

**SURVEYS OF SPRINGS IN THE COLORADO RIVER DRAINAGE IN
ARCHES NATIONAL PARK, CANYONLANDS NATIONAL PARK,
GLEN CANYON NATIONAL RECREATION AREA, AND
GRAND CANYON NATIONAL PARK**

PART I

Draft Final Report

John R. Spence
National Park Service
Glen Canyon National Recreation Area
PO Box 1507, Page, AZ 86040

Report to the

National Park Service
Water Resources Division-WASO
PO Box 25287
Denver, CO 80225

Account No. 1445-7431-NWZ (1997)
Account No. 1445-8250-NWZ (1998)

16 July 2002

EXECUTIVE SUMMARY

Water Resources Division funding was obtained to survey the plants, aquatic invertebrates and water chemistry and quality of springs associated with an 800 kilometer stretch of the Colorado River on the Colorado Plateau, southern Utah and northern Arizona. Springs in four NPS units were sampled, Arches National Park, Canyonlands National Park, Glen Canyon National Recreation Area, and Grand Canyon National Park. During 1997 and 1998 60 springs were visited. Springs were selected based on presence or availability of previous studies, as well as accessibility and water discharge rates. The distribution of sampled springs by park was, Arches NP (4), Canyonlands NP (4), Glen Canyon NRA (29) and Grand Canyon NP (23). Detailed data using ultra-pure techniques is presented on the water chemistry of sampled spring water. Field data was also collected on water temperature, pH, dissolved oxygen, and conductivity. Discharge rates were measured using a variety of methods, and varied from seeps that couldn't be quantified to >7000 ml/second. Spring water chemistry and pH values were differentiated by source geological strata, with significant differences in many elements between springs derived from limestones and springs derived from sandstones.

Aquatic invertebrates were collected from 45 springs. In all 140 insect genera and species in eight orders and 50 families were collected. Other invertebrate groups represented in the collection included sponges, leeches and worms, snails, ostracodes, arachnids, Collembola, and Amphipoda. Jackknife estimates place the total number of insect genera at the springs during the sampling period at 190-210. Because of the strong diurnal and seasonal emergence patterns of aquatic invertebrates, the taxa collected likely represent a relatively small portion of the total diversity at the sites. Relationships between the presence or absence of insect genera and elevation, water temperature, water conductivity, discharge volume, and solar radiation inputs were revealed by ordination and cluster analysis. New records for the hemipteran genus Ochterus are reported from three Grand Canyon springs. Three species of flies in the genus Clinocera (Diptera, Empididae) new to science were collected from seepy madicolous microhabitats in several Grand canyon springs. A potential undescribed species of fly in the genus Asymphyloptera (Diptera, Empididae) was collected from several Grand Canyon Springs. Sites at which these new species were found include springs in Bert's Canyon, Saddle Canyon, Elves Chasm, and Fern Glen.

The vascular plant flora of the sampled springs comprised 125 native species and 19 exotic species. Beta diversity was high between sites, and jackknife estimates indicated the total native flora of the site was likely under-sampled by 21%, with an estimated of 159 species present. The majority of the flora consisted of species with southwestern North America, widespread North America, or widespread temperate North America distributions. Additional data on distributions, pollination ecology, dispersal mechanisms, and growth forms is presented. A small Colorado Plateau endemic element of 12 species was documented, representing 10% of the native flora. The fern Adiantum capillus-veneris and the orchid Epipactus gigantea were the most widely distributed species. Tamarisk (Tamarix ramosissima) was the most widespread exotic species. A variety of unusual and interesting relict species from other elevations and regions were found.

The vegetation of the springs was analyzed with cluster analysis and ordination techniques. Four major vegetation types were produced, corresponding to herbaceous vegetation on backwall habitats, herbaceous vegetation of colluvial and detritus slopes, woody vegetation on colluvial and detritus slopes, and wetland vegetation associated with streams and pools. Relationships of vegetation structure and composition occurred with elevation, geology and geomorphology, water conductivity and solar radiation. A vegetation classification using the SRFR system is included, with 21 alliances represented. Backwall habitats were revealed as the most distinctive type among the springs. In many cases, sampled vegetation on a geomorphic type at a spring proved to be more similar to similar geomorphic settings in other, often distant, springs than to other vegetation at the same spring. Grand Canyon vegetation, particular on backwalls, was distinctly different from higher elevation spring vegetation in the other three parks.

Data on the presence of amphibians and various disturbances were also collected. Four amphibians were documented, including canyon treefrog (Hyla arenicolor), red-spotted toad (Bufo punctatus), Woodhouse's toad (Bufo woodhousei), and northern leopard frog (Rana pipiens). 47% of the springs showed evidence of recent human visitation and disturbances. However, most springs were relatively undisturbed, and native vegetation was for the most intact. Databases are included containing data on physical spring features, water quality parameters, water chemistry, flora, vegetation, aquatic invertebrates and disturbance types. Photographic points were established at all springs, and photos are included. Recommendations are made regarding future baseline inventories and establishment of long-term monitoring at selected springs in the four parks. Implications of future human-caused changes, including global warming, to spring biotas are discussed.

TABLE OF CONTENTS

VOLUME I

EXECUTIVE SUMMARY	2
I. INTRODUCTION	5
II. BACKGROUND AND REVIEW	8
II.A. WATER	8
II.B. VEGETATION	8
II.C. AQUATIC INVERTEBRATES	10
III. STUDY AREA	10
III.A. STUDY AREA DESCRIPTION	10
III.A.1. Climate	10
III.A.2. Geology and Geomorphology	11
III.A.3. Paleoecology and Past Climates	12
III.B. SITE SELECTION	12
IV. METHODS AND MATERIALS	15
IV.A. WATER QUALITY AND CHEMISTRY	15
IV.B. FLORA AND VEGETATION	15
IV.C. AQUATIC INVERTEBRATES	17
IV.D. OTHER SITE DATA	17
IV.E. DATA ANALYSIS	18
IV.F. COLLECTIONS AND CURATION	18
V. RESULTS	18
V.A. SITE ENVIRONMENTS	19
V.B. WATER	32
V.B.1. Field-measured Data	32
V.B.2. Water Chemistry	33
V.C. AQUATIC INVERTEBRATES	45
V.C.1. Results	45
V.C.2. Comments and Notes Provided by Dr. John McDonald	47
V.D. FLORA	59
V.D.1. Floristics	59
V.D.2. Origins and Distributions	59
V.D.3. Pollination Syndromes	59
V.D.4. Dispersal Ecology	59
V.D.5. Growth Forms and Vegetative Persistence	60
V.D.6. Exotic Species	60
V.D.7. Species Richness Estimates	60
V.D.8. Colorado Plateau Endemics	60
V.D.9. Relictual and Disjunct Species	61
V.D.10. Bryophytes	61
V.D.11. Discussion	61
V.E. VEGETATION	74
V.E.1. Community Analyses and Vegetation Structure	74

<i>V.E.2. Relationships with Physical Environment</i>	74
<i>V.E.3. Vegetation Classification</i>	75
<i>V.E.4. Comparisons and Discussion</i>	75
V.F. AMPHIBIANS	88
V.G. DISTURBANCE PATTERNS AT SPRINGS	88
V.H. PHOTOGRAPHIC DOCUMENTATION	88
VI. DISCUSSION AND CONCLUSIONS	88
VI.A. WATER	89
VI.B. AQUATIC INVERTEBRATES	89
VI.C. FLORA AND VEGETATION	89
VI.D. DISTURBANCE AND EXOTIC SPECIES	90
VI.E. IMPLICATIONS AND FUTURE WORK	91
VII. RECOMMENDATIONS	92
VII.A. ARCHES NATIONAL PARK	92
VII.B. CANYONLANDS NATIONAL PARK	92
VII.C. GLEN CANYON NATIONAL RECREATION AREA	93
VII.D. GRAND CANYON NATIONAL PARK	94
VIII. PRODUCTS	95
IX. ACKNOWLEDGEMENTS	95
X. LITERATURE	96

VOLUME II

XI. APPENDIX

- A1. Site physical data and location
- A2. Water chemistry
- A3. Aquatic invertebrates presence/absence
- A4. Flora presence/absence and ecology
- A5. Vegetation
- A6. Photos
- A7. Original data sheets
- A8. Original field sketches
- A9. Species lists and collections numbers and specimen data

I. INTRODUCTION

A significant portion of the Colorado River drainage system occurs on the Colorado Plateau (Figure I-1). Four park units administer major portions of this river corridor, Arches National Park, Canyonlands National Park, Glen Canyon National Recreation Area, and Grand Canyon National Park. Numerous springs and seeps occur along the river and in side canyons. Most of these water sources exist as isolated sites in arid or semi-arid climates, surrounded by arid-adapted communities. The Colorado River corridor parks support one of the most diverse floras and faunas in the U.S. Southwest. Grand Canyon NP, because of its great elevational relief and diverse geological strata, has a particularly rich biota. Much of the biodiversity in the river corridor parks centers around the permanent springs (Spence 2002a). Despite this, very little work has been done inventorying the biota associated with these sites. The flora and fauna associated with springs and seeps have never been adequately surveyed for any park unit.

Currently there are a variety of threats that could seriously impact the biota and water quality of isolated spring sites. One of the most urgent threats is the impacts of current and future recreational activity. Trampling and swimming at springs can damage vegetation, increase erosion, allow exotic species to invade, interfere with animal life cycles, and even eliminate aquatic life. Exotic riparian species, in particular tamarisk (*Tamarix ramosissima*), can invade and completely change the biotic community (NPS 1987). Many springs in the study area have already been affected by recreational activity and invasion of exotics.

Another threat to these fragile systems is global change. Impacts of climate changes, such as global warming, on the biota of springs and seeps, are not well understood. Declines in regional precipitation could potentially eliminate many of the obligate wetland plant and animal species at these sites. Ground water pumping and water diversion projects could also affect springs and seeps. Regional droughts have the potential to reduce water flows and affect biotic communities at many sites along the river corridor. With a continuation of drought conditions over a period of years, many plants and animals may become locally extinct before they can be discovered, identified and evaluated for significance. Baseline characterization of these systems is needed to properly evaluate the significance of any losses resulting from global climate change.

This final report documents the water quality, chemistry, flora, vegetation, and aquatic invertebrates of selected spring and seeps along the 800 km corridor of the Colorado River between Arches NP and Lake Mead, including springs around Lake Powell, and provides information on human-caused recreational impacts, as well as the presence of exotic and undesirable plant species. Fieldwork was conducted in 1997-1998. The data and analysis included in this report should be viewed as a baseline of conditions at these springs. Quantitative relationships between water chemistry, site physical environments, and native biotas are also analyzed. Finally, recommendations are made for monitoring water and biotic components of specific sites for each park. The report is organized into eight sections, including the introduction, background and review, methods and materials, results, discussion, recommendations, literature cited, and appendices.

Figure I-1. The study area, the Colorado River drainage in southern Utah and northern Arizona.

Figure to be added

II. BACKGROUND AND REVIEW

II.A. WATER.

Canyonlands NP and Arches NP have an ongoing water quality monitoring program that involves sampling at some spring sites, most of which are not directly associated with the Colorado River (NPS 1994; Long and Smith 1996). Glen Canyon NRA has recently completed an extensive sampling program of selected springs in side canyons around Lake Powell using ultra-pure techniques and including seasonal variation (Taylor *et al.* 1997). Cooley (1965) described locations, stratigraphy, and water quantity, while Lively-Schall and Foust (1988) analysed basic chemistry at numerous springs in Glen Canyon NRA. Brown and Moran (1979) identified the principal water sources in Grand Canyon NP, identifying 36 spring sites, while Goings (1985) studied water chemistry and geology at selected springs. Grand Canyon NP has ongoing studies at spring sites (NPS unpublished data), and a water resources management plan. Cooperative work with researchers at the University of Nevada at Las Vegas on south rim springs is ongoing.

II.B. VEGETATION

The original Colorado River riparian communities above Lee's Ferry are (or were through Glen Canyon) characterized by a mix of apache plume (*Fallugia paradoxa*), live oak (*Quercus turbinella*) and New Mexico olive (*Forestiera pubescens*) on higher terraces. High terrace vegetation of the Colorado River riparian about 65 km below Lee's Ferry in Marble Canyon is dominated by mesquite (*Prosopis glanduliflora*) and catclaw (*Acacia greggii*). Tamarisk (*Tamarix ramosissima*), arrowweed (*Tessaria sericea*), seepwillow (*Bacharis emoryi*), and coyote willow (*Salix exigua*) are abundant throughout the study area in lower zones inundated yearly in spring floods. Nettleleaf hackberry (*Celtis reticulata*), Gooddings willow (*Salix gooddingii*), and western redbud (*Cercis occidentalis*) are less common but still relatively widespread species.

The earliest descriptions of springs in the region come from Major J.W. Powell in his descents of the Colorado River (Powell 1895). Eastwood (1896) collected plants in the Bluff, Utah area and commented on the unusual character of the hanging gardens in the vicinity. Clover and Jotter (1944) described the principal species at springs along the Colorado and Green Rivers, starting at Green River in Utah and ending at Separation Canyon in the lower Grand Canyon. More recent vegetation studies in the study area have concentrated on hanging gardens (Welsh and Toft 1981; Welsh 1989a; Romme *et al.* 1993; Spence and Henderson 1993; Fowler *et al.* 1995; Graham 1997). Hanging gardens are unique herbaceous communities that develop under certain geologic and climatic features in arid to semi-arid climates. They are fed by groundwater aquifers in either fine-grained sandstones or limestones. They tend to develop on cliff faces or in undercut alcoves formed by spalling and groundwater sapping. As water flows down through joint systems or between the interstices of sandstone, it encounters aquicludes that force the water to flow more or less horizontally till it intersects a cliff face, where it emerges either as a single spring, series of springs, or as a seep line. At least two distinct habitats occur in many gardens, the seeping more or less vertical backwall, and the colluvial-detritus slopes at the base. Often a plunge-pool basin develops at the foot of the colluvial slope where water erodes a basin as it falls during flood events from the cliffs above. These pools often retain water for extended periods of time, and can foster the development of wetland communities.

Basic descriptive work on the floristics and geographic distribution of hanging gardens along the Colorado River includes Loope (1977), Welsh and Toft (1981), Rushforth and Merkley (1988; algae), Tuhy and MacMahon (1988), Welsh (1989a, b), Van Pelt *et al.* (1991), Romme *et al.* (1993), Fowler (1995), and Keate (1996). The most characteristic species of the gardens is the widespread tropical-subtropical fern *Adiantum capillus-veneris*, found in most gardens on the Plateau. Hanging gardens support interesting mixtures of species of different phytogeographic elements, including species representative of tall grass prairies, boreal-montane climates, and the Colorado Plateau (Welsh 1989a).

Spence and Henderson (1993) examined the floristics and dispersal ecology of tinajas (water filled rock tanks) and hanging gardens in the Waterpocket Fold of Capitol Reef National Park. They noted that the gardens were much less similar to each other in floristics than the tinajas were, suggesting either greater site-to-site habitat differences or a larger random component related to flooding or chance dispersal. The species in these gardens included many more species adapted for wind dispersal compared with tinaja floras.

Fowler (1995) examined vegetation and invertebrates in a variety of hanging gardens across the northern and central Colorado Plateau, testing his data against species-area relationships and the core-satellite hypothesis of Hanksi (1982). He documented differences in vegetation and floristics across the region, and noted that species that were locally abundant tended also to be geographically widespread. He also presented a preliminary vegetation classification with five principal types. Fowler found a weak positive relationship between species richness and garden area, but failed to differentiate between widespread riparian species that occur in adjacent riparian zones from species restricted to gardens (Fowler *et al.* 1995). He did not find any support for the core-satellite hypothesis.

Keate (1996) analyzed the physical differences between gardens and the distribution of hanging garden species around Moab, Utah. She realized that for some plant species gardens were not islands, so she restricted her analyses to narrow garden endemics that did not occur in adjacent riparian zones. Keate detected patterns in the distribution of endemics at several scales, including regional and local between-garden and within-garden scales. Important factors related to the presence of endemics included the extent of garden seepage development and distance above the adjacent riparian channel, a proxy variable for flooding. Gardens with more endemic species were higher above adjacent flood zones, had complex microhabitats, and low levels of solar radiation. Species richness of endemics was only weakly correlated with garden area.

Very little is known about other kinds of spring-supported vegetation in the region. Phillips *et al.* (1980, 1987) and Warren *et al.* (1982) described spring-supported vegetation in the Grand Canyon region. Most springs they studied supported stands of riparian-like woodlands, dominated by widespread riparian species like *Fraxinus pennsylvanica*, *Populus fremontii* and *Salix gooddingii*. Spence (1996) described and classified the vegetation associated with springs in 25 side canyons around Lake Powell and in the Escalante River Basin. He described the characteristics of 17 distinct vegetation types. Several unusual types occurred, including mixed deciduous woodlands dominated by Birchleaf Buckthorn (*Rhamnus betulifolia*) and thicket creeper (*Parthenocissus vitacea*), and types dominated by poison ivy (*Toxicodendron rydbergii*), common reedgrass (*Phragmites australis*), and spikerush (*Eleocharis palustris*). Very little information is available on bryophyte vegetation (e.g. Haring 1946; Woodbury 1958; Flowers 1959) at springs and seeps on the Colorado Plateau. Work on endemic wetland and riparian species on the Colorado Plateau includes Holmgren *et al.* (1976), McArthur *et al.*

(1989, 1998), Kelso (1991), Allphin and Harper (1994), Allphin et al. (1996), and Hudson et al. (2000). Stone (1998) summarizes the status of some of these species for Utah. A review of upland vegetation on the Colorado Plateau can be found in West and Young (2000).

II.C. AQUATIC INVERTEBRATES.

With the exception of Grand Canyon NP, virtually no baseline data on the aquatic macroinvertebrates of springs and seeps has been collected in the parks. Canyonlands NP has completed some preliminary work on aquatic macroinvertebrates associated with water sources (Wolz and Shiozawa 1995). Extensive work has been conducted on the aquatic macroinvertebrates of the Colorado River through Grand Canyon NP (eg., Sublette et al. 1998), although less is known about spring communities (L. Stevens, pers. comm., 1998). Stevens et al. (1995) discussed the ecology of the federally endangered Kanab Ambersnail (*Oxyloma haydenii kanabensis*), which occurs at the spring at Vasey's Paradise in Marble Canyon. Extensive survey work has been done on the aquatic invertebrates in tinajas in Capitol Reef National Park (Baron et al. 1998). Recent surveys of aquatic invertebrates have been done along the Escalante River in Glen Canyon NRA (Mueller et al. 1998). A general review of insects on the Colorado Plateau can be found in Harper et al. (1994).

III. STUDY AREA

III.A. STUDY AREA DESCRIPTION

The study area is the Colorado River corridor from Arches NP to Grand Canyon NP. Of the ca. 800 kilometers of Colorado River corridor, 50% occurs in Grand Canyon NP, 35% in Glen Canyon NRA, and 15% in Canyonlands and Arches NP's. Because of difficulties of access and a general lack of springs, the river corridor from Moab to Cataract Canyon through Canyonlands NP was not sampled. Instead, selected springs in the Island-in-the-Sky and Needles districts were sampled.

III.A.1 Climate

The entire study area lies below 2000 meters, and experiences an arid climate with hot summers, relatively mild winters, and <250 mm precipitation per year (Spence 2001). Data from seven climate stations along or near the river corridor are summarized in Table III-1. Mean annual precipitation ranges from a low of 152 mm at Bullfrog on Lake Powell to 247 mm at Phantom Ranch in the Grand Canyon. July maximum temperatures are high, ranging from 36 to 41° C. January minimum temperatures vary from -7.9° C at Moab to +2.7° at Phantom Ranch (Needles is at a higher elevation and is not situated on the Colorado River). The climate data from Phantom Ranch reflect the relatively mild winter conditions found along the Colorado River through Grand Canyon compared with upstream climates. Evapotranspiration rates are generally high throughout the year at all stations, with Phantom Ranch the highest at 1161 mm. Most long-term data sets (>30 years) along the river corridor and in the region show significant increases over time in minimum temperatures and moderate increases in winter precipitation (Spence 2001). There is little evidence for increases in maximum temperatures in the region, and no evidence for a strengthening of the monsoon that generally brings intense precipitation to the southwestern Colorado Plateau between July and September.

III.A.2. Geology and Geomorphology

The area under consideration (Figure I-1) consists of the central third of the Colorado Plateau, dominated by the Colorado River and the numerous associated tributaries such as the Green, San Juan, Escalante, Paria, and Little Colorado rivers, as well as literally hundreds of shorter side canyons. This portion of the Colorado Plateau is the lowest in elevation, with the Colorado River itself ranging from 1215 m at Moab to 370 m where the river reaches Lake Mead. Most of the surrounding landscape consists of mesas and cliffs of either sandstone or limestone. A distinct break in geology occurs at Lee's Ferry (370 kilometers above Diamond Creek). Below this break relatively older limestones interbedded with shales occur along the Colorado River, while above this break relatively younger sandstones and shales are found. Principal water-bearing strata include the Cedar Mesa, Entrada and Navajo Sandstones on the Colorado Plateau and the Redwall and Muav Limestones in Marble and Grand Canyons. Principal aquicludes include the Kayenta and Chinle Formations and the Bright Angel Shale. Springs are common in some strata, and extremely rare in others. The majority of springs studied are associated with layers of porous rocks (limestones or fine-grained eolian sandstones) which lie above aquicludes. Once the aquiclude is reached water tends to flow through cracks and joints horizontally until a canyon is reached, where the water issues as a spring. Many springs form in alcoves in the study area. The development and physical features of these alcoves and springs have been discussed in detail by Welsh and Toft (1981), Laity and Malin (1985), and May *et al.* (1995). General observations and literature on the springs of Grand Canyon NP can be found in a brief report written for this project by Eric Wilson, a graduate student in geology at Northern Arizona University (Wilson 1998).

III.A.3. Paleoecology and Past Climates

Many springs appear to harbor refugial populations of plants in the study area (Spence 1995, 2002a). The origins of these populations are not known, but an analysis of past climates and vegetation can provide a context to develop alternative hypotheses. The history of vegetation and presumed climates of the region prior to the Pleistocene that encompasses the study area can be found in Axelrod and Raven (1985). The central Colorado Plateau and Grand Canyon have an extensive history of late Pleistocene-Holocene paleoclimatic and paleoecological research (*e.g.*, Betancourt 1984; Betancourt *et al.* 1990; Cole 1991, 1997; Dryer 1994; Sharpe 1991, 1993; and Withers *et al.* 1993). Most of this work has focused on the last 25,000-30,000 years, comprising the last (Wisconsin) glaciation and the Holocene. Until about 11,000 years ago, conditions on the Colorado Plateau were cooler and wetter than at present. Extensive coniferous forests and sagebrush steppes covered the region. Along the Colorado River and its many tributaries, above *ca.* 1400 m, riparian and spring vegetation consisted of species that are typically montane today, such as *Abies concolor*, *Acer glabrum*, *A. grandidentatum*, *Betula occidentalis*, *Picea pungens*, *Pseudotsuga menziesii*, and *Rosa woodsii* among others. A varied fauna of large mammals occurred, including mammoth, mastodon, musk-ox, giant ground-sloth, and short-faced bear. Presumably, aquatic invertebrate assemblages in riparian zones and at springs also reflected the cooler and wetter conditions, although there is little evidence (Elias *et al.* 1992). With the change to drier and warmer Holocene conditions, most of the large mammals became extinct, and populations of the plant species either moved up slope to near their current elevational limits, or in some cases lingered in shaded alcoves associated with springs (Spence 1995). Conditions in some areas have apparently not changed substantially in the last 10,000 years (*e.g.*, Withers and Mead 1993), suggesting relatively stable climates. The mid-Holocene thermal maximum may have had some impacts on springs in the region, but no data is available on changes in climate patterns and regional aquifers. Proxy evidence of climate

change suggests that periods of aggradation alternated with periods of degradation in portions of the study area (e.g., Boison and Patton 1985, Patton and Boison 1986).

III.B. SITE SELECTION

For the study, sites were sampled from Arches NP, Canyonlands NP, Glen Canyon NRA, and Grand Canyon NP. Sites in Grand Canyon were only sampled along the river corridor. The original work plan called for visiting lesser known springs above the river corridor in the Grand Canyon, but this could not be done because of helicopter costs and the minimum tool policies of Grand Canyon NP. In general sites were selected within ca. 10 kilometers of the river. Springs at a variety of elevations were sampled, from river level to ca. 1750 m. Site access was often difficult, and a combination of boats, helicopters (Glen Canyon NRA only), four-wheel drive vehicles and hiking were utilized. Sites were selected where surface water existed, and were defined as either springs or seeps. In this study springs are defined as water sources that flow year round, although some seasonal variation in quantity may occur. Seeps are defined as water sources that stop emerging aboveground for at least a portion of the year. Sites were selected based on the following criteria:

- i) isolation from riparian zones;
- ii) relatively constant and well-developed water flows (not ephemeral);
- iii) well developed vegetation (see below);
- iv) geological formation (as many strata as possible to be sampled);
- v) accessibility.

Vegetation at springs and seeps in the study area is very complex, and can comprise predominantly herbaceous species, woody species, or a mixture of the two. Many springs have associated with them woodlands of deciduous tree or shrub species. Sites displaying a wide range of vegetation types and geological strata were sampled to provide details on how various strata and site environments affect floristics, vegetation structure, and aquatic macroinvertebrate faunas. Table III-1 lists the sites by geological strata present and park. The appendix details the locations, physical and biological characteristics, and photo documentation of each site.

Table III-1. Summary of means for selected climate variables from seven climate stations currently operating along the Colorado River, Lake Powell and in adjacent areas.

