VERNAL POOL SUBSTRATE AND PLANT COMMUNITY STUDY

FINAL REPORT

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Executive Summary

The California Department of Fish and Game and the US Fish and Wildlife Service have collaborated to provide management and funding for research to investigate the relationship between substrate and vernal pool plant communities.

In 1995 and 1996, this study was conducted in vernal pools at Beale Air Force Base, Yuba County, California, to determine whether vernal pool plant communities differ on different soil series. Pools of similar size and depth were sampled once in spring at peak flowering time on Pardee and Redding-Corning soils in 1995, and sampling of pools on San Joaquin soil was added in 1996. Percent cover data was gathered and means computed for TWINSPAN, which divided pools according to species abundance. DCA clustered pools with similar plant communities. Number of species occurring on each soil was used for calculation of species richness and Shannon diversity index. Although there was some overlap of pools on each of the soil series, TWINSPAN and DCA clearly separated soil by plant communities, while richness data results were mixed, with only San Joaquin soil showing a significant difference from the other soils. Diversity index results showed no significant difference among soils. Results indicate that soil series should be considered as an important factor in conservation of vernal pool plant communities.

1.0 INTRODUCTION

Vernal pools are ephemeral wetlands occurring in shallow depressions underlain by a layer of substrate that restricts percolation. Vernal pools fill during the rainy season and gradually dry during the spring and early summer. Many pools fill and empty more than once during the spring. Pools vary in size from a few square meters to several acres, and usually are located on semirolling grasslands, tucked in among mima mounds or hummocky topography. In California, vernal pools formed tens of thousands of years ago on ancient alluvial soils of the Central Valley, on coastal terraces, and on basaltic lava flow (Zedler, 1987).

Vernal pools have been considered habitat islands, with edaphic, hydrologic, and vegetative characteristics that are very different from the surrounding grasslands (Holland and Jain, 1977). Many of the plants and invertebrates supported by the pools are endemic species, indigenous to California vernal pools and adapted to the mediterranean climate. Additional native plant and animal species associated with these wetlands are not strict vernal pool endemics, but are usually or often found in vernal pools. A relatively large proportion of the species that are listed or are proposed for listing as Threatened or Endangered species by the State and/or Federal Government are associated with vernal pools (Holland, 1978). The primary threat to these species is habitat loss through agricultural conversion and urbanization (Stone et al., 1988). According to the California Department of Parks and Recreation, loss of vernal pools is estimated at 90% (Ferren et al., 1996).

Because of the policy of no-net-loss of wetlands, State and Federal agencies have required in-kind compensation for the loss of vernal pool habitats through the creation of artificial vernal pools. In some cases, the creation of vernal pools has occurred without considering differences in vernal pool soil types. Some biologists suspect that edaphic features may have a greater influence on plant communities in vernal pools than has been documented. W. A. Weitkamp (1996), states "An understanding of the vernal pool soils is essential to the maintenance and preservation of these unique ecological systems."

1.1 Vernal Pool Soils, Hydrology, and Plant Communities

All vegetation types are determined by interactions between climate, source biota, location history, and soil. However, in the vernal pool environment edaphic factors may have more influence than other factors in determining pool plant communities (Holland and Dains, 1990).

The soils directly under vernal pools may be different from the soil series mapped in a county soil survey. The Natural Resource Conservation Service maps soils at a scale of 1:24,000. At this resolution, vernal pools are often undescribed in soil map unit descriptions and occur as small inclusions in larger units. They are usually too small to be described separately on small-scale soil maps.

Vernal pools are basins that vary in the following characteristics: depth of the basin, soil depth and type above the layer that restricts the downward flow of water (aquiclude), the physical characteristics of the aquiclude, and the pathways by which water enters or leaves the pool. The depth of the basin is controlled by the configuration of side slopes of the pools, which in turn is a function of the topography of the soils. Soil types are classified by depth, physical characteristics such as structure textures of the different horizons, and mineralogy and chemistry. The nature of the aquiclude is also described by soil type and varies from extremely impervious clay layers above thick indurated hardpans, to cracked basalt that allows water to slowly percolate downward.

The hydrology in pools is a function of soil type, geomorphic position, and climate. The water level regime in vernal pools can be characterized by the potential pathways by which it receives or loses water (Hanes et al., 1990). The magnitude of these pathways can vary greatly from pool to pool and even over the course of the season in a single pool. Water can enter a pool from the following pathways: direct precipitation, inflow from a channel, overland flow from an adjacent upland, or subsurface flow from an adjacent upland. Water can leave a pool by the following pathways: evaporation, seepage through the pool bottom, outflow through a channel, and movement into the adjacent upland (Hanes et al., 1990).

In wetland communities, adaptation to inundation and to saturation duration is a primary factor determining the spatial distribution of plant species (Stone et al., 1988). Duration of saturation in vernal pools varies with topography, from the longer inundated pool bottom to the occasionally saturated pool margin. Saturation may also vary with type and depth of soil above the aquiclude. Plant communities vary along saturation gradients; zonation of plant communities is one of the most conspicuous features of a vernal pool, as evidenced by beautiful concentric rings of flowers. Plants that are adapted to ponded water are dominant in pool bottom communities and species of plants that tolerate or require periodic ponding and saturation are found in the transition zones from wetland to upland.

The shape of the side slopes and impermeable layer lining the pool bottom is important to the size of the transition zone that rings the pool. For example, a shallow, flat-bottomed pool leaves more edge area for transition plants, such as *Lasthenia fremontii* (Zedler, 1987). Plant species dominance also varies with the depth and texture of the soil above the hardpan, indicating that water-holding capacity may be as important to some species as flooding. At pool edges where clay depth is least, *Lasthenia fremontii* and *Deschampsia danthonioides* dominate, while *Eryngium* and *Navarretia* spp. grow where soils are deeper (Holland and Dains, 1990). Larger, deeper pools may offer more varied habitats over time and space. This may help to explain why, as some researchers have found, that more plant species can find a niche in larger, deeper pools that retain moisture longer, supporting a more diverse community (Baskin, 1994).

1.2 Classification of Plant Communities

A plant community describes the species that grow together in a particular habitat. Species composition and spatial patterns of the species present in the habitat describe the attributes of a community. Species richness is the number of species in a certain area within a community and species evenness is the distribution of species within the community. Diversity is a combination of the richness and evenness of the plants in a community. Diversity is the richness weighted by the evenness. Formulae, such as the Shannon diversity index, have been developed and are commonly used, allowing diversity to be expressed as a single index number (Barbour et al., 1987).

Classification methods attempt to group similar stands of plants in discrete communities to try to explain patterns in floristic variation. Classification of vegetation emphasizes either dominance of a few key species or uses indicator species that exhibit strong fidelity to certain habitat types; a good indicator species is present in one habitat type and absent in others. Classification of vegetation based on the entire flora is complex; researchers describe all species encountered in a given area and compare species distribution to the distribution of species in another area.

Cluster analysis is one method of classifying vegetation. The advantage of cluster analysis over simpler tabular methods is that the relatedness of different communities can be quantified. Several computer programs have been developed to perform cluster analysis. Two-Way Indicator Species Analysis (TWINSPAN) is a program frequently used by plant ecologists (Barbour et al., 1987).

Ordination procedures use a graphic display of species in two or more dimensions so that patterns of relationship can be seen. In an ordination diagram similar communities are closer together than dissimilar communities. Detrended correspondence analysis (DCA or DECORANA) is a an ordination computer program that is being used by plant ecologists to describe plant communities (Barbour et al., 1987).

1.3 Soil and Vernal Pool Plant Community Characterization Studies

Researchers have published reports correlating vernal pool plant communities with soil type (Jokerst, 1990; Holland and Dains, 1990).

In a 1987 study Jokerst (1990) described floristic communities in vernal pools forming on mudflows at the Johnson Ranch in western Placer County, California. After sampling percent cover and species composition and abundance in the pools, TWINSPAN was used to analyze plant communities among six geographically discrete clusters of mudflow pools. "Wetland generalists" (species that occur in more than one wetland type) were found to be dominant in the swale type pools, followed by "vernal pool obligates" (routinely found in vernal pools and rarely occurring in other types of wetlands), and upland plants. Species richness was weakly correlated with pool depth. Each group of pools shared the same species and this pattern of dominance.

Floristic comparisons were made among other mudflow sites, vernal pools forming on soils with hardpans, and vernal pools forming on basalt flows. It is difficult to judge the significance of the findings of this comparison study, as data was gathered for these comparisons in different years, by different researchers, and on land that has very different management and use histories. Jokerst stated that mudflow pools cannot be distinguished from hardpan pools on the basis of species composition alone, and that each pool was somewhat unique. He concluded that mudflow pools support a subset of Great Valley hardpan flora, as described by Holland (1986), and that many factors, such as presence of endemic plants and invertebrates, soil composition and chemistry, and hydrology should be used to distinguish between types of vernal pools.

Holland and Dains (1990) described a 1986 project to study patterns of plant communities and their relationship to soil types. The site was located at the Flying M Ranch in eastern Merced County, California, on an alluvial fan of the Merced River. The study involved 115 pools on eight different soil series, and in 1987 included 140 additional pools on 9 soil series. They used DCA and TWINSPAN to sort pools based on floristic patterns and soil type.

2.0 BEALE AIR FORCE BASE SOIL AND PLANT COMMUNITY STUDY

The study described in this report was performed in 1995 and 1996 at Beale Air Force Base. We described vernal pool plant communities on soils forming on basalt mudflow and two different soils that have hardpans. All of the pools had the same land use history, biota sources, and climate. In contrast to the Flying M Ranch and the Johnson Ranch studies, in the Beale study the soil series varied, but all pools sampled were approximately the same depth and volume. Like the other studies, percent cover and floristic composition were measured to determine if an association exists between soil type and plant communities, with sampling performed over a short period of time during maximum flowering. By sampling pools of the same size and depth on different soils, it was hoped that the effects of soil on floristic composition patterns could be distinguished.

2.1 Research Objectives:

Our objectives were to test the hypothesis that different soils (at the level of soil series) will support measurably different vernal pool plant communities. To test this hypothesis, we addressed the following questions:

1. Does species richness of vernal pools vary with soil type?
2. Does species diversity vary with soil type?
3. Do floristics (as described by cluster analysis and ordination programs) vary with soil type?
4. Do species present on each soil type vary in their fidelity to wetland habitats?

Do plant nutrients vary with soil type?

3.0 SITE DESCRIPTION

Beale Air Force Base is located on rolling grassland in eastern Yuba and western Nevada counties in California at an elevation of 60-250 feet, on ancient alluvial terraces with mound-intermound microrelief (Figure 1, Vicinity Map). Vegetation is predominantly grasses and forbs. Average air temperature is 16° C (61° F) and average annual precipitation is 46-56 cm (18-22"). Most of the rain falls during the winters and the summers are hot and dry. The average frost-free period is between 270-280 days.

