Oscillatoria tenuis</i>	HS	H	C
<i>Phormidium angustissimum</i>			C
<i>Phormidium tenue</i>	HSC		So
<i>Scytonema myochrous</i>	HSSo		CSo
<u>Chlorophyta</u>			
<i>Chlorococcum humicola</i>	HSo	SoT	C
<i>Oocystis species</i>		HS	
<u>Euglenophyta</u>			
<i>Euglena fusca</i>	C		
<i>Euglena proxima</i>	H		C
<i>Trachelomonas abrupta</i>	C		
<u>Chrysophyta</u>			
<i>Tribonema bombycinum</i>	SC		

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree Lichens.

Table 2. Continued*

Species	Betatakin	Keet Seel	Inscription House
<u>Bacillariophyta</u>			
Achnanthes coarctata	HC	HS	
Achnanthes exigua	SC	HS	
Achnanthes lanceolata	SC	HS	
Achnanthes lewisiana	HS		
Achnanthes linearis	HSCSo	H	So
Achnanthes microcephala	HSO	HSO	
Achnanthes minutissima	HSC	HS	C
Amphora coffeiformis	SC	S	
Amphora perpusilla	S	S	
Amphora veneta	HC	S	C
Anomoeoneis sphaerophora			C
Anomoeoneis zellensis	C	S	
Caloneis bacillum	HSCSo	HS	So
Caloneis lewisii	C		
Caloneis ventricosa var. truncatula	HC	HS	C
Cocconeis placentula var. euglypta	S		
Cocconeis placentula var. lineata	S	HS	
Cyclotella bodanica	So		
Cyclotella meneghiniana	H		
Cymbella cymbiformis var. nonpunctata			C
Cymbella incerta var. naviculacea	HC	HS	

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree Lichens.

Species	Betatakin	Keet Seel	Inscription House
<i>Cymbella mexicana</i> var. <i>janischii</i>	S	HS	
<i>Cymbella microcephala</i>	H	HS	
<i>Cymbella minuta</i> var. <i>silesiaca</i>	HS	HS	C
<i>Cymbella naviculiformis</i>	C		
<i>Cymbella norvegica</i>		S	
<i>Cymbella turgida</i>			CSo
<i>Cymbella</i> species 1	H	HS	
<i>Denticula elegans</i>	H	HS	
<i>Denticula elegans</i> f. <i>valida</i>	HSSo	HSSo	So
<i>Diatoma vulgare</i> var. <i>breve</i>	HSo		
<i>Epitemia adnata</i>	HSC	HS	
<i>Epitemia adnata</i> var. <i>minor</i>	C	HS	
<i>Fragilaria</i> species 1		S	
<i>Fragilaria lapponica</i>		HS	C
<i>Fragilaria vaucheriae</i>	HS		
<i>Gomphonema parvulum</i>	SC		C
<i>Hannaea arcus</i>		T	
<i>Hantzschia amphioxys</i>	HSCSo	HSSoT	HCSO
<i>Hantzschia amphioxys</i> f. <i>capitata</i>	HC	H	
<i>Melosira roeseana</i>	HCSO	HSSo	So
<i>Navicula abiskoensis</i>	C	S	C
<i>Navicula accomoda</i>	HC		C

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree Lichens.

Table 2. Continued*

Species	Betatakin	Keet Seel	Inscription House
<i>Navicula arvensis</i>	HC		C
<i>Navicula capitata</i> var. <i>hungarica</i>			C
<i>Navicula cincta</i>	C		
<i>Navicula contenta</i> f. <i>biceps</i>	C	HS	
<i>Navicula cryptocephala</i> var. <i>veneta</i>	HSC	HS	C
<i>Navicula cuspidata</i>	H		C
<i>Navicula excelsa</i>	HS	H	
<i>Navicula gallica</i>		HS	
<i>Navicula heufleri</i>	HC		C
<i>Navicula longicephala</i>	HSC	HS	
<i>Navicula luzonensis</i>	C		
<i>Navicula minima</i>	HSC	HS	
<i>Navicula mutica</i>	HSO	HSO	HSO
<i>Navicula mutica</i> var. <i>cohnii</i>	HSCSO	HSSO	HSO
<i>Navicula mutica</i> var. <i>nivalis</i>	H		
<i>Navicula mutica</i> var. <i>undulata</i>	H		So
<i>Navicula notha</i>	C		
<i>Navicula pupula</i>	HC		C
<i>Navicula pupula</i> var. <i>rectangularis</i>	C		
<i>Navicula radiosa</i>	C		
<i>Navicula secreta</i> var. <i>apiculata</i>	C		C

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree Lichens.

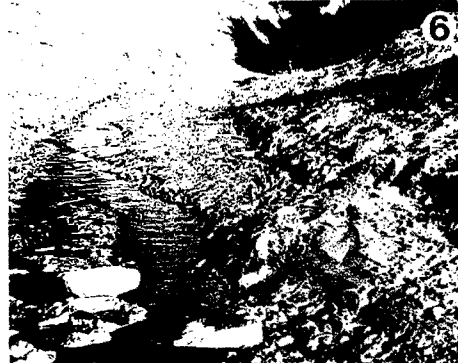
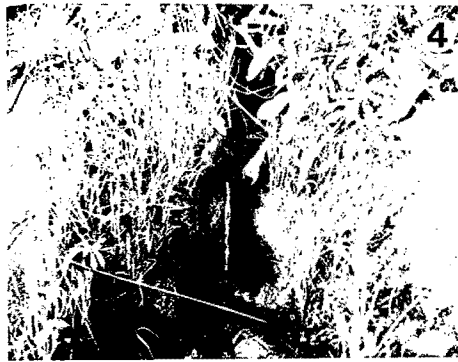
Species	Betatakin	Keet Seel	Inscription House
<i>Navicula seminuloides</i>	HC	H	
<i>Navicula seminulum</i>	C		
<i>Navicula seminulum</i> var. <i>hustedtii</i>		H	
<i>Navicula tantula</i>	H	HS	
<i>Navicula tripunctata</i>			So
<i>Navicula tripunctata</i> var. <i>schizonemoides</i>	HCSO	HS	C
<i>Navicula viridula</i> var. <i>rostellata</i>			C
<i>Navicula</i> species 1	HSSO	HSO	So
<i>Navicula</i> species 2			C
<i>Neidium affine</i> var. <i>amphirhynchus</i>	C		
<i>Nitzschia communis</i>	HSC		C
<i>Nitzschia hantzschiana</i>	HSC	HS	C
<i>Nitzschia linearis</i>	S	HS	C
<i>Nitzschia minutula</i>	HC		C
<i>Nitzschia palea</i>	HSC		C
<i>Nitzschia paleacea</i>	HSC	S	C
<i>Nitzschia pusilla</i>	C		
<i>Nitzschia romana</i>	C	S	C
<i>Nitzschia tryblionella</i> var. <i>debilis</i>	C		
<i>Nitzschia valdestriata</i>	C		
<i>Pinnularia appendiculata</i>	HSCSO	HSO	So
<i>Pinnularia borealis</i>	HSO	HS	So

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree Lichens.