Data	MO	ND	HI	BF	WW	LF	PR ¹
Elevation (m)	1219	1536	1220	1165	1136	978	784
Annual temperature (°C)	13.2	11.8	15.5	15.2	15.7	16.9	20.4
Maximum temperature (°C)	21.8	20.1	21.9	22.4	22.7	24.7	27.6
Minimum temperature (°C)	4.6	3.4	9.1	8.1	8.7	9.2	13.6
Annual precipitation (mm)	229	214	214	152	158	153	247
Maximum July temperature (°C)	36.6	36.0	36.9	37.4	36.9	39.5	41.0
Minimum January temperature (°C)	-7.9	-9.1	-3.7	-4.1	-3.1	-3.1	2.7
Evapotranspiration rate (mm) ²	791	727	919	899	911	993	1161
Duration of record (years)	110	34	21	26	32	84	34

¹MO=Moab, ND=Needles District CANY, HI=Hite Ranger Station GLCA, BF=Bullfrog Ranger Station GLCA, WW=Wahweap Ranger Station GLCA, LF=Lee's Ferry Ranger Station GLCA, PR=Phantom Ranch GRCA.

²Thornthwaite method.

Table III-2. General geology of the study sites selected in the study by park, along with age of formation.

<u>Park Unit</u>	<u>Geological Formation/Group</u>	<u>Age</u>	<u>Number of Sites</u>
ARCH	Entrada Sandstone	Jurassic	5
CANY	Navajo-Kayenta interface	Jurassic	3
GLCA	Cedar Mesa Sandstone	Permian	2
GLCA	Chinle Shale	Triassic	6
GLCA	Kayenta Sandstone	Jurassic	3
GLCA	Navajo-Kayenta interface	Jurassic	14
GLCA	Navajo Sandstone	Triassic-Jurassic	3
GLCA	Summerville Formation	Jurassic	1
GRCA	Bass Limestone	Precambrian	1
GRCA	Muav Limestone	Cambrian	18
GRCA	Precambrian strata	Precambrian	2
GRCA	Redwall Limestone	Mississippian	1
GRCA	Tapeats Sandstone	Cambrian	1
Totals	12	6	60

IV. METHODS AND MATERIALS

IV.A. WATER QUALITY AND CHEMISTRY

Water samples were collected using ultra-pure techniques in use by the USGS lab in Denver (Taylor *et al.* 1997). A disposable sterilized syringe with attached filters was used to collect water samples from cracks or other locations where water was issuing as close to the source as possible. The water was then stored in pre-cleaned plastic and glass bottles. Use of the syringe and filters minimized possible contamination that could occur as the water flows over vegetation, soil or other materials. Data collected on site using hand held meters or portable hydrolabs included pH, temperature, conductivity, and dissolved oxygen.

The water was analyzed at the USGS lab in Denver, Colorado (Taylor *et al.* 1997). Many of the methods used have only recently been developed, and represent state of the art approaches at extremely detailed levels of precision. Dissolved component analyses of trace elements include sodium, potassium, magnesium, calcium, strontium, iron, aluminum, arsenic, barium, beryllium, boron, cadmium, cesium, chromium, cobalt, copper, lead, lithium, manganese, mercury, molybdenum, nickel, rubidium, selenium, silver, thallium, vanadium, zinc, silica, alkalinity, chloride, sulfate, bromide, fluoride, nitrate, nitrite, ammonium, phosphate, carbonate, and bicarbonate. Because of holding time problems, some analyses could not be done for samples from remote sites accessed by backpacking or by boat along the Colorado River. Some elements have holding times as short as 24-48 hrs, and need to be quickly processed (Standard Methods 1992). Water samples were placed on ice immediately and kept cold until analyzed in the lab.

Water flow (quantity) was determined by one of several methods. In most situations, where the water was constrained into a channel, filling a standard volume over a specified time was used, either by building a temporary dam or installing a weir plate. In many situations, however, the water was issuing from a variety of sources, such as a wet wall. In these cases one or more photographs were taken of selected wetted areas, with a meter stick for scale in the photo. Where water was flowing within a defined area down a rock wall, plastic sheeting was used to temporarily channel the water into a container of known volume. In all cases, discharge is expressed in flow rates (milliliters/second). Data was compared between sites, and correlated with geological strata. All data is maintained in Microsoft ACCESS or EXCEL databases. Data will also be transferred to the STORET database.

IV.B. FLORA AND VEGETATION

The phreatophyte flora (*cf.* Green and Campbell 1968) of each site was described, and specimens of unknown species collected. The vegetation at the site was described using the prominence scale developed by Spence (1993, 1996):

- 6=dominant (>95% canopy cover)
- 5=abundant (51-95% canopy cover)
- 4=common (11-50% canopy cover)
- 3=uncommon (1-10% canopy cover)
- 2=occasional (<1% canopy cover)
- 1=rare (<<1% canopy cover, few individuals)

Each species was classified according to life form, geographic distribution, pollination mode, and dispersal category. Life forms (vascular plants) include:

- Annual forb
- Annual graminoid (grass, sedge or rush)
- Perennial forb
- Perennial graminoid
- Shrub
- Tree
- Vine

Each species was classified by dispersal categories based on the study of Spence and Henderson (1993), and include (example genus):

- Ballistic: dispersal of seeds by explosive mechanisms (*Viola*)
- Fleshy: fleshy fruit attractive to animals (*Vitis*)
- Floater: water dispersed fruits or seeds (*Typha*)
- Megawind: seed/fruits with large surface/volume ratios and low terminal velocities to aid in long-distance wind dispersal (*Adiantum*, *Epipactis*)
- Miniwind: limited wind dispersal away from parent (*Acer*, Asteraceae)
- Myrmecoid: ant-dispersed seeds/fruits (*Viola*)
- Smooth: no specialized morphological adaptations for dispersal (many taxa)
- Sticktight: seeds/fruits with sticky or barbed/hooked structures that can be dispersed on the feet, fur or feathers of animals (*Xanthium*).

Current geographic distributions include the following floristic elements, based primarily on the work of McLaughlin (1992):

- Madrean (southwestern US and northern Mexico)
- Colorado Plateau (endemic)
- Widespread NA temperate
- Widespread western North American
- Rock Mountain region
- Cosmopolitan

Presumed origins of the species were analyzed using the methods of Raven and Axelrod (1978), Stebbins (1982), and Axelrod and Raven (1985). The principal categories include the following:

- Cosmopolitan
- Boreal
- Madrean
- Temperate
- Tropical
- Western North American (old western autochthonous elements).

Pollination modes used are broad categories based on the concept of pollination syndromes, as the pollination ecology of most of the species in the study area has not been investigated. These categories are:

- Animal pollinated
- Wind pollinated
- Water pollinated
- Self-pollinated

As part of the project collections of bryophytes (liverworts, hornworts and mosses) were made. Nomenclature follows Spence (1988) for mosses except for more recent revisions of selected groups. Rough abundances were determined for species that can be reliably identified in the field. Nomenclature of vascular plants follows Spence and Zimmerman (1996), Phillips *et al.* (1987), and Welsh *et al.* (1993).

IV.C. AQUATIC INVERTEBRATES

Aquatic macroinvertebrates were collected at each study site by professional entomologists. Timed searches were used to sample all available microhabitats at each site. Standard methods and collecting equipment, including dip nets, aspirators, and surber samplers, were used. Collections were sorted by family and genus at the labs of SWCA, Inc., and sent to specialists at Purdue University for identification.

Principal habitats invertebrates were collected from were characterized for the study as:

- S=seep with laminar flow over vertical to near-vertical surface
- SP=spring with quantifiable flow and outlet
- P1=pool isolated from recharge except during flooding
- P2=pool associated with spring flow
- ST=stream or rivulet associated with high volume springs

The principal microhabitats that invertebrates were collected from were characterized for the study as:

- C=*Chara* sample from low velocity habitat
- LS=laminar seepage over rock, detritus or algae
- LP=leaf pack of allocthonous materials
- M=madicolous (seepy backwall) habitat
- SS=sediment sample from low velocity habitat
- SW=sweep of pool with net, including rock surfaces

IV.D. OTHER SITE DATA

The geological strata and associated geomorphological landforms at each site were identified and described. Five principal geomorphic settings were used:

- B=Backwall (vertical to sloping bedrock in alcove setting)

D=Colluvial (detritus) slopes
P=Plunge pools (pools of water resulting from springs or runoff in alcoves)
R=Sloping slickrock (bedrock in non-alcove setting)
S=Simple (spring sites lacking the above settings, generally emerging from colluvium)

Other site features recorded include elevation, aspect, exposure, any obvious natural disturbances, anthropogenic impacts, and presence of vertebrate species, in particular amphibians. Photographs were taken of each site from permanent photo points. Sites were georeferenced and mapped onto USGS 7.5 minute topographic maps. A Solar Pathfinder was used to determine total potential solar radiation at each site. Solar data consists of mean monthly inputs expressed as a percentage of maximum possible at the latitude of the spring.

IV.E. DATA ANALYSIS

Sites were classified and compared using standard multivariate ordination and classification techniques, including TWINSpan, SAHN clustering, DECORANA, NMS, and PCA. Comparisons between data sets (eg., water, macroinvertebrates, and plants) were made using canonical correlation analysis (CCA) or by correlating raw values with ordination scores. Presence-absence data was first transformed using the Beals smoothing function prior to ordination. Correlations between specific taxa and site characteristics were performed using the nonparametric Spearman's or Kendall's correlations. PCORD 2.0 (McCune and Mefford 1995) and SX4.1 (Analytical Software 1998) were used to analyze the data. Vegetation was classified using the SRFR classification (Spence 2002b). Data was manipulated and stored in Microsoft EXCEL databases (see Appendix).

IV.F. COLLECTIONS AND CURATION

Preliminary sorting, processing and identification of plant specimens was done at Glen Canyon NRA. Bryophytes were identified and prepared at Glen Canyon NRA. Sorting and preliminary identification (family/genus) of invertebrates was done in the labs of SWCA, Inc. Specialists were then consulted for identification below the family/genus level for select groups. All plant and invertebrate specimens will be housed in the park where they were collected, and will be stored and cataloged according to standard NPS natural history procedures.

V. RESULTS

In all 60 sites were visited for the project, 23 in 1997 and 37 in 1998. Of these, four were in Arches NP, four were in Canyonlands NP, 29 were in Glen Canyon NP, and 23 were in Grand Canyon NP. Water collections were taken for chemical analysis at 46 sites, and field measurements were made at 54 sites. Vegetation was sampled at 55 sites, while aquatic invertebrates were collected from 45 sites. Two sites were streams, and one site, Matrimony Spring, was a developed spring near Moab. The stream sites and Matrimony Spring are not included in the analyses except for the chemical data. Below the data is organized by subject material, including site environments, water, flora, vegetation, amphibians, bryophytes, disturbance, and other data.

V.A. SITE ENVIRONMENTS

Site physical data and field-measured water data can be found in the appendix. Sites ranged in elevation from 480 to 1650 m (Figure V-1). Although site area was not measured, all sites were <1 hectare in size, and most were <0.25 hectare. Some consisted of wet seeping walls of only 50-400 m² in extent (see site photos in the appendix). Two sites, Wall Spring and Lower Big Springs, were only about 20-30 m² in size. Site aspect included all compass directions, with the fewest sites facing west and the most facing south (Figure V-2). Solar radiation inputs (% of total possible) were generally higher for summer at a majority of sites compared with winter (Figure V-3). Amount of yearly solar radiation varied per site from 0% at Cabin Spring in CANY to 96% at Gypsum Canyon Spring in GLCA. For summer values, the range was 0% at Cabin Spring to 95% at Gypsum Canyon Spring. For winter values, the range was from 0% (several sites) to 96%, again at Gypsum Canyon Spring. This latter site was the most exposed of those sampled in this study.

Site geomorphology included a variety of types (Figure V-4). More than one type can occur at each site. Most common were seeping backwalls (B) in alcove settings and associated detritus slopes (D). These slopes were generally of colluvium produced by mast-wasting processes. A few sites in sandstones had some material of eolian origins as well. Plunge pools (P) occurred at 12 sites, generally in association with backwalls and detritus slopes of classic alcove hanging garden sites (Welsh and Toft 1981). Most of the above types are associated with springs that develop as linear seep lines rather than from a single source. A few sites in non-alcove settings consisted primarily of water seeping over exposed sloping slickrock (R). At least 19 sites consisted of a single spring source with water emerging in soil or eolian deposits (S). These sites were especially common at the base of talus where water that was seeping through the talus emerged at its base. An example of this are the many springs in Good Hope Bay that emerge at the base of extensive talus derived from the overlying Wingate cliffs that cover Chinle slopes. Figures V-5 and V-6 show schematic diagrams of the possible geomorphic types. Site-specific geomorphology and other physical features are discussed for each site in the appendix.

Figure V-1. The 60 spring study sites are plotted by elevation and river kilometer along the Colorado River drainage above Diamond Creek. The squares along the bottom of the chart depict specific locations along the river corridor. These are, from left to right, Diamond Creek (0 km), Phantom Ranch (225 km), Lee's Ferry (370 km), Bullfrog (550 km), Hite (625 km), confluence of the Colorado and Green rivers (700 km), and Moab (780 km).

Colorado River Springs

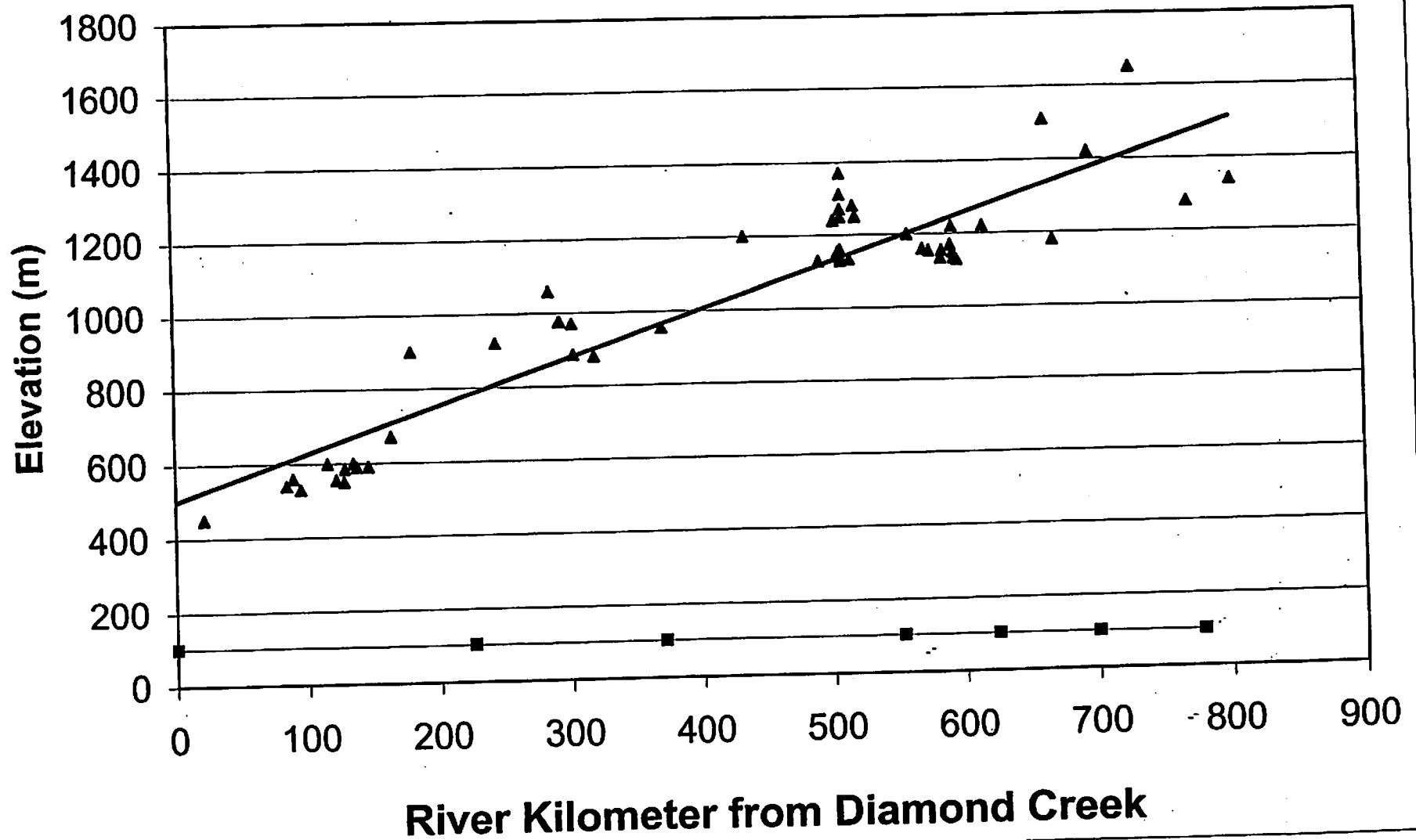


Figure V-2. Number of spring sites in each of four categories of aspect.

Spring Aspect

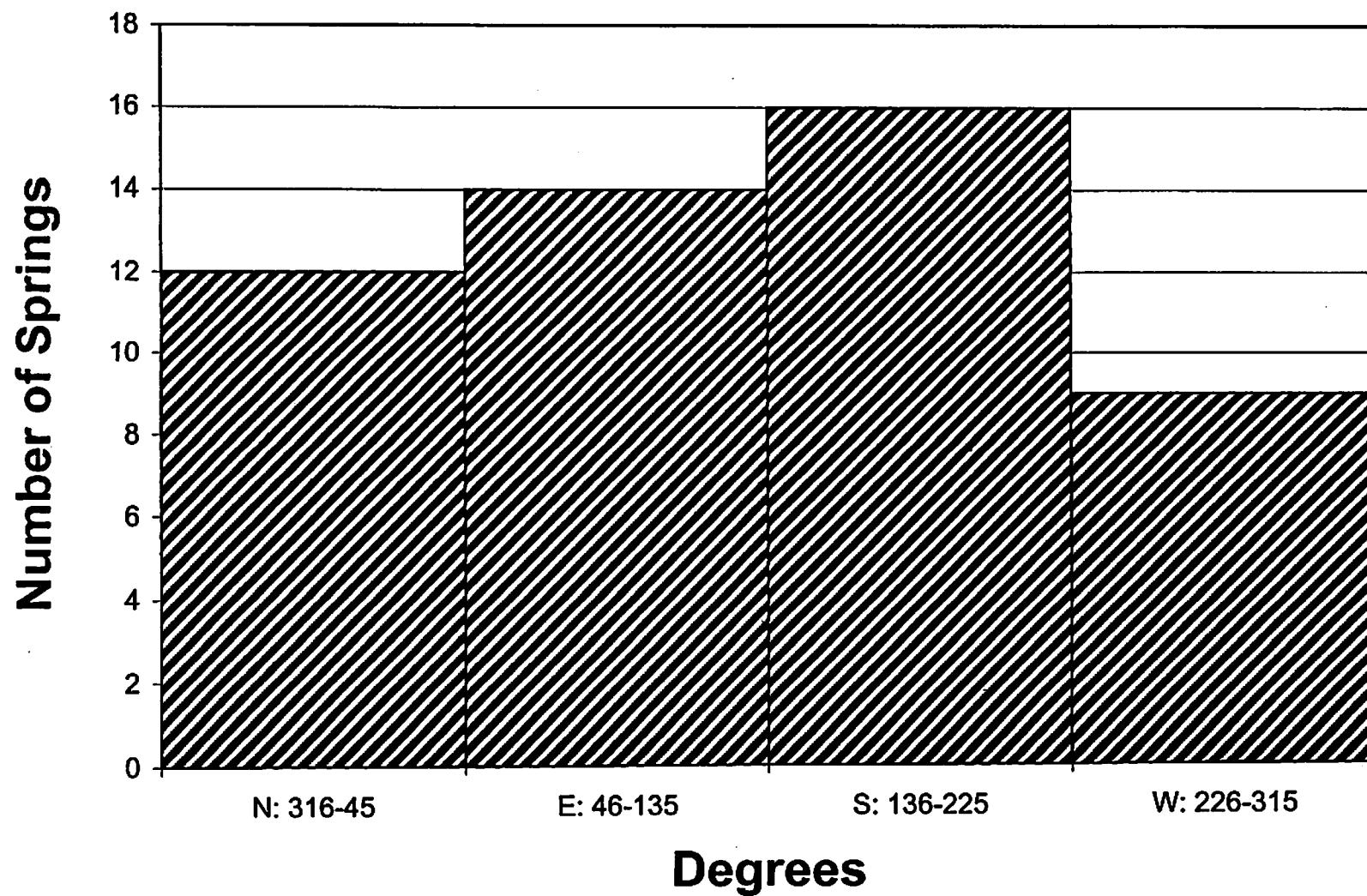


Figure V-3. Total amount of solar radiation input (out of 100%) for each spring site using a solar pathfinder. Number of sites are listed for summer (April-September), winter (October-March) and yearly totals for four different categories.

Solar Radiation Data

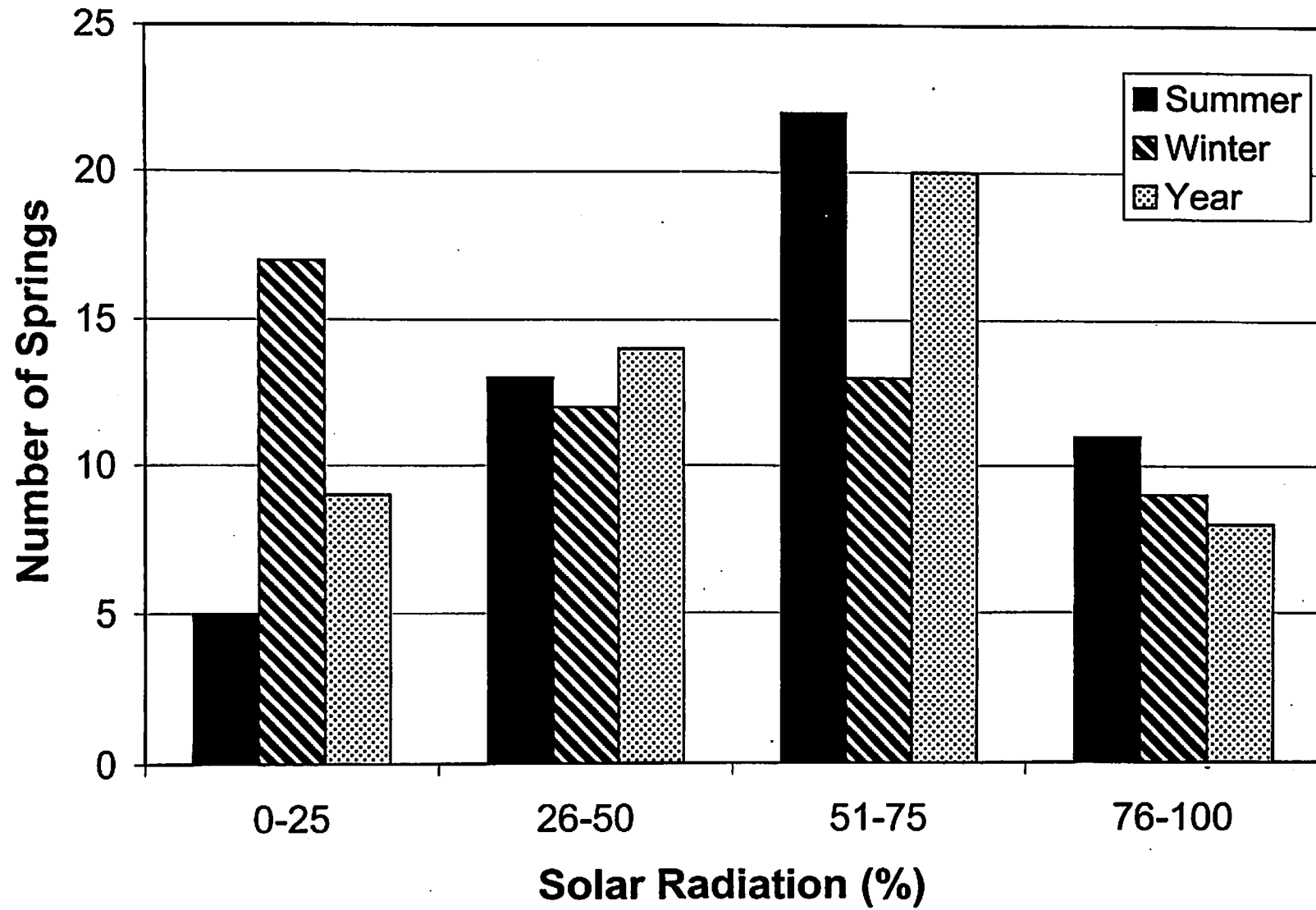


Figure V-4. Total number of different geomorphic units for the spring sites. The total number adds up to more than the number of sites because more than one geomorphic unit can occur at a site. For a description of the units see section III, Methods and Materials. Units are B=backwalls, D=detrital/colluvial slopes, P=plunge pools, R=riparian/stream zones, and S=simple springs.

