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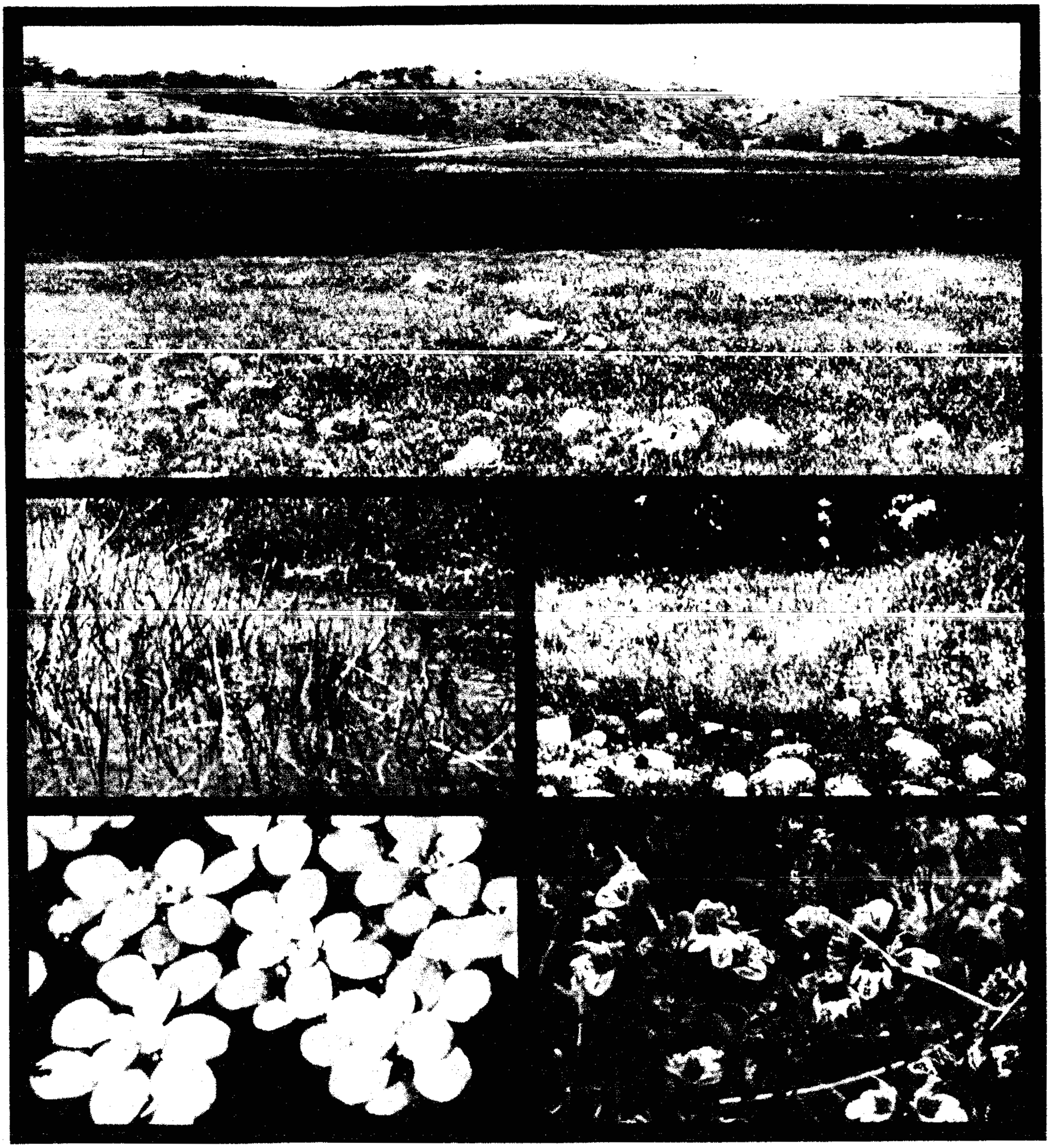

Fish and Wildlife Service

U.S. Department of the Interior

Cover Photos: Top: View of a large pool on the only reasonably intact vernal pool landscape in southern California--the Santa Rosa Plateau, Riverside County. Photo: author. Middle left: A vernal pool on Kearny Mesa in the winter condition, *Eryngium aristulatum* especially obvious. Photo: Ellen Bauder. Middle right: A Kearny Mesa vernal pool in late spring, the water gone and the late flowering species covering the pool bottom. Photo: Ellen Bauder. Bottom left: *Callitriche longipedunculata* floating on the surface of a vernal pool. Photo: Cam Patterson. Bottom right: *Pogogyne abramsii* growing on Kearny Mesa. Photo: author.

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THE ECOLOGY OF SOUTHERN CALIFORNIA VERNAL POOLS: A COMMUNITY PROFILE

by

Paul H. Zedler
Biology Department
San Diego State University
San Diego, CA 92182

Project Officers
Michael Brody
and
Wiley M. Kitchens
National Wetlands Research Center
Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

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PREFACE

The purpose of this profile is to summarize information on vernal pools, with an emphasis on those of southern California. Reference is made throughout the text to studies of the extensive Central Valley pools, but I have not systematically covered the literature of these pools, nor have I delved too deeply into work done on temporary wetlands elsewhere in the world. For those who wish to know more about temporary wetlands in general, the literature cited should provide a starting point.

Any questions or comments about or requests for this publication should be directed to:

Information Transfer Specialist
National Wetlands Research Center
U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, Louisiana 70458.

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	283.5	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556(°F - 32)	Celsius degrees

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ACKNOWLEDGMENTS

I am indebted to many for help at every stage in the writing and preparation of this document. My students and research associates who share an interest in vernal pools--Ellen Bauder, Carla Scheidlinger, and Cam Patterson--have played an especially important role. I have drawn on their knowledge and been sustained by their enthusiasm. Paula Jacks and Gerry Scheid helped with the graphics. Pam Garrett tackled the difficult and demanding job of forging a clean manuscript from the rough first draft. Because I thank her here, however, at least the task was not thankless. My faculty colleagues at San Diego State University have also been supportive. Ed Aguado, Phil Kern, and Steve Roberts lent their expertise. George Cox, also a vernal pool enthusiast, read an early draft of the manuscript and has tried to prevent me from making embarrassing errors. Tom Ebert was co-investigator with me on a vernal pool study and has influenced my views on pool ecology.

Contributions from other researchers interested in vernal pools or temporary wetlands were vital, and are acknowledged throughout the text. Robert Holland deserves special thanks for sharing his extensive knowledge of vernal pools in a thorough and information-packed review, and for being my guide on an enjoyable tour of the Jepson Preserve. Tom Griggs, Wayne Ferren, Millicent Quammen, and Jon Keeley also reviewed the manuscript and provided valuable comments and assistance.

The California Department of Transportation has supported most of the research that I have done on vernal pools. John Rieger, of the San Diego office, has been helpful in many ways, and made important contributions to my discussion of management problems. The U.S. Fish and Wildlife Service supported the cost of preparation of this document, and its personnel have always been willing to assist. Jim Bartel of the Endangered Species Office has been particularly generous with his time. I thank Wiley Kitchens and Mike Brody for their patience in guiding the project to completion. The Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon, funded the printing of this profile.

My family has also helped. Special acknowledgment must go to my colleague Joy Zedler, whose own contribution to this same series served as a model which I strove to equal but could not hope to better.

CHAPTER 1. VERNAL POOLS AND THEIR SIGNIFICANCE

1.1 WHAT IS A VERNAL POOL?

Because vernal pools are less known than other natural ecosystems, it is appropriate to begin with a definition: a vernal pool is a natural habitat of the Mediterranean climate region of the Pacific coast covered by shallow water for extended periods during the cool season but completely dry for most of the warm season drought. At their greatest extent vernal pools are usually small (3-50 m across) and always shallow (10-60 cm deep). Depth and duration are more important in defining a vernal pool than size (Figures 1,2). Some vernally moist habitats, especially in the Central Valley of California and the largest pools on the Santa Rosa Plateau of Riverside County, are as large at their maximum extent as many lakes (Lathrop 1976). But the shallowness and limited duration of these "vernal lakes" and "vernal marshes" insure that the biota found in them is essentially that of the smaller vernal pools.

Vernal pools are found only where there is a seasonally perched water table, and in California they are most common on coastal terraces and in the Central Valley (Holland and Jain 1977). They hold water long enough to allow some purely aquatic organisms to grow and reproduce, but not long enough to permit the development of a typical pond or marsh ecosystem. The water stands long enough to exclude or inhibit the growth of the species of the surrounding nonpool vegetation. As a result, in the summer the dried pool basins often are conspicuously barren compared to the shrublands or grasslands around them.

Vernal pools are amphibious ecosystems. The alternation of very wet and very dry creates an unusual ecological situation that supports a unique biota. To survive in a vernal pool a species must be able either to tolerate a wide range of conditions, or to grow and reproduce in the short time the pool is a favorable environment. It is not surprising then that many of the pool plants and animals are so specialized that they cannot persist for long, or even at all, outside temporary pools. A few of these species are also "endemics," species found only in a very restricted geographical area.

The changes in a vernal pool during the year are so great that it is in some ways more appropriate to consider it to be a sequence of ecosystems rather than a single static type. Strictly speaking, the vernal pool is only one phase. Much that is important happens before and after pool filling. For convenience in discussion, vernal pool development during the year can be broken into four stages (Figure 3).

In the wetting phase the first fall rains stimulate the germination of dormant seeds and the growth of perennial plants. A dense turf of seedlings and resprouts usually develops before the pools hold water for any extended period.

The aquatic phase (Figure 3, upper left) develops when the cumulative rainfall is sufficient to saturate the soils. This usually requires several days of intense rain. The aquatic plants and animals proliferate at this time. The nonaquatic species are subjected to varying degrees of stress depending on where they are located in the pool. Amphibians, aquatic insects, and birds are attracted to the pools.

The drying phase (Figure 3, upper right, lower left) begins as the pool

Figure 1. A typical small pool in mounded topography on Kearny Mesa, San Diego County. Photo by Ellen Bauder.

level recedes. The high soil moisture storage insures that plant growth can continue after the standing water is gone. The nonaquatic and amphibious plants that persisted through the aquatic phase flower and produce seed. Aquatic animals either disperse or become dormant.

The drought phase (Figure 3, lower right) may be said to begin when most of the fall-winter stimulated plant growth has succumbed to drought and turned brown. Some plants able to tap deeper moisture may continue to grow and flower even into early fall. Drying cracks appear. Summer rains, if they occur, generally do little to stimulate growth.

Vernal pools are a segment of a continuum of moisture and salinity conditions and no sharp line can be drawn to distinguish them from other wetlands. Their relationship to other types of wetlands may be illustrated by placing them on the major gradients along which wetlands are differentiated: 1) size (areal extent), 2) depth, 3) variation in area and depth within a year and between years, 4) water movement, 5) salinity, and 6) dominant vegetation. With respect to these, vernal pools are 1) small, 2) shallow, 3) variable within seasons but consistently present from year-to-year, 4) occasionally or never flowing, 5) nonsaline though sometimes alkaline and occasionally containing

Figure 2. The largest pool on the Santa Rosa Plateau, Riverside County, during the period of high water. Pools this large and well-vegetated are sometimes called vernal marshes. Photo by Carla Scheidlinger.

halophytes (e.g., Frankenia), and 6) containing as prominent species persistent (not successional) populations of annual plants though perennials such as Eleocharis spp. may be very abundant.

In the classification scheme of the U.S. Fish and Wildlife Service (Cowardin et al. 1979), vernal pools seem to be best classified as-- System: Palustrine (because they are small and shallow); Class: Emergent Wetland (because they usually contain some perennial hydrophytes, and sometimes these are dominant); Sub-class: Nonpersistent; Water regime: Seasonally Flooded. The main problem in applying this general scheme is the class designation. Vernal pools go through a sequence of dominant plants as the season progresses. Not uncommonly the first dominant is Isoetes (quillwort) a herbaceous perennial; the final dominants are annuals such as Pogogyne abramsii. Some vernal pools, because of the importance of annuals, might better be given the class designation "Unconsolidated Shore," but this name does not seem appropriate, though it correctly points to the affinities that vernal pool biotas have with the fluctuating margins of streams and ponds.

Vernal pools have not been consistently recognized as a distinct vegetation type until fairly recently, and have had a variety of names. Orcutt (1885), in what must be one of the earliest published description of vernal pools, described them as "miniature lagoons" and "little lakes." Early wildflower books, floras, and descriptions of California vegetation (e.g., Abrams 1911; Parsons 1918; Davidson and Moxley 1923) mentioned "wet meadows" or "wet places" when describing the habitat of vernal pool genera such as Downingia and Eryngium. J.T. Howell (1931) described the habitat of Pogogyne as "rain pools." Willis Linn Jepson (1867-1946) of the University of California at Berkeley and the dominant figure in California floristics for many years may have been the person who did the most to give currency to the term "vernal pool" since it appears frequently in his flora of 1925 (first edition 1923) and in his incomplete flora of 1936. Jepson seems to have made

Figure 3. Seasonal change in a vernal pool on Kearny Mesa, San Diego County, 1978. (A) 2 April. The pool is in the aquatic stage. In this wet year the pools held water later into the spring than usual. (B) 2 May. Early drying phase. The water has gone, but soil moisture is sufficient to support a dense population of flowering *Downingia cuspidata*. (C) 30 May. Late drying

phase. The surrounding vegetation has mostly turned brown, but some species are in flower. In the pool the most obvious flowers are *Brodiaea orcuttii.* (D) Drought phase in late summer. The vegetation in the pool is completely dormant, as is most of the herbaceous vegetation around the pool. All photos by Mary Lee Balko, Planning Dep., City of San Diego.

a distinction between vernal pools and "winter pools," because he lists both as habitats for some species.

Edith Purer's 1939 paper "Ecological study of vernal pools, San Diego County" was apparently the first to discuss in detail the ecological features of pools. It may be tentatively concluded that the joint efforts of Jepson and Purer helped to establish the term vernal pool, and more important, to bring the unique ecological and evolutionary aspects of vernal pools to the attention of scientists and the general public. In recent decades there has been growing appreciation of the scientific and aesthetic value of vernal pools, with increasing numbers of theses and research projects focussing on vernal pool organisms. Two symposia organized by Subodh Jain and his students at the University of California, Davis (Jain 1976a; Jain and Moyle 1984) have helped to stimulate interest in vernal pools.

1.2 GEOGRAPHIC DISTRIBUTION OF VERNAL POOLS

1.2.1 Distribution of Vernal Pools in California

Although this report will emphasize the southern coastal vernal pools, it is important to see these in their larger geographical context. Vernal pools occur in two main clusters in California, on the coastal terraces and level topography of the lower coastal mountains, and in the Central Valley (Figure 4). Vernal pools are also reported from Oregon (W. Ferren, Department of Biology, University of California, Santa Barbara; pers. comm.). Holstein (in Cheatham 1984) suggests a classification based on geography and substrate (Table 1). His scheme does not fit the southern pools as well as it might. First, San Diego Mesa is a local term referring specifically to one part of the coastal terrace distinct from, for example, Kearny Mesa. Second, vernal pools extend into Mexico. Thus instead of San Diego Mesa pools the name should probably be Borderland or Southern Terrace Pools. On the southern terraces there is a good but not perfect correlation of location and type of substrate. On Otay Mesa and Cocklebur Mesa (Camp Pendleton) the pools are in claypan substrates. However, on Kearny Mesa and Del Mar Mesa pools occur with both cemented hardpan and claypan substrates, though the former are more numerous (Greenwood 1984; J. Rieger; California Department of Transportation, pers. comm.). It is also not clear where the vernal pools of Santa Barbara, San Luis Obispo, Ventura, and other coastal counties fit into this scheme.

At the scale of the entire state, there is an evident correlation between vernal pools and level topography within the nondesert climatic zones. At a larger scale (Figure 5) the tendency for pools to occur in local clusters is evident. Another level of aggregation is revealed by detailed mapping of individual pools (see 2.3). Thus vernal pools may, like many other natural ecosystems, be viewed as a hierarchy of clusters from the local level to the largest geographical scale.

1.2.2 Worldwide Distribution of Temporary Pools

Although the vernal pools of California are unique, small, seasonally wet depressions are not unique to California (Thorne 1984). The necessary elements for the formation of temporary bodies of water are the presence of undrained depressions and variable rainfall. These conditions are met in many places in the world. In the United States temporary ponds probably occur in every state. They are reported for example, from Wyoming (D. Knight, Department of Biology, University of Wyoming, Laramie; pers. comm.), Alabama (Petranka and Petranka 1981), Colorado (Herrmann 1977), North Dakota (Eisenlohr et al. 1972), Georgia (Thorne 1984), and Texas (Merickel and Wangberg 1981). Temporary pools also occur in Canada (McKee and Mackie 1981).

The closest analogs to California vernal pools would be expected in regions of similar climate. In Australia there are many temporary pools (Bayly and Williams 1973; Morton and Bayly 1977). Some, like California vernal pools, are "soft-bottomed," and others are in bedrock depressions. In western Australia these

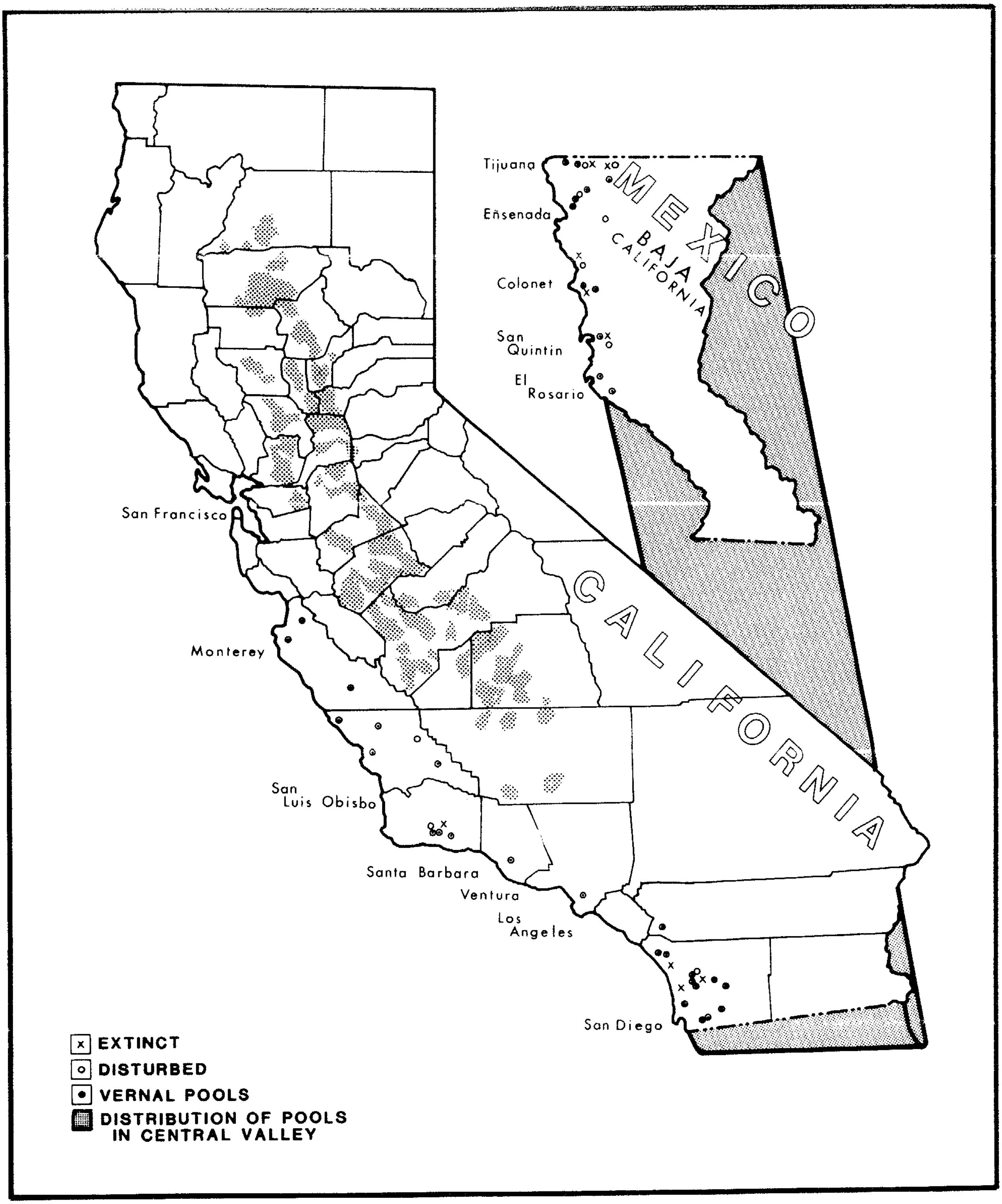


Figure 4. Distribution of vernal pools in California. The Central Valley distribution (stippled area) is based on the detailed maps in Holland (1978). The distribution of coastal pools is based on unpublished information of the author but was mostly obtained from colleagues around the State: W. Ferren, J. Griffin (Hastings Reservation, University of California), V. Holland, J. Keeley, D. Keil (Biological Sciences, Cal. Poly., San Luis Obispo), E. Lathrop (Biology, Loma Linda University), and R. Moran (formerly of the San Diego Natural History Museum).

Table 1. A classification of vernal pools by Holstein (*in* Cheatham 1984): the claypan-hardpan distinction is one also stressed by Holland (1978).

Northern vernal pools

- Hardpan pools--northern and eastern margin of the Great Valley
- Claypan pools--central and western floor of the Great Valley, but also on coastal terraces
- Basalt flows--scattered in Sierra foothills
- Northern sandstone tanks--inner coast ranges, elsewhere?

Southern vernal pools

- Interior basalt flows--Santa Rosa Plateau, Riverside Co.
- San Diego Mesa pools--Otay and Kearny Mesas, San Diego Co.

bedrock temporary pools often have a distinctive moss--*Isoetes*-cover on the bottom (I.A.E. Bayly, Department of Biology; Monash University, Melbourne, Australia, pers. comm.). Depressions in *Eucalyptus* forests in the eastern half of the arid zone of Australia are often dominated by a distinctive flora including a species of *Marsilea* (Beadle 1981). In the Mediterranean climate region of South Africa "seasonal vleis and pools" are common in some districts and support unusual plant and animal assemblages (Stephens 1929). "Pars," small closed basins which often are seasonally dry, are a characteristic feature of landscapes in southern Africa generally (Goudie and Thomas 1985).

Zohary (1973) described winter pools with a distinctive flora as present in the Middle East. In the high plains of Chile and Bolivia (the "altiplano") there are large numbers of vernal pools (Jaffuel 1932 cited by Purer 1939; S.H. Hurlbert, Department of Biology, San Diego State University, Calif.; pers. comm.). Temporary wetlands are also common in the northern Andes, and in Colombia the pools are dominated by *Isoetes* and *Crassula* and other genera characteristic of California vernal pools (J. Keeley, Department of Biology, Occidental College, Los Angeles, Calif.; pers. comm.) Simpson (1982) mentioned large numbers of enclosed basins in central Patagonia, including small depressions with temporary pools. Temporary pools are abundant in some parts of western Spain, and some of these support vegetation which is very similar to California pools with genera like *Callitriche*, *Lythrum*, *Isoetes*, *Myosurus*, and *Eryngium* present (Rivas Goday 1970). Mounded topography, apparently without pools, is also reported from Spain (Gasco Montes et al. 1979). Descriptions of the habitat of *Eryngium* sp. in the Flora Europea (Tutin *et al.* 1968) suggest that vernal pool-like habitats occur in Italy.

Temporary pools are found in Africa, Asia, and tropical South America. Vernal pools (Bowker and Bowker 1979) and small vernal marshes in mounded topography (G. Cox, Department of Biology, San Diego State University, Calif.; pers. comm.) occur in the highlands of Kenya. In north Africa there is a great diversity of temporary bodies of water, from "chotts" which occupy large Pleistocene lake basins and have areas up to many square kilometer, to small depressions that may be similar to vernal pools (Morgan and Boy 1982). Rzoska (1961) described the fauna of shallow warm-season ephemeral pools in the Sudan that support invertebrate faunas similar to those found in many California temporary pools. Temporary pools in parts of the humid tropics with seasonal rainfall, as in the Ivory Coast (Forge 1980) and in India (Venkataraman 1981). Raynal-Roques and Jeremie (1980) described rock pools in French Guiana that contain *Isoetes* and *Ophioglossum*, genera also found in association with California vernal pools.

Temporary bodies of water in basins of internal drainage are characteristic of desert regions of the world. The playas of extreme deserts differ from vernal pools mainly in the greater year-to-year variability in water levels (Louw and Seely 1982). Most are dry for extended periods, an example being Lake Eyre in Australia which fills only two to three times per century. Desert playas are also usually saline or alkaline, and generally have less plant cover, even in years of high rainfall. Playas in areas that receive rain more regularly than the extreme deserts approach the larger vernal pools of the Central Valley and Baja California in appearance and biota (R. Holland, California Department of Fish and Game; pers. comm.). Perhaps the major distinction in the Southwest United States is that vernal pools rarely or never form during the summer, whereas playa lakes and desert pools often are present in the warm season (e.g., Brown and Carpelan 1971).

Shreve (1964) briefly described playas in Baja California that have some similarities with vernal pools. He stated that in the southern Magdalena region in the lower third of the Baja California peninsula there are "many large playas and seasonal meadows." He reported Marsilea and Eryngium from these areas, suggesting there are ecological and floristic similarities with vernal pools. According to Reeder (1981) this same area is the type locality for Orcuttia fragilis Swallen, a little-known species of grass with close

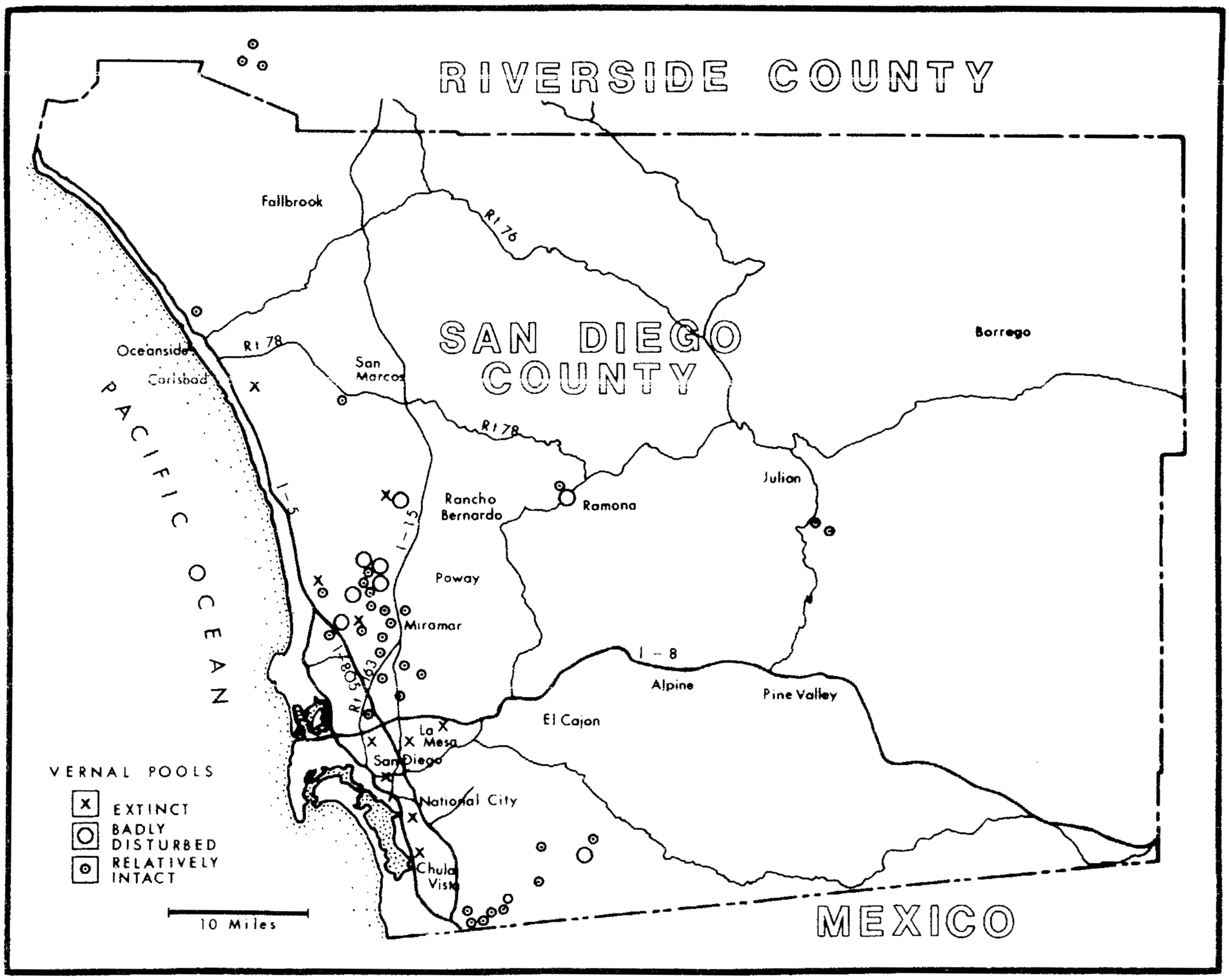


Figure 5. Distribution of vernal pools in San Diego County and adjacent Riverside County. Shown here are pools that were extant in about 1970. Many of these are now lost to development. Omitted here, for lack of accurate data, are the pools formerly on the San Diego and Linda Vista Mesas.

relatives in the coastal and Central Valley pools of California. Local residents who refer to these areas as "playitas" have said that water is present once every 4 or 5 years (R. Holland; pers. comm.).

This survey of a part of the literature on temporary pools, lakes, and wetlands makes clear that vernal pools are a special regional type of a worldwide phenomenon. Temporary bodies of water are a characteristic but relatively little-known feature of many of the world's landscapes. They are common today but were even more widespread in the past. The wetlands of each region have unique properties, but those of the Pacific coast, as we shall see, are among the most distinctive and interesting.

CHAPTER 2. THE PHYSICAL SETTING

2.1 REGIONAL CLIMATE

The most striking feature of vernal pools is their change from standing water in the winter to desert-like dryness in the summer, a moisture regime that is a consequence of the strongly seasonal rainfall of California's Mediterranean-type climate (Figure 6). The contrast between wet winters and dry summers is due to the shift of the belt of stormy westerlies from the south in winter to the north in summer (Major 1977). During the summer the subtropical high over the Pacific Ocean dominates the climate, causing subsiding air and a stable atmosphere. Skies are generally cloudless except along the coast where marine fogs form the "night and morning low clouds" that are often the only thing to report about southern California summer weather. In extreme southern California this summer pattern is broken occasionally by tropical storms that carry far enough north to increase humidity, bring clouds, and sometimes cause intense rainfall. For example, 0.41 inch of rain fell at the San Diego State University (SDSU) weather station on 15 August 1983. Along the coast and on the terraces where the vernal pools occur, summer storms of this kind contribute little to total yearly precipitation, but in the mountains and deserts to the east they are a major source of moisture. There is no record of summer rainfall ever stimulating significant growth in coastal vernal pools.

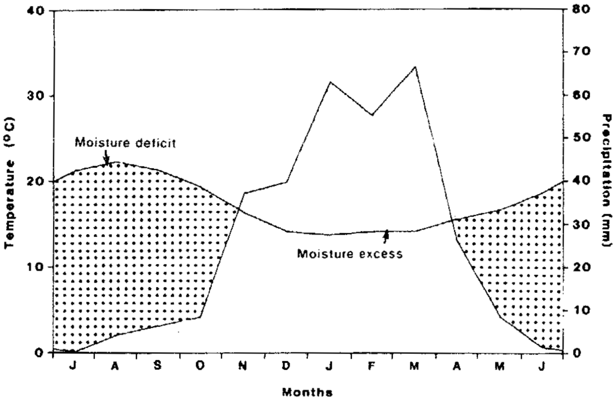


Figure 6. Climate diagram for San Diego as recorded at the San Diego State University Eidemiller Weather Station. Temperature averages are for 1958-83 and rainfall, 1959-83. The approximate period of excess moisture is the period in which native vegetation is most actively growing.

Although a third or more of the total precipitation in vernal pool areas normally falls before 1 January, in most years the pools hold water only briefly or not at all before this date. The prolonged drought dries the soils to a considerable depth, and the initial rains are absorbed in recharging the soils. Once saturated, the soils can support plant growth well after the rains stop. The soil aspects of water storage and loss will be discussed in section 2.4.

The seasonal change in water balance is most simply illustrated by comparing monthly potential evaporation with monthly rainfall. In Figure 7 potential evaporation (measured by the drop in water level of standard Class-A evaporation pan) and rainfall data are compared for the 1982-83 rainfall season at the SDSU weather station. The hydrologic year is considered to run from 1 July to 30 June. Evaporation rate is largely controlled by solar energy and air temperature, and accordingly it peaks just past midsummer and is minimal in midwinter. Precipitation typically peaks in late winter or early spring. In 1982-83 it exceeded evaporation only in February and March. The drastic shift from moisture excess in February and March to a severe deficit in April is also characteristic of most years. The tendency is for vernal pools to begin development slowly and to hold water in the mid-January to mid-March period, and then evaporate rapidly after the last substantial rains late in the season.