The three sites used in this study have been used for many years as annual range for cattle and are presently leased to local ranchers for grazing. All the sites have had similar management regimes, but minor variations in grazing intensity among the sites have undoubtedly occurred. The locations of the three study sites are shown on Figure 2, Site Location Map.

3.1 Soils and Geomorphology:

The landscape at Beale is the result of an interplay between various erosional and constructional processes acting on various geologic formations and processes. The development or modification of the landscape took place during the Pleistocene and Holocene epochs (Parsons, 1983). Geomorphic surfaces are mappable areas of the earth's surface that share a common history; the area of each geomorphic surface is of similar age and is formed by a set of processes during an episode of landscape evolution. A geomorphic surface can be erosional, constructional, or both. The surface may be planar, concave, convex, or any combination of these (Ruhe 1975). Geomorphic surfaces are associated with rock or sediment geologic formations. Each of the surfaces that make up the landscape is the result of an episode of landform development and will be covered with a characteristic assemblage of soils. Soils form on geomorphic surfaces in response to the factors of time, parent material, source biota, relief, and climate.

The three soil types that support vernal pools at Beale are mapped on three geomorphic surfaces (Lytle, 1987):

Low terraces are found at the lowest elevations (approximately 90') in the study area; the San Joaquin soils are mapped on this surface. These soils are forming on the Riverbank Formation (geologic formation).

High terraces are found at intermediate elevations (approximately 110') within the study site; the Redding-Corning soils are mapped on this surface. These soils are forming on the Arroyo Seco Gravels (geologic formation) which consists of sediments containing dark metamorphic, quartzitic, and andesitic pebbles and cobbles.

Hills are located at the highest elevation (approximately 150' to 175') in the study area; the Pardee Variant Complex soils are mapped on this surface. These soils are forming on an exposed knob of a volcanic mudflow known as the Mehrten Formation (geologic formation).

The relationship of the soils to the geomorphic surfaces that they are mapped on is shown in Figure 3. The series descriptions and discussion of soils and geomorphology in the Sacramento County Soil Survey was used to complete this figure (Tugel, 1993).

San Joaquin, 1 to 3 percent slopes - This moderately deep soil is on old alluvial terraces with mound inter-mound microrelief in areas that have not been leveled. It formed in alluvium derived from mixed sources. Included in this map unit are small areas of a soil that is less than 20 inches thick. This soil is often found in the intermound positions. Typically, the surface layer is light brown loam about 4 inches thick. The upper 12 inches of the subsoil is strong brown loam. The lower 9 inches is brown clay. A brown hardpan with many iron and manganese stains is at a depth of 20 to 40 inches.

Soils of the San Joaquin series are fine, mixed, thermic, Abruptic Durixeralfs. According to the Holland (1978) vernal pool classification, vernal pools forming on San Joaquin soils are "hardpan" pools.

Redding-Corning gravelly loam, 3 to 8 percent slopes - This map unit is on old alluvial terraces with mound inter-mound microrelief. This unit is 35 percent Redding and 35 percent Corning. The components of this unit are so intricately intermingled that it was not practical to map them separately at the scale used in the soil survey. Included in this map unit are small areas of soils that are similar to Redding and Corning soils except that they have very gravelly or cobbly textures, and are less than 20 inches deep.

The Redding soil is moderately deep. It formed in alluvium derived from mixed sources. Typically, the surface layer is brown gravelly loam about 6 inches thick. The subsurface layer is yellowish red gravelly loam about 7 inches thick. The upper 6 inches of the subsoil are yellowish red gravelly loam. The lower 14 inches are reddish brown clay. A yellowish red hardpan is at a depth of 20 to 40 inches.

The Corning soil is very deep. It formed in alluvium derived from mixed sources. Typically, the surface layer is yellowish red gravelly loam about 24 inches thick. The upper 7 inches of the subsoil is dark red gravelly clay. The lower 5 inches is brown gravelly clay. The lower part to a depth of 67 inches is mixed strong brown very gravelly sandy loam.

Soils of the Redding series are fine, mixed, thermic, Abruptic Durixeralfs. Soils of the Corning series are fine, mixed, thermic, Typic Palexeralfs. According to the Holland (1978) vernal pool classification, vernal pools forming on Redding-Corning soils are "hardpan" pools.

Pardee Variant complex, 0 to 3 percent slopes - This map unit is on hills. The surface typically has mound-intermound microrelief. This unit is 50 percent Pardee and 50 percent Pardee Variant. Pardee soils are on the mounds and Pardee Variant is in the inter-mounds. The components of this unit are so intricately intermingled that it is not practical to map them separately at the scale used. The Pardee soil is shallow and well drained. It formed in gravelly and cobbly alluvium derived from mixed sources overlying unrelated consolidated andesitic tuffaceous conglomerate. Typically, the surface layer is brown gravelly loam about 4 inches thick. The upper 7 inches of the subsoil is brown very cobbly loam. The lower 6 inches is strong brown very cobbly loam. Mixed gray and light brown, hard, consolidated, andesitic tuffaceous conglomerate is at a depth of 10 to 20 inches. Vernal pools form in the inter-mounds where depth to bedrock is approximately 8 to 10 inches.

Pardee soils are loamy-skeletal, mixed, thermic, Lithic Mollic Haploxeralfs. According to the Holland (1978) vernal pool classification, vernal pools forming on Pardee soils are "mudflow" pools.