Table 2. Continued*

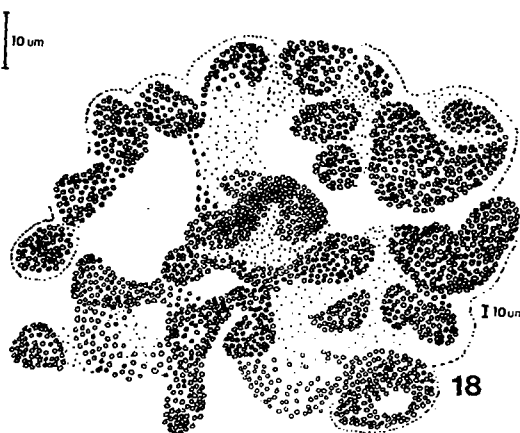
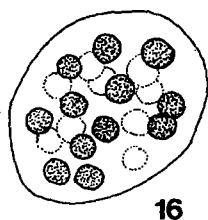
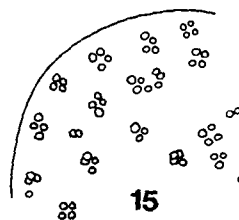
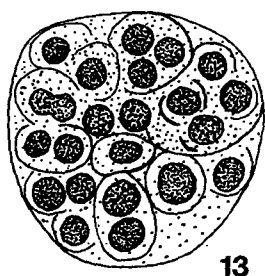
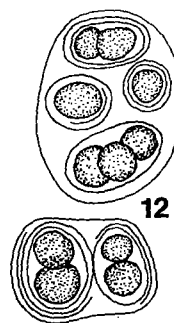
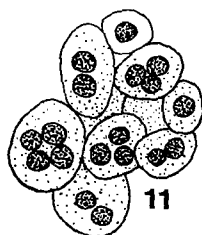
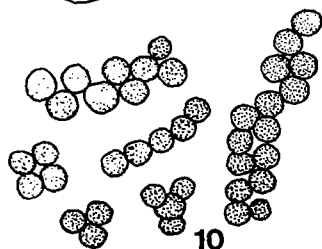
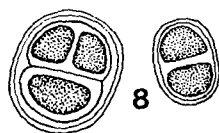
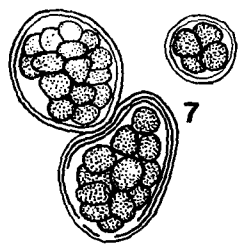
Species	Betatakin	Keet Seel	Inscription House
<i>Pinnularia borealis</i> var. <i>rectangularis</i>	C	H	
<i>Pinnularia brebissonii</i>			C
<i>Pinnularia microstauron</i>			So
<i>Pinnularia sudetica</i> var. <i>commutata</i>	C		
<i>Rhopalodia gibba</i>	HSC		
<i>Rhopalodia gibba</i> var. <i>ventricosa</i>	C		
<i>Rhopalodia gibberula</i>	C		
<i>Stauroneis anceps</i>	C		
<i>Stauroneis phoenicenteron</i>	C		
<i>Stauroneis wislouchii</i>	C	H	C
<i>Stephanodiscus astraia</i> var. <i>minutula</i>			So
<i>Surirella angusta</i>			C
<i>Surirella ovalis</i>	C		C
<i>Surirella spiralis</i>	S	S	

*H = Hanging Garden or Drip Wall; S = Spring; C = Creek; So = Soil;
T = Tree Lichens.



Figures 1-6.

- Fig. 1. Xeric drip wall at the base of the Betatakin trail.
- Fig. 2. Betatakin hanging garden.
- Fig. 3. Keet Seel hanging garden.
- Fig. 4. Betatakin spring.
- Fig. 5. Betatakin Creek.
- Fig. 6. Inscription House Creek.



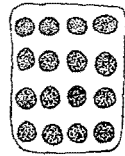
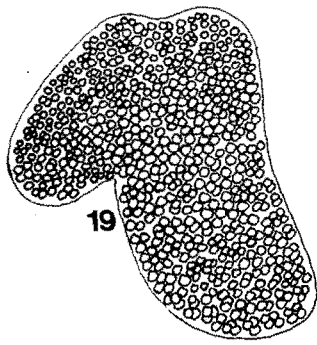
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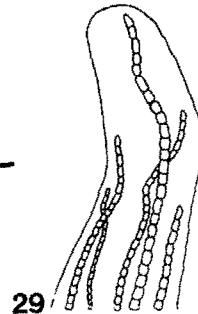
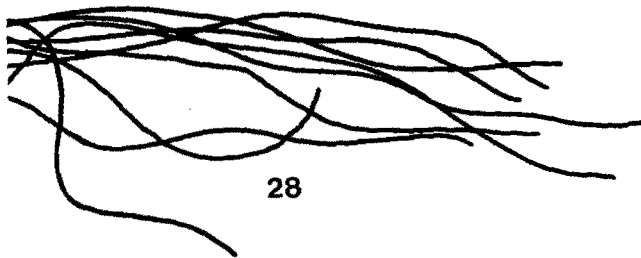
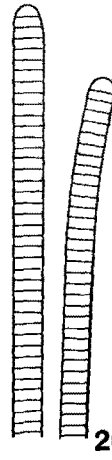
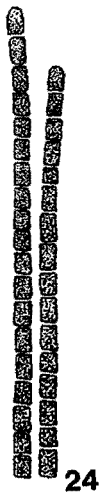
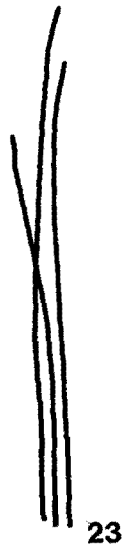
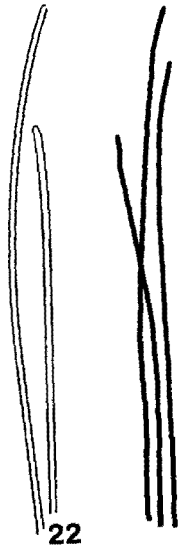
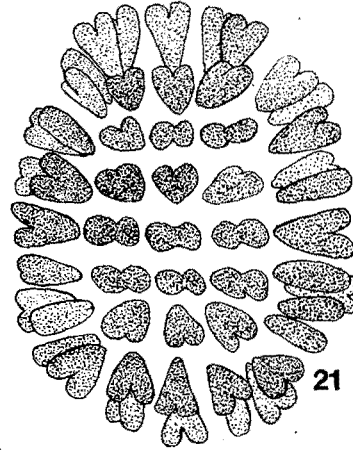
Figures 7-18.

- Fig. 7. Chroococcus rufescens
Fig. 8. Chroococcus turgidus
Fig. 9. Chroococcus varius
Fig. 10. Chlorogloea fritschii
Fig. 11. Gleocapsa aeruginosa
Fig. 12. Gleocapsa decorticans
Fig. 13-14. Gleocapsa magma
Fig. 15. Gleocapsa punctata
Fig. 16. Aphanocapsa grevillei
Fig. 17. Microcystis aeruginosa
Fig. 18. Microcystis aeruginosa low power, not drawn to scale

All illustrations drawn to the same scale except where noted.