In southern California rainfall is erratic within and between years as well as strongly seasonal. At San Diego, rainfall totals have ranged from 88 mm in 1960-61 to 660 mm in 1883-84. There is little or no correlation between rainfall in one year and that in the next (Figure 8). Within one season rainfall is similarly variable. Droughts of days to weeks can occur at any time (Major 1977, Figure 9). These uncertain growing conditions have probably been a significant selective force acting on vernal pool species.

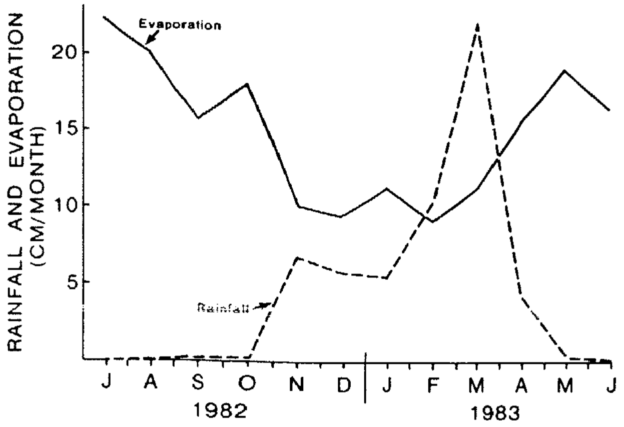


Figure 7. Rainfall and evaporation as recorded at the San Diego State University Eidemiller Weather Station for the 1982-83 hydrological year. Both are expressed on a per-month basis. Note that in this period it was not until February that rainfall exceeded evaporative demand.

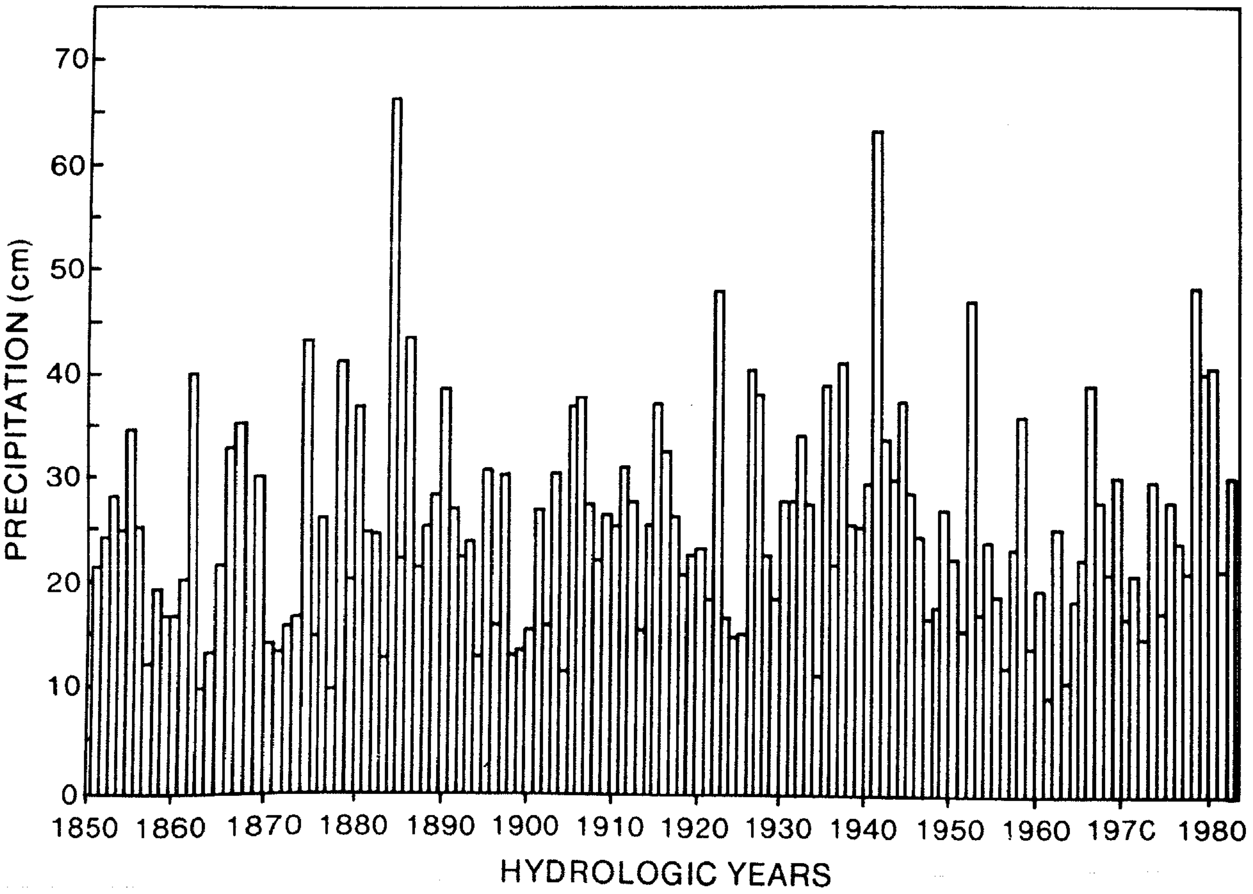


Figure 8. Annual precipitation recorded at the coast at San Diego, most recently at Lindbergh Field. Note the high variability and very low year-to-year correlation.

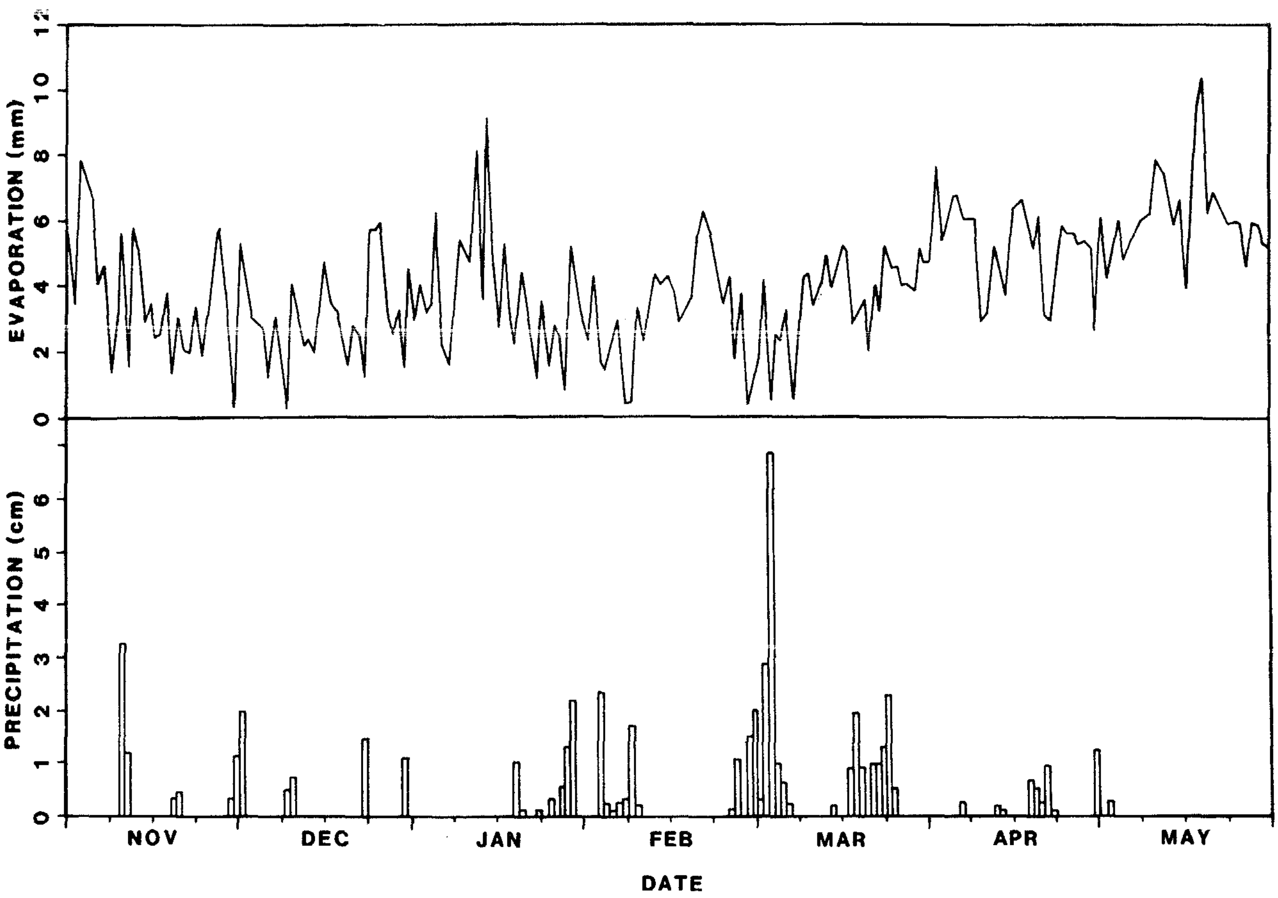


Figure 9. Daily precipitation and evaporation for the 1982-83 hydrological year recorded at the San Diego State University Eidemiller Weather Station. Note the high variability in both rainfall and evaporation.

2.2 VERNAL POOL LANDSCAPES

Although climate is a key element accounting for vernal pools, topography is also important. Pools can only form in closed depressions underlain by a nearly impermeable layer, and basins of this kind will only be abundant on generally level land surfaces. In California three major geomorphological situations provide these conditions: coastal terraces, the broader alluvial valleys, especially the Central Valley, and ancient basaltic lava flows. Most vernal pools are found in the first two situations. Figures 10, 11, and 12 are views in representative landscapes.

A topographic transect across San Diego County from the coast at Del Mar to the Kearny Mesa vernal pools shows the nature of the coastal terrace topography (Figure 13). The easternmost part of this transect just touches the mountainous terrain associated with the north-south trending Peninsular Ranges that dominate the middle third of San Diego County. From the base of these hills to the coast the topography is a deeply dissected plain with canyon-mesa topography. The alignment of the level surfaces shows that they are the remnants of a once-complete surface that slopes gently to the west. Through the vernal pool areas the transect crosses the Linda Vista Terrace. Once thought to be a single surface, careful study has revealed that it actually is a series of at least four terraces (P. Kern, Geology Department, San Diego State University, Calif.; pers. comm.).

The coastal terraces as they exist today are the end product of a process that occurred gradually over geological

Figure 10. View of a vernal pool landscape at the San Simeon State Beach, San Luis Obispo County. Bishop pine forest in the background. Photo by Mark Capelli.

Figure 11. Vernal pool landscape at Camp Pendleton, San Diego County. Soils here lack the hardpan but are very high in clay.

Figure 12. Vernal pool landscape at Kearny Mesa, San Diego County. Flowering shrub in the foreground is *Eriogonum fasciculatum*. Darker shrub in the background is *Adenostoma fasciculatum*. Area of low vegetation is a vernal pool basin. Photo by Ellen Bauder.

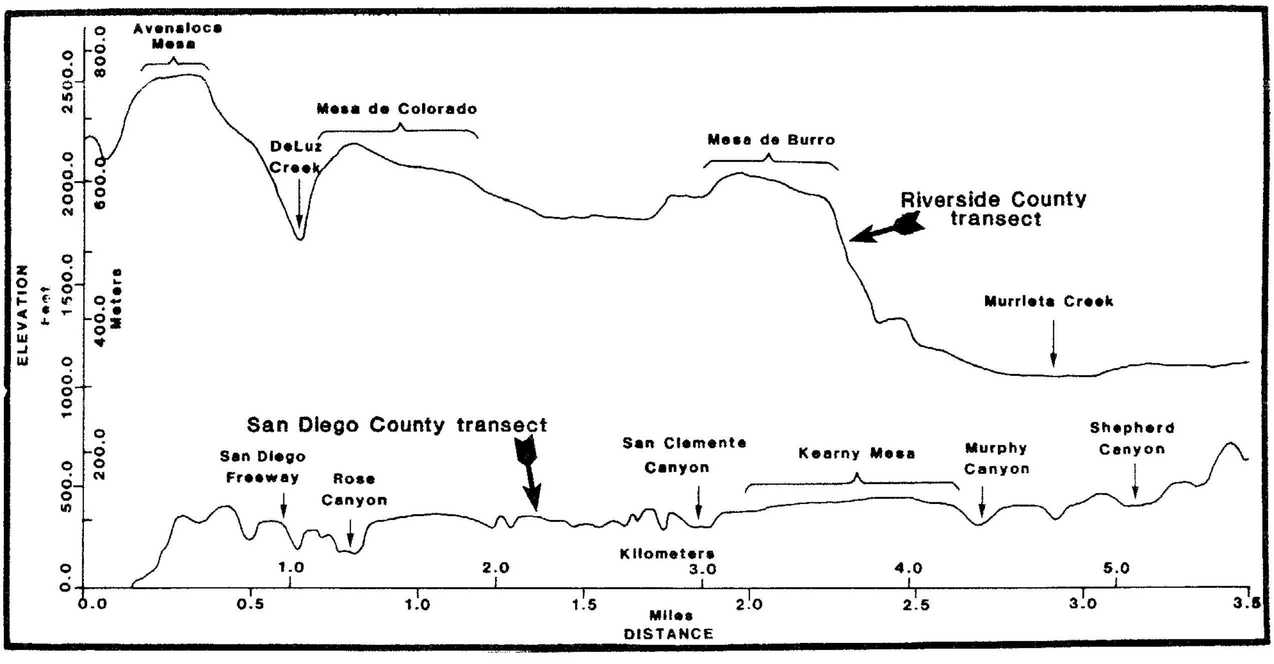


Figure 13. Topographic transects, vertical scale exaggerated, through vernal pool landscapes in San Diego and Riverside Counties. The San Diego transect, which begins at the Pacific Ocean, shows a coastal plain dissected by drainages. Some of the high points are dune ridges. Just beyond Shepherd Canyon the alluvial terrace meets the bedrock-controlled topography of the Peninsular Range. The Riverside County transect cuts through an old volcanic surface which remains a flat-topped mesa. Present-day vernal pool areas are located on Kearny Mesa and the areas to the east, and on Mesa de Colorado and Mesa de Burro.

time. This more or less continuous process can be arbitrarily divided into three main stages (Kennedy 1975; Kern 1977; Sharp 1978). In the first stage the sea rises, and the action of the waves cuts a gently sloping platform into the land (Figure 14). In the second stage the sea retreats, leaving a veneer of marine deposits which provide the most reliable means of dating the platform (Kern 1977). Erosion from the land onto the newly exposed terrace partially or completely conceals the now stranded seacliff and builds a thick layer of alluvium over the marine deposits. Dune ridges may also form on the surface, marking places where the retreating sea paused long enough to build large coastal features (Kennedy 1975). The final stage occurs when the process of uplift steepens the gradient from the ocean to the higher inland topography, causing deep drainages to be cut into the gently sloping terrace surface. After this, alluvium from inland is channelled through the newly formed river valleys and arroyos. The terrace surfaces stop aggrading and begin to weather and eventually form mature soils with strong differences between soil horizons.

From the standpoint of soil formation and microtopography, the age of such surfaces is best expressed as the time since deposition of water-borne alluvium ceased or slowed significantly. From present information, we cannot precisely determine when this occurred, but it can be bracketed by dates available for a low and a high terrace. Nestor terrace, well below the present vernal pool landscape, was being formed about 120,000 Before Present (B.P.) (Kern 1977). Amino acid racemization tests indicate an age of about 0.5 to 1.5 million years B.P. for the marine platform at Tierra Santa, toward the upper, therefore older, portion of the Linda Vista complex. The numbers suggest that the vernal pool landscapes of the San Diego coastal terraces are at least 100,000 years old, but may be as old as a million years. Knowing when the surfaces became terrestrial habitats does not, of course, tell us when vernal pool basins first formed. But it does argue for vernal pools having been in coastal California for a very long time, probably at least since late glacial times--25,000 years or more.

Although the topography of the vernal pool areas in Riverside County appears to be very similar in cross-section (Figure 13), its mode of formation is entirely different. These flat-topped hills were formed not by erosion, but by basaltic lava flows (Santa Rosa olivine basalt, Rogers 1965). These flows are thought to have occurred in the late Miocene about 8.3 million years ago (G. Peterson, Geology Department, SDSU; pers. comm.). It is assumed that the Mesa de Burro and the Mesa de Colorado are remnants of a once more extensive flow that moved over what was then relatively gentle topography.

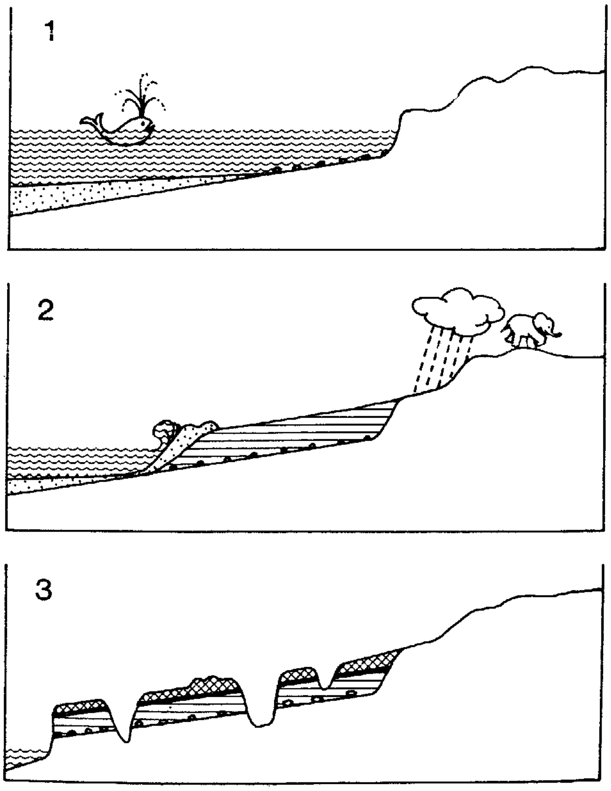


Figure 14. Postulated process of development of coastal terrace landscapes in southern California, such as that in Figure 11. The initial condition, not illustrated, was probably an older coastal terrace. In the first stage (1), the sea cuts into the land, forming a broad platform. In the second stage (2), uplift raises the land and terrestrial deposits are spread across the platform. Dune ridges may form. In the final stage (3), the sea level is well below the alluvial surface and drainages are incised into it. The soils of the alluvial surface weather to form the clay-rich lower horizons and hardpan.

Subsequent uplift and dissection have removed most of it. The long period of time that these surfaces have been exposed to weathering accounts for the strong soil development.

2.3 MOUNDS AND POOLS

Vernal pools occur in depressions, and so the microtopography of vernal pool areas is always somewhat undulating. The extreme minimum of local relief occurs when the pools are depressions in an otherwise level surface, but in most cases the surface has both convex and concave slopes, that is, mounds and depressions. Both situations occur in coastal California. On Kearny Mesa and Clairemont Mesa in San Diego County local relief of pools (difference between pool bottom and highest adjacent rise) varies between 38 and 120 cm (Zedler et al. 1979).

Because of the prevalence of mounded microtopography in parts of Australia, the Australian term "gilgai" for this topography has become generally accepted among soil scientists (Edelman and Brinkman 1962). According to Hallsworth et al. (1955) gilgai is the Aboriginal word for a small water hole. In the Western United States the Mima Prairie in Washington State has been known for its spectacular mounds for many years (Bretz 1913), and consequently in the West similar microtopography is described as "Mima mounds" wherever it occurs. The term "pimpled prairie" is used for mounded topography in the Southeastern United States, but fortunately has not come into general use. "Hogwallows," a name frequently used in California (e.g., Nikiforoff 1941; Holland and Jain 1977) was probably first applied in a jocular sense, because true hogwallows have few biological and almost no aesthetic similarities with vernal pools. Although "hogwallow" has the ring of folk authenticity, its use in formal contexts should perhaps be avoided. Therefore vernal pool should be the term for the bodies of water, and "mima mounds" may be used to describe the topography.

A typical example of mounded topography from Kearny Mesa in San Diego County may serve as an example (Figure 15). The tendency for uniformity in size and equal spacing of mounds is striking. The pools associated with the mounds are not so regular. They tend to fit around the mounds and assume various complex shapes, nearly circular if they occur in the middle of an intermound depression, or elongated or with boundaries that appear as a series of arcs if the level of inundation rises to the base of several mounds. In most situations many depressions do not hold water or do so only for brief periods, and therefore do not support a full complement of vernal pool species.

Although pools are generally associated with mounds, there are extensive areas of mounded topography where pools are rare or absent entirely (Cox 1984b). Thus the conditions for mound formation do not necessarily favor pool formation. This is not surprising, because surface drainage conditions are of critical importance in the retention of water.

2.4 SOIL CONDITIONS

The soils of vernal pool landscapes are typically formed in alluvial materials and are heavily weathered with subsoils high in clay. The parent material differs from place to place, gravelly alluvium or marine sandstone in San Diego County (Bowman 1973), dune sands in Santa Barbara County (Cole et al. 1944; Shipman 1972), and mixed alluvium in the inland valleys near Paso Robles in San Luis Obispo County (Lindsey 1983). Holland (1978) has a good discussion of the soils associated with the Central Valley pools. The nearly impermeable clay subsoil, leading to a seasonally perched water table, is clearly the key unifying factor.

The Redding soil, common on the San Diego mesas and also in vernal pool areas along the base of the Sierras, is a common vernal pool soil. According to the San Diego County soil survey (Bowman 1973), it is characterized by a yellowish- to light-brown surface layer (A horizon) of loam about 40 cm thick overlying a strongly acidic usually bright-red subsoil (B horizon) of gravelly clay and clay loam. An iron-silica hardpan layer of cemented cobbles or sand is usually present about 75 cm below the surface. Redding soils vary considerably from place to place, in part because of differences in the original parent material which grades from sand to very mixed alluvium with many large cobbles. Because the hardpan is nearly level, in mounded topography soil depth varies from a depression to the adjacent mound. At a site in San Diego County that we investigated the soil was 21 cm deep in the middle of the pool basin, but over a meter deep 6 m away in the center of a mound. The hardpan is also discontinuous, and when absent over large areas, the soils are classified as Olivenhain rather than Redding (Bowman 1973). Similar ranges of variation occur in other vernal pool areas, though the soil series may be different. Because of the extreme local variation, the soils of vernal pool areas must be considered as complexes rather than clearly defined series that can be characterized by a single profile description (Nikiforoff 1941).

The subsoil may contain a large proportion of expandable clays that shrink and swell with changes in soil moisture. Greenwood and Abbott (1980) reported that one-fifth to nine-tenths of the clay in the B horizon of the Redding soil they sampled was expandable and found volume increases of 7% to 37% for unconstrained samples. These large-volume changes

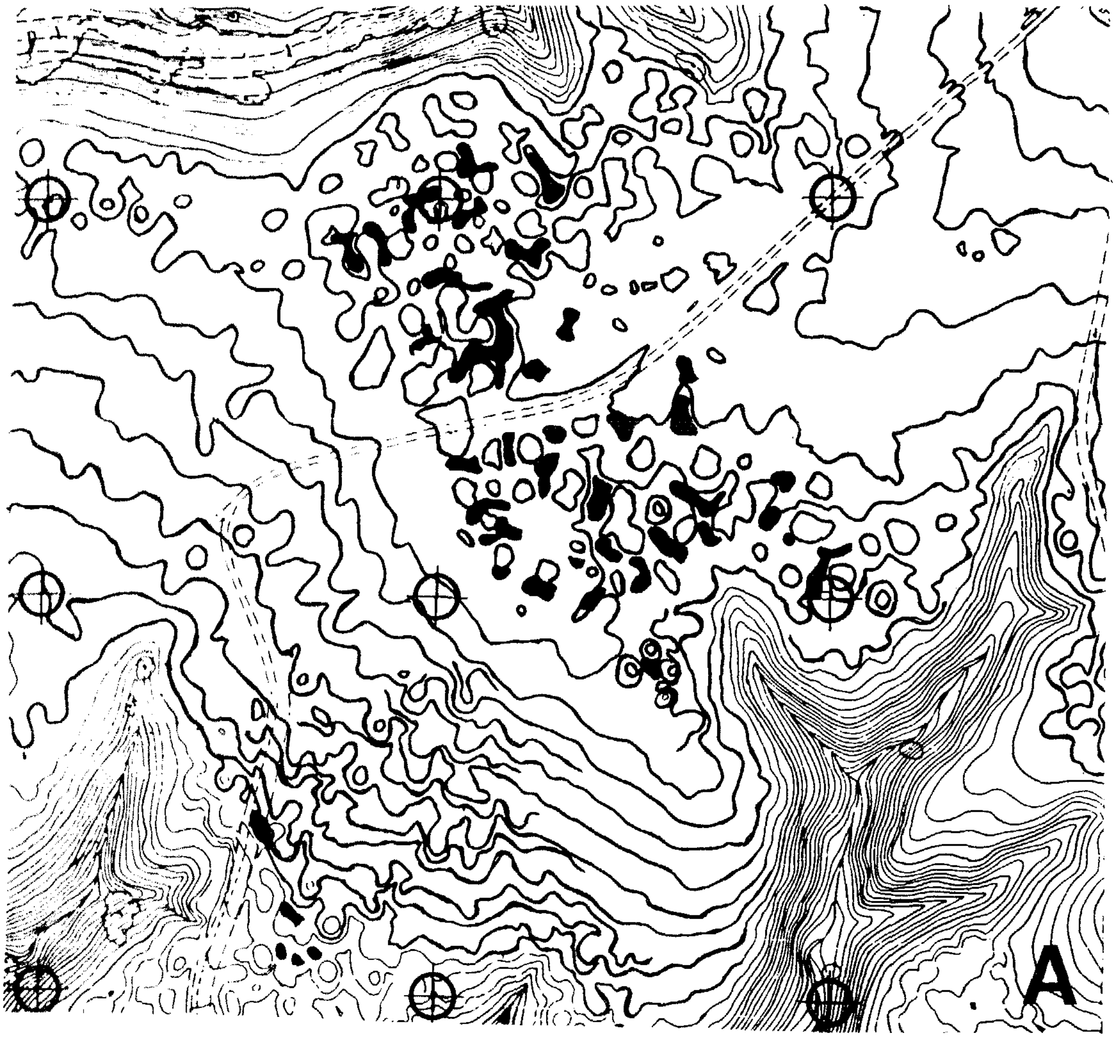
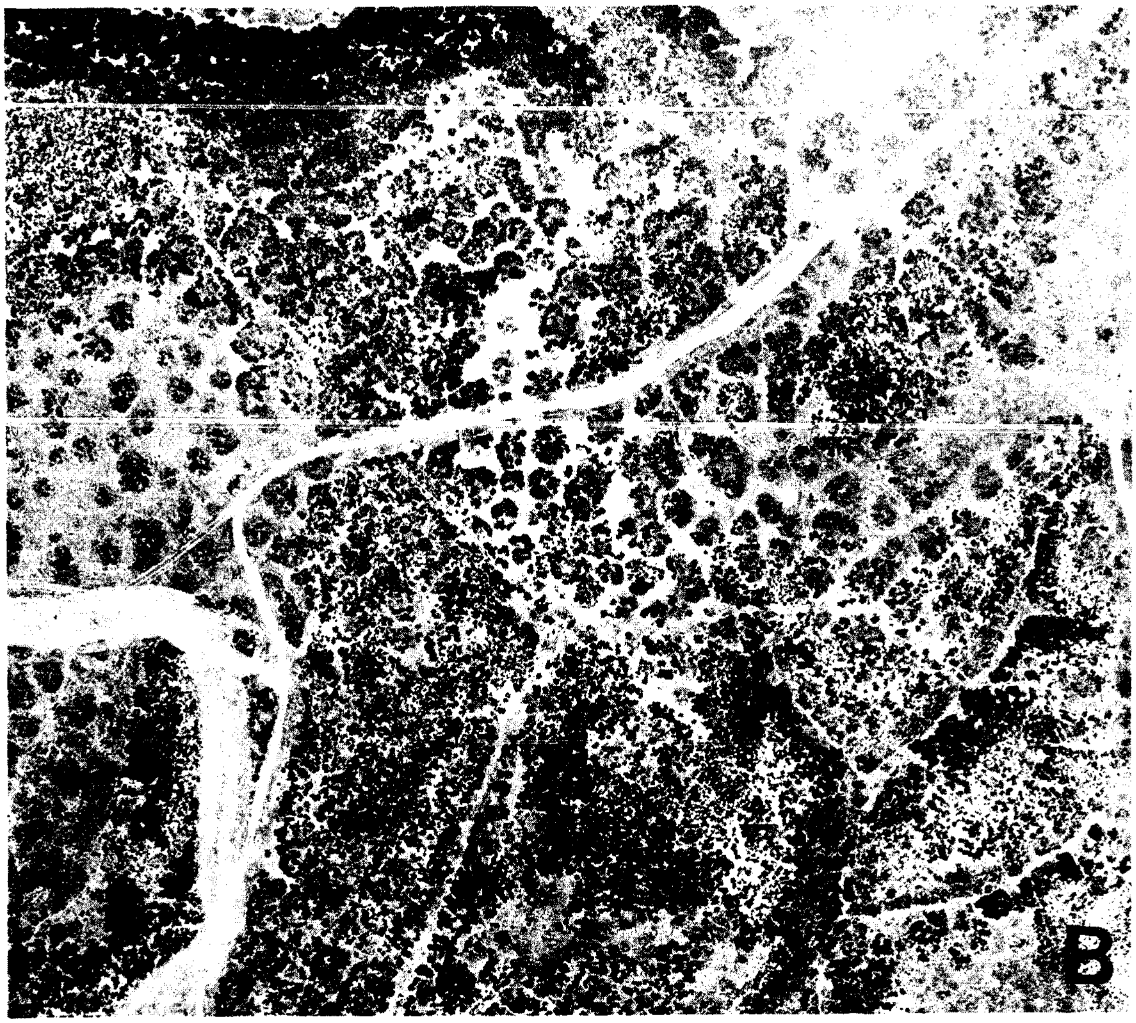


Figure 15. A topographic map (A) and the corresponding aerial photo (B) for an area of mounds and pools between Murphy and Shepherd Canyons on Kearny Mesa. The area is centered just south of the San Diego transect of Figure 13 at about the 4.5 km mark. North is at the top of the map and photo. The topographic map (A) has 2 ft (0.61 m) contours. Distance between the ticks (⊕) is 500 ft (152.4 m). Scale of the photo is

produce the cracks that are commonly seen in and near vernal pools during the summer, especially where the clay-rich horizons are near the surface. The network of cracks probably is a major means of water movement to deeper soil layers, especially early in the season (Emerson 1977). Excavations in soils during the early rains reveals a complex pattern of subsurface flow, with free water appearing below completely dry layers. The presence of subsurface cracks must account in part for this subsurface channelling. As the rainfall season continues, many of the cracks must seal as a result of the swelling of clays (Talsma and van der Lelij 1976) and, at the saturated surface at least, blockage by soil slurries. This closing of cracks could explain why more rainfall seems to be necessary to fill pools early in the season. Evidence from other studies of clay soils (e.g., Armstrong 1983) suggests that water movement through macropores may be important in establishing the level of perched water tables even after prolonged saturation.

There have been no comprehensive studies of the genesis of the Redding soil, but the high proportion of clays in



approximately the same. Vernal pools are shown in black on the topographic map. Vegetation in B is a complex mosaic of grassland, vernal pools (the lightest gray), coastal sage scrub, and chamise chaparral. Many of the mounds are brush-covered in areas otherwise covered by grass or vernal pools and therefore show up as dark patches. Map and photo courtesy of California Department of Transportation.

the B horizon, the association with a hardpan, and relatively low pH all suggest that Redding soils, along with those of most other vernal pool areas are relatively old and have been intensely weathered. The study of Torrent et. al. (1980) of a Chesterton soil in San Diego County supports this impression, and gives insight into the complex genesis of all soils of the higher terraces in southern California. The Chesterton soil is formed in aeolian sands deposited as dunes on the Pleistocene terrace surface. Therefore its age is similar to the Redding soil, but its parent material is somewhat different. The Chesterton, like the Redding, has a B horizon high in clay overlaying a hardpan (duripan) cemented with silica, and a seasonally perched water table can be present.

Torrent et al. (1980) did a detailed study of particle size distribution and chemical composition. Of particular interest are the data on slow-weathering heavy minerals, whose relative concentration in the sand fraction above and below the hardpan can be used to estimate the volume change of the soil (Barshad 1964). The data of Torrent et al. showed a markedly higher content of titanium oxide (TiO_2) in the soil material above the duripan. Since the soil formed in dune sand that probably had a fairly constant mineral composition at the time of deposition, the increase in concentration of TiO_2 above the duripan may be taken as an index of the relative loss of material above the duripan to chemical weathering. Since the average concentration of TiO_2 is about doubled, it appears that about 50% of the material in the sand fraction of the A and B horizons has been chemically weathered and either lost from the soil entirely or converted to silt- or clay-sized particles. It is difficult to imagine this degree of weathering without substantial lowering of the surface.