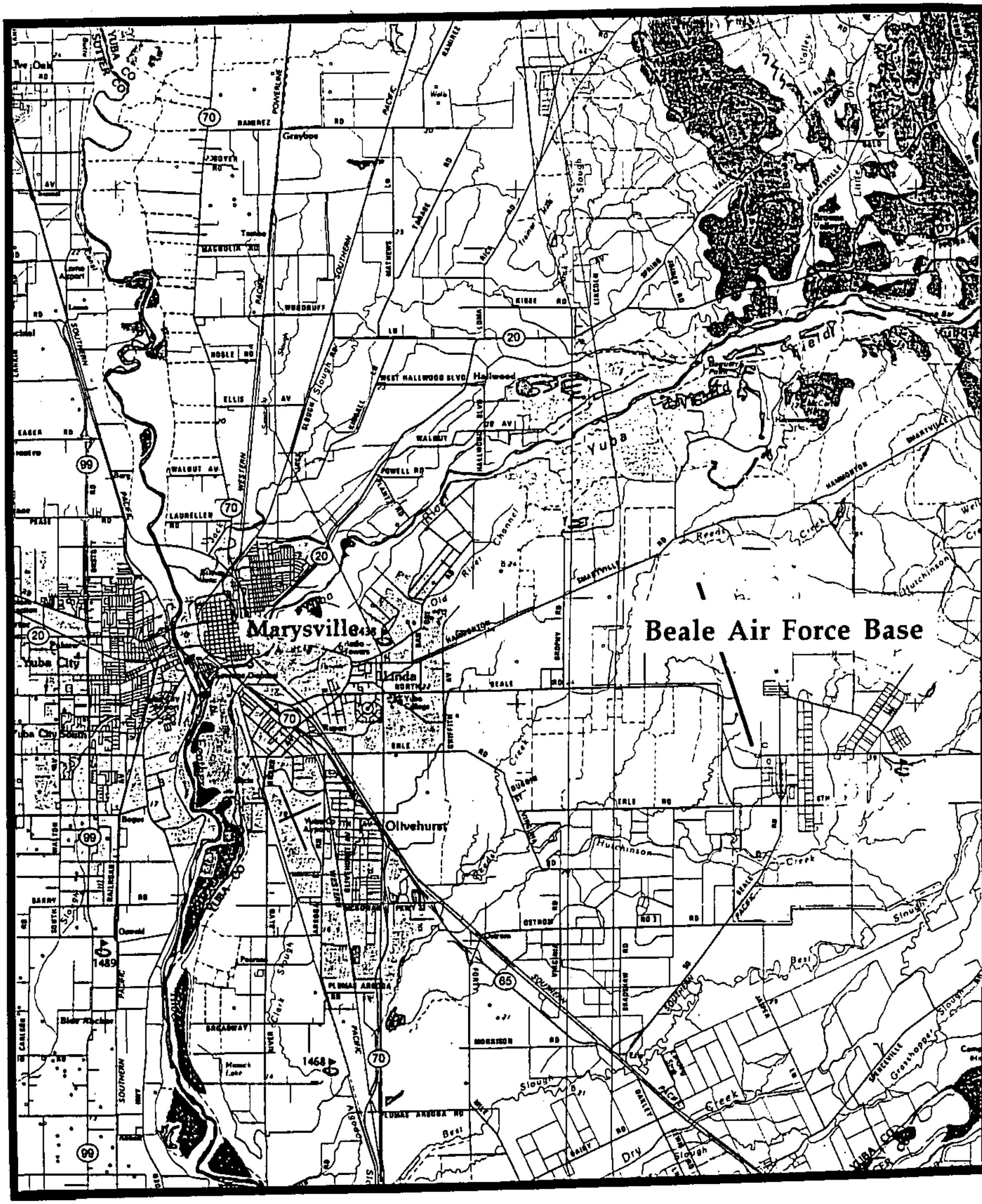

Figure 1. Site Map

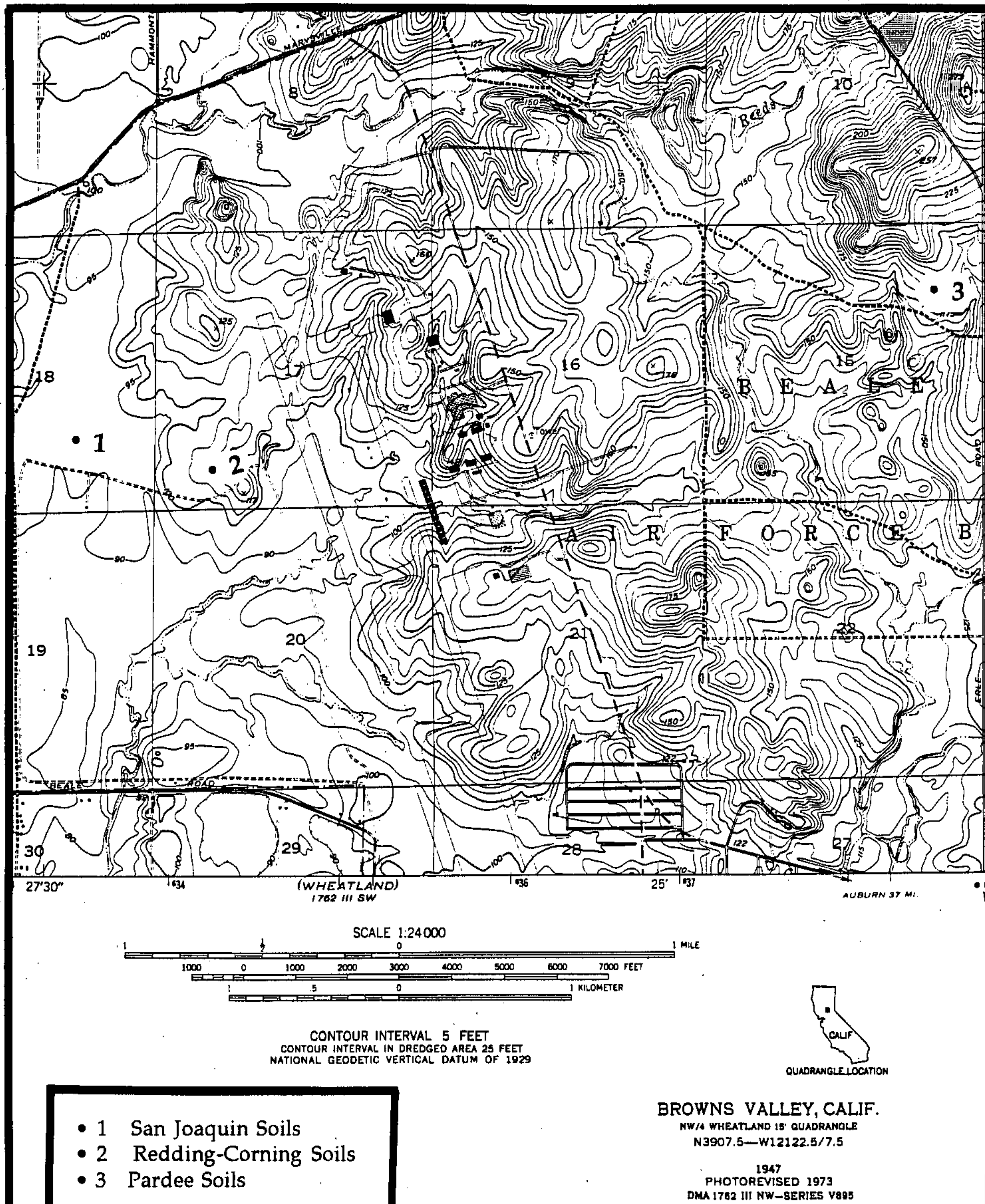

Figure 2. Site Locations

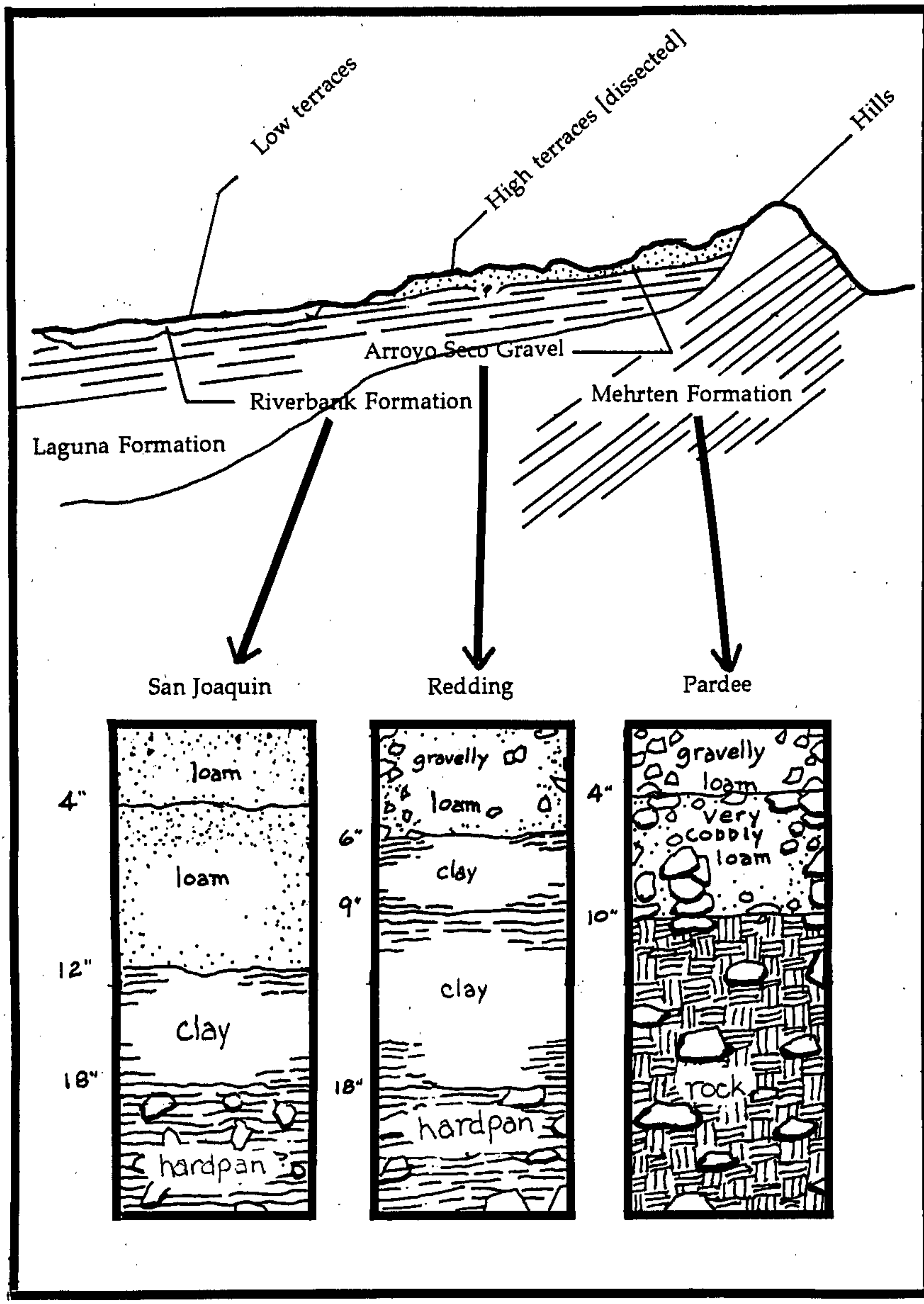

Figure 3. Cross section showing the relationship of geomorphic surfaces, soils, and geology at Beale Air Force Base.

4.0 METHODS

4.1 Plant Community Description:

To describe the plant communities on each of the three soil series, vernal pools of roughly the same size and depth were chosen. Pools were measured across their longest and shortest axes. A tape was stretched across each pool and depths were measured at their visually estimated deepest point. Between April 14-17, 1995, thirteen pools on the Pardee and thirteen on Redding-Corning soils were sampled. A line transect was placed across the length of each pool and ten evenly spaced 1/4 m^2 plots were sampled for absolute percent cover. Actual percent cover was estimated visually, aided by the use of counting frames marked with 50 percent, 25 percent and 12.5 percent. After completion of the quadrats, botanists surveyed the entire pool to note any species that had been missed by the transect for diversity calculations.

In 1996, the number of pools sampled and the number of plots sampled per pool were reduced. A sample curve analysis (number of pools and frames per pool sampled was plotted against number of species encountered) of the 1995 data showed that nine pools with eight frames per pool would lend essentially the same information as the sampling number used in 1995. The placement of the plots was modified from a one-line transect to two perpendicular transects that intersected in the center of the pool. This modification allowed four pool bottom plots and four edge plots to be sampled. Additionally, in 1996 we added San Joaquin soils to the study. Data were collected in the Pardee and Redding-Corning pools on April 13-14, 1996. The San Joaquin pools held water longer and were sampled on May 1, 1996. By this date the water level in the San Joaquin pools had dropped enough to allow sampling, and the plant communities were estimated to have reached the same phenotypic stage as that of the plant communities on the other two soils at sampling.

4.2 Statistical Analysis:

The percent cover of each species recorded in the plots was used to calculate a pool mean for each species. Species detected in the pool survey but not detected in the plots were assigned a percent cover of 0.5 percent cover and were included in the species mean calculations. "Rare" species were those with only a single occurrence and less than 1 percent cover. Rare species are usually deleted from a data matrix prior to multivariate analysis because the inclusion of rare species usually has very little affect on the output, or the inclusion of rare species may obscure the analysis of the data set (Gauch, 1982; Jokerst, 1990).

In 1995 data, 14 species that occurred only once in the 26 pools and had a mean percent cover of less than 1 percent were omitted from DCA and TWINSPAN calculations, as they were unnecessary for floristic analysis. In the 1996 data, the number of species omitted depended on the comparisons being made. When the communities from the three sites were compared, 28 species that occurred only once in the 27 pools and had a mean percent cover of less than 1 were omitted from DCA and TWINSPAN calculations.

Shannon diversity index, species richness, detrended correspondence analysis (DCA), and TWINSPAN were calculated for each year; details of each type of analysis are discussed below.

4.3 Diversity Index and Species Richness

Species richness is the total number of species present in a pool. The Shannon diversity index was used to calculate diversity for each pool, using the formula:

$$H' = -\sum p_i * \ln(p_i)$$

H' is the diversity index number, or the average degree of "uncertainty" in predicting the species of an individual chosen at random from a community (Shannon and Weaver, 1949; Ludwig and Reynolds, 1988), and p_i is the proportion of the total species' abundance represented by species *i* in a pool (species *i* abundance/total species' abundance). Abundance is represented by mean percent cover of a species in a pool. ANOVAS or two sample *t*-tests of richness and diversity were run to see if the Redding-Corning pools differed from the Pardee pools.

4.4 Floristic Characterization

Two statistical programs were used to characterize the relationships of species composition and soil types. DCA is an indirect ordination program that describes overall trends in the floristics of the pool types. DCA is an "indirect" ordination technique because environmental data (such as soil moisture) are not included in the analysis. Ordination arranges sampling units in relation to one or more coordinate axes such that their relative positions to the axes and to each other provides maximum information about their ecological similarities (Ludwig and Reynolds, 1988). In this study sampling units represent the individual vernal pools.

From the DCA output the following relationships were graphed: axis 1 by axis 2, axis 1 by axis 3, and axis 2 by axis 3. DCA axes maximize the multivariate correlation of the vernal pools. Similar pools were clustered together and dissimilar ones are separated. Three axes were produced which best explain the floristic variation in the data set. For each axis an eigenanalysis was performed to produce an eigenvalue, a number which represents the variance accounted for by that axis. An eigenvalue of 40 accounts for 40% of the variance in a community. Eigenvalues are additive; in typical community studies the first three eigenvalues may account for 40% to 90% of the variance. It is important to note that the mere presence of high eigenvalues has not been found to be a reliable indicator of the quality of the results (Hill, 1979a; Gauch, 1982).