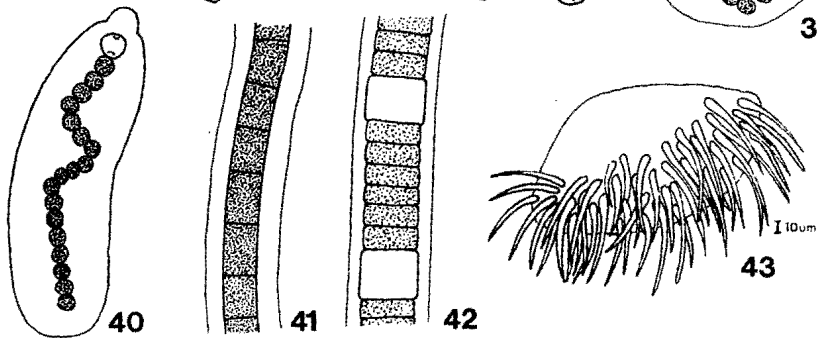
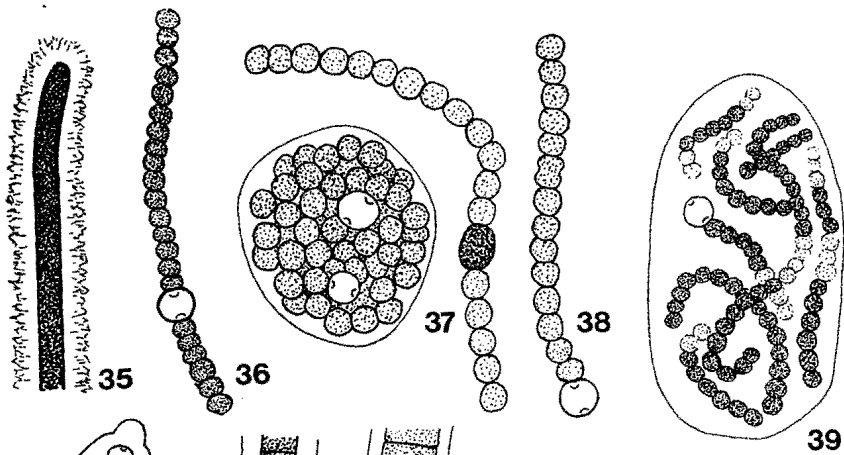
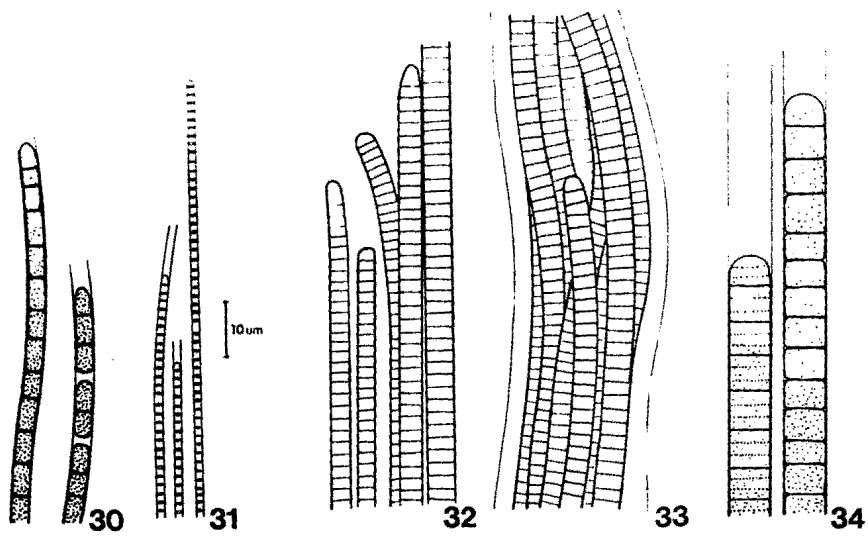
10 μ m



Figures 19-29.

- Fig. 19. Microcystis incerta
- Fig. 20. Merismopedia glauca
- Fig. 21. Gomphosphaeria aponina var. cordiformis
- Fig. 22. Oscillatoria angusta
- Fig. 23. Oscillatoria angustissima
- Fig. 24. Oscillatoria geminata
- Fig. 25. Oscillatoria obscura
- Fig. 26. Oscillatoria subbrevis
- Fig. 27. Oscillatoria tenuis
- Fig. 28. Phormidium angustissimum
- Fig. 29. Phormidium tenue

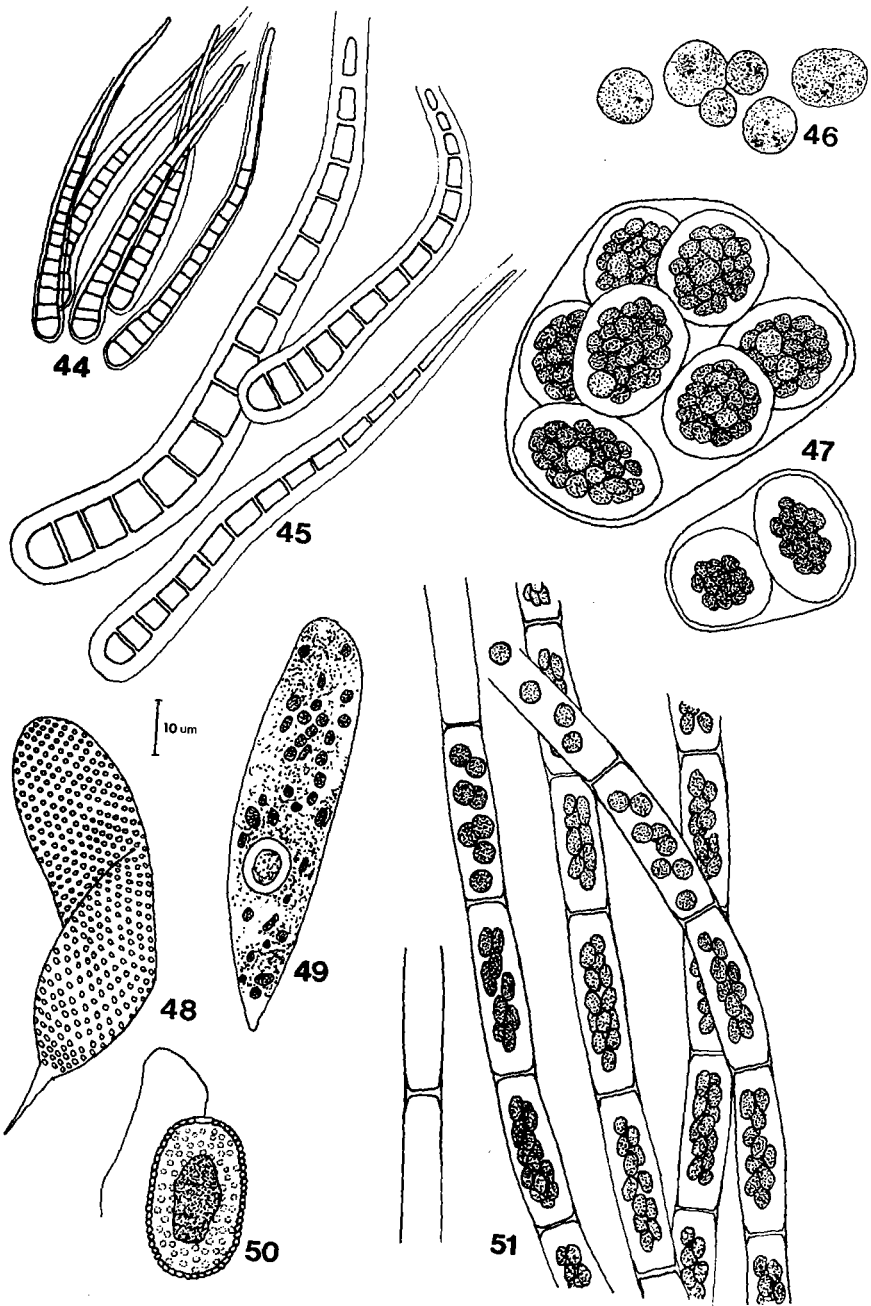
All illustrations drawn to the same scale.



Figures 30-43.

- Fig. 30-31. Lyngbya limnetica
- Fig. 32-33. Microcoleus vaginatus
- Fig. 34. Microcoleus vaginatus robust form
- Fig. 35. Microcoleus vaginatus lime incrustated form
- Fig. 36. Anabaena variabilis
- Fig. 37. Nostoc commune young colony
- Fig. 38. Nostoc commune
- Fig. 39. Nostoc muscorum
- Fig. 40. Nostoc paludosum
- Fig. 41-42. Scytonema myochrous
- Fig. 43. Calothrix marchica low power, not drawn to scale

All illustrations drawn to the same scale except where noted.



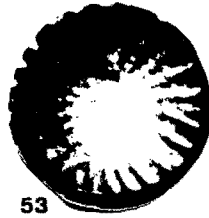
Figures 44-51.