To account for the complexity of the Chesterton soils, Torrent et al. (1980) postulated that the soil weathered initially under a warm subhumid climate, then a relatively dry climate when the duripan formed (c.f., Mabbutt 1977), and then again in a more humid environment that produced the discontinuity in clay minerals between the surface material and that protected from weathering below the duripan. Abbott (1981) came to broadly similar conclusions about these soils, emphasizing their relict nature. He suggested that present climate and vegetation could not produce the Redding or Chesterton soils and speculated that most of the soil development occurred in full glacial times when climatic conditions were similar to those of the present-day Pacific Northwest, or in a moist subtropical climate during interglacial periods. Clearly much remains to be learned about the genesis of vernal pool soils.

Data from Kearny Mesa in San Diego County illustrate some of the complexity of vernal pool soils (Table 2). A series of cores was taken from vernal pool areas on Montgomery Field and on private land near the junction of Carrol Canyon Road and Miramar Road. The textural analysis shows considerable variation in gravel content, surface soil texture, and depth to the hardpan. Of particular interest is the relatively higher content of clay in the surface horizons of the pool basins and pool margins.

2.5 POOL HYDROLOGY

The depth and duration of standing water are the most important environmental factors affecting vernal pools. For aquatic organisms like fairy shrimp, there is a strong direct link between water regime and survival. In other cases the influence may be indirect. For example, the standing water may exclude competitors that would otherwise dominate the habitat. Because of the fundamental importance of hydrological regime, it must be considered in vernal pool management and preservation. If each pool is an isolated hydrological system, preservation on a pool-by-pool basis would be possible; but if pools form interconnected hydrological networks, preservation of single pools might cause serious disruption of the hydrology.

2.5.1 Pool and Basin Morphometry

Vernal pools are of different shapes and sizes, and have different maximum depths and volumes. A difficulty in

Table 2. Soil textural analyses for cores from three vernal pool sites on Kearny Mesa, San Diego County. Data analyses by the California Department of Transportation Soils Laboratory, San Diego Office.

Topographic position	Depth (cm)	pH	Soil texture (%)[a]			Gravel[b]
			Clay	Silt	Sand	
Mound	0.00- 36.58	6.0	7	21	72	12
	36.58- 70.10	NA[c]	15	17	68	2
	70.10- 85.34	NA	20	16	64	4
	85.34-109.73	5.9	10	20	70	4
	109.73-140.21	---------- CEMENTED LAYER------------				
Nonpool depression	0.00- 27.43	6.6	9	14	77	2
	27.43- 51.82	NA	17	13	70	15
	51.82- 76.20	---------- CEMENTED LAYER------------				
Edge of pool	0.00- 33.53	6.0	19	15	66	0
	33.53- 54.86	5.5	25	6	69	7
	54.86- 76.20	-----------CEMENTED LAYER------------				
	76.20- 91.44	--------SILTY SAND, NOT SAMPLED ------				

[a] Silt and clay percentages sum to 100. U.S. Department of Agriculture size class categories were used.
[b] Gravel percentages are expressed relative to the total weight of the smaller particle size classes.
[c] NA indicates that the data were not recorded.

describing fluctuating bodies of water is that no measure of size or shape taken at a particular time is representative. A pool may have a large maximum size achieved only in unusually wet years but a smaller than average size in dry years. Pools often merge during periods of high water, and smaller shallower pools may scarcely hold water at all in extreme droughts. Therefore, a complete description of pool hydrology requires both detailed topographic mapping and monitoring of water levels over several years. Except for Greenwood and Abbott (1980), there do not appear to be any topographic maps of vernal pool basins at a sufficiently large scale to be useful for hydrological studies.

A survey of pools in the Kearny Mesa area of San Diego County measured the relative elevation of pools at 20-cm intervals along transects (Figure 16). These were positioned to pass near the deepest point in each pool and generally crossed the narrow dimension of noncircular pools. Although only cross-sections, they give an idea of pool size and shape.

The topography of the basins (Figure 16) is varied, but most approximate sectors of a circle. The minor dips and rises are attributable to a variety of causes, primarily the activities of animals, including humans. Pocket gophers burrow in the basins after the standing water has disappeared while the soil remains moist, pushing 5- to 15-cm high mounds to the surface. Vehicles, hikers, horses, and scientists studying pools can produce deep ruts when the soils are saturated. Some of the microtopography is caused by the large cobbles that are found in most pools and form an almost complete cover in others. The method used to plot the transects in Figure 16 avoided loose cobbles, but considered buried cobbles that could not easily be moved to be part of the bottom topography.

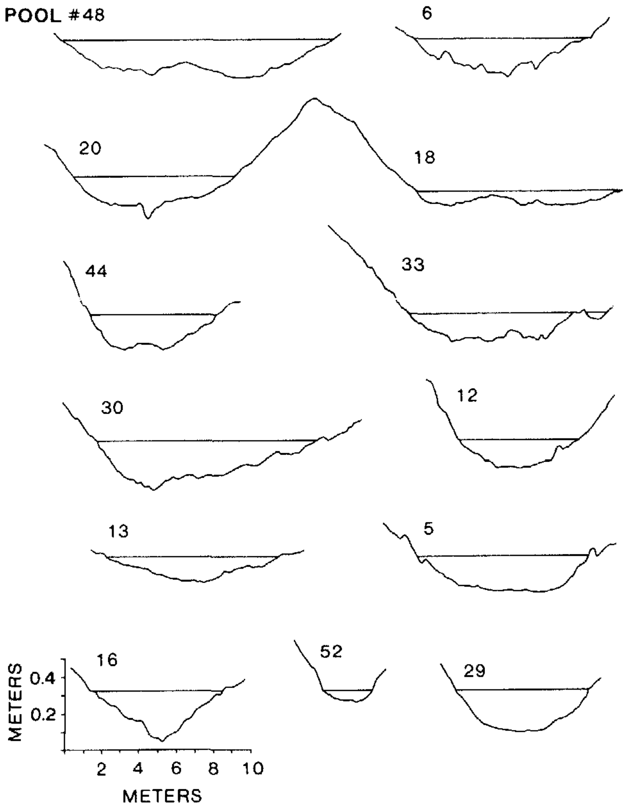


Figure 16. Topographic cross-sections (vertical scale exaggerated) of vernal pools from Kearny Mesa illustrating the variation in microtopography which is important in establishing the gradient in water duration. The relationship between pools and mounds is illustrated in the transect including 18, 20, and the intervening mound. The area where these two pools occurred has recently been developed.

The slope of the pool bottoms is of considerable importance, since it largely determines the steepness of the gradient in water duration and soil moisture from edge to center and hence the variety of growing conditions. Pool 20, for example, is relatively flat-bottomed, and the transitional zones are small, whereas in pool 12 the bands of intermediate water duration are much broader.

Pools 6 and 20 illustrate a common condition, the existence of small rises in the pool that can result in "islands," or in some cases reefs that divide a pool into two as it dries. The latter situation particularly may be an important influence on populations of aquatic animals.

Pools 20 and 18 are part of a continuous transect. Recalling that the transects have vertical exaggeration, the two pools show the common relation of pools to mound in those places where mounds are well developed. Of particular importance is the difference in the elevation of the maximum water levels, showing that the surface of the perched water table is not at a uniform elevation and therefore that in many cases adjacent pools can have quite different water regimes.

Precise measurement of the volume of vernal pools requires careful topographic mapping. However, one can estimate the approximate volume of the more symmetrical pools from the cross sections, and this suggests that this set of vernal pools would hold between 5 and 50 m^3 when full. Greenwood and Abbott (1980) mapped a large vernal pool in San Diego County and estimated its basin volume at about 540 m^3.

2.5.2. Observed Patterns in Change of Pool Levels

The simplest way to measure and express change in vernal pool water content is to measure the rise and fall of pool levels relative to a permanent reference stake. This has been done over a number of years at several sites in San Diego County (Figure 17). Pool levels are highly variable, rising in response to precipitation input, and then falling rapidly between rains, even in the relatively cool and moist winter months.

2.5.3 A Hydrological Model

The water regime of vernal pools is most easily discussed with reference to a simple input-output model (Figure 18). Despite the complexities of transfers of water in ecosystems, the water level is ultimately a consequence of the balance of income and loss. Following Hartland-Rowe (1972) the balance equation may be stated as follows:

$$IP + IR + IG = OR + OET + OSS + OG$$

Precipitation (IP). Vernal pool systems are driven by precipitation. They are caused by a temporary perched water table, which forms because for a brief

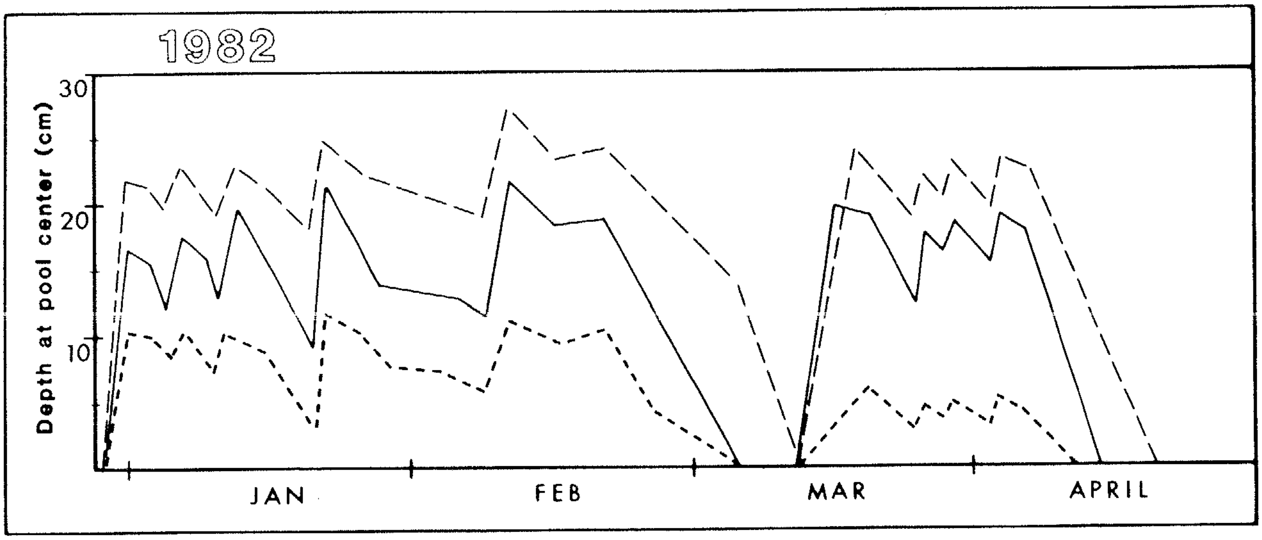


Figure 17. Water levels in three adjacent vernal pools from Kearny Mesa. In this set, the rise and fall are generally highly correlated, suggesting the pools share a common perched water table. This would not always be the case, however. (Scheidlinger and Patterson, unpubl. data).

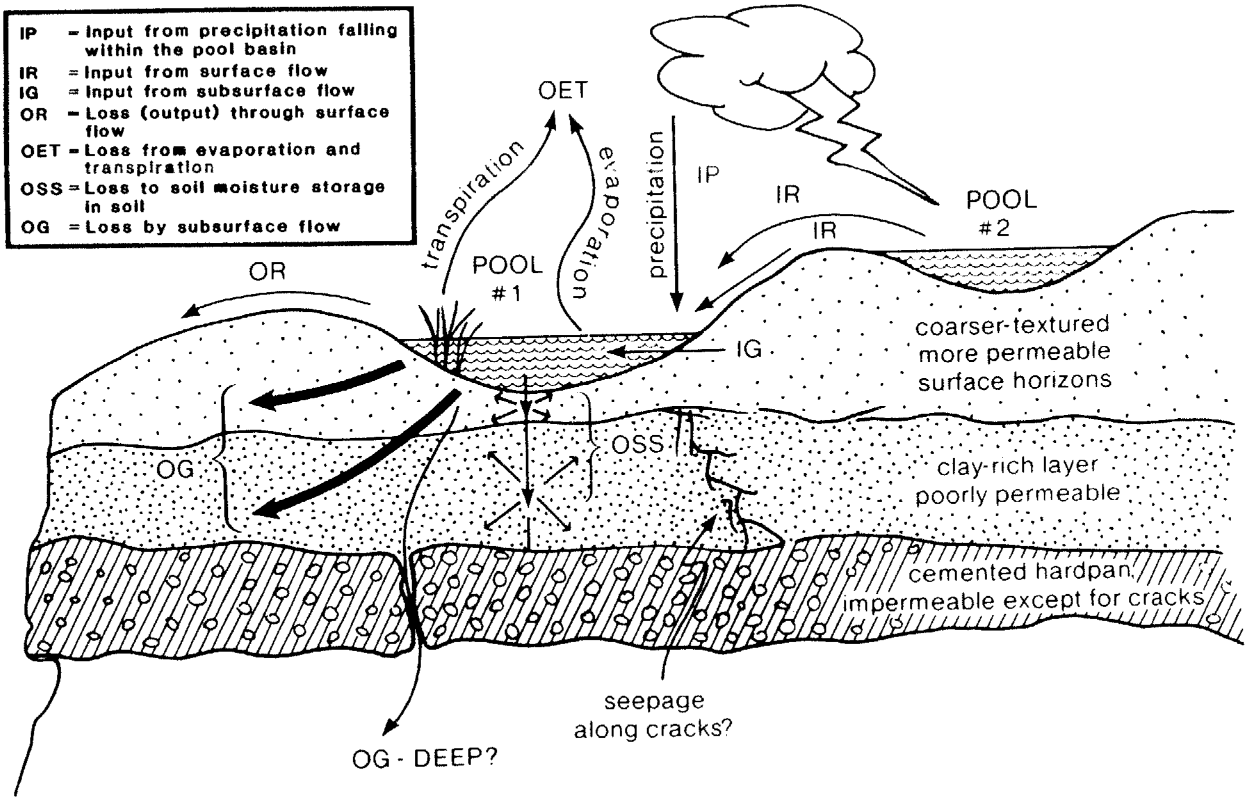


Figure 18. Input-output model of water regime for a hypothetical vernal pool (not to scale). The hardpan, shown here, is absent in many vernal pool areas, but the clay-rich subsoil is nearly always present.

period the rate of water input exceeds the rate of loss. In southern California winter rain tends to come in pulses--episodes of several days of rain interspersed with periods of sunny weather. Dry conditions caused by desert winds can also develop during the winter. These patterns are evident in both the rainfall and the evaporation data (Figure 9). The pool levels reflect this variability, fluctuating in a sawtooth pattern, filling rapidly and then slowly drying down (Figure 17).

Surface flow (IR, OR). Overland flow occurs when precipitation exceeds the rate of infiltration, and when a sloped water table intersects the surface. Although patterns vary, infiltration is usually greatest at the beginning of a rain, falls rapidly and then reaches a constant value (Linsley et al. 1982). For a given amount of rainfall, runoff will therefore be greater if rainfall comes in a single storm rather than several smaller ones.

Infiltration is decreased by the impact of rainfall on bare soil surfaces. It is increased when the soil is protected by plants and surface organic mulch which break the force of the raindrops, increase the residence time of water on sloped surfaces by the creation of microdams, and maintain greater surface porosity. For this reason surface runoff from heavily vegetated areas is minimal except on the steepest slopes. Vernal pool landscapes are sometimes not heavily vegetated, but the topography is also very gentle. The soils are also often relatively high in clay. Where this leads to surface cracking, infiltration would be increased, but clay and sand in the right proportions can make soils subject to crusting and sealing in response to surface wetting, thereby decreasing or even completely stopping infiltration (Emerson 1977). In the balance, surface runoff is probably significant on the sides of the larger mounds and on areas that have a reduced cover of herbs because of soil disturbance or a dense shrub canopy.

At all scales, runoff cannot begin until some minimum level of surface storage has been satisfied. After this, as more and more depressions are filled, increases in rainfall contribute to their outflow. At the smallest scale, surface storage involves microdepressions formed behind stones, twigs, leaf litter, etc. At a larger scale, storage includes the filling of pool basins. Overland flow into a pool is therefore a complicated function of 1) the topographic situation of the pool which determines the largest scale upstream storage, 2) the surface characteristics of the total watershed which determine the microdepression storage and rates of infiltration, 3) the moisture content of the soils at the time the rain begins, and 4) the rainfall rate. Some of these complexities are illustrated in Figure 19.

Detailed studies of vernal pool filling have apparently not been conducted, but the impression developed by workers in San Diego County is that most vernal pools begin to fill before surface runoff becomes evident. Thus the direct input to the basin and the slopes immediately adjacent is probably sufficient to fill most pools at least partially. But it appears that vernal pools can reach

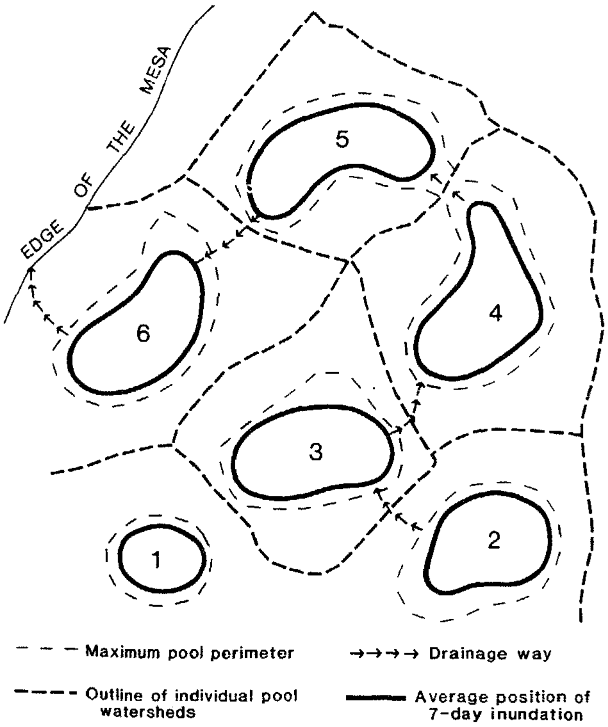


Figure 19. Hydrological relationships among six hypothetical vernal pools.

maximum depths only when there is widespread surface runoff and input from other depressions.

It is difficult to know what amount of water moves from temporary seepage areas formed where the perched water table intersects the surface. Such seepage areas can be observed, sometimes days or weeks after the last rain, but it seems likely that much more water moves as direct runoff, especially in the early weeks of the rainfall season.

For the purpose of characterizing the water budget of vernal pools it is useful to distinguish "within-drainage" runoff from "between-drainage" runoff. The first refers to the runoff that reaches a vernal pool without passing through another vernal pool basin, though it may pass through other depressions that hold water for brief periods. The second kind of runoff reaches a pool by overflow from an upstream pool or pools. These two cases are illustrated in Figure 19.

Input from subsurface flow (IG). The soils of vernal pool areas, which typically are high in clays, do not allow rapid sub-surface movement of water. Water transport (V) in saturated soil is primarily a function of the steepness of the gradient in water pressure and the hydraulic conductivity of the soil (K), as expressed in Darcy's law (Linsley et al. 1982). The hydraulic conductivity, which typically has units of cm/sec or m/day, is low to effectively zero for soils high in clay. For example, a field experiment in rice soils determined K values of about 2 mm/day for a soil with 62% clay.

Vernal pool soils on the mesas of San Diego County generally grade from a loam surface soil to a clay, clay loam, or sandy clay loam subsoil. It may be expected then that the movement of water through the soil will generally decrease sharply with depth, and in most cases drop to almost zero in the layers with 40% or more clay.

Suppose that there is a vernal pool with a maximum depth of 40 cm and diameter of 10 m located 10 m from another pool of similar or larger size 20 cm above it. The input from subsurface seepage would be, by Darcy's law with $K = 2.0$ mm/day and $s = 0.002$ m/m, about 1.6×10^{-5} m^3, equivalent to adding only a fraction of a millimeter to the depth of the pool when it is nearly full. This makes it obvious that inflow through heavy clay is unlikely to be a major input. In order for inflow to raise the level of the hypothetical pool 1 mm/day when it is near maximum depth, hydraulic conductivity would have to be about 10 m/day, a value which could only be achieved in coarse sand or gravel (Cedergren 1977). Subsurface flow is probably minimal except where pools are close together, the hydraulic head is unusually steep, or the pools are connected by animal burrows.

Loss from evaporation and transpiration (OET). The prediction of water loss from bodies of water has been the subject of considerable study. The Penman equation (Linsley et al. 1982), which predicts evaporation as a function of humidity, windspeed, air temperature, water temperature, and the intensity of solar radiation, has been widely used for this purpose.

Accurate prediction with the Penman equation requires measurement of the relevant meteorological variables at the site. Site specific data for vernal pools seem to be lacking, but data from nearby weather stations give a close approximation. The SDSU weather station is located about 10 km from the Kearny Mesa vernal pools and at approximately the same elevation. Using the daily values available from this station, it is possible to compare measured rates of drop in pools with the evaporation recorded in the same period. Since an evaporation pan has dimensions (diameter 122 cm, maximum depth 24.4 cm) in the same order of magnitude as vernal pools, the direct comparison is reasonable. If vernal pools behave as sealed basins with water temperature tending to follow air temperature, then there should be a close correspondence, on the average, between vernal pool evaporation and pan evaporation at a nearby weather station.

The comparison (Table 3) shows that the rate of drop in pools exceeded that in pans in all but two instances, and these negative differences were relatively

Table 3. Evaporation rates for 1982-83 from pools on Kearny Mesa, San Diego County, California, compared to evaporation from a Class A evaporation pan recorded at the San Diego State University Eidemiller Weather Station, about 10 km southeast of the pools at about the same elevation.

Pool[a]	Dates (month/date)	Water loss (mm/day)		Difference
		Pool	Pan--SDSU	(Pool-Pan)
C3[b]	12/1-12/8	3.4	3.0	+0.4
	12/10-12/16	3.6	2.9	+0.7
	12/24-12/29	4.4	4.5	-0.1
	1/5-1/11	4.5	3.7	+0.8
	2/8-2/15	4.3	3.4	+0.9
	2/15-2/21	7.1	4.4	+2.7
	3/3-3/14	4.8	4.0	+0.8
	3/25-4/14	5.9	5.1	+0.8
F3	1/30-2/2	7.7	3.2	+4.5
	2/8-2/15	5.9	3.4	+2.5
	3/8-3/14	6.1	4.0	+2.1
	3/25-3/27	11.8	4.4	+7.4
12-SL	2/9-2/13	21.1	3.6	+17.5
	2/13-2/18	8.2	3.4	+6.8
	3/22-3/29	16.1	4.2	+13.9
	3/29-4/4	10.2	5.4	+4.8
	4/4-4/8	10.1	6.4	+3.7
	4/25-4/27	24.0	5.5	+18.5
51	2/9-2/13	6.8	3.4	+3.4
	2/13-2/18	4.2	3.6	+0.6
	3/10-3/16	5.3	4.2	+1.3
	4/4-4/8	5.5	6.4	-0.9
34	2/9-2/13	12.3	3.4	+8.9
	2/13-2/18	9.0	3.6	+5.4
	3/10-3/16	8.7	4.2	+4.5
	4/4-4/8	21.3	6.4	+16.9
29	2/9-2/13	14.3	3.4	+10.9
	2/13-2/18	17.0	3.6	+13.4
	3/10-3/16	11.2	4.2	+7.0
	4/4-4/8	11.1	6.4	+4.7

[a] Data from pools C3 and F3 were collected by Carla Scheidlinger (Department of Biology, SDSU) and Cam Patterson (Department of Biology, SDSU). Data from the other pools are unpublished data of Ellen Bauder (Department of Biology, SDSU).

[b] Pool C3 is an artificially reconstructed pool which was dug deeper into the clay subsoil through the original pool and probably also partly compacted by the tractor used in the reconstruction. All other pools are natural, though not necessarily completely undisturbed, pool basins.

small. Though statistical significance may be lacking, there is the suggestion that the discrepancy between pan and pool rates varies more with pool than it does with period of observation, indicating that relatively fixed pool properties are a large element explaining the high rates of drop in the pools.

Why should pools drop so much more rapidly than evaporation pans? The most likely causes are 1) significantly higher water temperatures in pools compared to the pan because of absorption of heat by a dark pool bottom; 2) loss of water through plant transpiration; and 3) absorption or seepage into the soil.

The available data suggest that pool water temperatures are not sufficient to increase evaporation over the standard pan by the amounts recorded. For example, Pool 34 dropped at a rate 4.5 mm faster than the pan in mid-March, when mean daily air temperature was 10 degrees C. The temperature difference necessary to explain this discrepancy would have to be implausibly large.

Well-watered plants evaporate at very nearly the same rate per unit area as free-water surfaces experiencing the same physical conditions. Therefore the loss from transpiring plants would not increase the rate of drop of water levels unless the plants increased the evaporative surface by rising above the surface of the pool. But plant cover also shades the water surface and decreases wind velocity, and these can act to decrease evaporation. Detailed studies of prairie potholes in North Dakota, bodies of water larger and more permanent than vernal pools, showed that emergent hydrophytes (mainly *Typha*, *Juncus* and *Scirpus*) increased evaporation but also sometimes decreased it substantially (Eisenlohr et al. 1972). Vernal pools are much smaller and generally have less well-developed emergent vegetation. The relatively thin cover and short stature of the vernal pool hydrophytes make it unlikely that they are major contributors to water loss for most pools for most of the season.

Loss to storage in the soil and subsurface flow (OSS, OG). It seems apparent that the discrepancy between the rate of water loss from evaporation pans and pools must result from the loss of water into or through the soil. It is doubtful that the storage capacity of the subsoil alone could explain the observed rates of drop. According to Greenwood and Abbott (1980), the storage capacity of the soil beneath a pool on Del Mar Mesa with an unusually deep subsoil was 0.37 cm water/cm soil in the upper soil layers and 0.22 cm water/cm soil in the lower clay-rich layer, for a total storage capacity at saturation of over 32 cm, or substantially more than the total average rainfall of about 25 cm.

Although the water storage capacity of the soil is great, the rate of movement of the wetting front is slow. If we assume that a drop of 4 mm/day is attributable to the wetting of a clay layer, using the values of Greenwood and Abbott (1980) and assuming no lateral movement, the downward progression of the saturation front in the clay soil would be estimated at 18 mm/day. At this rate the soil beneath and adjacent to vernal pools, which is usually not much more than a meter deep over a hardpan, would be completely saturated by the end of the rainfall season. This contradicts direct observation that the clay subsoil usually is not saturated throughout its depth. Furthermore, many pools have much less than a meter of soil above the hardpan.

If absorption of water into the soil around the pools can account for only part of the increased rate of drop, the remaining possibility is that water is moving out of pool basins by mass-flow through macropores or channels, or lenses of coarser material. Though lenses of sand and sand-filled cracks are sometimes seen in cross-sections of soils near vernal pools, they are probably not universally present. A more likely pathway for mass-flow is through the network of micro-cracks that surround the soil aggregates and the larger cracks that are present because of shrink-swell processes.

The neutral to acid soils and low salinity of many vernal pool basins are consistent with the idea that mass-flow through the soil is a major source of water loss. The Kearny Mesa pools, for example, are not far from the coast and are on a relatively old land surface. If there were no drainage out of the pool basins, the soils and the pool waters should be saline or alkaline. Water must be moving through the soil column.

Water movement and water balance in vernal pool landscapes. From the previous information, it is possible to come to some general conclusions about the components of water balance in vernal pools. First, the precipitation input directly to the pool basin is probably significant in a majority of pools, and in some of the larger pools it may be the only significant source of water in many years (Greenwood and Abbott 1980). Many smaller pools probably require input of surface water from the overflow of adjacent pool or nonpool depressions.

Part of the water loss from the pools, especially the smaller ones, is probably a result of the absorptive capacity of the soils. But the main route of water loss is most likely cracks, old root channels, lenses of sand, animal burrows, and other macroscopic channels that allow mass flow out of the basins.

2.6 PHYSICAL AND CHEMICAL LIMNOLOGY OF VERNAL POOLS

For the period that water stands in vernal pools they are aquatic systems, but this phase has been little studied. Enough is known, however, to show that the vernal pool is a distinctive kind of aquatic habitat. Their small size, shallowness, and short period of persistence make them about as variable in physical and chemical properties as it is possible for a body of water to be.

2.6.1 Water Chemistry

Vernal pools in southern California, even though they are closed basins or have only very restricted surface drainage are generally fresh and clear (Figures 20, 21, 22). The waters have relatively low conductivities, and are acidic or just above neutral. The pH data, mostly late morning

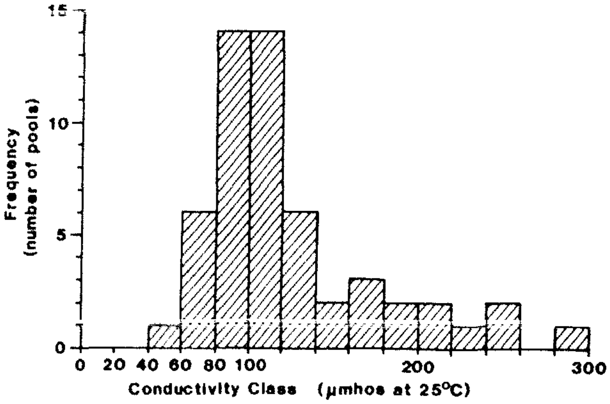


Figure 20. Frequency distribution showing the number of pools with water in various conductivity classes. Based on data collected on Kearny Mesa pools in spring 1979 by Mary Lee Balko, Planning Dep., City of San Diego.

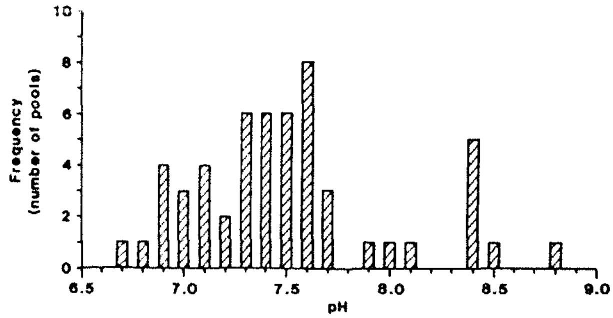


Figure 21. Frequency distribution showing the number of pools with midday water pH values in each pH class. The pH data are highly variable diurnally and within seasons as well as among pools. Based on data collected on Kearny Mesa pools in spring 1979 by Mary Lee Balko.

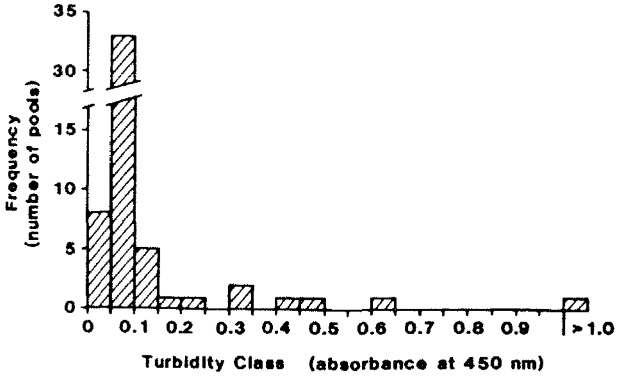


Figure 22. Frequency distribution showing the number of pools in different turbidity classes. Based on data collected on Kearny Mesa pools in spring 1979 by Mary Lee Balko.

to early afternoon measurements, must be interpreted with caution. Keeley (1981a, b) in his study of *Isoetes* in vernal pools in San Diego County and on the Santa Rosa Plateau has followed the diurnal course of pH, and found that it rises to a maximum in midday and drops to a minimum after midnight.

The diurnal range he observed (over 2 pH units) is almost as great as the range in midday values among pools. According to Keeley, this fluctuation is a consequence of the uptake of carbon dioxide (CO_2) by photosynthesizing plants during the day and its release by respiration at night. Higher daytime temperatures and the consequent decreased solubility of CO_2 may also play a role. Changes in pH of this magnitude would also affect the solubility of other elements. Morton and Bayly (1977) reported a much narrower diurnal range of pH for Australian temporary pools. For example, one pool ranged from a pH of 6.8 at 1100 h to a maximum of 7.05 at 1800 h.

Photosynthesis by algae and other plants also produces oxygen supersaturation (Keeley and Morton 1982). It is common to see bubbles rising to the surface during midday in shallow vernal pools from the algal cover on the bottom. I have also seen bubbles arising from submerged moss plants early in the season. The high oxygen content of the water, at least during midday, probably helps to alleviate and possibly eliminate the reducing conditions that would tend to develop in the saturated soil.

The few published studies of vernal pools that report dissolved and particulate organic matter and dissolved inorganic nutrients suggest that these features vary widely among pools. The large substrate-area to water-volume ratio insures that the water chemistry of vernal pools is intimately related to the substrate in which they are found, and to the surrounding vegetation and pools. At least in small shallow pools the decay of the previous year's dead vegetation must be a significant influence on the water quality of pools.