Geomorphological Units

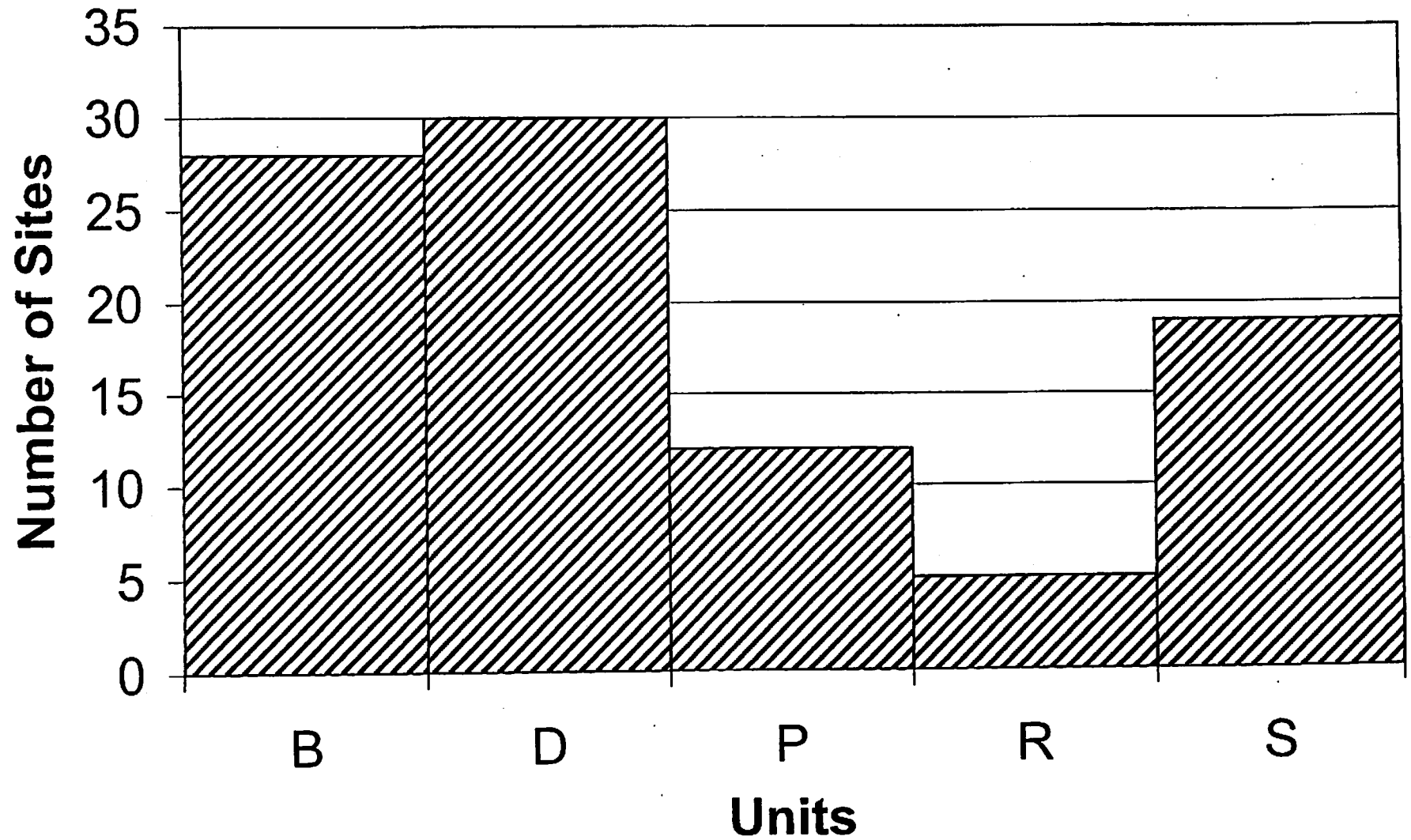


Figure V-5. Schematic diagrams of the principal geomorphic settings at a simple spring site.

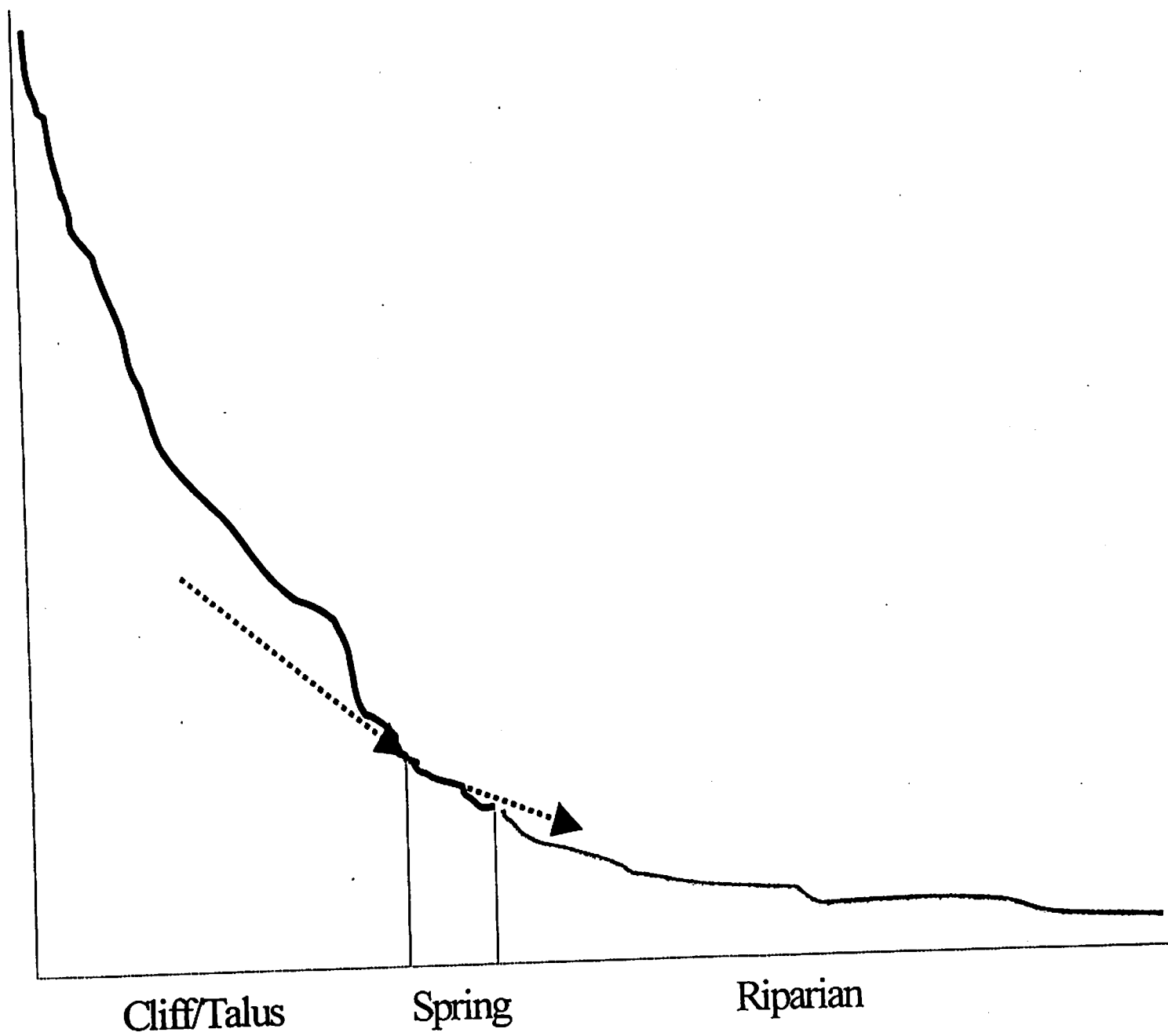
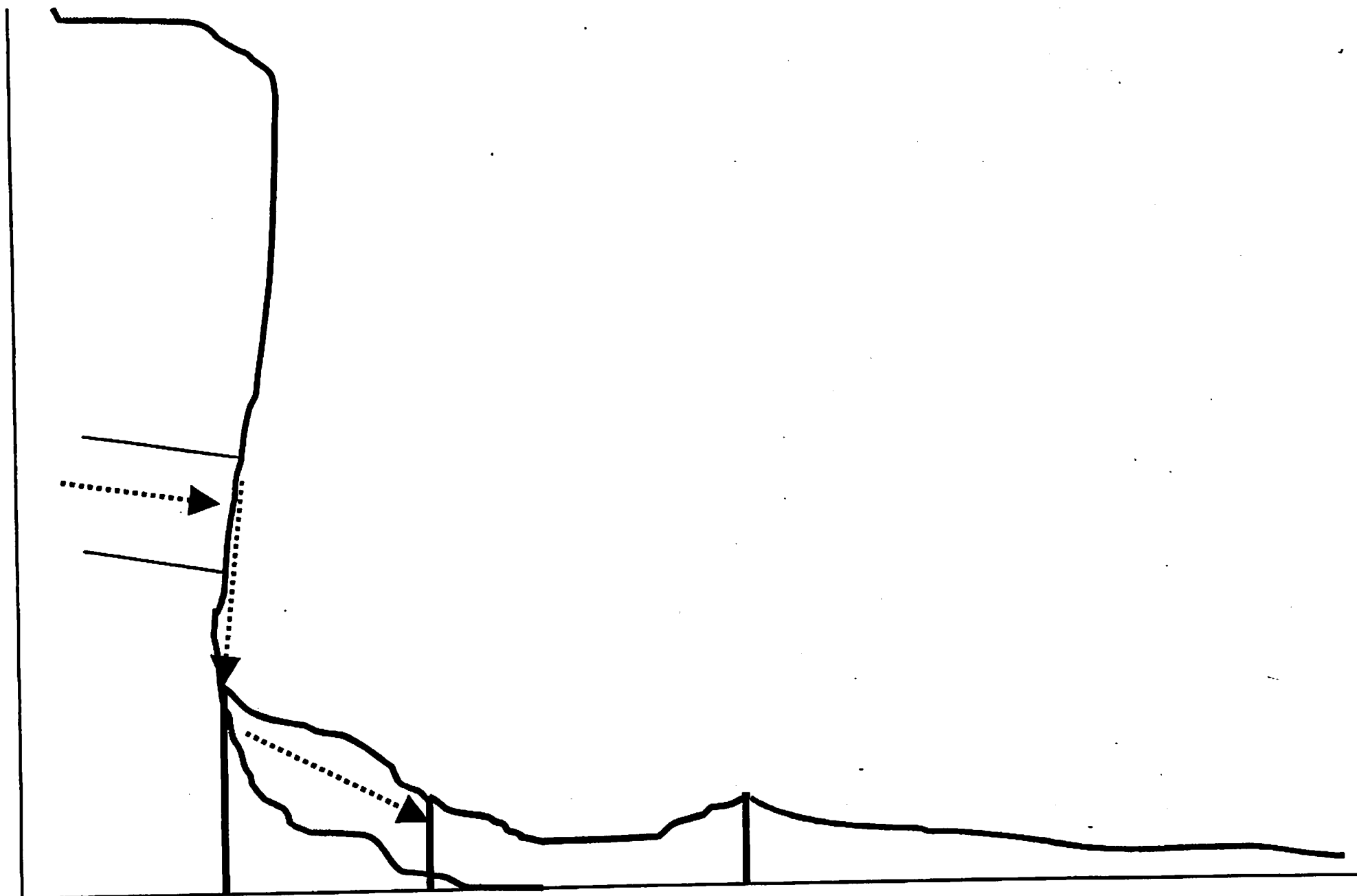


Figure V-6. Schematic diagrams of the principal geomorphic settings at a complex alcove spring and hanging garden site.



Backwall

Detritus Slope

Plunge Pool

Riparian

V.B. WATER

V.B.1. Field-measured Data

Water using the techniques outlined in Taylor *et al.* (1997) was collected from 55 sites. The remaining sites consisted of minor seeps with insufficient discharge to collect samples. Field-measured data can be found in the appendix. Parameters measured in the field were pH, water temperature, dissolved oxygen content, conductivity and discharge rates.

Spring water pH values ranged from 6.99-9.22, with a mean of 8.05 and a median of 8.0 (Figure V-6). Two sites had remarkably high pH levels, Bowns Canyon hanging garden in GLCA (9.07) and RM 213R spring in GRCA (9.22). There were no significant differences in pH between GRCA limestone sites and GLCA/ARCH/CANY sandstone sites.

Water temperature ranged from a low of 9° C at Elves Chasm to a high of 31.9° C at Swett Canyon Spring. The relationship between water temperature and elevation is plotted in Figure V-7. The relationship is weak ($r^2=0.115$), and positive, indicating the higher elevation sites had warmer water than the low elevation sites. When possible water temperature was recorded at the source, but in many cases this proved impossible. The high values may be the result of post-emergence changes in temperature. In particular, the very warm water at sites such as Swett Canyon spring, Easter Pasture Canyon hanging garden, and Knowles Canyon hanging garden are readings based on water well removed from the sources. The unusually low temperature at Elves Chasm may also be due to this problem. Three clusters of temperatures occur in Figure V-7. One consists of low elevation Grand Canyon sites with temperatures around 15-20°, a second small group of sites in Marble Canyon with colder temperatures around 13-15°, and a large cluster of mid-elevation sites around Lake Powell with temperatures around 18-25°.

Conductivity ranged from a low of 117 μ S at Bowns Canyon hanging garden to a high of 12,880 μ S at Pumpkin Spring in the lower Grand Canyon. Pumpkin Spring emerges in a carbonate-encrusted basin at river level in the Tapeats Sandstone and has highly unusual water chemistry (see below). A highly significant difference in conductivity occurs between springs emerging from sandstones and those emerging from Grand Canyon limestones and associated shales and Precambrian rocks. Mean conductivity of water emerging from Colorado Plateau sandstones was 243.5 μ S compared with 1897.5 μ S in Grand Canyon sites.

Problems were encountered with the DO meter used during the Colorado River trip through Grand Canyon, and this parameter was not measured for most springs in the canyon. Based on 25 samples, dissolved oxygen content varied from 2.1 to 10.4 mg/L with a mean of 7.17 mg/L.

Discharge rates varied from damp seeps without discernable flows to 7080 ml/second at Slimy Tick Canyon in GRCA. Rates were highly variable between most sites, and are also likely to be highly variable at different times of years and between years within sites. Discharge types ranged from single source springs to long linear seep lines in hanging garden and other alcove sites. This latter type was difficult to quantify, and rates only represent rough estimates at the time they were measured. The change in rates along the Colorado River is shown in Figure V-8. No relationship was evident between distance along the river (a proxy variable for elevation and geology) and discharge rates.

V.B.2. Water Chemistry

Water chemistry data is summarized in the appendix. This data supplements work from previous surveys in Glen Canyon NRA (Taylor *et al.* 1997). Some of the springs are the same in both studies, but many are new.

An analysis of spring water chemistry was done using ordination to study relationships between sites. A detrended correspondence analysis (DCA) ordination is shown in Figure V-9. Sites are plotted on the first two axes of the ordination. The first axis shows a gradient from primarily Grand Canyon springs on the left to Glen Canyon, Arches and Canyonlands springs on the right. The second axis shows a gradient primarily related to springs within Glen Canyon, and Arches and Canyonlands. Those elements that are most strongly correlated with the first two axes are shown in Table V-1. On axis I sites on the left of the diagram (e.g., P4298, P4698) have water enriched in Mo, Mg, SO₄, U, F, Ca, Re and K while sites to the right side of the chart (e.g., P1097, P2698) are low in these elements but high in Ba. On axis II sites at the bottom of the graph (e.g., P5598, P2798) are enriched in Ba, La and Sb, but low in Cs, Cd, Cr, Zn, Rb, and Al while sites at the top (e.g., P3498, P4798) are low in Ba, Sb and La but high in the other elements.

In order to determine whether geology is correlated with water chemistry, the geology of each site was mapped onto the ordination graph (Figure V-10). For each site number, principal geological formation was substituted. Sites to the left of the chart are primarily Grand Canyon sites associated with Muav and Bass Limestones as well as the Summerville Formation (GLCA P1997). Sites to the right are primarily those where the aquifers originate in sandstone, including the Navajo, Kayenta, Entrada and Cedar Mesa. The relationship between geology and water chemistry on the second axis is more difficult to interpret. At the top of the chart sites include a mix of geological substrates, including Tapeats Sandstone, Muav Limestone, Chinle Shale, Precambrian schists, and Navajo-Kayenta sandstones. Sites at the other end of the second axis are primarily those related to Entrada, Kayenta, and Navajo Sandstones. Sites associated with Chinle Shale often tend to be intermediate in water chemistry compared to end sites of the two axes. This may be related to residence time of water flowing through or in the Chinle after leaving the overlying Wingate Sandstone. Some springs occur at the top of the Chinle while others emerge well down in the Chinle.

Table V-1. The ten chemicals and elements that are most strongly correlated with each of the first two axes of the DCA ordination of water chemistry. The value is the Kendall rank correlation.

Chemical/Element	Axis I	Chemical/Element	Axis II
Mo	-0.675	Ba	-0.514
Mg	-0.653	Cs	+0.421
SO ₄	-0.603	Cd	+0.306
U	-0.552	La	-0.306
F	-0.527	Cr	+0.300
Ca	-0.509	Zn	+0.267
Re	-0.480	Rb	+0.263
Ba	+0.476	Al	+0.202
K	-0.455	Sb	-0.196

Figure V-6. Number of spring sites in each category of listed water pH ranges.

Spring Water pH

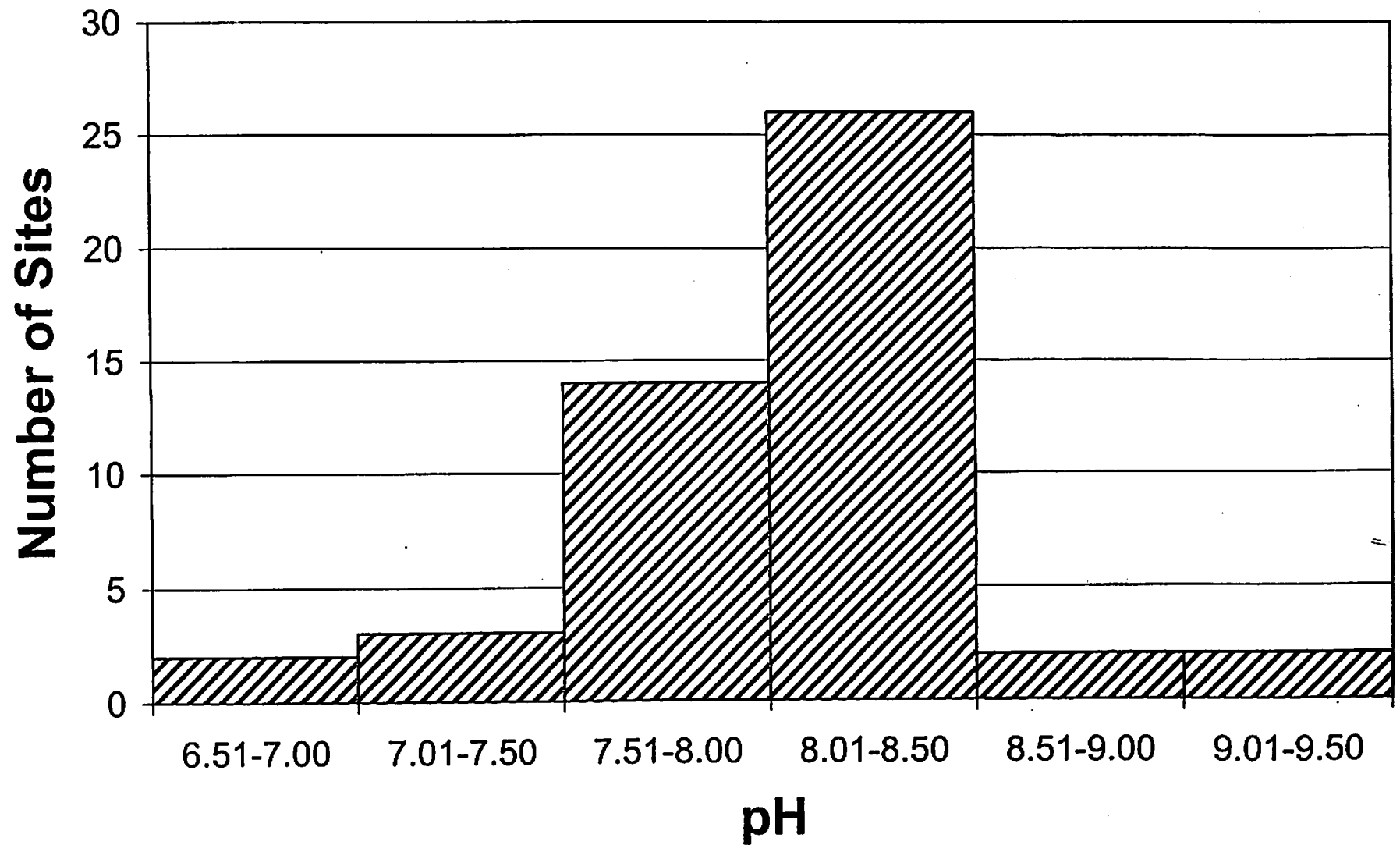


Figure V-7. Water temperature (°C) plotted against elevation of each spring site.

Relationship between elevation and pH

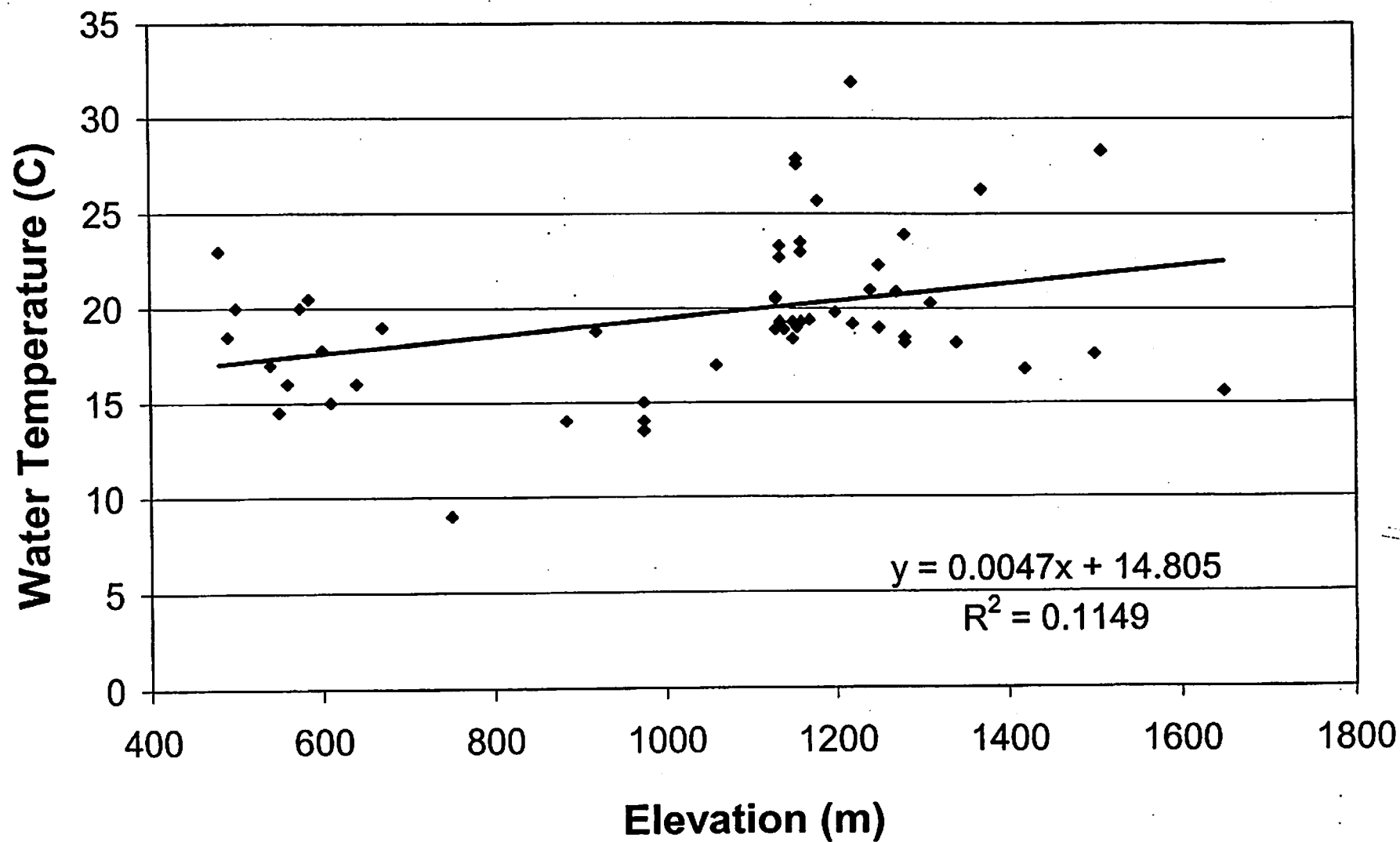


Figure V-8. Spring site water discharge rates are plotted by location along the Colorado River. Because of large differences in discharge, the $\log_{10}$ discharge rate was used.

Spring Discharge

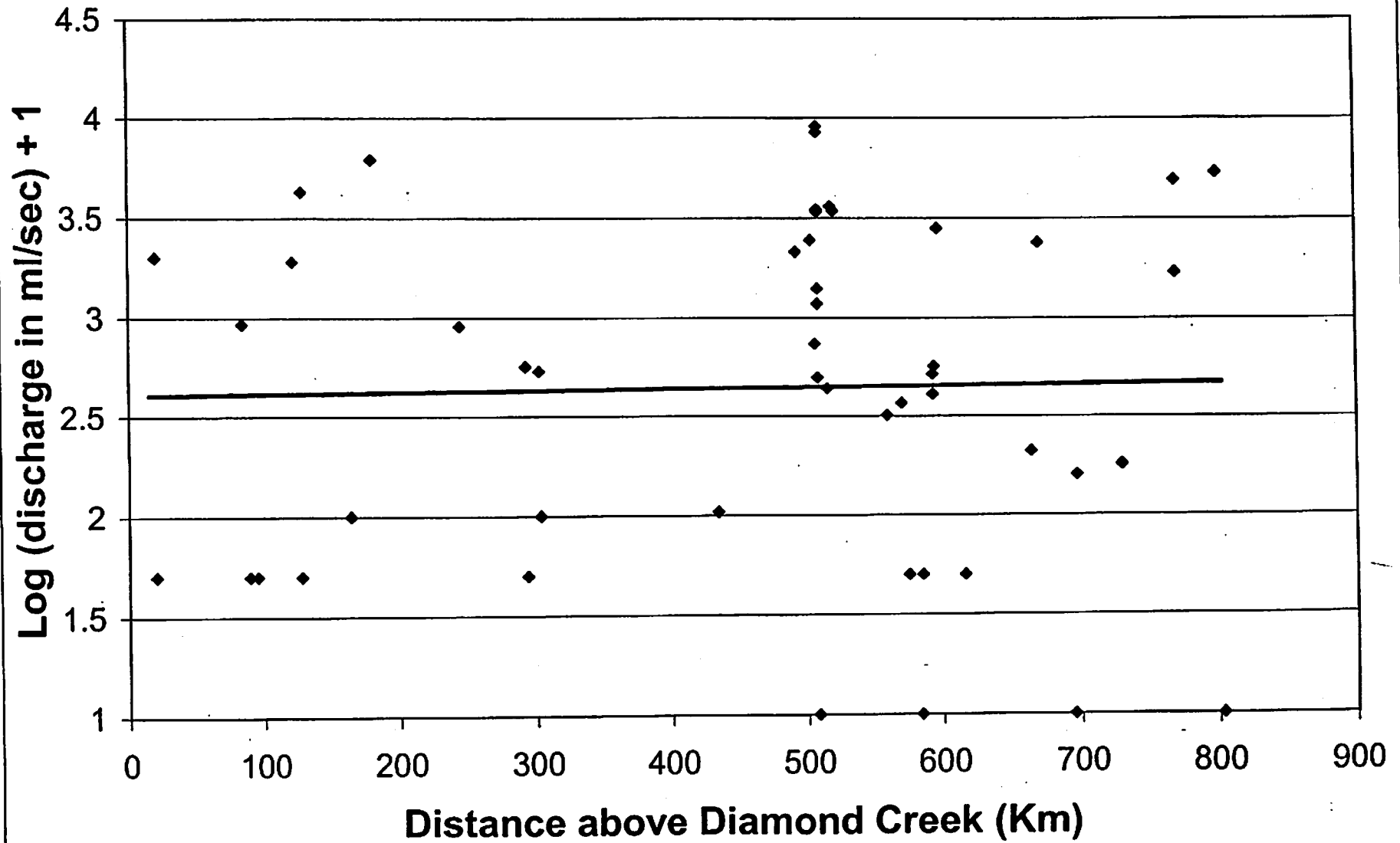


Figure V-9. Detrended correspondence analysis (DCA) ordination of spring water chemistry. The first two axes are shown. The spring site locations are GLCA (P1-23,P51-55), ARCH-CANY (P24-28), GRCA (P29-47).