- Fig. 44. Calothrix marchica
- Fig. 45. Calothrix parietina
- Fig. 46. Chlorococcum humicola
- Fig. 47. Oocystis species
- Fig. 48. Euglena fusca
- Fig. 49. Euglena oxyuris var. minor
- Fig. 50. Trachelomonas abrupta
- Fig. 51. Tribonema bombycinum

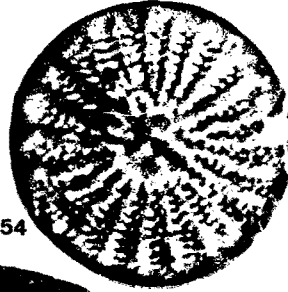
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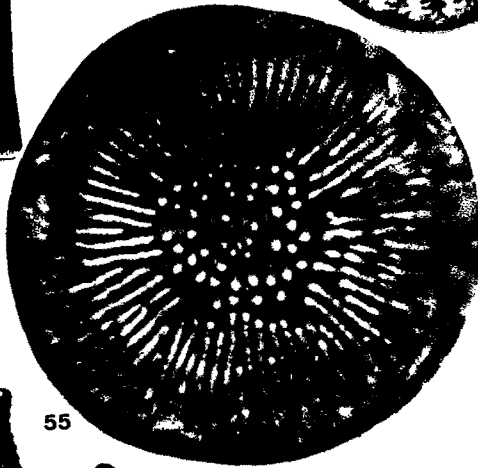
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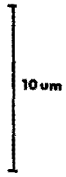
53



54



55



10 μ m



56



57



58



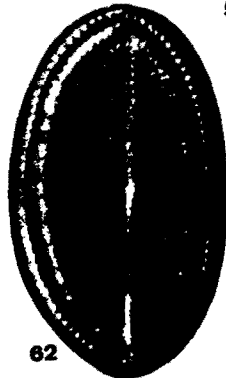
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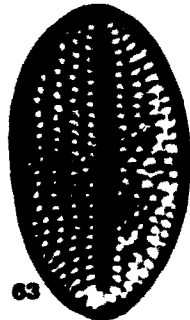
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61



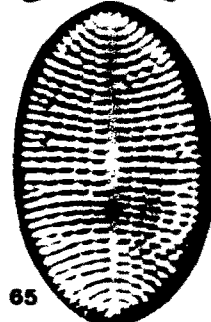
62



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64

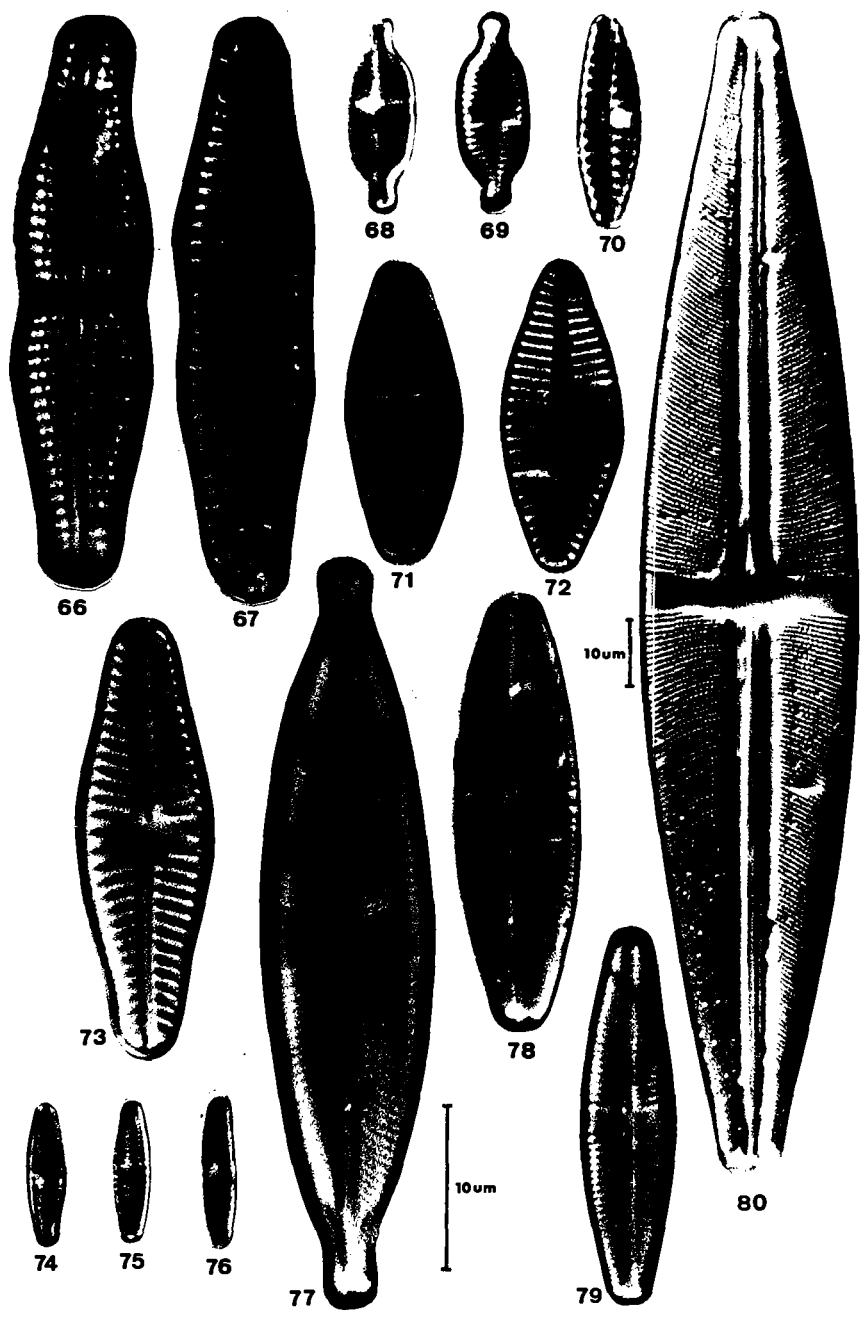


65

Figures 52-65.

- Fig. 52-53. Melosira roeseana
- Fig. 54. Stephanodiscus astraee var. minutula
- Fig. 55. Cyclotella bodanica
- Fig. 56. Diatoma vulgare var. breve
- Fig. 57-58. Fragilaria vaucheriae
- Fig. 59. Fragilaria lapponica
- Fig. 60-61. Fragilaria species 1
- Fig. 62. Cocconeis placentula raphe valve
- Fig. 63. Cocconeis placentula var. euglypta
- Fig. 64-65. Cocconeis placentula var. lineata

All photographs taken at 1000X except where noted.



Figures 66-80.