The importance of substrate on pool water is illustrated for an extreme case by the study of Barclay and Knight (1984) of a large pool in the Jepson Preserve near Dixon in the Central Valley. They reported high levels of both dissolved and particulate organic matter, moderate values of dissolved phosphorus (P), and low levels of dissolved organic nitrogen (N). The turbidity of this pool is high because of suspended clay which disperses from the largely barren surface of the pool basin upon filling. They believe that the high organic matter levels result from the decay of grass and shrub litter, and suspect that adsorption of organic matter and inorganic nutrients on the suspended clays plays an important role in the nutrient budget of this turbid pool.

The change in water properties as pools dry is a potentially important but little-studied aspect of pool limnology. Some data of Collie and Lathrop (1976) showed how significant these changes can be, at least for large pools. The conductivity of a 10.2-ha pool on the Santa Rosa plateau was nearly constant during the rainy season but rose exponentially as the pool dried (Figure 23), a consequence of the concentration of dissolved salts. This dramatic change must affect the gradient in soil properties, and may figure in the life histories of some of the vernal pool animals as a cue for the onset of the summer drought.

2.6.2 Light Penetration

In deep lakes the attenuation of light with depth is a major feature influencing the distribution of biota, but

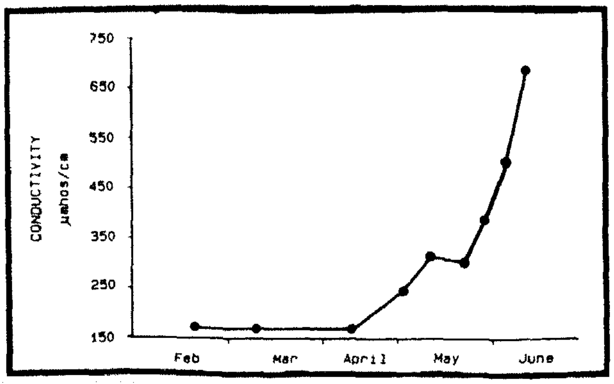


Figure 23. Increase in conductivity with drying in a large vernal pool on the Santa Rosa Plateau. Modified from Collie and Lathrop (1976).

it is obvious that this will be of scant importance in shallow vernal pools that have fluctuating water levels and clear water. Measurements by Keeley et al. (1983) in a shallow temporary pool indicate that 50% to 75% of the surface quantum solar flux remains at 5- to 10-cm depth. However, many pools develop thick covers of floating green algae and blue-green bacteria which must block a large proportion of the light. Others, most commonly disturbed pools, are cloudy with suspended clay (e.g., Barclay and Knight 1984). In these cases, the effect on the smaller plants that cannot expand leaf area above the surface of the water can be devastating. The relative barrenness of the deeper parts of some vernal pools late in the season may be in part a result of death of plants from insufficient light. In Australian temporary pools turbidities can be relatively high, and Morton and Bayly (1977) commented that photosynthesis may be light limited so that energy flow in the aquatic phase becomes detritus based. This is not likely to be the case for most of the coastal vernal pools in California.

2.6.3 Temperature

Water has a high heat capacity, and aquatic habitats are therefore usually characterized by narrower temperature ranges than terrestrial habitats. The same effect must operate in vernal pools, but much less strongly, since the pools are shallow enough to warm significantly during the day. For example, Keeley (1981a,b) reported diurnal temperature fluctuations of 6.9 and 8.5 degrees C for two Kearny Mesa vernal pools in April, when such fluctuations probably are near maximal. Morton and Bayly (1977) measured both air and water temperatures over a 24 h period in a vernal pool near Melbourne, Australia on 25 August, equivalent to late February in California. Water temperature followed air temperature with a time lag of about 2 h. Air temperature ranged from about 5 to 22.5 degrees C, while surface water temperature moved from 9 degrees C at about sunrise to 20 degrees C in midafternoon. While on many days the temperature fluctuations would not be as extreme as these figures indicate, on at least some days the aquatic animals and plants may suffer from heat stress.

2.7 THEORIES OF MOUND AND POOL FORMATION

2.7.1 The Mound Mystery

There are many interesting features of vernal pool topography, but none of these has excited as much speculation as the mounded topography. A satisfactory explanation of the cause of mounded topography has proven to be elusive, probably because there has been a high proportion of speculation per unit hard information. Various published (e.g., Cox 1984a,b) and unpublished (e.g., Nadolski 1969; Zedler et al. 1979) reviews of theories of mound origin have identified about 30 hypotheses.

The mounds are an intriguing geomorphological puzzle, but beyond that, we cannot have a satisfactory understanding of the evolution and assemblage of vernal-pool biotas unless we know when and how the basins formed. If vernal pools are ancient and stable landscape features, then the time for migration and evolution of organisms has been long, and we have a ready explanation for the presence of species of highly restricted distribution. But if vernal pools are short lived or were only recently formed, then we have the problem of explaining where the vernal pool biota was while it was waiting for the basins to be created. Existing theories of mound formation suggest very different chronologies for the origin and stability of pools. Our concepts of vernal pool function and origin will to a large extent depend on which hypotheses we choose to believe.

Because permanence and time of origin are so important, these provide the best way of organizing the various theories (Table 4). No doubt most of these still have proponents. I will discuss only those I perceive to be the leading candidates for the situation in California: B6, C1, C2, and part of B2.

2.7.2 Important Theories

Mound formation by swelling clays. Australia has extensive areas of mounded topography. These gilgai landscapes are usually found in association with soils high in montmorillonitic clays which because of their sandwich-like crystal structure absorb water and swell to a remarkable degree, as discussed earlier (see 2.4). It is argued that the forces generated on wetting can have a net upward component sufficient to lift mounds (Knight 1980). George Borst, formerly of the U.S. Soil Survey, suggested that these same processes may also operate in California mounded areas. He reported the presence of "slickensides" (distinctive surfaces caused by soil aggregates moving past one another) and an abundance of subsurface cracks, features which indicate the action of shrinking and swelling clays. However, in at least some places in San Diego County, the difference in elevation between depressions and mounds is much greater than the thickness of the clay layer underlying them. The tops of the mounds are also usually of distinctly coarser material than the deeper soil layers, and the clay-enriched horizons are usually nearly level (Nikiforoff 1941). These features are quite different from those of typical Australian gilgai (Hallsworth et al. 1955).

Table 4. A partial list of the theories for the origin of mounded topography. Publications marked with a single asterisk apply to the west coast of the United States; those with a double asterisk consider, at least in part, the situation in California. Others are for various regions.

A. Theories that suggest that the mounds are old and stable, and formed by processes that are no longer active. If the mounds were leveled, they would not reform.

1. Periglacial phenomena (Ritchie 1953*).
2. Depositional features (Krinitzsky 1949).

B. Theories that hold that mounds are probably old, but could be relatively young, and are relatively stable if not almost static. Processes involved are either no longer active or take place at such a slow rate that millenia are required for significant change.

1. Aeolian origin by deposition at the base of shrubs (Ellis and Lee 1919**; Krinitzsky 1949 in part; Quinn 1968).
2. Deflation (Abbott 1981**).
3. Mounds raised by ground water welling up from depth (Nikiforoff 1941**; Retzer 1945**).
4. Bulk density changes and soil collapse of poorly drained alluvium (Harris 1958)
5. Overburden pressure causes upwelling of clays (Paton 1974).
6. Differential "rheidity" plus shrink-swell (Beckman et al. 1981).
7. Subsidence: solution depressions by chemical weathering of alluvium, this chapter.

C. Mounds may be old, but could be young; the processes that formed them are still active. Mounds could reform if leveled.

1. Forces generated by swelling clays [Hallsworth et al. 1955; Knight 1980 (includes a review of literature on mechanisms for gilgai formation)].
2. Mounding by fossorial animals (Dalquest and Scheffer 1942*; Arkley and Brown 1954; Cox 1984a,b**).
3. Possibly B3, above.
4. Subsurface mass movement (soil-piping) (R. Holland; pers. comm.).

Deflation. Abbott (1980, 1981, 1983) has proposed a composite hypothesis for San Diego County. He suggested that shrinking and swelling cause triaxial intersections of cracks that collect water in the wet season. Clays from the margins of the cracks go into suspension, and then form curling flakes in the dry season. Given high winds and the low vegetation cover which he hypothesized existed during Pleistocene interglacial times, the clay in the dried mud curls could be blown out of the basins, leaving the gravel that covers most pool bottoms. He saw the shrinking and swelling of clays as essential to this process (Greenwood and Abbott 1980; Abbott 1983).

While pan-like deflation basins might form by such a mechanism, it is difficult to imagine how a landscape like that of Figure 15, where local relief between mound and pool often exceeds 1 m, could have been caused by wind. Since the theory depends on clay shrinkage, it cannot apply to areas where clay horizons are absent or very thin.

Gophers and mounds. In 1942 Dalquest and Scheffer argued that pocket gopher burrowing was the cause of the mounded topography of the Mima Prairie in western Washington. Subsequent publications (Price 1949; Arkley and Brown 1954; Cox 1984a) have proposed that gophers may be the cause of mounded topography throughout western North America. Cox and Gakahu (1983) presented evidence that mole rats may be responsible for mounds in Kenya. The gopher hypothesis is generally accepted as the explanation most likely to apply to the California mounds found in association with vernal pools (e.g., Barry 1981), and it therefore merits special consideration. The behavior and ecology of gophers will be discussed in section 4.6.

The basic elements of the theory are these: 1) The presence, initially, of a rather shallow substrate overlying a hardpan or a layer of large gravel or cobbles, but which is in other respects (texture, plant species present, etc.) favorable for fossorial rodents. The shallowness of the soil causes waterlogging for extended periods, restricts foraging, and makes the mounds increasingly favorable and the depressions increasingly less favorable as foraging and nesting sites for the gophers. 2) The animals have a highly territorial foraging pattern which centers around nesting sites. 3) The nesting sites are located in the deepest soils, partly because of greater food resources are found there, and partly because predators are most easily evaded in deeper soils. 4) There is a tendency during the creation of foraging tunnels for displaced soil to be moved back toward the center from which the foraging tunnels originate. This occurs either because the soil has a net backward movement within the foraging tunnels or because the mounds of dirt pushed to the surface at any point tend to contain material collected at a lower average elevation than the point of deposition, or both of these acting together. 5) Most of the habitat is exploited, so that a more or less evenly spaced distribution of mounds develops.

Given these assumptions, gopher foraging would accentuate the topography, making high points higher, and low points lower. The process should accelerate in the early stages because as the soil is accumulated at the high points, these become even better nest sites. The process should also tend to a uniform distribution of mounds, the scale of which should depend on the length of the foraging tunnels created by the gophers, and the population density.

Mounds built in this way should have certain features: they should contain few stones larger than the diameter of the burrow of a pocket gopher, whereas the depressions should be relatively enriched in larger sizes of gravel and stones. Burrowing within the soil might also cause large stones to settle in the mound, since the gophers could remove material from below stones and deposit it on the surface. These and other predictions of the theory appear to hold in many places. Until recently, the details of soil movement by gophers were largely supposition. Cox (1984a,b) has provided direct evidence for moundward movement of soil material, and has calculated that the creation of mounds by foraging is easily possible. He estimated that a typical mound would be formed in about 108 years.

Details of the gopher hypothesis may be criticized (e.g., Newcomb 1952), but a key question is how a single species of animal could have created a topography of such striking regularity over, in some cases, many hectares (Figure 15). For this to happen, the area would have to be continuously inhabited at maximum density for centuries, at least. A related problem is the regularity of the present landscape. Photographs in Nikiforoff (1941) and elsewhere show smoothly rounded mounds of uniform height and a tendency toward uniform size. Even if gopher foraging had the proposed effect on soil movement, a less uniform landscape might be expected. Another problem is that cross-sectional excavations show profile development within some mounds, suggesting that there has been soil genesis without significant soil disruption. For this to occur, the mounds must have been formed in the past and then subsequently weathered.

Another difficulty is presented by the heavily cobbled pools on Kearny Mesa (the more northern group in Figure 15) in which cobbles, some as large as 10 cm diameter are stacked on top of other cobbles, finer soil material being absent. In this case at least it is obvious that some erosive factor other than gophers has played a role.

A further difficulty, which could be resolved by careful field work, is that mounded topography should not, under the gopher hypothesis, be limited to extensive alluvial areas, but should be present wherever unconsolidated material overlies a layer which gophers cannot easily dig through. Isolated mounds would be expected in all sorts of topographic settings. Cox (1984b) provided evidence that mounds are found outside of alluvial areas, but a random sampling approach to show the correspondence between mounds and the postulated conditions is needed.

The subsidence theory. Elementary discussions of landscape evolution at the largest scales tend to emphasize mechanical erosion. Models are constructed in which landscapes are shaped by the movement and deposition of inert materials. The extant theories on mound formation take this view, stressing the pushing about or lifting and movement of soil particles and aggregates. But it is apparent that most of the surfaces that have mounded topography have had a long history of soil development, during which the mineralogy, texture, structure, and bulk density must all have been altered substantially. It would be surprising if these changes had no effect on microtopography, and it is possible that they are a major cuase of it.

A simple hypothesis, which I propose here, is that mounded topography in California is predominantly a result of the differential weathering and differential settling of alluvium or soil. Further, many of the vernal pool basins found in unmounded or slightly mounded areas may be solution basins formed by chemical weathering, or collapse basins formed by loss of structure.

It is surprising that the possibility of land subsidence has not been given more consideration in explaining mounded topography in the Western United States especially since Johnson (1900) proposed it to explain pits and depressions of the Great Plains. Arkley and Brown (1954) mentioned it without attribution only to dismiss it as an obviously inadequate explanation. There do not appear to be any published articles that propose the idea for California, nor does it seem to have been proposed for the Australian gilgai, although Blackburn et al. (1979) suggested that carbonate leaching may have accentuated existing gilgai relief in their study area.

A first point in support of the theory is that chemical weathering can produce surface features. Though data are still scattered, there seems little doubt that this is the case. The ability of subsurface weathering to produce undrained depressions is not questioned for the special case of karst topography (Smith and Atkinson 1976), in which the solutional erosion of limestone produces a variety of features. It is of particular interest that in some situations this subsurface removal can lead to an undulating topography with internally drained depressions (dolines) (Williams 1969, 1972; Gunn 1981).

The possibility of surface subsidence in landscapes of less-soluble lithologies has been not so much controversial as ignored. But when rates of chemical and mechanical weathering have been compared, the conclusion has been that the loss of material in solution is always significant and can exceed that removed by mechanical erosion in particular instances (Williams 1969; Cleaves et al. 1970; Carson and Kirkby 1972; Waylen 1979; Saunders and Young 1983). According to Saunders and Young (1983), it is now "firmly established" that solutional denudation is important for siliceous lithologies.

For geomorphological purposes, denudation rates are best expressed as surface drop. The effectiveness of solutional denudation may be measured by comparing it to total denudation rates 1 mm drop per 1000 years, and Saunders and Young (1983) assembled estimates of these rates from hundreds of publications. Comparing rates for surface wash and solution (their Figures 2 and 3, and Tables 3 and 4) leads to the conclusion that maximum rates of surface wash can exceed maximum rates of solutional denudation by an order of magnitude or more. Data are very sparse for Mediterranean climate regions, but surface wash is shown ranging from <1 to 7500 mm drop per 1000 years in steep topography, and solutional denudation is indicated, presumably on very limited data since no references are cited, as about 20 mm drop per 1000 years. As would be expected, rates of surface wash are greater on steeper slopes.

Interpreted uncritically, these numbers suggest that on the average any effects of solution in surface lowering would be completely overridden by slope wash. But the balance between surface wash and solutional processes will obviously depend on the steepness of the slope and the nature of the material being weathered (Carson and Kirkby 1972). The lower the slope, the more porous the substrate, and the more weatherable the minerals in the substrate the greater must be the relative contribution of solutional weathering to total surface denudation given a climate in which rainfall exceeds evaporation for at least some times of the year.

There is increasing evidence for the geomorphological importance of solutional weathering in other settings. Smith (1931) studied anomalous circular or oval depressions on level surfaces of sandy sediments on the coastal plain of South Carolina. He concluded on the basis of chemical analysis that these had formed by chemical solution enhanced by the increased moisture in the depressions and the production of acids by the lush vegetation which grew in them. Le Grande (1952) came to a similar conclusion in North Carolina. He argued that depressions about 60 m in diameter and 0.2 to 1 m deep were formed by "solution subsidence," since the depressions held water in the spring. He also attributed "slight undulations on the uplands" to the same cause. Johnson (1900), cited above, stated "(the) conclusion that the innumerable hollows in the High Plains surface, large and small alike, are due to ground settlement rather than to some process either of original construction or subsequent erosion, seems to be unavoidable."

Bremer (1973) (see also Buedel 1977, p. 211) worked on alluvial plains in the Amazon Basin of Brazil, where she reported both undulating topography in some situations, and in one alluvial landscape many closed depressions occupying small level areas surrounded by deeply incised drainages. She said that landforms and deposits present are "explainable only through a subterranean loss of material."

Brosh and Gerson (1975) were intrigued by depressions several meters deep and 100 or more across that they found on ridgetops in Uganda. They believe that percolation of rainwater, probably under different climatic conditions than those currently prevailing, and the removal of material in solution are the cause of the depressions. Since the depressions occur in quartzites, phyllites, sandstones, and shales they provide evidence that under the proper circumstances landscapes with even quite-resistant lithologies can have features caused by solutional weathering.

A study by Crabtree and Burt (1983) in England is of special relevance, since it showed that concentration of water in depressions can explain the evolution of hill-slope features. They studied subsurface erosion by burying polished bedrock tablets at a depth of 0.4 m across a hill-slope hollow and its adjacent spurs. By weighing the tablets before burial and after excavation 16 months later, they could assess the rate of bedrock weathering at different locations relative to the hollow. They found that the greatest loss (about 0.7%) was in the center of the hollow at the highest slope position, and that the average weight loss for the hollow was 0.42% versus 0.31 to 0.35 for losses on the spurs on either side of the hollow. The authors concluded that "solutional denudation appear(s) to be enlarging the hollow preferentially within a general pattern of slope decline over the hillslope." Their results support the conclusion of Carson and Kirkby (1972) that subsurface water erosion is a major factor in hillslope evolution.

Since there is accumulating evidence for surface depressions caused by solution even in situations dominated by relatively resistant bedrock in dissected topography, it seems certain that nearly level areas of alluvium exposed to weathering for more than 100,000 years would have some features attributable to the same cause. Way (1978) proposed that "buffalo basins" in Texas may have originated as "solution pits," and gave evidence for the potency of chemical weathering. Thus it seems plausible that solution depressions are present on the older alluvial terraces in California. But would these depressions form the almost regular pattern which is so obvious in air photos (Figure 15)?

A model for mound origin by weathering. The weathering hypothesis is based on the assumption that the rate of drop of the alluvial surface is proportional to the amount of "fresh" (i.e., relatively pure mineral-free) water that moves through it. It is assumed that if a particular block of material receives twice the quantity of "fresh" water, it will lose approximately twice as much material in solution, and therefore fall in elevation at twice the rate, assuming no mechanical erosion from high points to depressions.

The initial condition may be a nearly level surface with only minor microtopographic variation resulting from the conditions of deposition and from postdepositional movement by wind, water, and animals. Water collects in the microdepressions, and the throughflow in these small depressions is significantly greater than the surrounding mounds. The quantity of water accumulating in a depression is a function of the drainage area feeding it. In this initial phase removal of material by chemical solution will probably not contribute much to the drop in the surface. In fact, it is possible that the actual volume of the weathered minerals may be greater. However, saturated soils tend to lose structure, and as Harris (1958) and White and Law (1969) pointed out, there can be a development of patterned ground related solely to the loss of structure of soils in depressions. It is also possible for expansion of the drying soils of the mounds to accentuate this pattern. In this context the observations of Bull (1964) on the behavior of collapsing soils in California is relevant. He reports that "irrigated farmlands [on collapsing soils] tend to have hummocks and hollows caused by differential subsidence." Thus the initial pattern in the eventual mound field may be generated solely by collapse of material in the depressions without significant weathering. The symmetry may then arise by a mechanism like that postulated for polygonal karst by Williams (1972), in which the drainage of smaller depressions is captured by larger depressions.

The second phase of development is reached when the water moving through the soil profile beneath the depressions leads to a significantly greater loss of material from the depressions as a consequence of chemical weathering. The result is an acceleration of the process. As the depressions sink relative to the mounds, proportionately more of the runoff moves through the depressions, increasing the rate of drop. The process should eventually slow as more resistant minerals accumulate and as the local topography becomes steep enough to cause material to erode from mounds into the pool basins. Over the long time periods involved the possibility that there is significant dust input must also be considered (Muhs 1980).

The interaction of biological and physical factors might also have played a role. Besides the well-known relationship between plant cover and runoff, there is the possibility of organic acids enhancing weathering (Curtis 1976). Trudgill (1976) cited a case where algal respiration in temporary ponds increased calcium carbonate dissolution.

If the hypothesis of subsidence is correct, then one would expect to find certain features and processes in the present landscape: 1) There should be evidence of more intense weathering in depressions (including those without pools) than in mounds. 2) The rate of input of material from the mounds to the depressions by mechanical erosion should be slower than the rate of removal of material by weathering. 3) The mineral content of water percolating to the bottom of the solum beneath the mounds over the course of a year should be lower relative to the depth of soil than that of water moving through the soil beneath depressions.

There are few or no data on these three points, since there have been very few studies which have looked in detail at the small-scale toposequence of soils from mound to pool. Additional observations are clearly needed.

CHAPTER 3. THE BIOTIC SETTING

3.1 THE CALIFORNIA BIOTIC PROVINCE

The vernal pools of California, as defined here and in Holland and Jain (1977) lie entirely within the California Floristic Province (CFP) of Raven and Axelrod (1978). This region, essentially the nondesert part of California plus the Mediterranean climate areas of Oregon and Baja California, is one of high plant-species diversity and high endemism. Both these characteristics may be explained by the generally mild but geographically varying climates, the topographic and geological diversity of the region, and, for some climatic zones, geographic isolation from regions of similar climate (Raven and Axelrod 1978).

3.2 THE CURIOUS CASE OF AMPHITROPICAL DISJUNCTIONS OF VERNAL POOL PLANTS

One of the intriguing patterns in the plant geography of North America, and especially California, is that of "amphitropical disjunction": the occurrence of the same or similar species in the polar or temperate regions of North and South America, but not in the intervening tropical areas. A surprisingly large number of vernal pool genera and species have this distribution pattern. There are only two possible explanations for these extreme disjunctions: separation of once-continuous populations, or the long-distance dispersal of plants from one of the temperate areas into the other. For a variety of reasons explained in detail in Raven (1963), it appears that the second explanation applies to most of the instances of disjunction.

Of the about 130 species or species pairs involved in amphitropical disjunction (Raven 1963) about 10-15 are vernal pool plants, and a number of others are grassland plants associated with vernal pools (Thorne and Lathrop 1970, Table 5). It is thought that the vernal pool plants shared between North and South America were dispersed by migrating birds. As Raven (1963) points out, however, arrival at a distant location is of no consequence unless there is successful establishment. The newly arrived seed would have to germinate, and the plant grow and produce viable seeds. One would therefore expect plant groups with amphitropical disjunctions to be species of open habitats capable of producing seeds without cross pollination. No doubt migrating birds transport thousands of seeds long distances each year, but the vast majority of these fail to establish permanent populations.

Vernal pool plants fit the pattern of species that should make successful long-distance migrants. As discussed in subsequent sections, they are often self-fertile or apomictic, and have small seeds capable of long dormancy. Equally important, a vernal pool is a habitat relatively open to invasion. The hazards to survival are greatest up to the time of germination. Once established, a suitably adapted plant has a good chance of successful reproduction. The opposite condition holds in a dense forest, for example, where a germinated seed must face intense shade and competition from the roots of already established trees, shrubs, and herbs. In fact, none of the striking cases of amphitropical disjunction involve plants from heavily vegetated environments.

The amphitropical disjunctions are of interest in themselves, but also tell us something important about the function of vernal pools within California. If pool plants have been carried thousands of miles by birds, then the dispersal of vernal pool plants over tens or hundreds of miles must be proportionately more common. Within the CFP there must be a continuous trickle of propagules among habitats that are used by birds, which should be essentially all vernal pool habitat. This suggests that the presence or absence of the dispersable species is controlled more by local site and climatic factors than by geographical isolation.

3.3 RELATION OF VERNAL POOLS TO OTHER HABITAT TYPES

Vernal pools are never the dominant feature of the landscape and must be viewed in the vegetation context in which they occur. Because they are essentially restricted to level or gently sloping land, usually on alluvium, the associated vegetation types are those of the coastal mesas and inland alluvial valleys. Along the coast the remaining vernal pools are found mostly with annual grassland, though in places (parts of Kearny Mesa, San Diego County, Vandenberg Air Force Base (AFB), Santa Barbara County) the pools occur with evergreen chaparral usually dominated by chamise (*Adenostoma fasciculatum*). Further north, and on the Santa Rosa Plateau, vernal pools occur in or near oak woodland.

Although the island-like distinctiveness of vernal pools is striking, it is a

Table 5. Species and species groups of vernal pools that show amphitropical disjunction between temperate South America and North America. It is not necessarily true that the source area of North American groups found in South America was the vernal pools of California, since some species occur in many habitats besides vernal pools. All North American species are found in the coastal vernal pools except *Downingia humilis*.

N. American taxa	S. American taxa and location	Reference
Anagallis minima	same, Chile	TL
Blenospermum nanum	*B. chilense*, Chile	O
Boisduvalia glabella	3 spp., Chile and Argentina	TL
Crassula erecta	same, Chile	TL
Deschampsia danthoniodes	*D. monandra*, Chile	R
Downingia humilis	*D. pusilla*, Chile	R
Elatine chilensis	same, Chile	R,TL
Festuca megalura	same, Bolivia, Peru, Uruguay, Tierra del Fuego	R
Lasthenia glaberrima	*L. kunthii*, Chile	O
Legenere limosa	same, Argentina, Chile	H
Lilaea scilloides	same, Chile	TL
Lythrum hyssopifolium	same, Chile	TL
Myosurus minimus	*M. patagonicus*?, Argentina	R
Navarretia spp.	*N. involucrata*, Chile	H
Phalaris lemmonii	*P. platensis*, Argentina, Brazil	R
Pilularia americana	same, Chile	TL
Plagiobothrys spp.	Peru to Chile	R
Psilocarphus brevissimus	same, Argentina, Chile	R
P. tenellus	*P. berteri*, Chile	R
Spergularia platensis	same, Argentina, Chile	R

Reference code: R = Raven (1963) O = Ornduff (1963)
TL = Thorne and Lathrop (1970)
H = R. Holland (pers. comm.).

mistake to assume that "pools" and "non-pools" are the only categories of vegetation in vernal pool landscapes. In an area of rolling mounded topography, such as that on Kearny Mesa, there are many depressions in which the vegetation is distinctly different from that of the mounds but which are also clearly not vernal pools. There is a continuum of water-duration characteristics from basins of long duration in which vernal pools in the strict sense develop, and those in which surface water and the perched water table exert some influence but do not lead to the formation of a true aquatic ecosystem. Unfortunately, there are no studies that have examined the full range of vegetation of vernal pool landscapes. Schlising and Sanders (1982) did, however, sample the surrounding vegetation in their study of pools at Richvale in the Central Valley, and Kopecko and Lathrop (1975) included the "dry grassland zone" in their study on the Santa Rosa Plateau. Del Moral and Deardorff (1976) presented a comprehensive analysis of vegetation of the Mima Prairie in Washington, but this landscape does not contain pools.

3.4 BIOTIC CHANGES IN THE LAST 200 YEARS

The introduction of European land-use practices in the 18th century dramatically altered the vegetation of the state, especially the grasslands and open woodlands near vernal pools. First, the domesticated grazing animals both introduced and favored the spread of Mediterranean and Eurasian weedy plants (Heady 1977), especially annual grasses. These plants, presumably because of their tolerance to grazing, but also perhaps because of their freedom from insect herbivory and pathogens, spread into every corner of the state with astounding rapidity. The annual grasses became dominant, displacing the native perennial bunch grasses (e.g., Melica spp., Stipa spp.)

So thoroughly have these plants become naturalized that there has been in some cases considerable confusion over the introduced status of some species. For example, Festuca (Vulpia) megalura, a small annual grass, long thought to be native (e.g., Munz 1974), is now said to be introduced (Lonard and Gould 1974). Heady (1977), pointing out the present importance of introduced annuals and the impossibility of rangeland management eliminating these species, proposed that we acknowledge their status by referring to them as "new natives."

There have been changes in grassland landscapes beyond the shift in species composition. It is also obvious that the present and original distribution of grassland is not the same, though opinions differ on how much change there has been and in what direction. Heady (1977) believes that, excluding developed lands (farms, cities, etc.), the distribution of grassland is about the same today as it was 200 years ago. Dodge (1975), on the other hand, argues that grazing and decreased fire frequency have favored the spread of brush at the expense of grassland. I will follow Oberbauer (1978) here in suggesting that the major change in the vicinity of vernal pools has been for the combined effects of wood cutting, grazing, fire, and introduced plants to cause grassland to increase in area relative to oak woodland and shrublands. This is the case in the Landmark site on Kearny Mesa, where a sharp line, apparently dating to past clearing, separates the "grassland" vernal pools from those that occur in dense chamise chaparral (see Figure 60). The pattern is not so obvious in Figure 15, but the story is probably the same. Patches of chamise chaparral occur on the mesa top, probably remnants of the original vegetation, but the dominant vegetation type is an open annual grassland-coastal sage scrub that almost certainly is the result of past grazing and fire.

Cox (1984b, and pers. comm.), because he believes that pocket gophers formed the mounds and could only have done so in a grassland situation, also believes that the heavy brush cover is a recent phenomenon. This may be, but lacking other more direct evidence for the recent expansion of chamise chaparral, his idea must be viewed as an interesting hypothesis.

Though there is ample room for argument, a reasonable extrapolation of the present situation into the past suggests that most vernal pools were probably in or near perennial-dominated grassland or an open shrub-grassland, but it seems just as certain that some pools (e.g., Kearny Mesa in San Diego County and Burton Mesa in Santa Barbara County) occurred in relatively heavy shrub cover. The pools of the northern Central Valley may have occurred in oak woodland and oak savanna (R. Holland; pers. comm.), a situation similar to some of the gilgai pools of Australia (Beadle 1981).

CHAPTER 4. ORGANISMS OF VERNAL POOLS

A problem in characterizing the biota of any ecosystem is that of reducing the complexity to a manageable level. In the sections that follow I will discuss selected examples of vernal pool taxa. Some of these are strictly vernal pool specialists, while others range widely and include vernal pools in their range of habitats. Because it was the botanical component that first directed attention to California vernal pools, I begin by considering the higher plants, the most conspicuous of the unique elements of the pool biota. The species emphasized are those that occur in the coastal vernal pools, but I draw upon studies from the Central Valley done with the same or similar species.

4.1 LARGER (VASCULAR) PLANTS

Because vernal pools are only a very local phase in a larger community, a complete listing of all plant species that occur within 100 m of the vernal pools of coastal California would probably include the greater part of the flora of grasslands, oak woodlands, coastal sage scrub, chaparral, and weed patches. Furthermore, even though vascular plants are much better known than vernal pool organisms of other taxonomic groups, detailed species lists with annotations of occurrence of plants in pools are limited. Therefore, to keep the list reasonably short while including the more interesting species, I have listed all plants that have been reported as being common in or restricted to vernal pools (Table 6). I have also included the more frequent species that are associated with vernal pools, although the weediest plants to be expected only in very disturbed pools have been excluded. The list given here should be compared to the comprehensive list of genera for all California vernally moist habitats given in Thorne (1984).

To differentiate among the categories of plants associated with pools, I have adopted the following classification system:

Pool restricted (Table 6A): Plants whose distribution in coastal California is completely or substantially restricted to vernal pool basins. Some of these may also be common in other habitats outside of our area. This group includes those plants usually thought of as indicators of vernal pool habitat. Putting this simply, if a number of plants of this group occur together in a particular place, it is virtually certain that the habitat is a vernal pool.

Occurring in pools, but also common in other aquatic, marshy, or seasonally wet habitats (Table 6B): These are plants that locally may be restricted to vernal pool basins or occur mainly in vernal pool basins, but which also occur in other aquatic, marsh, or seepage habitats in coastal California.

Occurring in pools, but more common in terrestrial habitats (Table 6C): These plants are found within the inundated area of vernal pools, but even locally are more common outside of pools. Their populations do not depend on vernal pool habitat, either locally or regionally.

Associated with pools (Table 6D): This group includes plants that are common in the vicinity of pools and which may be considered to be indicators of vernal pool landscapes but not specifically of vernal pools. Populations of these plants are not dependent on vernal pool basins for habitat, but presumably benefit from other features often associated with vernal pools, such as soils high in clay, or seasonally high soil moisture.