DCA of water chemistry data

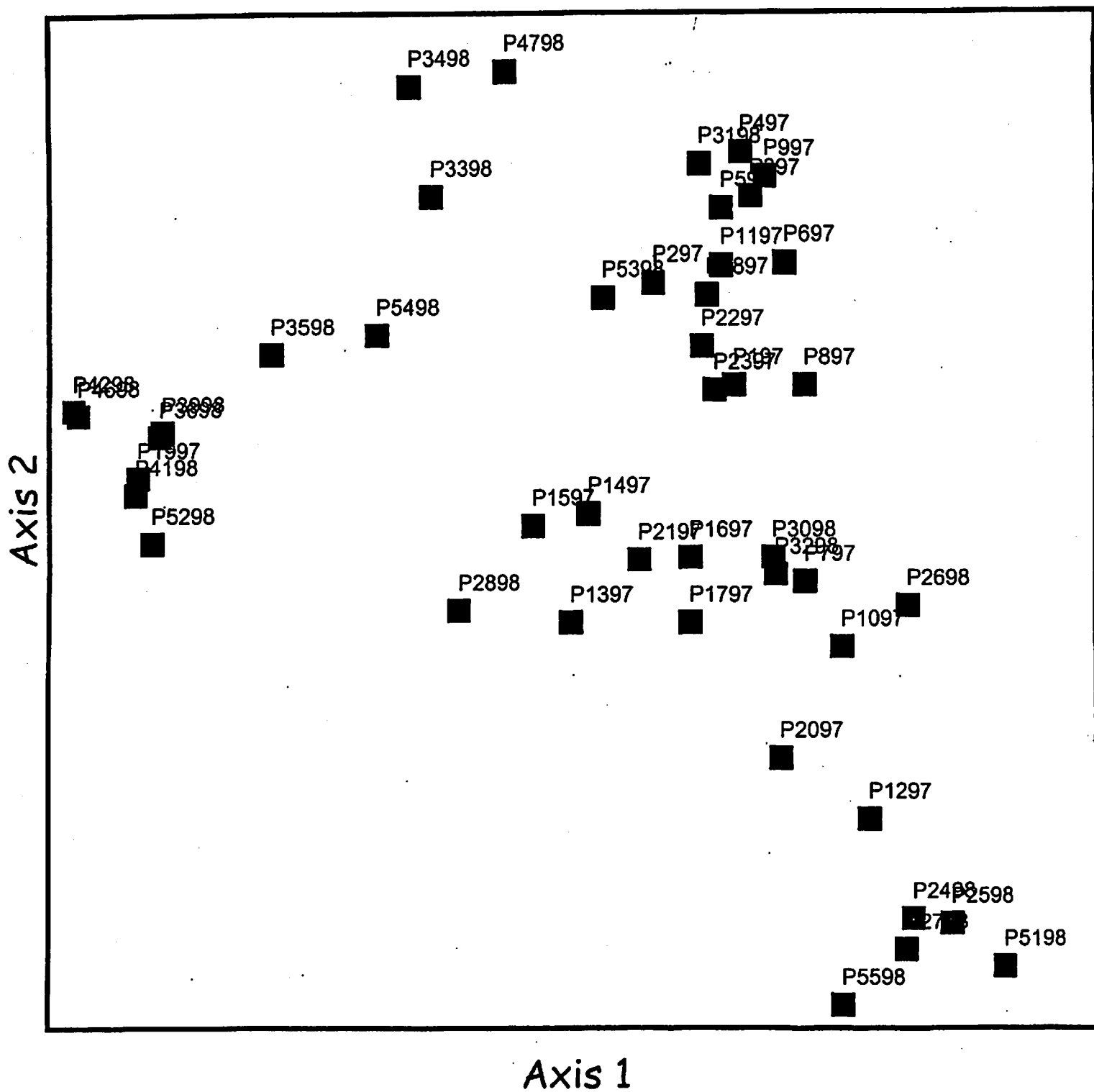
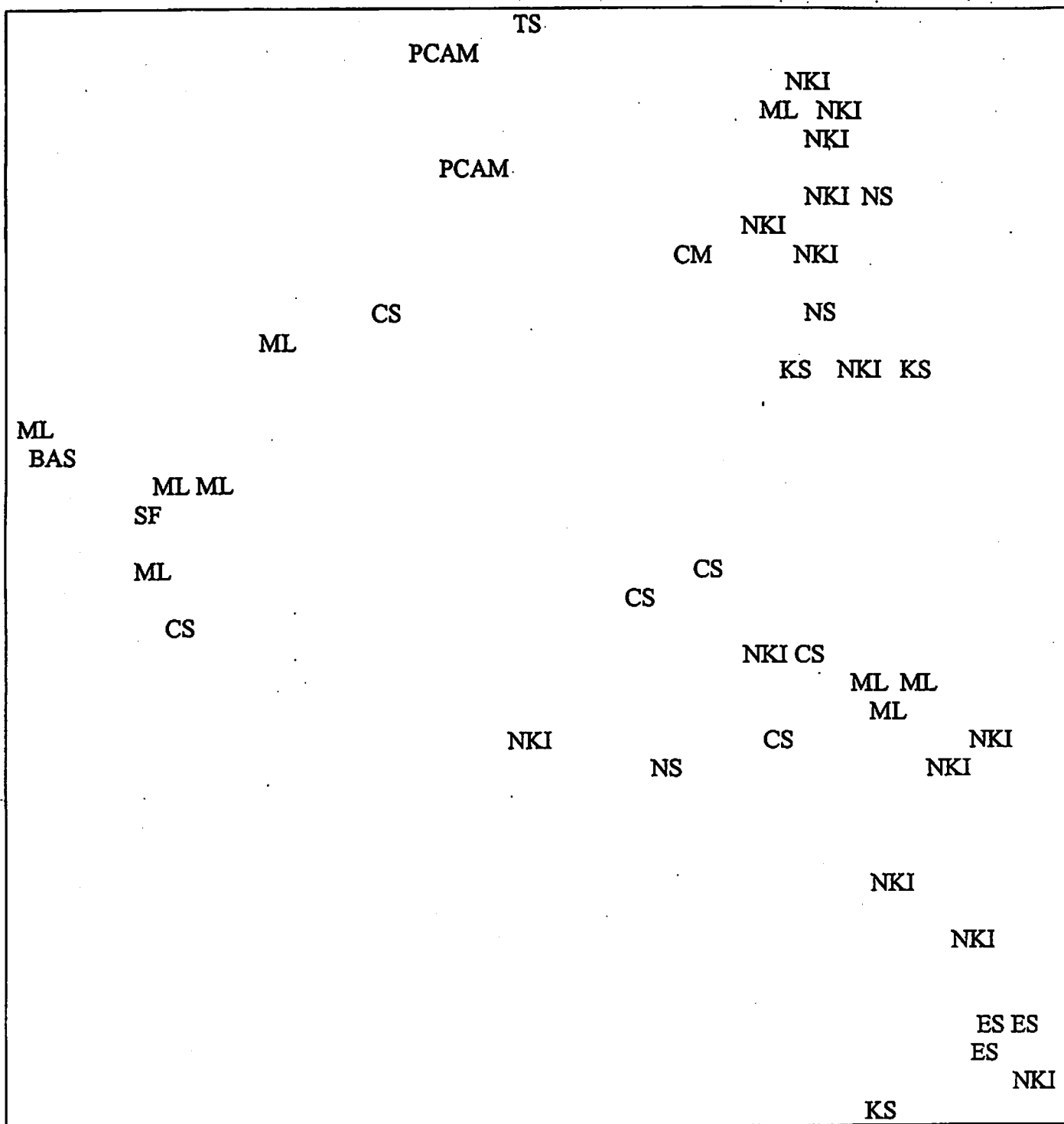


Figure V-10. The results of the water chemistry ordination (Figure V-8) with geology plotted for each spring site. The position of the sites on the first two axes is the same as in Figure V-8. Geological strata are identified by the acronyms BAS=Bass Limestone, CM=Cedar Mesa Sandstone, CS=Chinle Shale, ES=Entrada Sandstone, KS=Kayenta Sandstone, ML=Muvav Limestone, NS=Navajo Sandstone, NKI=Navajo-Kayenta interface, PCAM=Precambrian group, and TS=Tapeats Sandstone.



V.C. AQUATIC INVERTEBRATES

V.C.1. Results

Because of the dynamic nature of invertebrate communities, including great variation in the presence of taxa on daily, monthly and yearly periods, a single visit for one-two hours at a site is unlikely to do more than find the most common species or those that have recently emerged. Additionally, many taxa can occur as either adult or larval stages, and often only one stage is present, causing considerable identification problems. The collections consist of several thousand invertebrates, of which most insect groups were identified to genus level, and a few to species level. Other groups, including annelids, snails, ostracodes and miscellaneous taxa, remain un-identified. It is anticipated that in the future some of these collections will be identified by experts.

In all 140 insect genera in eight orders were collected. Table V-2 shows the breakdown in order, family and genus richness for the three principal portions of the study area. Including non-insect groups, at least 57 families were represented. The collection data by site can be found in Appendix X. The species accumulation curve among sites was fairly steep (Figure V-11), and the calculated jackknife values were 186 genera (first-order) and 211 genera (second-order), suggesting fairly high beta diversity.

Parks with more sites had greater generic richness, as expected. Although richness was greatest in Glen Canyon NRA because of more sites visited, the Grand Canyon region was almost as diverse with only about 56% of the number of sites, and it is likely that richness would have been higher in the Grand Canyon if more sites had been sampled. Generally, sites with the most diverse geomorphology and habitats had the most diverse insect faunas.

In order to examine faunal relationships among sites, an analysis of generic presence/absence was done using cluster analysis. The method chosen for clustering was the flexible beta sorting method, with Sorenson's method as the coefficient of similarity. Flexible beta sorting was chosen primarily because it reduces chaining in the dendrogram compared to other clustering algorithms. The resulting dendrogram is shown in Figure V-12. The percent chaining in this figure was low at 4.1%.

The analysis produced two groups (I-II), a small group of eight sites with similar but highly distinctive faunas, and a large group of the remaining sites. Within the larger group, two additional levels of division are recognized, denoted by groups A, B, and C and terminal groups 1-6. These six groups as well as group II of faunistically similar sites are discussed below. The groups and associated physical site characteristics are summarized in Tables V-2 and V-3.

Group IA1 included seven Glen Canyon sites with fairly strong discharges and associated streams, but lacking in madicolous (backwall) habitats. Only one site had a pool. Some sites had sloping wet slickrock surfaces (R). Most were moderately sunny, and had warm water temperatures and low conductivity. These sites were the most diverse in genera among the sites (mean=16.0). Some sites in this group were in close proximity, including the three springs on the Escalante Arm of Lake Powell, and three springs on the south shore of Good Hope on the lake. Their similar faunas may represent either similar environments or perhaps dispersal between nearby sites. Common genera at the sites included *Paracymus* (Coleoptera), *Caloparyphus* (Diptera), *Dicranota* (Diptera), *Procladius* (Diptera), *Tabanus* (Diptera), *Petrophila* (Lepidoptera), *Hydroptila* (Trichoptera), and *Argia* (Zygoptera).

Group IA2 included low-discharge seeps and springs with pools in alcove sites in Arches NP and Glen Canyon NRA. Some sites may dry out in the summer, except perhaps for the larger pools. There were some minor madicolous habitats present. The sites were moderately sunny with warm water temperatures, fairly high conductivity, and low discharge rates. Mean genus richness was intermediate at 14.7. The coleopteran beetle *Octhebius* was present at all sites. Other representative genera of this group included *Argia* (Zygoptera), *Caloparyphus* (Diptera), *Dasyhelea* (Diptera), *Dicranota* (Diptera), and *Natarsia* (Diptera).

Springs sites with streams and associated pools from Glen Canyon NRA and Canyonlands NP characterized group IB3. There were no madicolous habitats present. Some sites were seeps that may dry out in summer. Sites were primarily sunny except for two, Cave Spring and Cabin Spring, that never saw the sun (0% solar input). Water temperatures were variable, conductivity was moderately low, and discharge rates were mostly low and partly ephemeral. Genus richness was moderately low at a mean of 7.5. Representative genera include *Apsectrotanypus* (Diptera), *Aquarius* (Hemiptera), and *Archilestes* (Zygoptera).

Group IB4 consisted of Grand Canyon springs with streams and pools with well-developed madicolous habitats. Sites were fairly shaded, and had distinctly cool water temperatures (mean=14.9° C), moderately high conductivity, and relatively low discharge rates. Most sites in this group are in either Marble Canyon (Buck Farm, Bert's, and Saddle Canyons) or in the Muav Gorge and upper portions of the Lower Canyon stretches through Grand Canyon (Ledges, Fern Glen and Mohawk Canyon). Sites were relatively rich in genera (mean=15.4). Representative genera include *Baetis* (Ephemeroptera), *Bezzia* (Diptera), *Clinocera* (Diptera), *Microvelia* (Hemiptera), *Ochrotrichia* (Trichoptera), *Tinodes* (Trichoptera), and *Argia* (Zygoptera).

Sites spanning the entire river corridor comprised group IC5, with five from Grand Canyon, two from Glen Canyon, and one from Canyonlands. Sites included simple springs associated with moderately sunny alcoves and madicolous habitats. Water was high in conductivity, temperatures were variable, and discharge rates were low, with many probably ephemeral. Perhaps because of this, these sites were relatively low in diversity, with a mean of 8.6 genera per site. Representative genera of this group included *Tropisternus* (Coleoptera), *Caloparyphus* (Diptera), *Natarsia* (Diptera), *Stratiomys* (Diptera), and *Argia* (Zygoptera).

Two springs with associated streams comprised group IC6. One was in Glen Canyon (Good Hope Bay spring C) and the second in the Grand Canyon (lower Deer creek spring). Both of these sites may have flooded just prior to the site visits, as both were extremely poor in invertebrates, with only two genera collected, *Argia* (Zygoptera) and *Tipula* (Diptera).

Group II consisted of eight sites, seven from Glen Canyon and one from Grand Canyon. They included moderately exposed alcove sites with intermediate levels of radiation, low conductivity, moderately warm water temperatures, and variable but generally high discharge rates with most springs likely to be permanent. Madicolous, pool and stream habitats were present. One site, Slimy Tick Canyon, although grouped with the Glen canyon sites, was very different in most site characteristics. Generic richness was high, with a mean of 15.9 per site. Representative genera for this group included *Acilius* (Coleoptera), *Callibaetis* (Ephemeroptera), *Coenagrion* (Zygoptera), and *Neocorixia* (Hemiptera).

To better understand the relationship between site invertebrate faunas and environment, a detrended correspondence analysis (DCA) was performed. The invertebrate data were first transformed using the Beals smoothing transformation. The ordination is shown in Figure V-13, with the sites plotted on the first two axes. The correlations between the sites on the first two axes and 20 environmental variables are listed in Table V-5. On the first axis, the most strongly correlated variables include elevation, water temperature and conductivity. Sites to the right (e.g., P897, P1097) are at high elevations, have warm water and low conductivity. Sites to the left (e.g., P1497, P4498) are at lower elevations, have cooler water and higher conductivity. On Axis II the most strongly correlated variables include water conductivity, temperature, discharge rates, and summer, August, and September solar radiation. Sites at the bottom on Axis II (e.g., P3598, P3198) have water with low temperatures, high conductivity and low discharge rates, and low levels of radiation during the summer. Sites at the top (e.g., P1597, P1497) have warmer water with low conductivity, high discharge rates and higher summer radiation levels. Overall, the ordination suggest that aquatic invertebrate presence-absence among sites is related to site elevation, water temperature, conductivity and discharge rates, and levels of summer solar radiation. Water pH and levels of winter solar radiation were not strongly correlated with the invertebrate data.

V.C.2. Comments and notes provided by Dr. John McDonald

Because most of the insect taxa could not be identified to species level, relatively little can be said about specific distributions. Another major limitation of the data is that only those species present and common were likely to have been collected. Variables that can influence what species are present include:

- A. Time of year: many species spend long periods of time in a diapausing life cycle stage, including some that may spend months in an egg stage.
- B. Time of day: many species exhibit pronounced circadian activity cycles, often independent of the amount of sunlight, but influenced by heat and dryness.
- C. Time of day: some site sites were sampled in the morning while others were sampled in the afternoon, which can affect what species may be present.
- D. Amount of sunlight: amount of sunlight varies over the day at sites, and this can affect the species seen.
- E. Uneven or clumped distribution of larvae in various substrates. Sampling once for a short period of time may miss such aggregations.
- F. Recent flash flooding: this can drastically affect the invertebrate community as time is required for species to re-colonize.
- G. Skill of the collectors: abilities and techniques can make a difference in what is collected.

With this in mind the above quantitative analyses should be considered suggestive only. Madicolous habitats (seepy backwalls) were one of the more interesting and unusual habitats in the study. In general, two principal groups of springs, sites in shaded wetter canyons, and sites in exposed, sunny and drier canyons. The fauna associated with these two types were different. Shaded wet sites tended to have species in the families Empididae (Diptera) as well as various Trichoptera. Drier sunnier sites tended to have species of the Stratiomyidae (Diptera). Some genera were widespread throughout the study area, including *Callibaetis* larvae, *Argia* larvae, *Microvelia* adults, Stratiomyid larvae, and various Chironomid larvae. Species of aquatic Coleoptera were common at many sunnier sites, including species

in the families Dytiscidae and Hydrophilidae. Also common were larvae of Hydroptilidae (Zygoptera). Diptera were particularly common and widespread. At least 24 genera of Chironomidae and 11 genera of Tipulidae were collected, but most sites tended to support only a few genera. Adult *Clinocera* (Empididae) were found at all shaded madicolous habitats in the Grand Canyon. Larve of either *Pericoma* or *Telmatoscopus* (Psychodidae) and Stratiomyidae were also found at almost all sites.

New or interesting species included the following:

1. The Hemipteran *Ochterus* sp. was found at three sites in the Grand Canyon (Bert's Canyon, Hance Rapid Spring and Elves Chasm). This is an eastern species that reaches west to Texas. It has been reported once before from the Grand Canyon.
2. *Asymphyloptera* sp. (Empididae, Diptera) is a Neotropical genus, with one species recorded from Arizona. The collections from the Grand Canyon (Saddle Canyon, Elves Chasm, and Fern Glen) may represent a second undescribed species.
3. Five species of the genus *Clinocera* (Empididae, Diptera) were collected, of which three are new to science. These species occurred in deeply shaded cool madicolous sites in the Grand Canyon (Bert's Canyon, Elves Chasm, and Fern Glen).
4. A species of *Wiedemannia* (Empididae) new to science was collected at Vasey's Paradise in the Grand Canyon.
5. A freshwater sponge (Hydrozoa) was collected from the permanent plunge pool at the Rana Canyon site in Glen Canyon.

Some invertebrate collections from the study have not been examined by experts yet. In particular, numerous collections of snails were made, and the potential for new finds is good. The snail collections will be examined by Dr. Larry Stevens in 2002.

Table V-2. Summary of aquatic invertebrates collected from 45 springs in Arches National Park (ARCH), Canyonlands National Park (CANY), Glen Canyon National Recreation Area (GLCA), and Grand Canyon National Park (GRCA).

PARK	NUMBER OF SITES	ORDERS¹	FAMILIES²	GENERA³
ARCH-CANY	5	7	25	54
GLCA	27	9	46	101
GRCA	15	8	36	87
Totals	47	9	57	140

¹Insect orders only

²Includes non-insect invertebrate families (e.g., Acarina, Amphipoda, Arachnoidea, Collembola, Oligochaeta, Bsammatomophora, Ostracoda).

³Insect genera only

Table V-3. Summary of groups formed by a cluster analysis of genera of aquatic invertebrates at 45 springs. Sorenson's coefficient of similarity was used, with the flexible beta algorithm ($\beta=-0.25$).

GROUP	INVERTEBRATE HABITATS	NUMBER OF GENERA	SITE CHARACTERISTICS AND GEOMORPHOLOGY
IA1	S, ST (P2)	16.4	S,DR,DB rocky and simple springs with moderate discharge streams in GLCA
IA2	P2 (ST,S)	14.7	B,D,P,SR,S mix of simple low discharge or ephemeral springs and alcove sites with streams and pools in ARCH and GLCA
IB3	P2,S,ST (SP)	7.5	B,D,P,S low discharge or ephemeral alcoves and simple springs with pools, one cave site, in CANY and GLCA
IB4	P2,S,ST,SP (P1)	15.4	B,D,S moderate discharge seepy walls and slopes with pools in canyons in GRCA
IC5	S (P2,SP)	8.6	B,D,P,DR,S low discharge or ephemeral simple springs in alcoves with some hanging gardens in CANY, GLCA and GRCA
IC6	ST	1.5	S moderate discharge permanent streams in GLCA and GRCA
II	P2, S (ST)	15.9	B,D,P complex alcove sites with moderate permanent discharge

Table V-4. Environmental variables associated with the seven groups of invertebrate genera defined by the cluster analysis (Figure V-11).

Group	Solar Input (%)	PH	Conductivity (μS)	Water Temperature (°C)	Discharge (ml/sec)	Number of Genera
IA1	53	7.8	265	20.0	575	16.4
IA2	59	8.2	462	22.7	98	14.7
IB3	52	7.9	300	20.3	94	7.5
IB4	31	7.9	1,122	14.8	127	15.4
IC5	57	8.0	1,105	21.1	92	8.6
IC6	63	8.3	230	22.1	-	1.5
II	50	8.0	187	21.0	280	15.9

Table V-5. Kendall rank correlations between 45 spring site invertebrate faunas on the first two axes of a DCA ordination and site environmental variables. Variables with correlations of 0.200 or better or bolded.

Environmental variable	DCA Axis I	DCA Axis II
Site Elevation	0.344	0.183
Water pH	0.064	-0.153
Water conductivity	-0.198	-0.351
Water temperature	0.246	0.246
Spring discharge	0.007	0.204
Solar radiation input		
January	0.106	0.085
February	0.068	0.123
March	-0.005	0.214
April	-0.061	0.196
May	-0.110	0.180
June	-0.138	0.184
July	-0.137	0.183
August	-0.098	0.201
September	-0.005	0.225
October	0.081	0.155
November	0.100	0.076
December	0.122	0.071
Summer	-0.091	0.214
Winter	0.074	0.130
Year	0.020	0.185

Figure V-11. Genus accumulation curve for the 45 spring at which aquatic invertebrates were collected.

