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GLEN CANYON NATIONAL RECREATION AREA

**A SURVEY AND CLASSIFICATION OF THE RIPARIAN
VEGETATION IN SIDE CANYONS AROUND LAKE POWELL**

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INTRODUCTION

A diversity of wetland plant communities occurs on the Colorado Plateau. For convenience, these can be grouped into six main kinds: marshland, riparian, hanging garden-spring, strand, lake, and tinaja (waterpocket). These categories are summarized in Table 1 (tables begin on p. 34) with principal plant and environmental characteristics. All wetland communities (in the general sense) can be defined as vegetation composed at least partly of obligate phreatophytes (or water-loving plants) growing in sites, where either the water table is at or near the ground surface, or which are periodically flooded. Phreatophytes are species which require abundant available water during the growing season, generally by exploiting a ground water table, or which otherwise lack features (morphological or physiological) that could prevent or reduce water loss. The classification presented in Table 1 is intended primarily as a heuristic tool rather than an exact classification. Some kinds of vegetation are not well described by this system (bogs, lacustrine, some springs, algal and charophyte vegetation), and some sites will be transitional between these categories, e.g., strand-riparian, or marshland-lake. Furthermore, obligate riparian species or phreatophytes are not always easily characterized, as they occupy one end of a continuum of water use, with the opposite end comprising arid-adapted species. Campbell and Green (1968) used the term pseudoriparian for those plant species that can exist away from permanent water sources, but which reach their greatest size and maximum abundance where water is freely available.

This report presents the results of the first two years of a three-year NRPP-funded ecological survey of the riparian vegetation within Glen Canyon National Recreation Area (NRA). The 1992-93 fieldwork concentrated on riparian (streamside) communities in selected side canyons of Lake Powell. The third year of the project (1994) was spent establishing a monitoring program in selected riparian sites.

Three main types of riparian zones occur in Glen Canyon NRA; ephemeral, intermittent, and permanent (Driscoll et al. 1984). Ephemeral zones are characterized by a deep water table that lies well below the streambed, with water only present during precipitation events or in brief periods following snowmelt. Intermittent zones have some surface water, seasonally or permanently in some stretches, derived via groundwater discharge. Permanent zones support year round flows. This study concentrated on intermittent and permanent riparian zones, because ephemeral drainages usually lack riparian vegetation. Because of variable combinations of disturbance, topography, substrate and channel type, animal activity, and available plant species, riparian vegetation in these canyons is both complex and variable. Survey work concentrated primarily on vegetation occurring within the channels or on the fluvial terraces of streams. Some marshland vegetation (eg., beaver ponds) occurred, however, within the matrix of predominantly riparian vegetation. This vegetation was included within the survey. All vegetation surveyed and reported in this study was found above the highest water level reached by Lake Powell in the period 1980-1986 (ca. 1130 m or 3706 feet), when it was at full pool.

Data is presented on riparian plant species distribution, growth form, and cover from general floristic surveys as well as quantitative descriptions of 148 plots. The primary goals were to, 1) produce a classification of the riparian vegetation around Lake Powell, 2) present a detailed description of the resulting vegetation types, 3) examine the relationships between vegetation and the physical environment, 4) discuss the origin and dynamics of the riparian vegetation, 5) make recommendations for the third year of the project, and 6) make recommendations on how to monitor and manage these riparian communities. Derived from the basic data is a preliminary classification of riparian vegetation, with analyses of species richness,

evenness, diversity, and preliminary comparisons between the vegetation and environmental features. Finally, the riparian zones of those canyons investigated are ranked by criteria of water resources, biodiversity, disturbance, and communities present.

The report is organized into a brief literature review of riparian research in the region, area description, site selection, data collection, analysis and interpretation methods, results, discussion, and recommendations. The appendices include a full plant species list, glossary of statistical and mathematical methods, and key to the vegetation types.

LITERATURE REVIEW

Riparian vegetation in the American southwest is less well known than adjacent upland desert vegetation (Brown 1982). The most detailed study in the region is that of Szaro (1989, 1990) on riparian vegetation of Arizona and New Mexico. He described 28 vegetation communities derived from 152 plots. Padgett et al. (1989) provides a classification and description of high elevation riparian communities of forestlands of southern Utah. Other important regional studies include those of Baker (1989a,b, 1990) in western Colorado, Webb and Brotherson (1988) in southwestern Utah, Harper et al. (1992) in Zion National Park, and Heil et al. (1993) and Romme et al. (1993) in Capitol Reef National Park.

Most research on the vegetation along the Colorado River in the area now within the boundaries of Glen Canyon NRA deals with upland desert communities (Schultz et al. 1987; Tuhy and MacMahon 1988; West 1988; Spence 1990). Very little published work is available on riparian and wetland vegetation. Perhaps the best known communities are the hanging gardens (Welsh and Toft 1981; Welsh 1984, 1989; Stanton et al. 1992; Spence and Henderson 1992; Spence 1995). Riparian vegetation along the Colorado River and its tributaries was first studied by Clover and Jotter (1944) and Woodbury et al. (1959). Irvine (1976) and Irvine and West (1979) described the ecology of the principal woody species along the Escalante River. Waring (1992) studied the developing shoreline communities around Lake Powell. Agenbroad et al. (1990) examined the paleoecology and dynamics of fluvial deposits in Bowns Canyon. Withers and Mead (1993) discussed the paleoecological record and inferred climate for the Willow and Forty Mile drainages on the Escalante River. Other work on riparian vegetation in the area include Camp (1978) and Tuhy and MacMahon (1988). Spence (1991) surveyed several hanging gardens and adjacent riparian zones in the Great Bend part of the San Juan arm of Lake Powell. Spence and Henderson (1993) provide a detailed analysis of vegetation and floristic patterns in tinaja vegetation in the southern Waterpocket Fold in Capitol Reef National Park, directly north of and adjacent to Glen Canyon NRA. Graf (1978) analysed the spread of *Tamarix chinensis* along the Colorado River and its impacts on water flows and geomorphology.

Tuhy and MacMahon (1988) classified the riparian and wetland vegetation of Glen Canyon NRA and surrounding areas into six communities; hanging gardens, perennial riparian, ephemeral washes, and three "pseudoriparian" shrub types, characterized by *Sarcobatus vermiculatus*, *Artemisia tridentata*, and *Atriplex canescens* respectively. The last two are generally not considered riparian because the dominant species are not riparian obligates. Ephemeral wash is principally a geomorphic-topographic type, and satisfactory classification of the vegetation of this type has not yet been achieved (cf. Romme et al. 1993; see below in results).

AREA DESCRIPTION

Glen Canyon NRA comprises 1.25 million acres of canyons, benches, mesas, and the waters of Lake Powell. Numerous riparian zones exist, ranging from the

well-developed riparian scrub along the Colorado River to dry washes with ephemeral stream flows. Rivers include portions of the Colorado, Dirty Devil, Escalante, San Juan, and Paria. Numerous smaller permanent streams also exist within the recreation area.

The geology of Glen Canyon NRA is very complex. Strata range in age from Permian to Cretaceous, and include sandstone, siltstone, mudstone, and shale units. Much of the central part of the recreation area, and many of the canyons investigated in this study, are incised in the Glen Canyon Group, which consists of the Navajo, Kayenta, and Wingate sandstones. Canyons formed in these sandstones tend to be sheer-walled, narrow, and rocky. The Navajo Formation is permeable to water, while the underlying Kayenta Sandstone is much less permeable. Hence springs and seeps emerge at the contact of these units and are important controlling factors in the distribution of many riparian vegetation types. Superimposed on the geological strata are numerous Quaternary alluvial, colluvial, and eolian deposits. Many side canyons around Lake Powell have extensive deposits of Holocene alluvium, deposited mainly in the period from ca. 1250-1350 to 1880 AD, although some alluvium from Bowns Canyon is much older (Graf 1987; Agenbroad et al. 1990). Some canyons, however, record different periods of incision and sedimentation (Boison and Patten 1985; Patton and Boison 1986).

The prevailing climate in Glen Canyon NRA is arid and warm. The lowest elevations in Glen Canyon NRA are in the Lees Ferry area (950 m), while the highest elevations occur on the Kaiparowits Plateau and Orange Cliffs (2280-2290 m). Climate data from four stations within or near the recreation area are presented in Table 2. Mean annual temperature varies from 13-15° C, while all stations except Hite record annual precipitation totals under 200 mm (7.8"). Using adiabatic lapse rates (based on Betancourt 1984), precipitation at 2100 m would be ca. 320 mm, and mean annual temperature ca. 9° C. Precipitation often falls as snow in winter months. Most areas below 1400 m experience 210-220 frost-free days per year. At the climate stations, annual potential evapotranspiration rates are very high, varying from 1400-1500 mm depending on locality (Ascroft et al. 1992). Precipitation peak is in August-September, and results from southern monsoonal storms. Flash flooding is often frequent at this time of year. Little data is available on past flood activities on the rivers and permanent streams in the recreation area. Webb and Baker (1987) document major flood frequency along the Escalante River. Four large (100- or 500-year floods) have occurred in the last 400 years, and all may have occurred between 1909 and 1932. Studies from other areas, particularly the Paria River (Graf et al. 1991; Webb et al. 1991), indicate that major terrace incision and streambed degradation has been concentrated in relatively short periods. These periods of climatic instability can be linked to episodes of the Southern Oscillation-El Niño (ENSO) event. The last degradational period was from ca. 1880 to 1940. Between 1940 and 1990, most streams on the Colorado Plateau were aggrading their beds.

The predominant upland vegetation types include arid blackbrush, shadscale, saltbush shrublands, grasslands, and semiarid pinyon-juniper woodlands above ca. 1450 m. Much of the park consists of cliffs, steep talus, and expanses of slickrock supporting little vegetation.

METHODS AND MATERIALS

A. Canyon selection

A preliminary inspection of aerial photos, in conjunction with information on stream flows and surface water (Lively-Schall and Foust 1988), was used to select study canyons. Primary selection criteria included, 1) the canyon was entirely or largely within Glen Canyon NRA, 2) the canyon was relatively undisturbed by livestock and human-related activities, and 3) the canyon

supported riparian vegetation. Excluded were canyons with mostly bare or poorly vegetated stream channels largely lacking in riparian vegetation. The principal sites selected are listed in Table 3. Sites visited included (uplake and clockwise from dam) Last Chance Creek, Dry Rock Creek, parts of the Escalante River, Willow Gulch, Forty Mile Gulch, Scorpion Gulch, Upper Fence Canyon, Chopslot Canyon, Neon Canyon, Cow Canyon, Lower Fence Canyon, Bowns Canyon, Long Canyon, lower Hall's Creek, upper Miller's Creek, Two Mile Canyon, Clearwater Canyon, Knowles Canyon, Forgotten Canyon, Slickrock Canyon, Lake Canyon, Ribbon Canyon, lower Wilson's Creek, and Alcove Canyon. In addition, springs on the southeast shore of Good Hope Bay were surveyed.

B. Field survey techniques

During the canyon surveys, species found in the riparian zones were recorded when encountered. In general, only species considered riparian obligates, or species characteristic of the riparian zone, were noted. Critical or difficult specimens were collected for later identification. In representative homogeneous patches of riparian vegetation temporary plots (relevés) were placed for quantitative description. The plots were 100 m² in extent and circular wherever possible (radius=5.65 m). In some cases dimensions varied, such as where riparian zones were narrow. In these cases plot dimensions were more elongate (rectangular) in shape, but retained the 100 m² size. In a few cases, smaller plots were used. Some patches of Typha and Phragmites vegetation surveyed, for example, were as small as 40-50 m². These plot sizes were chosen because they were common sizes used in description of herbaceous and woody vegetation. Useful summaries of field techniques can be found in Shimwell (1971), Mueller-Dombois and Ellenberg (1974), Bonham (1989), and Rowlands (1994).

Physical data recorded for each plot included date, location, aspect, elevation, amount of litter, soil (or other substrate) and rock, topographic position, flood terrace position, signs of disturbance (biotic, physical), presence of surface water, and exposure. The terrace and exposure levels were arbitrarily defined (Table 4), and were only approximate guidelines to these features. Other variables used in data analysis included distance from plot to upstream barrier or canyon end (headwaters), canyon depth, width, and the ratio of width to depth. These data were derived primarily from site observations, aerial photography, and U.S.G.S. 7.5 minute topographic maps. Finally, a synthetic potential flood intensity variable was calculated for each plot using a combination of geomorphic features. Potential flood intensity (PFI) was defined as

$$PFI = \log_{10}(\text{upstream distance}) * (1/\text{terrace}) * (1/\text{canyon W/D ratio})$$

This equation assumes that flood intensity increases downstream, at least in the narrow rocky canyons of the region, but is modified at any point by height of vegetation above flood channel (higher levels reduce and lower levels increase flood intensity) and canyon profile (wide canyons reduce and narrow canyons increase flood intensity).

Within each plot species presence, height, abundance, and reproductive status, was noted (Table 4). In general, vegetation sampling lasted ca. 15-20 minutes per plot. This time interval was chosen as a compromise between completeness of plot description and number of plots surveyed. In preliminary tests using this technique, about 80-90% of the species present within test plots were located. Species likely to be overlooked include small annuals, or species that are morphologically similar when sterile. This was a problem primarily in spring and early summer, when critical genera like Baccharis, Juncus, Carex, Solidago, and many grasses, were not in flower.

Species abundance, defined as a combination of canopy cover (amount of ground

covered by foliage as projected vertically) and number of individuals and their size, was recorded visually with a modified Daubenmire scale (Table 4).

The scale intervals were chosen to reduce observer bias and increase repeatability of the measure. Height was estimated visually to the nearest meter over one meter, and the nearest decimeter under one meter. Heights above ca. 5 meters were only approximate. The time spent to measure height using a more detailed technique, or by use of an instrument, would have been prohibitive. For woody species, average lowest and highest heights were noted. Presence of flowers or fruits, from the current or previous years, was recorded for all species. A sample riparian data form is included (see Appendix 4).

C. Data analysis

Only a brief description of the methods are presented below. Complete details on mathematical and statistical methods can be found in Appendix 1. Classification of plot vegetation data was done using objective multivariate techniques. Recent work (e.g., Baker 1989a; Padgett et al. 1989; Szaro 1989) has demonstrated the value of multivariate analysis in the interpretation of complex matrices (species X plots) of riparian data. The most common mathematical classification techniques come under the general name of cluster analysis. Several different techniques have been used, including both agglomerative and divisive clustering, which can be either hierarchical or nonhierarchical in nature. There are good reasons for using hierarchical techniques, primarily because hierarchy is a desirable property of a classification (cf. Spence 1992a). Sequential, agglomerative, hierarchical, non-overlapping clustering of vegetation plots using Euclidean distance as the measure of association and Ward's flexible linkage as the clustering algorithm, were used to produce a preliminary clustering of the riparian vegetation. Ordination of the data by principal components analysis was used to study gradients and relationships within the vegetation as well as with environmental variables. Ordinations display relationships among a set of data visually by reducing the dimensionality of the multivariate data set to a series of fewer linear synthetic variables representing the variation in the data. These techniques were designed primarily to portray relationships rather than to classify data into discrete groups. The specific reasons for using these techniques are presented in Appendix 1. The basic data matrix comprised 148 plots by 161 species (162 species were actually recorded but the two *Typha* species were combined for analysis). For each species by plot occurrence, a value was assigned using the 6-point abundance scale, or given a 0 if the species did not occur in the plot in question.

Seven measures were selected to describe and compare groups (=vegetation types) resulting from the cluster analysis. Measures of species richness, diversity and evenness were computed for each plot, and then averaged for each vegetation type. Richness was defined as the number of species found in the plot. Diversity was defined as the Shannon index, while evenness was the Shannon index divided by the $\log_{10}$ of species richness. Specific details are noted in the appendix. Prevalent and modal species were extracted from each vegetation type by the method of Curtis (1959). Prevalent species are characteristic species that attain high frequencies in a particular vegetation type, while modal species are those that reach maximal regional abundance in a particular vegetation type. The index of homogeneity was used to indicate how similar plots within a vegetation type are to each other. The index of distinctiveness determines how distinct each vegetation type is from other types. For identified vegetation types, an index of geographic range was computed as the percentage of canyons each type occurred in. Finally, numbers of ecologically or geographically disjunct species and Colorado Plateau endemics were determined for each type. Details can be found for these measures in Appendix 1. Riparian reléve data are stored in the dBASE III+ file 'RIPDAT.DBF'. Location data for rare and unusual species is located in

the dBASE file 'RARESPP.DBF'.

RESULTS

A. Floristics

A total of 162 species were encountered in at least one plot. Of these, 79 (48%) were native obligate riparian species. Another 18 species (11%) were introduced (non-native). The final 65 species (41%) encountered in the plots were considered native non-riparian, either facultative or pseudoriparian species (in the sense of Campbell and Green 1968), or desert species. All species found in plots during the 1992-1993 field work, as well as other observed riparian species (38 species), are listed in Appendix 2. Problems of identification were encountered with certain groups, principally grasses, Juncus, Baccharis, and Typha. These are noted in Appendix 2. Species nomenclature follows Spence and Zimmerman (1994).

Table 5 presents a summary of life forms for the three groups of species, total native obligate riparian flora (N=111), native non-riparian flora (N=65; plots only), and introduced flora (N=22; plot only; species numbers include taxa not recorded from plots as well). Perennial forbs, perennial graminoids, and shrubs were most common overall. The obligate riparian flora contained relatively more grasses and trees than the non-riparian flora, and included all ferns, fern allies, and lianas. The introduced flora included mostly herbaceous species, and many annuals, especially of forbs. Elaeagnus angustifolia and Tamarix chinensis were the only introduced woody species.

The most widespread species was Equisetum hyemale (76 plots), ubiquitous in the riparian zones of Glen Canyon NRA. Some populations of this species were of the E. hyemale-E. laevigatum hybrid known as E. X ferrissii. Other native species which occurred in 20 or more plots, in order, were Populus fremontii (62), Baccharis salicina (56), Juncus arcticus (53), Artemisia ludoviciana (48), Elymus canadensis (42), Salix exigua (41), Castilleja linariifolia (32), Clematis ligusticifolia (31), Euthamia occidentalis (31), Phragmites australis (29), Apocynum cannabinum (28), Oxytenia acerosa (27), Oenothera longissima (25), Salix goodingii (25), Panicum virgatum (22), Typha species (22; mostly T. domingensis), Chrysothamnus viscidiflorus (21), Muhlenbergia asperifolia (21), and Solidago canadensis (20). Most of these were riparian obligates. The most widespread introduced species were Bromus tectorum (40 plots), Tamarix chinensis (37), and Melilotus alba (18). Of the 162 species encountered in the plots, 37% occurred only in one or two. Native obligate riparian species accounted for 56% of the total flora.

B. Vegetation communities

During the 1992-93 field seasons, 143 plots were surveyed in 25 canyons and Good Hope Bay (Table 3). Five plots surveyed in 1991 in an unnamed canyon (unofficially called Garden) west of Alcove Canyon were also included (data from Spence 1991).

An initial cluster analysis of the 1992 plot data grouped 80 plots into three major clusters, corresponding to forest, scrub, and herbaceous types (Spence 1992b). Because of the large size of the data set, the combined 1992 and 1993 plot data were analysed in three separate groups corresponding to these three categories. This was necessary because the data matrix (148X161) exceeded the matrix array limitations of SYSTAT 5.02. The a priori assumption was made that the primary segregation of the vegetation into the three life form groups would be maintained in the larger data set. Each of these groupings is discussed below.

The final classification of vegetation types is presented in Table 6. Types

are grouped into the three categories, forest and woodland, scrub, and marshland (herbaceous vegetation). Some types were recognized based on only one or a few plots that were extracted from other groups. These types were tentatively recognized because of relatively distinct vegetation physiognomy or floristics.

Most of the vegetation types recognized are probably equivalent with the series level in the U.S. Forest Service system. Within each of the larger or more complex types several series and "phases" based on floristics could be distinguished, with the latter probably equivalent to Forest Service community or habitat types, or floristic associations in the sense of Baker (1989a) and Szaro (1989). The term adopted in this study is vegetation type, so as not to imply exact correspondence with series, community and habitat types, or floristic associations.

Below, data on floristics, structure and site environment are presented for each type. A summary of chief vegetation and site features is provided in tables for all types comprising three or more plots. Each type was assigned to one or more series in the SRFR classification (Spence et al. 1995). Finally, comparisons were made with other regional classifications, particularly those on the Colorado Plateau. Appendix 3 is a key to the vegetation types.

1. FOREST AND WOODLAND

In all, 53 plots were dominated by one or more of several tree species. The three plots with Douglas fir from upper Miller's Creek were not included in the analysis as they were very distinct from all other vegetation types in the region (Spence 1992b, 1992c), and no additional work was done on them in 1993-94. The dendrogram resulting from a cluster analysis of the 50 plots is presented in Figure 2. Two main clusters emerged, corresponding to the Populus fremontii type (labeled group 2) and mixed deciduous woodland (labeled group 1) type. These two types were the same as those identified in the 1992 report (Spence 1992b).

1. Populus fremontii woodland (Table 7; group 2 in Figure 2).

Stands of Populus fremontii were rare along the Colorado River through Glen Canyon (Woodbury et al. 1959), but common in some side canyons. Many examples of this type occurred as isolated stands of old trees on high terraces (TCE=4-5) well above stream channels. Younger stands consisting predominantly of saplings and seedlings were found on wet substrates in streambeds and lower terraces. Occasionally, cottonwoods occurred within the riparian scrub type, generally as saplings. The type was represented in most canyons investigated ($I_G=65.2\%$).

Plots consisted of three or four layers. A tall tree layer of P. fremontii (to 30 m) dominated. In many cases a subcanopy layer of smaller P. fremontii and Salix goodingii also occurred, varying from 5-10 m in height. A shrub layer, between 1-2 m, was usually present in more open and drier examples. Finally, a herbaceous layer to 1 m was usually present. Lianas were rare, represented by only Clematis ligusticifolia.

The most common prevalent species included P. fremontii, Artemisia ludoviciana, Salix goodingii, Baccharis salicina, Tamarix chinensis, and Elymus canadensis. A large number of modal species occurred, many of which were upland desert species that were only common in this type, generally on the higher terraces. Richness, diversity and evenness were generally intermediate compared to other types, and lower than for the mixed deciduous woodland type.

Two phases could be delineated within the P. fremontii type (Figure 2). One occurred mostly on high terraces, and was characterized by large cottonwood individuals (to 30 m) with Chrysothamnus viscidiflorus, C. nauseosus, and Artemisia dracunculus forming a low (1-2 m) understory. Bromus tectorum was a common grass. Of these plots, 73% showed signs of livestock grazing. Cottonwood saplings and seedlings were absent in this phase. The second phase occurred on lower terraces and occasionally in streambeds where flooding was absent. Salix goodingii was often codominant in this phase. The understory was dominated by a mixture of obligate riparian tall shrubs or low trees, including Baccharis salicina, and Tamarix chinensis. In this phase, 67% showed some sign of livestock grazing. Salix exigua was rare in both phases.

Populus fremontii woodlands were most similar vegetationally to the Baccharis-Salix riparian scrub type. In sites where flood activity is low or has ceased, the scrub type may be successional to cottonwood woodland. Many dense shrub sites had abundant cottonwood seedlings and saplings that, in the absence of flooding, would eventually overtop the shrub species. Cottonwood riparian woodlands are widespread in the western U.S., and well studied. Understory vegetation varies greatly from study to study, however. Romme et al. (1993) described a P. fremontii-Chrysothamnus nauseosus community on river terraces in Capitol Reef N.P. that was similar to the Glen Canyon NRA type. Szaro (1989) described a P. fremontii-Salix goodingii association which was similar to the P. fremontii-Salix goodingii phase in this study.