Fig. 66-67. Achnanthes coarctata

Fig. 68-69. Achnanthes exigua

Fig. 70-73. Achnanthes lanceolata

Fig. 74-75. Achnanthes linearis

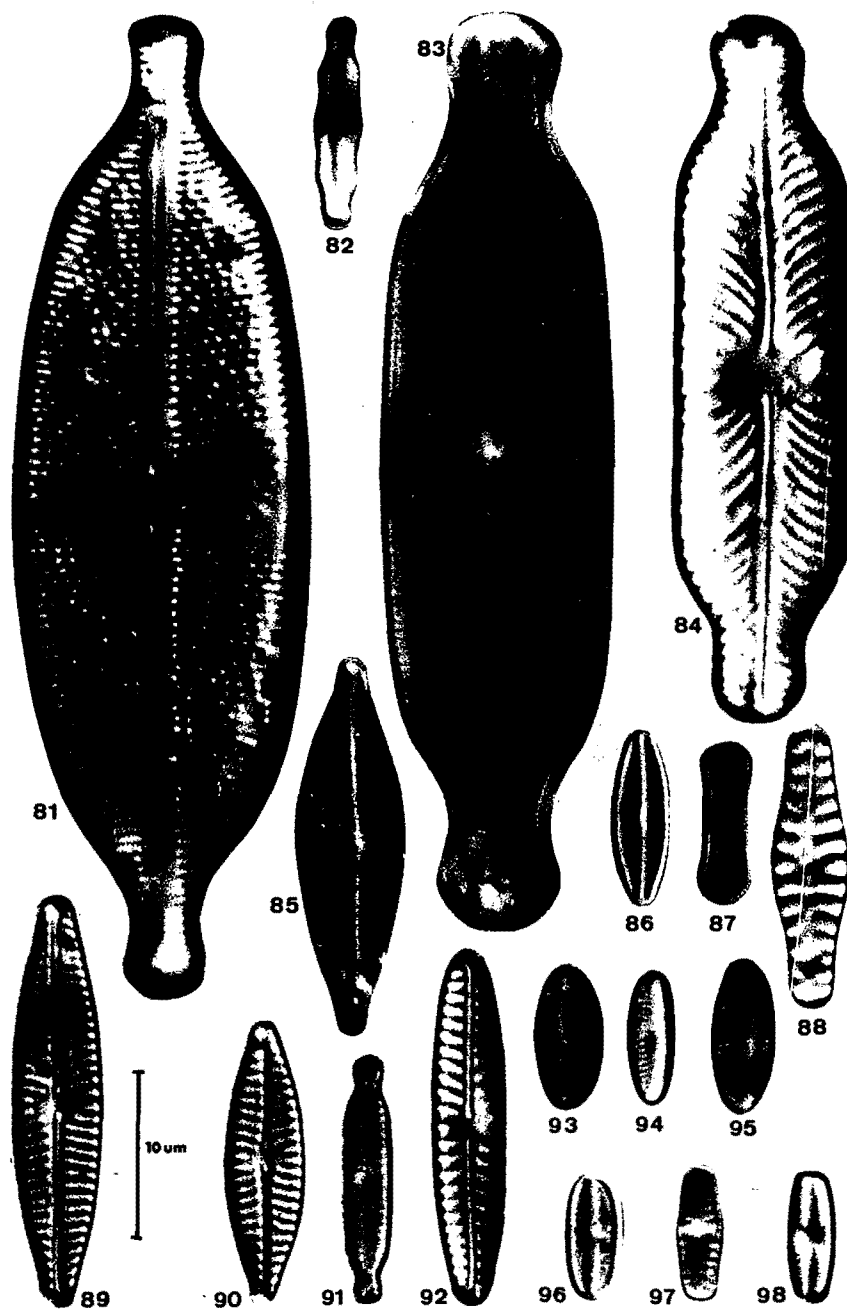
Fig. 76. Achnanthes minutissima

Fig. 77. Stauroneis anceps

Fig. 78-79. Stauroneis wislouchii

Fig. 80. Stauroneis phoenicenteron 400X, not to the same scale

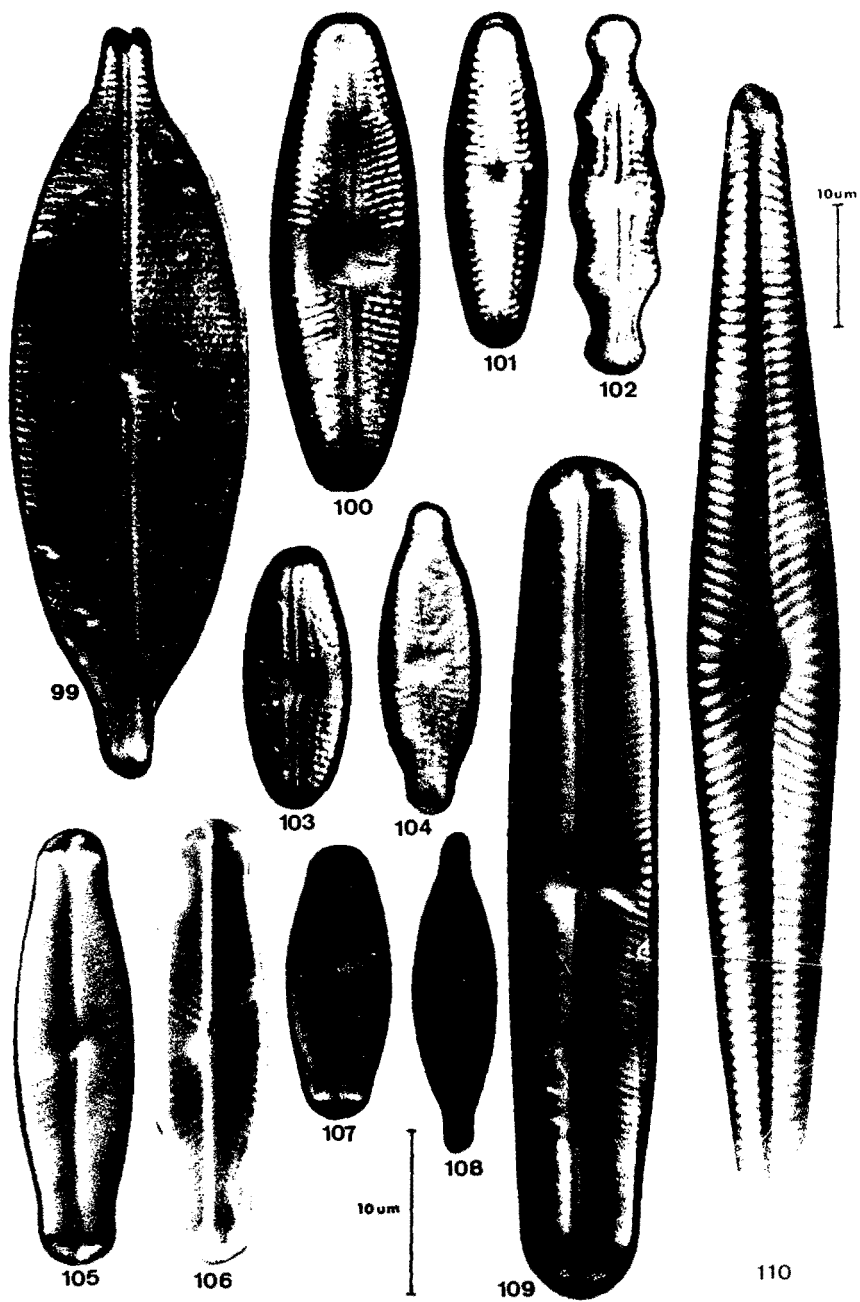
All photographs taken at 1000X except where noted.



Figures 81-98.

- Fig. 81. Anomoeoneis sphaerophora
- Fig. 82. Anomoeoneis zellensis
- Fig. 83. Neidium affine var. amphirhynchus
- Fig. 84. Navicula abiskoensis
- Fig. 85. Navicula accomoda
- Fig. 86. Navicula arvensis
- Fig. 87. Navicula contenta f. biceps
- Fig. 88. Navicula capitata var. hungarica
- Fig. 89. Navicula cincta
- Fig. 90. Navicula cryptocephala var. veneta
- Fig. 91. Navicula longicephala
- Fig. 92. Navicula heufleri
- Fig. 93. Navicula excelsa
- Fig. 94. Navicula gallica
- Fig. 95. Navicula luzonensis
- Fig. 96. Navicula minima
- Fig. 97. Navicula seminulum
- Fig. 98. Navicula tantula