TWINSPAN is a classification program which divides the samples (vernal pools) into groups according to species presence or absence and abundance, defined as percent cover. It provides indicator species for the groups it classifies (Hill, 1979b).

TWINSPAN provides a Two-Way Ordered Table of species by pools, showing the divisions using binary code (0s and 1s). Dendrograms of the first three divisions made by TWINSPAN were created for each analysis.

To quantitatively analyze year-to-year changes in percent cover within a soil type due to differences in sampling from 1995 to 1996, a Wilcoxon signed rank test of species' mean percent cover was used.

4.5 Fidelity to Wetland Habitats

We compared the degree of fidelity of the plant species on each soil type to wetlands in general and vernal pools in particular. Two different fidelity classifications were used. The first was developed by the US Fish and Wildlife Service (USFWS). Their classification characterizes wetland vegetation by the probability that a given species will occur in a wetland. Obligate wetland species almost always occur in wetlands (estimated probability >99%) and facultative wetland species usually occur in wetlands (estimated probability 67% -99%) (Reed, 1988).

The second classification system is a working list developed by field biologists at Jones and Stokes Associates, an environmental consulting firm that has conducted numerous floristic surveys in vernal pool habitats in the Great Central Valley of California. Jones and Stokes developed lists of wetland plant species that are likely to be found in vernal pools and plants that occur in a variety of seasonal wetlands; they defined these species as obligate vernal pool species and wetland generalist species respectively.

The results of the USFWS classification are shown in Table 5 and the results of the Jones and Stokes classification are shown in Table 6. It should be noted that this comparison only groups the species for each soil type; it does not address percent cover. Cover is another characteristic that would reflect the affinity of wetland and/or vernal pool plants to each soil type.

4.6 Soil Description and Fertility Analysis:

Soil descriptions were performed using hand dug pits while soil fertility analysis was done by Monarch Labs, Chico, California, on bulked samples from 5 pool bottoms and from 5 associated upland soil from each series. Replicate samples were not analyzed; the statistical significance of these data can not be determined. Nitrate was determined by an electrode test, phosphorus (P) by the Olsen method, and potassium (K), calcium (Ca), and magnesium (Mg), were extracted by ammonium acetate for atomic absorption analysis. Manganese (Mn), iron (Fe), copper (Cu), and zinc (Zn) were extracted with DPTA for atomic absorption analysis. Soil pH was determined on saturated pastes.

5.0 RESULTS

Discussion of statistical analysis is summarized from the data analysis reports prepared by Jean Hubbell, 1995, J. Hubbell and Elizabeth Hubert 1996.

5.1 Diversity Index and Species Richness

In 1995, a total of 99 plant species across two soil types were sampled at Beale. Native species represented 83%, while non-natives were 17% of the total species. In 1996, a total of 84 plant species across three soil types were sampled. Native species represented 80%, while non-natives were 20% of the total species. Both species richness and diversity were calculated, first using all species and then only native species. In 1996, species richness data from San Joaquin pools, using either natives (31) or all species (38), was significantly different from Pardee pool's species richness (22 for natives and 25 all species) (both p's < 0.0001, Tukey's HSD) and Redding-Corning's species richness (26 for natives and 30 for all natives) ($p = 0.009$, $p = 0.033$, Tukey's HSD).

Species diversity in the San Joaquin pools was not significantly different from either of the other pool types. There were no significant differences between Redding-Corning and Pardee pools for either richness or diversity of all species in either year sampled (1995 richness $p = 0.329$, diversity $p = 0.503$; 1996 richness $p = 0.112$, diversity $p = 0.194$). However, diversity and richness within Redding-Corning and Pardee pools varied significantly from 1995 to 1996. The mean species richness and diversity results are shown on Tables 1 and 2.

Table 1. Mean richness and mean Shannon diversity index (H') comparing data from different soil types in 1996. p-values are from t-tests to compare soil types. All values with the same subscripts are not significantly different.

	Mean Richness		Mean Diversity (H')	
Soil Type	all species	natives only	all species	natives only
Pardee				
1996	25a	22c	2.1e	1.9f
Redding-Corning				
1996	30a	26c	2.3e	2.2f
San Joaquin				
1996	38b	31d	2.3e	2.0f
	Richness p values all species	**Richness p values natives only**		
Pardee vs Redding-Corning	0.112	0.101		
San Joaquin vs Pardee	<0.0001	<0.0001		
San Joaquin vs Redding-Corning	0.009	0.033		
	Diversity p values all species	**Diversity p values natives only**		
Pardee vs Redding-Corning vs San Joaquin	0.194	0.170		

Table 2. Mean richness and mean Shannon diversity index (H') for the different soil types in each year. Note: 1995 numbers were calculated using only pools that were sampled in both years. p-values are from t-tests to compare 1995 to 1996 within a soil type.

	Mean Richness		Mean Diversity (H')	
Soil Type	all species	natives only	all species	natives only
Pardee				
1995	39	35	2.7	2.2
1996	25	22	2.1	1.9
p values	0.001	0.001	<0.0001	0.032
Redding-Corning				
1995	37	34	2.8	2.4
1996	30	26	2.3	2.2
p values	0.014	0.002	0.034	0.192

In 1995, mean richness in the Redding-Corning pools was 36 species, and was not significantly different from the mean species richness (39) of the Pardee pools. If richness is calculated using only native species, the Redding-Corning and Pardee means are 34 and 35. In addition, in 1995 mean species diversity as shown by the Shannon index, calculated using all species and only native species, did not differ significantly between pool types.

Diversity in 1996 did not differ among soil types. The Shannon diversity index does differ within a soil type from 1995 to 1996, when all species were used for Redding-Corning pools, and for Pardee pools when only native species were used.

5.2 Floristic Characterization

DCA: For 1995 mean percent cover data, plots of the DCA axes shown in Figure 4 demonstrate the clustering of pools on the same soil type. Axes 1 and 2 represent 39% of the variation in the data set (axis 1 EIG=0.261, axis 2 EIG=0.131). Eigenvalues for axes 1 and 2 for each of the DCA plots are shown in Table 3.

For 1996 data, plots of DCA axes shown in Figure 5 demonstrate clustering of pools on the same soil types. Clustering appears to be more evident for San Joaquin than the other 2 soil series. Axes 1 and 2 represent 54% of the variation in the data set (axis 1 EIG=0.251, axis 2 EIG=0.160). When DCA was run using only pools that were sampled in both years, axes 1 and 2 represent 47% of the variation (axis 1 EIG=0.312; axis 2 EIG=0.155) in 1995. In 1996 axes 1 and 2 represent 41% of the variation (axis 1 EIG=0.363; axis 2 EIG=0.181).

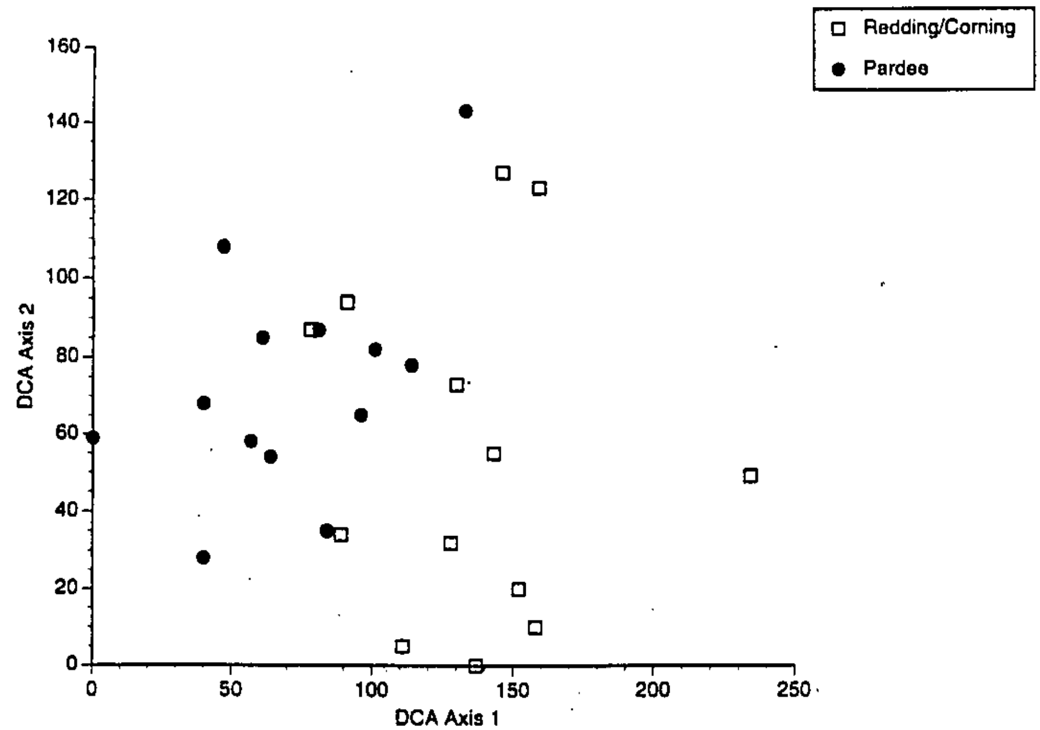

Figure 4. 1995 Detrended Correspondence Analysis (DCA) ordination of the floristic variation among vernal pools sampled on Redding-Corning soils ("hardpan" pools) and Pardee soils ("mudflow" pools). The first and second axes are shown. Each symbol represents and individual vernal pool.

Figure 5. 1996 Detrended Correspondence Analysis (DCA) ordination of the floristic variation among vernal pools sampled on San Joaquin soils ("hardpan" pools), Redding-Corning soils ("hardpan" pools), and Pardee soils ("mudflow" pools). The first and second axes are shown. Each symbol represents and individual vernal pool.