Table 6A. Vascular plants that occur within pool basins and that are largely restricted to vernal pools within the study area of coastal California. These are the plants which are indicators of vernal pools, as vernal pools have been defined in this study. If several of these species are found together with plants of Table 6B, the area in which they are found is probably a vernal pool. Plants with an I/ in the "Type" column are introduced species.

Plants	Type[a]	Regions[b]	Phenol.[c]
Apiaceae			
Eryngium aristulatum	P	SD,BC,SR,SLO	D
Eryngium armatum	P	SB,SLO	W/D?
Eryngium parishii	P	BC	
Eryngium vaseyi	P	SLO	W/D
Asteraceae			
Blennospermum nanum	A	SR,SLO	W
Gnaphalium palustre	A	BC,SR,SB	
Hemizonia perennis	P?	BC	
Lasthenia glaberrrima	A	SLO	W/D
Psilocarphus brevissimus	A	SD,BC,SR,SLO,SB	W/D
Psilocarphus oregonus	A	SLO,SB	
Psilocarphus tenellus	A	SD,BC,SR	W/D
Boraginaceae			
Plagiobothrys acanthocarpus	A	SD,BC	W/D
Plagiobothrys bracteatus	A	BC	
Plagiobothrys stipiitatus	A	SLO	
Plagiobothrys undulatus	A	BC,SR,SLO,SB	W/D
Brassicaceae			
Sibara virginica	A/B	SD,BC,SLO	
Callitrichaceae			
Callitriche heterophylla	A?	SR	
Callitriche longipedunculata	A	SD,BC,SR	A
Callitriche marginata	A	SD,BC,SR,SLO,SB	A/W
Campanulaceae			
Downingia bella	A	SR	W
Downingia cuspidata	A	SD,BC,SR,SLO,SB	W
Crassulaceae			
Crassula aquatica	A	SD,BC,SR,SB	A/W
Elatinaceae			
Bergia texana	A	BC,SLO	
Elatine brachysperma	A	SD,BC,SR,SLO,SB	W
Elatine californica	A	SR,SLO	A/W
Elatine chilensis	A	SR	A/W
Elatine heterandera	A	SLO	

(continued)

Table 6A. (Concluded).

Plants	Type[a]	Regions[b]	Phenol.[c]
Isoetaceae			
Isoetes howellii	P	SD,SR	A
Isoetes orcuttii	P	SD,BC,SR,SLO	A
Lamiaceae			
Pogogyne abramsii	A	SD	W/D
Pogogyne nudiuscula	A	SD,BC	W/D
Lilaeaceae			
Lilaea scilloides	A	SD,BC,SR,SLO	A
Lythraceae			
Lythrum hyssopifolia	A/P	SD,BC,SR,SLO,SB	W
Marsileaceae			
Marsilea vestita	P	SD,BC,SR,SLO	A
Pilularia americana	P	SD,BC,SR,SLO,SB	A/W
Onagraceae			
Boisduvalia glabella	A	BC,SLO,SB	
Poaceae			
Alopecurus howellii	A	BC,SR,SB	
Deschampsia danthonioides	A	SD,BC,SR,SLO	A/D
Orcuttia californica	A	SD,BC,SR	W/D
Phalaris caroliniana	I/A	SR	
Phalaris lemmonii	A	SD,SLO,SB	W
Phalaris paradoxa	I/A	SB	
Polemoniaceae			
Navarretia prostrata	A	SR,SLO	
Primulaceae			
Anagallis minimus	A	SD,BC,SR,SB	W
Ranunculaceae			
Myosusrus minimus	A	BC,SR,SLO	W
Scrophulariaceae			
Mimulus latidens	A	BC,SLO	
Solanaceae			
Petunia parviflora	A	BC	

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[a] See text.

[b] Region codes: SD = San Diego
BC = Baja California
SR = Santa Rosa Plateau
SLO = San Luis Obispo
SB = Santa Barbara.

[c] Phenology symbol. See text.

Table 6B. Vascular plants that are found in vernal pools, but that are more common in other aquatic, marsh, or seepage areas. Species with I/ in the "Type" column are introduced.

Plants	Type	Regions	Phenol.
Asteraceae			
Cotula coronopifolia	I/P	SD,BC,SR,SB	A/W
Convolvulaceae			
Cressa truxillensis	P	BC	
Cyperaceae			
Eleocharis acicularis	P	BC,SR,SLO,SB	A/W
Eleocharis bella	A	SD	A/W
Eleocharis macrostachya	P	SD,SR,SLO,SB	A/W
Eleocharis montevidiensis	P	SR	
Frankeniaceae			
Frankenia grandifolia	SS	SB	
Juncaceae			
Juncus bufonis	A	SD,BC,SR,SLO,SB	W
Juncus mexicanus	P	SD	A/W
Juncus phaeocephalus	P	SLO	
Juncus rugulosus	P	SD	
Juncus sphaerocarpus	A	SR	
Juncus tenuis	P	SB	
Juncus tiehmii	P?	SR	
Juncus triformis	A	SD	
Lamiaceae			
Stachys ajugoides	P	SB	
Lemnaceae			
Lemna minima	P?	SR	A
Malvaceae			
Sida leprosa	A	BC,SR,SB	W?
Poaceae			
Crypsis niliaca	I/A	BC	
Crypsis schoenoides	I/A?	BC	
Distichlis spicata	P	SB	
Elymus triticoides	P	SLO	
Hordeum brachyantherum	P	SB,SLO	
Polypogon monspeliensis	I/A	SD,SB,SLO	W
Polygonaceae			
Rumex crispus	I/P	SB	A/W
Portulacaceae			
Montia fontana	A	SD,SR	W?
Potomogetonaceae			
Potamogeton pusillus	A	SR	A
Ranunculaceae			
Ranunculus aquatilis	P	SR	A
Scrophulariaceae			
Veronica peregrina	A	SD,BC,SR,SLO,SB	

Table 6C. Vascular plants that are often found in vernal pool basins but that are as common or more common in other terrestrial habitats. In a particular area these species may be limited to vernal pool basins, but more usually they will be found both in and adjacent to pools. Species with I/ in the "Type" column are introduced.

Plants	Type	Regions	Phenol.
Amaryllidaceae			
Brodiacea jolonensis	PB	SB	W/D
Brodiacea orcutii	PB	SD,SR	W/D
Muilla clevelandii	PB	SD	W/D
Muilla maritima	PB	SD	W/D
Asteraceae			
Achyrachaena mollis	A	SB	W?
Ambrosia pumila	P	BC	
Filago californica	A	SB	
Grindelia robusta	SS	SB	
Hemizonia australis	A	SB	
Hemizonia fasciculata	A	SD,SB	D
Hemizonia parryi	A	BC	
Hemizonia pungens	A	BC	
Holocarpha virgata	A	SD	
Hypochoeris glabra	I/A	SD,SB	W/D
Madia sativa	A	SB	
Brassicaceae			
Lepidium latipes	A	BC	
Lepidium nitidum	A	SR,SB	
Caryophyllaceae			
Spergularia bocconii	I/A	SD	
Spergularia marina	A	SB	
Spergularia platensis	A	BC	
Spergularia villosa	I/P	SB	
Convolvulaceae			
Convolulus arvensis	I/P	SB	
Euphorbiaceae			
Eremocarpus setigerus	A	SD,SB	D
Euphorbia spathulata	A	BC	
Fabaceae			
Trifolium amplectens	A	SD,SR	W

(continued)

Table 6C. (Concluded).

Plants	Type	Regions	Phenol.
Gentianaceae			
Centaurium venustum	A	SD	W/D
Geraniaceae			
Erodium botrys	I/A	SD	W/D
Erodium cicutarium	I/A	SD	
Erodium moschatum	I/A	SD	
Lamiaceae			
Trichostema lanceolatum	A	SD,BC	D
Plantaginaceae			
Plantago bigelovii	A	SD,BC,SR,SB	
Plantago erecta	A	SD	
Plantago lanceolata	I/P	SB	
Poaceae			
Bromus mollis	I/A	SD	W/D
Danthonia californica	P	SLO	
Elymus glaucus	A?	SLO	
Festuca dertonensis	I/A	SB	
Festuca megalura	I?/A	SD	W/D
Festuca myuros	I/A	SD	W/D
Gastridium ventricosum	I/A	SD	
Hordeum californicum	P	SB	
Hordeum geniculatum	I/A	SB	
Hordeum glaucum	I/A	SD	
Hordeum leporinum	I/A	SB	
Hordeum pusillum	A	BC	
Lolium perenne	I/P	SD,SB	
Polemoniaceae			
Navarretia atractyloides	A	SD	W/D
Navarretia fossalis	A	BC	W/D
Polygonaceae			
Polygonum aviculare	I/A	SB	
Ranunculaceae			
Ranunculus californicus	P	SR,SLO	
Scrophulariaceae			
Mimulus guttatus	P-A	SR	
Orthocarpus densiflorus	A	SD,SB	

Table 6D. Vascular plants that are common near vernal pools but which usually do not occur in the pool basin (i.e., within the area of standing water). Species with I/ in the "Type" column are introduced.

Plants	Type	Region	Phenol.
Amaryllidaceae			
Allium haematochiton	PB	SD	
Sisyrinchium bellum	P	SD,SLO	
Asteraceae			
Anthemis cotula	I/A	SB	
Baccharis pilularis	S	SB	
Baccharis sarothroides	S	SD	
Centaurea melitensis	I/A	SB	
Lasthenia chrysostoma	A	SD,SR	W/D
Microseris douglasii	A	SD	
Convolvulaceae			
Convolvulus simulans	A	BC	
Crassulaceae			
Crassula erecta	A	SD,SR	
Hydrophyllaceae			
Nama stenocarpum	A	BC	
Lamiaceae			
Acanthomintha ilicifolia	A	BC	
Liliaceae			
Chlorogalum parviflorum	PB	SD	
Poaceae			
Agrostis diegoensis	P	SD	
Agrostis microphylla	A	SD	
Avena barbata	A	SD,SB	
Bromus diandrus	I/A	SD	
Bromus rubens	I/A	SD	
Stipa pulchra	P	SD	
Polemoniaceae			
Navarretia hamata	A	SD	W/D
Navarretia intertexta	A	SR	W?
Ophioglassaceae			
Ophioglossum californicum	P	SD,BC	W
Selaginellaceae			
Selaginella cinerascens	PR	SD	W

Notes to Table 6: This list has been compiled from a variety of sources. The main ones are a list compiled by M. Beauchamp and others for San Diego County cited by Zedler et al. (1979); W. Ferren (1984) and various unpublished reports and personal communication for Santa Barbara, Ventura, and Monterey Counties; Moran (1984) and personal communication for Baja California; Lathrop and Thorne (1983) for Santa Rosa Plateau; and Hoover (1970) for San Luis Obispo County.

To give some clue as to the type of plant, Table 6 includes the family of the plant and an indication of growth form. These growth forms, together with the letter designation used in Table 6, are as follows:

Annual (A): A plant that lives for a year or less, regenerating the next year from dormant propagules.

Perennial: A plant whose vegetative structure survives for more than one growing season. Perennials may produce sexual propagules in several seasons (polycarpic) or only in the last season in which they are alive (monocarpic). Some plants can function as either annuals or perennials, depending on growth conditions. These are indicated as A/P or P/A, the first letter indicating the predominant mode.

Among perennials there is a range of growth forms from ones smaller than most annuals to massive woody plants. The following simplified growth form categories are used:

Perennial herb (P): Plants in which the top of the plant dies back each year.

Bulb perennial (PB): Perennial herbs which arise from bulbs.

Rhizomatous perennials (PR): Plants that spread extensively by underground stems (rhizomes), potentially forming large patches of genetically identical individuals (clones). Since all perennials have some sort of underground stem, this group represents an extreme where there is a particularly high potential for spread.

Subshrub (SS): Plants that are primarily herbaceous, with most of the top dying back each year, but with a woody base from which the stems arise.

Shrub (PS): Plants that regenerate leaves, stems, etc., from above-ground woody parts.

Table 6 also gives an indication of the stages of the annual cycle of a vernal pool in which each species first flowers and fruits. These categories give a rough idea of species phenology: Some species (phenology symbol "A") can flower and fruit entirely within the aquatic phase before the pool dries. A "W" species can flower or fruit only in the later stages of the standing water phase, or in the early drying stage when the surface is still saturated. A "D" species cannot complete its life cycle unless the soil surface is completely dry and the pool is no longer saturated. These categories are very rough, and the many blanks indicate the lack of quantitative data.

4.1.1 Vascular Plants of the Aquatic Phase

The aquatic habitat poses special problems for higher plants. While being surrounded by water relieves desiccation stress and reduces the need for supporting tissue, there are also severe disadvantages. The diffusion of gases is two to three orders of magnitude slower in water than in air. Because of this, aquatic plants are subject both to reduced photosynthesis because of lack of CO_2 and inhibited respiration because of lack of oxygen. During the day, oxygen produced in photosynthesizing tissues accumulates to excessive levels and can inhibit photosynthetic efficiency because of photorespiration. Light also rapidly diminishes with depth even in pure water, and with the addition of suspended and dissolved material light penetration is reduced even further.

Though plant life originally evolved in water, the vascular aquatic plants are decendants of terrestrial species. The reinvasion of water by land-adpated plants required that structures and physiology designed to deal with drought had to be modified to be efficient in the water. These changes have tended in the same direction, and water plants of quite different ancestry have ended up having similar leaves and growth structure.

Because of the buoyancy in water, aquatics need not have a well-developed support system, so woody tissues are almost completely lacking. Leaves tend to be thin and are often finely divided to facilitate gas exchange. The greater the surface area per volume, the greater the gas exchange per unit weight of photosynthesizing or respiring tissue. Stems, leaves, and roots often have large air spaces to allow gas diffusion to take place within the plant. For some plants, the diffusion of oxygen through these air spaces is necessary to allow roots to respire while surrounded by anaerobic mud.

Associated with these obvious morphological features are biochemical and physiological traits that are not as yet fully understood. A basic physiological problem is the lack of oxygen, which is needed as an electron acceptor for the final stage of metabolism. A lack of oxygen therefore leads to an accumulation of metabolites which in turn induces a shift to anaerobic metabolism. The anaerobic pathways partially solve the energy problem but create another by leading to the buildup of toxic end products such as acetaldehyde and lactic acid. Ethanol also accumulates, but is said not to be toxic in concentrations usually observed (Jackson and Drew 1984). When inundated for long periods, plants not specially adapted to aquatic conditions must either become dormant, or risk death from metabolic poisons.

Because vernal pools are temporary aquatic habitats that often dry more than once in a growing season, none of the characteristic vascular plants are submerged aquatics. Aponogeton, an aquatic and an apparent escapee from aquarium culture, occurs in the vernal pool area of Kearny Mesa in San Diego County, but at a site that is artificially impounded and which holds water for almost the entire year (Keeley and Keeley 1979). Instead, most of the plants that peak in vigor and dominance during the period of standing water in vernal pools are amphibious--able to deal with standing water, but also able to survive at least brief periods of emergence.

Not surprisingly, species prominent in the aquatic phase largely belong to families in which most members are aquatic plants (Isoetaceae, Marsileaceae, Elatinaceae, Callitrichaceae, Lemnaceae; Sculthorpe 1967). Plants tolerant of flooding, but requiring drying in order to complete their life cycle are from genera (Downingia, Pogogyne, Eryngium, Juncus, Lythrum) with many species that can grow in damp or seasonally flooded habitats. This suggests that it is not an easy matter to adapt to the aquatic habitat, and that when in geological time pools appear they tend to be filled with plants that disperse from other aquatic habitats rather than with local organisms that evolve to exploit the wet conditions. The more unique and isolated the aquatic habitats, however, the more likely that a locally restricted form will be able to evolve to exploit the ecological opportunity offered.

Isoetes. Isoetes species are the most important of those that can withstand long inundation. The genus Isoetes is worldwide in its distribution, but nowhere a major component of vegetation. Some species grow completely submerged, while many others occur in seasonally moist habitats. Often they are found in small and remote habitats, such as rock pools on the top of Ayers Rock in Australia (Aston 1973).

Two species of Isoetes are common in vernal pools, and one (I. orcuttii) is often the dominant plant in San Diego County vernal pools in the aquatic phase (Figure 24). On the Santa Rosa Plateau two species of Isoetes comprised a fifth of the vegetation cover within the zone of standing water (Kopecko and Lathrop 1975).

Isoetes is a derivative of the ancient (Devonian) group of arborescent lycopods (club-mosses) that gave rise to Lepidodendron, the genus of trees that was prominent in the coal forming swamps of the Pennsylvanian (Stewart 1983). Isoetes' nearest living relatives outside the family Isoetacea are in the genus Selaginella, a group that includes S. cinerascens, a rare species found near vernal pools in San Diego County and Baja California.

Through geological time the lycopsids have been pushed from dominant forms like Lepidedendron to small plants that survive because of their ability to exploit unusual or marginal habitats--bogs (Lycopodium inundatum), rock outcrops (Selaginella spp.), alpine marshes (Stylites), and the understory of shady coniferous forests (Lycopodium

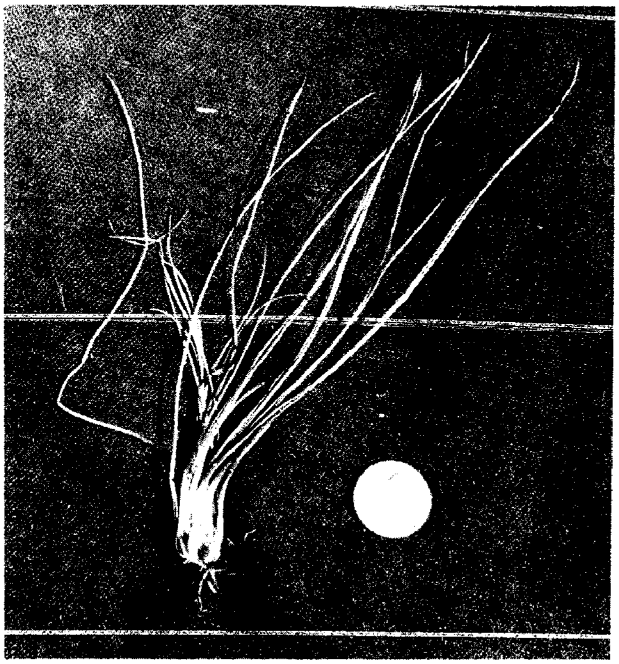

Figure 24. *Isoetes orcuttii.* **Note the swollen base where the microspores and megaspores are produced. This very large individual was collected from a large artificial pool late in the season.**

lucidulum). Vernal pools are another special habitat in which plants built to an ancient design can still persist, because no better solution has been found to the problems of surviving there than those first perfected in the coal swamps.

Morphologically *Isoetes* resembles a small rush or stiff-leaved grass, hence its common name of quillwort. The leaves arise from a two- or three-lobed bulblike perennial structure (corm). They are perennials, but it is not known how long individual plants live. Both the leaves and roots of *Isoetes* have large air chambers, a feature common to aquatic plants. In cross section the leaves of *Isoetes* reveal four air chambers, while the roots have a curious morphology, consisting mostly of an open air chamber (Foster and Gifford 1974).

At the base of all but the youngest leaves there are swollen chambers (sporangia) which contain either female "megaspores" or pollen-size male "microspores" in great numbers. The spores are produced during the growing season but not released until growth has ceased and the sporangia have broken open because of drying or decay of the tissues. Since the leaf bases are below the soil surface, the spores also are released there, but the presence of cracks in the soil and the small hole left by the withering of the leaves allow some dispersal on the surface before the next rainy season. It has also been reported that spores are extruded at the time of initial wetting by the swelling of tissues.

After release and in the presence of moisture, the megaspores undergo development, and split open to reveal several "archegonia." Spermatazoids are released by the microspore and fertilize the archegonia. The resulting embryo grows into the next generation of photosynthesizing, spore-producing *Isoetes*. Like mosses and ferns, *Isoetes* requires at least surface moisture to effect fertilization. This may be part of the reason that most species of Isoetes are aquatic plants and all are found in at least seasonally moist habitats.

Isoetes species are widely distributed in California, despite the fact that they seem to have no obvious adaptations for dispersal. It seems probable that dispersal is accomplished by water over short distances and animals, especially birds, over longer distances. Since the spores are relatively small, they may also be moved by wind.

In keeping with the aquatic habits of its near relatives, *Isoetes* flourishes in the pools in the earlier stages when there is standing water or soils are saturated. As the soil dries later in the spring, the leaves of *Isoetes* rapidly turn yellow and die. *Isoetes* appears to have limited drought tolerance (McMillan et al. 1968).

Keeley (1981a,b, 1983; Keeley and Busch 1984) in conjunction with studies on the metabolism of submerged vernal pool plants, noted an unexpected accumulation of malic acid in *Isoetes* plants during the night. Subsequent work revealed that *I. howellii* and *I. orcuttii* along with every other *Isoetes* species studied to date, exhibit "Crassulacean acid metabolism" (CAM), a special set of biochemical pathways that allow plants to photosynthesize during the day without having to open their stomates to absorb CO_2. In contrast to the normal pattern, in CAM plants the stomates open at night, and CO_2 is stored in organic acids. During daylight hours the stomates are closed and photosynthesis proceeds utilizing CO_2 released from the acids.

Previously this mechanism had been observed almost exclusively in plants subject to pronounced drought such as tropical epiphytes and desert succulents. The advantage of nocturnal gas-exchange in conserving water for such plants is very clear (Fitter and Hay 1981). The presence of CAM in a group of aquatic plants was unexpected, and is still not fully explained. Keeley (1981a,b; 1983) hypothesizes that CAM is of use to Isoetes because it occurs in habitats where diurnal CO_2 concentrations are low either because of competition from other rapidly photosynthesizing plants or because of extremely oligotrophic (nutrient-poor) conditions. In the case of vernal pools, Keeley assumes that it is competition with algae and other vascular plants that is important. In confirmation of this he has reported diurnal shifts of more than 2 pH units that seem to be a consequence of CO_2 depletion. Also consistent with his hypothesis is the observation that Isoetes leaves exposed to air as the pools dry gradually lose or never develop CAM (Keeley and Busch 1984).

The aquatic ferns, Pilularia americana and Marsilea vestita. These two diminutive ferns are closely related, despite the strikingly different foliage. Marsilea, which has shamrock-like leaves up to 3 cm in diameter that float on the surface of the water, is a plant not likely to escape notice when present in abundance. Pilularia (Figure 25), on the other hand, is a tiny fern that when full grown resembles seedlings of a rush or grass. But despite its small size its developing leaves show the distinctive fiddlehead growth pattern (circinate veination) of its larger relatives.

The taxonomic affinity of Marsilea and Pilularia is based on the similarity of their unique fruiting structures. The spore-producing sori, which in most ferns occur as small brown structures on the underside of leaves, in the Marsileaceae are developed within a spherical or bean-shaped sporocarp which in vernal pool species develops at the base of the plant below the soil surface. Furthermore, the sporocarps contain male and female spores (heterospory) instead of the single spore type of most ferns (homospory). The process by which the spores are released and fertilization is effected to produce the next generation is rather complex and is described in Sculthorpe (1967). The important point from an ecological point of view is that the sporocarp provides a protective structure that allows both for dispersal to new habitats and survival of drought and other stresses. Allsopp (1952, cited in Tryon and Tryon 1982) reported that Marsilea spores remain viable for up to 70 years. Proctor and Malone (1965) established that sporocarps of M. mucronata fed to ducks and killdeer will germinate after passing through the intestinal tract. They hypothesized that dispersal by birds may be important in spreading this species. Thorne and Lathrop (1970) also suggested that bird dispersal of sporocarps may be important in Pilularia.

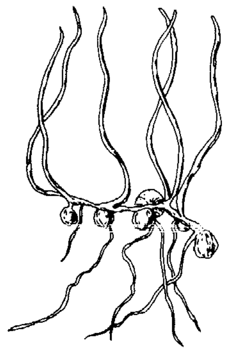

Figure 25. ***Pilularia americana.*** **Drawing by Joyce Hayashi.**

Both Pilularia and Marsilea are capable of withstanding prolonged inundation, and both disappear rapidly on drying. McMillan et al. (1968) investigated the growth of P. americana and M.

vestita native in Texas at several depths of water and on several soils. They found that *P. americana* would survive and produce sporocarps at all depths of inundation, but that it could not tolerate complete desiccation. In California vernal pools, however, *P. americana* regularly survives severe summer drought. *Marsilea vestita*, on the other hand, though it grew at all depths, was incapable of producing sporocarps except when its leaves reached the surface of the water. This suggests that it is an amphibious plant rather than a strictly aquatic one. Further evidence of its amphibious nature is that *Marsilea* produces different leaf shapes in the water and in the air. This phenomenon will be discussed more fully in the next section.

Callitriche species. The species of *Callitriche* known commonly as "water starworts" are prominent members of the aquatic phase of vernal pools. Though the California species are all annuals, morphologically and ecologically they are like miniature water-lilies. Seeds germinate when winter rains fill the pools, and the threadlike stems idly grow to the surface, forming a floating rosette of leaves (Figure 26). The bright green clusters of leaves on the surface of a dark pool suggest how the common name may have originated. *Callitriche* is able to withstand considerable inundation, in keeping with its membership in a family (Callitrichaceae) in which most species are aquatic.

The stems and leaves show a marked response to inundation, and *Callitriche* species have served as textbook examples (e.g., Sculthorpe 1967) of the phenomenon of aquatic heterophylly--the production of dissimilar leaf forms in the air and in water (Figure 27). Heterophylly allows the plant to have the leaf morphology appropriate to the habitat at the time the leaves form. When in water, a thin epidermis, a large surface-to-volume ratio to foster gas exchange, and the presence of gas-conducting tissue are beneficial. In air, mechanical tissue for support, a protective cuticle, thick epidermis, and a smaller surface-to-volume ratio are needed to retain water and prevent wilting. When inundated, the *Callitriche* leaves tend to be longer and narrower, almost linear in the extreme; while the floating leaves are rounded and much shorter, and have fewer stomates (Sculthorpe 1967; Deschamp and Cooke 1983).

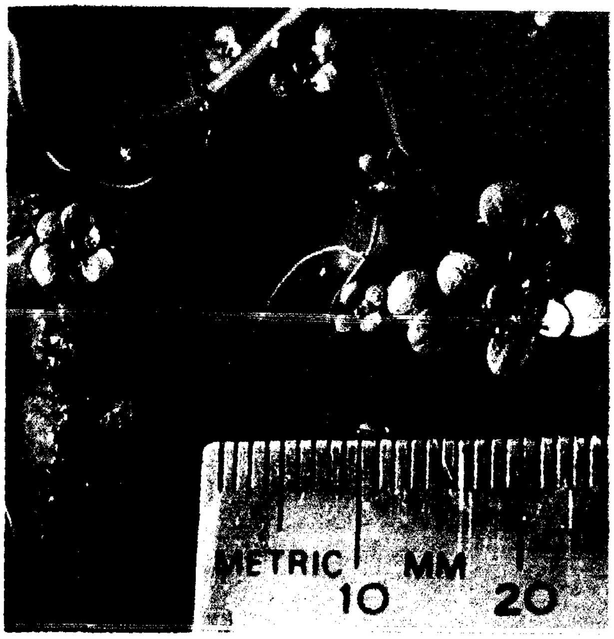

Figure 26. Floating leaves and threadlike stems of *Callitriche longipedunculata*. The male flowers, which consist of a single stamen, can be seen arising from the leaves. The black rice-grain shaped form in the upper right of the photo is a flatworm, *Bothromostoma*. Algal masses are visible in the water. This pool, partly disturbed by vehicles, is turbid with suspended clay.

Deschamp and Cooke (1983) showed that the switch from water to land forms in *C. heterophylla* is controlled by turgor pressure. When the leaves are under more severe drying stress in the air, the cells of the leaves are shorter and have convoluted jigsaw-puzzle shapes, while in water, with little stress, they expand to become long and thin. Because this shift is not normal in land plants, the use of increase in water stress as a signal of emergence by *Callitriche* is probably an evolved response to life in a fluctuating environment. All plants possess some ability to modify structure to suit the environment, but *Callitriche*, like many vernal pool plants, shows amplified plasticity in which a small environmental signal induces large change.

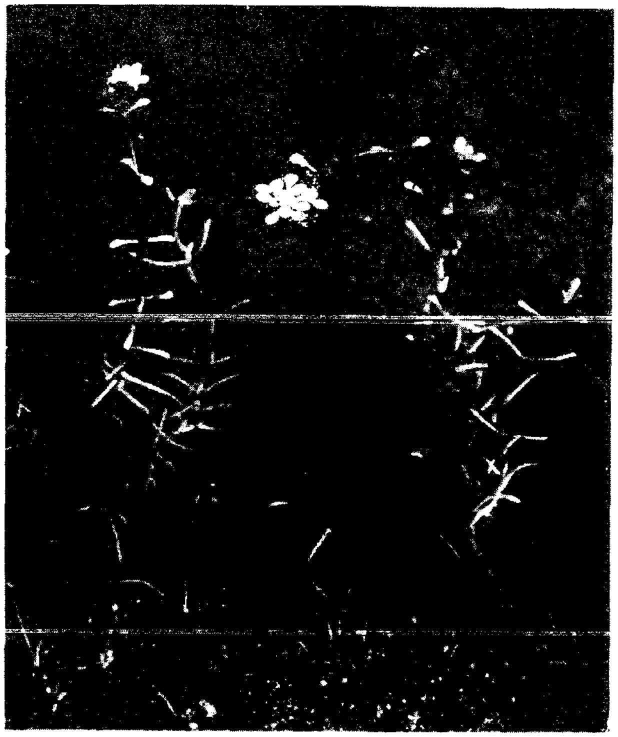

Figure 27. Floating and submerged leaves of *Callitriche heterophylla* showing leaf dimorphism. Photo by Cameron Patterson.

Callitriche species have both male and female flowers on the same plant. The male flowers are reduced to a single anther, while the female flowers produce four seeds (McLaughlin 1974). McLaughlin (1974) reported that seeds are formed by both aerial and submerged flowers, and this seems to be true for species of the coastal vernal pools as well. She speculated that the submerged seeds were formed by apomixis (i.e., without fertilization being necessary) or possibly by the transfer of pollen under the water. Philbrick (1984) has reported an unusual mode of self-fertilization for submerged Callitriche flowers in which pollen grains germinate inside the unopened anthers and send pollen tubes down the filament, through intervening vegetative tissue, and into the nearby female flowers to effect fertilization. It is not known how widespread this phenomenon is.

It is not surprising that self fertilization should be found in Callitriche. Annual plants of many unstable environments have developed a variety of mechanisms to insure that propagules are formed without the need to cross-pollinate with another individual. Most plants produce at least some progeny by out-crossing and it is obviously the case that out-crossing sexual reproduction, for all its inefficiency, is the best approach to long-term survival. However, persistence in highly changeable environments with short and unpredictable growing seasons requires fast and reliable formation of new seeds, and plants in such habitats have been commonly found to forgo the luxury of cross-pollination partially or entirely. A tendency toward apomixis or self-pollination is therefore expected in vernal pool plants.

Callitriche species do not require standing water, but they appear to be very sensitive to dry conditions. When the water level drops, C. longipedunculata seems to disappear rapidly, and is never observed after the point where the surface soil has been thoroughly dried. Callitriche marginata appears to be better able to grow exposed, though it too is mainly a plant that functions in the early part of the pool cycle when temperatures are cool and water is still at the surface. However, the taxonomy of Callitriche is confused, and it is possible that C. marginata is a different growth form of C. longipedunculata.

Another interesting feature of the Callitriche species is the production of fruits beneath ground (Mason 1969). The stems of the plants grow along the surface, and the pedicels flex strongly downward, in effect planting the seeds in the substrate. The insertion of the seeds directly into the substrate presumably has the advantage to the plant of avoiding predation while insuring a suitable germination microhabitat. Lilaea scilloides, discussed next, also produces seeds below the soil surface. Ferren and Schuyler (1980) noted that many intertidal vascular plants of eastern North America have reflexed stalks, and they speculated that this is because it is advantageous to have seeds deposited close to the parent plant. Reduced dispersal appears to be common in many marshy situations.

Lilaea scilloides, flowering quillwort. This species is widespread in the New World, but rarely abundant in any one place. Its common name, flowering quillwort, refers to its growth form which vaguely resembles that of the true quillwort, Isoetes, though the plant is more suggestive of a rather lax rush (Figure 28). Lilaea scilloides, an annual, evidently germinates with the earliest rains and then grows up to the surface. In the later aquatic stage it usually raises a few leaves above the water surface, making it more of an emergent plant than a submerged hydrophyte.