Regeneration was absent in cottonwood stands on higher terraces (TCE=4-5). Past livestock activity may have eliminated recruitment, but this does not explain why regeneration was often occurring on lower sites in grazed areas. Depth to the water table and flood activity may control recruitment in this species. Fremont cottonwood requires a relatively high water table to establish, but is sensitive to flooding (Asplund and Gooch 1988). Establishment generally occurs in overflow backwater areas that remain wet for long periods of time, but are only flooded infrequently. The model developed by Asplund and Gooch from Burro Creek in western Arizona appears to be applicable to cottonwood stands in Glen Canyon NRA. Aerial views of the gallery forests along the Escalante River display many of the characteristics of their model.

Older stands perched on high terraces (P. fremontii-C. viscidiflorus) may be relictual from the period prior to arroyo cutting (ca. 1880-1930), which isolated terraces and lowered water tables throughout the region (cf. Graf et al. 1991; Webb et al. 1991). Populus fremontii woodlands are classified in the SFRF system as (1401.05) Colorado Plateau cold-temperate lowland forest and woodland, P. fremontii series.

2. Mixed deciduous woodland (Table 8; group 1 in Figure 2).

This type consisted of mixed stands of several tree species. Stands occurred in shaded watered alcoves and stream terraces well above the canyon bottoms and stream channels, and were often associated with springs. The sites were generally stable, with little disturbance, other than occasional tree falls, slope failure, rock fall, and deer browsing. Only two plots (12%) showed sign of livestock grazing. Distribution of this type included about one third of canyons investigated ($I_0=34.8\%$). The composition and structure of two plots, COW11 and CLW1, was discussed in Spence (1992c).

Usually four layers were evident in the vegetation. A low tree or tall shrub stratum up to 7-8 m (rarely to 10 m) dominated. In a few stands a tall, emergent layer (20-25 m) formed by Populus fremontii occurred. A dense low shrub and herbaceous layer, mostly under 1 m, was characteristic of wet sites. Lianas of Clematis and Parthenocissus were common, often festooning individuals in the low tree stratum.

Defining species included Rhamnus betulifolia, Acer negundo, Quercus gambelii, Parthenocissus vitacea, and Smilacina stellata. All these were prevalent and modal species (Table 7). Other woody species included Betula occidentalis, Populus fremontii, Celtis reticulata, Salix exigua, and Ostrya knowltonii. Additional prevalent herbaceous species included Apocynum cannabinum, Equisetum hyemale, and Adiantum capillus-veneris. Many rare species were unique to these woodlands, including Carex curatorum, Calamagrostis scopulorum, Rhus glabra, Mahonia repens, Rosa woodsii, and Aralia racemosa. These explain the high value for I_D , 80.5%, indicating that this type was very distinctive. I_H was relatively low, indicating considerable site to site variation. Much of this results from the high beta diversity in the herbaceous layer. In this latter respect mixed woodlands are similar to hanging gardens, which also exhibit high beta diversity (Spence 1995).

Mixed deciduous woodlands were often associated with hanging gardens in alcoves. The woody vegetation on many wet detritus slopes adjacent to gardens belonged to this type. Drier detritus slopes lacked the rich woody and herbaceous layers, and lianas, and supported predominantly Quercus gambelii. There were many similarities in the herbaceous layer of this type and hanging gardens, although strict garden specialists were generally rare or absent. There is some evidence that floristic composition of both mixed deciduous woodlands and hanging gardens are controlled by site, i.e., the canyon they occur in. The woodlands of Garden Canyon, for example, showed strong floristic similarity to the hanging gardens in this canyon. The same environmental factors may be controlling both types (see discussion).

Most of the plots in this vegetation type can be classified as (1401.10) Rhamnus betulifolia Colorado Plateau cold-temperate woodland in the SRFR classification. In some places, however, species other than the Rhamnus were dominant. These included Acer grandidentatum, A. negundo, Ostrya knowltonii, and Quercus gambelii. Classification of these plots into SRFR series can be found in Table 7. Romme et al. (1993) described a Rhamnus-Acer-Quercus woodland community from southern Capitol Reef National Park, in the narrows of Hall's Creek, which appears to belong to this type. It may be restricted to the Colorado Plateau along the Colorado River. Woodbury et al. (1959) reported a mixed deciduous woodland in areas now drowned by Lake Powell, which is presumably of this type.

Mixed deciduous woodland harbored more relict and rare species than any other type considered in this study. These woodlands were probably more widespread during the Pleistocene, when conditions were wetter and cooler in the region.

With the warming and drying trend of the Holocene, they would have become gradually restricted to shaded wet sites. Many species presumably became locally extinct as conditions became unfavorable, particularly in sites that lacked permanent water. This is discussed in greater detail in the section on biogeography and history.

3. Pseudotsuga menziesii-Acer grandidentatum forest (Table 9).

This type comprised three plots in the stand of Pseudotsuga menziesii at the head of Miller's Creek, a tributary of Hall's Creek draining the Waterpocket Fold. It was considered a riparian type because of the presence of a stream in the grove. The site was in a north facing alcove at a relatively high elevation of 1770 m. Diversity, evenness and richness were low. Prevalent species included P. menziesii, Acer grandidentatum, Smilacina stellata, Ostrya knowltonii, Habenaria zothecina, and Mahonia repens. Structurally, the vegetation consisted of a tall closed canopy (20-30 m) of P. menziesii, a low tree canopy (3-7 m) of Acer grandidentatum and Ostrya knowltonii, and a very sparse low herbaceous layer. Shade was very dense under the tree canopy. The rare C2 species Habenaria zothecina was found along the banks of the stream

itself. More information on the structure and dynamics of this stand can be found in Spence (1992c).

This type is not closely related to other riparian communities in Glen Canyon NRA. It is a relictual montane stand that represents a type of riparian woodland that was probably more widespread during the Pleistocene in the region (Spence 1992c; see below). This hypothesis is supported by fossils of P. menziesii and A. grandidentatum that have been recovered together from alcove sites in the Forty Mile-Willow drainages, dated at ca. 12,000 BP (Withers and Mead 1993). A pack rat midden was collected in the alcove behind the stand on June 17, 1992. Recently, this has been dated at 13,310 $\pm$ 140 radiocarbon years BP (Saxon Sharpe, pers. comm. 1994). This date was based on a sample of limber pine (Pinus flexilis) needles, a species that no longer grows in the area. The limber pine needles were mixed with abundant douglas fir needles.

Padgett et al. (1989) described conifer-dominated riparian communities from higher elevations in which P. menziesii occurs. None of their described community types are similar to the stand in upper Miller's Creek. In the Forest Service terminology this stand would be classified as a P. menziesii series, P. menziesii-Acer grandidentatum community type. It is classified in the SRFR system as (1301.01) Colorado Plateau montane forest, P. menziesii series.

B. SCRUB

Preliminary analyses of plots dominated by shrub species indicated that those in which poison ivy, Toxicodendron rydbergii, was dominant, were floristically and structurally much closer to herbaceous-dominated (marshland) plots. The T. rydbergii plots were therefore analysed with the herbaceous plots. In all, 36 shrub plots were surveyed. Of these, three were tinajas from the 1992 field season. These three plots were not included as they were shown to be very distinct from other vegetation types (Spence 1992b), and no further work was done on them in 1993-94. A further six plots from ephemeral streams were not included.

Figure 3 shows the results of a cluster analysis of the 27 plots retained for the analysis. Two main clusters were produced, one characterized by Salix exigua and Baccharis salicina (group 1 in Figure 3), and the second by Salix lutea and Betula occidentalis (groups 2-3 in Figure 3). This latter cluster was further divided into two groups, characterized by either S. lutea or B. occidentalis. Two plots (labeled 1B in Figure 3), were distinctive by the presence of russian olive, Eleagnus angustifolia, mixed with the native riparian species. The three main groups recognized in the classification include the clusters 1-3 in Figure 3. Clusters 2-3 are classified as distinct because they have different dominant shrub species. These three types, along with T. rydbergii vegetation and Salix goodingii tinajas, are described below.

4. Salix exigua scrub (Table 10; group 1 in Figure 3).

Salix exigua scrub is one of the most widespread vegetation types along intermittent and permanent streams in Glen Canyon NRA ($I_c=80.8\%$). Before the construction of Glen Canyon Dam a mixed riparian scrub comprising Baccharis, Salix, and Tamarix was also found along the banks of the Colorado River. In side canyons of the lake, the type generally occupied low terraces (TCE=2-3) just above stream beds. Where flood activity was absent or rare, the scrub species, principally the clonal Salix exigua, were invading the stream bed itself. In most canyons investigated, the riparian scrub zone was not continuous, and in some was often poorly developed. It was generally rare or absent where bedrock was common, and best developed on sandy alluvial terraces.

The two most characteristic species were Salix exigua and Baccharis salicina (some may be B. emoryi, see Appendix 2). The willow was the more common of the two at most sites. Individuals of these species averaged 3 m in height, although occasionally they reached 6 m. Generally, a low herbaceous layer of Equisetum hyemale and Juncus arcticus occurred. Tamarix chinensis was a common associate, although it rarely dominated. Saplings of Populus fremontii were occasionally present.

This type could be divided into two phases, related to terrace position. On higher infrequently flooded terraces the Baccharis dominated, although S. exigua remained common. On lower sites that were probably flooded every year, S. exigua dominated, with Baccharis relatively uncommon. Juncus arcticus and Equisetum hyemale were abundant in this second group, and generally absent from the higher terraces. Tamarix was scattered throughout both groups. Two plots from the Escalante River (CHO4, NEO2) were distinctive in the presence of the introduced tree russian olive, Elaeagnus angustifolia. Along this river Scirpus pungens was also much more common than Juncus arcticus, and often replaced it as the herbaceous dominant.

Species richness and diversity were the lowest of any scrub type. However, a variety of herbaceous species occurred unpredictably in low abundances, and produced some floristic diversity from site to site ($I_H=49.5\%$).

Although widespread, this riparian scrub type has not been adequately described on the Colorado Plateau. Salix exigua is especially widespread, and vegetation dominated by this species has been described from Arizona, New Mexico, and Utah (Padgett et al. 1989; Szaro 1989). Other studies discussing this type include Loope (1977) and Irvine and West (1979). Salix exigua vegetation is classified as SRFR (1402.05) Colorado Plateau cold-temperate lowland tall shrubland, S. exigua series.

5. Betula occidentalis scrub (Table 11; group 3 in Figure 3).

An unusual variant of riparian scrub was found in the upper end of the south fork of Cow Canyon and in lower Fence Canyon. On intermediate terraces along the permanent streams in these canyons scrub dominated by river birch, Betula occidentalis, was found. Other prevalent species included Euthamia occidentalis, a variety of other forb and shrub species, and Rhamnus betulifolia. Sites were shaded for much of the day. Both Salix exigua and the rare S. lutea occurred in low amounts. Structurally, the vegetation consisted of scattered patches of shrubs (2-5 m in height) within a relatively lush forb layer.

Several montane relicts have been found along the stretch in Cow Canyon where this type occurs (Spence, unpublished data), including Mahonia repens, Rosa woodsii, and Viola nephrophylla. Mixed deciduous woodlands and hanging gardens were common, and harbored many unusual species. This scrub type was considered relict because Betula occidentalis is found typically at much higher elevations in this area, generally along montane streams above 2000 m. Fully 23% of the species found in this type were in the disjunct category, which includes higher elevation relicts as well as southern temperature species (see section on biogeography). Interestingly, Padgett et al. (1989) described high elevation B. occidentalis community types from southern Utah that shared several species with the Cow Canyon sites, including Salix lutea, S. exigua, Smilacina stellata, and Equisetum hyemale. Scrub with Betula has been reported from Betatakin Canyon in Navajo National Monument (Brotherson et al. 1985). Betula is also found along streams in Zion National Park and vicinity (Webb and Brotherson 1988), where it was also often found at low elevations in shaded sites. This type is classified as (SRFR 101306.06) Colorado Plateau montane tall shrubland, B. occidentalis series.

6. Salix lutea scrub (Table 12; group 2 in Figure 3).

In protected shaded sites along permanent streams scrub dominated by yellow willow, S. lutea, was found. It was only extensive in Forty Mile Gulch and Forgotten Canyon, although the willow was more widespread, occurring as a rare associate in other scrub and forest types.

This type was structurally similar to Salix exigua scrub. It generally occurred on low to intermediate terraces along well watered stretches of streams in slot canyons where exposure to the sun was minimal. A lush understory of herbaceous species was usually associated with the shrubs. Prevalent species in addition to the willow included Apocynum cannabinum, Clematis ligusticifolia, and Equisetum hyemale. Rarer prevalent species included several generally associated with wet sites such as springs and hanging gardens, eg., Epipactis gigantea, Solidago canadensis, and Smilacina stellata. Disjunct species accounted for 23% of the total flora.

Padgett et al. (1989) and Szaro (1989) report Salix lutea as a minor component in montane riparian vegetation characterized by Alnus tenuifolia and Betula occidentalis, generally found at elevations above 1600 m.

7. Salix goodingii scrub (Table 13).

Tinajas are large waterpockets that occur in slickrock along incipient drainages that channel precipitation. They differ from other waterpockets by the presence of permanent water and associated dense riparian vegetation (Spence and Henderson 1993). Rock pools along main ephemeral drainages may be vegetationally similar, but destructive flash floods are probably more frequent than in sites on slickrock. The best developed tinajas are found on Navajo sandstone, and are especially common along the Waterpocket Fold in Capitol Reef National Park. Disturbance is high, and flood events probably damage vegetation on a regular basis, and may even scour out tinajas, at least occasionally. Size varies from a few square meters to about 100 square meters.

Three tinajas were sampled in 1992, all in the Waterpocket Fold west of lower Hall's Creek. Prevalent species included Salix goodingii, Artemisia ludoviciana, Panicum oligosanthos, Schizachyrium scoparium, and Juncus tenuis. Tinajas generally exhibit high beta diversity, and the three surveyed sites differed floristically in several respects from those found further north (Spence and Henderson 1993). However, S. goodingii was almost always present in larger and deeper tinajas. A constant, defining, herbaceous species was Panicum oligosanthos, which is widespread in tinajas along the Waterpocket Fold (Heil et al. 1993). Spence and Henderson (1993) found, with a larger sample of tinajas, that vegetation patterns were related to pool depth and protection (shading) from the sun.

Tinaja vegetation was fairly distinctive ($I_p = 68.0\%$), and exhibited high richness, diversity, and homogeneity. Biogeographically disjunct species and Colorado Plateau endemics were absent. Tinajas are interesting communities that deserve more attention and study than received to date. Only Romme et al. (1993) and Spence and Henderson (1993) have studied tinaja vegetation on the Colorado Plateau.

8. Toxicodendron scrub (Table 14; group 4 in Figure 4).

Seven plots were dominated by the physiognomically highly distinctive poison ivy, Toxicodendron rydbergii. Although poison ivy is a shrub (or sometimes a vine), its broad mesophytic leaves and generally low stature suggests it may be ecologically similar to broad-leaved dicot forbs.

Plots were on shaded intermediate terraces or protected alcoves in relatively deep or narrow canyons. Surface water was not generally present, with most plots associated with subsurface water only. Toxicodendron rydbergii formed a variable layer (1-4 m tall) with a lush and dense understory of herbaceous species. In addition to T. rydbergii, other prevalent species included Equisetum hyemale, Apocynum cannabinum, Artemisia ludoviciana, Tamarix chinensis, and Euthamia occidentalis. Richness, diversity and evenness were all intermediate compared to other scrub types. Some site to site floristic variation occurred ($I_H=47.5\%$). This vegetation type was the least distinctive of any in the present study, with an I_D of 9.5%.

Vegetation dominated by poison ivy has not been reported from the region. This may be related to scale, since most examples were relatively small in extent (mostly <100 m²), and occurred as scattered patches in alcoves in shaded terraces. Neither Padgett et al. (1989) nor Szaro (1989) mention T. rydbergii. In Utah, the species is generally found in rich moist soil sites along streams.

C. MARSHLAND

Much of the vegetation in the survey was dominated by one or more of a variety of herbaceous species. Strong differences in site characteristics and floristics occurred among these herbaceous plots. A cluster analysis of 50 plots is shown in Figure 4. Eight principal clusters were formed, numbered 1-7. An additional four plots that remained outside these principal clusters were assigned the letters A, B, C, and D. Each of the numbered groups were characterized by one or more dominant species; Phragmites australis (group 1), Eleocharis palustris (2), Typha species (3), Toxicodendron rydbergii (4), Panicum virgatum (5), Equisetum hyemale and Juncus arcticus (6), and Solidago canadensis (7). The four lettered plots consisted of low flooded sites (e.g., beaver dams) with little in common. Below, each of the resulting vegetation types is described and discussed.

9. Phragmites marshland (Table 15; group 1 in Figure 4).

Reedgrass, Phragmites australis, is a vigorous clonal species, and often formed almost pure stands, varying from a few square meters up to almost a hectare in some areas. It seemed to favor a high but subsurface and reliable water table, although it may tolerate some inundation. Floods probably control the species' presence along stream channels, as clones have been shown to suffer high mortality during heavy flooding (cf. Stevens and Waring 1985).

This type occurred in two settings, exposed seeps on canyon slopes well above stream channels, and in stream channels in the upper ends of well watered canyons where flood activity was minimal. Median terrace position was 6 (hillsides). Plots were located in about one third of investigated canyons ($I_D=39.1\%$).

Prevalent species, in addition to Phragmites, included Equisetum hyemale, Oxytenia acerosa, Bromus tectorum, and Aster glaucodes. Diversity, richness, and evenness were all low compared to other herbaceous vegetation types. The type was not very distinct ($I_D=39.6\%$) or homogeneous ($I_H=48.6\%$). A variety of species occurred unpredictably in low abundances in the reedgrass plots.

Although widespread on the Colorado Plateau, Phragmites vegetation has not yet been described or classified. This may be a result of scale, as most examples are relatively small compared to other kinds of vegetation. This type was classified as (1404.12) Colorado Plateau cold temperate grassland, P. australis series.

10. Typha marshland (Table 16; group 3 in Figure 4).

Where beaver ponds or quiet pools along permanent streams occurred, patches of Typha domingensis and T. latifolia were found. Most were small, and often consisted of a narrow fringe around the water. However, in some cases they became quite extensive, occupying up to a hectare or more. Four plots were established in Typha vegetation. Patches were seen in most canyons with permanent water.

Sites were generally in the lowest part of stream channels (median terrace position=1), and were typically saturated, with standing water often present.

A dense tall (to 3 m) stand of Typha was typical, with forbs and other monocots scattered among the cattails. Other prevalent species included Euthamia occidentalis, Equisetum hyemale, Scirpus pungens, Baccharis salicina, Epilobium ciliatum, and Carex hystricina. Richness, diversity, and evenness were all low in this type. Typha marshland was less homogeneous ($I_H=56.0\%$) and distinctive ($I_G=50.0\%$) than many other herbaceous types. The type was most similar to Eleocharis palustris marshland (see below).

The distribution of most sites was probably related to beaver activities. Another important factor was probably an absence of destructive flooding, resulting from barriers created by the beaver dams. In some cases, Typha marshes became quite extensive in the well-watered upper portions of canyons where flooding probably was at a minimum, such as in Cow, Garden, or Bowns canyons. They were also common in some canyons below the high water level of Lake Powell, such as in Lake Canyon and lower Hall's Creek.

Although Typha wetlands are widespread throughout western North America, they are relatively uncommon on the Colorado Plateau. No other published work has been done on these wetlands on the plateau. They are classified as (1405.01-1405.02) Colorado Plateau cold temperate lowland marshland, T. latifolia and T. domingensis series.

11. Panicum virgatum marshland (Table 17; group 5 in Figure 4).

This type comprised sites along stream channels without extensive flooding and dominated by switchgrass, Panicum virgatum. Copperweed, Oxytenia acerosa, was generally present and often codominant. Scratchgrass, Muhlenbergia asperifolia, was usually present. Soils were shallow, and bedrock often showed at the surface. Carbonate deposits on the surface occurred at all sites, suggesting that the controlling factor might be the presence of basic carbonates and salts. Most sites were on drier intermediate terraces (TCE=2-3) in exposed sites, generally along intermittent stream reaches. The vegetation consisted of tussocks of P. virgatum, from 1-2 m high, with a low herbaceous layer of grasses and forbs. Oxytenia acerosa, when present, usually occurred as dense patches in the grass layer.

Species richness, diversity and evenness were intermediate compared to other herbaceous types, but relatively distinct ($I_G=59.8\%$). In many respects this type was very similar to the mixed forb type, differing primarily in the abundance of the three most common species. Both the Muhlenbergia and Panicum were found in the mixed forb type, although copperweed was generally not present. The Panicum virgatum type was only found in 26% of investigated canyons, and was most common in Alcove Canyon and Forgotten Canyon. No other studies in the region have documented this type. It is classified as (1404.13) Colorado Plateau cold temperate lowland grassland, P. virgatum series.

12. Mixed forb marshland (Table 18; group 6 in Figure 4).

This type was found in broader stretches of several canyons, where stream

meandering and deep alluvium occurred. It was best developed on low flood plains (median terrace position=2), and was often associated with beaver dams. The potential flood intensity index was one of the highest observed (PFI=1.004), with only the scrub types and Typha plots having a higher index. The type was most common in Alcove, Bowns, and Slickrock canyons, where it formed extensive stretches along stream channels.

All sites consisted of a mixture of Equisetum hyemale, Euthamia occidentalis, and Juncus arcticus. Of these, the Juncus was generally the most common. Other prevalent species included Muhlenbergia asperifolia, Bromus tectorum, Castilleja linariifolia, and Elymus canadensis. The only prevalent woody species was Baccharis salicina, which was often found in small numbers as saplings or young individuals. Two phases could be distinguished, one consisting of dense stands of E. hyemale with abundant Juncus arcticus, and the other with abundant Euthamia and J. arcticus, and less E. hyemale.

Species richness, diversity and evenness were all low. There was moderate site to site variation ($I_H=58.4\%$), and the type was moderately distinctive ($I_D=66.7\%$). Structurally, the vegetation consisted of a relatively dense monolayer of Equisetum, Juncus, and forbs, generally less than 2 m tall. There was strong seasonal change in this type. In early season, the forbs, especially Euthamia, were just starting growth, and Equisetum was most conspicuous. By late summer the Euthamia had reached maturity and was flowering, and often was the most conspicuous component.

This mixed forb type was unusual in that it occurred on sites that generally supported riparian scrub rather than herbaceous vegetation. There are several possible explanations for why this type occurs where it does. Deep alluvium, as in Bowns Canyon, was often present, and some aspect of soil chemistry, water-holding properties, or alluvial-stream dynamics could explain its presence. Sites may be flooded by meltwater in spring long enough to prevent the establishment of woody species.

Tall herbaceous (particularly forb) vegetation is prone to damage by flood activity, especially strong floods that could uproot individuals and completely remove the plant cover. Mixed forb plots had very high potential flood indices. Several of the best-developed stands were associated with beaver dams and other barriers. Such barriers would increase the likelihood of standing water in early season, and may also prevent damage by dissipating destructive floods. If standing water and a high water table is the principal controlling factor, barriers would be expected to occur downstream from mixed forb stands, but if reduction of damaging floods is the primary factor, barriers should be found upstream of stands. Future work, mapping stands in relation to alluvium, stream characteristics, and barriers, will be necessary to test these hypotheses.

The mixed forb marshland type has not been previously reported from the Colorado Plateau. It is classified as (1405.10) Colorado Plateau cold temperate marshland, Equisetum hyemale-Juncus arcticus series.

14. Solidago canadensis marshland (Table 19; group 7 in Figure 4).

Patches of Canadian goldenrod, Solidago canadensis, were occasionally found along perennial streams. They generally occurred in two settings; shaded intermediate terraces (median terrace position=3) in deep narrow canyons, or associated with Phragmites australis on open sunny slopes around springs.