Genus-Accumulation Curve

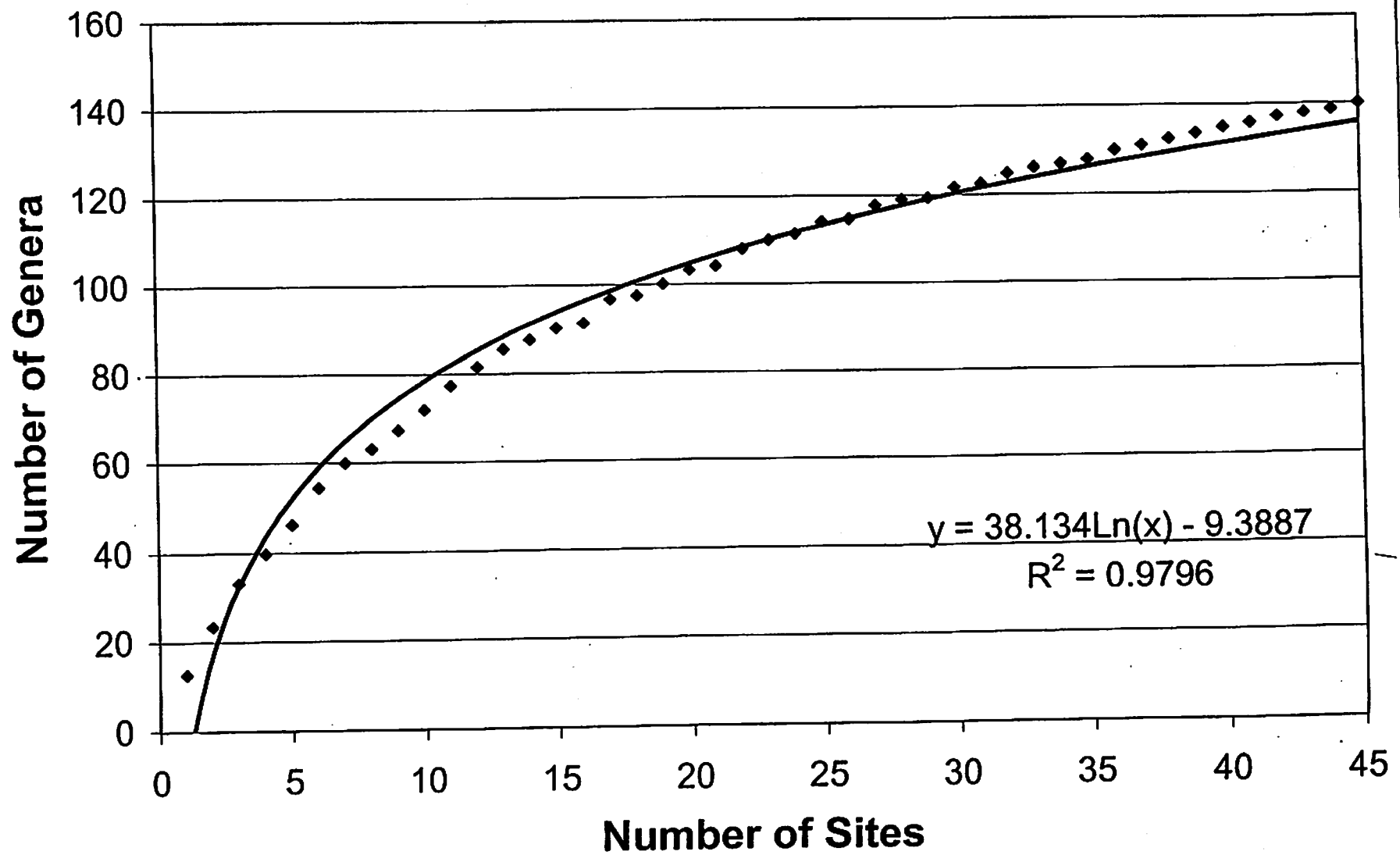


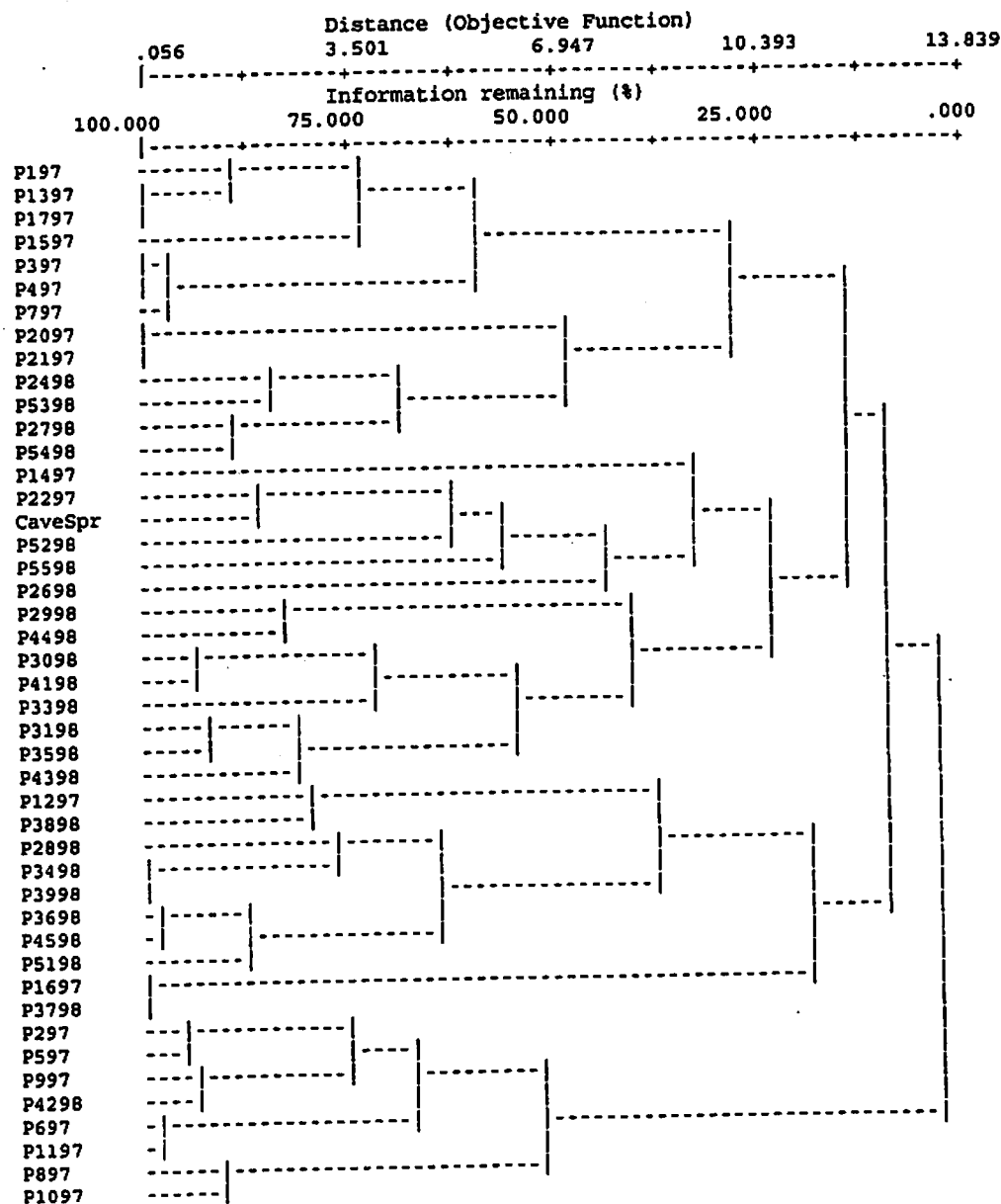
Figure V-12. Cluster analysis of the invertebrate genera among the 45 springs. The clustering algorithm was beta flexible sorting ($\beta=-0.25$) with Sorenson's coefficient of similarity. The spring locations are GLCA (P1-23,P51-55), ARCH-CANY (P24-28), GRCA (P29-45).

***** CLUSTER ANALYSIS: SORESENSEN DISTANCE , FLEXIBLE BETA *****
 PC-ORD, Version 3.17
 2 Apr 2001, 15:37

Cluster Analysis of aquatic invertebrate data

Flexible beta value selected is -.250

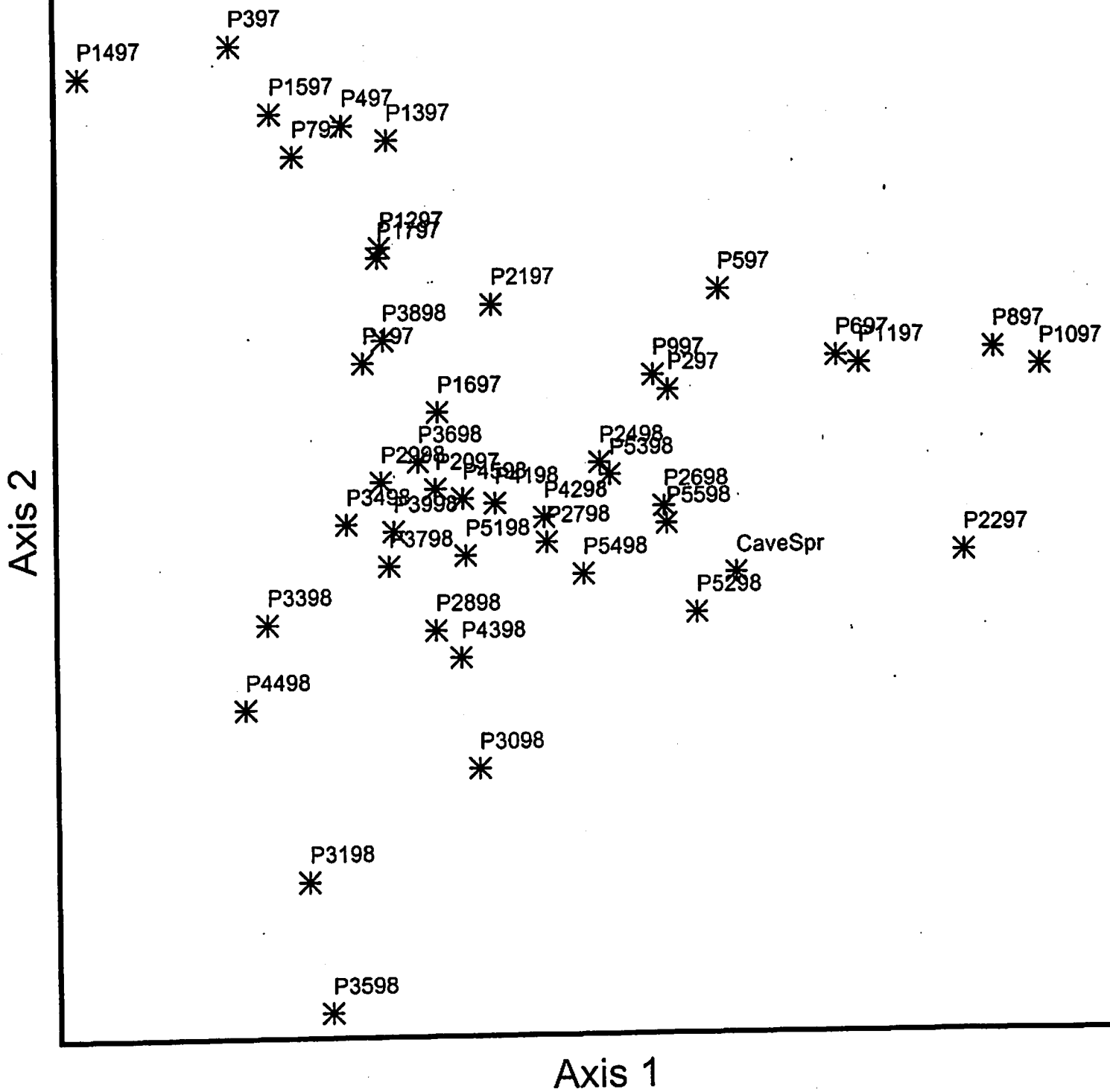
Percent chaining = 4.09



***** Cluster analysis completed *****

Figure V-13. Detrended correspondence analysis (DCA) ordination of the invertebrate genera at 45 springs. The data were first transformed using the Beal's smoothing transformation. The first two axes are plotted. Site locations are Glen Canyon NRA (P1-23, P51-55), Arches and Canyonlands NP's (P24-28), and Grand Canyon NP (P29-45).

DCA of aquatic invertebrate data



V.D. FLORA

V.D.1. Floristics

In the study area, 125 species of obligate native wetland and riparian species were recorded. Number of plots per species is plotted in intervals in Figure V-14. The most widely distributed species (number of sites) were *Adiantum capillus-veneris* (43 plots), *Epipactus gigantea* (37), *Brickellia longifolia* (29), *Phragmites australis* (29), *Solidago velutina* (28), and *Rhamnus betulifolia* (27). There were 34 species that occurred at a single plot or site, and 14 additional species found at only two plots or sites. Species richness among sites ranged from 6 to 34, with a mean richness of 12 species per plot. Large complex hanging gardens tended to be the richest, while springs with associated riparian woodlands tended to be the least rich. Among the three regions, Glen Canyon sites supported 89 species, Grand Canyon 82 species, and Arches-Canyonlands 50 species.

V.D.2. Origins and Distributions

Tables V-6 and V-7 summarize the distribution of the species among six groups of presumed origin and six current distribution patterns. The majority of the riparian and wetland flora has temperate, Madrean or boreal affinities, with relatively few species of western (autochthonous), cosmopolitan (unknown) and tropical origins. Turning to current distributions, the southwestern element is the largest, with 40 species (33% of the flora), followed by temperate-widespread North American species (25%) and widespread western North American species (16%). The Colorado Plateau endemic element comprises 12 species (10%). The current distributions of four taxa not identified to species level could not be determined.

V.D.3. Pollination Syndromes

Presumed pollination modes include four main types, animal (predominantly insect), water, wind, and selfing. The majority of the dicot flora consists of insect pollinated species, although some species with red flowers (e.g., *Aquilegia*, *Castilleja*, *Lobelia*, *Mimulus*) may also be hummingbird pollinated. A small group of six species may be primarily selfers, including *Hutchinsia procumbens*, *Parietaria pennsylvanica*, and *Viola nephrophylla*. A second small group of seven species are primarily water-pollinated, such as *Potamogeton foliosus*, *P. natans*, *Polygonum amphibium*, and *Zannichellia palustris*. A large group of species, including grasses, sedges and rushes and their allies, are primarily wind pollinated. Table V-8 summarizes pollination syndromes of the spring flora.

V.D.4. Dispersal Ecology

Dispersal types for the 125 species of wetland and riparian species is summarized in Table V-9. The most common dispersal type, smooth (44% of total), are for species that lack any specialized dispersal mechanisms. The second most common type, miniwind (20%) consists of species with plumes, pappuses, awns or large volume to weight ratios that may confer advantage in getting seeds and fruits dispersed away from the parent plants. Among specialized dispersal mechanisms, the most common in the flora is fleshy fruits that are attracted to animals, primarily birds. Representative genera include *Parthenocissus*, *Rhamnus*, *Rhus* and *Vitis*. *Quercus gambelii*, with its large nut, is included in this group as well. Other specialized mechanisms, including megawind, sticktight and floater groups, are not

common in the total flora. All specialized types (excluding smooth and miniwind), account for 36% of the flora.

V.D.5. Growth Forms and Vegetative Persistence

A majority of the riparian and wetland flora is herbaceous (74%) and perennial (93%). A breakdown into six growth forms is found in Table V-10. Perennial forbs are best represented, followed by perennial graminoids and trees/shrubs. Relatively few species are annuals, perennial aquatic forbs, or vines. Vegetative spread via rhizomes and stolons is relatively common, with 46% of the flora able to propagate vegetatively.

V.D.6. Exotic Species

Nineteen species of exotic plants were recorded among the sites. Glen Canyon had the most species, with 14, followed by Arches-Canyonlands with 11 species and Grand Canyon with seven species. The most widespread species were *Agrostis semiverticillata*, *A. stolonifera*, *Polypogon monspeliensis*, *Sonchus asper*, and *Tamarix ramosissima*. Relatively few species were common, and the mean number of sites per species was 2.9 for Glen Canyon, 3.1 for Grand Canyon, and 1.5 for Arches-Canyonlands. Tamarisk was the most widely distributed species, occurring at 22 sites. Several potentially invasive exotics, including bindweed (*Convolvulus arvensis*), Russian olive (*Elaeagnus angustifolia*), and cocklebur (*Xanthium strumarium*), were rare and limited to one or two sites in low abundance. None of the exotics was dominant at any of the sites where they were found.

V.D.7. Species Richness Estimates

Species richness was determined for both geographic areas as well as habitats within sites. Overall Glen Canyon sites were most diverse, while Arches and Canyonlands sites were least diverse. The first order jackknife estimates suggest that the observed riparian and wetland flora represented only 76-84% of the total flora. In particular, the data in Table V-11 suggests that Grand Canyon, Arches and Canyonlands sites were under-sampled by >20% for flora. The total observed flora, 125 species, is estimated to represent 79% of the actual flora expected among the sites. Richness also varied considerably between habitats (Table V-12). Colluvial slopes associated with alcoves and hanging garden sites were the most diverse, while riparian-like woodlands were the least diverse. The first-order jackknife estimates suggest that the four principal environments were under-sampled by 10-17%.

V.D.8 Colorado Plateau Endemics

A small group of about 20 species of vascular plants are endemic to the Colorado Plateau and restricted to wet sites (Spence 2002a). Of these, 11 (possibly 12 if the *Carex* in Grand Canyon is *C. specuicola*) were collected or seen during this study (10% of total flora). Six of the remaining species are endemic to Zion national Park. Only two endemics were not found in this study, *Erigeron kachinensis* and *Phacelia indecora*. Table V-13 summarizes their ecology, distribution, closest presumed relatives and probable origins. Most of the endemics are associated with hanging garden environments, in particular the wetter colluvial slopes and backwalls. On these substrates some endemics, such as *Aquilegia micrantha*, *Carex curatorum* or *Cirsium rydbergii*, are often dominant species. A more detailed analysis

of the distributions and origins of these species can be found in Spence (2002a). Most are of northern or boreal-temperate origins rather than of cosmopolitan or Madrean origins.

V.D.9 Relictual and Disjunct Species

Relictual species are those that either, 1) occur at much higher elevations on the Colorado Plateau but then re-appear in low elevations in association with shaded cool canyons and springs, 2) are disjunct from their centers of abundance and distribution, or 3) are found typically at lower elevations but also in scattered populations at much higher elevations in the study area. A good example of a relict is the grass *Calamagrostis scopulorum*, a mountain species that is widespread in low elevation hanging gardens on the Colorado Plateau. Others include *Carex rossii*, *Rosa woodsii*, *Sisyrinchium demissum*, and *Rubus neomexicanus*. In all 17 species (14% of total flora) in the study are considered to be relictual in the region, not including the lower Grand Canyon. For example, *Cladium californicum* is a common species in the Grand Canyon, but occurs in about 10 small populations around Lake Powell. Most of these species are relicts from periods when the climate was cooler and wetter than at present (the late Pleistocene), although a few Sonoran species are probably relictual from times when it was warmer than at present. The origins of these patterns have been analyzed in more detail in Spence (1995, 2002a).

V.D.10 Bryophytes

Bryophyte species richness at springs varied from none to 10+ species. The appendix lists all species identified to date, including 30 species. Some collections remain to be identified to species, and it is likely that species diversity will increase as they are completed. Mosses were most common, while liverworts were relatively rare. On backwalls, the most common species were primarily acrocarps in the family Pottiaceae, especially *Eucladium verticillatum*, *Hymenostylium recurvirostrum*, and *Didymodon tophaceus*. *Amblystegium serpens* and *A. riparium* were common pleurocarpous mosses. *Philonotis fontana* and *Brachythecium frigidum* were common on wet soil and mud around the edges of plunge pools and along stream channels. Liverworts identified to date include *Marchantia polymorpha* and *Pellia neesiana*.

V.D.11 Discussion

The 125 native species of phreatophytes documented in this study represents about 40% of the 300 or so species (Spence, unpublished) that occur below 1800 meters on the Colorado Plateau. Site richness varied between 6-35 species, with the richest springs in Glen Canyon NRA and Arches NP. Particularly species-rich were springs associated with hanging gardens in large alcove settings. Overall, Glen Canyon springs were slightly more species-rich compared with the other three parks. Backwalls were floristically the most distinctive, with a variety of characteristic and often endemic species, including *Adiantum capillus-veneris*, *Aquilegia micrantha*, *Calamagrostis scopulorum*, *Carex curatorum*, *Flaveria macdougalii*, *Mimulus eastwoodiae*, *Petrophytum caespitosum*, and *Zigadenus vaginatus*. Colluvial slopes were the most species-rich, as they include a variety of herbaceous species as well as riparian-like woodlands. Woodlands and wetlands associated with plunge pools were the least floristically rich. Jackknife estimates suggest that the total flora at the springs sampled is approximately 160 species. This richness estimate reflects the generally high beta diversity (turnover in species composition) among springs along the Colorado River. A remarkable result of this study is that different geomorphic types (e.g., backwalls, colluvial slopes) can support strongly different floras in the same alcove or spring.

Wong (1999) compared her hanging garden flora with data from this study, and showed that some springs in Zion NP were clustered with sites in Glen Canyon as well as the Grand Canyon, rather than with other Zion sites. This study has shown that the same geomorphic types in different springs and parks often show stronger floristic and vegetation composition than different types at the same site. Reasons for this are unclear, but may be a result of one or two mechanisms. Species assemblages may be relictual from cooler and wetter times in the past, with the environmental features of each site sorting out the suite of species that survives, or species may be widely and easily dispersed. The second hypothesis is not well supported by an analysis of dispersal mechanisms, as 64% of the species lacked specialized features (Table V-9). Elsewhere (Spence 2002a), I analyzed these hypotheses in greater detail and suggested that the relictual-environmental sorting hypothesis is better supported. It remains a remarkable fact that, for example, the backwall at Rana Canyon on the Escalante River in Glen Canyon (GLCA11-97), is floristically and structurally most similar to the backwall at Sleepy Hollow in Arches (ARCH03-98), despite a distance of >200 km.

The majority of the indigenous species are of either boreal, southwestern (Madrean) or temperate origins, and either temperate-widespread or southwestern in distribution. Despite the proximity of the Colorado Plateau and Colorado River to the southern Rocky Mountains, the spring flora shows very little influence of the Rocky Mountain floristic region (5%). The endemic element, species that are restricted to the Colorado Plateau, comprised 10% of the flora, although the majority of species were found in the higher elevation sites in Glen Canyon, and Arches and Canyonlands. Grand Canyon only had four endemic species, compared with nine in Glen Canyon and five in Arches and Canyonlands. Elsewhere, I have pointed out (Spence 2002a), that endemics are most common in the higher elevation sandstone-derived springs of the eastern Colorado Plateau, in particular in Arches and Canyonlands, and Natural Bridges NM. The relatively small sample size from the first two of these parks is probably the main reason why relatively few endemics were found.

Most species were either woody plants, perennial forbs, or perennial graminoids. Very few annual, aquatic, and vine growth forms occurred. The majority of the flora was also either wind or animal pollinated, with very few water or self pollinated species. In all, 36% of the flora showed some type of specialized long-distance dispersal mechanism (excluding the miniwind category), primarily of wind or animal dispersal types. Relatively little published work from other floras or areas on the Colorado Plateau exist to compare with the results of this study. Three studies that are available include Malanson and Kay (1980), Harper *et al.* (1992) and Spence and Henderson (1993). Malanson and Kay (1980) showed that in gardens along the Virgin River in Zion NP species with good dispersal abilities were significantly over-represented in flood-prone gardens compared with less flood-prone gardens. In a study of the riparian flora of Zion NP, Harper *et al.* (1992) classified the principal riparian species by dispersal and pollination type. Unlike this study, the majority of the widespread riparian species in Zion NP showed various adaptations through specialized dispersal and pollination mechanisms, primarily by wind and animals. Since rarer phreatophytes were not included in their analysis, it is not a complete treatment and is difficult to compare with this study. Spence and Henderson (1993) examined the dispersal mechanisms of 45 riparian species at hanging gardens and tinajas in southern Capitol Reef NP. The riparian flora was dominated by species lacking specialized long-distance mechanisms (64%) compared with those exhibiting specialized long-distance mechanisms (36%). These results are very similar to the current study, except for a much higher proportion of species in the megawind (eg., spores, dust seeds) category (27%) in the Capitol Reef study compared with this study (10%). This was attributed primarily to the scattered and strongly isolated study sites, most of which were highly

disturbed by flooding. Willson et al. (1990) point out that, depending on vegetation type and continent, the percentage of a temperate site flora that lacks any obvious form of dispersal mechanism (smooth in the present study), ranges between 20-50%. In the current study, 44% of the phreatophyte flora lacks these features, which is towards the high end for temperate floras.

Species with small wind-dispersed seeds or spores (the megawind category), however, were generally more widespread than species with other categories. The two most widespread species in the study were *Adiantum capillus-veneris* and *Epipactus gigantea*. The fern disperses via spores and the orchid via "dust" seeds. However, Spence (2002a) analyzed the distribution (number of sites) of 76 species that were largely restricted to springs and hanging gardens (i.e., non-riparian species) and found no significant departure from expectation towards more long-distance dispersed species.

Bryophytes show relatively widespread distributions within the study area, with some species found at all elevations in suitable habitat. Because they can disperse via spores, most bryophyte species tend to be widespread. Their absence at sites is more likely to reflect a lack of suitable micro-environmental conditions that are necessary for establishment and persistence.

Table V-6. Distributions and presumed origins of 125 riparian and wetland species associated with springs and seeps in the study area. The current distributions of four species could not be determined.

Probable Origin	Number of Species	Percent of Flora	Current Distributions	Number of Species	Percent of Flora
Boreal	23	18	Boreal-Temperate	14	12
Cosmopolitan	8	6	Endemic	12	10
Madrean	25	20	Rocky Mountains	5	4
Temperate	49	40	Southwestern	40	33
Tropical	12	10	Temperate-widespread	30	25
Western NA	8	6	Western-widespread	20	16
Totals	125	100	Totals	121	100

Table V-7. The current distributions of 121 native species in three regions in the study area.

Current Distribution	Glen Canyon	Arches-Canyonlands	Grand Canyon
Boreal-temperate	14	8	6
Widespread temperate	27	14	21
Widespread w. NA	17	11	10
Colorado Plateau	9	5	4
Rocky Mountain	4	3	4
Southwestern	18	9	37
Totals	89	50	82

Table V-8. Pollination syndromes of 125 riparian and wetland species associated with springs and seeps in the study area.

Pollination Syndrome	Number of Species	Percent of Flora
Animal pollinated	68	54
Wind pollinated	44	35
Water pollinated	7	6
Self pollinated	6	5
Totals	125	100

Table V-9. Dispersal mechanisms among the 125 riparian and wetland species associated with springs and seeps in the study area.

Dispersal Mechanism	Number of Species	Percent of Flora
Smooth	55	44
Miniwind	25	20
Megawind	12	10
Fleshy Fruits/Nuts	16	12
Sticktights	12	10
Floaters	5	4
Totals	125	100

Table V-10. Growth forms among the 125 riparian and wetland species associated with springs and seeps in the study area.

Growth Form	Number of Species	Percent of Flora
Annuals	9	7
Aquatics	3	2
Forbs	42	34
Graminoids	33	26
Vines	6	5
Trees/Shrubs	32	26
Totals	125	100

Table V-11. Species richness estimates by region of the 125 riparian and wetland species associated with springs and seeps in the study area. Expected species number is based on the first-order Jackknife estimate. The mean Shannon diversity index for each park is also listed.

Region	Observed Species	Expected Species	Percent of Total (Observed/Expected)	Richness per Site	Diversity per Site
GLCA	73	87	84%	13.0	2.41
GRCA	81	107	76%	11.6	2.29
ARCH-CANY	48	62	77%	11.0	2.16
Total Flora	125	159	79%	12.1	2.33

Table V-12. Species richness estimates by principal habitats of the 125 riparian and wetland species associated with springs and seeps in the study area. Expected species number is based on the first-order Jackknife estimate. The mean species richness and Shannon diversity index for each habitat is also listed.