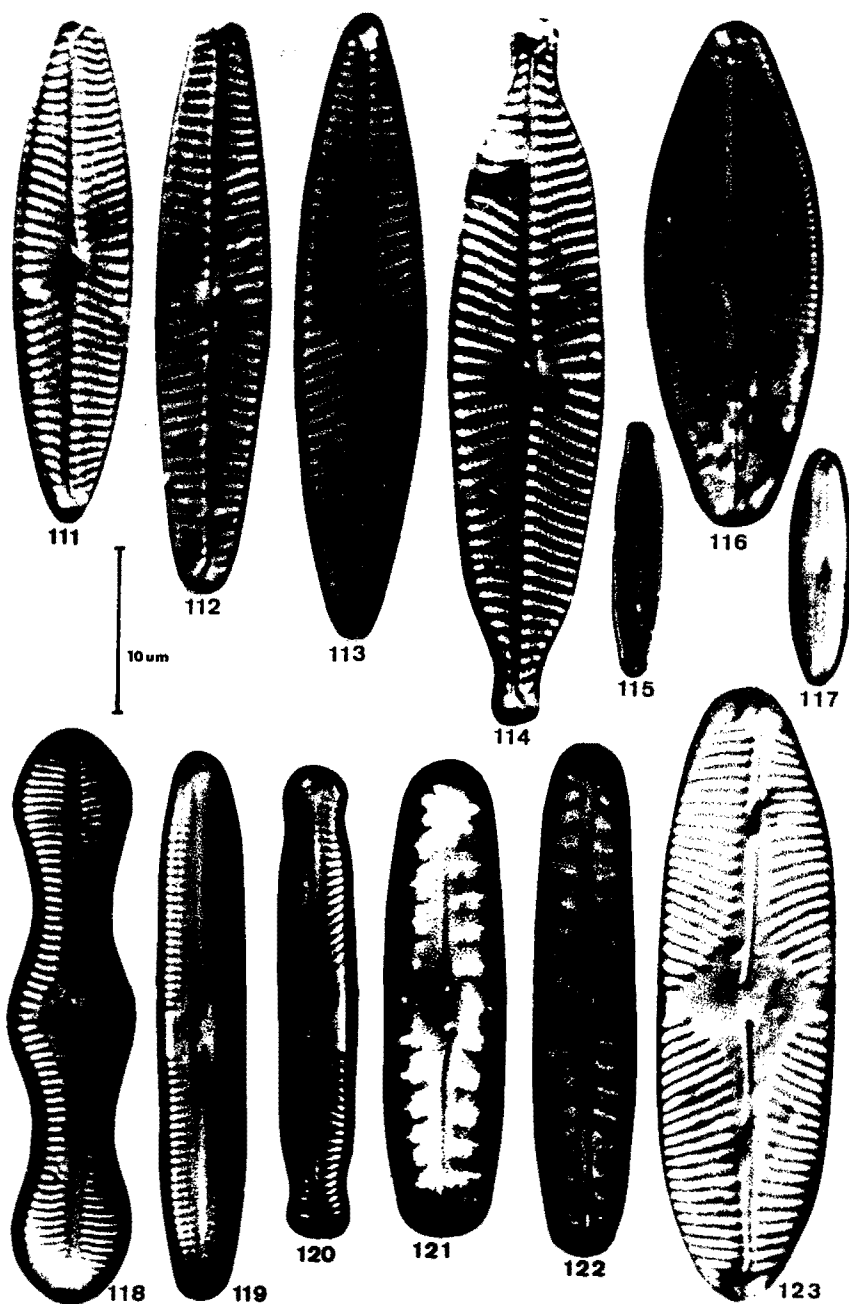
All photographs taken at 1000X except where noted.



Figures 99-110.

- Fig. 99. Navicula cuspidata
- Fig. 100-101. Navicula mutica
- Fig. 102. Navicula mutica var. nivalis
- Fig. 103. Navicula mutica var. cohnii
- Fig. 104. Navicula mutica var. undulata
- Fig. 105-107. Navicula pupula
- Fig. 108. Navicula secreta var. apiculata
- Fig. 109. Navicula pupula var. rectangularis
- Fig. 110. Navicula radiosa not to the same scale

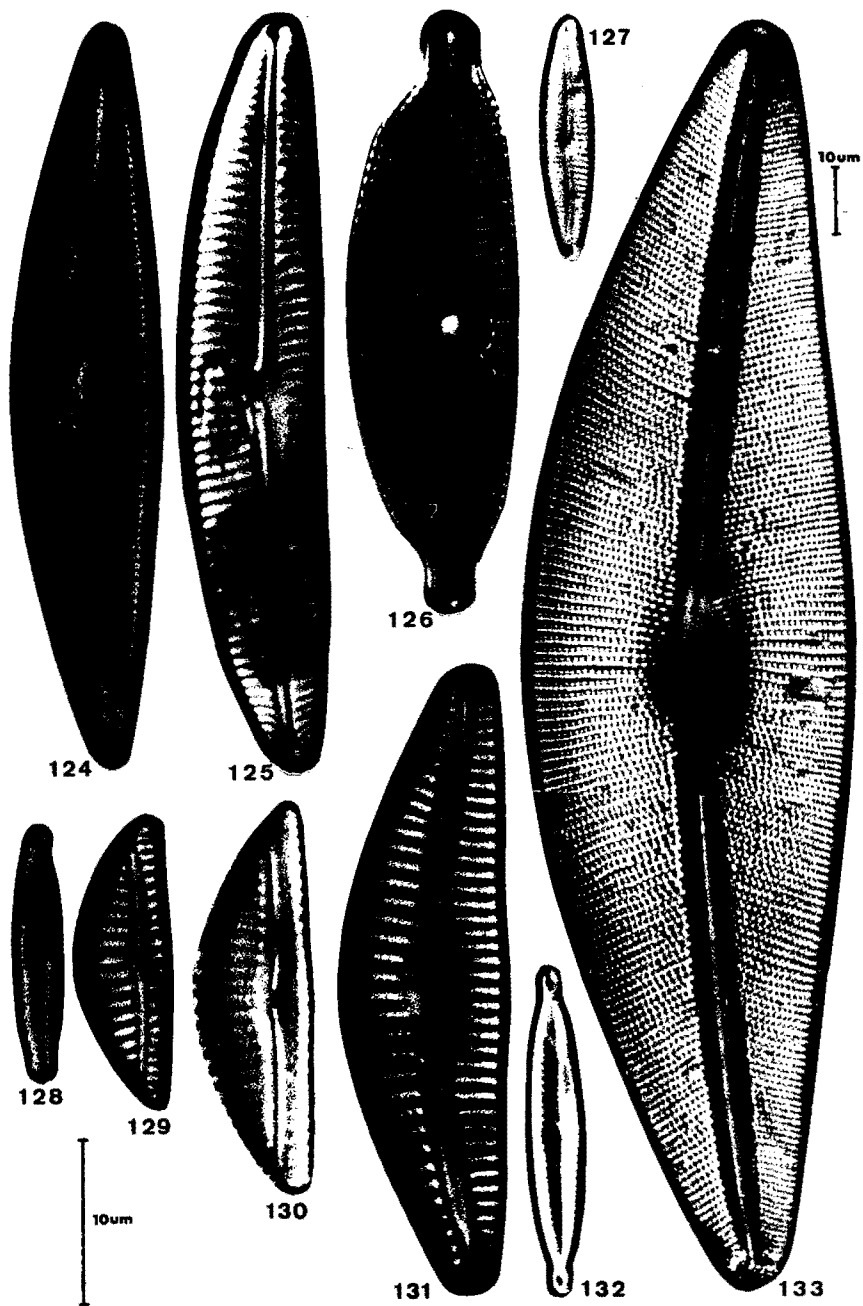
All photographs taken at 1000X except where noted



Figures 111-123.