In addition to the Solidago, other prevalent species included Phragmites australis, Juncus arcticus, Equisetum hyemale, Clematis ligusticifolia, and Artemisia ludoviciana. Diversity, richness, and evenness were all high. Plots were relatively homogeneous ($I_H=60.7\%$), but not very distinctive

($I_D=35.3\%$). Sites were generally protected from flooding, although median terrace position was 3. The vegetation structure consisted of a relatively dense layer of goldenrod with other herbaceous species dispersed throughout. Floristically, this type intergraded with the Phragmites type. Some plots consisted of equal mixtures of the two species, and were difficult to classify in either.

No other reports of Solidago dominated vegetation have been reported from the region. This type is classified as a (1406.10) cold temperate lowland forbland, Solidago canadensis series.

15. Eleocharis-Lobelia marshland (Table 20; group 2 in Figure 4).

Dense patches of spikerush, Eleocharis palustris, occur within Glen Canyon NRA. They were found on open (exposed) slopes or in small side drainages around seeps with permanent above ground flows. Sites were not flood prone, and appeared to be stable. Eleocharis palustris (some may have been the related E. rostellata) dominated, forming a dense sward. A variety of other graminoid species of Carex and Juncus were often also present. In late summer Lobelia cardinalis became conspicuous. One plot with some Eleocharis (BOC1), although clustered with group 2, was dominated by a mixture of Juncus and Equisetum, and was classified with the mixed forb type.

Richness, diversity and evenness were all high. Eleocharis vegetation was only moderately distinct ($I_D=50.1\%$), but fairly homogenous ($I_H=60.8\%$). Prevalent species included E. palustris, Phragmites australis, Baccharis salicina, L. cardinalis, Solidago sparsiflora, Panicum acuminatum, and Oenothera longissima. Structurally, the vegetation consisted of a low very dense (approaching 100% cover) sward of monocots with scattered emergent forbs, Phragmites, and rarely, shrubs. Some forb species were characteristic of hanging gardens, such as Cirsium rydbergii and S. sparsiflora. Overall, this type supported a relatively large number of disjuncts and Colorado Plateau endemics.

Eleocharis communities generally occur at higher elevations in southern Utah. Padgett et al. (1989) describe a E. palustris community type from central and southeastern Utah at elevations from 2200-3000 m, which is, however, floristically very different from the Glen Canyon NRA type. The Eleocharis type is classified as a (1405.07) Colorado Plateau cold temperate marshland, E. palustris series.

D. MINOR VEGETATION TYPES AND UNCLASSIFIED PLOTS

16. Cladium californicum marshland (plot C (ALC10) in Figure 4).

Sawgrass, Cladium californicum, is a rare species found in Utah only along the Colorado and San Juan rivers in Glen Canyon NRA. The principal center of distribution for this species is the lowland riparian zones, springs and hanging gardens along the Colorado River through the Grand Canyon and in the Mohave Desert. The species is probably relictual from an earlier period, perhaps the middle Holocene, when conditions were warmer along the Colorado River drainage. The species is common in hanging gardens along the Colorado River through Grand Canyon N.P. (personal observations; also Spence 1994).

Most populations of sawgrass have apparently been drowned by Lake Powell (Welsh et al. 1993). Recently, several stands were discovered in Alcove and Garden canyons (Spence 1991). Some populations were in hanging gardens, but at least two were found along stream channels. This type was recognized despite its rarity because of its unusual composition and regional importance.

Physiognomically, this type consisted of dense stands of sawgrass mixed with

some Typha, Carex, Juncus, Scirpus and forbs. The investigated site (ALC10) was drier than other sites where sawgrass is generally found, and may not be typical. It occurred along the margin of the stream in Alcove Canyon, in an area with shallow soils, exposed slickrock, and carbonates at the surface. Patches of the Panicum virgatum type were found in the vicinity. Other sites away from hanging gardens tended to be associated with smaller wet side drainages downstream from hanging gardens. Sawgrass vegetation is classified as (1505.01) Sonoran warm temperate lowland marshland, C. californicum series.

17-18. Beaver pond marshlands (groups A/B in Figure 4).

Two plots were associated with beaver ponds, one in Scorpion Gulch (SCO9) and the second in lower Fence Canyon (LFC2). Sites were stream channels along permanent streams. In both cases, a small pond occurred, with fringing herbaceous vegetation. The dominant species of the two plots were different.

LFC2 was dominated by Carex lanuginosa, with lesser amounts of C. hystricina and Equisetum hyemale. SCO9 was characterized by Scirpus microcarpus, a montane bulrush that generally occurs at higher elevations. The site was in a narrow shaded canyon (EXP=4). Until more plots are sampled around beaver ponds, no attempt is made here to classify the vegetation.

A related plot (COW2, plot B in Fig. 4) occurred in a plunge pool associated with a hanging garden in Cow Canyon. A rich mixture of herbaceous species occurred in this plot, with no clear dominance by any species. Floristically it was closest to the beaver pond plots, but lacked the two species that dominated those.

19. Miscellaneous types

A. Low elevation ephemeral stream channels.

A variety of shrub species occurs along dry streambeds, including Brickellia longifolia, Fallugia paradoxa, and Chrysothamnus nauseosus. Psoralidium lanceolatum and Lepidium montanum were common forbs. Tuhy and MacMahon (1988) briefly mention this type, and point out that beta diversity is very high. Romme et al. (1993) described similar types (dry and mesic canyon bottom communities) from Capitol Reef National Park.

In a few side canyons, on dry sandy stream terraces, arrowweed, Tessaria sericea, occasionally becomes dominate. Arrowweed occurs throughout Glen Canyon NRA in riparian zones, but is usually rare. Tessaria is one of the principal riparian scrub species along the Colorado River from Glen Canyon Dam downstream. The reason for its failure to dominate or at least occur more commonly in most canyons around Lake Powell is not known.

B. High elevation ephemeral stream channels.

Rocky ephemeral stream channels above ca. 1400 m are characterized by a rich mixture of deciduous shrub species, including Amelanchier utahensis, Chrysothamnus linifolius, Fallugia paradoxa, Fraxinus anomala, Holodiscus dumosus, Ostrya knowltonii, Quercus gambelii, Rhus aromatica, Shepherdia rotundifolia, and Symphoricarpos longiflorus. This type of vegetation is found at moderate elevations (1400-2000 m) at the bases of cliffs, in defiles, and dry (largely ephemeral) shaded stream channels, especially rocky channels.

It was common in such sites along the Waterpocket Fold through Capitol Reef National Park (personal observations; Romme et al. 1993), although without Ostrya knowltonii, which extends no further north than Hall's Creek Narrows. This type is probably common within Glen Canyon N.R.A., in the Kaiparowits Plateau and its canyons, the Waterpocket Fold, the Orange Cliffs, and other areas where the park reaches the necessary elevations. It is classified as Colorado Plateau cold-temperate tall shrubland. No work at the series level

has been done yet on this vegetation. Romme et al. (1993) have described very similar vegetation from Capitol Reef National Park. They classified it into two communities, one consisting of higher elevation or protected sites with more available moisture, and the second of lower more open sites with less available moisture. They pointed out the difficulty of classifying these communities to series because of their high beta diversity and the numerous co-occurring species of shrubs.

20. Unclassified sites

Several plots remained unclassified by the above classification. Two plots consisted of Quercus gambelii scrub, a widespread "pseudoriparian" type that occurs in most canyons around Lake Powell. The majority of unclassified plots consisted of a mixture of herbaceous and woody species (especially Brickellia longifolia), occupying low sites, particularly current stream channels and sites with frequent flooding. They had little in common other than low cover and topographic-terrace position. These intermittent and ephemeral floodplains and flood channels are common in Glen Canyon NRA, but will be difficult to classify by floristics because of high beta diversity.

C. Vegetation-Environment Relationships

In order to detect gradients in vegetation structure correlated with environmental variables, ordinations of the three groups of plots, forest and woodland, shrub, and marshland, were performed (see Appendix 1 on ordination method). PCA axis loadings for each plot were then correlated with physical site variables using Spearman's rank correlation to detect relationships between plot ordination location and physical variables (see Table 21).

The first two axes of the ordination of the forest and woodland plots (Figure 5) accounted for 35% of the variation in the data. Plots on the left side and upper parts of the ordination (1-14) were mixed deciduous woodland plots, as were 15-17. Those labeled 18-50 were all Populus fremontii plots. The first axis (22% of the variation) separated the two principal types, and integrated those variables that differentiate the two communities (e.g., exposure, terrace position, and distance from headwaters). The second axis was similar, but showed in addition strong correlations with water and canyon width to depth ratio.

The ordination of 27 riparian scrub plots is shown in Figure 6. Plots were separated by a combination of exposure, stream bearing, and distance from headwaters. Most of the Betula occidentalis and Salix lutea plots were segregated from the S. exigua plots in this ordination. The first axis (22% of variation) was most strongly correlated with distance from headwaters, exposure and stream bearing. The second axis (13%) showed strong correlations with canyon width to depth, distance from headwaters, exposure, and the potential flooding index.

The ordination of herbaceous vegetation plots is shown in Figure 7. The first two axes accounted for 15% and 13% of the variation respectively. The first axis separated sites in wide shallow canyons (left side of ordination) from sites in narrower, deeper and more protected canyons. The second axis separated the Phragmites australis and Solidago canadensis plots from the remainder. The variables most strongly correlated with this axis were terrace position and water type, with the Phragmites and Solidago plots on slopes associated with perched springs, and the remaining plots located in canyon bottoms and associated with stream channels. Plot 9 in Figure 7 was intermediate between the two groups. Although it was a Solidago plot, the plot was located in a canyon bottom.

Patterns of diversity, evenness and richness were correlated with site

physical variables using Spearman's rank correlation test (Table 22). Species richness and diversity in forest plots was not strongly correlated with any physical variable. Evenness showed moderately strong correlations with quadrant and stream bearing, with more even vegetation in east and south-facing sites. Species variables of the riparian scrub plots showed strong correlations with several physical variables. Both species richness and diversity were strongly positively correlated with canyon depth, exposure, canyon width to depth ratio, and the potential flood index. Sites in narrower, more protected, or deeper canyons tended to be richer and more diverse than sites in more exposed or shallower canyons. Areas more flood-prone tended to have more diverse and species-rich vegetation. Evenness was most strongly correlated with exposure and water, with higher (more even) values in more exposed (sunnier) sites with permanent water. Marshland plots were not strongly correlated with any physical variables. For richness and diversity values, the strongest relationship was with canyon width to depth ratio. For evenness, marshland plots were most strongly correlated with water, with more even values at plots with permanent water. An analysis of the entire data set indicated that no species variable was strongly correlated with any site physical variables. Again the strongest correlations were between diversity and evenness and the water variable, with more diverse and more even vegetation at sites with permanent water, particularly springs.

D. Biogeography and paleoecology

Information on species ecology and distribution in Welsh et al. (1993) and Albee et al. (1988) was used to classify the riparian flora into distributional groups. These groups consisted of species with broadly similar geographic and elevational distributions on the Colorado Plateau and the southwestern U.S. Most species were found to be widespread western or southwestern species, either in riparian zones and wetlands, or in upland desert sites. Three small groups of species, however, showed interesting distribution patterns. They were named the southwestern, boreal-montane disjunct, and Colorado Plateau endemic groups (Table 23).

Species in the southwestern group reach their northern distributions in the west and Utah in particular within or near Glen Canyon NRA. They are more widespread to the south in Arizona, and are often common species in the southern U.S. and the Great Plains. Most species penetrate into Utah along the Colorado River. This temperate group includes both prairie grasses, eg., Andropogon glomeratus, Panicum virgatum, and Sorghastrum nutans, as well as riparian and wetland species, such as Aralia racemosa, Cladium californicum, Parthenocissus vitacea, and Rhamnus betulifolia. Two species with somewhat different distributions, Ostrya knowltonii and Rhus glabra, were also included in this group. The Rhus is a temperate species common in the eastern U.S., and found in scattered sites as far north as southern British Columbia in the west. The Ostrya has its primary concentration on the Colorado Plateau and Mogollon Rim, but is also found disjunct in the Guadalupe Mountains of Texas. The affinities of both these species lie with southern temperate taxa, and are classified as southwestern.

The boreal-montane disjuncts comprise species that generally occur at higher elevations on the Colorado Plateau (the montane and subalpine zones of Spence et al. 1995) than those in the study area. Most are common in forests and along streams above about 2000 m, although one grass, Calamagrostis scopulorum, is most common at elevations above 3000 m. Species in this group included Acer grandidentatum, Betula occidentalis, Mahonia repens, Rosa woodsii, and Smilacina stellata.

A third small group comprises species restricted to the Colorado Plateau. Most plateau endemics are upland or desert species (see analysis in Schultz 1993), but a small number are found in hanging gardens. Most of these species

are not restricted to gardens, although they are generally most common in them. Seven species were found in riparian vegetation: Aquilegia micrantha, Carex curatorum, Cirsium rydbergii, Habenaria zothecina, Mimulus eastwoodiae, Primula specuicola, and Yucca toftiae.

These three groups comprised 36 species (Table 23), or 23% of the flora found in the vegetation plots. Their distributions among the vegetation types was not random. Four types supported the majority of disjunct or endemic species; mixed deciduous woodland (26 species), Pseudotsuga menziesii forest (7), Betula occidentalis scrub (6), and Salix lutea scrub (8). The only species that commonly occurred in other types were Panicum virgatum, which was the dominant species in the P. virgatum vegetation type on open intermediate terraces along some streams, and Salix goodingii, which was common in the Populus fremontii type.

Per cent disjunct species (in the southwestern and boreal-montane disjunct categories) per plot was correlated with site physical variables using Spearman's rank correlation. For all forest plots, disjunct species were most strongly correlated with terrace and exposure variables (Table 24). Plots on higher terraces and in alcoves in more protected sites tended to have more disjunct species than plots on lower, more open terraces. In riparian scrub, the variable most strongly correlated with disjuncts was exposure. Distance from headwaters was also strongly negatively correlated. Per cent disjuncts increased in more protected plots, and closer to headwaters or barriers. Marshland vegetation generally supported few disjuncts. Plots with disjuncts were most strongly correlated with deep canyons rather than shallow canyons.

The largest concentrations of both disjuncts and Colorado Plateau endemics was in the mixed deciduous woodland (26 species, 72% of total). Because of the large number of such species in this type, correlations of the three elements, southwestern, montane, and endemic, with site variables were performed (Table 25). Linear regressions were also computed between the disjunct categories (dependent variable) and the most strongly correlated physical site variables (independent variables).

Boreal-montane disjunct species were most strongly correlated with water type, with the majority associated with permanent springs ($r^2=23.8\%$, $p=0.027$). Southwestern species showed strongest correlations with water and exposure ($r^2=48.7\%$, $p=0.004$). Spring sites in more exposed southern or western aspects tended to support more southern species than drier and more northern and eastern or more protected sites. For Colorado Plateau endemics, significant correlations occurred with both exposure and canyon depth ($r^2=32.8\%$, $p=0.024$).

Exposed sites in shallow canyons supported the largest concentrations of endemics. There was also a strong negative but not significant correlation with the flooding index, with more endemics in sites which were potentially less flood prone.

Data on the paleovegetation of the region is summarized in Betancourt et al. (1990). More recently, Withers and Mead (1993) presented data on macrobotanical remains from the Willow and Forty Mile drainages. Betancourt (1984, 1990) indicated that in the late Wisconsin (prior to ca. 12000 BP) a mixed conifer woodland occupied areas between 1300-2000 m on the Colorado Plateau. At present, this woodland is found above 2200 m in the region. Along streams, elements of the Wisconsin woodlands would have penetrated to much lower elevations. Prominent species in these woodlands included Pseudotsuga menziesii (Douglas fir), Picea pungens (blue spruce), Pinus flexilis (limber pine), and Juniperus scopulorum (Rocky Mountain juniper). At the present time, other species found along streams in association with these species include Acer negundo, Betula occidentalis, Mahonia repens, Rosa woodsii, and Smilacina stellata. Other kinds of vegetation present in the late Wisconsin included sagebrush steppe dominated by Artemisia tridentata,

and shale badland communities dominated by (as today) various members of the Chenopodiaceae. Quercus gambelii (Gambel oak) was not important, and may have occurred primarily along drainages below ca. 1500 m, where it probably co-occurred with Acer grandidentatum (big-tooth maple) and Celtis reticulata (hackberry). Rare associates of these streamside woodlands may have included Cercis occidentalis (western redbud), Ostrya knowltonii (Knowlton hophornbeam), Rhus glabra (smooth sumac), and Rubus neomexicanus (New Mexico raspberry).

Withers and Mead (1993) identified and dated plant remains from several alcoves in Forty Mile and Willow gulches. Their radiocarbon dates ranged from ca. 7500 to 12,700 yrs BP. Numerous plants were identified, many of which still occur in the drainages. Common riparian species included Celtis reticulata, Quercus gambelii and Acer negundo. Species that occurred in the alcoves prior to 8500 yrs BP included Acer grandidentatum, Betula occidentalis, Cladium californicum, Pseudotsuga menziesii, Rosa woodsii, and Smilacina stellata. None of these species are currently found in Forty Mile and Willow gulches. However, all except Douglas fir are known from nearby Cow and lower Fence Canyons.

Betancourt (1990) thought that the woodlands and hanging gardens of moist protected alcoves in canyons of the Colorado Plateau represented important relictual centers for montane plants. Remnants of the originally widespread late Wisconsin woodlands may have persisted in these sheltered habitats since the breakup of the formation at the end of the Wisconsin some 11,000 years ago. The alternative hypothesis is that many of these species may have dispersed more recently into the alcoves from montane areas, possibly through the activities of birds. Charles Wood (pers. comm. 1992) suggested that some canyons may have functioned as "mega-alcoves", with their protected and wet upper portions supporting various kinds of both relictual and disturbance sensitive vegetation. This can be called the "Wood hypothesis". An important component of the Wood hypothesis is that these areas had significantly reduced levels of disturbance that could have eliminated disturbance-sensitive species. Principal canyons that may have functioned as refugia include Cow, Bowns, Garden, Ribbon, and others that are incised into the Navajo Sandstone formation. These canyons are characterized by lush riparian and hanging garden vegetation at their upper ends, associated with permanent springs. In all these canyons, downstream reaches are drier and support less diversified vegetation. Although data are not available on flooding, an important assumption of the Wood hypothesis is that flooding is minimal in the upper reaches of these canyons.

E. Canyon rankings

Surveyed canyons were ranked according to various criteria, including presence of unusual or rare species, diversity of vegetation types, disturbance, water resources, and suitability for continued NRPP ecosystem research (Table 21).

Perennial flows occurred in at least some stretches of 15 canyon riparian zones investigated. Those canyons lacking perennial flows included Alcove Canyon, Chopslot Canyon, Clearwater Canyon, Dry Rock Creek, Garden Canyon, Knowles Canyon, Last Chance Creek, Moody Creek, Neon Canyon, and Two Mile Canyon.

Most of the canyons were grazed prior to the formation of Lake Powell, with several still affected (e.g., upper Forty Mile Gulch, Last Chance Creek, Lake Canyon, Long Canyon, Scorpion Gulch, and upper Willow Gulch). In Long Canyon several horses were seen in September 1992 (they were removed in 1993). They had caused extensive damage in most of the riparian zone and benches in the canyon. Beaver activity was seen in many canyons supporting permanent water.

Cow Canyon had the richest flora and the largest number of unusual or relict species (see Table 23) with 13. Nearby lower Fence Canyon ranked second with nine species. Upper Miller's Creek (7 species), Clearwater Canyon (5), Ribbon Canyon (5), and Wilson's Creek (4) were ranked third through fifth respectively.

Suitability for vegetation research was based on the diversity and extent of riparian vegetation types in each canyon, and complexity of landforms. Although Alcove Canyon was highly diverse, its small size limited the development of some vegetation, particularly Populus fremontii and riparian scrub types. Overall, the upper ends of Bowns, Cow, Long, and Lower Fence canyons supported the most diverse and extensive riparian communities and complex topography. Lower Wilson's Creek supported the best example of P. fremontii woodland seen during the survey. Apparently, this site has never been grazed by livestock (Tuhy and MacMahon 1988; Spence, personal observations).

Suitability for hydrology studies was based on stream flows, with permanent zones ranked highest. Geomorphology denotes the complexity and extent of landforms, particularly alluvial deposits, beaver dams, and floodplains. Finally, those canyons with extensive alluvium, and well developed patches of mixed deciduous woodland, were ranked highest for paleoecology studies. In addition to extensive deposits in Bowns and Long canyons, some alluvial deposits and well developed mixed woodland was noted in Garden and Ribbon canyons. The presence of potentially deep and stable alluvium and soils around springs in Good Hope Bay suggested some potential for paleoecological studies.

These canyons do not necessarily represent the best sites for research in Glen Canyon NRA. Several canyons in the Escalante drainage, including Coyote and Explorer, still need to be investigated, particularly for vegetation studies. The vegetation in Iceberg, Knowles, and Ticaboo canyons should also be studied. Finally, survey work in Cataract Canyon, and along the San Juan River (e.g., Johns Canyon, Slickhorn Canyon) also needs to be completed.

DISCUSSION

Virtually nothing was known about the riparian vegetation along the Colorado River through Glen Canyon prior to construction of the dam. Clover and Jotter (1944) were the first to describe the vegetation along the river corridor. They mention two main types of riparian vegetation, groves of mixed deciduous trees, including patches of cottonwoods, and a mixed scrub of Baccharis, Salix, and Tamarix. Woodbury et al. (1959) reported that mixed riparian scrub, with Baccharis, Salix, and Tamarix, was the most widespread riparian type along the river. In side canyons and at canyon mouths patches of Populus fremontii and mixed deciduous woodland were found. Except for some brief floristic surveys by Irvine and West (1976), Welsh (1984), and Tuhy and MacMahon (1988), the vegetation of many of the side canyons around Lake Powell has never been studied.

Many of the investigated canyons were probably inaccessible prior to the lake ("hanging" canyons), due to the presence of pour offs, now flooded, in their channels. This is especially likely with canyons such as Alcove, Garden, Bowns, Forgotten, Ribbon, and Slickrock. The presence of Lake Powell has had profound implications for riparian vegetation in many of these originally inaccessible canyons, as they have been colonized in the last 20-30 years, probably for the first time, by beaver. Extensive damage due to beaver activities can be seen in several canyons, with cottonwood in particular being damaged.

Because some canyons in Glen Canyon NRA have not yet been surveyed, the

classification presented in this report remains preliminary. Some types represented by many plots, such as P. fremontii woodland, are likely to be retained, but some types poorly represented in the data set may require modification and reclassification with additional work. Also, additional types may be discovered as more canyons are surveyed. These vegetation types are best considered idealized "types", or "nodes", around which vegetational variation occurs. Vegetation similar to an idealized plot, based on prevalent and modal species, probably does not exist. Rather, these idealized types are class constructs that comprise a variety of similar vegetation which share one or more of a set of diagnostic or defining (dominants in this study) species.

The vegetation classification presented in this report will be a useful tool in future work on wildlife management and research, and livestock grazing management. Also, it will provide a useful focus for future research on the classification, ecology, origins and history of riparian communities on the central portion of the Colorado Plateau. Several of the types that were recognized have not been reported elsewhere in the region. These include the Toxicodendron scrub, mixed forbland, Panicum virgatum marshland, Carex lanuginosa marshland, and Cladium californicum marshland. All of these are best represented in the well watered, "hanging" canyons, including Alcove, Garden, Bowns, Slickrock, and Ribbon. Many are rare, often represented in only one or a few canyons, and are small in extent. Other vegetation types have been previously described, and are widespread in the region. Many of these types occur throughout Glen Canyon NRA where permanent or intermittent riparian zones are found. These include the P. fremontii woodland, Salix-Baccharis scrub, Phragmites marshland, Typha marshland, and mixed deciduous woodland. Others, such as Pseudotsuga menziesii forest, Eleocharis palustris marshland, or Betula occidentalis scrub, are more common at higher elevations, and are represented in Glen Canyon NRA as restricted relict patches which have suffered extensive extinction and modification compared to typical higher elevation stands.