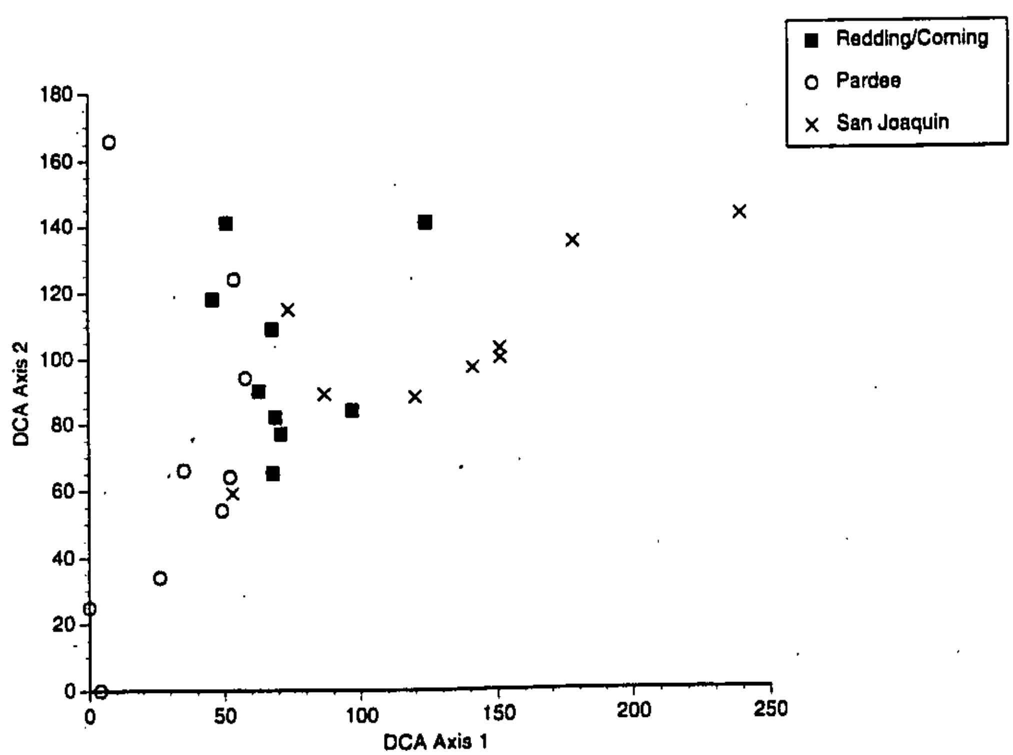

Table 3. Eigenvalues, percent variation accounted for by axes 1 and 2 for each of the soil types sampled in 1995 and 1996.

Year	Soil Types	Axis 1	Axis 2	% Variation
1995	Redding-Corning, Pardee	0.261	0.131	39
1995	Redding-Corning, Pardee (pools sampled both years)	0.312	0.155	47
1996	Redding-Corning, Pardee (pools sampled both years)	0.251	.160	41
1996	San Joaquin, Redding-Corning, Pardee	0.363	0.181	54

TWINSPAN's first division of the pools is by soil series, as shown in the dendrograms for 1995 and 1996 (Figures 6 and 7). With the 1995 data, using only pools sampled in both years, *Plagiobothrys stipitatus* var. *stipitatus* and *Brodiaea* species are the indicator species of Redding-Corning pools and *Lolium multiflorum* is the indicator species of Pardee pools. With analysis of the 1996 data, *Leontodon taraxacoides* is the indicator species of San Joaquin pools, separating San Joaquin pools from Pardee and Redding-Corning pools. TWINSPAN indicator species are shown in Table 4.

Table 4. Indicator species for the different soil types for each of the data sets for which TWINSPAN was run each year. ANOVAS or *t*-tests were run to determine if percent cover of the indicator species was significantly different among the soil types. NS indicates tests were nonsignificant. If the tests were significant, the *p*-value is shown.

Data set	Year	Soil Type	Indicator Species	Significance
All pools, all species	1995	Pardee	*Lolium mult.*	NS
"	1996	Pardee	*Juncus buf.*	NS
"	1995	Redding-Corning	*Lasthenia platy.*	NS
"	1996	San Joaquin	*Leontodon tax.*	$p = 0.001$
Natives as indicators	1995	Pardee	*Centunculus mini.*	$p = 0.004$
			Poa anua	$p = 0.032$
			Lasthenia fremont.	$p = 0.003$
"	1996	Pardee	N/A	
"	1995	Redding-Corning	*Lasthenia platy.*	NS
"	1996	Redding-Corning	N/A	
"	1996	San Joaquin	*Limnanthes alba.*	$p = 0.003$
			Mimulus tricolor.	$p < 0.0001$
			Ranunculus bonari.	$p = 0.015$
Pools Sampled 1995 and 1996	1995	Pardee	*Lolium multi.*	NS
"	1996	Pardee	N/A	
"	1995	Redding-Corning	*Plagiobothrys stip.*	NS
"	1996	Redding-Corning	*Castilleja camp.*	NA
			Pilularia americana.	$p = 0.033$
			Juncus buf.	NS

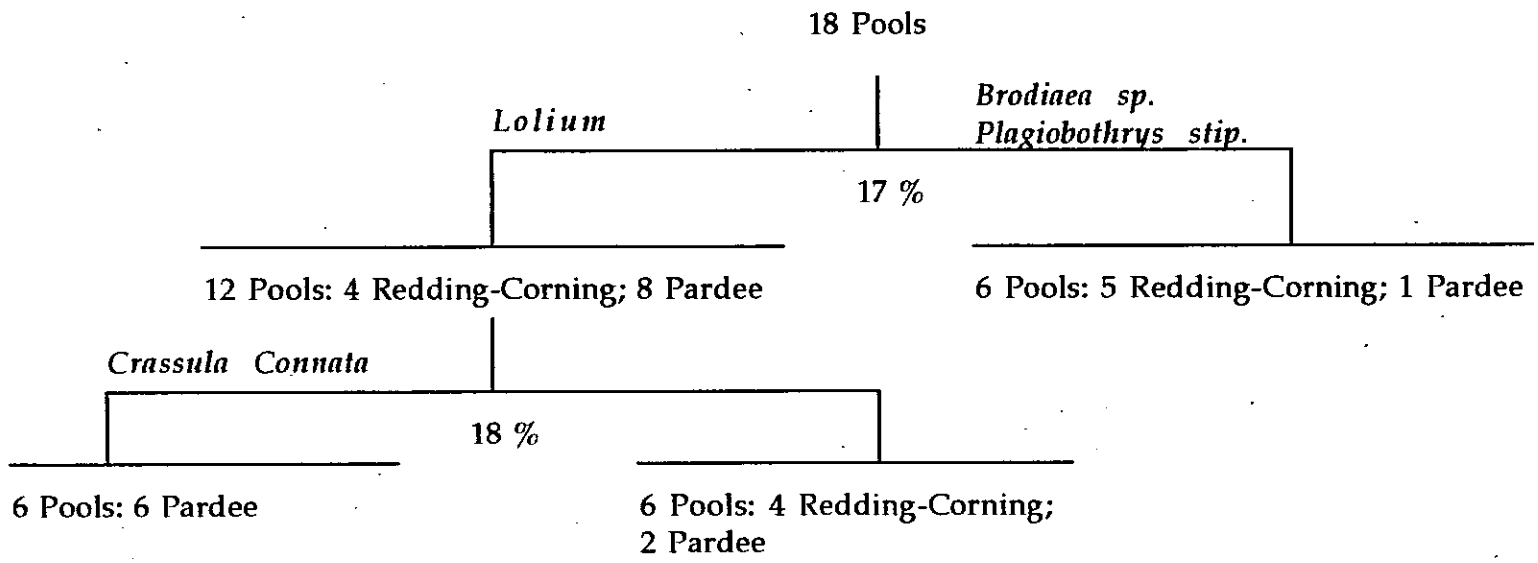

Figure 6. 1995 dendrogram of TWINSPAN groupings and their respective indicator species for vernal pools sampled in both 1995 and 1996 on Redding-Corning and Pardee soils. Percents beneath the divisions are eiganvalues and represent the percent of variation in the data set explained by that division.

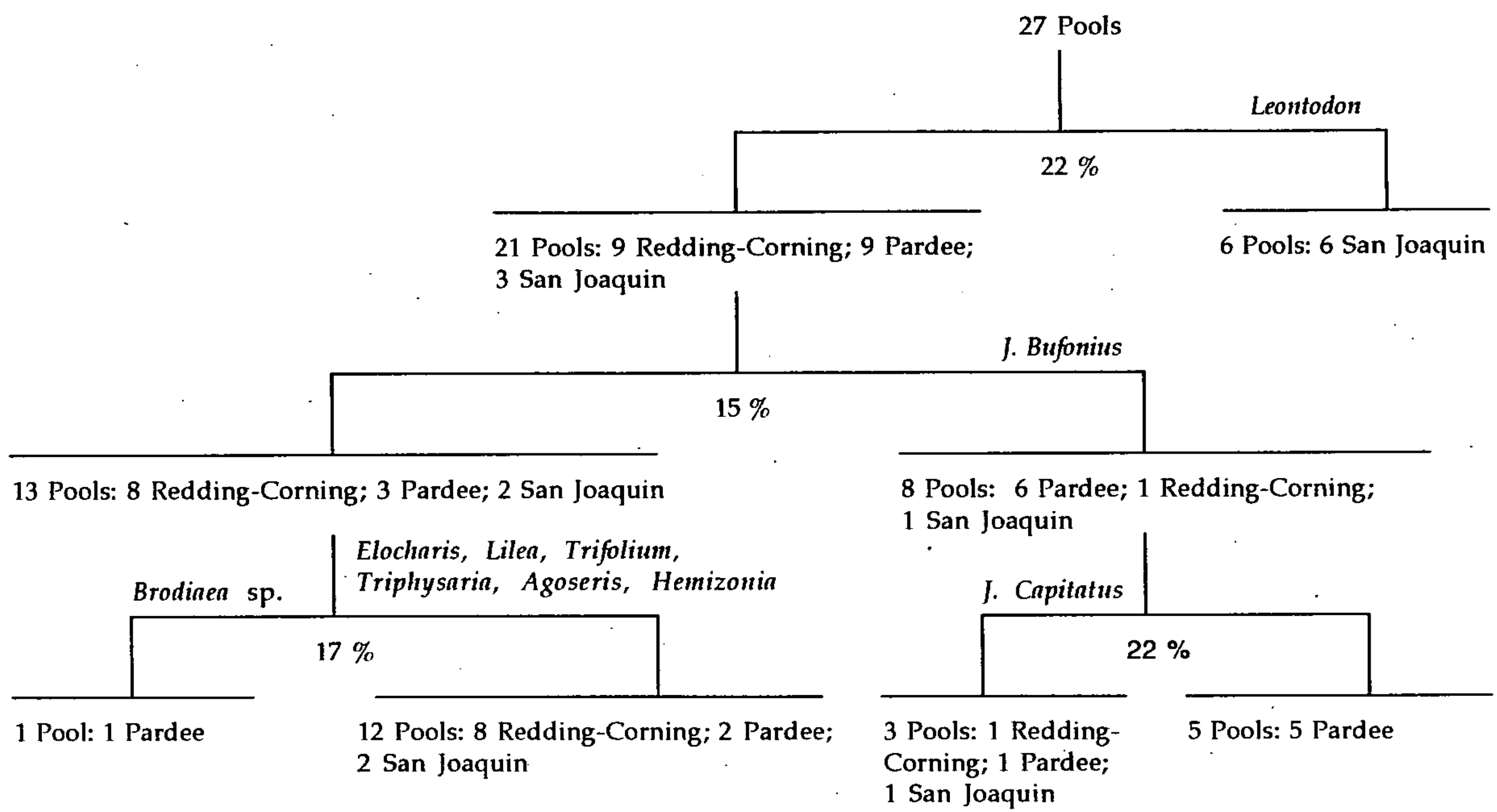

Figure 7. 1996 dendrogram of TWINSPAN groupings and their respective indicator species for vernal pools sampled on San Joaquin, Redding-Corning, and Pardee soils. Percents beneath the divisions are eiganvalues and represent the percent of variation in the data set explained by that division.