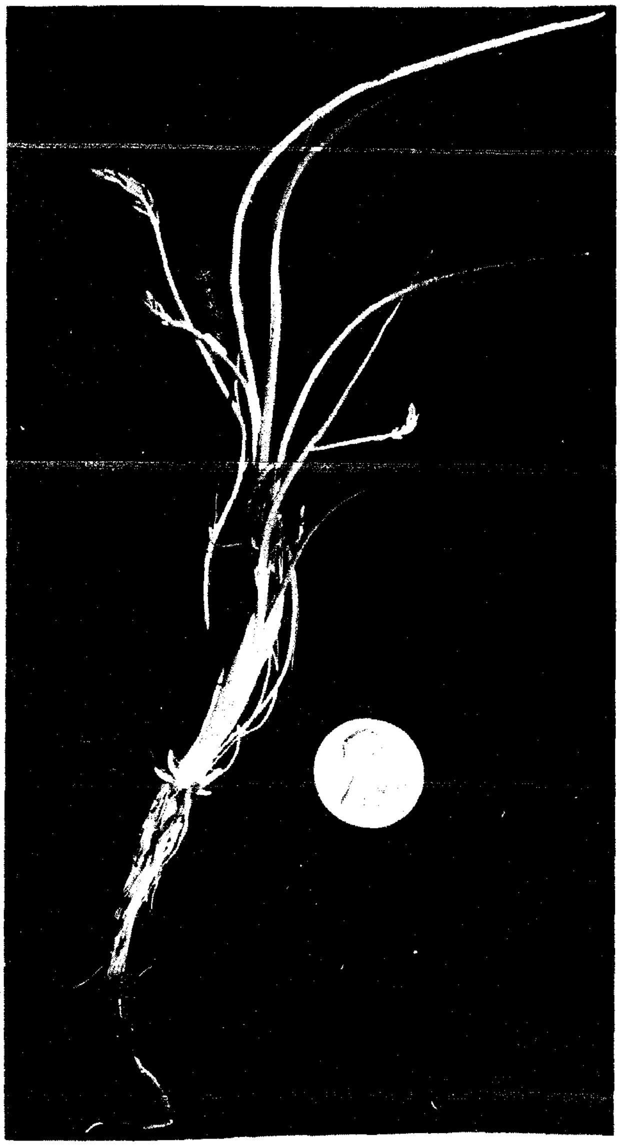

Figure 28. *Lilaea scilloides*. Both the aerial and basal flowering and fruiting structures are visible in this picture.

A peculiarity of this plant is the production of flowers both at the base of the plant (generally buried in the mud) and also on an aerial stem that rises above the water surface. The flowers on the aerial stem are either perfect, or sometimes only male or female, while those at the base are female only. To solve the problem of pollination when flowers are below water, the plant produces long threadlike styles 5-20 cm long, reminiscent of corn-silk, which float to the surface of the water. Pollen shed from emergent staminate flowers floats to the stigmas, effecting fertilization and insuring some degree of cross-pollination (R. Holland; pers. comm.).

One wonders why Lilaea has the two distinct modes of fruit production. The underlying reason must be the need of plants of varying habitats to hedge their bets. It is apparently advantageous to get some seeds into the soil to insure survival into the next year and to protect them from predation and physical stress but also a good idea to have more widely dispersible propagules. It is obvious that the system works because Lilaea is very widespread.

Other species. There are other species of the aquatic phase that deserve mention. Eleocharis (spike-rush) is widely distributed genus of mostly small plants that grow in wet places. Members of the sedge family (Cyperaceae), they represent a streamlined reduction of plant form to the minimum. As the common name suggests, the aerial part of the plant consists of rushlike leaves. These are amply provided with aerenchyma, a specialized tissue filled with large air spaces. Most Eleocharis species are "emergent hydrophytes," plants whose roots and lower stems are submerged, but which must have their leaves above water in order for the plant to function.

Like many other emergent hydrophytes, E. macrostachya, the most common perennial Eleocharis of the vernal pools, spreads by underground stems (rhizomes) to form extensive vegetative clones (Figure 29). In some of the larger pools on Kearny Mesa, in

San Diego and on the Santa Rosa Plateau, for example, E. macrostachya is nearly continuous across the entire bottom of the pool. Eleocharis macrostachya begins growth with the earlier rains, and usually sets seed before the pools are completely dry. Growth appears to cease shortly after the surface soil dries below the point of saturation. Some vernal pool species of Eleocharis are annuals, and these persist through the dry season as dormant seeds.

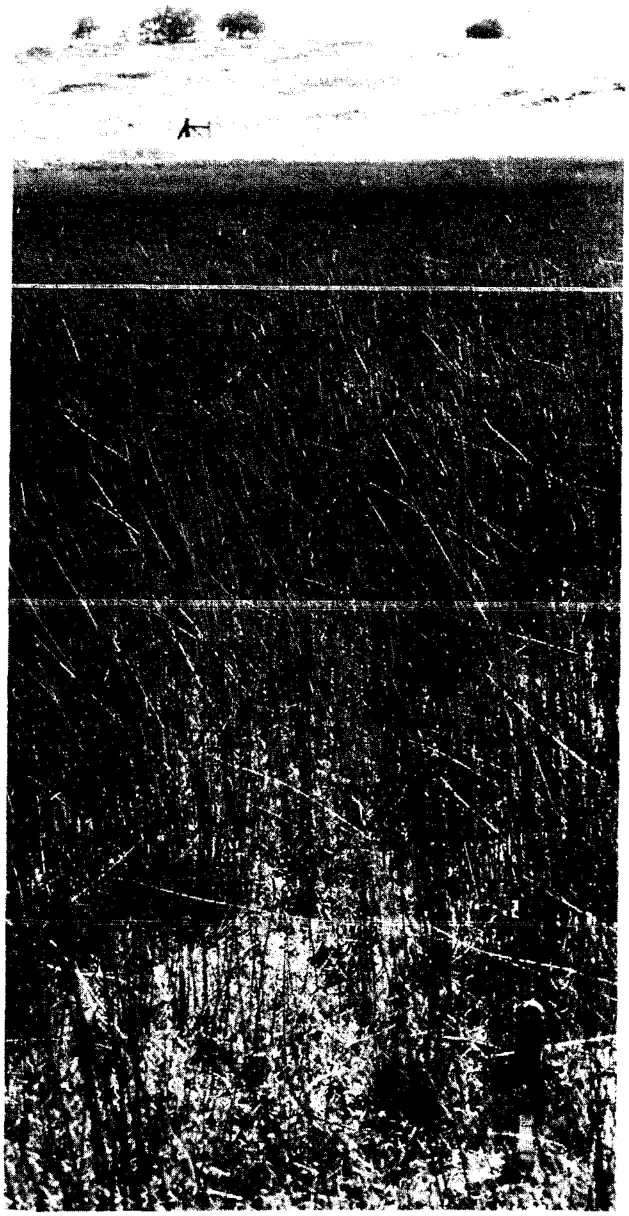

Figure 29. ***Eleocharis macrostachya*** **on the Santa Rosa Plateau. Some ecologists would prefer to call pools with this degree of dominance by a perennial emergent a vernal marsh.**

The flowers and fruits of Eleocharis are inconspicuous, being borne among brownish or reddish scales at the tips of some of the leaves. Flowers are wind pollinated, and produce small hard-coated seeds which disperse in some cases by floating and probably also internally and externally on birds (Sculthorpe 1967).

Morton (1984) has studied the photosynthetic characteristics of E. acicularis on the Santa Rosa Plateau. This species is a perennial that spreads by stolons and that on the Santa Rosa Plateau spends most of its active growth period submerged. Morton (1984) speculated that E. acicularis possesses a flexible photosynthetic system that can adapt to submergence and emergence. Following Keeley's reasoning for CAM in Isoetes (Keeley 1981; Keeley and Busch 1984), he argued that C_4 tendencies noted in the photosynthetic system when the plants are submerged are a response to limited CO_2. In any case the shifts in physiological function noted by Morton suggest that vernal pool plants are specially adapted to deal with fluctuating water levels.

Elatine is another vernal pool genus from a family of aquatic and marsh plants (Figure 30). The vernal pool species of Elatine seem to be specialists for the aquatic and immediate postaquatic phase. These diminutive plants are easy to overlook, and are not evident until the pools have held water for some time. Laboratory observations have shown that Elatine can germinate, grow, and even flower and fruit when completely submerged, making it one of the few seed plants in vernal pools that can go from germination to seed set without exposure to the air.

Elatine brachysperma is a good example of the extreme plasticity that characterizes many vernal pool plants. Given favorable conditions, E. brachysperma can grow to be a plant several centimeters long with hundreds of capsules and thousands of seeds. Under less favorable conditions it begins flower and fruit production shortly after the first true

Figure 30. ***Elatine*, probably *brachysperma*, growing in an experimental container with some *Crassula aquatica* which has distinctive four-parted fruits. Photo by Ellen Bauder.**

leaves are formed. A plant 3-5 mm high with two to three leaves can produce one or more fruits, each with several seeds. To accomplish this, the plant bypasses outcrossing sexual reproduction, since fruits and seeds are present in flowers that never open. It is not known if this is accomplished by autogamy (self-fertilization within the flower) or by apomixis (bypassing of sexual reproduction entirely). It may be that the larger plants produce seeds at least in part by outcrossing.

The advantage of being plastic in a vernal pool is clear. If the year is good and the place of germination favorable, the plant can produce a superabundance of seeds. In a bad year the ability to flower when scarcely past germination insures that at least a few seeds will be produced. This approach to survival may be contrasted with plants of more predictable habitats, for which a more or less prolonged period of vegetative growth is a precondition for flowering.

Crassula aquatica is remarkable for its diminutive size--a miniature aquatic for a miniature aquatic system. Like several other vernal pool plants, it is widespread and not restricted to vernal pools, though in coastal California this is its main habitat.

In view of its membership in the Crassulaceae it is not surprising that Keeley and Morton (1982) found that C. aquatica exhibits CAM, the special biochemical system that allows gas exchange to take place in the dark, already discussed in conjunction with Isoetes. Rather surprisingly, they also found that C. erecta, a close relative that is only accidental in vernal pools, lacks CAM metabolism. They see this difference as evidence for the theory that the function of CAM in the vernal pool setting is to obtain carbon dioxide in an environment where it is limiting.

Crassula aquatica produces a three- to five-parted fruit typical of the Crassulaceae but of almost microscopic size. The seeds are minute, scarcely visible to the human eye, so that even though a large C. aquatica may be only 2-5 cm high, it could potentially produce hundreds or thousands of seeds. Though its breeding biology is unknown, it is probably at least partly autogamous.

Overview of plants of the aquatic phase. This brief survey of some of the more important species makes clear several themes among the plants of the aquatic phase.

1) Most of the more "aquatic" species have broad ranges, vernal pools being only one of the habitats in which they occur. A few (e.g., Eleocharis acicularis, Crassula aquatica) span continents. Many of these species are perennials.

2) Plasticity in growth, with heterophylly as a special case, is characteristic of the majority of species. Indeterminate flowering, the continuous production of flowers and fruit while conditions are favorable, is another form of plastic response.

3) Despite modifications that seem to be designed to restrict dispersal rather than promote it, the species of the aquatic phase possess a remarkable capacity for finding new habitat. For most species this can only be explained by animal, and especially bird, dispersal.

4) Either autogamy or apomixis, both of which bypass the need for pollination, seems to be characteristic of most species.

5) Since seeds are well adapted for surviving drought, annual aquatics are well equipped to survive in vernal pools. The more surprising cases are the perennial species (Eleocharis, Isoetes) that require water to grow well but whose perennial structures are somehow able to endure what must be severe drought.

4.1.2 Temporary Pool Specialists -- Amphibious Plants

This group of plants includes those species that can spend part of their life as aquatics but that can flourish only if the pools dry. Following Sculthorpe (1967) and others, they may be called "amphibious plants" to underline their tolerance of wet conditions but preference or requirement for aerial existence. Included in this group of amphibious plants are most of the showy vernal pool flowers that form displays in the late winter and spring.

Pogogyne abramsii and P. nudiuscula. The more strictly aquatic plants of vernal pools tend to have broad geographical ranges. In contrast, the amphibious plants are sometimes very narrow endemics, and included among them is the only species of the southern pools that is listed by the U.S. Fish and Wildlife Service as rare and endangered--Pogogyne abramsii.

Pogogyne abramsii, for which the common name "San Diego mesa mint" has recently been formulated, is a small annual member of the mint family (Lamiaceae), with the typical mint morphology of opposite leaves, square stem, and bilaterally symmetrical lavender flowers borne in small clusters ("cymules," Munz 1974) in the axils of bracts (Figure 31). It is distinguished from its close relative P. nudiuscula found in southern San Diego County and northern Baja California by the dense stiff hairs in the inflorescences. Both species possess a powerful mint fragrance.

Three other species are in California: P. zizyphoroides which occurs in vernal pools in the Central Valley, P. douglasii, which is found in pools and other wet habitats from Mendocino County south through the Central Valley to Kern County, and P. serpylloides, which grows in a variety of moist habitats from San Luis Obispo County northward.

Figure 31. ***Pogogyne abramsii*****. Approximate scale: 1/4. Drawing by Joyce Hayashi.**

In contrast to most of the annual plants associated with vernal pools, P. abramsii appears to require insect pollination for its seed set, and it may be partially self-incompatible (A. Howald, Santa Barbara, unpubl. data; C. Scheidlinger, pers. comm.; E Bauder, pers. comm.).

In common with most other mints, Pogogyne has a four-parted ovary, each portion of which can produce a single seed, though in natural populations many do not (Scheidlinger 1981). The seeds, more properly "nutlets," about 0.75 to

1.25 mm long, are covered with stiff hairs, but seem to have no special features to insure dispersal (Figure 32). Most seeds remain inside the dried calyx and fall to the soil surface when the branches break off during summer or the plants are collapsed with the first fall rains. Seedlings can often be found emerging from the previous year's calyx (Scheidlinger 1981).

Though not as extreme as the self-planting mechanisms of Callitriche and Lilaea, Pogogyne's retention of the seeds is clearly a trait designed to restrict dispersal. It is easy to build an explanation of why this should be a good idea for a vernal pool plant. Pogogyne grows in a habitat in which the local environmental gradients are extremely steep. Vernal pools are a small percentage of the total land area, so that dispersal of seeds away from the parent plant would tend to land them in an inhospitable environment. Natural selection should act against dispersal when it results mostly in a wastage of propagules, especially in an annual plant in which the persistence of the population is entirely dependent on seeds.

Seed retention restricts dispersal in time as well as in space. Sharitz and McCormick (1973) theorized that the seed retention they observed in the granite outcrop species Sedum smallii may be a mechanism for preventing seeds from being carried away by floodwater prior to germination, and cited an earlier suggestion of D.N. Wiggs and R.B. Platt that retention may offer protection against high temperatures. Few seeds are probably washed from vernal pools by flowing water, but seeds on the often-bare mineral soil of vernal pools would be exposed to extreme heat and vulnerable to seed predators.

Like many other annuals, P. abramsii is sensitive to germination microhabitat. In cobbled pools plants are usually denser at the edges of large rocks. In less rocky basins with clay-rich soil, P. abramsii often is found more abundantly along cracks, suggesting that establishment is more successful there (Figure 33).

An annual plant growing in a variable environment would seem to run a great risk of local extinction. If the plant is also rare, local extinctions may not be offset

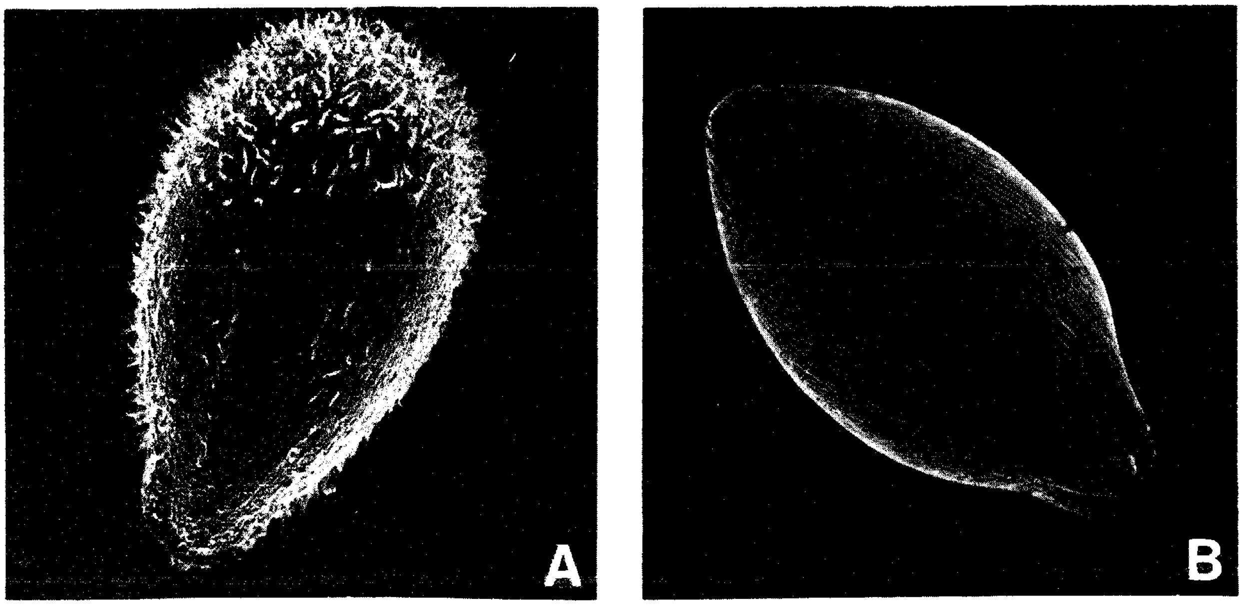

Figure 32. **Seeds of (A)** ***Pogogyne abramsii*** **and (B)** ***Downingia cuspidata*****. The lengths of the seeds are approximately 1.3 and 0.7 mm, respectively. Scanning electron microscope photographs by Chris Urbach.**

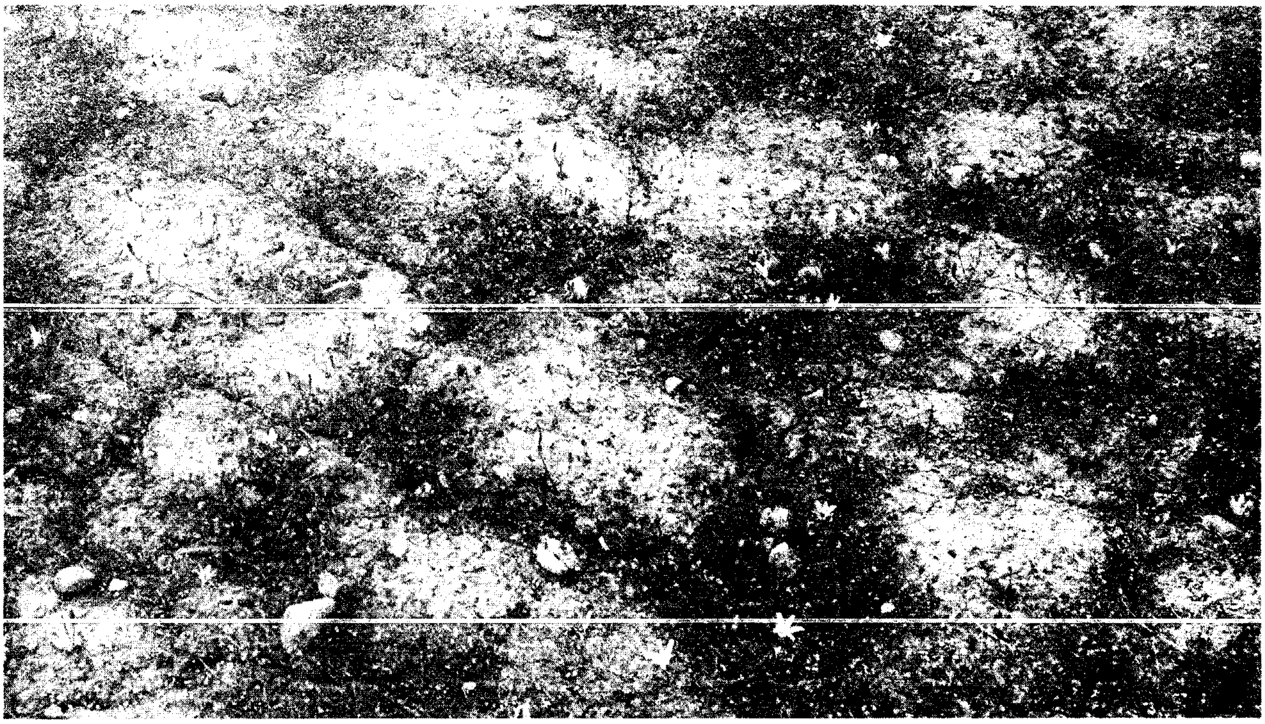

Figure 33. ***Pogogyne abramsii*** **flowering and fruiting in a dried vernal pool. There is a strong tendency for more and larger plants to be located along the roughly polygonal cracks of the vernal pool. It seems likely that this is partly a consequence of seeds finding a suitable germination microhabitat there.**

by reinvasion. How then does a rare annual like P. abramsii survive? Scheidlinger (1981, 1984) studied the population ecology of P. abramsii on Kearny Mesa with this question in mind. She found that P. abramsii germinates with the first significant fall rains, as early as late September or early October In most years, growth begins before extended periods of inundation, which generally do not occur until late December or January. This initial inundation-free period of growth may be important in allowing the P. abramsii to become large enough to reach the surface of the water when inundation does occur.

When inundated, P. abramsii has a markedly different leaf shape and growth form than when exposed after pool drying. The leaves below water are rounded, the distance between internodes relatively great, and the stems usually little branched. When the pools dry, the plants rapidly adopt a terrestrial form and tend to be highly branched. The leaves become narrow and folded, not unlike those of many other chaparral and desert annual plants. This change from broader to narrower leaves is the opposite of the pattern shown by Callitriche, discussed above.

The tendency for stems to elongate when inundated is also present in other vernal pool taxa, notably Callitriche and Psilocarphus. The same response is common in other aquatic plants (Sculthorpe 1967; I. Ridge, Open University, England; unpubl.), and clearly it is an accommodation to fluctuating water levels Evidence suggests that the response is stimulated by accumulation of ethylene, a gas which is a product of normal plant growth. In a plant growing in air, the ethylene diffuses away rapidly, but in water diffusion is much slower and ethylene accumulates in the intercellular spaces (Musgrave et al. 1972). In most plants, increase of ethylene around growing points causes stem thickening and reduced elongation, but in many aquatic species it stimulates growth by interaction with growth hormones (Fitter and Hay 1981).

Irene Ridge, of the Open University in England, (pers. comm.) has surveyed the literature for reports on species which show an ability for rapid stem elongation under water. The 28 species span the taxonomic spectrum, including *Callitriche*, *Marsilea*, and rice (*Oryza sativa*). Ridge's current work, as well as some published studies, strongly suggest that ethylene is implicated in the response of most, if not all, of these species (Jackson and Drew 1984). Other species of marsh habitats (e.g., *Typha latifolia*, cattails, and *Mentha aquatica*, mint) showed little or no elongation response but were less adversely affected by the ethylene than most terrestrial species.

P. abramsii, despite its desert-plant appearance in the dried pool, has specific physiological adaptations to the pool environment. In addition to the depth accommodation response, inundated plants also produce abundant roots from submerged nodes (Bauder, unpubl.). This may function to establish the plant in mud as the water recedes and may offset the damage from the collapse of the weak elongated stems as the water falls. This would explain why the production of roots from stem nodes is common in plants that grow in exposed mud (Mason 1969). However, the adventitious roots may be produced simply to replace the roots in the substrate whose functioning and growth are inhibited by lack of oxygen (Jackson and Drew 1984). Measurements of root/shoot ratios of inundated plants with adventitious roots and noninundated plants would provide a first test of these hypotheses.

Scheidlinger's population study of *P. abramsii* showed that population parameters as well as morphology and physiology are strongly affected by time and depth of inundation. She followed seedlings that emerged at three depths in the pool basin and recorded, among other things, mortality and seed production (Table 7).

Although mortality of *P. abramsii* was higher in the inundated plants, the surviving plants were larger (Scheidlinger 1981), and produced many more seeds per plant. A similar pattern has been reported for *Orcuttia californica* (Stagg 1977, cited in Griggs and Jain 1983). Scheidlinger hypothesized that this pattern may be the result of competition, which she believes is more intense in the deeper part of the pool because of the dense stands of *Isoetes*. *Isoetes*, a perennial, may be able to grow to a large

Table 7. Emergence, survival to flowering, and seed production per plant of *P. abramsii* (mesa mint) at three depths in a pool on Kearny Mesa, San Diego County (Scheidlinger, unpubl.).

	Number of seedlings		
Depth	Emerging in fall	Flowering in spring	Number of seeds/plant
Shallow (7 cm max.)	69 (11)	31 (6)	21 (3)
Intermediate (12 cm max.)	48 (15)	18 (8)	49 (7)
Deep (17.5 cm max.)	31 (4)	6 (3)	183 (17)

Values are the means of four dm^2 quadrats (with standard error).

size more quickly than *P. abramsii* seedlings. However, an alternative explanation is that the stress of inundation causes mortality in both *P. abramsii* and species that will compete with it after the pool has dried. The plant density during the crucial growth period at the time of initial drying will therefore be lower in the deeper parts of the pool and higher on the margins while at the same time there will be higher soil moisture in the deeper parts of the pool.

Whatever the cause, *P. abramsii* exhibits very marked plasticity in form, from tiny plants with a few flowers to large individuals with hundreds. This plasticity is a trait which it shares with all of the other annuals of vernal pools, and indeed with annuals from many other habitats (Hickman 1975). Scheidlinger (1981) emphasized that this ability to adapt to the current circumstances is undoubtedly of vital importance in the adjustment of *P. abramsii* to a spatially and temporally varying habitat.

Scheidlinger also carried out a series of observations and experiments on the local distribution of *P. abramsii*. She selected a complex of pools on Kearny Mesa and recorded the presence or absence of *P. abramsii*. She found a pattern in which *P. abramsii* was most likely to be missing in smaller "upstream" pools, whereas it was usually present in larger pools and smaller "downstream" pools. The introduction of seeds of *P. abramsii* into four of the unoccupied pools in the fall of 1979 led to the establishment of populations that persisted at densities comparable to those of naturally occupied pools for the next 2 years (Scheidlinger 1984).

Scheidlinger's data suggest that *P. abramsii* populations are to some extent dispersal-limited. That is, the average population size would be larger if the between-pool dispersal were greater. However, since the majority of pools are occupied, even high rates of dispersal could not increase the total population by very much. For example, the unoccupied pools in her study have an area something less than one-fifth of the total area of pools, so a 20% increase would be achieved if these empty pools supported *P. abramsii* populations at a density equal to those of the occupied pools.

The physiology, life history, and distribution of *P. abramsii* contrast strongly with the aquatic plants that were discussed in the previous section. Unlike these mostly widespread species, *P. abramsii* is a local endemic. Although similarly plastic in growth form and showing clear adaptations to inundation, the pools must dry for it to complete its life cycle successfully. Most striking is the apparent lack, in *P. abramsii*, of apomictic or self-pollinated seeds. A single seed transported to a new habitat would have scant chance of success unless another pool with *P. abramsii* was within the foraging distance of insect pollinators. Perhaps more than any other plants in the southern California vernal pools, the *Pogogyne* species seem specifically designed for life in a semidesert aquatic habitat.

Coyote thistle (Eryngium species). *Eryngium* is a large genus of about 200 species especially abundant in the American tropics. Many of these species are associated with seasonally or permanently wet habitats. The occurrence of several species of *Eryngium* in California vernal pools is therefore not surprising. However, unlike the situation with most of the more strictly aquatic plants, the California species of *Eryngium* are endemic to the area. *Eryngium aristulatum*, for example, occurs only in the Californias, and *E. aristulatum* var. *parishii* is restricted to a small area from Riverside County to northern Baja California. The genus is almost cosmopolitan, but the species often of limited distribution.

At first glance, it is difficult to believe that *Eryngium* is in the carrot family (Apiaceae), but its structure and its carroty smell and taste reveal its true affinities. Instead of the usual flat-topped compound umbel of tiny white flowers, *Eryngium* has a dense head of inconspicuous flowers surrounded, in our species, by spine-tipped bracts (hence, "coyote thistle").

The heterophylly displayed by *Eryngium* foliage is pronounced (Figure 34). When the pools are inundated, the bright green leaves are reduced essentially to petioles with little or no lobing. These are displayed vertically, and are soft and without spines or with small, soft spines, and rise above the water like rushes. Some leaf divisions and the leaf midrib are hollow, presumably to facilitate oxygen diffusion or storage (see the discussion of plants of the aquatic phase). As the pool dries, the leaves become greyish green, more dissected, and tend to be horizontal rather than ascending. At the time of flowering, usually well after the water is gone, *E. aristulatum* plants are spiny desert plants flattened against the ground (Figure 35).

Like *P. abramsii*, *E. aristulatum* has limited means of dispersal. The heads break off the plants and fragment. Some of the seeds that remain attached to the spiny bracts may be dispersed by animals, but this is conjecture. The plant seems designed to find new habitat in the immediate vicinity of established plants, and not to disperse widely. But R. Holland (pers. comm.) reported that the fruiting

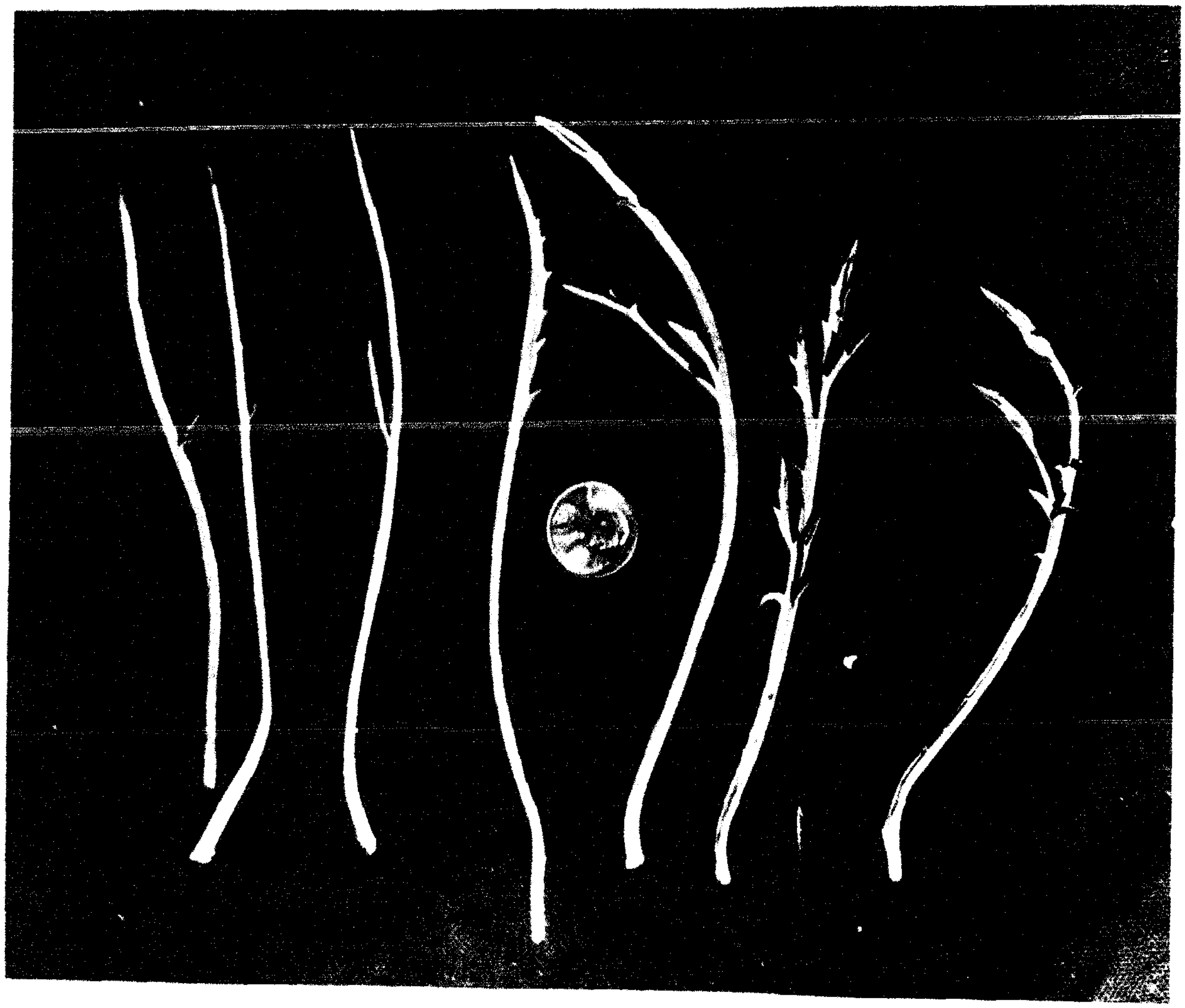

Figure 34. Leaves of *Eryngium aristulatum* illustrating the change in leaf form from the aquatic to the terrestrial stage. The leaf at the extreme left is typical of those that are emergent when the standing water is present. These leaves are bright green, hollow, and have no effective spines. At the extreme right is a leaf typical of flowering plants: it is grayish green, much more lobed, and protected by sharp spines.

heads of another species, E. vaseyi, break off in late summer and can be dispersed like tumbleweeds.