There are few regional studies to compare with the results of this project. The only areas on the Colorado Plateau that can rival the riparian vegetation around Lake Powell for complexity and distinctiveness are in Grand Canyon and Zion national parks. There are currently no classifications or detailed surveys of the riparian vegetation in these canyons. Zion Canyon is a deep canyon incised into the Glen Canyon group of sandstones. It is well known for numerous endemics, boreal-montane species, and complex patches of different kinds of riparian communities. There are strong similarities in the vegetation of this canyon and the east-west trending canyons off the Escalante River, in particular Cow and Fence. The presence of shared rare species, such as Aralia racemosa and Rhus glabra, suggests similar environments and perhaps similar past vegetation. In both canyons, species characteristic of higher elevation coniferous forests can be found in sheltered, well watered, locations. This is particularly true in Zion Canyon, where stands of Douglas fir and white fir can be found as low as 1800 m. Source areas for these species are relatively close in Zion Canyon, while the same species are much more isolated in the Escalante drainage. The Escalante area patches of mixed deciduous woodland with their associated boreal-montane species are more likely to be relictual due to this extreme isolation. If these species and communities are relictual from the late Wisconsin and early Holocene, they are of major scientific importance. Research in these communities can lead to a much better understanding of how species persist or die out during climate changes.

Various lines of evidence provide support for the relict hypothesis to explain the presence of the boreal-montane species in side canyons around Lake Powell. First, most species in this group occur normally at much higher elevations on the Colorado Plateau. The presence of typical coniferous forest species like Mahonia repens or Carex rossii at 1150-1200 m in an arid climate is highly

unusual. Second, most of these species occur together in particular communities. Their distributions are not random, but consist of repeatable assemblages of species within a narrow environmental range. The presence of deep shade (such as in alcoves or in narrow and deep east-west trending canyons), permanent water, and a dense overstory of tree species are site characteristics strongly correlated with these boreal-montane species. Third, many of these species are known as fossils from the late Wisconsin and early Holocene in riparian and alcove sites in the Escalante drainage (Withers and Mead 1993), at a time when coniferous forests occurred at much lower elevations.

Southwestern species reach their northernmost limits in or near the study area. These include Cladium californicum, Rubus neomexicanus, Rhamnus betulifolia, and Parthenocissus vitacea. It was to be expected that these species would be found in warmer southern or western exposures, and associated with permanent water. Unexpected was the association of several of these species with boreal-montane taxa in mixed deciduous woodland. In fact, the Rhamnus and Parthenocissus are among the dominant species in these woodlands. The presence of species with very different distributions and ecologies in the same habitat is difficult to explain. One possibility is that two sets of environmental conditions are explaining the presence of these two groups of species. Boreal-disjunct species may persist because of the combination of relatively cool shaded microclimate and permanent water, while the presence of water may be the most important feature for southwestern species. Elevation of sites was only weakly correlated with numbers of southwestern species, suggesting that climate was not an important controlling factor. Clearly, more work is needed analysing habitat relationships and abundances of these groups of species.

Correlations between vegetation and site physical variables were evident for several types. Perhaps the single most important variable was topographic position (terrace, alcove, stream channel, etc.), which integrates a variety of factors, including water table depth, flood intensity and frequency, microclimate, and substrate characteristics. Mixed deciduous woodland and stands of older P. fremontii tended to occur in alcoves or high terraces where flood activity was minimal. Scrub types were often on medium-height terraces where some flooding occurred, but probably not every year. Marshland types were generally found either in low sites with a high water table, or where springs emerged at the surface, and in both cases where flood activity was minimal.

Most regional riparian vegetation studies have indicated that flooding is the most important single variable influencing vegetation patterns. Topographic, especially terrace, position, is not always a good indicator of flood frequency and intensity, however. Stream barriers and canyon length and width can strongly influence flood activity. Beaver dams in particular can reduce downstream flooding, although their presence can also increase the intensity of a flood if dam failure occurs. Flood activity can be minimal in canyons lacking the necessary length and width to capture and funnel extensive runoff. The synthetic flood intensity index, PFI, showed moderately strong correlations with vegetation structure and composition. In particular, correlations were strongest with forest and woodland plots. In general, most forested plots had relatively low PFI values, suggesting some sensitivity to flooding. Mixed deciduous woodland only occurred in areas where very little potential flooding could occur, and the PFI was the lowest of any vegetation type. Many riparian scrub plots near stream channels showed very high values of the PFI. However, plots of the presumed relict Betula occidentalis scrub occurred only in sites with very low values of the PFI. As a first approximation, the PFI seemed to be a useful variable relating plot location to flood intensity.

Other physical features that could be related to vegetation included canyon aspect or stream bearing, and exposure. For example, the east-west orientation of Cow Canyon may have been partly responsible for the presence of numerous relict species, the Betula and Salix lutea scrub, and well developed mixed deciduous woodland. Also, the upper end of this canyon is very deep (up to 350 m in places) and narrow, which would reduce the amount of sunlight reaching the canyon floor.

It may be possible to predict the type of vegetation a site will support by a set of physical-environmental factors. A simple predictive model can be developed in the form of

$$\text{vegetation type} = \text{function} (A, B, C, D, E, F, G)$$

where:

- A = topographic position (alcove, terrace, channel, etc)
- B = terrace height (if A = terrace)
- C = depth to water table or presence of permanent water
- D = substrate type and texture (slickrock, sand, organic soil, etc.)
- E = soil chemistry (salts)
- F = site or canyon aspect (stream bearing)
- G = recent flood activity

Testing of this model could provide clues to the repeatability of vegetation patterns and responses to the selected environmental factors. Failure to predict the vegetation type a site should support could lead to the development of alternative hypotheses, based on competition, other forms of disturbance, or chance colonization or survival events. Such a model, in conjunction with stand data, could also be useful in determining flood frequency along riparian zones.

Correlations of species richness, diversity and evenness with environmental features like elevation, flood activity, and stream bearing, are often weak in riparian vegetation (Baker 1989a,b; Szaro 1990). Most studies, however, have noted a positive relationship between species diversity and flooding, with high diversity in sites that are frequently flooded. In this study, weak positive correlations were found between all three species variables and terrace-topographic position. There was a tendency, in particular, for diversity to be somewhat higher in stream beds and low terraces compared with higher terraces. These trends are supported in part by general theoretical considerations on the relationships among diversity, competition, and environment (eg., Huston 1979; White 1979). Where disturbance is minimal competition should be more intense, leading in particular to lowered evenness (dominance by one or a few species). This was not found to be the case in this project. Evenness peaked in sites least likely to be flooded, such as alcoves, and especially around permanent water sources. Evenness and diversity values were also high in those types supporting large numbers of relict species, suggesting that some historical component may be involved in evenness and diversity. However, although these sites were not flood-prone, other disturbances such as rockfall may occur and explain the high diversity and evenness values. Species diversity and richness should be lower in highly disturbed sites, such as stream channels frequently flooded, compared to sites where disturbance is less frequent or intense. This was not the case in this study, nor in other regional riparian studies (Baker 1989a; Szaro 1990).

The riparian vegetation in many canyons was distinctly patchy, a feature that other southwestern studies have noted (cf. Szaro 1990). The upper ends of canyons with perennial flows, including those in Alcove, Bowns, Cow, and Ribbon, were especially distinctive in this respect. These upper canyons consisted of mosaics of mixed deciduous woodland, P. fremontii stands, Typha

and Phragmites patches, Toxicodendron scrub, and Salix-Baccharis scrub. C. Wood (pers. comm. 1992) suggested that the complex and patchy nature of the riparian vegetation in these upper canyon settings results from a lack of disturbance, especially by flooding, and by the abundant available water. The lack of disturbance would lead to competitive interactions and sorting out of species and vegetation patches along subtle but stable environmental gradients. Support for this hypothesis includes the lower overall values of evenness, diversity and richness in protected sites, and the presence of numerous relict species that have been able to persist in the absence of disturbance. Many of these relicts rarely reproduce sexually, and would be expected to be especially vulnerable to high levels of disturbance.

A subsidiary hypothesis to explain the patchiness and overall lack of predictability of vegetation in these upper canyon sites can be developed based on flood frequency and chance survival. Past flood activity may have controlled the distribution of many species in parts of these riparian zones.

However, as flooding is highly variable in time and space, differential survival of individuals or clones of particular species would have occurred. With subsequent cessation or reduction of flooding, survivors may have been at a competitive advantage compared to species dispersing into the site by seed.

This may have led to site tenacity, i.e., a species that survived a flood event would be more likely to reoccupy and dominate the site than a species dispersing into it. Strongly clonal, rapidly growing herbaceous species, such as Phragmites and Typha, in particular, would be expected to produce mosaics of different patches related to postflood clonal survival, with site tenacity (competitive ability) controlled by differences in water tables and substrate.

This hypothesis may explain the mosaic of different vegetation patches in the channels of many of these upper canyon zones. Collection of field data on the ability to survive flooding and experiments on the growth rates of selected species could provide tests of this hypothesis.

MANAGEMENT IMPLICATIONS

The riparian plant communities of Glen Canyon NRA are of major scientific importance. Prior to this survey, only a very incomplete picture of the kinds of vegetation that occurred in the side canyons around Lake Powell was available. In this report these communities have been shown to be very complex, diverse, and to support remarkable numbers of relict boreal-montane species as well as other types of rare species. They represent survival centers for a variety of species and communities that appear to date from the Wisconsin, and that have persisted throughout the Holocene. Because of these considerations, representative sites need to be preserved for scientific research. Much can be learned from these communities about persistence of species in the face of climate change and how disturbance affects riparian vegetation. Below, the most important sites for monitoring and for Research Natural Area designation are discussed.

1. Canyon selection

Among canyons surveyed during 1992-94, several stand out as being most important, by virtue of well-developed riparian vegetation. These are Alcove, Bowns, Cow, Long and Ribbon canyons, lower Hall's Creek, and lower Wilson Creek. Of these, only Alcove and lower Wilson's appear to have never been grazed, apparently supporting pristine riparian communities. However, the vegetation in Alcove Canyon appears to have changed dramatically at some point in the recent past (Spence, pers. observations). This leaves only lower Wilson's Creek as being both undisturbed and lacking any obvious sign of recent vegetation change. Among the other five, Long Canyon has been seriously affected by feral horses, Hall's Creek was grazed to 1986, and Bowns, Cow and Ribbon have not been grazed since the 1960's. Beaver are found in all except possibly Long Canyon.

Bowns, Cow and Long canyons are all centered on the east side of the Escalante River and west of the lower Waterpocket Fold, within the Natural Zone. They are similar geologically, but differ substantially in geomorphology and water flows. The upper ends of Bowns and Cow canyons support perennial streams, while the situation in Long Canyon is reversed, with perennial flows only in the lower part, and none in the upper end. This upper end of Long Canyon is unusual because it supports the only P. fremontii gallery forest seen in the survey other than in lower Wilson's Creek, in Lake Canyon (badly disturbed), and along the Escalante River. Extensive alluvial deposits occur in Bowns Canyon, while more limited deposits are found in upper Cow and Long canyons. Cow Canyon is very long, and access to perennial stream stretches and associated vegetation is more difficult than similar sites in Bowns Canyon. Of these three, Bowns Canyon is probably the best candidate for work on riparian vegetation structure, woody species dynamics, hydrology, and long-term monitoring. It also has an excellent paleoecological record, and good habitat for amphibians. The bird fauna was not surveyed, but is probably similar to that in Long Canyon. The one drawback to Bowns is that its patches of mixed deciduous woodland are less extensive than in Cow or Long canyons. Hall's Creek, although recovering from past grazing, and supporting a wide diversity of vegetation, is excluded because of the additional factor of grazing. Ribbon Canyon supports good stands of mixed deciduous woodland, but has little P. fremontii woodland and only intermittent and poorly developed riparian scrub.

Because of questions concerning resources available for ecosystem monitoring work, the suggested canyons are ranked from highest potential to lowest potential. This way, a cut off level can be applied anywhere along this ranking:

1. Wilson's Creek
2. Bowns Canyon
3. Cow Canyon
4. Slickrock Canyon (well developed mixed forblands; some human disturbance)
5. Long Canyon
6. Upper Fence Canyon (off Escalante River; excellent Populus fremontii-Salix goodingii vegetation in upper reaches; some grazing).

Two canyons not yet surveyed may also be good candidates, Coyote Gulch and Iceberg Canyon.

2. 1994-95 field work and monitoring plans

One of the goals of the NRPP riparian ecosystem project at Glen Canyon NRA was to establish a long-term monitoring program for selected ecosystem attributes.

In the likely event of future climate change resulting from global warming, monitoring of perennial stretches of riparian communities will provide valuable data. Five attributes have been selected for monitoring; vegetation, streambank morphology, stream depth and flow, avian communities, and herp communities. Monitoring a sixth community attribute, aquatic invertebrate communities, is also recommended (see below).

In 1994, long-term monitoring programs were initiated in Wilson's Creek and Cow Canyon. Vegetation, streambank morphology, and water depth data were collected from six transects in each canyon. Three avian monitoring plots were surveyed at each site. Field work for 1995 will concentrate on establishing field plots in Bowns Canyon and a fourth canyon yet to be selected. Details on the monitoring program will be prepared following the 1995 season. This report will document monitoring protocols for all ecosystem attributes.

3. Research Natural Area designations

Because of the relatively undisturbed nature and scientific value of many of the side canyons around Lake Powell, it is recommended that Research Natural Area designation be pursued for selected canyons. In addition, future management plans could include restrictions on recreational activities (e.g., camping, developed trails) in these sites. The most important sites are: Cow and Fence canyons (as a combined unit), lower Wilson's Creek, upper Bowns Canyon, Ribbon Canyon, and the upper end of the main fork of Forgotten Canyon. Future survey work may also suggest that Iceberg Canyon be placed on this list. Currently, very little recreational activity occurs in most of these canyons, although several are easily visited by boat.

4. Other Recommendations

Several additional recommendations are listed below. Implementation of these will depend upon management concerns, and available funds and personnel.

1. The riparian vegetation in those canyons where long-term monitoring programs exist should be mapped using GPS. Future GPS surveys will allow an assessment of changes in sizes and status of the communities.
2. Monitoring of water quality and aquatic invertebrate communities should be established as part of the long-term monitoring of riparian communities. The baseline data generated can be used to study the effects of recreational, mining, or grazing activities in disturbed streams elsewhere in the recreation area.
3. Trapping and removal of beaver should be done in canyons where they appear to be having a major impact on woody riparian species. Beaver are capable of completely destroying riparian gallery forests of favored species such as Populus fremontii and Salix goodingii. Their activities could destroy the monitoring programs put into place.
4. Monitoring of riparian communities should be extended to those currently impacted by activities such as grazing, mining, or heavy recreational use.

LITERATURE CITED

- Agenbroad, L., J. Mead, R. Hevly, S. Clay-Poole, and G. Judges-Edwards. 1990. Quaternary studies: Canyonlands National Park and Glen Canyon National Recreation Area. Final Report to the National Park Service, Rocky Mountain Region, Lakewood, CO. Quaternary Studies Program, Dept. of Geology, N. Arizona University.
- Ashcroft, G.L., D.T. Jensen, and J.L. Brown. 1992. Utah climate. Utah Climate Center, Utah State University, Logan.
- Asplund, K.K. and M.T. Gooch. 1988. Geomorphology and the distributional ecology of Fremont cottonwood (Populus fremontii) in a desert riparian canyon. Desert Plants 9: 17-27.
- Baker, W.L. 1989a. Classification of the riparian vegetation of the montane and subalpine zones in western Colorado. Great Basin Natur. 49: 214-228.
- Baker, W.L. 1989b. Macro- and micro-scale influences on riparian vegetation in western Colorado. Ann. Assoc. Amer. Geogr. 79: 65-78.
- Baker, W.L. 1990. Species richness of Colorado riparian vegetation. J. Veg. Sci. 1: 119-124.
- Boison, P.J. and P.C. Patton. 1985. Sediment storage and terrace formation in Coyote Gulch basin, south-central Utah. Geology 13: 31-34.
- Brotherson, J.D., E.E. Evenson, S.R. Rushforth, J. Fairchild, and J.R. Johansen. 1985. Spatial patterns of plant communities and differential weathering in Navajo National Monument, Arizona. Great Basin Natur. 45: 1-13.
- Brown, D.E. (ed.) 1982. Biotic communities of the American southwest-United States and Mexico. Desert Plants 4: 1-342.
- Camp, P. 1978. Ecological reconnaissance, Hall's Creek, Capitol Reef National Park. Unpublished report to the National Park Service, Capitol Reef National Park. Dept. of Biology, Utah State University.
- Campbell, C.J. and W. Green. 1968. Perpetual succession of stream-channel vegetation in a semiarid region. J. Arizona Acad. Sci. 5: 86-98.
- Curtis, J.T. 1959. The vegetation of Wisconsin: an ordination of plant communities. U. Wisconsin Press, Madison, WI.
- Digby, P.G.N. and R.A. Kempton. 1987. Multivariate analysis of ecological communities. Chapman and Hall, London.
- Driscoll, R.S., D.L. Merkel, D.L. Radloff, D.E. Snyder, and J.S. Hagihara. 1985. An ecological land classification framework for the United States. U.S. For. Ser. Misc. Publ. 1439.
- Graf, J.B., R.H. Webb, and R. Hereford. 1991. Relation of sediment load and flood-plain formation to climatic variability, Paria River drainage basin, Utah and Arizona. Geol. Soc. Amer. Bull. 103: 1405-1415.
- Graf, W.L. 1987. Late Holocene sediment storage in canyons of the Colorado Plateau. Geol. Soc. Amer. Bull. 99: 261-271.
- Grieg-Smith, P. 1983. Quantitative plant ecology (3rd ed.). Blackwell

Scientific Publ., Oxford.

- Harper, K.T., S.C. Sanderson, and E.D. McArthur. 1992. Riparian ecology in Zion National Park, Utah. pp. 32-42 In: Symposium on the ecology and management of riparian shrub communities. U.S.D.A. For. Ser. Gen. Tech. Rep. INT-289.
- Heil, K.D., J.M. Porter, R. Fleming, and W.H. Romme. 1993. Vascular flora and vegetation of Capitol Reef National Park, Utah. USDI Dept. of Interior, National Park Service, Tech. Rep. NPS/NAUCARE/NRTR-93/01.
- Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113: 81-101.
- Irvine, J.R. 1976. Riparian environmental-vegetation interrelationships along the lower Escalante River, Glen Canyon National Recreation Area, Utah. M.Sc. thesis, Utah State University, Logan, Utah.
- Irvine, J.R. and N.E. West. 1979. Riparian tree species distribution and succession along the lower Escalante River, Utah. Southwestern Natur. 24: 331-346.
- Lively-Schall, W. and R.D. Foust. 1988. Surface water within Glen Canyon National Recreation Area. Final report to the National Park Service, Glen Canyon National Recreation Area. Northern Arizona University.
- Loope, W.L. 1977. Vegetation in relation to environment in Canyonlands National Park, Utah. Ph.D. dissertation, Utah State University, Logan.
- Manly, B.F.J. 1986. Multivariate statistical methods: a primer. Chapman and Hall, London.
- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.
- Padgett, W.G., A.P. Youngblood and A.H. Winward. 1989. Riparian community type classification of Utah and southeastern Idaho. U.S.D.A. For. Ser. Intermountain Region R4-Ecol-89-01.
- Patton, P.C. and P.J. Boison. 1986. Processes and rates of formation of Holocene alluvial terraces in Harris Wash, Escalante River basin, south-central Utah. Geol. Soc. Amer. Bull. 97: 369-378.
- Romme, W.H., K.D. Heil, J.M. Porter, and R. Fleming. 1993. Plant communities of Capitol Reef National Park, Utah. USDI Dept. of Interior, National Park Service, Tech. Rep. NPS/NAUCARE/NRTR-93/02.
- Schultz, L.M. 1993. Patterns of endemism in the Utah flora. pp. 249-269 In Sivinski, R. and K. Lightfoot (eds.). Southwestern rare and endangered plants. New Mexico For. Res. Cons. Div. Misc. Publ. No. 2.
- Schultz, L.M., E.E. Neely and J.S. Tuhy. 1987. Flora of the Orange Cliffs of Utah. Great Basin Natur. 47: 287-298.
- Shimwell, D.W. 1971. The description and classification of vegetation. Univ. Washington Press, Seattle.
- Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy. W.H. Freeman and Company, San Francisco.
- Spence, J.R. 1990. A review of various vegetation classification schemes for

- use on the Colorado Plateau, with suggestions for future consideration. Unpublished report, Resource Management Division, Capitol Reef National Park.
- Spence, J.R. 1991. Hanging garden vegetation and flora survey, San Juan Arm, Lake Powell, Glen Canyon National Recreation Area. Unpublished report to the National Park Service, Glen Canyon NRA. Manzanita BioStudies, Torrey, Utah.
- Spence, J.R. 1992a. Adapting the Brown, Lowe and Pase classification to the Colorado Plateau. Final Report to the National Park Service, CPSU, N. Arizona University. Manzanita BioStudies, Torrey, Utah.
- Spence, J.R. 1992b. A survey and classification of the riparian vegetation in side canyons around Lake Powell, Glen Canyon NRA. Unpublished report, Resource Management Division, Glen Canyon NRA.
- Spence, J.R. 1992c. Relict vegetation surveys, Glen Canyon National Recreation Area. Unpublished report, Resource Management Division, Glen Canyon NRA.
- Spence, J.R. 1992d. A breeding bird census workplan for side canyons of Lake Powell, Glen Canyon National Recreation Area. Unpublished report, Resource Management Division, Glen Canyon NRA.
- Spence, J.R. 1994. A preliminary survey of hanging gardens and related vegetation along the Colorado River, Grand Canyon National Park. Resource Management Division, Glen Canyon NRA.
- Spence, J.R. 1995. Resource paper on the hanging gardens of the Colorado Plateau. Unpublished report, Resource Management Division, Glen Canyon NRA.
- Spence, J.R. and N.R. Henderson. 1993. Tinaja and hanging garden vegetation of Capitol Reef National Park, southern Utah, U.S.A. J. Arid Environ. 24: 21-36.
- Spence, J.R., W.H. Romme, L. Floyd-Hanna, and P.G. Rowlands. 1995. A preliminary vegetation classification for the Colorado Plateau. In Proceedings of the second biennial conference on research on the Colorado Plateau. National Park Service (in press).
- Spence, J.R. and J.A.C. Zimmerman. 1994. Preliminary flora of Glen Canyon National Recreation Area. Unpublished report, Resource Management Division, Glen Canyon NRA.
- Szaro, R.C. 1989. Riparian forest and scrubland community types of Arizona and New Mexico. Desert Plants 9: 69-138.
- Szaro, R.C. 1990. Southwestern riparian plant communities: site characteristics, tree species distributions, and size-class structures. Forest Ecology and Manage. 33-34: 315-334.
- Stanton, N.L., S.J. Buskirk, and J.F. Fowler. 1992. Biogeography of invertebrates and plants in hanging gardens of the Colorado Plateau. Annual report to the National Park Service, Rocky Mountain Region. U. of Wyoming.
- Stevens, L.E. and G.L. Waring. 1985. The effects of prolonged flooding on the riparian plant community in Grand Canyon. pp. 81-86 In Riparian ecosystems and their management: reconciling conflicting uses. U.S.D.A.

For. Ser. Gen. Tech. Rep. RM-120.