Habitat	Observed Species	Expected Species	Percent of Total (Observed/Expected)	Richness per Site	Diversity per Site
Backwalls	58	79	73%	8.8	2.00
Colluvial Slopes	97	121	80%	15.3	2.61
Marshlands	59	81	73%	12.4	2.40
Riparian Woodlands	49	64	77%	11.5	2.28

Table V-13. The twelve Colorado Plateau endemic vascular plant species found during the study. Information on ecology, distribution, closest relatives and probable origin are included.

Species	Ecology ¹	Distribution	Presumed Congener ²	Probable Origin ³
<i>Aquilegia micrantha</i>	hgw	ARCH,CANY,GLCA	<i>A. flavescens</i>	BT
<i>Carex curatorum</i>	hgw, rip	ARCH,CANY,GLCA,GRCA	<i>C. scirpoidea</i>	BT
<i>C. cf. specuicola</i>	hgw	GLCA,GRCA	<i>C. aurea</i>	BT
<i>Cirsium rydbergii</i>	hgw	ARCH,CANY,GLCA	<i>C. calcareum?</i>	BT
<i>Cirsium sp. Nov.</i>	hgw	GRCA	<i>C. virginense?</i>	BT
<i>Flaveria macdougallii</i>	hgw	GRCA	<i>F. sonorensis</i>	Madrean
<i>Mimulus eastwoodiae</i>	hgw	ARCH,CANY,GLCA	<i>M. guttatus</i> group	BT
<i>Perityle specuicola</i>	hgd	ARCH,CANY,GLCA	<i>P. tenella</i>	Madrean
<i>Platanthera zothecina</i>	hgw, rip	ARCH,CANY,GLCA	<i>P. sparsiflora</i>	BT
<i>Primula specuicola</i>	hgw	ARCH,CANY,GLCA	<i>P. mistassinica</i>	BT
<i>Yucca toftiae</i>	hgd, rip	GLCA	<i>Y. angustissima</i>	Madrean
<i>Zigadenus vaginatus</i>	hgw	ARCH,CANY,GLCA	<i>Z. volcanicus</i>	Madrean

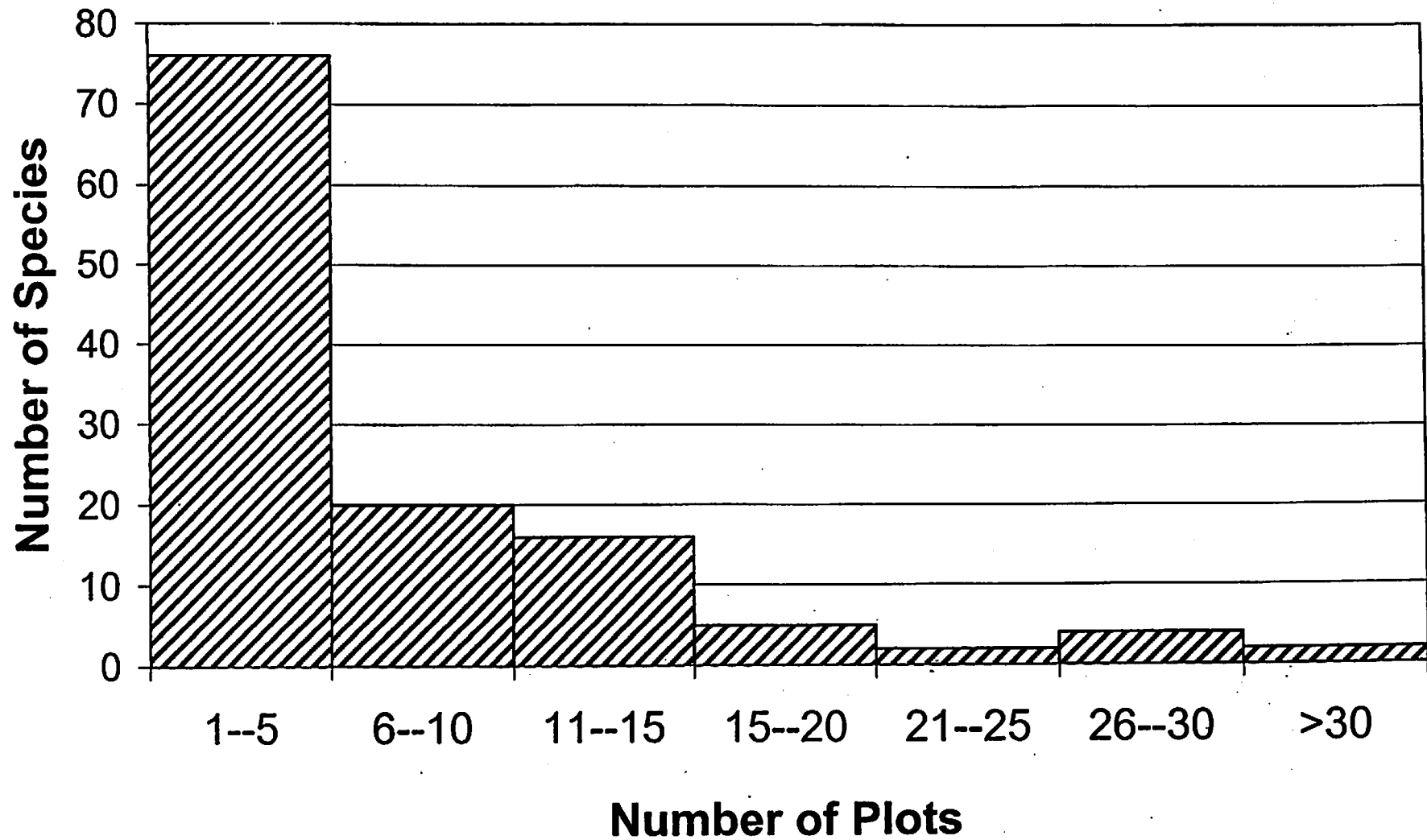
¹hgw=hanging garden wet, hgd=hanging garden dry, rip=riparian

²Presumed closest species, a ? indicates the assignment is tentative

³BT=boreal-temperate, Madrean=southwestern US-Mexico

Figure V-14. The distribution of the 125 native species at 90 plots among the 55 spring sites.

Species distribution among plots



V.E. VEGETATION

V.E.1. Community Analyses and Vegetation Structure

A combination of ordination, TWINSpan and classification techniques was used to analyze vegetation structure. The total number of plots for the analyses was 90, because many springs had two or more different types of sampled geomorphic units present. Four major groups of sites were revealed, corresponding to hanging garden backwalls, hanging garden colluvial slopes, wetlands dominated by species like *Phragmites australis* and *Typha domingensis*, and riparian-like woodlands. The last two groups overlapped in floristic composition and vegetation structure, and were combined for subsequent ordinations. Different geomorphic units within a spring site grouped with similar geomorphic units at other sites rather than with different units at the same spring, indicating strong within-site differentiation. For example, the backwall at site GLCA10-97, Rana Canyon hanging garden, was grouped with backwall sites from Glen Canyon, Canyonlands, and Arches, rather than with other sampled units at the site. The floristically and structurally most similar site to the Rana Canyon backwall was the backwall at site ARCH03-98, Sleepy Hollow alcove, in Arches NP. The two springs are separated by a distance of >200 km. Descriptions and common species for each of the four vegetation types can be found in Table V-14.

The principal groupings of vegetation types are shown in Figure V-15. Six major groups of plots, indicated as A-F, resulted from a cluster analysis using Euclidean Distance and Ward's flexible sorting algorithm. The dissimilarity in vegetation structure between clusters increases from right to left. The first division (1) of plots separates Grand Canyon backwalls and colluvial slopes from Colorado Plateau and all wetlands and riparian-like woodlands, including those from the Grand Canyon. The second division separates Colorado Plateau backwall vegetation (A) from all other types (B-C). The third major division separates Glen Canyon colluvial slopes and sloping slickrock springs (D) from the remaining springs and plunge pool wetlands (B-C). The fourth division separates Marble Canyon sites from lower Grand Canyon sites. The final fifth division separates Colorado Plateau simple springs and plunge pool wetlands from Grand Canyon springs and plunge pool wetlands. In order of separation, division 1 segregates Grand Canyon hanging gardens and associated colluvial slopes from all other plots, division 2 is primarily related to differences between Colorado Plateau hanging garden backwalls and other types of vegetation, division 3 separates wetland and riparian woodland vegetation from Glen Canyon hanging garden colluvial slopes, division 4 differentiates sites in Marble Canyon from lower Grand canyon, and division 5 separates Grand Canyon wetlands and woodlands from Colorado Plateau wetlands and woodlands. The two principal factors segregating sites are elevation (geography) and the presence or absence of hanging garden backwalls.

V.E.2. Relationships with Physical Environment

Relationships between vegetation structure and physical site data were explored using non-metric dimensional scaling (NMS) ordinations. Three separate analyses were done on backwalls, colluvial slopes, and combined wetland and riparian woodlands. A secondary matrix of site physical data was then projected onto the ordinations, and Kendall correlations were computed between the physical site data and the first two ordination axes. The Kendall correlations are listed for the three ordinations in Table V-15.

The backwall ordination (Figure V-16) relates sites primarily to an elevation-conductivity gradient on the first two axes. High elevation sites with low conductivity (primarily ARCH-CANY-GLCA) are at the positive end. These sites occur primarily on sandstones. Low elevation-high conductivity sites (primarily GRCA) are at the negative end of the gradient, and are mostly on limestone. The second axis is also correlated with solar radiation, in particular winter radiation. Site P197 (San Juan hanging garden) receives ca. 65% of total winter radiation, while site P4398 (Fern. Glen) receives no winter radiation. The colluvial slope ordination (Figure V-17) correlates vegetation structure on the first axis with an elevation-conductivity gradient. Low elevation-high conductivity sites are on the right (e.g., P3598, P4098) while high elevation-low conductivity sites are on the left (e.g., P2498). The second axis is moderately correlated with water temperature and weakly with winter radiation. The combined wetland and woodland ordination (Figure V-18) showed that elevation and solar radiation were most strongly correlated with vegetation structure. Sites to the left of the ordination are deeply shaded and receive little if any direct sun, while sites to the right side of the ordination are more open and sunny.

V.E.3. Vegetation Classification

A preliminary classification of the vegetation at the 55 sites was attempted using the SRFR 4.0 classification (Spence 2002b). The results are listed in Table V-16. Only types which were either known from previous studies in the region, or that occurred at least twice in the study area are classified. The SRFR classification is hierarchical, and uses five principal levels, floristic province, climate zone, formation, physiognomic class, and alliance. In all 21 alliances are recognized in the study area, distributed among two provinces (Colorado Plateau and Sonoran), six formations (aquatic vascular, forbland, marshland, shrubland, forest, and woodland), and eight classes (rooted aquatic, short forbland, short marshland, tall marshland, cold-deciduous shrubland, evergreen shrubland, cold-deciduous forest, and evergreen woodland). Many other alliances restricted to single sites could be recognized, but until more work is done regionally they are not formally recognized here.

V.E.4. Comparisons and Discussion

The principal factors that seem to control vegetation structure at springs along the Colorado River are elevation, water conductivity and solar radiation. Elevation can be considered a proxy variable for climate, with warmer Sonoran climates along the Colorado River through Grand Canyon, and cooler Colorado Plateau climates at higher elevations. One important component of climate is probably the extent of winter freezing that occurs at springs. Work on hanging gardens at Zion NP (Welsh 1989b) suggests that sheet ice formation and shearing can have a major impact on backwall and associated colluvial slope vegetation. The distribution of many Sonoran species in the study area probably also reflects variable tolerances to winter freezing. The importance of solar radiation in the ordinations also suggests that local microclimate plays an important role in shaping vegetation composition and structure. Some species and vegetation alliances tend to occur in deeply shaded sites with little if any direct solar radiation. The amount of solar radiation at different times of the year may also be important.

Geology, as defined in part by water chemistry (especially conductivity) appears to be another factor related to vegetation structure. Limestone springs with high water conductivity are distinctly different in structure and composition than sandstone springs with low conductivity. However, this factor is strongly correlated with elevation as most limestone sites are at low elevations in the Grand Canyon and most sandstone sites are at higher elevations on the Colorado Plateau. Few if any spring sites that emerge

from limestone are known at higher elevations in the region, while relatively few springs derived from sandstone occur in the Grand Canyon. Those that emerge in the Tapeats Sandstone have distinct water chemistry compared with sandstone such as the Navajo and Cedar Mesa. Because of this inter-correlation, it is difficult to determine if substrate or climate is the principal factor explaining site vegetation and species composition.

The backwall habitat is shown to be quite distinct in vegetation structure and floristic composition compared with other vegetation types. Many of the endemic species encountered in the study occur in this type. Strong floristic similarities in backwalls occur among springs that are often great distances apart. The strong similarities between distant sites on the Colorado Plateau are unusual, and should be investigated. The species assemblages on these backwalls may represent relictual concentrations of species that have persisted since the cooler and wetter conditions of the Pliocene, although long-distance dispersal cannot easily be ruled out. A more detailed analysis of backwalls can be found in Spence (2002a).

The relatively high level of species richness and beta diversity in the study area (e.g., Table V-12) results in numerous vegetation alliances. The alliances recognized in Table V-16 only represent the more common and widespread types. Because of the complex interactions between climate, geology, water, solar radiation and site disturbance, the springs are likely to support many additional restricted or less known alliances. To date, little work has been done on the classification of spring-supported vegetation on the Colorado Plateau. Fowler (1995) described five principal types, identified by *Adiantum capillus-veneris*, *Aquilegia* species, *Adiantum-Aquilegia*, *Phragmites australis*, and *Adiantum-Cirsium*. These types were also found in the present study, along with numerous additional alliances. Spence (1996) described three additional types that were not encountered in this study, classified as *Toxicodendron rydbergii* deciduous shrubland, *Eleocharis rostellata-Lobelia cardinalis* low marshland, and *Solidago canadensis* tall forbland. Romme *et al.* (1993) described two communities associated with springs in southern Capitol Reef National Park. These were the *Rhamnus betulifolia* type, similar to Alliance 19 (Table V-16), and a general hanging garden type, dominated by *Adiantum capillus-veneris*, *Aquilegia micrantha*, and *Mimulus eastwoodiae*. Other brief descriptions of hanging garden and spring vegetation can be found in Loope (1977), Phillips *et al.* (1980, 1987), Brotherson *et al.* (1985), Tuhy and MacMahon 1988, Van Pelt *et al.* (1991), Spence (1993, 1995, 1996), Spence and Henderson (1993), and Holiday (2000).

Table V-14: Four principal spring vegetation types derived from cluster analysis and TWINSpan.

Vegetation Type	Description	Characteristic Species	Photo Point Examples ¹
Hanging Garden Backwalls	Relatively stable vertical to sloping seepy backwalls, some spalling and rockfall; predominantly herbaceous	<i>Adiantum capillus-veneris</i> <i>Aquilegia micrantha</i> <i>Flaveria macdougalii</i> <i>Mimulus eastwoodiae</i> <i>Petrophytum caespitosum</i> <i>Primula specuicola</i>	
Hanging Garden Colluvial Slopes	Wet slopes derived from mass-wasting processes and eolian sand deposits, unstable, subject to slumping, flash flooding, rockfall; floristically rich, generally dominated by herbaceous species	<i>Aquilegia micrantha</i> <i>Aquilegia chrysantha</i> <i>Calamagrostis scopulorum</i> <i>Carex curatorum</i> <i>Cirsium rydbergii</i> <i>Epipactus gigantea</i> <i>Panicum acuminatum</i>	
Wetlands	Wet soil around plunge pools or along streams, subject to flash flooding and scour; grasses, sedges and rushes, often mixed with woody species	<i>Baccharis emoryi</i> <i>Carex aquatilis</i> <i>Cladium californicum</i> <i>Juncus balticus</i> <i>Phragmites australis</i> <i>Salix exigua</i> <i>Typha domingensis</i>	
Riparian-like Woodlands	Wet soil around plunge pools, on colluvial slopes or along streams, subject to flash flooding; overstory of trees with a variable but often lush and wet understory	<i>Celtis reticulata</i> <i>Clematis ligusticifolia</i> <i>Brickellia longifolia</i> <i>Equisetum hyemale</i> <i>Populus fremontii</i> <i>Quercus gambelii</i> <i>Rhamnus betulifolia</i>	

¹See Appendix X: Photo documentation

Table V-15. Kendall correlations between site physical data and the first two NMS ordination axes of site vegetation for three main vegetation types. See Appendix X for physical data.

Variables	Backwalls		Colluvial Slopes		Wetlands and Woodlands	
	Axis I	Axis II	Axis I	Axis II	Axis I	Axis II
Elevation	-0.585	-0.145	0.659	0.035	0.591	0.022
Aspect	-0.093	0.213	0.213	0.061	0.048	-0.186
PH	0.070	0.051	-0.004	0.009	-0.244	0.084
Conductivity	0.592	0.171	-0.405	0.237	-0.565	-0.080
Temperature	-0.198	-0.277	0.273	-0.359	0.230	0.113
Discharge	0.073	-0.129	0.108	0.004	0.113	0.157
January	-0.135	-0.308	0.013	-0.355	-0.148	0.341
February	-0.129	-0.264	0.026	-0.411	-0.122	0.262
March	-0.021	-0.291	0.026	-0.368	-0.272	0.110
April	-0.035	-0.120	0.048	-0.140	-0.346	-0.128
May	0.042	-0.005	-0.117	-0.130	-0.381	-0.287
June	0.093	0.084	-0.141	-0.145	-0.364	-0.349
July	0.053	0.040	-0.148	-0.104	-0.371	-0.298
August	-0.009	-0.156	-0.017	-0.179	-0.367	-0.207
September	0.000	-0.295	0.070	-0.381	-0.262	0.048
October	-0.096	-0.279	0.075	-0.373	-0.162	0.257
November	-0.143	-0.287	-0.002	-0.382	-0.119	0.348
December	-0.092	-0.310	0.034	-0.360	-0.120	0.330
Summer	0.039	-0.109	-0.039	-0.259	-0.341	-0.174
Winter	-0.136	-0.320	0.041	-0.337	-0.159	0.268
Total Year	-0.076	-0.242	0.017	-0.349	-0.254	0.159

Table V-16. SRFR classification of the vegetation at 55 springs in the study area (from Spence 2002b). 21 alliances in two climate zones, six formations, and eight physiognomic classes are recognized.

Province	Zone	Formation	Class	Alliance	Geomorphic Types	Park
1. Colorado Plateau	Cold-temperate	Aquatic	Rooted Aquatic	Potamogeton foliosus (POFO)	Plunge pools	GLCA
2. Colorado Plateau	Cold-temperate	Forbland	Short Forbland	Adiantum capillus-veneris (ADCA)	Backwalls, colluvial slopes	ARCH, CANY, GLCA
3. Colorado Plateau	Cold-temperate	Forbland	Tall Forbland	Cirsium rydbergii (CIRY)	Backwalls, colluvial slopes	ARCH, CANY, GLCA
4. Colorado Plateau	Cold-temperate	Forbland	Short Forbland	Mimulus eastwoodiae (MIEA)	Backwalls	ARCH, CANY, GLCA
5. Sonoran	Warm-temperate	Forbland	Short Forbland	Mimulus cardinalis (MICA)	Colluvial slopes	GRCA
6. Sonoran	Warm-temperate	Forbland	Tall Forbland	Vitis arizonica (VIAR)	Colluvial slopes	GRCA
7. Sonoran	Warm-temperate	Forbland	Tall Forbland	Oxytenia acerosa (OXAC)	Colluvial slopes	GRCA
8. Colorado Plateau	Cold-temperate	Forbland	Short Forbland	Aquilegia micrantha (AQMI)	Backwalls, colluvial slopes	ARCH, CANY, GLCA
9. Sonoran	Warm-temperate	Forbland	Short Forbland	Adiantum capillus-veneris (ADCA)	Backwalls, colluvial slopes	GRCA
10. Colorado Plateau	Cold-temperate	Marshland	Short Marshland	Juncus balticus (JUBA)	Colluvial slopes, plunge pools, simple springs	ARCH, CANY, GLCA
11. Colorado Plateau	Cold-temperate	Marshland	Short Marshland	Equisetum hyemale (EQHY)	Colluvial slopes, plunge pools, simple springs	ARCH, CANY, GLCA
12. Colorado Plateau	Cold-temperate	Marshland	Tall Marshland	Phragmites australis (PHAU)	Colluvial slopes, plunge pools, simple springs	ARCH, CANY, GLCA
13. Colorado Plateau	Cold-temperate	Marshland	Tall Marshland	Typha domingensis (TYDP)	Plunge pools, colluvial slopes	ARCH, CANY, GLCA
14. Sonoran	Warm-temperate	Marshland	Tall Marshland	Cladium californicum (CLCA)	Colluvial slopes, wetlands	GRCA
15. Sonoran	Warm-temperate	Marshland	Tall Marshland	Phragmites australis (PHAU)	Colluvial slopes, simple springs	GRCA
16. Colorado Plateau	Montane	Shrubland	Cold-deciduous Shrubland	Betula occidentalis (BEOC)	Colluvial slopes	GLCA, CANY
17. Colorado Plateau	Cold-temperate	Shrubland	Cold-deciduous Shrubland	Salix exigua (SAEX)	Plunge pools, colluvial slopes, simple springs	ARCH, CANY, GLCA
18. Sonoran	Warm-temperate	Shrubland	Evergreen Shrubland	Tessaria sericea (TESE)	Simple springs, colluvial slopes	GLCA, GRCA
19. Colorado Plateau	Cold-temperate	Woodland	Evergreen Woodland	Rhamnus betulifolia (RHBE)	Colluvial slopes	GLCA, GRCA
20. Colorado Plateau	Cold-temperate	Forest	Cold-Deciduous Forest	Quercus gambelii (QUGA)	Colluvial slopes	ARCH, CANY, GLCA
21. Colorado Plateau	Cold-temperate	Forest	Cold-deciduous Forest	Populus fremontii (POFR)	Simple springs	ARCH, CANY, GLCA

Figure V-15. Principal clusters in a cluster analysis of 90 vegetation plots at 55 sites using Euclidean Distance and Ward's flexible sorting algorithm. Six principal clusters are identified, with locations and vegetation types of plots within each cluster listed. The numbers indicate the primary divisions into clusters.

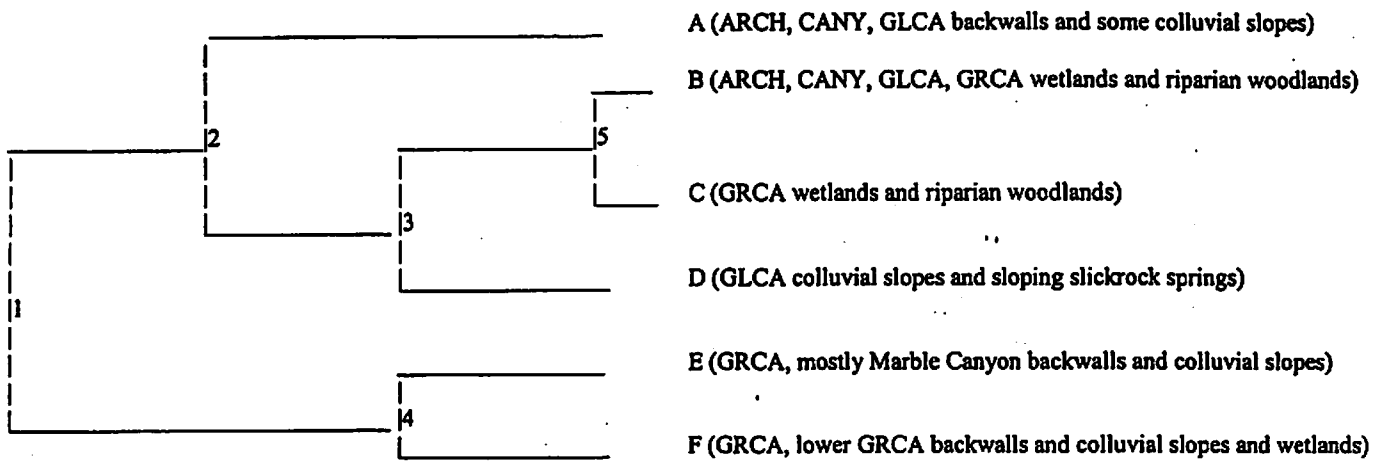


Figure V-16. The results of a non-metric multidimensional scaling ordination of backwall vegetation plots. The first two axes are portrayed, along with those physical site variables most strongly correlated with them. Site locations are GLCA (P1-23,P51-55), ARCH-CANY (P24-28), GRCA (P29-47).