Seeds of E. aristulatum collected from the bottoms of pools in summer have been found to germinate readily when introduced into suitable pool basins (C. Patterson; pers. comm.). Newly established plants flowered three growing seasons after being introduced as seed. Munz (1974) reported that Eryngium species are biennial as well as perennial. From observation of permanent transects it is known that E. aristulatum lives for at least 3 years, and that it is able to reach large size under favorable conditions (C. Scheidlinger, pers. comm.; E. Bauder, unpubl.). Individual plants on the coastal mesas of Camp Pendleton have rosettes 30 cm and more in diameter.

The Eryngium species are among the few perennial dicots in vernal pools and are the only long-lived perennial in the group of amphibious vernal pool plants occurring in the southern vernal pools. The large number of annual species and

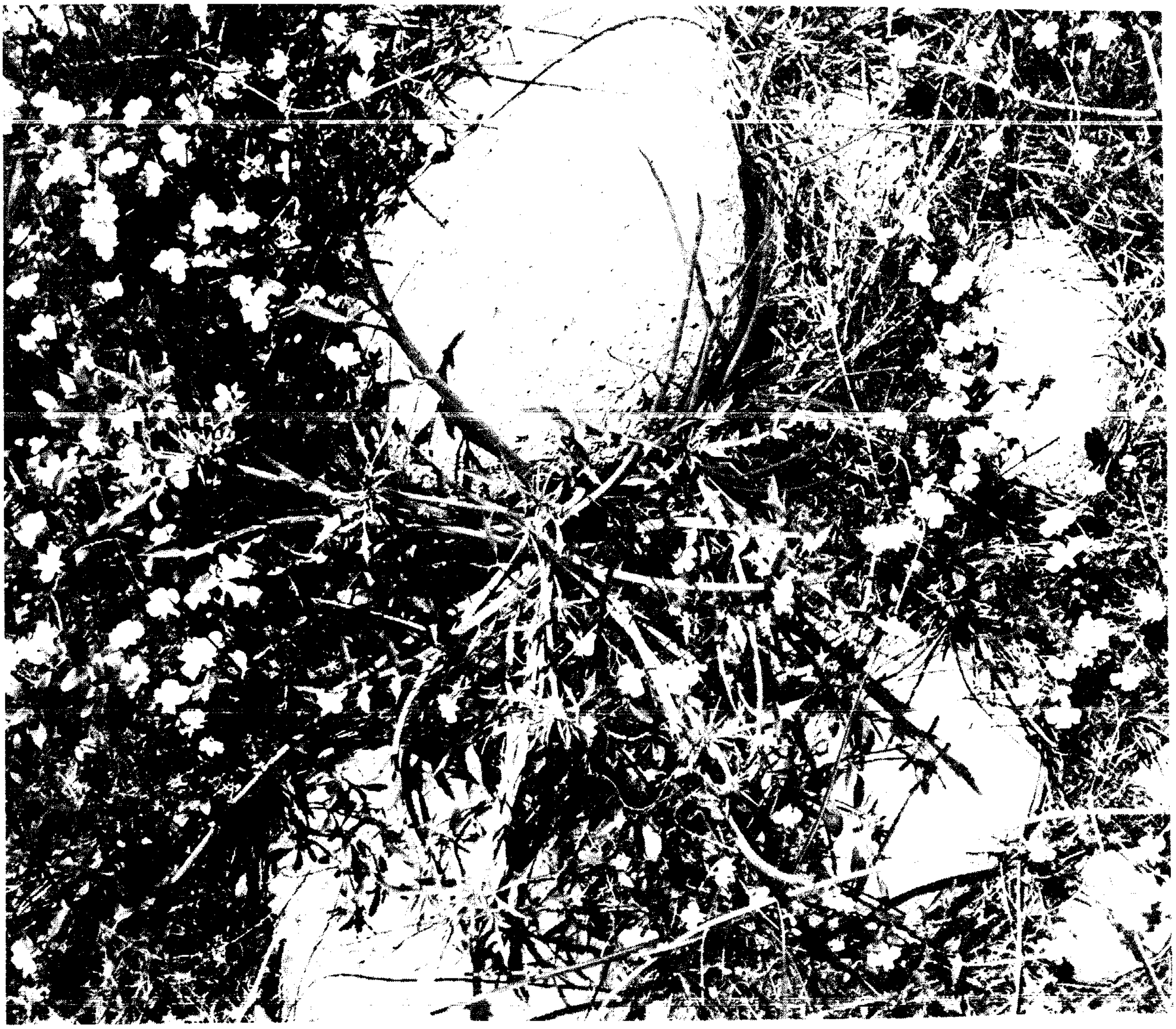

Figure 35. Flowering plant of *Eryngium aristulatum* on Kearny Mesa. The tiny flowers are surrounded by spiny bracts. Also in this picture: *Downingia cuspidata* (large flowers) and *Pogogyne abramsii* (visible above medium-size cobble at lower right).

comparative lack of perennials may be explained by the extreme desiccation which vernal pools undergo in summer, which may be fatal to perennating structures. *Eryngium* has a very patchy distribution in San Diego County and appears to favor pools with deep clay subsoil. This may be because these sites do not dry as rapidly or as completely as those with shallower or more coarsely textured soils.

Downingia. This genus consists of about 13 species found in western North America and South America (Munz 1974). All of the species are associated with vernal pools or other mostly temporary wetlands (Weiler 1962). Two species are reported from the coastal vernal pools, and several others from the pools of the Central Valley (Holland and Jain 1977). *Downingia* is one of the most colorful of the vernal pool plants, with multicolor blue, white, and yellow bilaterally symmetrical flowers that reveal its membership in a family with many other well-known wildflowers such as the scarlet lobelia (*Lobelia cardinalis*). In the later aquatic stage, but more typically in the early drying phase, *Downingia* can form carpets of blue in vernal pools. Sometimes it forms a band below the edge of the pool. Vernal pools are at their best on a bright spring day with meadowlarks calling and *Downingia* spread across the bottoms of the newly dried basins. Though not the rarest plants of vernal pools, *Downingia* are among the most beautiful.

All *Downingia* species are small annuals, and those of the coastal vernal pools are definitely amphibious plants. They are rarely found outside of places where water stands for at least a short time, yet the plants would be completely incapable of completing their life cycle if the level of the water did not drop sufficiently to allow them to produce flowers above water. Since these are mostly small plants (2-10 cm tall) this means they have no chance of persisting in deep permanent pools. They are specialists for areas of seasonally fluctuating water levels.

Downingia seedlings evidently germinate in early stages of inundation. Experiments (Myers 1975; E. Bauder unpubl.) show that *D. cuspidata* does not require immersion for germination, and also that it appears to require very definite pretreatment in order to germinate at high percentages, since many experimental attempts have given very low germination. For example, Linhart (1972) reported erratic results in laboratory experiments on the germination of *D. concolor*, though he did get almost complete germination on wet soil for some seed lots. Hoover (1937) indicated complete failure of his attempts.

Once germinated, *D. cuspidata* is very well equipped to withstand inundation. The stems of seedlings at an early stage of growth have large air chambers (Weiler 1962), and have a few linear leaves (Figure 36). In some pools, seedlings can be so dense that through the clear water it appears that a coarse grass turf is developing. *Downingia* is heterophyllous, with the submerged leaves seeming to be more linear, thinner, and to lack a waxy cuticle, but the differences between aerial and submerged leaves are not as conspicuous as in other amphibious plants. For *Downingia* it is rather that the whole form of the plant is adapted to the aquatic environment. Like *Pogogyne*, *D. cuspidata* has an elongation response to inundation, but the contrast between submerged and emerged growth form is less striking. *D. cuspidata* also produces abundant adventitious roots from submerged nodes.

Flowering is generally in March or April, well after the more strictly aquatic plants, but the variability is great. In very wet years, flowering will be delayed until the plants can emerge from the water. The showy flowers with their distinctive markings are designed to attract pollinators, reported by Weiler (1962) to be mainly bees and flies.

Like other members of the Campanulaceae, *Downingia* has a complex system for ensuring cross pollination. It is protandrous, meaning that the stamens mature and shed pollen before the stigma is receptive. In addition, the stamens, which are joined together, have "trigger hairs" which when disturbed by a visiting insect cause a burst of pollen to be released. Despite the special features to insure outcrossing, Weiler (1962) found that most

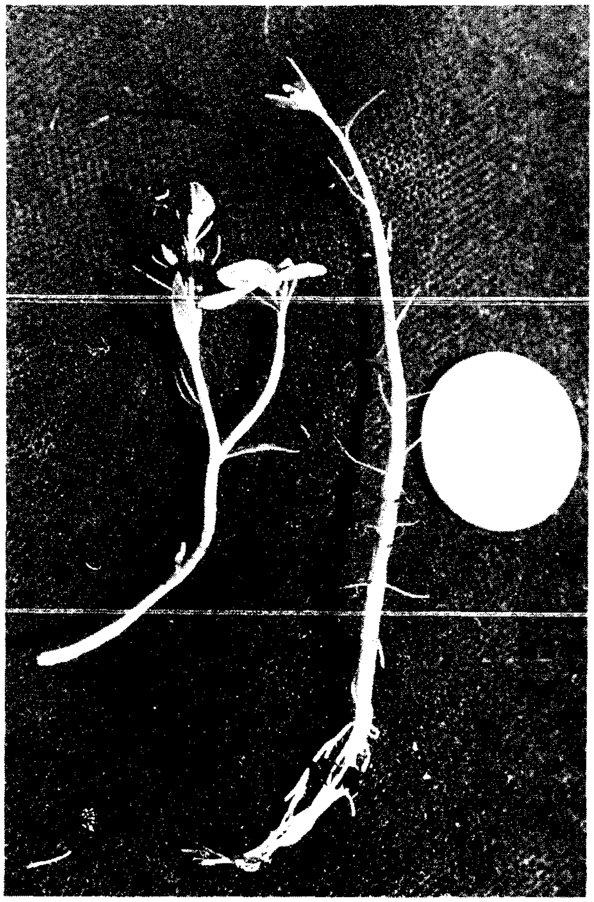

Figure 36. ***Downingia cuspidata*****. Plant at right was collected from standing water and has the expanded hollow stems and narrow leaves typical of the aquatic stage of this species. The plant at the left was collected from a dried pool and has the terrestrial form with broader leaves and reduced air spaces in the stem. The flowers are also shown in Figure 35.**

species of *Downingia*, including *D. cuspidata*, set small numbers of seeds by self-pollination in greenhouses where pollinators were not present. There are also species in which self-pollination is the rule. In these the flowers are smaller and less brightly colored (Weiler 1962).

After pollination, a long (2-4 cm), narrow capsule filled with many minute dustlike seeds develops (Figure 32). In common with other vernal pool plants the shedding of seeds seems a haphazard process dependent on the gradual disintegration of the capsule. Long-distance dispersal presumably occurs by the transport of seeds in mud by birds and other animals.

Psilocarphus. This small genus of annuals in the composite family is conspicuous at the time of fruiting because of the white, cottony heads (Figure 37). These diminutive plants are among the most frequent vernal pool plants and often are the most abundant annual species present. *Psilocarphus* also occurs in slightly moist open areas that are too dry to qualify as vernal pools by most definitions.

Like *Pogogyne*, *Psilocarphus* species usually germinate with the first fall rain and grow for some time in an aerial environment. Though they commonly occur in areas with minimal inundation, they are very tolerant of standing water. When growing in water, the leaves, like those of *Downingia* are linear. Upon exposure, later in the season, the leaves become broader relative to their length. The stems elongate when submerged, suggesting that they have a physiological ability to respond to inundation. After the pool has dried, the larger plants become highly branched.

The ecological value of the cottony covering of the fruits is unknown. It may assist dispersal by wind or water. Because the seeds are retained after the death of the plant, a more likely function is to protect the seeds against heat or seed predators. Ants may have difficulty handling the fruits because of the cobwebby hairs.

Deschampsia and *Orcuttia*. Considering the importance of grasses in many ecosystems, it is not surprising that grasses should also have invaded habitats with fluctuating water levels. The most famous grass of this kind is rice (*Oryza sativa*), an amphibious species whose unique features allowed it to become the cornerstone of the great civilizations of the orient. (The possibility of finding a plant even fractionally as valuable as rice is one justification for preserving temporary wetlands.)

Deschampsia danthonioides (hairgrass) is the most common of the vernal pool grasses. It is a delicate annual usually

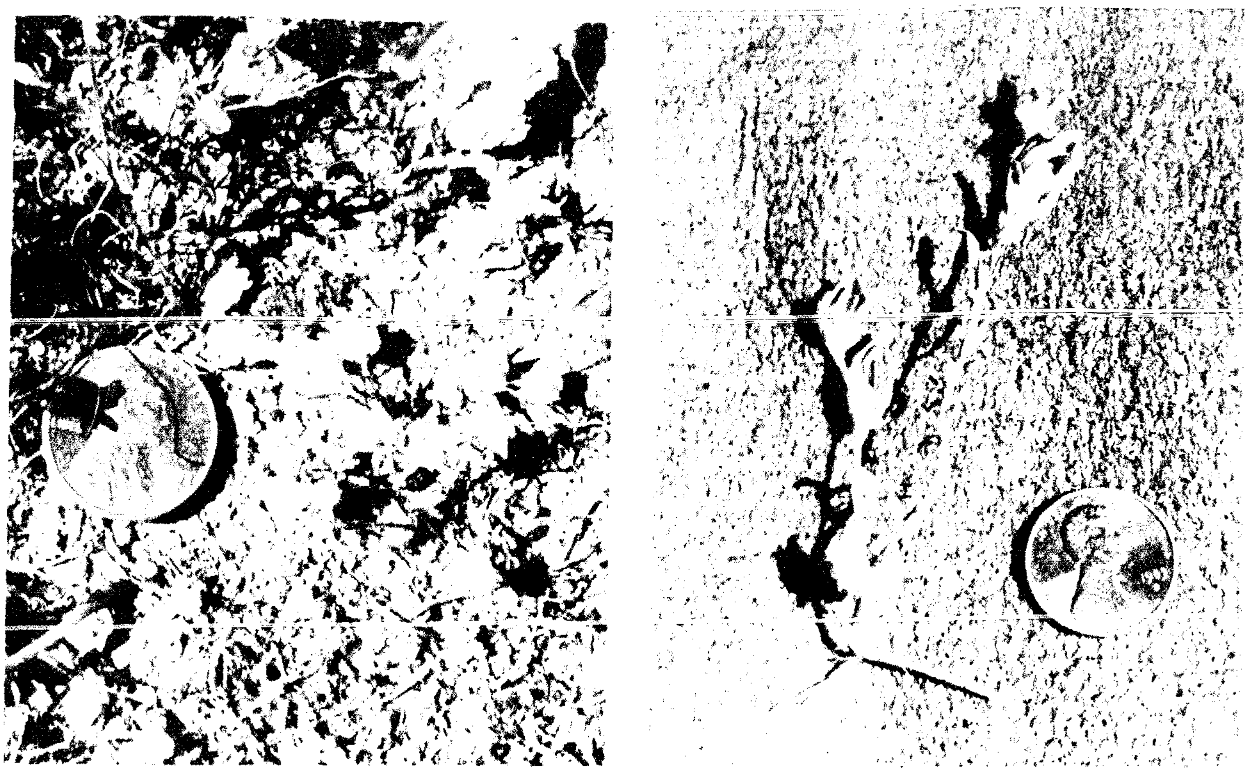

Figure 37. Fruiting *Psilocarphus brevissimus*. (A) a plant *in situ* with multiple branches and the typical woolly fruiting heads. (B) a less branched plant with the dried stem leaves, some of which were inundated, and the bract-like leaves around the heads.

of short stature (10-20 cm). The flowering heads (panicles) are very open, with long branches each with only a few small two-flowered spikelets at the ends (Figure 38). As with *Downingia*, *D. danthonioides* often appears *to form a ring in the pool basin*, usually at the upper margin.

Lin (1970) reported that in an experimental setting *D. danthonioides* requires prolonged *inundation before* germination occurs (in his experiment, three flooding episodes for an unknown number of days below water). If this is indicative of its field performance, one would expect *D. danthonioides* to germinate with the *first persistant inundation* of December or January.

When inundated at an early stage of growth, its floating leaves make *D. danthonioides* very conspicuous. Like *some other grasses* (e.g., *Glyceria borealis*, Fassett 1951) and the *water starwort* (*Callitriche*), *D. danthonioides* floats *its leaves* on *the surface rather* than raising them above the water. This presumably is accomplished by an elongation reaction similar to that discussed for *Pogogyne*. As the water recedes, *D. danthonioides* reverts to a *standard grass morphology*, and by the time of fruiting, which usually occurs after the pool has dried, it is difficult to believe that the plant had been functioning a few weeks earlier as a floating aquatic plant.

Grasses are overwhelmingly wind pollinated. Many are self-fertile, and others have complex breeding patterns in which the proportion of self-fertilized seeds varies within and between plants and years. If *D. danthonioides* follows the common pattern *of annual grasses* it probably is capable of selfing but also has at least limited exchange of pollen between plants. Like so many other vernal pool plants, the seeds that are produced are small and numerous.

Figure 38. *Deschampsia danthonioides*. By this stage the plants are mostly brown. Photo by Ellen Bauder.

Orcuttia californica, though one of the rarest grasses of the coastal vernal pools, is perhaps better known than any other because of the taxonomic studies of J. R. Reeder and the ecological and genettical studies of Tom Griggs. Though not plants to excite the interest of the uninformed, Orcuttia (Reeder, 1982, has transferred some Orcuttia species to a new genus, Tuctoria) and the closely related single-species genus Neostapfia are botanically among the most interesting plants of vernal pools. Of all vernal pool plants, these small annuals are the most likely to have evolved specifically in vernal pool habitat or in whatever habitat most closely resembled vernal pools in the past. These grasses are so distinctive and well differentiated from other species that their classification within the grass family (Poaceae) has been a matter of some debate. Reeder (1965) created a new tribe within the Poaceae specifically for these genera, a move which underlines their distinctiveness.

Orcuttia are small grasses with short leaves and dense inflorescences. Their most conspicuous trait may be the sticky (viscid) secretions that cover all parts of the leaves and stems, and which impart a "rather pleasant odor" that may "alert a collector that some members of the plant are in the area even before the plants are seen" (Reeder 1982). The value of the sticky surface to the plant is unknown, but it may serve to deter grazing. Reeder and Reeder (1980) noted that O. fragilis, a rare species of Baja California, Mexico, was ungrazed despite its occurrence in heavily used rangeland. Since Orcuttia, which reaches maximum development after the water has receded, would likely be most succulent just when the grasses of surrounding nonpool habitats were turning brown, there may have been intense selection against edible Orcuttia. Fitting with this idea is the fact that many of the plants of the last stages of pool drying are spiny (Eryngium), highly aromatic (Pogogyne), viscid and ill-smelling (Trichostema lanceolatum, "vinegar weed"), or otherwise not suggestive of pleasant taste or texture (e.g., Eremocarpus setigerus, dove weed; Hemizonia fasciculata, tar weed).

Orcuttia californica, which is the only species of this genus in the coastal vernal pools, may be presumed to have a life history similar to that of O. tenuis described by Griggs (1981). In this species germination takes place under water. Griggs reports that germination is not immediate, but requires the growth of fungus over the seed. While the biochemical or physical effect of the fungus is not known, Griggs found that the dormancy of the seeds could not be broken without the fungal growth. As he observed, this requirement for 2 weeks of fungal growth would assure that germination cannot occur except in years when pools are filled for extended periods. It may be an evolutionary response to the serious problem of germination at an inauspicious time, such as in response to a heavy summer storm (Griggs 1981). Regardless of the mechanism, it is known that Orcuttia can be absent (as observable plants) from pools in certain years or even for several years.

Once germinated, the seedlings of Orcuttia are typically entirely submerged and initially grow slowly, forming an Isoetes-like rosette of leaves. Eventually they also produce long, narrow floating leaves, as in Deschampsia. As the water recedes and the plants become exposed, the leaves are shorter and broader. The plant flowers after the water is gone. John Keeley (pers. comm.) has found that carbon isotope ratios for Orcuttia, Tuctoria, and Neostapfia indicate that they are all C$_4$ grasses. This fits with their late development in conditions when temperatures are higher, day length greater, and light intense. The earlier developing Deschampsia is probably a C$_3$ species.

Data on O. californica var. viscida (Griggs and Jain 1983) illustrate its population dynamics. With a density of 126 individuals per square meter, seed production was 500 per individual. For Orcuttia, the number of seeds stored in the soil can be substantially larger or smaller than a single year's seed production, but it is always significant. For O. californica var. viscida it amounted, in the year sampled, to about 5600/m^2, less than 10% of the current seed production.

Overview of the amphibious plants. The plants of the amphibious group are diverse, but certain generalizations can be made about them:

1) Most of the narrow endemics of vernal pools are amphibious species--Pogogyne, Orcuttia, etc. This may be because plants of this group must have an especially close fit to the physical and biotic environment in which they occur.

2) The plasticity in growth form, like the aquatics, is large.

3) Most of the amphibious species have no obvious adaptations for dispersal except small seed size, and most have a tendency to retain seeds on the plant. The main advantage of this may be to protect the seeds against predation, especially by ants.

4) In contrast to a majority of the more aquatic species, many amphibious plants seem to be outcrossing in whole or in part.

5) The ability of the annual amphibious plants to survive in a fluctuating environment seems to be a combined function of timing of critical life history events and plasticity. The considerable plasticity minimizes the probability of complete failure of seed production even though each year brings a unique sequence of environmental events. For most species only a moderate level of seed dormancy is probably required as an insurance policy against total ruin in a very bad year.

6) Outbreeding is more common in the amphibious plant species than the aquatics. It is tempting to conclude that this provides greater variability, but the work of Brown and Jain (1979) on inbreeding and outbreeding Limnanthes casts doubt on this.

4.1.3 Plants of the Drought Phase

The cycle of species in the vernal pool does not end with the drying of the surface and the onset of the summer drought. The amphibious species, notably Eryngium and Pogogyne, may still be active as late as early July. Some of the grassland-associated herbaceous species flower in late spring or summer, but most of these are incidental in vernal pools. There are a few plants, however, that are present in the dried basins consistently enough to be considered characteristic even though they are not restricted to pools. The following two species are examples of this group.

Eremocarpus setigerus (dove weed) is one of the species that begins growth very late in the season. A member of the Euphorbia family, this broad-leaved silvery annual is a native plant common in grasslands, especially in disturbed places. In vernal pools, seedlings of E. setigerus are first noticed in the dried or drying pool bottoms (Figure 39). These plants grow well into the hottest part of the summer, when they may be the only obvious signs of life in the desiccated pools. In late summer or autumn

Figure 39. Seedling of *Eremocarpus setigerus* in the basin of a dried vernal pool in April. The surrounding plants are brown and dead.

the plants eventually die, and in the early stages of pool filling the blackened rotting remains of E. setigerus are a characteristic feature of some pools. Evidently the seeds of this plant have the ability to persist in the moist soil without being stimulated to germinate. Since moisture clearly is not limiting, it may be that there is a heat requirement for the seeds to break dormancy. Whatever the mechanism, this tendency for late development is characteristic of dove weed (Bartolome cited in Heady 1977).

Trichostema lanceolatum (vinegar weed) is another plant of similar behavior. Like dove weed, T. lanceolatum appears late in the season and persists into the dry summer when other annuals have died. Despite its membership in the mint family, vinegar weed has a bitingly pungent non-mintlike odor, which may serve in part to discourage herbivory.

4.1.4 Species of the Pool Margins

There are many species (Tables 6 C and D) that are characteristic of vernal pool habitats, but that are not true vernal pool specialists. They either occur outside of the pool boundaries proper, or if they occur in pool basins, their presence is dependent on the input of propagules from adjacent nonpool habitat. These nonpool species can tolerate the limited periods of standing water that exist toward the pool margins, especially if they have grown large enough before inundation to have some leaves above the surface of the water (E. Bauder, pers. comm.). Since vernal pools typically vary considerably in depth or duration or both from year to year, it is also possible for annual species intolerant of flooding to invade pool basins in dry years (Bauder, unpubl.). There are also depressions of intermediate moisture status where vernal pool plants occur mixed with nonpool plants. To at least some extent, then, vernal pool plants and the nonpool species that surround pools contend for the same growing space. A brief consideration of the natural history of the plants that occur in the transitional areas from pool to typical terrestrial habitat is therefore necessary.

While many coastal vernal pools are surrounded by shrubs (Figure 12), herbaceous grassland species typically occur adjacent to pools. Because of the importance of annual grasses in rangelands, these have been studied relatively intensively compared to other wild plants (Heady 1977). Three genera contribute most of the dominant species--Bromus, Festuca (sometimes also known as Vulpia), and Avena. All have the same basic life history. Germination occurs with the first heavy fall rains, growth continues through the winter, and seeds are produced in early to late spring, to lie in the litter and surface soil until the next fall.

The reason for the success of the introduced annual grasses evidently lies in their ability to adjust to California's drought-flood climate. They begin growth promptly when moisture becomes available, grow rapidly while conditions are favorable, and switch to seed production as drought intensifies. In good years and in favorable habitats the annual grasses grow large, tiller (produce additional stems) extensively, and have high seed production. In bad years and on less productive sites plants are small and seed production reduced. Even in the most severe droughts the annual grasses have a remarkable ability to produce at least some seeds (Ewing and Menke 1983).

Bromus mollis (soft chess) is one of the annual grasses most commonly found within and next to vernal pool basins (Figure 40). Since it is also a desirable range species it has been the subject of a number of studies, and it may serve as an example of the annual grasses generally. A study by Young et al. (1981) revealed the importance of seeds and germination behavior in the life history of *B. mollis*. By harvesting soil samples in the field and germinating them in the greenhouse, they were able to measure both the abundance of seeds in the soil at different times of year, and the rate and degree of germination. They found, as expected, that seed reserves of *B. mollis* were highest in late spring after the ripening and dispersal of seeds. The rate of germination of seeds in the soil was found to be slow in June and increased

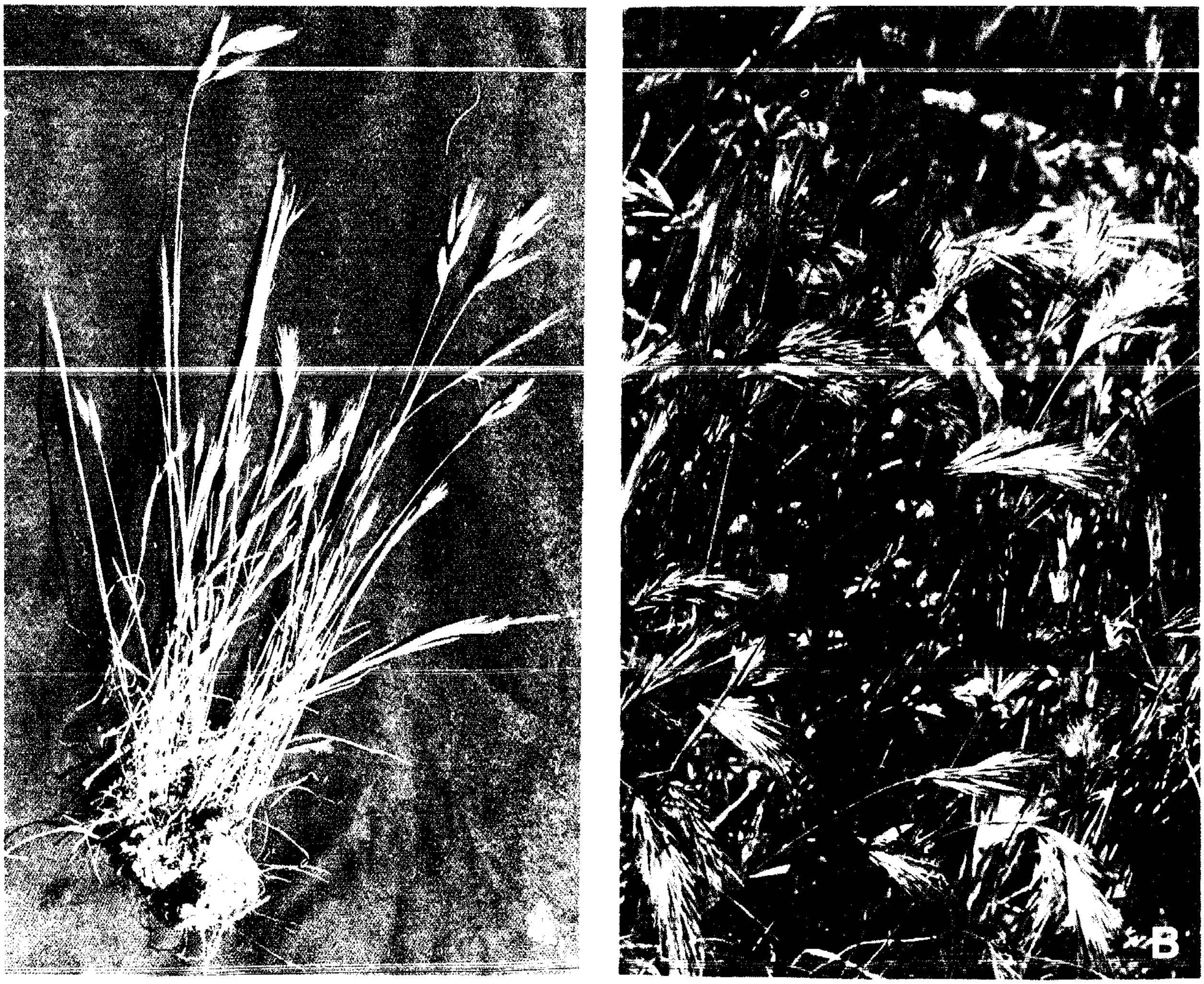

Figure 40. Annual grasses of the pool margins. (A) *Bromus mollis* (tallest plants), *Hordeum* sp. (thick wheat-like heads mostly in the center of the photo), and *Vulpia* sp. (finer narrow heads, as at extreme left). (B) *Bromus rubens*.

into the fall. The final percentage germination also tended to increase. Compared to some other plants in the annual grassland (e.g., clover, *Trifolium hirtum*) very few germinable seeds of *B. mollis* (about 20/m^2) survived in the soil for more than a year.

Bromus mollis obviously relies heavily on the current seed production, and the requirement of the seeds for a period of afterripening minimizes the possibility of premature germination. Summer storms, if they stimulated germination, could expose the seedlings to an extended drought and complete failure of seed production. However, once the time is right (about October), the seeds are prepared to germinate within a week, betting, as it were, that the fall rains are on the way, and that they will be sufficient to allow at least some seeds to be produced. It is rare for this bet not to pay off, but even when it doesn't the small survival of ungerminated seeds gives *B. mollis* another chance in the next year.

The genetic structure of *B. mollis* populations has been studied by Jain et al. (1970). They found that it was predominantly self-fertile. No population had an outcrossing rate higher than 10%. But, despite the restricted crossing among plants, *B. mollis* was far from genetically uniform. It is somewhat surprising that much of this variation exists within populations, in contrast to other self-fertile plants where local populations often tend to be genetically uniform.

A characteristic of introduced annuals that is especially well developed in the species of *Bromus* is the presence of stiff barb-like hairs on the lemma (chaff-like covering over the grain) and the almost needlelike base of the lemma which combine to give the fruiting structures a remarkable ability to become firmly embedded in clothing, and no doubt, animal fur. Grazing animals sometimes get the grass spikelets into the skin, or worse, since one of the common names of *B. diandrus* is "ripgut brome." There seems little doubt that the amazing spread of these introduced grasses is in part a result of their transport by grazing animals. Of necessity, vernal pool researchers adapt their footwear to avoid the need to pick seeds from their socks. In the Central Valley old tennis shoes without socks or nylon spats over shoes have been used (R. Holland, pers. comm.) while in San Diego County, despite an abundance of rattlesnakes, beachcomber zoris have found favor in the period when grasses are ripening seeds (T. Ebert, Department of Biology, SDSU; pers. comm.).

Not all of the introduced species are grasses. One of the most ubiquitous plants in the upper margins of vernal pools in San Diego County is *Hypochoeris glabra*, a plant in the chicory tribe of the sunflower family (Asteraceae) resembling a delicate dandelion (Figure 41). Aspects of the population ecology of this species were the topic of thesis work by Baker (Baker 1977; Baker and O'Dowd 1982), the field work parts of which were conducted in a vernal pool area of Kearny Mesa, San Diego County. Like other annual

Figure 41. Fruiting heads of *Hypochoeris glabra* in an area adjacent to vernal pools on Kearny Mesa. This density of plants is not unusual in areas with a history of disturbance.

plants discussed, *H. glabra* shows remarkable plasticity of growth. In addition, it produces two kinds of achenes (fruits) on the same plant. Both are topped with the dandelionlike tuft of stiff plumed hairs (pappus) But in one the pappus is borne at the end of a long thin projection (beak) while in the marginal achenes this projection is absent. The beaked achenes are readily carried by the wind, whereas the unbeaked achenes tend to be moved relatively little by the wind and also have short hairs that cause them to cling tenaciously to cloth and fur. The achenes, especially the beaked ones, are avidly collected by ants. *Hypochoeris glabra* thus has seeds that can be dispersed widely by either wind or animals, and it is adept at exploiting new habitats wherever they might appear.