- Tuhy, J.S. and J.A. MacMahon. 1988. Vegetation and relict areas of Glen Canyon National Recreation Area. Final report to the National Park Service, Glen Canyon National Recreation Area. The Nature Conservancy.
- Waring, G.L. 1992. A study of the developing riparian communities along the shoreline of Lake Powell, Arizona and Utah. Final report to the National Park Service, Glen Canyon National Recreation Area. Museum of Northern Arizona.
- Webb, G.M. and J.D. Brotherson. 1988. Elevational changes in woody vegetation along three streams in Washington County, Utah. Great Basin Natur. 48: 512-529.
- Webb, R.H. and V.R. Baker. 1987. Changes in hydrologic conditions related to large floods on the Escalante River, south-central Utah. pp. 309-323 In Singh, V.P. (ed.). Regional flood frequency analysis. D. Reidel, Boston.
- Webb, R.H., S.S. Smith and V.A.S. McCord. 1991. Historic channel change of Kanab Creek, southern Utah and northern Arizona. Grand Canyon Nat. Hist. Assoc. Monogr. No. 9: 1-91.
- Welsh, S.L. 1984. Flora of Glen Canyon National Recreation Area. Final report to the National Park Service, Glen Canyon N.R.A.
- Welsh, S.L. 1989. On the distribution of Utah's hanging gardens. Great Basin Natur. 49: 1-30.
- Welsh, S.L. and C.A. Toft. 1981. Biotic communities of hanging gardens in southeastern Utah. National Geogr. Soc. Res. Rep. 13: 663-681.
- Welsh, S.L., N.D. Atwood, S. Goodrich and L.C. Higgins (eds.). 1987. A Utah flora. Great Basin Natur. Mem. 9: 1-894.
- West, N.E. 1988. Intermountain deserts, shrub steppes, and woodlands. Ch. 7 In: Barbour, M.G. and W.D. Billings (eds.). North American terrestrial vegetation. Cambridge U. Press, New York.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45: 229-299.
- Withers, K. and J.I. Mead. 1993. Late Quaternary vegetation and climate in the Escalante River basin on the central Colorado Plateau. Great Basin Natur. 53: 145-161.
- Woodbury, A.M., S.D. Durrant and S. Flowers. 1959. Survey of vegetation in the Glen Canyon reservoir basin. Anthropol. Pap. University of Utah No. 36 (Glen Canyon Ser. No. 5).

TABLES

Table 1. A brief and subjective topographic-vegetation classification of wetland and riparian vegetation with reference to the Colorado Plateau below 2000 m. Genera characteristic of sites on the Colorado Plateau are included.

1. MARSHLAND: permanently saturated flat low lying sites with high water table or periodic surface water and organic rich soils dominated by herbaceous monocots. Disturbance low. Characteristic genera: Carex, Equisetum, Juncus, Scirpus, Typha.

2. RIPARIAN: seasonally to permanently saturated stream and river margins with high water table, soils variable, sometimes absent, vegetation variable, often woody. Disturbance high. Characteristic genera: Baccharis, Equisetum, Juncus, Populus, Salix, Tamarix.

3. HANGING GARDEN-SPRING: permanently to seasonally saturated sites perched above low lying water table, spring-fed, with little soil development, usually in alcoves, vegetation predominantly herbaceous. Disturbance variable, low to high. Characteristic genera: Adiantum, Calamagrostis, Carex, Eleocharis, Mimulus, Phragmites, Primula, Solidago.

4. STRAND: permanently to seasonally saturated recent deposits (eg., sand bars) or rock surfaces along rivers and fluctuating lakeshores, no soil development, water table high, periodically flooded, vegetation very sparse and open, woody and herbaceous. Disturbance high. Characteristic genera: Cyperus, Echinochloa, Elymus, Tamarix.

5. LAKE: still or slowly moving water, generally organic soil present, vegetation herbaceous, often floating on water surface. Disturbance low. Characteristic genera: Potamogeton, Zannichellia, Chara.

6. TINAJA: permanently to mostly seasonally saturated, periodically flooded pools eroded in bedrock, organic soil often present in basin, vegetation woody and herbaceous. Disturbance high. Characteristic genera: Juncus, Panicum, Phragmites, Salix.

Table 2. Climate data for selected sites in and near Glen Canyon National Recreation Area, Most data is from Ashcroft, et al. (1992).

	<u>Page</u>	<u>Big Water</u>	<u>Bullfrog</u>	<u>Hite</u> ¹
Elevation (m)	1320	1250	1165	1219
Mean Annual Temperature (C)	14.2	13.7	15.2	15.3
Mean Annual Precipitation (mm)	165	176	151	221
Period of Record	1957-1993	1963-1992	1967-1990	1978-1992

¹Hite Ranger Station. Hite Marina (1125m) recorded values of 16.1° C and 136 mm for the period 1968-1978.

Table 3. The study sites for riparian survey and ecosystem NRPP project around Lake Powell. The dates visited are noted in parentheses. The number of plots recorded in each canyon is listed.

<u>Canyons visited 1991-1993</u>	<u>Code</u>	<u>Number of Plots</u>
1. "Garden" Canyon (7/27/91)	GAC	5
2. Two Mile Canyon (4/22/92)	TMC	4
3. Good Hope Bay (4/23/92)	GHB	3
4. Lake Canyon (4/23/92)	LAC	1
5. Wilson's Creek (5/26-27/92)	LWC	4
6. Alcove Canyon (5/28/92)	ALC	11
7. Ribbon Canyon (6/8-9/92)	RIC	11
8. Hall's Creek (6/18-19/92)	HAC	11
9. Last Chance Creek (7/10/92)	LCC	5
10. Cow Canyon (7/28-31/92)	COW	18
11. Clearwater Canyon (8/13-14/92)	CLW	1
12. Bowns Canyon (8/19/92)	BOC	3
13. Slickrock Canyon (8/20/92)	SLC	2
14. Long Canyon (9/2-4/92)	LOC	6
15. Miller's Creek (9/23-25/92)	UMC	4
16. Moody Creek (06/24/93)	MOD	1
17. Knowles Canyon (7/12/93)	KNC	2
18. Willow Gulch (7/27/93)	WIG	6
19. Forty Mile Gulch (7/28/93)	FMG	7
20. Lower Fence Canyon (7/29/93)	LFC	7
21. Dry Rock Creek (8/20/93)	DRC	1
22. Scorpion Gulch (8/23-24/93)	SCO	10
23. George's Camp (8/24/93)	GEC	4
24. Chopslot Canyon (8/25/93)	CHO	4
25. Neon Canyon (8/26/93)	NEO	2
26. Upper Fence Canyon (8/26/93)	UFC	5
27. Forgotten Canyon (9/9/93)	FOC	10
Total: 26 canyons + Good Hope Bay		148

Table 4. Notation and definitions used in recording of plot vegetation and site environment data.

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1. GROWTH FORM: Tr=tree; Sh=shrub/subshrub; Pf=biennial/perennial forb; Pg=biennial/perennial graminoid; Li=liana; Fr=fern/fern ally; Cr=cryptogam; Af=annual-biennial forb; Ag=annual-biennial graminoid.
 2. ABUNDANCE: 6=Dominant (95-100% canopy cover); 5=Abundant (50-95% canopy cover); 4=Common (10-50% canopy cover); 3=Uncommon (1-10% canopy cover); 2=Occasional (<1% canopy cover but easily found, or one large individual of a shrub or small tree); 1=Rare (<<1% canopy cover, difficult to find or one or two small individuals present).
 3. TERRACE: 1=current wetted stream channel; 2=margins or lowest obvious terrace (0-50 cm, flooded often and yearly); 3=intermediate terrace (50-100 cm, flooded occasionally, usually at least once every 1-3 years); 4=high terrace (100-200 cm, flooded every 5-10 years); 5=highest terrace (>200 cm; flooded ca. every 100 years); 6=completely protected from floods (eg., alcoves).
 4. EXPOSURE (hours exposed during May-August period): 1=exposed at least 8 hrs/day, canyon w/d ratio >3:1; 2=exposed 5-8 hrs/day, morning or afternoon sun partially blocked by cliffs, w/d ratio 2-3:1; 3=exposed 3-5 hrs/day, partially shaded by cliffs, with only morning or afternoon sun; 4=exposed 1-3 hrs/day, in narrow deep canyon, w/d ratio <1:1; 5=mostly protected, exposed to sun <1 hr/day, often in alcove.
-

Table 5. Life form spectra for four groupings of the riparian flora; total, obligate riparian, facultative riparian, and introduced.

	Life Form							
	Tr	Sh	Pf	Pg	Af	Ag	Li	Fr
Total (N=199)	12	32	63	58	18	9	3	5
Obligate riparian (N=111)	9	11	31	42	5	5	3	5
Facultative Riparian (N=65)	2	20	29	10	5	0	0	0
Introduced (N=22)	2	1	3	5	8	4	0	0

Tr = tree
 Sh = shrub or subshrub
 Pf = biennial/perennial forb
 Pg = biennial/perennial graminoid

Af=annual forb
 Ag=annual graminoid
 Li=liana or vine
 Fr=fern or fern ally

Table 6. A classification of the principal riparian, seep, and tinaja vegetation based on 148 plots, informally grouped into three major physiognomic groups. N=number of plots, S=average species richness, H'=Shannon diversity index, E=evenness index, I_H=index of homogeneity, I_D=index of distinctiveness, I_G=index of geographic distribution, DISJ=per cent disjunct species, and CPE=per cent Colorado Plateau endemics.

	N	S	H'	E	I _H	I _D	I _G	DISJ	CPE
A. FOREST AND WOODLAND									
1. <u>Populus fremontii</u>	33	11.7	1.01	0.96	56.8	37.6	65.2	2.3	0.6
2. <u>Mixed Deciduous</u>	17	13.1	1.07	0.97	44.4	80.4	34.8	33.9	5.5
3. <u>Pseudotsuga menziesii</u> - <u>Acer grandidentatum</u>	3	6.3	0.73	0.94	78.0	34.8	4.2	70.5	11.4
B. SCRUB									
4. <u>Salix exigua</u>	17	9.4	0.91	0.95	49.5	55.6	47.8	1.4	0
5. <u>Betula occidentalis</u>	4	13.3	1.10	0.97	69.1	26.3	8.7	23.5	0
6. <u>Salix lutea</u>	6	10.3	0.97	0.96	59.5	51.4	8.7	23.0	1.9
7. <u>Salix goodingii</u>	3	11.7	1.03	0.95	73.7	68.0	4.3	0	0
8. <u>Toxicodendron rydbergii</u>	7	10.7	0.98	0.96	47.5	9.5	30.4	10.0	5.1
C. MARSHLAND									
9. <u>Phragmites australis</u>	9	7.7	0.79	0.93	48.6	39.6	39.1	2.2	0
10. <u>Typha</u>	4	7.0	0.78	0.94	56.0	50.0	13.0	0	0
11. <u>Panicum virgatum</u>	9	10.4	0.95	0.95	53.3	59.8	26.1	10.7	0
12. <u>Mixed forb</u>	10	7.7	0.83	0.95	58.4	66.7	21.7	5.4	0
13. <u>Solidago canadensis</u>	5	11.2	1.01	0.96	60.7	35.3	21.7	9.0	0
15. <u>Eleocharis palustris</u>	3	11.0	0.98	0.99	60.8	50.1	13.0	4.2	12.5
16. <u>Cladium californicum</u>	1	13.0	1.01	0.91	-	-	4.2	15.4	0
17. <u>Carex lanuginosa</u>	1	12.0	1.04	0.97	-	-	4.2	16.7	0
[18. unclassified or ephemeral riparian plots					16]				

Table 7. Summary of the principal vegetational and physical characteristics of the Populus fremontii woodland type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	33
Total species	90
S	11.7 (2.9)
H'	1.010 (0.119)
E	0.959 (0.017)
I _H	56.8%
I _D	37.6%
I _G	65.2%
DISJ	2.3%
CPE	0.6%
Terrace position	3.04 (1.53)
Exposure	2.74 (0.74)
PFI (flooding index)	0.76 (0.77)
DIST (log ₁₀ m)	3.01 (0.77)
Canyon depth (m)	116.4 (53.5)
Canyon width (m)	320.0 (264.9)
Width/depth ratio	2.61 (1.61)
Stream bearing	156.9° (87.3°)
Elevation (m above 1130)	145.9 (100.5)
Domestic livestock sign (% of plots)	60.6%
Median water type: permanent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate lowland forest and woodland, (1401.05) Populus fremontii series, (1401.06) Salix goodingii series.

Prevalent species (*=modal species also)

- | | |
|---------------------------------|------------------------------------|
| 1. <u>Populus fremontii</u> * | 7. <u>Castilleja linariifolia</u> |
| 2. <u>Artemisia ludoviciana</u> | 8. <u>Equisetum hyemale</u> |
| 3. <u>Salix goodingii</u> * | 9. <u>Bromus tectorum</u> * |
| 4. <u>Baccharis salicina</u> | 10. <u>Juncus arcticus</u> |
| 5. <u>Tamarix chinensis</u> | 11. <u>Clematis ligusticifolia</u> |
| 6. <u>Elymus canadensis</u> | |
-

Table 8. Summary of the principal vegetational and physical characteristics of the mixed deciduous woodland type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	17
Total species	75
S	13.12 (3.18)
H'	1.069 (0.104)
E	0.966 (0.013)
I _H	44.4%
I _D	80.4%
I _G	34.8%
DISJ	33.9%
CPE	5.5%
Terrace position	5.62 (0.94)
Exposure	4.09 (0.87)
PFI (flooding index)	0.283 (0.069)
DIST (log ₁₀ m)	1.816 (0.593)
Canyon depth (m)	161.8 (71.6)
Canyon width (m)	302.6 (176.9)
Width/depth ratio	2.19 (1.77)
Stream bearing	176.5° (80.85)
Elevation (m above 1130 m)	116.2 (74.9)
Recent livestock sign (% of plots)	11.8%
Median water type: permanent spring	

SRFR ASSIGNMENTS: Colorado Plateau cold temperate woodlands, (1401.10) Rhamnus betulifolia series, (1401.07) Acer negundo series, (1401.09) Ostrya knowltonii series; Colorado Plateau cold-temperate lowland tall shrublands, (1402.02) Quercus gambelii series; Colorado Plateau montane forest, (1301.08) Acer grandidentatum series.

Prevalent species (*=modal species also)

- | | |
|------------------------------------|--|
| 1. <u>Rhamnus betulifolia</u> * | 8. <u>Celtis reticulata</u> * |
| 2. <u>Acer negundo</u> * | 9. <u>Clematis ligusticifolia</u> |
| 3. <u>Smilacina stellata</u> * | 10. <u>Betula occidentalis</u> |
| 4. <u>Quercus gambelii</u> * | 11. <u>Adiantum capillus-veneris</u> * |
| 5. <u>Parthenocissus vitacea</u> * | 12. <u>Solidago sparsiflora</u> * |
| 6. <u>Equisetum hyemale</u> | 13. <u>Toxicodendron rydbergii</u> |
| 7. <u>Apocynum cannabinum</u> * | |
-

Table 9. Summary of the principal vegetational and physical characteristics of the Pseudotsuga menziesii forest type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	3
Total species	10
S	6.3
H'	0.733
E	0.944
I _H	71.7%
I _D	80.2%
I _G	4.2%
DISJ	70.5%
CPE	11.4%
Terrace position	6.00 (0)
Exposure	4.00 (0)
PFI (flooding index)	-
DIST (log ₁₀ m)	1.00 (0)
Canyon depth (m)	-
Canyon width (m)	-
Width/depth ratio	-
Stream bearing	15° (0°)
Elevation (m above 1130 m)	545 (0)
Recent livestock sign (% of plots)	0%
Median water type: permanent spring	

SRFR ASSIGNMENT: (1301.01) Colorado Plateau montane forest, Pseudotsuga menziesii series.

Prevalent species (*=modal species also)

- | | |
|-----------------------------------|---------------------------------|
| 1. <u>Pseudotsuga menziesii</u> * | 4. <u>Ostrya knowltonii</u> * |
| 2. <u>Acer grandidentatum</u> * | 5. <u>Habenaria zothecina</u> * |
| 3. <u>Smilacina stellata</u> | 6. <u>Mahonia repens</u> |
-

Table 10. Summary of the chief features of the the principal vegetational and physical characteristics of the Salix exigua type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	17
Total species	48
S	9.412 (3.411)
H'	0.910 (0.157)
E	0.949 (0.003)
I _H	49.5%
I _D	55.6%
I _G	47.8%
DISJ	1.4%
CPE	0%
Terrace position	2.47 (0.99)
Exposure	2.53 (0.82)
PFI (flooding index)	1.02 (1.24)
DIST (log ₁₀ m)	3.38 (0.61)
Canyon depth (m)	122.5 (76.6)
Canyon width (m)	314.4 (262.8)
Width/depth ratio	3.00 (1.91)
Stream bearing	170.0° (82.4°)
Elevation (m above 1130 m)	94.7 (74.1)
Recent livestock sign (% of plots)	41%
Median water type: permanent stream	

SRFR ASSIGNMENT: (1402.05) Colorado Plateau cold temperate tall shrubland, Salix exigua series.

Prevalent species (*=modal species also)

- | | |
|--------------------------------|-------------------------------|
| 1. <i>Salix exigua</i> * | 5. <i>Melilotus alba</i> * |
| 2. <i>Baccharis salicina</i> * | 6. <i>Tamarix chinensis</i> * |
| 3. <i>Equisetum hyemale</i> | 7. <i>Juncus arcticus</i> |
| 4. <i>Populus fremontii</i> | 8. <i>Elymus canadensis</i> |
-

Table 11. Summary of the principal vegetational and physical characteristics of the Betula occidentalis scrub type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	4
Total species	30
S	13.25 (2.5)
H'	1.101 (0.105)
E	0.972 (0.002)
I _H	69.1%
I _D	55.6%
I _G	8.7%
DISJ	23.5%
CPE	0%
Terrace position	3.00 (0.50)
Exposure	3.75 (0.50)
PFI (flooding index)	0.59 (0.08)
DIST (log ₁₀ m)	3.06 (0.25)
Canyon depth (m)	163.7 (23.9)
Canyon width (m)	290.0 (51.0)
Width/depth ratio	1.76 (0.06)
Stream bearing	202.5° (69.5°)
Elevation (m above 1130)	91.3 (48.2)
Domestic livestock sign (% of plots)	0%
Median water type: permanent stream	

SRFR ASSIGNMENT: Colorado Plateau montane tall shrubland, (1302.06) Betula occidentalis series.

Prevalent species (*=modal species also)

- | | |
|---------------------------------|------------------------------------|
| 1. <u>Betula occidentalis</u> * | 8. <u>Aster glaucodes</u> * |
| 2. <u>Equisetum hyemale</u> | 9. <u>Chrysothamnus nauseosus</u> |
| 3. <u>Elymus canadensis</u> * | 10. <u>Panicum virgatum</u> |
| 4. <u>Solidago canadensis</u> | 11. <u>Salix exigua</u> |
| 5. <u>Juncus arcticus</u> | 12. <u>S. lutea</u> |
| 6. <u>Rhamnus betulifolia</u> | 13. <u>Apocynum cannabinum</u> |
| 7. <u>Artemisia ludoviciana</u> | 14. <u>Clematis ligusticifolia</u> |
-

Table 12. Summary of the principal vegetational and physical characteristics of the Salix lutea scrub type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	6
Total species	30
S	10.33 (2.73)
H'	0.966 (0.110)
E	0.964 (0.006)
I _H	59.5%
I _D	51.4%
I _G	8.7%
DISJ	23.0%
CPE	1.9%
Terrace position	2.50 (0.71)
Exposure	3.92 (0.20)
PFI (flooding index)	1.223 (0.357)
DIST (log ₁₀ m)	2.443 (0.651)
Canyon depth (m)	132.5 (54.9)
Canyon width (m)	120.0 (62.9)
Width/depth ratio	0.875 (0.343)
Stream bearing	218.3° (98.9°)
Elevation (m above 1130)	100.0 (67.0)
Domestic livestock sign (% of plots)	0%
Median water type: permanent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate lowland tall shrubland, (1402.08) Salix lutea series.

Prevalent species (*=modal species also)

- | | |
|-------------------------------------|-----------------------------------|
| 1. <u>Salix lutea</u> * | 6. <u>Solidago canadensis</u> |
| 2. <u>Apocynum cannabinum</u> * | 7. <u>Populus fremontii</u> |
| 3. <u>Clematis ligusticifolia</u> * | 8. <u>Smilacina stellata</u> |
| 4. <u>Equisetum hyemale</u> | 9. <u>Epipactus gigantea</u> * |
| 5. <u>Phragmites australis</u> | 10. <u>Parthenocissus vitacea</u> |
-

Table 13. Summary of the principal vegetational and physical characteristics of the Salix goodingii type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	3
Total species	20
S	11.7
H'	1.027
E	0.955
I _H	73.7%
I _D	68.0%
I _G	8.7%
DISJ	5.0%
CPE	0%
Terrace position	1.00 (0)
Exposure	1.00 (0)
PFI (flooding index)	-
DIST (log ₁₀ m)	-
Canyon depth (m)	-
Canyon width (m)	-
Width/depth ratio	-
Stream bearing	-
Elevation (m above 1130)	150 (0)
Domestic livestock sign (% of plots)	0%
Median water type: intermittent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate lowland tall shrubland, (1402.09) Salix goodingii series.

Prevalent species (*=modal species also)

- | | |
|-------------------------------------|------------------------------------|
| 1. <u>Salix goodingii</u> * | 7. <u>Heterotheca villosa</u> |
| 2. <u>Artemisia ludoviciana</u> * | 8. <u>Erigeron bellidiastrum</u> * |
| 3. <u>Panicum oligosanthos</u> * | 9. <u>Elymus canadensis</u> |
| 4. <u>Schizachyrium scoparium</u> * | 10. <u>Celtis reticulata</u> |
| 5. <u>Juncus tenuis</u> * | 11. <u>Phragmites australis</u> |
| 6. <u>Rhus aromatica</u> | |
-

Table 14. Summary of the principal vegetational and physical characteristics of the Toxicodendron rydbergii type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	7
Total species	41
S	10.71 (2.93)
H'	0.979 (0.140)
E	0.964 (0.016)
I _H	47.5%
I _D	9.5%
I _G	30.4%
DISJ	10.0%
CPE	5.1%
Terrace position	3.29 (1.03)
Exposure	3.71 (0.76)
PFI (flooding index)	0.875 (0.689)
DIST (log ₁₀ m)	2.079 (0.843)
Canyon depth (m)	112.1 (57.9)
Canyon width (m)	127.1 (94.3)
Width/depth ratio	1.046 (0.517)
Stream bearing	152.9° (98.6°)
Elevation (m above 1130)	126.4 (108.0)
Domestic livestock sign (% of plots)	14%
Median water type: intermittent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate lowland low shrubland, (1403.19) Toxicodendron rydbergii series.

Prevalent species (*=modal species also)

1. <u>Toxicodendron rydbergii</u> *	6. <u>Euthamia occidentalis</u>
2. <u>Equisetum hyemale</u>	7. <u>Bromus tectorum</u>
3. <u>Apocynum cannabinum</u>	8. <u>Acer negundo</u>
4. <u>Artemisia ludoviciana</u>	9. <u>Oenothera longissima</u>
5. <u>Tamarix chinensis</u>	10. <u>Panicum acuminatum</u> *

Table 15. Summary of the principal vegetational and physical characteristics of the *Phragmites australis* type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	10
Total species	38
S	7.70 (3.27)
H'	0.792 (0.219)
E	0.931 (0.386)
I _H	48.6%
I _D	39.6%
I _G	39.1%
DISJ	2.2%
CPE	0%
Terrace position	4.53 (2.01)
Exposure	2.65 (0.41)
PFI (flooding index)	0.560 (0.590)
DIST (log ₁₀ m)	2.523 (1.085)
Canyon depth (m)	99.5 (66.6)
Canyon width (m)	171.5 (75.9)
Width/depth ratio	1.935 (0.655)
Stream bearing	197.0° (85.9°)
Elevation (m above 1130)	92.2 (72.0)
Domestic livestock sign (% of plots)	20%
Median water type: intermittent perched spring	

SRFR ASSIGNMENT: Colorado Plateau cold temperate grassland, (1404.12)
Phragmites australis series.