- Fig. 111. Navicula tripunctata
- Fig. 112-113. Navicula tripunctata var. schizonemoides
- Fig. 114. Navicula viridula var. rostellata
- Fig. 115. Navicula species 1
- Fig. 116. Navicula species 2
- Fig. 117. Caloneis bacillum
- Fig. 118. Caloneis lewisii
- Fig. 119. Caloneis ventricosa var. truncatula
- Fig. 120. Pinnularia appendiculata
- Fig. 121. Pinnularia borealis
- Fig. 122. Pinnularia borealis var. rectangularis
- Fig. 123. Pinnularia brebissonii

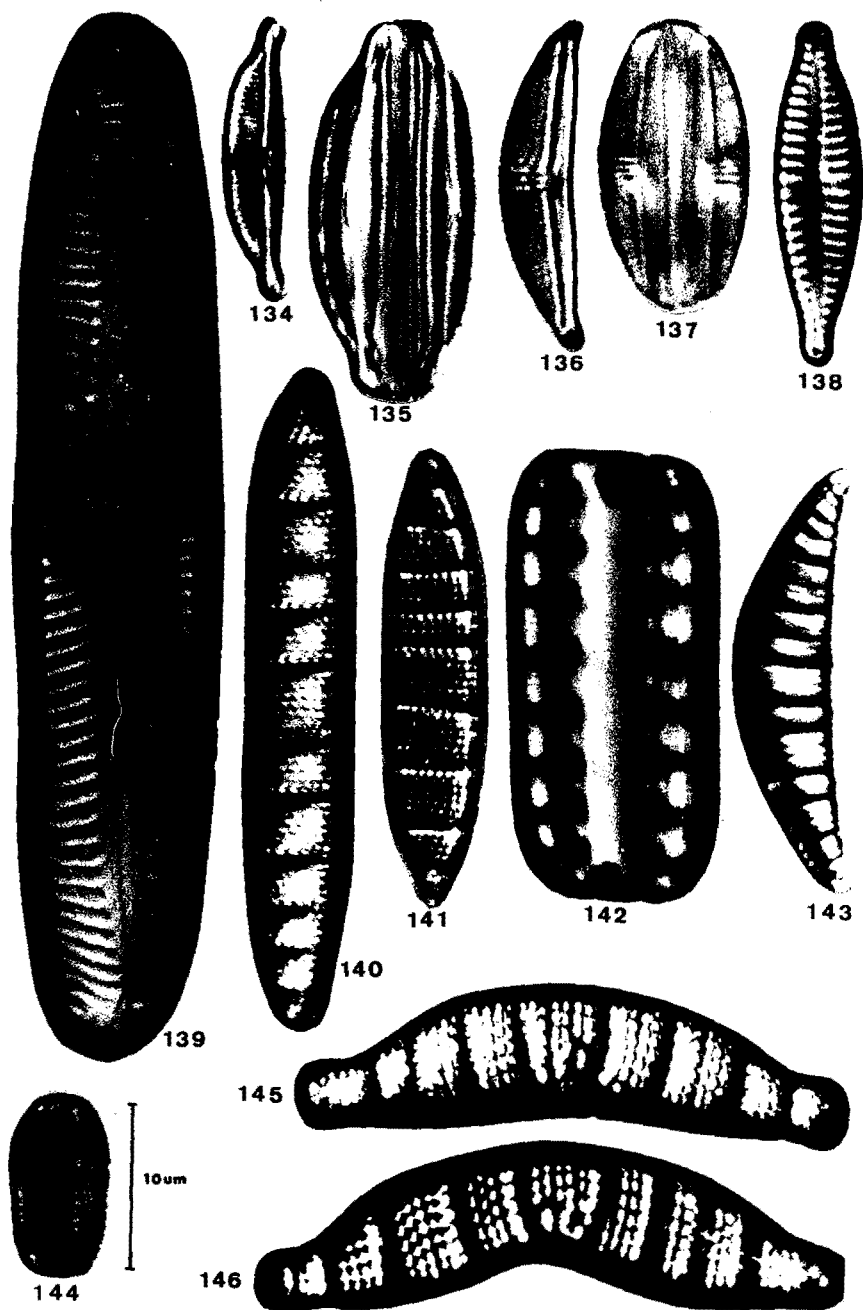
All photographs taken at 1000X except where noted.



Figures 124-133.

- Fig. 124. Cymbella incerta var. naviculaceae
Fig. 125. Cymbella norvegica
Fig. 126. Cymbella naviculiformis
Fig. 127-128. Cymbella microcephala
Fig. 129-130. Cymbella minuta var. silesiaca
Fig. 131. Cymbella cymbiformis var. nonpunctata
Fig. 132. Cymbella species 1
Fig. 133. Cymbella mexicana var. janischii 400X, not to the
 same scale

All photographs taken at 1000X except where noted.



Figures 134-146.

Fig. 134-135. Amphora coffeiformis

Fig. 136-137. Amphora veneta

Fig. 138. Gomphonema parvulum

Fig. 139. Pinnularia sudetica var. commutata

Fig. 140. Denticula elegans

Fig. 141-142. Denticula elegans f. valida

Fig. 143. Rhopalodia gibberula

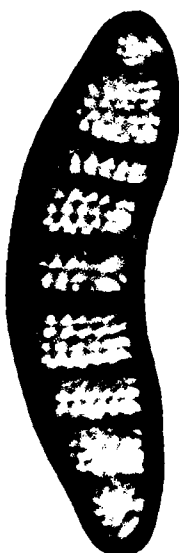
Fig. 144. Amphora perpusilla

Fig. 145-146. Epithemia adnata var. minor

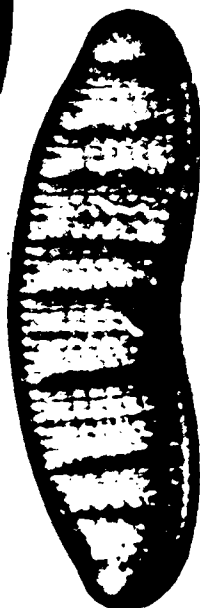
All photographs taken at 1000X except where noted.



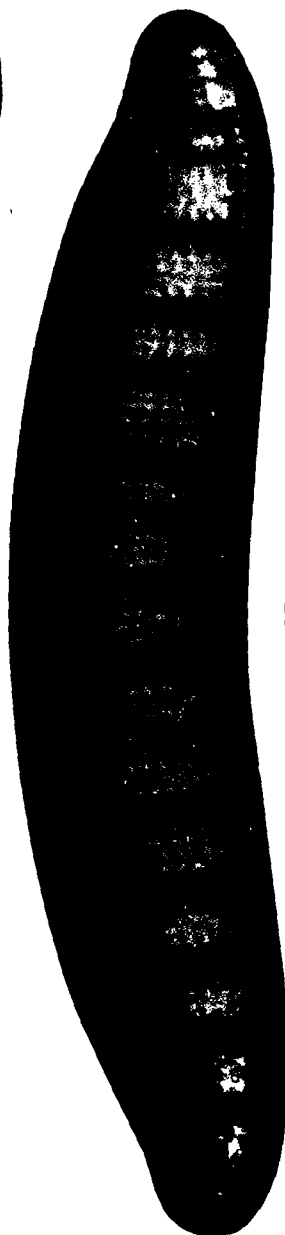
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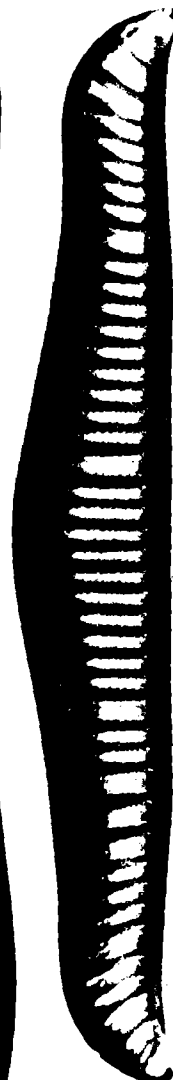
148