NMS of backwall data

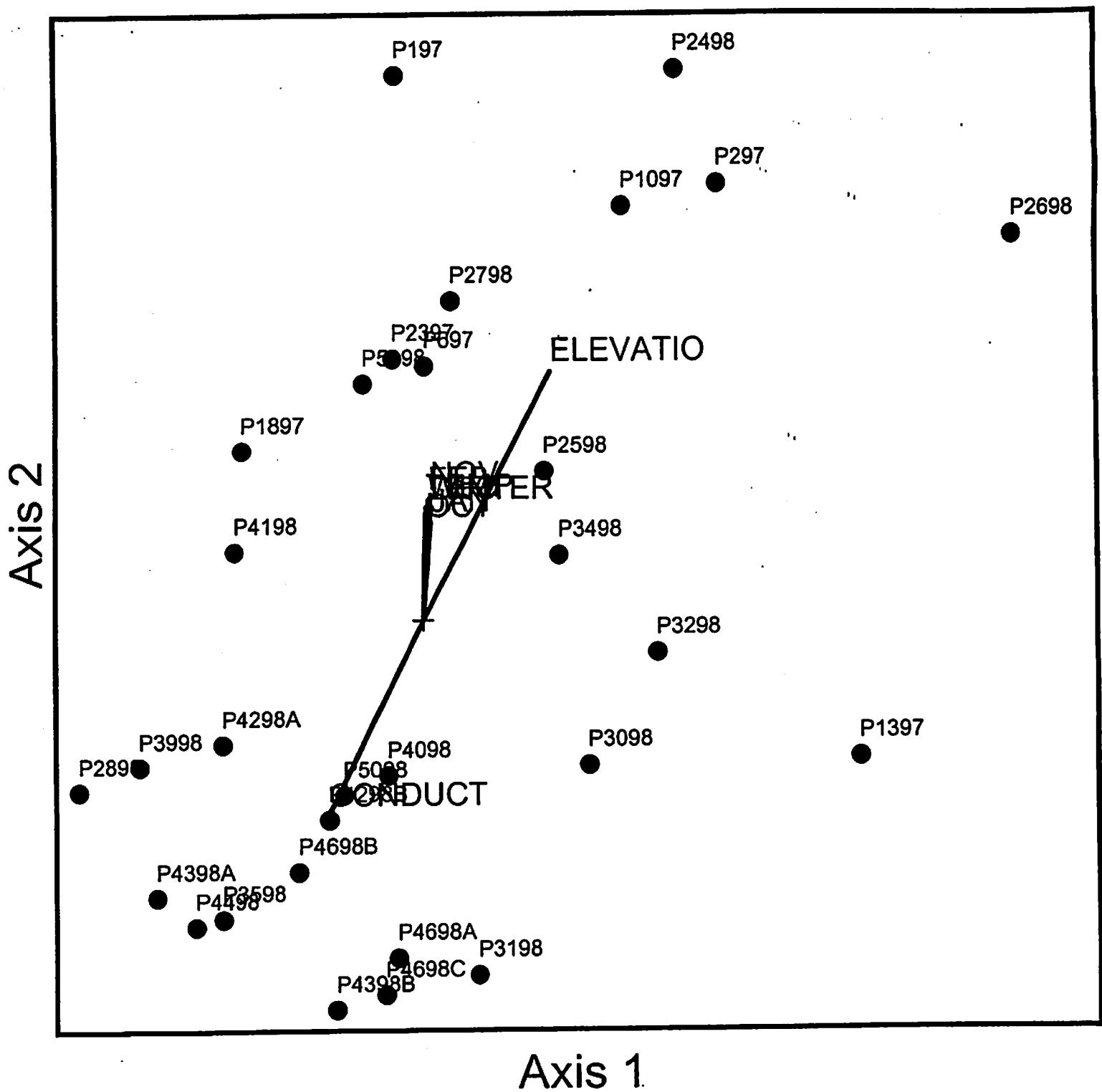


Figure V-17. *The results of a non-metric multidimensional scaling ordination of colluvial slope vegetation plots. The first two axes are portrayed, along with those physical site variables most strongly correlated with them. Site locations are GLCA (P1-23,P51-55), ARCH-CANY (P24-28), GRCA (P29-47).*

NMS of colluvial slope data

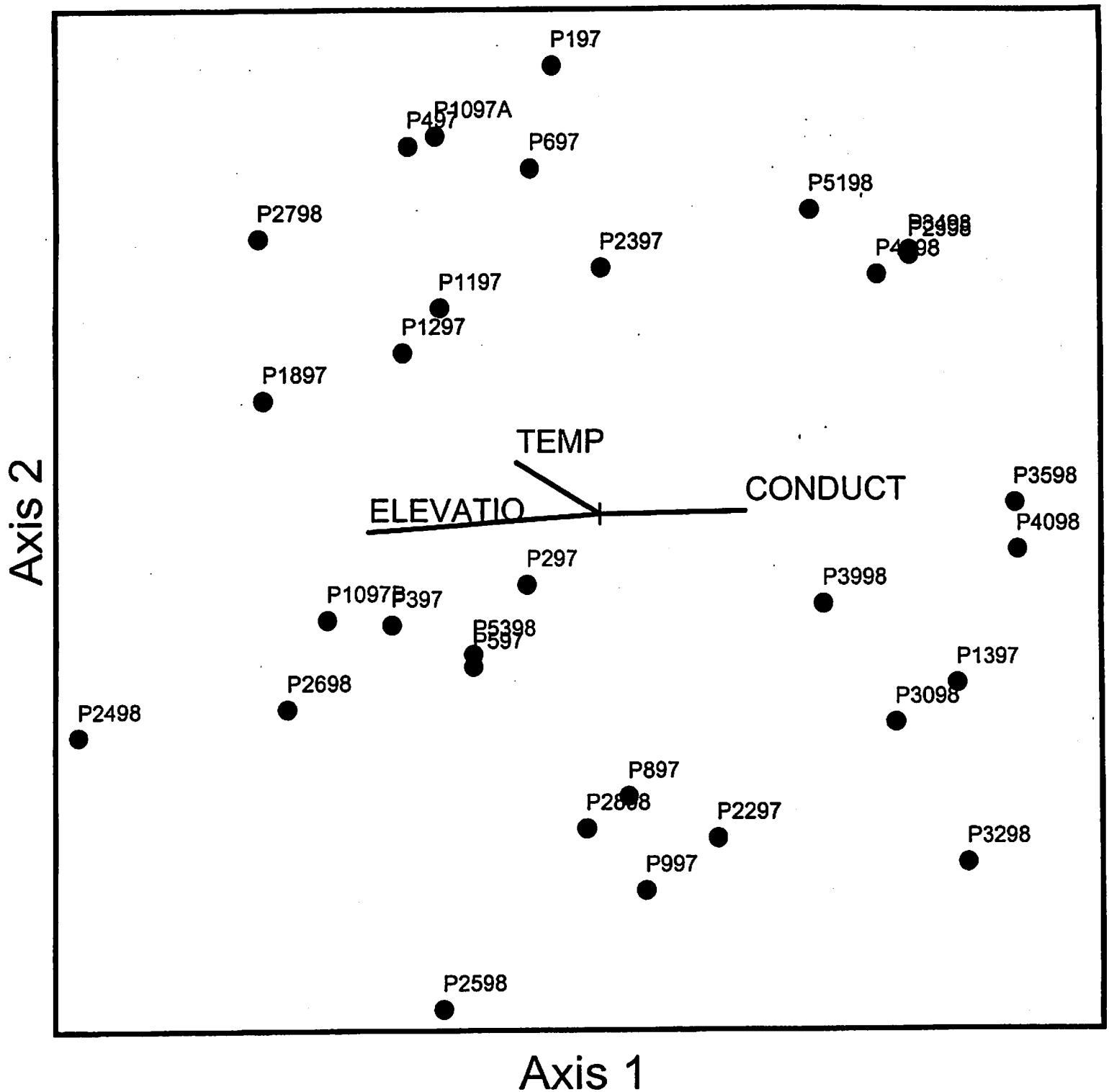
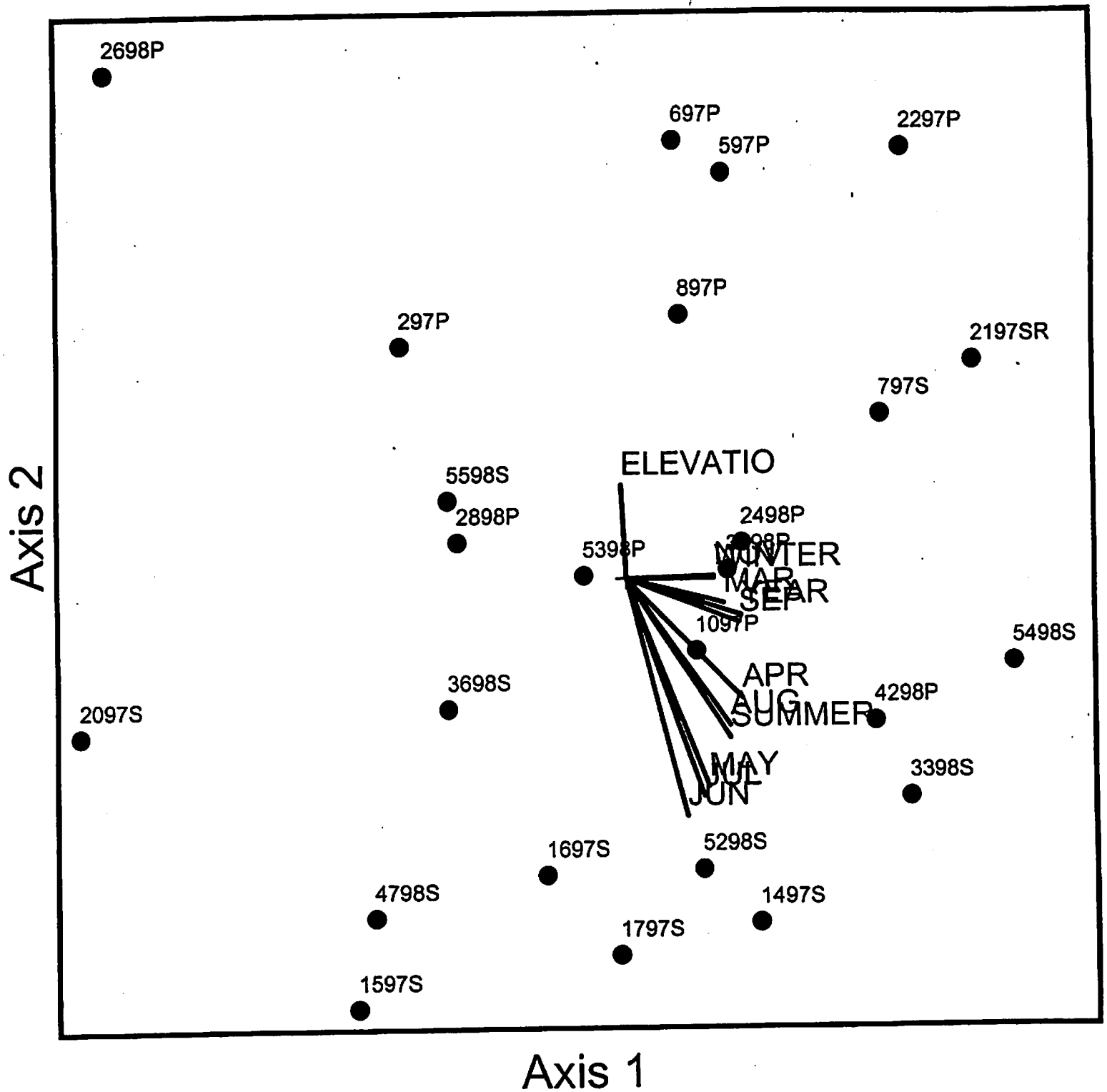


Figure V-18. *The results of a non-metric multidimensional scaling ordination of wetland and woodland vegetation plots. The first two axes are portrayed, along with those physical site variables most strongly correlated with them. Site locations are GLCA (P1-23,P51-55), ARCH-CANY (P24-28), GRCA (P29-47).*

NMS of wetland and woodland data



V.F. AMPHIBIANS

Four species of amphibians were seen during the study, canyon treefrog (*Hyla arenicola*), northern leopard frog (*Rana pipiens*), red-spotted toad (*Bufo punctatus*), and Woodhouse's toad (*Bufo woodhousei*). They were uncommon, occurring at relatively few sites. The leopard frog was restricted to Glen Canyon NRA, where it was found at three sites. Woodhouse's toad was found in both Glen Canyon and Grand Canyon at four sites. Red-spotted toads occurred in both parks at six sites. The canyon treefrog was the most widespread, found in seven sites in Glen Canyon and Grand Canyon. It is likely that the Grand Canyon tree frogs along the Colorado River represent a distinct undescribed species different from those at higher elevations (Dr. Michael Douglas, pers. comm. 1998). No amphibians were seen at the sites in Arches and Canyonlands, although all except the leopard frog are known from both parks. The overall low number of sites at which amphibians occurred is probably because many of these species are nocturnal, and are more likely to be active at night.

V.G. DISTURBANCE PATTERNS AT SPRINGS

Notes on disturbance were taken at each site. Among sites with vegetation, 47% showed recent sign of human activity, 5% showed recent sign of domestic livestock activity, 26% showed recent sign of native ungulate activity (mule deer, bighorn), and 61% showed either recent sign of flooding or were in settings where flooding existed and would have impacts on the vegetation. The distribution of exotics was analyzed with respect to human trampling, native ungulates, and flooding. Springs with human activity were not more likely to support exotics (Student's $t=0.61$, $p=0.547$ for a 2-tailed test), while springs that were flood prone did not have more exotics (Student's $t=0.49$, $p=0.628$ for a 2-tailed test). Springs with native ungulate sign did not have more exotics than sites lacking ungulate sign (Student's $t=0.40$, $p=0.695$ for a 2-tailed test). The distribution of exotic species appeared to be random, at least with respect to recent disturbance activity. The three sites with livestock activity had 0, 2 and 4 exotic species respectively. Sleepy Hollow (ARCH01-98) had the highest number of exotics with a remarkable 10 species. Three sites (GLCA09-97, GLCA10-97, GRCA11-98) had five species each, while the remaining sites had four or fewer. Nineteen springs (33%) had no exotic species.

V.H. PHOTOGRAPHIC DOCUMENTATION

Photographic documentation of each site can be found in the appendix. All photographs are available as *.jpg files on the enclosed CD. Selected examples of different types of springs are shown. Hand sketches of each site showing prominent features, locations where water was collected, location of photo points, and other features can be found in the appendix as well.

VI. DISCUSSION AND CONCLUSIONS

This study has presented baseline data on plants, aquatic invertebrates, water chemistry, and spring discharge and physical environment at 60 springs in the Colorado River drainage from Arches National Park to lower Grand Canyon National Park. As such, it is the first comprehensive multidisciplinary survey of its kind in the region. The same methods and personnel were present at all sites, providing continuity in collecting protocols.

VI.A. WATER

The springs derive from a wide cross-section of aquifers, ranging from the Cedar Mesa in Arches NP, through the Glen Canyon Group throughout much of the river corridor, to the Muav and Redwall aquifers in the Grand Canyon. In all 12 different geological formations were involved, although the majority of the sampled springs were in either the Navajo or the Muav formations. Water chemistry showed great variation regionally, with the most likely explanations being the geological formation the water flows through. As one would expect, water derived from the sandstone aquifers in the upper portion of the study area was significantly different from waters derived from the limestone aquifers in the Grand Canyon region in chemical composition. Interestingly, water temperature showed a slight trend for cooler temperatures at the low elevation sites in the Grand Canyon, and higher temperatures in the higher elevation sandstone sites. Reasons for this are not known, although it may be related to time after emergence. Discharge rates varied from minor seeping that could not be quantified to heavy flows in the order of 1000 ml/second or more. It is likely that discharge varies at most springs from year to year because of the highly variable precipitation patterns during winter months (Spence, personal observations; Spence 2001). In general, most water pH values were between 7.5 and 8.5, but two springs, Bowns Canyon (GLCA) and RM 213R spring (GRCA) had remarkably high pH values at 9.07 and 9.22 respectively.

VI.B. AQUATIC INVERTEBRATES

Because spring visits generally lasted only two hours or less, very little can be said about associated aquatic invertebrate communities. Sites varied from extremely diverse assemblages in shaded cool wet alcove gardens, to very depauperate assemblages in drier sunnier sites and along recently flooded streams. Generic distribution patterns and diversity appeared to be most strongly correlated with water chemistry and temperature, elevation and solar radiation, and likely also disturbance. Another factor positively related to generic richness was discharge rate, with larger springs tending to support more taxa. Particularly interesting were the insects associated with seepy backwalls (madicolous habitats). These habitats tended to support an interesting and unusual array of Dipteran flies, some of which are new to science, particularly in the family Empididae.

VI.C. FLORA AND VEGETATION

The springs sampled in this study support a rich diversity of plant species and vegetation communities. However, as yet relatively little research has been conducted on their structure, dynamics, and origins. A variety of interesting research programs could be established using the isolated spring biotas of the region, some of which are suggested below.

Vegetation of the hanging gardens is quite distinct from other kinds of wetland and riparian vegetation in the American southwest. The floras of gardens include a mix of species from a variety of geographic elements, such as southwestern, boreal-temperate, montane-disjunct, widespread temperate, and Colorado Plateau. The backwall habitat is particularly distinctive, supporting unusual assemblages dominated by Colorado Plateau endemic and montane-disjunct species. Other workers (e.g., May et al. 1995) have suggested that hanging garden backwall habitats may have occurred on the Colorado Plateau since the Pliocene, and thus may have been in existence for >2 million years.

Overall, elevation appears to be the principal controlling factor in vegetation structure. Elevation is in this case a proxy variable for climate, with distinct vegetation types in lower elevations of Grand and Marble Canyons and in higher elevations of the Colorado Plateau. This is also reflected in the much larger southwestern element, including primarily Sonoran-Mojavean species, in the springs in lower elevation sites. A secondary factor may be geology, since most Plateau springs are associated with sandstones while most Grand Canyon springs are associated with limestones. Conductivity and pH tend to be higher in limestone springs compared with sandstone springs. Water from limestone springs is somewhat more basic than water from sandstone springs ($T_{\text{Student's}}=1.94, p=0.060$). However, the presence of numerous species in springs of both types suggests that water chemistry may not be an important factor. Solar radiation showed some relationships to certain types of vegetation. Radiation was not strongly related to backwall and colluvial slope richness. However, woodland vegetation supported more species where summer radiation was low, while wetland and plunge pool vegetation richness was higher in sites with higher levels of fall radiation. Clearly, these relationships are tentative, and additional work is required to determine the role of solar radiation in influencing vegetation structure and species richness patterns.

Although this study has focused on the Colorado River and some of its major tributaries, other rivers draining off the Colorado Plateau also support spring-related vegetation. These include the upper Green River and its tributaries in and around Dinosaur National Monument, upper Rio Grande River, upper and middle reaches of the Little Colorado River, and streams draining off the Mogollon Rim. The riparian corridors associated with these rivers connect Colorado Plateau regions with adjacent floristic provinces, especially the southern Rocky Mountain, Apachean and Chihuahuan regions (cf. McLaughlin 1989). Floristic and vegetation surveys in these areas would provide valuable additional information on the roles of climate, dispersal and extinction in structuring spring-related vegetation in the region.

VI.D. DISTURBANCE AND EXOTIC SPECIES

Of the 19 species of exotic plants discovered at the springs, several are invasive and have the potential to severely alter spring vegetation and ecosystem dynamics. Among the most serious are *Agrostis stolonifera*, *Convolvulus arvensis*, *Elaeagnus angustifolia*, *Melilotus* species, *Tamarix ramosissima* and *Xanthium strumarium*. The spread of tamarisk in the Colorado River system provides a good example of how quickly a species can invade a region and become widespread and pervasive. Tamarisk first appeared in the lower Colorado River system in the late 1890's, then spread up the Colorado River rapidly (Graf 1978). It was at Lees Ferry by 1920, and Moab by 1925. In approximately 30 years it moved >1500 km up the Colorado River corridor. Tamarisk was a well established and common component of the Colorado River riparian ecosystem by the 1930's (Clover and Jotter 1944). Other invasive exotics may have similar potential to spread rapidly in the system and alter spring communities.

Surprisingly, although a majority of the springs showed evidence of human activities (eg., trampling) there was no relationship between human-caused disturbances and the presence of exotic species. There was a slight tendency for flood-prone springs to have more exotics, but the differences were not significant. Only three sites had recent sign of domestic livestock, whether feral or authorized. Currently, the majority of the spring and their associated vegetation and fauns are relatively intact. However, with increased recreational activity this could change.

V.I.E. IMPLICATIONS AND FUTURE WORK

The availability of inventory and monitoring data is critical as a baseline to interpret changes in natural systems in units of the National Park Service. Without such baseline data, losses in biodiversity could occur in the future without our knowledge. A variety of threats face the spring communities inventoried in this study. Many of the principal threats have probably not yet seriously affected the vegetation, water and invertebrate communities. The evidence on disturbance suggests that, although impacts have occurred and exotics are present, the native vegetation is still largely intact at most springs. However, with the future threats of global warming, new exotic plant and invertebrate invasions, and increased recreational impacts, these fragile communities are likely to come under increased pressure from human-related activities.

Springs in the region are fed primarily by aquifers that are re-charged by local precipitation events. Currently, about 50-70% of regional precipitation is in the cooler winter and early spring months, with the rest from either the summer monsoons or from fall storms from the Pacific (Petersen 1994; Spence 2001). Global warming predictions indicate that substantial changes in precipitation patterns could occur. The principal models are contradictory regarding precipitation changes. Two older models (the GISS and GFDL) predict stronger summer monsoon and possible decreases in winter precipitation, while more recent models suggest the opposite pattern (Spence 2001). The relevance of these changes in precipitation patterns to spring discharge rates is unclear, however, for several reasons. First, the water recharging the springs varies considerably in estimated age. Kimball and Christensen (1996) point out the water discharging from springs in Zion Canyon varies in age from essentially modern to 4000 yrs old. Second, we do not yet know recharge and depletion rates for most aquifers in the region. Third, the relative contributions of winter versus summer precipitation have yet to be determined with certainty. Despite these uncertainties, springs on the Colorado Plateau and their associated aquatic and wetland biotas could be at risk in the future. Further research on the origin, age and depletion rates of regional aquifers is urgently needed.

Evidence has been presented elsewhere (Spence 2002a) that suggests that vicariance (survival in situ) best explains the current isolated distribution patterns of Colorado Plateau endemics and boreal-montane relicts at the springs (cf. Nekola 1999). One promising area of research at these springs is to study genetic change in these isolated populations. If isolated populations have persisted since the Pleistocene, then a variety of genetic changes could occur. One of these changes is the fixation or at least the occurrence of unique alleles. Populations that have persisted for a long period of time and have descended from more than one original genotype are likely to exhibit greater genetic variability and have more unique alleles compared with a population that is the result of a long-distance dispersal event. The only studies to date that have looked at genetic changes include those of Allphin *et al.* (1996) on the hanging garden endemic *Erigeron kachinensis* and Kimberling *et al.* (1996) and Miller *et al.* (1999) on northern leopard frogs (*Rana pipiens*). Allphin and co-workers noted that a high elevation population of the endemic *Erigeron kachinensis* was genetically and morphologically distinct from hanging garden populations. Kimberling and co-workers showed that populations of leopard frogs in northern Arizona and in isolated canyons off of Lake Powell had genetically diverged from one another to varying degrees. The species was originally widespread along the Colorado River through Glen Canyon, but current remnant populations in side canyons are genetically different from one another. These changes may have occurred in the last 30 years since the isolation of side canyon populations resulting from the filling of Lake Powell. Other interesting and important research possibilities on spring water age and

origin, phytophagous invertebrate assemblages on relict and endemic plant species, and pollination and reproductive ecology of selected plant species could be initiated. To date, little if any work has been done in most of these areas (cf. Flanagan et al. 1997; Hudson et al. 2000).

VII. RECOMMENDATIONS

Below a variety of recommendations are made regarding future work that should be continued or initiated at the four NPS units inventoried in this study. Developing a long-term monitoring program of selected springs and their resources would greatly increase our knowledge of how they vary over time, and provide timely information on both short-term and long-term changes and their causes..

VII.A. ARCHES NATIONAL PARK

Because Arches NP has ongoing water quality monitoring (Long and Smith 1996), sites are selected primarily based on invertebrate and plant species composition. Two sites are chosen that are included in the park's water quality monitoring, Sleepy Hollow and Seven Mile Spring. They are reasonably accessible by day-hiking or by backpacking. Water discharge rates at both sites are relatively easy to obtain. Sleepy Hollow was the most diverse site investigated in the park for both plants and invertebrates, and is a good candidate for long-term monitoring. It was also the most diverse spring in the entire study for invertebrates. In all 40 genera of aquatic invertebrates were collected during a two hour visit. There are several interesting and rare plant species at the spring, including *Cornus sericea*, *Platanthera zothecina* and *Zigadenus vaginatus*. Currently, however, the site is threatened by numerous exotic species, including the invasives *Agrostis stolonifera*, *Convolvulus arvensis*, *Melilotus* species, *Tamarix ramosissima* and *Xanthium strumarium*. With additional work documenting the abundance and presence of aquatic invertebrates and their seasonal dynamics, it would be a good choice for invertebrate monitoring.

The following recommendations are made:

- Continue to collect water quality data
- Continue to determine discharge rates
- Conduct research to determine water sources and times and sensitivity to climate change
- Conduct intensive seasonal sampling to establish a complete baseline for aquatic invertebrates
- Develop protocols for future routine invertebrate monitoring
- Gather baseline data on vegetation and species cover or performance
- Develop protocols for floristic and vegetation sampling
- Remove invasive exotic species from spring sites, particularly at Sleepy Hollow

VII.B. CANYONLANDS NATIONAL PARK

Sites in Canyonlands NP were not particularly diverse biologically. In particular, invertebrate assemblages were relatively genus poor. However, the time of the visit and the relatively short period of time collecting at each spring precludes any conclusions about aquatic invertebrate diversity. Springs that supported vegetation and at least some aquatic invertebrates included Cabin Spring and lower Big Springs. These two springs are recommended for long-term monitoring. They are both included in

Canyonlands NP water quality monitoring (Long and Smith 1996). Cabin Spring supported some unusual and rare plant species, including large populations of *Berberis fendleri*, *Cornus sericea*, *Platanthera zothecina*, and *Zigadenus vaginatus*. Some exotics are present at both springs, but only *Agrostis stolonifera* is of some concern as it can be invasive and may threaten native species. Water discharge rates were relatively easy to determine at both springs. Additional invertebrate sampling, especially at Cabin Spring, might reveal greater richness than this study has shown.

The following recommendations are made:

- Continue to collect water quality data
- Continue to determine discharge rates
- Conduct research to determine water sources and times and sensitivity to climate change
- Conduct intensive seasonal sampling to establish a complete baseline for aquatic invertebrates
- Develop protocols for future routine invertebrate monitoring
- Gather baseline data on vegetation and species cover or performance
- Develop protocols for floristic and vegetation sampling
- Remove invasive exotic species from the spring sites

VII.C. GLEN CANYON NATIONAL AREA

Because a spring water quality monitoring program is not yet in place in Glen Canyon NRA, a variety of site are recommended covering much of the NRA. In general, access is not a problem for many springs, as they are easily visited by boat off of Lake Powell. Setting up a long-term monitoring program on selected springs at Glen Canyon NRA would provide data on the largest and best developed set of alcove hanging gardens on the Colorado Plateau, and perhaps the world. Numerous extremely large complex alcove gardens with high biodiversity, many relict and endemic species, and diverse aquatic invertebrate fauns exist. Because of their size and in some cases distance from the lake, some of the larger gardens may be difficult to effectively monitor, hence two groups of springs are recommended, one comprising smaller more easily accessible springs, and the second large and important, but generally more difficult to reach, hanging gardens.