Prevalent species (*=modal species also)

- | | |
|----------------------------------|-------------------------------|
| 1. <i>Phragmites australis</i> * | 5. <i>Aster galucodes</i> |
| 2. <i>Equisetum hyemale</i> | 6. <i>Apocynum cannabinum</i> |
| 3. <i>Oxytenia acerosa</i> | 7. <i>Salix exigua</i> |
| 4. <i>Bromus tectorum</i> | 8. <i>Baccharis salicina</i> |
-

Table 16. Summary of the principal vegetational and physical characteristics of the Typha type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	4
Total species	18
S	7.00 (2.71)
H'	0.779 (0.148)
E	0.944 (0.280)
I _H	56.0%
I _D	50.0%
I _G	13.0%
DISJ	2.2%
CPE	0%
Terrace position	1.00 (0)
Exposure	3.19 (0.63)
PFI (flooding index)	1.527 (0.835)
DIST (log ₁₀ m)	2.737 (0.408)
Canyon depth (m)	110.0 (78.7)
Canyon width (m)	227.5 (187.1)
Width/depth ratio	2.202 (1.250)
Stream bearing	63.7° (18.9°)
Elevation (m above 1130)	177.5 (131.2)
Domestic livestock sign (% of plots)	25%
Median water type: permanent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate marshland, (1405.02) Typha domingensis series.

Prevalent species (*=modal species also)

- | | |
|--|--------------------------------|
| 1. <u>Typha domingensis</u> */ <u>T. latifolia</u> * | 5. <u>Baccharis salicina</u> |
| 2. <u>Euthamia occidentalis</u> | 6. <u>Epilobium ciliatum</u> * |
| 3. <u>Equisetum hyemale</u> | 7. <u>Carex hystricina</u> |
| 4. <u>Scirpus pungens</u> * | |
-

Table 17. Summary of the principal vegetational and physical characteristics of the Panicum virgatum type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	9
Total species	41
S	10.44 (2.79)
H'	0.954 (0.121)
E	0.948 (0.004)
I _H	53.3%
I _D	59.8%
I _G	26.1%
DISJ	10.7%
CPE	0%
Terrace position	2.61 (0.74)
Exposure	2.75 (0.47)
PFI (flooding index)	0.955 (0.540)
DIST (log ₁₀ m)	3.423 (0.341)
Canyon depth (m)	187.7 (20.8)
Canyon width (m)	310.0 (76.7)
Width/depth ratio	1.642 (0.306)
Stream bearing	229.4° (67.6°)
Elevation (m above 1130)	50.0 (57.7)
Domestic livestock sign (% of plots)	11%
Median water type: intermittent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate grassland, (1404.13) Panicum virgatum series.

Prevalent species (*=modal species also)

- | | |
|--------------------------------------|------------------------------------|
| 1. <u>Panicum virgatum</u> * | 6. <u>Ipomopsis aggregata</u> * |
| 2. <u>Oxytenia acerosa</u> * | 7. <u>Oenothera longissima</u> |
| 3. <u>Equisetum hyemale</u> | 8. <u>Gutierrezia microcephala</u> |
| 4. <u>Muhlenbergia asperifolia</u> * | 9. <u>Populus fremontii</u> |
| 5. <u>Juncus arcticus</u> | 10. <u>Dalea oligophylla</u> * |
-

Table 18. Summary of the principal vegetational and physical characteristics of the mixed forb type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	10
Total species	36
S	7.70 (1.89)
H'	0.830 (0.121)
E	0.947 (0.025)
I _H	58.4%
I _D	66.7%
I _G	21.7%
DISJ	5.4%
CPE	0%
Terrace position	1.80 (0.67)
Exposure	2.85 (0.34)
PFI (flooding index)	1.004 (0.649)
DIST (log ₁₀ m)	2.959 (0.399)
Canyon depth (m)	148.5 (57.3)
Canyon width (m)	283.0 (74.7)
Width/depth ratio	2.128 (0.990)
Stream bearing	232.0° (22.0°)
Elevation (m above 1130)	65.5 (55.9)
Domestic livestock sign (% of plots)	0%
Median water type: intermittent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate marshland, (1405.10) Juncus arcticus-Equisetum hyemale series.

Prevalent species (*=modal species also)

- | | |
|---------------------------|-----------------------------|
| 1. Juncus arcticus* | 5. Elymus canadensis |
| 2. Equisetum hyemale* | 6. Muhlenbergia asperifolia |
| 3. Euthamia occidentalis* | 7. Castilleja linariifolia* |
| 4. Baccharis salicina | 8. Bromus tectorum |
-

Table 19. Summary of the principal vegetational and physical characteristics of the Solidago canadensis type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	4
Total species	27
S	11.75 (3.59)
H'	1.009 (0.138)
E	0.960 (0.002)
I _H	60.0%
I _D	25.0%
I _G	21.7%
DISJ	9.0%
CPE	0%
Terrace position	3.75 (1.50)
Exposure	3.12 (0.48)
PFI (flooding index)	0.656 (0.377)
DIST (log ₁₀ m)	2.922 (0.864)
Canyon depth (m)	123.7 (35.0)
Canyon width (m)	205.0 (77.2)
Width/depth ratio	1.697 (0.751)
Stream bearing	182.5°108.4°
Elevation (m above 1130)	53.8 (67.9)
Domestic livestock sign (% of plots)	0%
Median water type: permanent stream	

SRFR ASSIGNMENT: Colorado Plateau cold temperate forbland, (1406.09) Solidago canadensis series.

Prevalent species (*=modal species also)

- | | |
|-----------------------------------|---------------------------------------|
| 1. <u>Solidago canadensis</u> * | 7. <u>Panicum acuminatum</u> * |
| 2. <u>Phragmites australis</u> | 8. <u>Thelypodium integrifolium</u> * |
| 3. <u>Equisetum hyemale</u> | 9. <u>Salix exigua</u> |
| 4. <u>Juncus arcticus</u> | 10. <u>Baccharis salicina</u> |
| 5. <u>Clematis ligusticifolia</u> | 11. <u>Elymus canadensis</u> |
| 6. <u>Artemisia ludoviciana</u> | |
-

Table 20. Summary of the principal vegetational and physical characteristics of the *Eleocharis palustris* type. Mean values are given for most variables, with one standard deviation in parentheses.

Number of plots	3
Total species	24
S	11.00 (1.73)
H'	0.986 (0.009)
E	0.494 (0.002)
I _H	60.8%
I _D	50.1%
I _G	13.0%
DISJ	19.3%
CPE	10.2%
Terrace position	4.33 (2.89)
Exposure	2.00 (0)
PFI (flooding index)	0.370 (0.477)
DIST (log ₁₀ m)	2.000 (0.300)
Canyon depth (m)	98.3 (51.1)
Canyon width (m)	370.0 (338.7)
Width/depth ratio	3.410 (1.869)
Stream bearing	113.3°32.1°
Elevation (m above 1130)	120.0 (130.8)
Domestic livestock sign (% of plots)	0%
Median water type: permanent perched spring	

SRFR ASSIGNMENT: Colorado Plateau cold temperate marshland, (1405.07)
Eleocharis palustris series.

Prevalent species (*=modal species also)

- | | |
|----------------------------------|----------------------------------|
| 1. <i>Eleocharis palustris</i> * | 7. <i>Oenothera longissima</i> * |
| 2. <i>Phragmites australis</i> | 8. <i>Juncus ensifolius</i> |
| 3. <i>Baccharis salicina</i> | 9. <i>Scirpus pungens</i> * |
| 4. <i>Lobelia cardinalis</i> * | 10. <i>Cirsium rydbergii</i> |
| 5. <i>Solidago sparsiflora</i> * | 11. <i>Equisetum hyemale</i> |
| 6. <i>Panicum acuminatum</i> | |
-

Table 21. Spearman's rank correlations between site physical variables and PCA axis loadings of the first three axes for the three groupings, forest and woodland, scrub, and marshland. N is the number of plots in the analysis. The strongest three correlations in each group on each axis are highlighted.

<u>Forest and Woodland</u> (N=50)	STB	QUA	CAD	CAW	WDR	DIS	TCE	EXP	ELE	WAT	PFI ¹
PCA I	-0.01	0.02	-0.28	-0.01	0.22	0.52	-0.59	-0.60	0.15	-0.38	0.42
PCA II	0.01	0.12	0.18	-0.07	-0.39	-0.75	0.51	0.60	-0.15	0.54	-0.35
PCA III	0.05	0.06	0.24	0.22	0.07	0.31	0.49	-0.19	-0.07	-0.08	-0.39
<u>Scrub</u> (N=27)											
PCA I	-0.56	-0.41	-0.04	0.30	0.45	0.64	-0.17	-0.53	-0.17	-0.07	-0.26
PCA II	0.46	0.22	0.18	-0.32	-0.66	-0.66	-0.25	0.69	-0.05	0.08	0.58
PCA III	-0.27	-0.45	-0.02	-0.17	-0.21	0.02	0.19	0.13	0.12	-0.29	0.05
<u>Marshland</u> (N=47)											
PCA I	0.35	0.42	0.58	0.49	-0.01	0.58	-0.26	-0.10	-0.29	-0.38	0.21
PCA II	-0.07	-0.08	-0.35	-0.34	0.11	-0.16	0.45	-0.16	0.01	0.36	-0.30
PCA III	-0.07	-0.11	-0.07	-0.03	-0.11	-0.21	-0.36	0.30	0.15	0.07	0.11

¹STB=stream bearing, QUA=azimuth quadrant, CAD=canyon depth, CAW=canyon width, WDR=canyon width/depth ratio, DIS=downstream distance from headwaters, TCE=terrace position, EXP=exposure, ELE=elevation, WAT=water type, PFI=potential flood index.

Table 22. Spearman's rank correlations between species richness, diversity, and evenness, and physical site variables for the plot groupings forest and woodland, scrub, and marshland. N is the number of plots. The strongest three correlations in each contrast are highlighted.

Forest and Woodland (N=50)	STB	QUA	CAD	CAW	WDR	DIS	TCE	EXP	ELE	WAT	PFI ¹
S	0.10	-0.08	0.08	0.01	0.01	-0.06	0.02	0.01	0.13	0.00	0.02
H'	0.03	-0.14	0.07	0.01	0.01	-0.07	0.05	0.05	0.14	0.04	-0.02
E	-0.20	-0.29	0.02	0.02	0.05	0.03	0.19	0.05	0.16	0.18	-0.19
Scrub (N=27)											
S	0.10	0.14	0.42	0.21	-0.30	-0.04	0.11	0.26	-0.01	0.30	0.29
H'	0.14	0.21	0.40	0.17	-0.39	-0.13	-0.06	0.31	0.03	0.24	0.39
E	0.12	0.20	-0.19	-0.23	-0.24	-0.29	-0.14	0.36	0.23	-0.09	0.36
Marshland (N=47)											
S	0.01	-0.04	0.19	-0.07	-0.27	0.03	0.07	0.18	-0.03	0.14	0.06
H'	0.02	-0.03	0.15	-0.07	-0.23	0.01	0.06	0.19	-0.03	0.19	0.05
E	-0.09	-0.08	-0.03	-0.05	-0.11	0.08	-0.04	0.19	0.09	0.32	0.03

¹STB=stream bearing, QUA=azimuth quadrant, CAD=canyon depth, CAW=canyon width, WDR=canyon width/depth ratio, DIS=downstream distance from headwaters, TCE=terrace position, EXP=exposure, ELE=elevation, WAT=water type, PFI=potential flood index.

Table 23. List of Colorado Plateau endemic, southwestern temperate, and boreal-montane species. Montane species are those defined to normally occur above the level of pinyon-juniper woodlands on the Colorado Plateau..

Colorado Plateau endemic

Aquilegia micrantha
Carex curatorum
Cirsium rydbergii
Habenaria zothecina
Mimulus eastwoodiae
Primula specuicola
Yucca toftiae

Southwestern temperate (m=montane)

Adiantum capillus-veneris
Andropogon glomeratus
Aralia racemosa (m)
Cercis occidentalis
Chloracantha spinosa
Cladium californicum
Imperata brevifolia
Lobelia cardinalis
Ostrya knowltonii (m)
Panicum virgatum
Parthenocissus vitacea
Rhamnus betulifolia
Rhus glabra (m)
Rubus neomexicanus (m)
Salix goodingii
Sorghastrum nutans

Boreal-montane

Acer grandidentatum
Betula occidentalis
Calamagrostis scopulorum
Carex rossii
Cystopteris fragilis
Galium aparine
Glyceria striata
Mahonia repens
Pseudotsuga menziesii
Rosa woodsii
Smilacina stellata
Scirpus microcarpus
Salix lutea
Viola nephrophylla

Prunus virginiana (extinct)

Table 24. Spearman's rank correlations between number of disjunct species (montane and southwestern groups) and site physical variables for the plot groupings forest and woodland, scrub, and marshland. N is the number of plots. The strongest three correlations in each contrast are highlighted.

	STB	QUA	CAD	CAW	WDR	DIS	TCE	EXP	ELE	WAT	PFI ¹
<u>Forest and Woodland</u> (N=50)	0.04	0.02	0.28	0.02	-0.29	-0.64	0.66	0.64	-0.29	0.55	-0.50
<u>Scrub</u> (N=27)	0.37	0.21	0.43	0.00	-0.43	-0.50	0.02	0.60	-0.06	0.01	0.32
<u>Marshland</u> (N=47)	0.13	-0.03	0.40	0.21	-0.25	0.03	0.21	0.00	0.05	-0.05	-0.05

¹STB=stream bearing, QUA=azimuth quadrant, CAD=canyon depth, CAW=canyon width, WDR=canyon width/depth ratio, DIS=downstream distance from headwaters, TCE=terrace position, EXP=exposure, ELE=elevation, WAT=water type, PFI=potential flood index.

Table 25. Spearman's rank correlations between three groups of rare and disjunct species and site physical variables for the mixed deciduous woodland vegetation type (N=17 plots). Regression equations are presented for selected comparisons.

<u>Variable</u> ¹	<u>Boreal-Montane</u>	<u>Southwestern</u>	<u>Endemic</u>
STB	-0.13	0.20	0.28
QUA	0.16	0.38	0.05
CAD	0.39	0.21	-0.54
CAW	0.54	0.21	-0.25
WDR	0.19	-0.10	0.24
DIS	0.14	-0.62	-0.18
TCE	0.38	0.03	0.12
EXP	-0.31	0.47	0.44
ELE	-0.30	-0.20	-0.29
WAT	0.55	0.56	-0.38
PFI	-0.09	-0.26	-0.39
PCAI	-0.19	-0.34	-0.32
PCAI ^{II}	0.65	0.11	-0.57
PCAI ^{III}	0.00	0.21	0.07

<u>Regression Equations</u>				
<u>Dependent Variable</u>	<u>Equation</u>	<u>F</u>	<u>R²</u>	<u>P</u>
Boreal-Montane	Y=-6.71+7.33 (WAT)	5.99	0.238	0.027
Southwestern	Y=-26.01+4.68 (WAT)+6.88 (EXP)	8.59	0.487	0.004
CP Endemic	Y=-6.90+6.06 (EXP)-0.06 (CAD)	4.90	0.328	0.024

¹STB=stream bearing, QUA=azimuth quadrant, CAD=canyon depth, CAW=canyon width, WDR=canyon width/depth ratio, DIS=downstream distance from headwaters, TCE=terrace position, EXP=exposure, ELE=elevation, WAT=water type, PFI=potential flood index, PCAI-III=ordination axis loadings for plots.

Table 26. Rankings for 17 canyons and Good Hope Bay in nine variables, and suitability for future research in four areas. Riparian vegetation is the number of different types represented in each canyon. The riparian vegetation in Knowles Canyon was not surveyed.

	A	B	C	C	G	L	L	G	R	S	T	L	K	W	F	L	F	D
	L	O	O	L	H	O	C	A	I	L	M	W	N	I	M	F	O	R
<u>Variable</u>	C	C	W	W	B	C	C	C	C	C	C	C	C	G	G	C	C	C
Water flows	2	3	3	2	3	2	1	2	2	2	2	3	2	3	3	3	2	1 ¹
Present livestock	-	-	-	-	-	+	+	-	-	-	-	-	-	+	+	-	-	-
Past livestock	-	+	+	-	-	+	+	-	+	+	+	-	+	+	+	+	+	+
Beaver	+	+	+	-	-	-	-	+	+	+	-	+	-	+	+	+	-	-
Rare plant species	1	2	13	5	1	2	1	2	5	0	0	4	0	3	1	9	1	0
Riparian vegetation	9	8	8	4	3	5	3	9	7	5	5	4	?	7	8	10	8	0
Hanging gardens	2	2	3	1	0	2	2	3	3	2	1	1	2	1	1	3	2	0 ²
Birds	3	2	3	1	1	3	1	2	2	2	1	3	2	2	2	3	2	1 ²
Herps	2	3	3	1	1	2	1	2	3	1	1	3	1	1	1	2	2	1 ²
<u>Research</u>																		
Vegetation	2	3	3	1	2	3	3	2	2	2	1	3	2	2	2	3	2	1 ³
Hydrology	2	3	2	1	1	2	1	2	2	2	1	3	1	1	1	2	2	1 ³
Geomorphology	1	3	2	1	1	2	3	1	1	2	2	2	1	1	1	2	1	1 ³
Paleoecology	1	3	3	1	2	1	1	2	2	1	1	1	2	3	3	3	2	1 ³

¹1=predominantly ephemeral, 2=predominantly intermittent, some surface flows but not continuous, 3=perennial flows

²0=absent, 1=poorly developed or low diversity, 2=moderately well developed or diverse, 3=extremely well developed or diverse

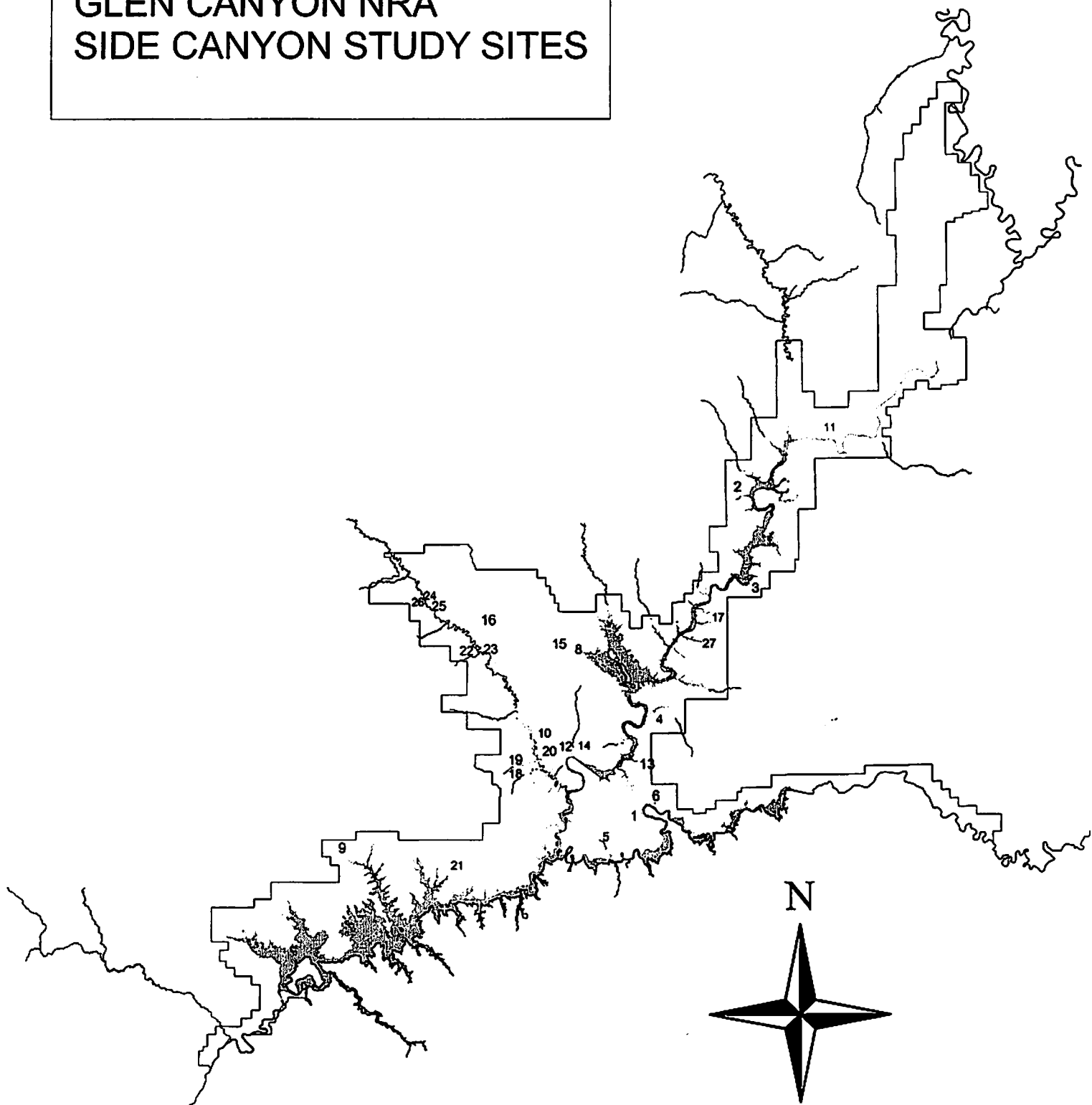
³1=not particularly good, 2=some potential for subject area work, 3=excellent potential for study

FIGURES

Figure 1. Glen Canyon National Recreation Area, with study sites indicated. Study sites are listed below.

1. "Garden" Canyon
2. Two Mile Canyon
3. Good Hope Bay
4. Lake Canyon
5. Wilson's Creek
6. Alcove Canyon
7. Ribbon Canyon
8. Hall's Creek
9. Last Chance Creek
10. Cow Canyon
11. Clearwater Canyon
12. Bowns Canyon
13. Slickrock Canyon
14. Long Canyon
15. Miller's Creek
16. Moody Creek
17. Knowles Canyon
18. Willow Gulch
19. Forty Mile Gulch
20. Lower Fence Canyon
21. Dry Rock Creek
22. Scorpion Gulch
23. George's Camp
24. Chopslot Canyon
25. Neon Canyon
26. Upper Fence Canyon
27. Forgotten Canyon

GLEN CANYON NRA SIDE CANYON STUDY SITES



10 0 10 20 30 Kilometers

Figure 2. Dendrogram of the forest and woodland plots using Ward's linkage algorithm and euclidean distance. Groups are mixed deciduous woodland (1) and Populus fremontii woodland (2). Plot site acronyms can be found in Table 3.