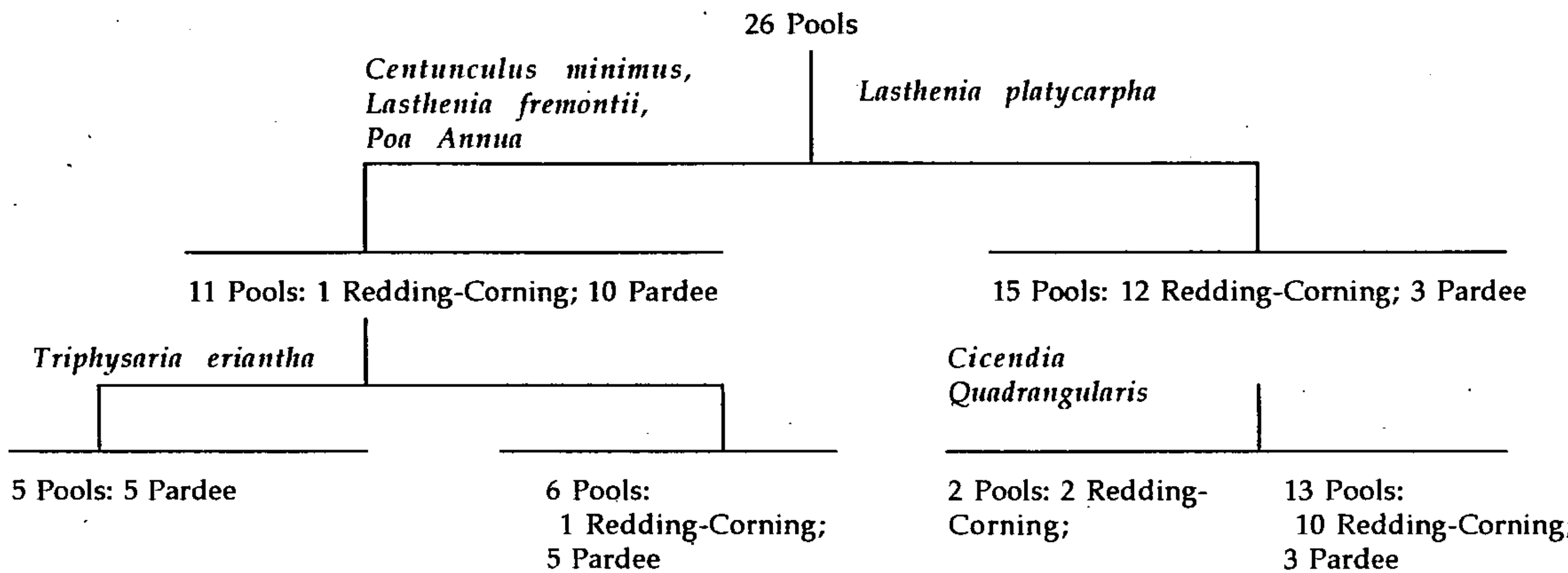

Figure 8. 1995 dendrogram of TWINSPAN groupings and their respective indicator species with *Lolium multiflorum* suppressed for vernal pools sampled on Redding-Corning and Pardee soils. Percents beneath the divisions are eiganvalues and represent the percent of variation in the data set explained by that division.

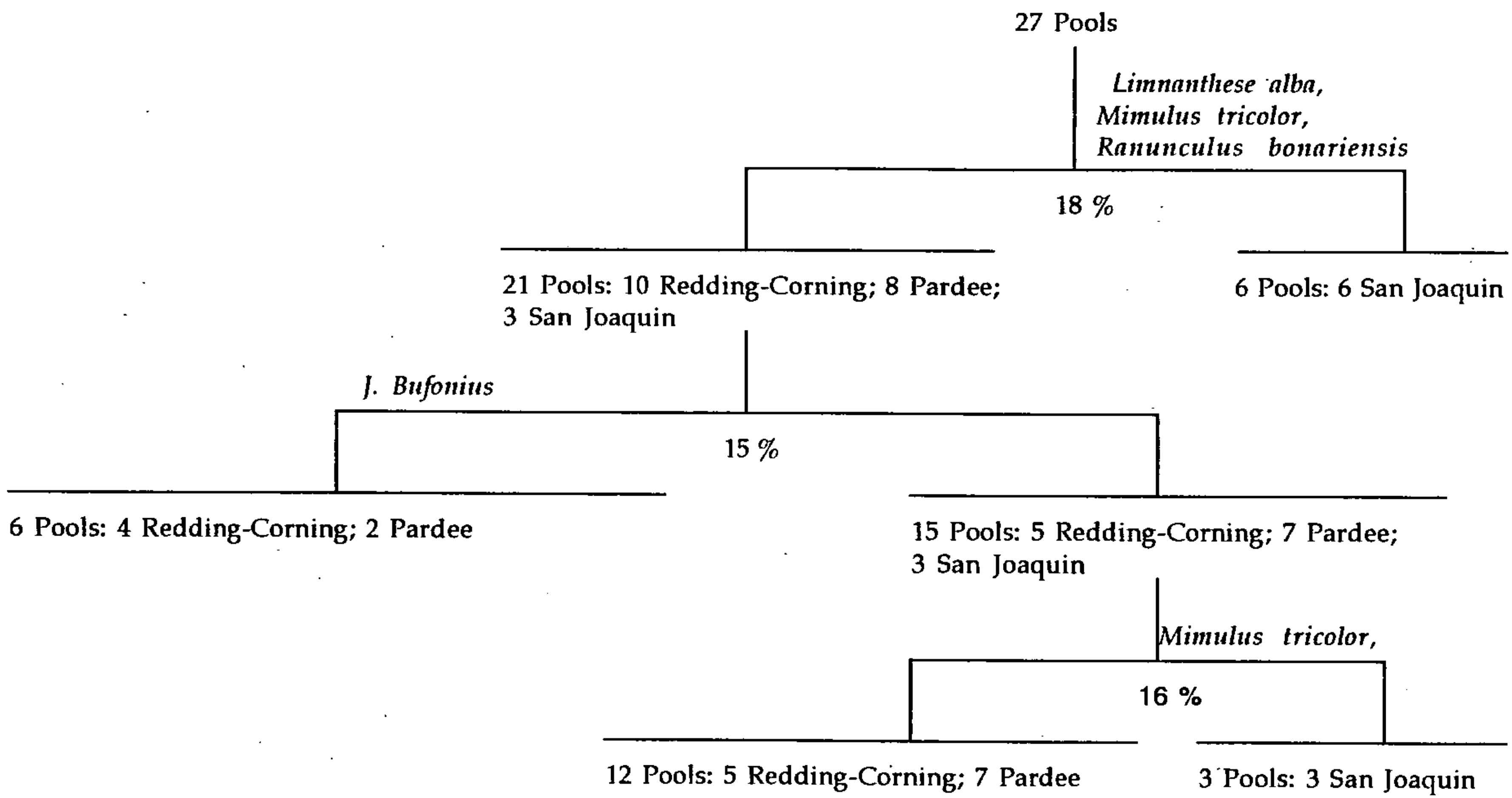

Figure 9. 1996 dendrogram of TWINSPAN groupings and their respective indicator species with *Leontodon taraxacoides* suppressed for vernal pools sampled on San Joaquin, Redding-Corning, and Pardee soils. Percents beneath the divisions are eiganvalues and represent the percent of variation in the data set explained by that division.

In 1996 TWINSPAN's second division of the pools is again by soil series; *Juncus bufonius* is the indicator species of Pardee pools, separating Pardee pools from Redding-Corning pools.

In both 1995 and 1996 the species that separated the soils were non-natives *(Lolium multiflorum* and *Leontodon taraxacoides).* To determine how the pools would be separated using native indicator species, we re-ran TWINSPAN suppressing non-native indicator species and obtained essentially the same results (Figures 8 and 9). Again, pools were separated by soil series in the first division.

Finally, we were concerned that differences in the soil types might be obscured by analyzing the edge and bottom plots together. Vernal pool vegetation is zonated; edge vegetation is often different from pool bottoms. DCA and TWINSPAN analyses were repeated, separating edge and bottom plots, to explore whether differences in soil series are determined by edge or bottom plots alone. There were no differences between the DCA and TWINSPAN results using either the pool bottom and pool edge data or the combined pool data.

The Wilcoxen signed rank test showed that percent cover was not significantly different from year-to-year within either soil type. Lack of significant difference suggests that environmental and sampling technique variations did not significantly affect the results.

5.3 Fidelity to Wetland Habitats

The results of the characterization of the species present in the vernal pools on each soil type is shown in Tables 5 and 6.

Table 5 USFWS Indicator Status Plants Present on three soil types at Beale Air Force Base in 1996. Bold typeface indicates native taxa.