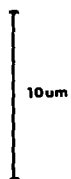
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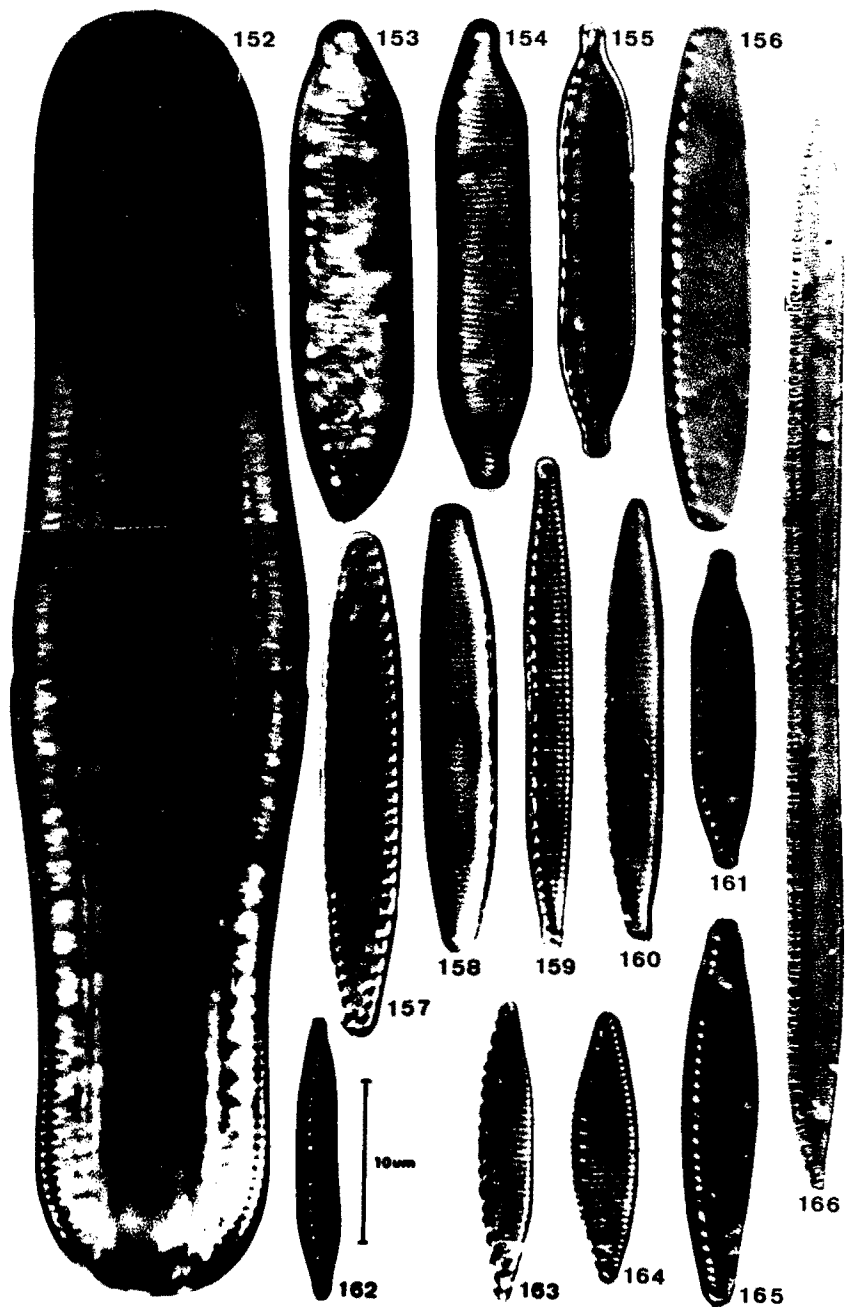
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Figures 147-151.

Fig. 147-150. Epithemia adnata

Fig. 151. Rhopalodia gibba var. ventricosa

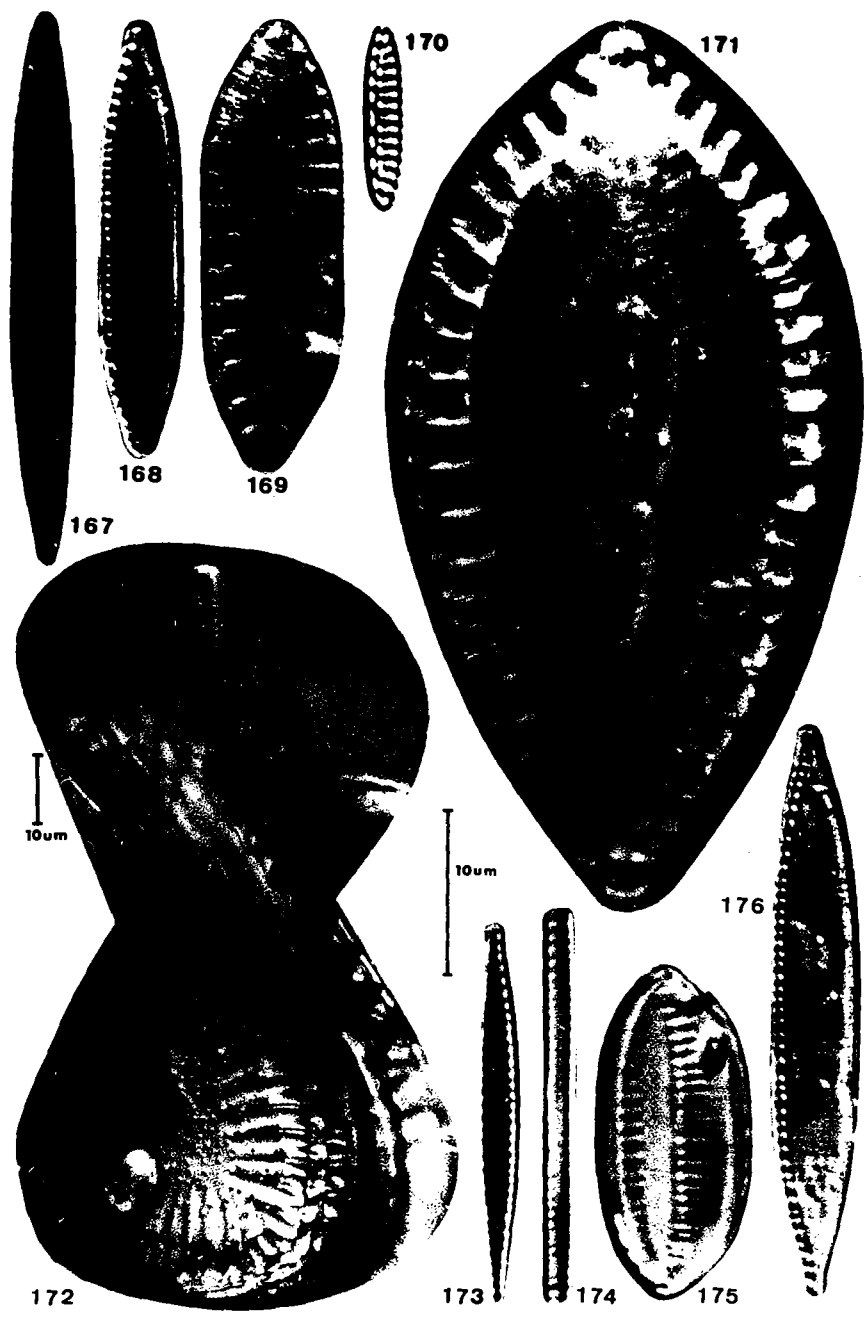
All photographs taken at 1000X except where noted.



Figures 152-166.

- Fig. 152. Rhopalodia gibba
- Fig. 153-154. Hantzschia amphioxys
- Fig. 155. Hantzschia amphioxys f. capitata
- Fig. 156-158. Nitzschia communis
- Fig. 159-163. Nitzschia hantzschiana
- Fig. 164. Nitzschia romana
- Fig. 165. Nitzschia pusilla
- Fig. 166. Nitzschia linearis not to the same scale

All photographs taken at 1000X except where noted.



Figures 167-176.

- Fig. 167-168. Nitzschia palea
Fig. 169. Surirella angusta
Fig. 170. Nitzschia valdestriata
Fig. 171. Surirella ovalis
Fig. 172. Surirella spiralis 400X, not to the same scale
Fig. 173-174. Nitzschia paleacea
Fig. 175. Nitzschia tryblionella var. debilis
Fig. 176. Nitzschia palea

All photographs taken at 1000X except where noted.