EUCLIDEAN DISTANCE

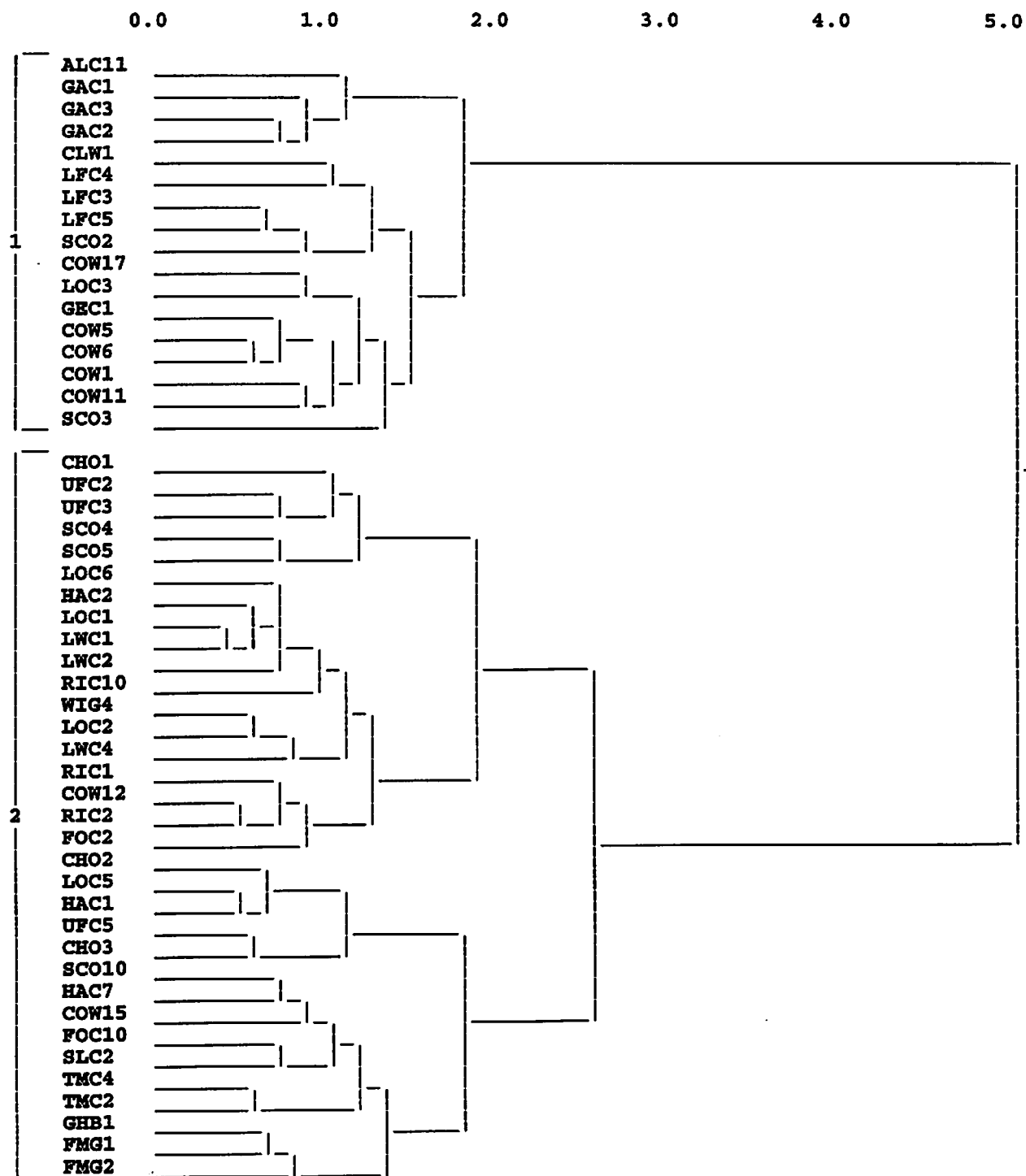


Figure 3. Dendrogram of the scrub plots using Ward's linkage algorithm and euclidean distance. Groups are Salix exigua scrub (1A), Salix-Elaeagnus scrub (1B), Salix lutea scrub (2), and Betula occidentalis scrub (3). Plot site acronyms can be found in Table 3.

EUCLIDEAN DISTANCE

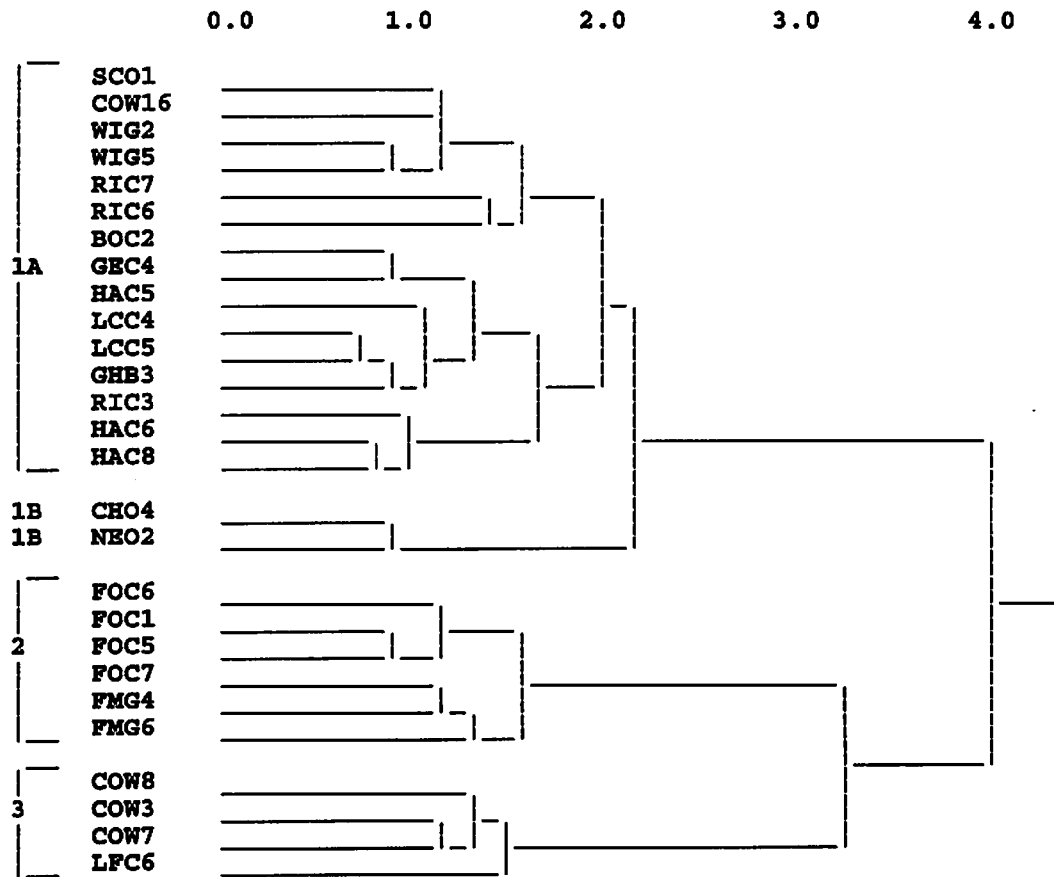


Figure 4. Dendrogram of the marshland plots using Ward's linkage algorithm and euclidean distance. Groups are Phragmites marshland (1), Eleocharis palustris marshland (2), Typha marshland (3), Toxicodendron rydbergii scrub (4), Panicum virgatum marshland (5), mixed forbland (6), and Solidago canadensis forbland (7). Plots A-D represent miscellaneous unclassified plots. Plot site acronyms can be found in Table 3.

EUCLIDEAN DISTANCE

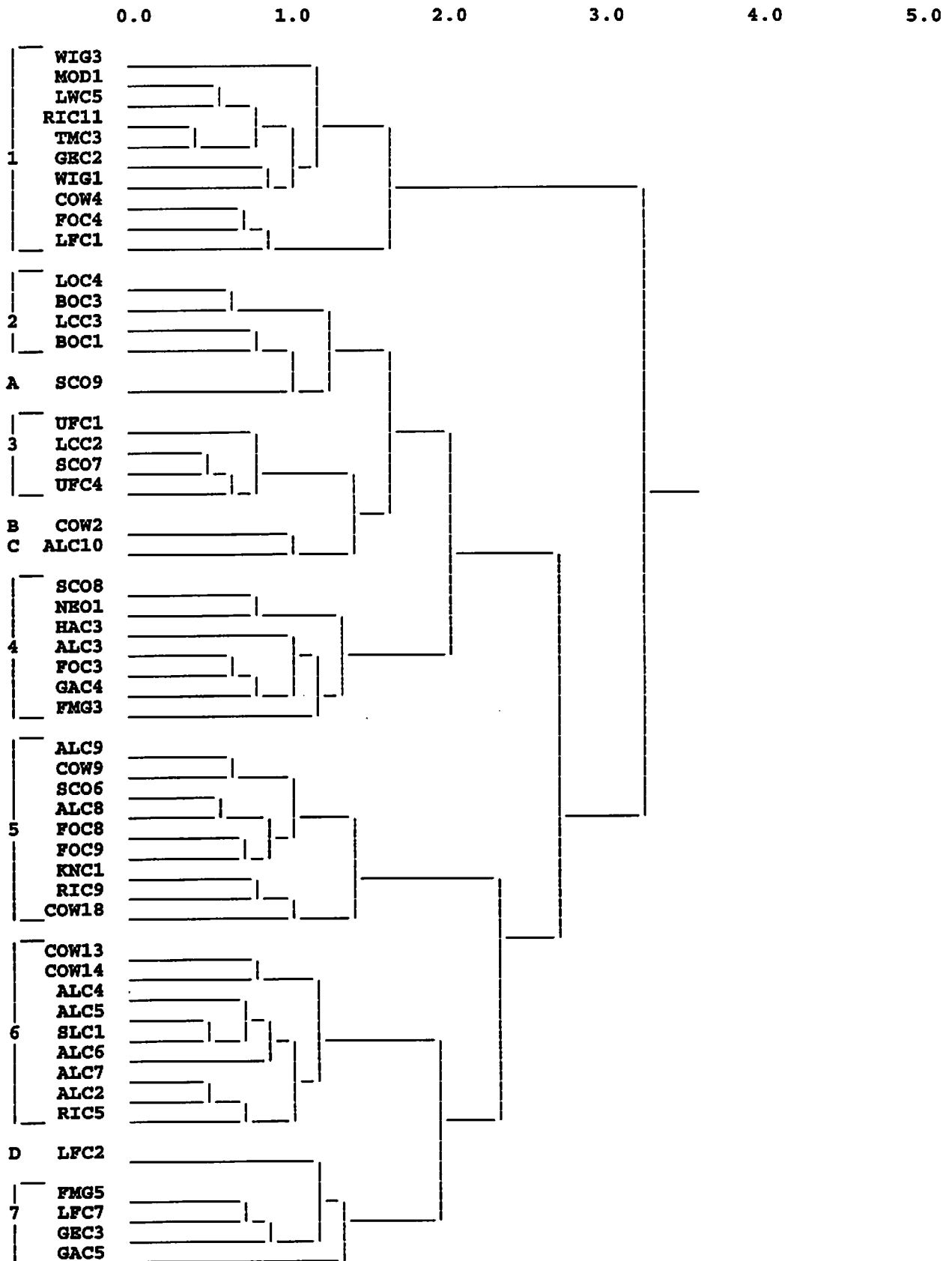
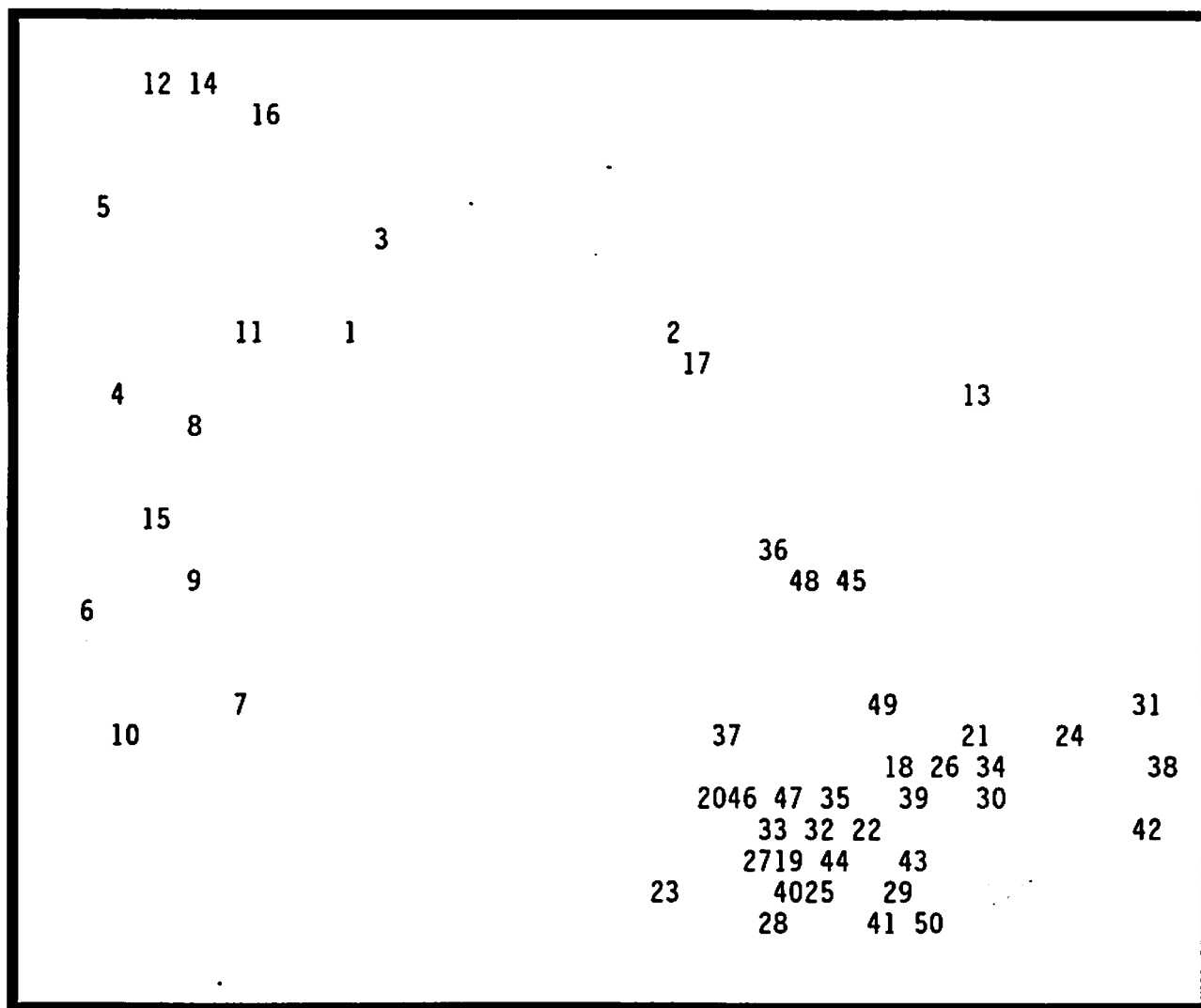


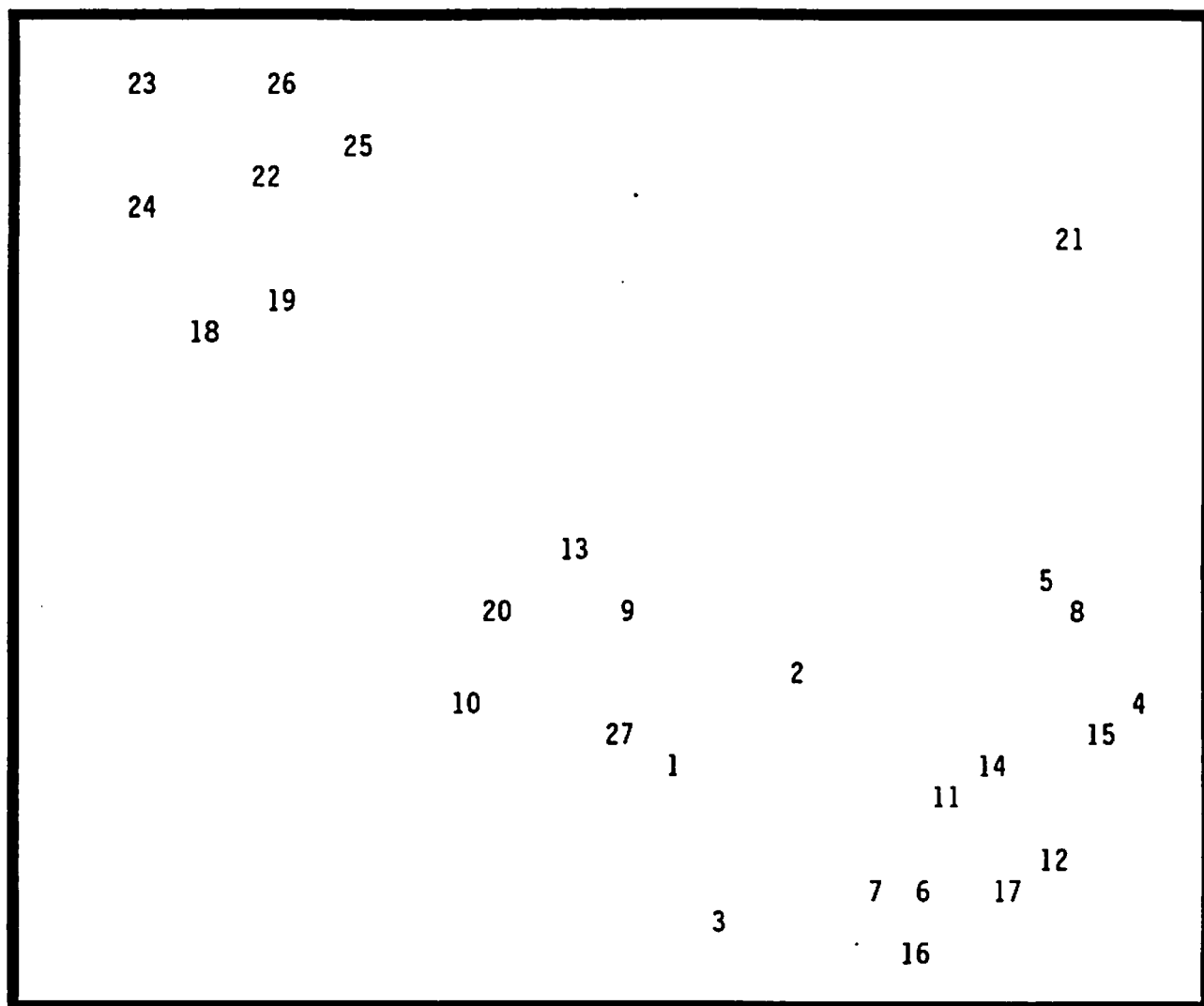
Figure 5. Principal components analysis of the forest and woodland plots.
The first two axes are plotted. Plot site acronyms can be found in Table 3.



PCA I

1=COW1	11=GEC1	21=COW12	31=LWC2	41=CH03
2=COW5	12=SC02	22=COW15	32=LWC4	42=SC04
3=COW6	13=SC03	23=HAC1	33=RIC1	43=SC05
4=COW11	14=LFC3	24=HAC2	34=RIC2	44=SC010
5=COW17	15=LFC4	25=HAC7	35=SLC2	45=CH01
6=CLW1	16=LFC5	26=LOC1	36=FOC2	46=WIG4
7=ALC11	17=LOC3	27=LOC2	37=FOC10	47=RIC10
8=GAC1	18=GHB1	28=LOC5	38=FMG1	48=UFC2
9=GAC2	19=TMC2	29=LOC6	39=FMG2	49=UFC3
10=GAC3	20=TMC4	30=LWC1	40=CH02	50=UFC5

Figure 6. Principal components analysis of the scrub plots. The first two axes are plotted. Plot site acronyms can be found in Table 3.



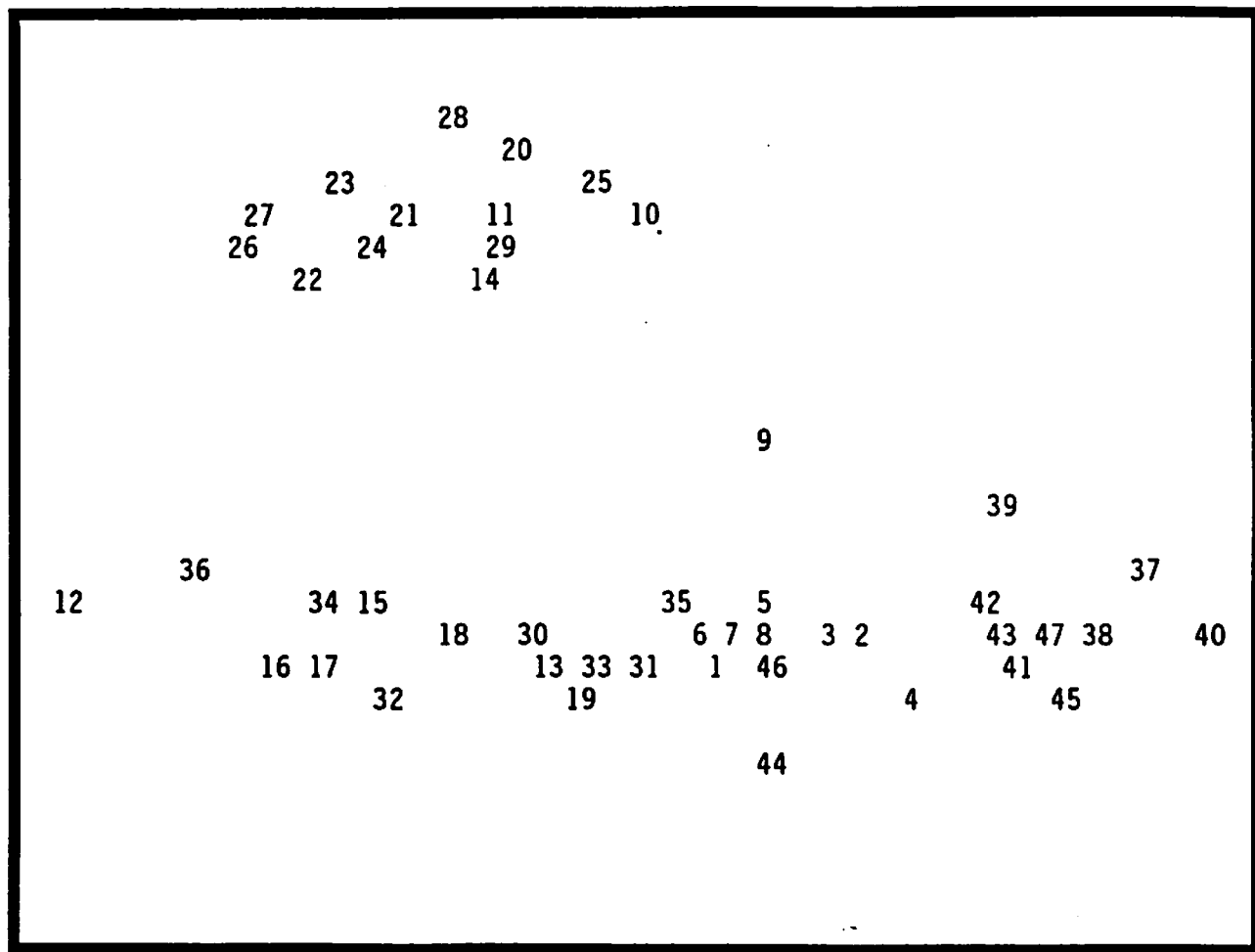
PCA I

1=GHB1
2=COW16
3=HAC5
4=HAC6
5=HAC8
6=LCC4
7=LCC5
8=RIC3
9=RIC6
10=RIC7

11=SC01
12=GEC4
13=FMG6
14=WIG2
15=WIG5
16=CH04
17=NE02
18=COW3
19=COW7
20=COW8

21=LFC6
22=FOC1
23=FOC5
24=FOC6
25=FOC7
26=FMG4
27=BOC2

Figure 7. Principal components analysis of the marshland plots. The first two axes are plotted. Plot site acronyms can be found in Table 3.