Scientific Name	Indicator Status	Pardee	Redding Corning	San Joaquin
Achyrachaena mollis	FAC	X	X	X
Agoseris heterophylla	UPL	X	X	
Aira caryophyllea	UPL			X
Allium amplectens	UPL	X	X	X
Alopecurus saccatus	OBL	X		
Briza minor	FACW	X	X	X
Brodiaea minor	UPL	X	X	X
Bromus hordeaceus	FACU	X	X	X
Callitriche marginata	OBL	X	X	X
Cardamine oligosperma	FACW		X	
Castilleja attenuata	UPL			X
Castilleja campestris	OBL	X		X
Centunculus minimus	FACW	X	X	X

Scientific Name	Indicator Status	Pardee	Redding Corning	San Joaquin
Cicendia quadrangularis	UPL	X	X	X
Crassula aquatica	OBL	X	X	X
Crassula connata	UPL		X	X
Cuscuta howelliana	UPL	X	X	X
Deschampsia danthonioides	FACW	X	X	X
Dichelostemma capitatum ssp. ***capitatum***	UPL			X
Dichelostemma multiflorum	UPL			X
Downingia bicornuta	OBL	X	X	X
Downingia cuspidata	OBL		X	
Downingia ornatissima	OBL	X	X	X
Eleocharis acicularis	OBL	X	X	X
Eleocharis macrostachya	OBL		X	X
Eremocarpus setigerus	UPL	X		X
Eryngium vaseyi	FACW	X	X	X
Gratiola ebracteata	OBL	X	X	X
Hemizonia fitchii	UPL		X	X
Hordeum murinum ssp. *gussoneanum*	FAC	X	X	X
Hypochaeris glabra	UPL	X	X	X
Isoetes orcuttii	OBL	X	X	X
Isoetes nutallii	OBL	X		
Juncus bufonius	FACW	X	X	X
Juncus capitatus	FACU	X	X	X
Juncus uncialis	OBL	X	X	X
Lasthenia californica	FACU	X	X	X
Lasthenia fremontii	OBL	X	X	X
Lasthenia platycarpha	FACW	X	X	
Layia fremontii	UPL	X	X	X
Legenere limosa	OBL		X	
Leontodon taraxacoides	FACU	X	X	X
Lepidium nitidum	UPL		X	X
Lolium multiflorum	FAC	X	X	X
Lythrum hyssopifolium	FACW	X	X	X
Medicago sp.	UPL		X	X
Microseris douglasii.	UPL			X
Microseris sp.	UPL	X		X
Mimulus tricolor	OBL			X
Minuartia californica	UPL	X		
Myosurus minimus	OBL			X
Navarretia leucocephala var . ***leucocephala***	OBL	X	X	X
Navarretia tagetina	UPL	X		X
Pilularia americana	OBL	X	X	X
Plagiobothrys greenei	FACW	X	X	X
Plagiobothrys stipitatus* var. *micranthus	OBL	X	X	X
Plagiobothrys stipitatus* var. *stipitatus	OBL	X	X	X
Plantago coronopus	FAC	X		
Plantago elongata	FACW		X	
Poa annua	FACW-	X	X	

Scientific Name	Indicator Status	Pardee	Redding Corning	San Joaquin
Pogogyne zizyphoroides	OBL	X	X	X
Psilocarphus brevissimus	OBL	X	X	X
Psilocarphus oregonus	OBL	X	X	X
Psilocarphus tenellus* var. *tenellus				
Ranunculus bonariensis	OBL	X	X	X
Scribneria bolanderi	UPL			X
Sidalcea calycosa	OBL			X
Taeniatherum caput-medusae	UPL	X	X	
Trifolium depauperatum	FAC-	X	X	X
Trifolium dubium	FACU			X
Trifolium variegatum	FACW-		X	
Trifolium wildenovii	UPL			X
Triphysaria eriantha	UPL	X	X	X
Triteleia hyacinthina	FACW	X	X	X
Veronica peregrina* ssp. *xalapensis	OBL		X	
Vulpia bromoides				
Vulpia microstachys	FACU	X	X	
Total Number of Species		53	56	60
Percent OBLIGATES		38%	38%	37%
Percent FAC wet		17%	20%	13%
(FACW-, FAC, FAC +) Percent FAC		9%	9%	5%
(FAC-, NI, UPL, FACU) Percent Upland		36%	34%	45%

*As determined by the US Fish and Wildlife Service, Biological Report 88 (26.10), May 1988: National List of Plant Species that Occur in Wetlands: California (Region O).

Table 6 Vernal pool obligate* species and wetland generalists occurring in vernal pools on three soil types at Beale Air Force Base in 1996.

	Pardee	Redding-Corning	San Joaquin
Alopecurus saccatus		VP	
Callitriche marginata	WG	WG	WG
Castilleja campestris		VP	VP
Crassula aquatica	WG	WG	WG
Downingia bicornuta	VP	VP	VP
Downingia ornatissima	VP	VP	VP
Eleocharis acicularis	WG	WG	WG
Eleocharis macrostachya	WG		
Gratiola ebracteata	VP	VP	VP
Isoetes nuttallii	WG		
Isoetes orcuttii	WG	WG	WG
Juncus uncialis	VP	VP	VP
Lasthenia fremontii	VP	VP	VP
Lilaea scilloides	WG		
Limnanthes alba			VP
Mimulus tricolor			VP
Myosurus minimus			WG
Navarettia leucocephala	VP	VP	VP

	Pardee	Redding-Corning	San Joaquin
Pilularia americana	WG	WG	WG
Plagiobothrys stipitatus var. *stipitatus*	WG	WG	
P. stipitatus var. *micranthus*	WG	WG	WG
Pogogyne zizyphoroides	VP	VP	VP
Psilocarphus brevissimus	VP	VP	VP
P. oreganus	VP	VP	VP
Sidalcia calycosa			WG
Veronica perigrina ssp. *xalapensis*	WG		
Vernal Pool Obligates*	9	11	12
Wetland Generalists*	11	7	8
Total Wetland Obligates**	20	18	20

*Based on an analysis made by Jones & Stokes included in Floristic Analysis of Volcanic Mudflow Vernal Pools by James D. Jokerst in Vernal Pool Plants--Their Habitat and Biology , D.Ikeda and R. A. Schlising [eds.] , Studies from the Herbarium No. 8, California State University, Chico.

**As determined by the US Fish and Wildlife Service, Biological Report 88 (26.10), May 1988: National List of Plant Species that Occur in Wetlands: California (Region O).

5.4 Soil Analysis

Examination of soils at each of the three sites confirmed the NRCS (Natural Resource Conservation Service) soil map.

Results of the soil fertility analysis is shown in Table 7.

Table 7. Analysis of plant nutrients on Pardee, Redding-Corning, and San Joaquin soil series.

	PPM								
Soil Series.	NO3-	P	K	Mg	Ca	Zn	Cu	Mn	Fe
Pardee-Upland	120	11	130	310	2010	1.6	0.8	74	54
Pardee Pools	78	11	100	490	2630	1.2	0.8	58	62
Redding-Corning Upland	9	7	110	200	1180	1.3	1.1	34	69
Redding-Corning Pools	14	6	60	440	1100	0.6	1.1	34	74
San Joaquin Upland	19	5	50	260	1260	0.6	1.1	58	23
San Joaquin Pools	29	7	90	240	1130	1.0	2.3	125	103

6.0 DISCUSSION

6.1 Floristic Characterization

DCA and TWINSPAN provided the clearest picture of differences among plant communities on Redding-Corning, Pardee, and San Joaquin soil series. Floristics generally differed among pools on the three soil types, suggested that these are somewhat different plant communities. Our 1996 data suggests that the plant communities on the San Joaquin soils generally differed from those on Redding-Corning and Pardee. DCA eigenvalues for these analyses are moderately strong. When Redding-Corning and Pardee communities were analyzed using only pools sampled in both years, the communites were separated by soil type in both 1995 and 1996. However, it can be seen in the DCA plots that soil type separation is not perfect; some overlap of the vernal pools (points on the graphs) from different soil types occurred.

TWINSPAN supported the DCA findings that plant community composition varies with soil series. However, as in the DCA graphs, the dendrograms showed that soil type separation is not perfect; some overlap of the vernal pools from different soil types occurred.

Our findings agreed with those of Holland and Dains (1990) in their Flying M Ranch study, that vernal plant communities vary with soil type. They also used DCA and TWINSPAN to sort pools on the basis of floristic patterns and soil; they concluded that floristic composition varies with soil. However since vernal pools are small inclusions in soil map units and are often not described, comparisons between plant communities and soil series cannot provide information about potential specific causal relationships for the variation. Additionally, their study included detailed profile descriptions of vernal pools soils and plant communities. They concluded that vernal pools are exceedingly complex ecosystems, consisting of interactions among semi-independent factors, and that hydrology is probably as important as the soil profile (Holland and Dains, 1990).

The differences seen in plant communities at Beale may be due to hydrologic characteristics related to the soil series and geomorphic surface the soil is forming on. Even though the San Joaquin and Redding-Corning soils both have hardpans and clay layers that pond water, the San Joaquin soils were wetter longer than the Redding-Corning soils. The San Joaquin pools are at the lowest elevation of the three soil types studied; water may be flowing to San Joaquin pools through surface or subsurface flow from upslope positions. The Pardee and Redding-Corning soils may be acting as watersheds for the San Joaquin pools.

Another explanation of the observed differences in the plant communities may be related to sampling time: San Joaquin pools were sampled 14 days later to allow the vegetation to reach the same phenological stage of the communities on the other soil types; the longer growing season may have allowed some plants to be identified that could not be observed in the other pool types.

We found that there was considerable variation in the indicator species produced by TWINSPAN for each soil type. For both Redding-Corning and Pardee soil types, indicator species changed from year to year and for each data set analyzed. Indicator species work best in communities where there is a dominant species or unique species. The inconsistencies of indicator species on the Redding-Corning and Pardee soils suggest that these communities lack a dominant species. This variability indicates that these communities are dynamic and lack consistent dominant species. The pools should be differentiated at the community level, not by individual species. San Joaquin may have more reliable indicator species, but data must be gathered in additional years to check if the determined indicators are stable in multiple seasons.

6.2 Species Richness and Diversity

In 1995, there were no significant differences in species richness or diversity between the Redding-Corning and Pardee soil types in 1995, but in 1996 when San Joaquin pools were added to the study, Redding-Corning and Pardee pools differed significantly in richness from San Joaquin. San Joaquin pools were wet longer than the others and displayed the greatest richness of the three types. Duration of saturation may affect species richness, as drydown over a prolonged period of time could provide more niches for germination and growth of additional species.

Species richness declined significantly on both Pardee and Redding from 1995 to 1996. For example, fourteen species detected on Pardee in 1995 were not detected in 1996. Greater numbers of species in 1995 could have been due to unusually abundant rainfall during the winter and spring preceding the growing season. The timing and amount of rainfall may have provided favorable conditions to support greater numbers of species in 1995.

The species richness of individual pools studied at Beale was higher than that reported by other researchers (Holland and Jain, 1977). In 1995 the Pardee pools had mean richness of 38 species per pool. Richness for individual pools ranged from 29 to 49. Holland and Jain (1977) found in their Rancho Seco study that individual pools had lower species richness (20.5 species/pool; range 16-25 species/pool) than pools at the Beale site. Only 3 of the 60 species encountered were present in all pools and 7 species were encountered in only 1 pool. Bauder stated that in her experience pools averaged 20 species per pool in San Diego County (Bauder, 1996). The increased richness per pool at Beale Air Force Base may in part be due to more favorable environmental conditions, management regimes, or differences due to sampling intensity or methods.