The first group of springs that could form the basis of a monitoring network include:

GLCA 0197: San Juan Arm hanging garden
GLCA 0297: Ribbon Canyon Granddaddy Garden
GLCA 0397, 0497 and 0797: one of the three Escalante Arm springs
GLCA 1397: Wall Spring in Ticaboo Canyon
GLCA 1797: Good Hope Bay spring
GLCA 0398: Easter Pasture Canyon (access may be difficult from above?)

In addition, Sumac Hanging Garden on the main arm of the lake near lake buoy 73 should be selected. It was not sampled in this study.

The second group of springs are more remote, but are important as they support populations of rare endemic and boreal-temperate relict species. Most are large alcove hanging gardens:

GLCA 0697: Bowns Canyon garden
GLCA 0997: Cow Canyon garden
GLCA 1097: Cave Pool garden in Cow Canyon
GLCA 1197: Rana Canyon garden
GLCA 2297: Cottonwood Canyon garden

In addition, other prime candidates include numerous other gardens and springs not sampled in this project in Cow, lower Fence, Explorer, and Iceberg Canyons.

The following recommendations are made:

- Initiate a long-term monitoring program for selected springs in Glen Canyon NRA
- Conduct research to determine water sources and times and sensitivity to climate change
- Conduct intensive seasonal sampling to establish a complete baseline for aquatic invertebrates
- Gather baseline data on vegetation and species cover or performance
- Develop protocols for floristic and vegetation sampling
- Remove invasive exotic species from the spring sites

V.D. GRAND CANYON NATIONAL PARK

Grand Canyon NP has numerous springs, and currently conducts monitoring at many of them. Hence these recommendations limit themselves to those springs sampled along the river corridor, and which sites may be useful for long-term vegetation and aquatic invertebrate sampling. Based on water discharge rates, vegetation cover and species composition, and invertebrate richness, the following sites are recommended for long-term biodiversity monitoring:

GRCA 0298: Bert's Canyon spring
GRCA 0698: Hance Spring
GRCA 0798: Elves Chasm
GRCA 1198: RM 147R spring
GRCA 1298: Matkatamiba Canyon spring
GRCA 1398: Ledges spring
GRCA 1498: Slimy Tick Canyon spring
GRCA 1598: Fern Glen springs

Several of the sites support populations of the endemic *Flaveria macdougallii*, while aquatic invertebrate diversity was relatively high at some sites. Another important reason for selecting these sites is that many support unusual and rare insects on the madicolous (dripping backwall) habitat. These include new sites for a species of *Ochterus* (Hemiptera), undescribed species of Clinocera (Diptera), and a possible undescribed species in the neotropical genus *Asymphyloptera* (Diptera).

Some recommendations are made below for potential long-term monitoring at these springs:

- Conduct research to determine water sources and times and sensitivity to climate change
- Conduct intensive seasonal sampling to establish a complete baseline for aquatic invertebrates
- Develop protocols for floristic and vegetation sampling

- Gather baseline data on vegetation and species cover or performance
- Remove exotic species present at the springs

VIII. PRODUCTS

The data collected in this study have been or will be presented at scientific meetings and will be published in various journals and books. These include:

1. The basic vegetation and floristic results were presented at a conference entitled "Desert Springs of North America Symposium" held at the Desert Museum, Tucson on 4-6 August 200.
2. The presentation at the conference was written up as a chapter entitled "Spring-supported vegetation along the Colorado River, central Colorado Plateau: floristics, vegetation structure and environment" in the proceedings volume "Desert Springs of North America" to be published by University of Arizona Press.
3. The water chemistry will be published in the National Park Service Technical Report Series NPS/NRWRD/NRTR by Dr. Howard Taylor et al.
4. The bryophytes collected during the study will be published in a manuscript in preparation by J. Spence and L. Stevens entitled "Bryophytes at springs on the Colorado Plateau" to be submitted to either Western North American Naturalist or Southwestern Naturalist.
5. The floristic results of this study will be included in a presentation on the floristics of desert springs in the American Southwest" at the Ecological Society of America meetings in Tucson in August, 2002.
6. The floristic and vegetation data collected during this study will be incorporated into three manuscripts in preparation (J. Spence; vegetation structure and floristic composition of Colorado Plateau hanging gardens; ecology, distribution and origins of low-elevation mixed deciduous riparian woodlands in southern Utah; and a classification of the riparian and wetland vegetation of Glen Canyon NRA).

This final report will include complete hard and electronic copies of all data collected, photos of springs, original field notes and data forms, and specimens of aquatic invertebrates and bryophytes to be deposited in each park units' collections.

IX. ACKNOWLEDGEMENTS

Many people helped make this project a success. Dr. Howard Taylor of the USGS enthusiastically supported the project and contributed considerable in-kind support for the water chemistry analyses. Without the support of Dr. Bill Liebfreid of SWCA, Inc. the aquatic invertebrate collection and processing would not have been feasible. Jerry Monks of SWCA, Inc. happily provided his field expertise in the pursuit of invertebrates. Dr John MacDonald and his graduate student Colin Brammer

of Purdue University identified most of the invertebrate collections, and Dr. McDonald was involved in much of the fieldwork. Help on botanical specimens was provided by Dr.'s Tina Ayers, David Hammond and Randy Scott of Northern Arizona University.

The Colorado River float trip to access springs in the Grand Canyon was organized and supported by Grand Canyon Monitoring and Research Center. The support of Dr. Barry Gold, director, as well as Jeff Behan and Mike Yard, is gratefully acknowledged. Boatmen Eric Wilson, Dave Baker and Ken Baker did an excellent job keeping everyone safe. Suzanne Rhodes was invaluable on the trip, providing her expertise in botany and logistics. Dr. Larry Stevens, boatman, scientist, and gentleman, was instrumental in the success of the trip, and also provided useful advice and information on many springs along the river corridor derived from his vast experience running the river.

Helicopter support for the Glen Canyon NRA work was provided by the Bureau of Reclamation. The pilot Steve Chubbick, kept us all safe and was a good source of information on previous work and spring locations in Glen Canyon NRA. He always provided help in the field, even after he tangled with the cactus! His retirement will be greatly missed at Glen Canyon.

National Park Service people involved in this project included Kevin Berghoff, water quality specialist at Glen Canyon NRA from 1996-1999, and Charlie Schelz, botanist for the Southeast Utah Group. Charlie's support on the field work in Arches and Canyonlands NP's was invaluable. Despite his fall, Kevin continued to collect water quality data on the Colorado River field work, and only two sites were missed. John Ritenour, chief of resource management at Glen Canyon NRA, provided advice and support during the project. Dan Spotskey, GIS specialist at Grand Canyon National Park, provided the locational data for the springs in the Grand Canyon.

X. LITERATURE

Allphin, L. and K.T. Harper. 1994. Habitat requirements for Erigeron kachinensis, a rare endemic of the Colorado Plateau. Great Basin Naturalist 54: 193-203.

Allphin, L., M.D. Windham and K.T. Harper. 1996. A genetic evaluation of three potential races of the rare Kachina daisy. Pp. 68-76 in Maschinski, J., H.D. Hammon and L. Holter (eds.). Southwestern rare and endangered plants: Proceedings of the second conference. U.S.D.A. Forest Service Technical Report RM-GTR-283.

Analytical Software. 1998. STATISTIX for Windows. Analytical Software, Tallahassee, FL.

Axelrod, D.I. and P.H. Raven. 1985. Origins of the cordilleran flora. Journal of Biogeography 12: 21-47.

Baron, J.S., T. LaFrancois and B.C. Kondratieff. 1998. Chemical and biological characteristics of desert rock pools in intermittent streams of Capitol Reef National Park, Utah. Great Basin Naturalist 58: 250-264.

Betancourt, J.L. 1984. Late Quaternary plant zonation and climate in southeastern Utah. Great Basin Naturalist 44: 1-35.

- Betancourt, J.L., T.R. Van Devender and P.S. Martin. 1990. Packrat middens. The last 40,000 years of biotic change. University of Arizona Press, Tucson. 467 pp.
- Boisan, 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., W.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 Naturalist 45: 1-13.
- Brown, B.T. and Moran, S. 1979. An Inventory of Surface Water Resources in Grand Canyon National Park, Arizona. Unpublished Final Report to the Division of Resource Management Grand Canyon National Park Part I (Water Resources Inventory) of the 208 Water Quality Project. 60 pp.
- Campbell, C.J. and W. Green. 1968. Perpetual succession of stream-channel vegetation in a semiarid region. Journal of the Arizona Academy of Science 5: 86-98.
- Clover, E.U. and L. Jotter. 1944. Floristic studies in the canyons of the Colorado and tributaries. American Midland Naturalist 32: 591-642.
- Cole, K.L. 1990. Reconstruction of past desert vegetation along the Colorado River using packrat middens. Palaeogeography, Palaeoclimatology, Palaeoecology 76: 349-366.
- Cole, K.L. and L.K. Murray. 1997. Middle and late Holocene packrat middens from Capitol Reef National Park. Pp. 3-24 in van Riper III, C. and E.T. Deshler (eds.). Proceedings of the third biennial conference on research in Colorado Plateau National Parks. U.S.D.I. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-95/11.
- Cooley, M.E. 1965. Stratigraphic sections and records of springs in the Glen Canyon region of Utah and Arizona. Mus. N. Arizona Tech. Ser. No. 6, Flagstaff, AZ.
- Dryer, J.D. 1994. Late pleistocene vegetation change at Stanton's Cave, Colorado River, Grand Canyon National Park, Arizona. M.Sc. thesis, Quaternary Studies, Northern Arizona University, Flagstaff. 100 pp.
- Eastwood, A. 1896. Report of a collection of plants from San Juan County, in southeastern Utah. Proceedings of the California Academy of Science II, 6: 271-329.
- Elias, S.A., J.I. Mead and L.D. Agenbroad. 1992. Late Quaternary arthropods from the Colorado Plateau, Arizona and Utah. Great Basin Naturalist 52: 59-67.
- Flanagan, L.B., C.S. Cook and J.R. Ehleringer. 1997. Unusually low carbon isotope ratios in plants from hanging gardens in southern Utah. Oecologia 111: 481-489.

- Flowers, S. 1959. Vegetation of Glen Canyon. Pp. 21-61 In Woodbury, A.M. (ed.). Ecological studies of flora and fauna in Glen Canyon. University of Utah Anthropological Papers No. 40 (Glen Canyon Series No. 7).
- Fowler, J.F. 1995. Biogeography of hanging gardens on the Colorado Plateau. Ph.D. dissertation, Dept. of Zoology and Physiology, University of Wyoming, Laramie.
- Fowler, J.F., N.L. Stanton, R.L. Hartman and C.L. May. 1995. Level of endemism in hanging gardens of the Colorado Plateau. Pp. 215-223 in van Riper III, C. (ed.). Proceedings of the second biennial conference on research in Colorado Plateau National Parks. U.S.D.I. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-97/12.
- Goings, D. 1985. Spring flow in a portion of Grand Canyon National Park. M.Sc., University of Nevada, Las Vegas.
- Graf, W.L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin 89: 1491-1501.
- Graham, T.B. 1997. The Knowles Cañon hanging garden, Glen Canyon National Recreation Area, five years after burning: Vegetation and soil biota patterns. Pp. 173-190 in van Riper III, C. and E.T. Deshler (eds.). Proceedings of the third biennial conference on research in Colorado Plateau National Parks. U.S.D.I. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-95/11.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite hypothesis. Oikos 38: 210-221.
- Haring, I.M. 1946. Mosses of the Grand Canyon National Park, Arizona, II. Bryologist 49: 90-96.
- Harper, K.T., S.C. Sanderson and E.D. McArthur. 1992. Riparian ecology in Zion National Park. Pp. 32-42 In Symposium on the ecology and management of riparian shrub communities. USDA Forest Service General Technical Report INT-289.
- Harper, K.T., L.L. St. Clair, K.H. Thorne and W.M. Hess (eds.). 1994. Natural history of the Colorado Plateau and Great Basin. University Press of Colorado, Niwot. 294 pp.
- Holiday, S. 2000. A floristic study of Tsegi Canyon, Arizona. Madrono 47: 29-42.
- Holmgren, A.H., L.M. Schultz and T.K. Lowrey. 1976. Sphaeromeria, a genus closer to Artemisia than to Tanacetum (Asteraceae: Anthemideae). Brittonia 28: 255-262.
- Hudson, L.E., R.A. Coleman and S. Charles. 2000. A preliminary population study of Platanthera zothecina (Higgins & Welsh) Kartesz & Gandhi (Orchidaceae) at Navajo National Monument, Arizona. North American Native Orchid Journal 6: 103-118.
- Keate, N.S. 1996. Quantitative analysis of hanging garden endemic plant species richness in the Moab region, Utah. Ph.D. dissertation, Dept. of Geography, University of Utah, Salt Lake City.

- Kelso, S. 1991. Taxonomy of Primula sects. Aleuritia and Armerina in North America. Rhodora 93: 67-99.
- Kimball, B.A. and P.K. Christensen. 1996. Residence time of water discharging from the hanging gardens of Zion Park. Water Resources Bulletin 32: 531-539.
- Kimberling, D.N., A.R. Ferreira, S.M. Shuster and P. Keim. 1996. RAPD marker estimation of genetic structure among isolated northern leopard frog populations in the south-western USA. Molecular Ecology 5: 521-529.
- Laity, J.E. and M.C. Maslin. 1985. Sapping processes and the development of theater-headed valley networks on the Colorado Plateau. Geological Society of America Bulletin 96: 203-217.
- 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 NRA. Northern Arizona University.
- Long, B.A. and Smith, R.A. 1996. Water quality data analysis and interpretation for spring monitoring sites, Southeast Utah Group. National Park Service Tech. Rep. NPS/NRWRD/NRTR-96/77.
- Loope, W.L. 1977. Relationships of vegetation to environment in Canyonlands National Park. Ph.D. dissertation, Dept. of Range Science, Utah State University, Logan.
- Malanson, G.P. 1980. Habitat and plant distributions in hanging gardens of the Narrows, Zion National Park, Utah. Great Basin Naturalist 40: 178-182.
- _____. 1982. The assembly of hanging gardens: effects of age, area, and location. American Naturalist 119: 145-150.
- Malanson, G.P. and J. Kay. 1980. Flood frequency and the assemblage of dispersal types in hanging gardens of the Narrows, Zion National Park, Utah. Great Basin Naturalist 40: 365-371.
- May, J.F. Fowler and N.L. Stanton. 1995. Geomorphology of the hanging gardens of the Colorado Plateau. Pp. 3-24 in van Riper III, C. (ed.). Proceedings of the second biennial conference on research in Colorado Plateau National Parks. U.S.D.I. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-95/11.
- McArthur, E.D., S.C. Sanderson and K.T. Harper. 1989. Expansion of the known distribution of the rare Zion Tansey, Sphaeromeria ruthiae (Asteraceae). Southwestern Naturalist 34: 441-443.
- McArthur, E.D., R. Van Buren, S.C. Sanderson and K.T. Harper. 1998. Taxonomy of Spaheromeria, Artemisia, and Tanacetum (Compositae, Anthemideae) based on randomly amplified polymorphic DNA (RAPD). Great Basin Naturalist 58: 1-11.
- McCune, B. and M.J. Mefford. 1995. PC-ORD. Multivariate analysis of community data. Version 2.0. MjM Software Design, Gleneden Beach, Oregon. 126 pp.

- McLaughlin, S.P. 1992. Are floristic areas hierarchically arranged? Journal of Biogeography 19: 21-32.
- Miller, M.P., D.N. Kimberling, and P. Keim. 1999. Re-analysis of genetic structure among populations of Rana pipiens in Arizona and Utah. Southwestern Naturalist 44: 527-530.
- Mueller, G., L. Boobar, R. Wydoski, K. Comella, R. Fridell and Q. Bradwisch. 1998. Aquatic survey of the lower Escalante River, Glen Canyon National Recreation Area, June 22-26, 1998. USDI U.S. Geological Survey Open File Report 99-101.
- National Park Service. 1987. Tamarisk control in southwestern United States. USDI National Park Service University of Arizona Cooperative Park Studies Unit Special Report No. 9.
- National Park Service. 1994. Southeast Utah Group water quality monitoring plan. National Park Service, SEUG, Moab, UT.
- Nekola, J.C. 1999. Paleoreugia and neoreugia: the influence of colonization history on community pattern and process. Ecology 80: 2459-2473.
- 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. Geological Society of America Bulletin 97: 369-378.
- Petersen, K.L. 1994. Modern and pleistocene climatic patterns in the west. Pp. 27-54 in Harper, K.T., L.L. St. Clair, K.H. Thorne and W.M. Hess (eds.). Natural history of the Colorado Plateau and Great Basin. University Press of Colorado, Niwot. 294 pp.
- Phillips, B.G., R.R. Johnson, A.M. Phillips III and J.E. Bowers. 1980. Resource values of the aquatic and riparian vegetation of Roaring Springs, Grand Canyon. U.S.D.I. National Park Service. Proceedings of the second conference on research in the National Parks. National Park Service, Washington, D.C.
- Phillips, B.G., A.M. Phillips III and M.A.S. Bernzott. 1987. Annotated checklist of vascular plants of Grand Canyon National Park. Grand Canyon Natural History Association Monograph No. 7.
- Powell, J.W. 1895. The exploration of the Colorado River and its canyons. 1961 Dover Reprint, New York. 400 pp.
- Raven, P.H. and D.I. Axelrod. 1978. Origin and relationships of the California flora. University of California Publications in Botany 72. 134 pp.
- Romme, K.D. Heil, J.M. Porter and R. Fleming. 1993. Plant communities of Capitol Reef National Park, Utah. Cooperative Park Studies Unit, Northern Arizona University, Flagstaff. U.S.D.I. National Park Service Technical Report NPS/NAUCARE/NRTR-93/02.
- Rushforth, S.R. and G.S. Merkley. 1988. Comprehensive list by habitat of the algae of Utah. Great Basin Naturalist 48: 154-179.

Sharpe, S.E. 1991. Late-Pleistocene and Holocene vegetation change in Arches National Park, Grand County, Utah and Dinosaur National Monument, Moffat County, Colorado. M.Sc. thesis, Quaternary Studies, Northern Arizona University, Flagstaff. 95 pp.

Sharpe, S.E. 1993. Late-Wisconsin and Holocene vegetation in Arches National Park, Utah. Pp. 109-122 in Rowlands, P.G., C. van Riper III, and M.K. Sogge (eds.). Proceedings of the first biennial conference on research in Colorado Plateau National Parks. U.S.D.I. National Park Service Transactions and Proceedings Series NPS/NRNAU/NRTP-93/10.

Spence, J.R. 1988. A checklist of the mosses of the Intermountain West, U.S.A. Great Basin Naturalist 48: 394-401.

_____. 1993. A preliminary survey of hanging gardens and related vegetation along the Colorado River, Grand Canyon National Park. Report to Glen Canyon Environmental Studies and Grand Canyon National Park. National Park Service, Resource Management Division, Glen Canyon National Recreation Area. 15 pp.

_____. 1995. Characterization and possible origins of isolated Douglas Fir stands on the Colorado Plateau. Pp. 71-82 in Waugh, W.J. (ed.). Climate change in the Four Corners region. Proceedings of a symposium, Grand Junction, September 12-14, 1994. Dept. Energy NTIS CONF-9409325.

_____. 1996. A survey and classification of the riparian and spring vegetation in side canyons around Lake Powell, Glen Canyon National Recreation Area, Utah. Unpublished final report, National Park Service, Resource Management Division, Glen Canyon National Recreation Area. 90 pp.

_____. 2001. Climate of the central Colorado Plateau, Utah and Arizona: Characterization and recent trends. Pp. 187-203 in van Riper III, C., K.A Thomas and M.A. Stuart (eds.). Proceedings of the fifth biennial conference of research on the Colorado Plateau. U.S.D.I. U.S. Geological Survey Report Series USGSFRES/COPL/2001/24.

_____. 2002a. Spring-supported vegetation along the Colorado River, central Colorado Plateau: floristics, vegetation, structure and environment. In L. SE. tevens and V. Meretsky (eds.). Desert Springs of North America: Ecology and Conservation. U. Arizona Press, Tucson (in press).

_____. 2002b. The Spence/Romme/Floyd-Hanna/Rowlands vegetation classification, Version SRFR 4.0. Unpublished report, National Park Service, Resource Management Division, Glen Canyon National Recreation Area. 14 pp.

_____ and N.R. Henderson. 1993. Tinaja and hanging garden vegetation of Capitol Reef National Park, southern Utah, U.S.A. Journal of Arid Environments 24: 21-36.

_____ and J.A.C. Zimmerman. 1996. A preliminary flora of Glen Canyon National Recreation Area. Unpublished report, National Park Service, Resource Management Division, Glen Canyon National Recreation Area. 27 pp.

Standard methods for the examination of water and wastewater, 18th ed. 1992. American Public Health Association, Washington, DC.

Stebbins, G.L. 1982. Floristic affinities of the high Sierra Nevada. Madrono 29: 189-199.

Stevens, L.E., Protiva, F., Kubly, D., Meretsky, V.J., and Petterson, J. 1995. The ecology of the Kanab Ambersnail (Succineidae: Oxyloma haydeni kanabensis Pilsbry) at Vasey's Paradise, Grand Canyon, Arizona. Draft Final Report submitted to Glen Canyon Environmental Studies Program. 34 pp.

Stone, R.D. 1998. Inventory of sensitive species and ecosystems in Utah. Endemic and rare plants of Utah: An overview of their distribution and status. Utah Division of Wildlife Resources, Salt Lake City, Utah. 566 pp.

Sublette, J.E., L.E. Stevens and J.P. Shannon. 1998. Chironomidae (Diptera) of the Colorado River, Grand Canyon, Arizona, USA, I: systematics and ecology. Great Basin Naturalist 58: 97-146.

Taylor, H.E., K. Berghoff, E.D. Andrews, R.C. Antweiler, T.I. Brinton, C. Miller, D.B. Peart, and D.A. Roth. 1997. Water quality of springs and seeps in Glen Canyon National Recreation Area. USDI Nat. Park Service Tech. Rep. NPS/NRWRD/NRTR-97/128.

Taylor, H.E., J.R. Spence and K. Berghoff. 2002. Water quality of springs and seeps of National Park Service units along the Colorado River, Arizona and Utah. USDI Nat. Park Service Tech. Rep. NPS/NRWRD/NRTR (in preparation).

Tuhy, J.S. and J.A. MacMahon. 1988. Vegetation and relict communities of Glen Canyon National Recreation Area. Final report to the National Park Service. The Nature Conservancy and Department of Biology and Ecology Center, Utah State University, Logan, Utah.

Van Pelt, N.S., C.D. Schelz, J.S. Tuhy, D.W. Johnson and J.R. Spence. 1991. Survey and analysis of relict plant communities within national park system units of the Colorado Plateau. Volumes I-III. Final report to the National Park Service, Rocky Mountain Region. The Nature Conservancy, Great Basin Field Office, Salt Lake City, Utah.

Warren, P.L., K.L. Reichhardt, D.A. Mouat, B.T. Brown and R.R. Johnson. 1982. Vegetation of Grand Canyon National Park. National Park Service, Cooperative National Park Resources Studies Unit, University of Arizona, Tucson. Technical Report No. 9.

Welsh, S.L. 1989a. On the distribution of Utah's hanging gardens. Great Basin Naturalist 49: 1-30.

Welsh, S.L. 1989b. Hanging gardens of Zion National Park. Final report to the National Park Service. Endangered Plant Studies, Inc., Orem, Utah.

Welsh, S.L. and C.A. Toft. 1981. Biotic communities of hanging gardens in southeastern Utah. National Geographic Society Reports 13: 663-681.

Welsh, S.L., N.D. Atwood, L.C. Goodrich and L.C. Higgins. 1993. A Utah flora. 2nd Ed. Brigham Young University Press, Provo.

West, N.E. and J.A. Young. 2000. Intermountain valleys and lower mountain slopes. Pp. 255-284 in Barbour, M.G. and W.D. Billings (eds.). North American terrestrial vegetation, 2nd Ed. Cambridge University Press, New York. 708 pp.

Wilson, E. 1998. Geology of springs along the Colorado River, Grand Canyon National Park, Arizona. Report to the National Park Service, Glen Canyon NRA. Department of Geology, Northern Arizona University.

Willson, M.E., B.L. Rice and M. Westoby. 1990. Seed dispersal spectra: a comparison of temperate plant communities. Journal of Vegetation Science 1: 547-562.

Withers, K. and J.L. Mead. 1993. Late Quaternary vegetation and climate in the Escalante River Basin of the central Colorado Plateau. Great Basin Naturalist 53: 145-161.

Wolz, E.R. and Shiozawa, D.K. 1995. Aquatic macroinvertebrates of the Needles District, Canyonlands National Park, Utah. Report to the National Park Service. Brigham Young University. 25 pp.

Wong, D. 1999. Community analysis of hanging gardens at Zion National Park, Utah and the Colorado Plateau. M.Sc. thesis, Dept. of Biology, Northern Arizona University, Flagstaff.

Woodbury, A.M. 1933. Biotic relationships of Zion Canyon, Utah, with special reference to succession. Ecological Monographs 3: 147-245.

Woodbury, A.M. 1958. Preliminary report on biological resources of the Glen Canyon reservoir. University of Utah Anthropological Papers No. 31 (Glen Canyon Series No. 2).

Volume II (in preparation)

The following data sets and their file formats will be included in the appendix.

XI. APPENDIX

- A1. Site physical data and location (Excel)
- A2. Water chemistry (Excel)
- A3. Aquatic invertebrates presence/absence (Excel)
- A4. Flora presence/absence and ecology (Excel)
- A5. Vegetation (species abundance by spring by geomorphology; Excel)
- A6. Photos (.jpg files on CD)
- A7. Original data sheets (duplicates)
- A8. Original field sketches (duplicates)
- A9. Species lists and collections numbers and specimen data

Aquatic invertebrate specimens

Bryophyte specimens