PCA I

1=SLC1
2=ALC4
3=ALC5
4=ALC6
5=RIC5
6=BOC1
7=ALC2
8=ALC7
9=LFC7
10=GEC3

11=FOC4
12=HAC3
13=ALC3
14=FMG5
15=FMG3
16=GAC4
17=FOC3
18=NEO1
19=SC08
20=COW4

21=TMC3
22=RIC11
23=GAC5
24=LWC5
25=WIG1
26=WIG3
27=LFC1
28=GEC2
29=MOD1
30=LCC2

31=SC07
32=UFC1
33=UFC4
34=BOC3
35=LCC3
36=LOC4
37=COW9
38=ALC8
39=ALC9
40=SC06

41=FOC8
42=FOC9
43=KNC1
44=RIC9
45=COW18
46=COW13
47=COW14

APPENDICES

APPENDIX 1: MATHEMATICAL AND STATISTICAL METHODS

The mathematical and statistical methods used in the report are presented and discussed below. Cluster analysis and principal components analysis were done using the SYSTAT package, version 5.02. All other computations were done by hand. Because the raw data matrix (148x164) was larger than the cluster analysis routine in SYSTAT could handle, the data were first subjected to a either a correlation analysis or Euclidean distance analysis in the correlation routine. The smaller symmetric association (distance) matrix that was produced by this was then input into either the cluster analysis or principal components analysis routines.

1. Cluster analysis

Good discussions of cluster analysis as a classification tool are found in Sneath and Sokal (1973), Grieg-Smith (1983), Manly (1986), and Digby and Kempton (1987). For construction of the dendrograms of vegetation plots, several linkage algorithms were tried, including single, average (UPGMA), complete, and Ward's. The last method produced the most interpretable results, and appeared to provide a balance between the chaining inherent in single linkage, and the many small clusters often produced by complete linkage (Sneath and Sokal 1973). In all cases, Ward's method also produced tighter and more interpretable clusters than average linkage.

Euclidean distance was chosen as the association measure, as it has many desirable geometrical properties (Sneath and Sokal 1973), and is also commonly used in ecological work. Euclidean distance is computed between two plots i and j by the equation:

$$d_{ij} = \sqrt{\sum_{k=1}^S (x_{ik} - x_{jk})^2}$$

where k is any species common to one or both plots i and j , x is the abundance of the k th species in plots i and j , and S is the number of species found in the plots i and j .

2. Principal components analysis

Ordination methods reduce complex multivariate data sets, common in ecology, to a small set of new variables which summarize the major relationships in the data (Sneath and Sokal 1973). These new variables (eigenvectors) are linear combinations of the original variables (generally plant species in vegetation work). The eigenvector scores for each site of plot can be plotted on XY coordinates for visual display. Values called eigenvalues are also computed which represent the amount of variation in the original data set summarized. The first eigenvalue represents the largest amount of variation explained in the ordination. In most work, the first two or three eigenvectors are plotted, as they account for the largest proportion of the variation in the data.

Principal components analysis was selected as it is a widely used, well understood ordination technique. A centered variance-covariance matrix was computed from the untransformed species by site matrix. The first two eigenvectors were plotted and graphed for each of the three data sets forest and woodland, scrub, and marshland (herbaceous).

3. Species diversity and evenness

Species richness (S) is the number of species present within a plot. Species

diversity (H') was computed using the Shannon information index:

$$H' = \sum_{i=1}^S (p_i \log_{10} p_i)$$

where S is the number of species, and p is the proportion of the total abundance contributed by the i th species. Diversity measures the overall complexity, or amount of "information" (unpredictability), in a set of data, with higher values reflecting more diverse sites.

Species evenness (Pielou's J) is:

$$E = H' / \log_{10} S$$

and measures the evenness of the distribution of abundances among the states (species). Vegetation dominated by a single species, with many rare species, would be very uneven, while vegetation in which all species were more or less equally abundant would be very even. E varies between 0 (very uneven) and 1.0 (very even).

4. Prevalent and modal species

Prevalent and modal species are defined by Curtis (1959). Prevalent species are those that reach highest frequency (percentage of plots) in a defined vegetation type. Modal species are those that reach maximum abundance in a vegetation type in a region, such as Glen Canyon NRA. Species can be both modal and prevalent, or one or the other.

5. Community indices of homogeneity and distinctiveness

Both measures are from Curtis (1959), and require at least two plots to calculate, although more provide a better estimate. The index of homogeneity points out how similar all the plots within a vegetation type are to each other, and is calculated as:

$$I_H = \frac{\text{sum \% frequency of prevalent species}}{\text{sum \% frequency of all species}}$$

Values range from 0% (least homogeneous) to 100% (most homogeneous). The index of distinctiveness determines how distinctive vegetationally a type is from all other types, and is calculated as:

$$I_D = \frac{\text{sum \% frequency modal species}}{\text{sum \% frequency prevalent species}}$$

and can vary from 0% (least distinctive) to 100% (most distinctive). A variety of other ways of calculating distinctiveness and homogeneity are available as well. For example, average Euclidean distances could be computed for each type, both within as a measure of homogeneity, and between as a measure of distinctiveness. However, the number of computations to do this would be extremely large. An alternative method using species presence-absence includes probability indices (Spence 1991; Spence and Henderson 1993).

APPENDIX 2: SPECIES LIST

A list of species found in riparian and wetland vegetation, based on the 1992-94 field seasons, and information in Welsh (1984) and Tuhy and MacMahon (1988). The four-letter acronym used in recording data and as the species name in the SYSTAT data files is listed. Life forms (LF) can be found in Table 4. Each species is identified as native obligate riparian (*), native facultative or pseudoriparian (#), or introduced (!).

1. List of species found in at least one of the 148 plots (N=no. of plots).

<u>Species</u>		<u>LF</u>	<u>N</u>
Acer grandidentatum*	(ACGR)	Tr	3
A. negundo*	(ACNE)	Tr	17
Adiantum capillus-veneris*	(ADCA)	Fr	5
Agrostis stolonifera!	(AGST)	Pg	20
Ambrosia acanthicarpa#	(AMAC)	Af	8
Amelanchier utahensis#	(AMUT)	Sh	5
Andropogon glomeratus*	(ANGL)	Pg	1
Apocynum cannabinum*	(APCA)	Pf	28
Aquilegia micrantha*	(AQMI)	Pf	2
Aralia racemosa*	(ARRA)	Pf	1
Artemisia filifolia#	(ARFI)	Sh	2
A. dracunculus#	(ARDR)	Pf	2
A. ludoviciana#	(ARLU)	Pf	48
Asclepias speciosa#	(ASSP1)	Pf	1
Aster chilensis*	(ASCH)	Pf	5
A. glaucodes*	(ASGL)	Pf	10
A. spinosus*	(ASSP2)	Pf	1
A. subulatus*	(ASSU)	Af	1
Atriplex canescens#	(ATCA)	Sh	1
Baccharis glutinosa*	(BAGL)	Sh	1
B. salicina*	(BASA)	Sh	56
Betula occidentalis*	(BEOC)	Sh	9
Brickellia californica#	(BRCA)	Sh	1
B. longifolia#	(BRLO)	Sh	16
Bromus tectorum!	(BRTE)	Ag	40
Calamagrostis scopulorum*	(CASC)	Pg	5
Carex aurea*	(CAAU)	Pg	8
C. curatorum*	(CACU)	Pg	2
C. hystericina*	(CAHY)	Pg	8
C. lanuginosa*	(CALA)	Pg	1
C. rossii#	(CARO)	Pg	2
Castilleja linariifolia#	(CALI)	Pf	32
Cercis occidentalis*	(CEOC)	Tr	6
Celtis reticulata#	(CERE)	Tr	8
Chrysothamnus linifolius#	(CHLI)	Sh	4
C. nauseosus#	(CHNA)	Sh	13
C. viscidiflorus#	(CHVI)	Sh	21
Cirsium arizonicum#	(CIAR)	Pf	6
C. rydbergii*	(CIRY)	Pf	9
Cladium californicum*	(CLCA)	Pg	1
Clematis ligusticifolia*	(CLLI)	Li	31
Comandra umbellatum#	(COUM)	Pf	1
Conyza canadensis#	(COCA)	Af	10
Cryptantha species#	(CRsp)	Pf	1
Cystopteris fragilis*	(CYFR)	Fr	1
Datura meteloides#	(DAME)	Pf	1
Dalea oligophylla#	(DAOL)	Pf	8
Descurainia pinnata#	(DEPI)	Af	2

Distichlis spicata*	(DISP)	Pg	14
Echinochloa crus-galli*	(ECCR)	Ag	1
Elaeagnus angustifolia!	(ELAN)	Tr	2
Eleocharis palustris*	(ELPA)	Pg	4
Elymus canadensis*	(ELCA)	Pg	42
E. elongatus!	(ELEL1)	Pg	4
E. elymoides#	(ELEL2)	Pg	1
E. repens!	(ELRE)	Pg	1
E. trachycaulis#	(ELTR)	Pg	4
Epilobium ciliatum*	(EPCI)	Pf	10
Epipactis gigantea*	(EPGI)	Pf	13
Equisetum arvense*	(EQAR)	Fr	4
E. hyemale*	(EQHY)	Fr	76
Erigeron bellidiflorus#	(ERBE)	Pf	2
E. utahensis#	(ERUT)	Pf	6
Euphorbia parryi#	(EUPA)	Pf	1
Euthamia occidentalis*	(EUOC)	Pf	31
Fallugia paradoxa#	(FAPA)	Sh	3
Forestiera pubescens*	(FOPU)	Sh	1
Fraxinus anomala#	(FRAN)	Sh	3
Galium aparine*	(GAAP)	Af	4
Glyceria striata*	(GLST)	Pg	3
Glycyrrhiza lepidota*	(GLLE)	Pf	1
Gnaphalium chilense*	(GNCH)	Af	1
Gutierrezia microcephala#	(GUMI)	Sh	11
Habenaria zothecina*	(HAZO)	Pf	5
Heterotheca villosa#	(HEVI)	Pf	4
Holodiscus dumosus#	(HODU)	Sh	1
Hymenopappus filifolius#	(HYFI)	Pf	1
Ipomopsis aggregata#	(IPAG)	BP	19
Juncus arcticus*	(JUAR)	Pg	53
J. ensifolius*	(JUEN)	Pg	7
J. tenuis*	(JUTE)	Pg	3
J. torreyi*	(JUTO)	Pg	3
Juniperus osteosperma#	(JUOS)	Tr	1
Lactuca serriola!	(LASE)	Af	5
Lathyrus cf. brachycalyx#	(LABR)	Pf	1
Lepidium montanum#	(LEMO)	Pf	7
Lobelia cardinalis*	(LOCA)	Pf	3
Machaeranthera canescens#	(MACA)	BP	6
Mahonia fremontii#	(MAFR)	Sh	1
M. repens#	(MARE)	Sh	5
Melilotus alba!	(MEAL)	Af	18
Mirabilis multiflora#	(MIMU)	Pf	1
Muhlenbergia andina*	(MUAN)	Pg	6
M. asperifolia*	(MUAS)	Pg	21
M. thurberi*	(MUTH)	Pg	1
Nasturtium officinale!	(NAOF)	Pf	1
Oenothera longissima#	(OELO)	BP	25
Opuntia species#	(OPsp)	Pf	4
Ostrya knowltonii*	(OSKN)	Tr	5
Oxytenia acerosa*	(OXAC)	Pf	27
Panicum acuminatum*	(PAAC)	Pg	15
P. oligosanthes*	(PAOL)	Pg	3
P. virgatum*	(PAVI1)	Pg	22
Parthenocissus vitacea*	(PAVI2)	Li	18
Penstemon eatonii#	(PEEA)	Pf	1
P. rostriflorus#	(PERO)	Pf	1
Phragmites australis*	(PHAU)	Pg	29
Pinus edulis#	(PIED)	Tr	1
Plantago patagonica#	(PLPA)	Af	1

<i>Poa fendleriana</i> #	(POFE)	Pg	5
<i>Polypogon monspeliensis</i> !	(POMO)	Ag	4
<i>P. semiverticillata</i> !	(POSE)	Pg	5
<i>Populus fremontii</i> *	(POFR)	Tr	62
<i>Primula specuicola</i> *	(PRSP)	Pf	1
<i>Psoralidium lanceolatum</i> #	(PSLA)	Pf	3
<i>Psoralethamnus thompsonae</i> #	(PSTH)	Sh	1
<i>Pseudotsuga menziesii</i> #	(PSME)	Tr	3
<i>Purshia mexicana</i> #	(PUME)	Sh	1
<i>Quercus gambelii</i> #	(QUGA)	Tr	13
<i>Ranunculus cymbalaria</i> *	(RACY)	Pf	1
<i>Rhamnus betulifolia</i> *	(RHBE)	Tr	17
<i>Rhus aromatica</i> #	(RHAR)	Sh	11
<i>R. glabra</i> *	(RHGL)	Sh	1
<i>Rosa woodsii</i> *	(ROWO)	Sh	8
<i>Rubus neomexicanus</i> *	(RUNE)	Sh	1
<i>Saccharum ravennae</i> !	(SARA)	Pg	1
<i>Salsola iberica</i> !	(SAIB)	Af	1
<i>Salix exigua</i> *	(SAEX)	Sh	41
<i>S. goodingii</i> *	(SAGO)	Tr	25
<i>S. lutea</i> *	(SALU)	Sh	10
<i>Schizachyrium scoparium</i> #	(SCSC)	Pg	4
<i>Scirpus microcarpus</i> *	(SCMI)	Pg	1
<i>S. pungens</i> *	(SCPU)	Pg	3
<i>Shepherdia rotundifolia</i> #	(SHRO)	Sh	3
<i>Smiliacina stellata</i> *	(SMST)	Pf	17
<i>Sonchus asper</i> !	(SOAS)	Af	5
<i>Solidago canadensis</i> *	(SOCA)	Pf	20
<i>S. sparsiflora</i> *	(SOSP)	Pf	12
<i>Sorghastrum nutans</i> *	(SONU)	Pg	5
<i>Sporobolus cryptandrus</i> #	(SPCR)	Pg	5
<i>S. giganteus</i> #	(SPGI)	Pg	3
<i>Stipa comata</i> #	(STCO)	Pg	4
<i>S. hymenoides</i> #	(STHY)	Pg	12
<i>S. speciosa</i> #	(STSP)	Pg	1
<i>Stanleya pinnata</i> #	(STPI)	Pf	2
<i>Stephanomeria tenuifolia</i> #	(STTE)	Pf	1
<i>Symphoricarpos longiflorus</i> #	(SYLO)	Sh	3
<i>Taraxacum officinale</i> !	(TAOF)	Pf	2
<i>Tamarix chinensis</i> !	(TACH)	Sh	37
<i>Tessaria sericea</i> *	(TESE)	Sh	1
<i>Thelypodium integrifolium</i> *	(THIN)	Af	5
<i>Toxicodendron rydbergii</i> *	(TORY)	Sh	18
<i>Tradescantia occidentalis</i> *	(TROC)	Pf	2
<i>Tragopogon dubius</i> !	(TRDU)	Af	1
<i>Typha domingensis</i> */ <i>T. latifolia</i> * (TYDO) (TYLA)		Pg	22
<i>Veronica americana</i> *	(VEAM)	Pf	2
<i>Viola nephrophylla</i> *	(VINE)	Pf	4
<i>Xanthium strumarium</i> !	(XAST)	Af	11
<i>Xylorhiza tortifolia</i> #	(XYTO)	Pf	1
<i>Yucca toftiae</i> #	(YUTO)	Pf	2
<i>Yucca species</i>	(YUsp)	Pf	1

2. Other native obligate riparian species reported from Glen Canyon NRA.

<i>Agrostis exarata</i>	Pg
<i>Asclepias latifolia</i>	Pf
<i>Aster falcatus</i>	Pf
<i>A. hesperius</i>	Pf
<i>Baccharis emoryi</i>	Sh
<i>Bothriochloa barbinodis</i>	Pg

B. laguroides	Pg
Carex parryana	Pg
C. vesicaria	Pg
Centaurium calycosum	Af
Cyperus acuminatus	Pg
Eleocharis rostellata	Pg
Elymus smithii	Pg
Equisetum laevigatum	Fr
Fimbristylis spadicea	Ag
Galium biflorum	Pf
G. triflorum	Pf
Hedeoma drummondii	Pf
Juncus articulatus	Pg
J. bufonius	Ag
Juncus longistylis	Pg
Panicum capillare	Ag
P. obtusum	Pg
Parietaria pennsylvanica	Af
Potomageton natans	Pf
P. foliosus	Pf
Sarcostemma cynanchoides	Li
Sarcobatus vermiculatus	Sh
Scirpus acutus	Pg
S. microcarpus	Pg
S. pallidus	Pg
S. validus	Pg
Silene antirrhina	Af
Spartina gracilis	Pg
Sphenopholis obtusata	Ag
Zanichellia palustris	Pf
Zigadenus vaginatus	Pf

IDENTIFICATION NOTES

Baccharis. Most of the seepwillows in the current study were B. salicina, which is the most common species from the Escalante area north. However, some was likely to have been B. emoryi, which differs in characters of the flowers and fruits. In early season (prior to ca. June), the two cannot be easily distinguished. They are probably ecologically similar. Flowering times differ, with B. emoryi in late summer and fall, and B. salicina in early summer.

Eleocharis. Most is probably E. palustris, but some may have been E. rostellata. The two species can only be easily distinguished when in flower or fruit.

Opuntia. The species was either O. phaeacantha or O. polyacantha.

Typha species. When sterile the two species are very difficult to separate. Ecologically, they are probably similar, but T. domingensis is probably more common. For the purposes of data analysis the two species were combined.

APPENDIX 3: KEY TO THE RIPARIAN VEGETATION TYPES OF GLEN CANYON NATIONAL RECREATION AREA

A key to the riparian vegetation types in Glen Canyon NRA is presented below. The abundance terms used are those found in Table 3. Several additional types are included in the key based on Tuhy and MacMahon (1988) and my own observations.

1. Woody species (shrubs and/or trees) common to dominant 2
1. Woody species absent or rare, never dominant 16
2. Pseudotsuga menziesii present relict P. menziesii forest 3
2. P. menziesii absent 3
3. Trees at least 6 m tall or more, either Acer negundo, Populus fremontii, Quercus gambelii, Rhamnus betulifolia, or Celtis reticulata present and common 4
3. Trees of above species rare or absent, sites dominated by either Salix, Baccharis, or Tamarix species generally less than 6 m in height, or by low shrubs 5
4. Populus fremontii dominant, other tree species generally absent except Salix goodingii, understory generally open, or composed of Chrysothamnus or Baccharis and Salix shrubs, vines rare P. fremontii woodland
4. Mixed dense woodland comprising Acer, Quercus, Rhamnus, and Celtis present, P. fremontii occasionally present as emergent, understory often lush and herbaceous, vines often common mixed deciduous woodland
5. Tall scrub along permanent or intermittent stream channels, composed of Baccharis, Salix, Tessaria, or Tamarix 6
5. Above species absent, low woody shrubs or Toxicodendron present 11
6. Sites in waterpockets or tinajas in slickrock in ephemeral, incipient drainages, Salix goodingii and Panicum oligosanthos present Salix-Panicum tinaja
6. Sites along riparian zones, Salix goodingii absent, or present with Baccharis, Tessaria, Tamarix, or other Salix species 7
7. Tessaria sericea present and dominant Tessaria scrub
7. T. sericea absent or rare, not dominant 8
8. Betula occidentalis present, common, herbaceous understory with Solidago, Elymus and Equisetum present Betula occidentalis scrub
8. B. occidentalis absent, herbaceous layer variable, lush to sparse, Baccharis, Salix, or Tamarix present and dominant 9
9. Tamarix dominant, other species rare Tamarix scrub
9. Baccharis and/or Salix dominant, Tamarix present but uncommon 10
10. Salix lutea present and common, herbaceous understory usually lush with Solidago, Smilacina and/or Apocynum Salix lutea scrub
10. Salix exigua or Baccharis species present and dominant, S. lutea rare or usually absent, understory usually sparse or of Equisetum, Juncus or Scirpus Salix exigua scrub
11. Toxicodendron rydbergii present and common to dominant, in wet protected sites Toxicodendron scrub
11. Toxicodendron absent, sites usually ephemeral channels 12
12. Sites on fluvial terraces or bottomlands at middle or higher elevations (mostly >1370 m), either Artemisia, Atriplex, Chrysothamnus, or Sarcobatus

- present and dominant 13
12. Sites in rocky stream beds or above species absent or uncommon, at low to high elevations 15
13. Sarcobatus vermiculatus present, common to dominant, Distichlis spicata usually present, carbonates or salts often at surface, usually on low terraces or channel bottoms Sarcobatus vermiculatus shrubland
13. S. vermiculatus absent or rare, sites usually on well developed or sandy soils on obvious terraces 14
14. Artemisia tridentata common to dominant, on deep loamy soils, Chrysothamnus species absent or rare Artemisia tridentata shrubland
14. Atriplex canescens common to dominant, on sandy soils, Chrysothamnus species often present Atriplex canescens shrubland
15. Holodiscus dumosus, Symphoricarpos longiflorus, and Ostrya knowltonii present with numerous other shrub species high elevation mixed shrubland
15. Holodiscus and Ostrya absent, Symphoricarpos absent or rare, sites dominated by a mix of Amelanchier, Brickellia, Chrysothamnus, Fallugia, Purshia, or Rhus species low elevation mixed shrubland
16. Lush herbaceous vegetation of both graminoids and forbs present, with either Euthamia occidentalis or Solidago canadensis present and common or dominant 17
16. Monocot graminoids (Typha, Phragmites, Juncus, Eleocharis) dominant, forbs generally scarce, or if common then is usually Oxytenia acerosa 18
17. Solidago canadensis dominant, often with Apocynum or Smilacina, usually in well watered sites in narrow canyons Solidago canadensis forbland
17. Euthamia occidentalis or Solidago canadensis present but usually not dominant in vegetation dominated by dense layer of Juncus arcticus and/or Equisetum hyemale Equisetum-Juncus marshland
18. Panicum virgatum and Muhlenbergia asperifolia present, carbonates often present on soil surface, Oxytenia usually present Panicum virgatum grassland
18. Panicum and Oxytenia absent or rare, obligate riparian species of Juncus, Scirpus, Typha, Phragmites, Elymus or Cladium present and common 19
19. Typha dominant, surface water generally present, sites mostly in stream channels or associated with beaver dams Typha marshland
19. Typha absent, or if present not common, surface water present or absent, sites often above stream channels on hillsides, or on terraces 20
20. Cladium californicum present and common to dominant, often with Typha species Cladium californicum marshland
20. Cladium absent 21
21. Phragmites dominant, surface water generally absent, Eleocharis absent or rare Phragmites marshland
21. Eleocharis species common to dominant, Lobelia cardinalis and Phragmites often present but not common, surface water generally present Eleocharis marshland

APPENDIX 4

SAMPLE FIELD PLOT FORM

1. Name of the person or persons who made the observations: _____

2. Date and time of day: _____

3. Name of the place or places where the observations were made: _____

4. Name of the person or persons who made the observations: _____

5. Name of the place or places where the observations were made: _____

6. Name of the person or persons who made the observations: _____

7. Name of the place or places where the observations were made: _____

8. Name of the person or persons who made the observations: _____

9. Name of the place or places where the observations were made: _____

GLCA RIPARIAN VEGETATION DATA FORM 1

Map	Location	Date	Observers
UTM		Releve	Elevation
Geomorphology			
Aspect	Substrate	Terrace	PFI
Exposure	Water	Canyon D	Canyon W
Geology			
Disturbance			
Code	Species	Prominence	Collection
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			

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Code	Species	Prominence	Collection
16			
17			
18			
19			
20			
21			
22			
23			
24			
25			
Stratum	Height	Cover	
Tree			
Shrub			
Graminoid			
Forb			
Bryophyte			
Lichen			
Litter			
Soil			
Rock			
Notes			