Our data supported the findings of previous researchers that vernal pool plant community's species richness shows a high percentage of native species when compared to the surrounding naturalized grassland (Zedler, 1990; Jokerst, 1990; Holland, 1978).

6.3 Fidelity to Wetland Habitats

The species lists on all three soil types had approximately the same percentage of obligate wetland species (USFWS), and a smaller number of FACw, and FAC, and upland species made up a greater percentage of the total species encountered in San Joaquin pools. Pardee and Redding-Corning are quite similar in the number of species found within each wetland indicator status category. This result is somewhat surprising. The shallow soils in Pardee pools were not expected to support as many obligate wetland species as the deeper San Joaquin and Redding soils. The number of upland species in San Joaquin pools is also puzzling. San Joaquin soils were wetter longer than either of the other soils and because of longer inundation would be expected to have a species list dominated by wetland species. In contrast to our findings, Stone (1990) found that inundation prevents invasion by upland plants. The San Joaquin pools did have slightly more vernal pool obligates than the other two soils according to the Jones and Stokes classification scheme.

6.4 Soil Analysis

The results of the macronutrient analyses are surprising; Pardee has more N, P, and K than either of the other two soils. Pardee is a very shallow rocky soil and would be expected to be less fertile than the deeper soils. The level of Manganese found in all three soils (both pools and uplands) is very high (ranging from 34 to 125 ppm). Concentrations of Mn^{+2} in acid to neutral soils is commonly 0.01 to 1 ppm. Mn in the soil solution is increased in acid soils in low-redox conditions. In acid flooded soils, Mn^{+2} concentrations can be high enough to be toxic to plants (Tisdale et al., 1993). We have found high concentrations of Mn at in the vernal pool soils at Vina Plains (unpublished data) and Hobson (1996) stated that he had also found high Mn concentrations in vernal pools. If these results are widespread, manganese concentrations may help to explain the high degree of endemism seen in vernal pool plant communities, as high levels of manganese may be excluding some non-native species. Replicate soil samples were not run; it is not possible to determine if these results are significant.

7.0 CONCLUSIONS

Some of the soils that support vernal pools are 600,000 years old, resulting in well-developed profiles with impermeable silica or iron cemented hardpans and / or dense clay layers underlying vernal pools (Holland and Jain, 1977). As a restricting layer almost universally underlies vernal pools, the type of impermeable layer was used by Holland (1978) to classify pools. His classification recognizes mudflow, claypan, and hardpan pools. In claypan pools, a hard clay layer lies directly over siltstone, which may weather, adding to the clay in the pool bottom and allowing slow vertical drainage. If pool soil is underlain by a duripan, which may have been sculpted by flowing water in ancient times, it is classed as a hardpan pool. The hardpan may be as thick as one meter (Holland and Jain, 1981) but pools that are not well sealed may allow vertical seepage of water out of the pool through breaks or cracks in the hardpan. This system has been used extensively to describe vernal pools throughout California.

We found indications that all hardpan pool plant communities may not be alike. The plant communities in the Redding-Corning pools (hardpan pools) and the Pardee pools (mudflow pools) are more similar to each other than to the plant community found in the San Joaquin pools (hardpan pools). From our data it would be difficult to classify vernal pools from the type of impermeable layer as it relates to plant communities. Although detailed soil descriptions of the vernal pool soils in our study sites were not made, the observed differences are probably not due to differences in soil texture or depth above the hardpan. The soil depth and textures of the San Joaquin and Redding-Corning soils are similar.

Vernal pools can also be grouped hydrologically by the dominant pathways that water enters and leaves a pool. The relative magnitude of these fluxes will depend on soil type, geomorphic position, and seasonal climate. Analysis of the dominant hydrologic fluxes in vernal pools is a useful tool in vernal pool classification (Hanes et al., 1990). Our study did not address hydrology; we noted that in late April, the San Joaquin pools still had substantial amounts of standing water while the Pardee and Redding-Corning pools were drying down.

Our data suggest that at Beale Air Force Base plant communities are varying with geomorphic surface and thus soil type. These findings support Smith and Verril's (1996) suggestion that geomorphology and soils can be used to provide a framework for the systematic classification of vernal pools. Hydrologic regime may also vary with geomorphic surface and soil type, but further research needs to be done to clarify this relationship.

7.1 Areas for Future Research

Four areas emerge as high priorities:

(1) Data should be collected in additional years at Beale and on the same soils at other sites, to further test the hypothesis that different soils (at the level of soil series) will support measurably different vernal pool plant communities. This information is critical because our data suggest that the San Joaquin pools' plant communities were different from the other communities, but these pools were sampled in only one year.

(2) The questions about the source of water on the San Joaquin soils are important; many creation plans assume that direct precipitation is the main source of water in vernal pools. If San Joaquin pools do have relatively large watersheds, these areas should also be conserved when the pools are protected. Rainfall and pool ponding information is needed to clarify the hydrologic relationships between the soils at Beale.

(3) Detailed descriptions of the soil profiles in each of our study areas may provide information about the cause of the longer ponding period in the San Joaquin pools. The

surface texture of the soils in our study areas was similar. However, vernal pool soils are usually mapped as undescribed inclusions; a detailed study of these soils would describe the depth and texture of soils overlying the hardpan or mudflow.

(4) The role that high levels of manganese and iron are playing in vernal pool plant communities should be explored further. These data could help to explain the high degree of endemism seen in vernal pool plant communities.

(5) The relationship between soils and vernal pool invertebrate communities has not been characterized. Information about this relationship may provide valuable insight for conservation of these communities.

REFERENCES

Barbour, M. G., J. H. Burk, and W. A. Pitts. 1987. Terrestrial Plant Ecology. Second Ed. Benjamin/Cummings Pub. Co., Inc. Menlo Park CA.

Baskin, Yvonne. 1994. California's ephemeral vernal pools may be a good model for speciation. Bio Science 44:384-388.

Bauder, E. 1996. Personal Communication. Department of Biology. San Diego State University, CA 92182-0057.

Ferren, W. R. Jr., Fiedler, P. L., and R. A. Leidy. 1996. Wetlands of California, Part I: history of wetland habitat classification. Madrono 43:105-124.

Gauch, H. G., 1982. Multivariate Analysis in Community Ecology. Cambridge University Press. Cambridge MA.

Hanes, W., T., Hecht, B., and L.P. Stromberg. 1990. Water relationships of vernal pools in the Sacramento region, California. *In* D. Ikeda and R. A. Schlising [eds.], Vernal Pool Plants--Their Habitat and Biology, Studies from the Herbarium No. 8, 49-60. California State University, Chico.

Hill, M.O. 1979a. DECORANA -- a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca NY.

Hill, M.O. 1979b. TWINSPAN -- a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca NY.

Hobson, B. 1996. Personal Communication. Department of Land Air Water Resources, University of California, Davis. Davis CA 95616.

Holland, R. F. 1978. Geographic and edaphic distribution of vernal pools in the Great Central Valley, California. Special Publication No. 4., California Native Plant Society, Berkeley, California.

Holland, R. F. 1986. Preliminary descriptions of the terrestrial natural communities of California. California Department of Fish and Game, Sacramento. Unpublished.

Holland R. and V. I. Dains 1990. The edaphic factor in vernal pool vegetation. *In* D. Ikeda and R. A. Schlising [eds.], Vernal Pool Plants--Their Habitat and Biology, 31-48. Studies from the Herbarium, No. 8, California State University, Chico.

Holland, R. F. and S. Jain. 1977. Vernal pools. *In* M. G. Barbour and J. Major [eds.], Terrestrial Vegetation of California, 515-533. Wiley-Interscience, New York NY.

Holland R. F. and S. Jain. 1981. Insular biogeography of vernal pools in the Central Valley of California. Amer. Nat. 117:24-37.

Jokerst, J. D. 1990. Floristic analysis of volcanic mudflow vernal pools. *In* D. Ikeda, and R. A. Schlising [eds.], Vernal Pool Plants--Their Habitat and Biology, 1-30. Studies from the Herbarium No. 8, California State University, Chico.

Ludwig, J. A. and J.F. Reynolds. 1988. Statistical Ecology. Wiley Interscience. NY.

Lytle, D: 1987. Yuba County Soil Survey. United States Department of Agriculture. Mapping Complete Awaiting Publication. National Resource Conservation Service.

Parsons, R.B. 1983. Initial geomorphic Concepts, Upper Consumnes River, Sacramento County, California. (Memo with field mapping legend).

Reed, P.B. 1988. National list of plant species that occur in wetlands: California (Region 0). US Department of the Interior, US Fish and Wildlife Service. Washington DC.

Ruhe, R.V. 1975. Geomorphology: Geomorphic Processes and Surficial Geology. Houghton-Mifflin Co., Boston MA .

Smith, D.W. and W.L. Verrill. 1997. Vernal pool landscapes and soils of the Central Valley, California. *In* C. Witham et al. [eds.], Proceedings of the Conference on the Ecology, Conservation, and Management of Vernal Pool Ecosystems. California Native Plant Society, Sacramento, CA.

Shannon, C.C. and W. Weaver. 1949. The mathematical theory of communication. University of Illino is Press, Urbana IL.

Stone, R. D. 1990. California's endemic vernal pool plants: some factors influencing their habitat and endangerment. *In* D. Ikeda and R. A. Schlising [eds.], Vernal Pool Plants--Their Habitat and Biology, 89-107. Studies from the Herbarium No. 8, California State University, Chico.

Stone, R. D., Davilla, W. B., Taylor, D. W., Clifton, G. L., Stebbins, J. C. 1988. Status survey of the grass Tribe Orcuttieae and *Chamaesyce hooveri* (Euphorbiaceae) in the Central Valley of California. Technical Report for the Office of endangered Species, U. S. Fish and Wildlife Service. Sacramento, CA.

Tisdale, S. L., W. L. Nelson, Beaton, J. D., Havlin, J. L. 1993. Soil Fertility and Fertilizers. Macmillin P ublishing Co. New York NY.

Tugel, A. 1993. Sacramento County Soil Survey. United States Department of Agriculture. Soil Conservation Service.

Weitkamp, W. A., Graham, R. C., Anderson, M. A., and C. Amrhein. 1996. Pedogenesis of a vernal pool entisol-alfisol-vertisol catena in southern California. Soil Sci. Soc. of Am. J. 60:316-323.

Zedler, P. 1987. The ecology of southern California vernal pools: a community profile. U. S. Fish Wildl. Serv. Biol. Rep. 85 (7.11).

Zedler, P. 1990. Life histories of vernal pool vascular plants. *In* D. Ikeda, and R. A. Schlising [eds.], Vernal Pool Plants–Their Habitat and Biology, 1-30. Studies from the Herbarium No. 8, California State University, Chico.