Like *B. mollis*, *H. glabra* seeds need afterripening to achieve maximum germination. Baker found that germination of *H. glabra* was only moderate immediately after collection of the seeds, and that it gradually increased with time. Furthermore, she showed that germination was less at higher temperatures Both of these characteristics would tend to favor germination in the fall and winter, minimizing the possibility of germinating in response to rainfall during the warm months.

Erodium is a dicot genus of introduced plants that is as thoroughly naturalized as the annual grasses. Certain species tolerate saturated soils, and they are frequently found within the pool basins. The life history of *Erodium* is similar to that of the annual grasses. *Erodium* has self-planting seeds, a trait shared with some other members of the geranium family and many grasses (e.g., *Stipa* spp.). At maturity the seed retains a long bristlelike projection (actually part of the style of the flower). When dry this structure is coiled. Wetting the dried fruit causes the coils to unwind, and with repeated changes in humidity the sharp pointed seed is pushed into the soil. This elaborate mechanism, requiring a relatively great investment of energy into each fruit, also insures a good chance of success for the seeds by removing them from the soil surface, where they may be eaten or destroyed by physical stress. When seeds do germinate, they are well placed for growth. In confirmation of this, Roberts (1968) observed almost complete survival of *Erodium* seedlings after initial emergence, with significant mortality occurring only after seed set and the onset of drought.

Like *B. mollis* and *H. glabra* , *E. botrys* seeds show an afterripening effect, with germination being more rapid and more complete for seeds that have been in the soil longer (Young et al. 1981). They seem to be more liable to germinate with early rains but also seem to have considerable drought tolerance and thus have a better chance than many annuals of surviving from germination in summer to the fall rains that will insure reproductive success (Young et al. 1981).

As is evident from Table 6 there are many native species associated with vernal pools. Most of these undoubtedly were present in the original grasslands, and a number are perennials rather than annuals. This distinction is most striking in the grasses. Few native species of any prominence are annuals, whereas the native *Stipa* (needlegrass) species can be important locally. In contrast to the introduced annuals, the native perennial species seem to have little capacity for rapid population expansion. Seed production is relatively modest for the size of the plants, and in very dry years there may be little or none. The program of these perennials seems to be to sacrifice seed production in favor of the survival of the vegetative part of the plant. Because of this, perennial grasses do not possess the ability of the annuals to move into vernal pool basins in dry years.

One group of natives that is of interest aesthetically as well as scientifically are the "bulb" plants, especially the genera *Allium*, *Brodiaea*, *Chlorogalum*, *Dichelostemma*, and *Muilla* (Figure 42). Some of these can be very abundant around vernal pools and add considerably to the show of flowers. *Muilla clevelandii*, of San Diego County, is a very restricted endemic.

Ecologically, these species all follow the same recipe for success in a semiarid climate. They have deep-seated

Figure 42. *Muilla maritima* in flower. Fruiting heads of *Erodium* sp. and *Hypochoeris glabra* are also in the photo.

bulbs or bulblike corms. They begin growth with the early rains, and generally flower in late winter. Unlike many of the annuals, the seeds of bulb plants probably do not survive for more than a year if they fail to germinate. Since the established plants probably can live for many years, the failure of seedling establishment in any one year is of little consequence. The deeply implanted bulbs are well protected against the extremes of drought and heat, and will be able to flower again in the next year. Some species also are reported to remain completely dormant in unusually unfavorable years (P. Rundel, Biomed. Lab., University of California, Los Angeles; pers. comm.). *Brodiaea orcuttii* is one member of this *ecological group* that in some places in San Diego County is locally restricted to pool basins. It is not known if these populations of *B. orcuttii* possess any special *physiological or* developmental adaptations to vernal pools.

There is also a large assemblage of native annual species associated with pools, some of which appear to have considerable tolerance of flooding. For example, the annual clover *Trifolium amplectens* is often found growing in standing water, although it also grows in nonpool situations. The beautiful yellow composite goldfields (*Lasthenia chrysostoma*) often is abundant at the upper margins of pools.

Hemizonia species deserve special mention, since they are among the most frequent native annuals in and near vernal pools (Figure 43). This genus is distinctive in the grassland for being late in the phenological sequence. As members of the tarweed subtribe in the composite family (Asteraceae) they possess the pungent fragrance peculiar to that group. In the late spring and early summer when the annual grasses have already turned completely brown, *Hemizonia* species will often be nearly the only green herb in evidence. They evidently have the ability to draw upon deeper reserves of water and withstand intense heat and drought better than other species of annuals, introduced or native. This ability, combined with some inundation tolerance, means that *Hemizonia* can sometimes be found in considerable abundance in the basins of dried vernal pools.

Selaginella cinerascens, a clubmoss endemic to southern California and northern Baja California, is the dominant element of an unusual vegetation cover characteristic of areas of clay soil crust adjacent to vernal pools in San Diego County. The vegetation patches are typically a few to hundreds of square meters in area, and are made up of clones of *S. cinerascens* with scattered, mostly stunted grasses and forbs, and areas of bare or lichen-encrusted soil. The *Selaginella*, which is a perennial that spreads across the surface and rarely rises more than a half centimeter above it, is obviously well suited to growing on shallow compacted or crusted soils that inhibit the

Figure 43. *Hemizonia fasciculata* adjacent to a pool on Kearny Mesa.

growth of lusher vegetation. It is apparent that these surfaces are drought stressed even during the winter growing season, and the dominance of S. cinerascens may well be because of its ability to tolerate repeated dehydration during the growing season. Though the community is growing on soil, it resembles most closely the lichen-clubmoss associations that develop on bare rock surfaces. A suitable name for these distinctive areas, underlining the depauperate nature of the vegetation, is "selaginella balds."

4.2 MOSSES, LIVERWORTS, AND LICHENS

4.2.1 The Bryophytes -- Mosses and Liverworts

Vascular plants are the obvious dominants of the vernal pool landscapes, but close examination reveals an abundance of bryophytes. Bryophytes lack the complex rooting structures of higher plants and a vascular system for the conduction of water, so they require ample moisture for growth and reproduction. But bryophytes also are able to withstand almost complete desiccation, and this, along with their small size and capacity for rapid recovery when moisture is available, allows them to exploit habitats that vascular plants find too severe-- rock faces, soil crusts, tree bark, etc. and enables them to occur in extremely arid regions.

In the vicinity of vernal pools mosses are most in evidence in moist depressions and at the upper margins of pools within and outside of the basins. They may also be seen on the bottoms of vernal pools, but it is not known if these are true aquatic mosses or merely terrestrial mosses with some degree of inundation tolerance. At the moist margins of pools a nearly complete understory of small moss can develop, filling in the habitat between the larger plants where for brief periods excess moisture and nutrients are available.

Most mosses are perennials, so that the vernal pool mosses probably regenerate each year from growing points in or just above the soil surface. Establishment of new moss plants is by spores produced in the stalked capsules characteristic of most species. However, little appears to be known about the rate of establishment of spores or the mortality of the vegetative individuals for mosses of arid regions (Scott 1982). Because of interest in the desiccation tolerance of mosses, the rate of recovery of rewatered moss has been studied in some detail. Many species are known to be able to recover from years of desiccation. Typically, desiccation-tolerant mosses are able to recover their photosynthetic capacity so rapidly on rewetting that they have a positive carbon balance within hours (Proctor 1982).

Little seems to have been done on the ecology or taxonomy of vernal pool associated mosses, yet they may play an important role in the functioning of the system. One may speculate that the mosses may be important to invertebrates, supporting mites, pseudoscorpions, bristletails and other insects, and other small surface active organisms (Gerson 1982). They may also be locally important in providing protective mulch for the seeds and seedlings of the higher plants. It seems unlikely that they would be serious competitors of higher plants, but there may be important effects of mosses on decomposition and nutrient release to the higher plants where moss cover is very dense. Mosses may also reduce soil erosion by protecting against raindrop impact, binding the surface, and slowing the movement of water across the soil surface.

Liverworts, because of their larger size and distinctive fruiting structures, are more likely to attract attention than mosses. Like the mosses, liverworts show a remarkably rapid response to rain, often being the first plants to turn visibly green. While liverworts are widely distributed in California, they are particularly prominent around vernal pools (Luckenbach 1973), though no species is confined to vernal pool basins. D.K. Severson of the Department of Biology, University of San Diego has identified six species, including both thalloid and leafy forms, from the northern part of the National Landmark on Miramar Naval Air Station on Kearny Mesa in San Diego County:

Asterella bolanderi (Aust.) Underw.
A. palmeri (Aust.) Underw.
Fossombria longiseta Aust.
Riccia californica Aust.
R. glauca L.
R. trichocarpa M.A. Howe

The Riccia species are probably mostly annual, originating each year from spores, though perennial species are known. These species play a pioneering role on bare soil, forming rosettes that may be important in reducing soil erosion. The other two genera are perennial. In Asterella the leaves become strongly incurled when dry, appearing like black lines on the soil surface (D.K. Severson, pers. comm.).

The ecological role of the perennial liverworts may be compared with both the mosses and Selaginella cinerascens. All of these groups exploit the brief periods when soil moisture is high and evaporation not excessive. Presumably these plants would be much less abundant if rainfall were to increase, allowing the development of a dense grass or herb cover. If so, bryophytes and Selaginella species should be less prominent members of the community as one moves north.

4.2.2 Lichens

Lichens are ubiquitous and extremely hardy organisms that consist of an alga and fungus growing in close association. In the vernal pool region lichens are most in evidence on the bark of trees and shrubs and on exposed boulders. Others form rounded, nondescript thalli just below the soil surface in the selaginella balds and other places with sparse plant cover. In these situations they probably play an important role in preventing soil erosion. While a diverse group with interesting physiological and morphological characteristics, they are plants primarily of drier microhabitats and therefore play little direct role in vernal pools.

4.3 ALGAE

All of the plants loosely known as algae, including the blue-green algae, which taxonomically are more properly grouped with the bacteria, will be considered under this heading. In vernal pools, as in aquatic systems generally, the algae are of major importance in the aquatic stage as primary producers and nitrogen fixers. Unfortunately there are no estimates of the productivity of algae in vernal pools, but in some instances it appears to equal and very probably exceed that of the vascular plants. The standing biomass of algae differs widely among pools. Some pools never have obvious algal blooms, and maintain clear water throughout their existence. In other cases, dense floating mats of filamentous algae develop, shading the plants below water, thereby reducing their growth and probably also causing some mortality for those unable to raise leaves above the surface. A characteristic feature of pools in the drying phase, especially of those that have had dense algal mats, is the presence of crust on the pool bottom formed by the coalescence of the algae. This sometimes forms a thin sheet, not unlike the nori used as sushi wrappers.

The organisms of the aquatic phase of vernal pools are the least studied, and algae in particular seem to have been virtually ignored up to this time. The species list in Table 8 is based on data collected by Norma Lang's phycology class at U. C. Davis in March 1984 from pools south of Dixon, California, in the Central Valley.

Aside from the mat-forming algae already mentioned, one of the most obvious algae is *Nostoc*, a genus of colonial blue-greens that forms small semitransparent balls in the water of vernal pools. They are nitrogen fixers, possessing the enlarged clear cells known as heterocysts that are believed to be the site of fixation in the blue-green algae.

Table 8. Algal genera reported from vernal pools near Dixon, California. Identifications by Norma Lang's Botany 118 class at University of California, Davis, 1984.

- *Cyanophyceae*
  - *Anabaena*
  - *Nostoc*
  - *Oscillatoria*
- *Chlorophyceae*
  - *Ankistrodesmus*
  - *Apiocystis*
  - *Chlamydomonas*
  - *Closterium*
  - *Cosmarium*
  - *Eudorina*
  - *Micrasterias*
  - *Oedogonium*
  - *Scenedesmus*
  - *Spirogyra*
  - *Staurastrum*
  - *Tetraspora*
  - *Ulothrix*
  - *Volvox*
  - *Zygnema*
- *Charophyceae*
  - *Chara*
- *Euglenaphyceae*
  - *Euglena*
  - *Phacus*
  - *Trachelomonas*
- *Xanthophyceae*
  - *Ophiocytium*
  - *Tribonema*
  - *Vaucheria*
- *Bacillariophyceae*
  - *Melosira*
  - *Synedra*

4.4 MICROBIOTA

Microorganisms are viruses, bacteria, fungi, protozoa, and algae that range in size from one to a few tens of micrometers (Campbell 1983). Microorganisms are important in every aspect of energy and material transfer in ecosystems and are certainly key elements of vernal pool ecosystems. But little is known about the microorganisms of vernal pools, and the best that can be done is to suggest which groups of microorganisms might be most important, and how they might affect system functioning.

The autotrophic microorganisms include the blue-green algae which were discussed with the prokaryotic algae in the previous section. Although these are probably the most important primary producers in vernal pools, there are photosynthetic bacteria in other groups (e.g., green and purple sulphur bacteria, purple non-sulphur bacteria) that can be important in aquatic systems, both by their contribution to productivity and to sulphur cycling (Wetzel 1983).

Many of the organisms in these groups are facultative autotrophs that switch to heterotrophy in the appropriate circumstances. Others have rather exacting requirements and exist in zones of steep gradients in oxygen availability. Since such conditions might exist in vernal pools, it may be that photosynthetic bacteria other than blue-green algae are important. The phototrophic protozoans (e.g., *Chlamydomonas*) may also be included in the list of potential photosynthesizers. Their role in vernal pools is unknown.

Chemosynthesis is the reduction of carbon dioxide through the utilization of inorganic molecules such as hydrogen sulphide. In most ecosystems the main source of the appropriate molecules is the decomposition of organic matter, so that chemosynthesis is really a kind of secondary productivity, and may be thought of as grazing on inorganic molecules released in decay (Rheinheimer 1971).

Because of the anaerobic conditions that exist in saturated vernal pool soils, chemosynthetic bacteria may be of some importance during the aquatic stage.

The free-living predators, decomposers, and saprophytes encompass a diverse group of microorganisms that consume living or dead plant and animal material and effect many biochemical transformations in the process. Of greatest overall importance is the role they play in the release of nutrients to primary producers. They also provide a source of food for the smaller predaceous animals.

Anaerobic conditions are an indirect effect of decomposition by microorganisms in saturated soils. Oxygen diffuses much more slowly in water than it does in air. Thus when the air in soil containing organic matter is replaced with water, the action of decay organisms augmented by the respiration of higher plant roots quickly depletes the oxygen. Though oxygen does diffuse into the soil, the rate is so slow relative to the demand that, even when waters above the soil are supersaturated with oxygen, the aerobic layer at the surface may be only a few millimeters thick (Watanabe and Furusaka 1980).

Once the anaerobic conditions are established, there is a shift in microbial function resulting both from a change in the species to anaerobic forms and facultative changes within aerobic species to adjust to the lack of free oxygen. Instead of carbon dioxide being the final stage in carbon metabolism, organic acids and methane (swamp gas) are produced along with other reduced forms such as hydrogen sulphide that would be quickly oxidized or metabolized in an aerobic environment (Campbell 1983).

Because of the importance of nitrogen as a nutrient, one of the anaerobic transformations of special interest in aquatic systems occurs when nitrates are used as an oxygen source by some bacteria, resulting in the release of nitrogen gas. In certain conditions this process, along with volatilization of ammonia, can result in significant losses of nitrogen from the system. There are also anaerobic nitrogen-fixers, however, so that determining the effect of water-logging on nitrogen balance is complex. There are data to suggest that for rice paddies the effect of flooding is to increase nitrogen contents relative to unflooded soils. This is assumed to be the result of increased fixation. The same may be true for vernal pools.

Heterotrophic microbial symbionts, especially parasites, may be assumed to be important in their effects on both plants and animals. A description of their influence in vernal pools must await further study. Mutualist symbionts, living in association with higher plant hosts, undoubtedly contribute a portion of the nitrogen available in vernal pool ecosystems, but it seems likely that free-living nitrogen fixers may be of greater importance.

Symbiotic mycorrhizal fungi, which form an intimate association with the roots of their plant hosts, undoubtedly are present and play a role in increasing the absorption of nutrients. Nothing is known about this group with reference to vernal pools.

4.5 INVERTEBRATES

4.5.1 Zooplankton and Other Small Aquatic Animals

Strictly speaking, plankton are organisms that are suspended in the water column, so that their movements are mainly dependent on water currents. The organisms to be discussed under this heading will also include some that spend most of their time moving across the bottom (some ostracods) and others that are relatively strong swimmers (fairy shrimp).

The small animals of vernal pools have not been extensively studied in California, though temporary waters elsewhere have attracted the attention of limnologists and others (e.g., Wiggins et al. 1968). The main source of information used here is a thesis and subsequent work done for the California Department of Transportation on Kearny Mesa in San Diego County by Balko (1979). The list in Table 9 is of the larger zooplankton (interpreted broadly) and does not include smaller organisms such as protozoans or larger animals such as insect larvae and amphibians.

Cladocerans. Balko identified more than eight species of cladocerans, a suborder of crustaceans common in freshwater habitats throughout the world. They are small animals (generally less than 3 mm) with a compound eye, a distinct head, a carapace covering the body, and insectlike jointed appendages. They move through the water with jerky motions that along with their gross morphology make their common name, water fleas, especially apt.

Although some cladocerans are predaceous, most are filter feeders that collect organic material from the water by movements of the legs that pass a current of water under the body (Pennak 1978). While it appears that ingestion is fairly indiscriminate, much of the energy and nutrition is probably derived from algae, protozoans, bacteria, and other living organisms.

The life cycle of cladocerans is well suited to temporary pools, although the species listed (Table 9) are not restricted to temporary waters (Balko and Ebert

Table 9. List of zooplankton species collected in Kearny Mesa vernal pools of San Diego County by M.L. Balko in 1978, 1979, and 1980 (Balko 1979; Balko and Ebert, MS.). Presence is based on occurrence in the 54 pools of the 1979 sampling.

Species	Presence (%)[a]
Class Crustacea	
Sub-class Branchiopoda	
Order Anostraca (fairy shrimp)	
Branchinecta lindahli	24
Order Cladocera (water fleas)	
Alona sp. 1	83
Alona sp. 2	7
Macrothrix hirsuticornis	54
M. rosea	67
Moina wierzejskii	24
Simocephalus exspinosus	17
Unidentifed species[b]	11 (2)[c]
Sub-Class Copepoda (copepods)	
Cyclops vernalis	100
Eucyclops speratus	2
Sub-class Ostracoda (seed shrimp)	
Bradleycypris cf. *affinis*	--
B. sp. n. McKenzie	26
Cyprioconcha macra	--
C. steveni	6
Eucypris virens	39
Heterocypris incongruens	--
H. aff. *salinus*	54
H. aft. *symmetricus*	28
Limnocythere reticulata	--
L. sp. n. McKenzie	37
Pseudoilycypris sp.	4
3 unidentified	53 (2)
Phylum Rotifera (rotifers)	
Brachionus quadridentata	28
Hexarthra sp.	59
Lecane formosa	39
L. luna	33
L. ohiensis	31
L. sp. A	4
L. sp. B	6
Lepadella patella	30
L. sp. A	20
Monostyla closterocerca	13
M. elachis	2
M. lunaris	26
M. sp. A	4
M. sp. B	6
Platyias quadricornis	17
Polyarthra sp.	76
Trichocera sp.	33
Scardium longicaudum	31
Squatinella tridentata	7
22 unidentified illoricates	100 (9)

[a] 100% = species was collected at least once in all pools.
-- = species was present but presence data are not available.
[b] unidentified = occurrence of one or more unidentified species.
[c] () = maximum number of unidentified species found in a single pool.

1984). With the first filling of the pools females emerge from resting eggs on the pool bottom. These grow by a series of molts. Upon reaching adult size, the females begin the production of parthenogenetic eggs. These are retained within the body until hatching, so that fully formed young are released. In the early stages of population growth these young will also be parthenogenetic females that will in turn produce more parthenogenetic females. Since some species produce up to 40 eggs, the potential for population expansion in this period is enormous. In most species males are not produced until some change in environmental or biological conditions that presages a deterioration in growing conditions is sensed. It has been proposed that increases in population density, temperature, or salinity, or a decrease in food, may be the triggers (Pennak 1978). In vernal pools, either density or salinity would be good predictors of imminent drying, since both would inevitably increase as the water evaporates.

With the appearance of males mating takes place to produce sexual resting eggs. It is apparently also possible for resting eggs to be produced asexually in at least some species of cladocerans (S. Hurlbert, pers. comm.). The resting eggs are encased in special protective structures and are dormant, unlike the parthenogenetic eggs produced in the favorable season. The resting eggs are able to tolerate drying and extremes of heat and cold, and provide the means by which these aquatic organisms manage to persist through the intervening period of desertic conditions until the pools fill again.

Copepods. Balko found only two species of copepods, one of which, Cyclops vernalis, was nearly always present. Both species occur in many freshwater habitats and are not restricted to vernal pools. Copepods are crustaceans and like the cladocerans are widely distributed, have segmented bodies, and move through the water with short darting movements. The two species reported for vernal pools are cyclopoid copepods, having mouth parts suitable for seizing and biting and feeding on unicellular plants and animals, other zooplankton, and probably organic debris as well. The life history of copepods differs from that of the cladocerans in that parthenogenesis is much more unusual, and the eggs are borne outside the body in masses resembling bunches of grapes. However, like the cladocerans, copepods are capable of rapid population increase when conditions are favorable. Survival through the dry season is accomplished in most species by encystment of posthatch copepods in the bottom mud, though resting eggs may also be produced (Alexander 1976). The encysted copepods appear to respond very quickly to moisture, since they are among the first organisms to appear when cores from vernal pools are moistened in the laboratory (Alexander 1976).

Ostracods. Ostracods are yet another group of crustaceans, and of the three groups considered are probably the most obvious in vernal pools. They are small (generally less than 3 mm) organisms that superficially resemble miniature clams, with bodies and segmented appendages enclosed within a bivalve shells. Unlike the copepods and cladocerans, most ostracods move about on the bottom rather than swimming or floating in the open water. In vernal pools some of the species are very abundant and very active, flitting about the bottom in nearly continuous motion. According to Pennak (1978), most ostracods are omnivorous scavengers, feeding on bacteria, molds, and fine detritus. It is also reported that the species of vernal ponds have only a single generation per year, in contrast to the cladocerans and copepods. Oversummering is accomplished by the production of sexual eggs that withstand the drought. Some species are said to be able to survive as advanced instars in a torpid state buried in the mud (Balko and Ebert 1984). Even if this behavior does not allow them to survive through the summer, it may permit them to withstand brief dry periods within a season.

Though apparently not considered of major importance in larger aquatic systems, in vernal pools the ostracods may well achieve greater abundance and have a greater impact on the pool food web than any of the other crustaceans. Their specialization on bottom feeding and on organic detritus is probably ideal in shallow pools, where the filling of the pools must stimulate the decomposition of the algal crust and higher plant biomass. In many drying pools masses of white ostracod shells are conspicuous.

In contrast with the widespread cladocerans and copepods discussed above, some of the ostracods collected by Balko from the San Diego pools were previously undescribed. K.G. McKenzie, an authority on ostracod systematics at Riverina College, Australia, has described several new species and a new genus from Balko's San Diego collections (Balko and Ebert 1984). These taxa may prove to be endemic to the San Diego vernal pools, but since vernal pool zooplankton populations are so poorly studied, it is not possible to say this with certainty.

Many species of both rotifers (McCollough and Lee 1980) and protozoans (Cox 1982) are rarely collected yet have very broad distributions. Like some of the aquatic plants discussed earlier, small aquatic animals have a remarkable ability to find suitable habitats wherever they occur.

Rotifers. Rotifers are a large and diverse group of small (mostly less than 0.5 mm long) animals. They are overwhelmingly a freshwater group and though they occur in large lakes they are especially adept at finding and flourishing in even the tiniest bodies of water, such as tree holes and small depressions in boulders. Their occurrence in vernal pools is therefore not surprising. Although highly diverse in morphology, many rotifers are symmetrically cigar-, vase-, or spittoon-shaped organisms that have circular rows of cilia at the anterior end. These cilia, beating at high frequency and in sequence about the circumference, create the illusion that there are small wheels rotating, and it is this that gives the animals their name. Most rotifers, and probably most of those listed in Table 9, are omnivorous, ingesting bacteria along with fine detritus, although algae are probably the major food of most species. Some rotifers (Trichocerca) are carnivorous and feed on other rotifers and small metazoans.

As with some cladocerans, males are rare in rotifer populations. In fact, males are unknown for many species. In some of these cases the animals may have gone completely to parthenogenesis, in others it is probable that the males appear for such brief periods that they have not been collected. Those male rotifers that are known are generally smaller than the females, short lived, and because of undeveloped digestive organs and the lack of a mouth or anus, incapable of feeding.

In the order that includes most of the species listed (Ploima) the typical rotifer life history has a dormant stage of cold- and drought-resistant resting eggs. The new generation initiated by the hatching of these eggs is entirely female. These females, in their short 1-2 week lifespan produce eggs that give rise to more females. This continues for a number of generations until an environmental or population change triggers the production of males, copulation, and the formation of the resting eggs (Pennak 1978). According to Pennak (1978), some rotifers can also survive drought by drying down and shrinking into a cystlike form. This would be a valuable adaptation for vernal pool rotifers since it would prevent the untimely disappearance of a pool from wiping out populations in which resting eggs had not been formed.

Trochosphaera solstitialis, a rare species found in temporary ponds in Texas, suggests some of the discoveries that may await detailed study of vernal pool animals. In this species females hatch from resting eggs and give rise to more females by parthenogenetic ovovivipary (hatching of eggs within the body of the parent) early in the season. Later males begin to appear, hatching from eggs within the female's body. These males remain within the female's body and release their sperm to effect internal fertilization. It is believed that this leads to the formation of resting eggs (McCollough and Lee 1980).

The alternation of parthenogenetic and sexual systems of reproduction is a prominent feature of rotifer life histories, and as we have seen, is also present in other zooplankton. While a full evolutionary explanation of the patterns of reproduction is still lacking, it is generally agreed that in organisms that possess both modes of reproduction sexual reproduction generally occurs just before the onset of conditions of the greatest risk or uncertainty (Williams 1972). The variability thus insured may be important to organisms of temporary pools, where the onset of rains and duration of standing water are both unpredictable. A purely asexual species might lose out completely in unusual years, whereas an exclusively sexual species would probably have a lower rate of population expansion in favorable conditions. This would be an especially severe disadvantage for organisms that depend on invasion into new habitats (Jain 1976b).

Fairy shrimp. Most of the zooplanktonic organisms discussed to this point are obviously well suited to life in vernal pools, but are not necessarily specialists for temporary waters. But the division Eubranchiopoda of the Crustacea are largely restricted to temporary pools, and clearly have had a long evolutionary history in such situations. None occur in running waters, and although some species are tolerant of extreme salinities, none are true marine organisms (Pennak 1978). The division is broken into three distinct orders, the Notostraca (tadpole shrimps), the Conchrostraca (clam shrimps), and the Anostraca (fairy shrimps). All three are well represented in temporary waters in California (Alexander 1976). For example, *Triops*, a tadpole shrimp, has been reported as a pest in rice fields where it eats the young rice shoots (Grigarick et al. 1985). Although both clam shrimp and tadpole shrimp probably occur in the coastal vernal pools, neither was detected in the samples in San Diego County, and I will confine discussion to the fairy shrimp, and the single species which seems to be most common, *Branchinecta lindahlii* (Figure 44). Alexander (1976) discusses

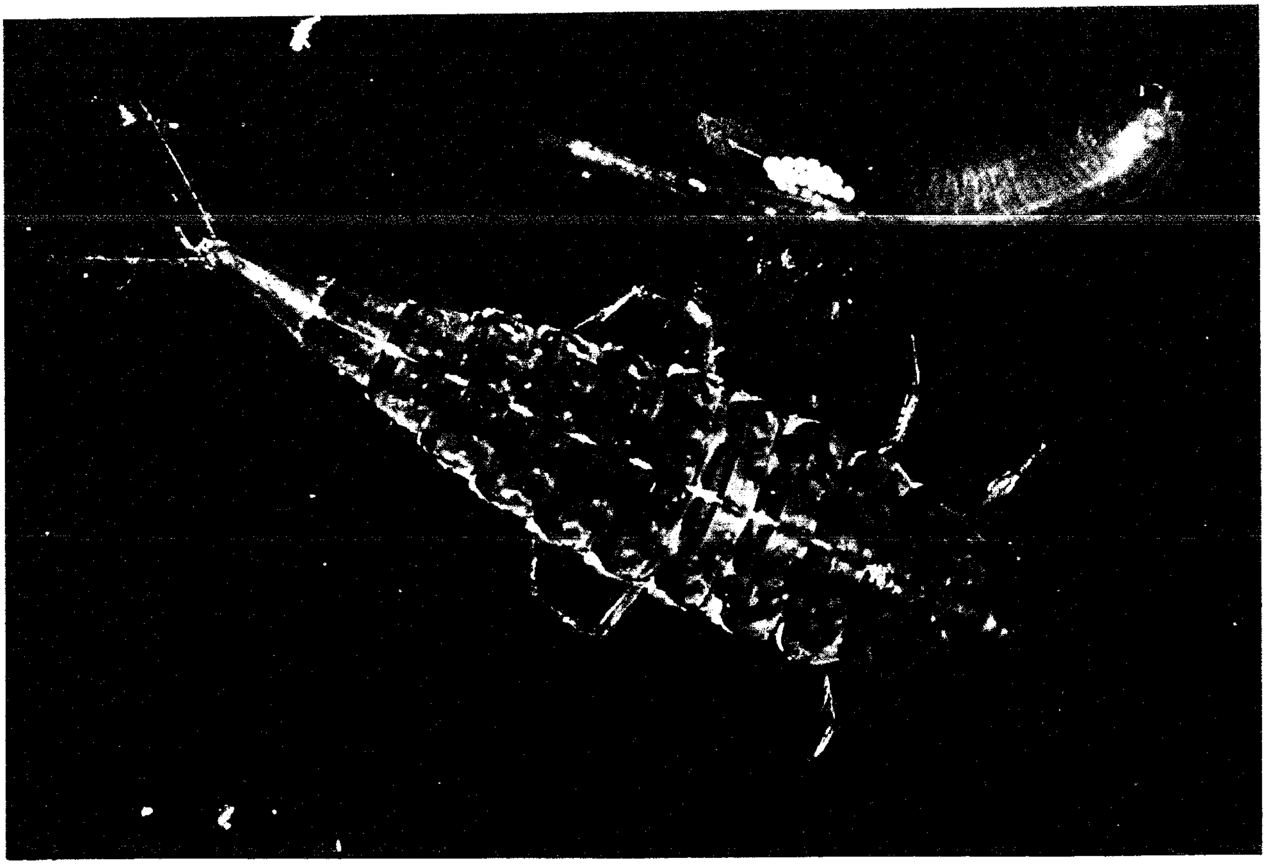

Figure 44. *Brachinecta*, probably *lindahlii* (smaller organism) with egg case, and the carnivorous larvae of a dytiscid water beetle. Photo by Andy Olson, Biology Dep., San Diego State University.

aspects of the ecology of Central Valley species.

Branchinecta lindahlii was collected in about half of the vernal pools surveyed by Balko (Table 9), which in view of their short persistence, may be an underestimate. It emerges from resting eggs, and like other crustaceans, undergoes a series of molts before reaching adult size. It has 20 body segments, 11 of which bear legs. A distinctive behavior, making it almost impossible to confuse it with any other vernal pool animal, is its typical habit of swimming slowly and gracefully on its back by a rhythmic beating of its legs. While in motion it is filtering bacteria, algae, rotifers, protozoans, and fine detritus. Like many other zooplankton, males are often rare in fairy shrimp, and parthenogenetic egg production is common. In Artemia salina, the common brine shrimp, which has a world-wide distribution, the majority of populations in Europe are exclusively parthenogenetic. Interestingly, the few sexual populations are in more or less natural habitats while the parthenogenetic ones occupy artificial habitats such as salt evaporation ponds (Browne and Macdonald 1982). This supports the view that parthenogenesis is an advantage in colonizing new habitats.

Like many other anostracans, B. lindahlii appears to have only a single generation per year, emerging early, producing resting eggs, and then disappearing. Dormant eggs of a related desert species, B. mackini, have been reported to hatch within 24 to 36 hours of being thoroughly wetted (Brown and Carpelan 1971). No doubt, hatching in vernal pools is equally rapid. According to Broch (1965 cited in Donald 1983), some anostracan eggs require high oxygen levels in order for development to proceed to the point where hatching is possible. If this is true for B. lindahlii, the eggs may be prevented from hatching while covered with water and may require exposure in a dry pond to complete development. This may explain the single generation of B. lindahlii in vernal pools. The suppression of hatching of newly produced eggs may have arisen because of high rates of loss of second and subsequent generations to predators. Ample food may be available later in the aquatic phase of a pool but there is also a gradual increase in the numbers and size of predaceous insects such as dragonflies and dytiscid beetles that would probably take a heavy toll of the slow-moving fairy shrimp. Aberrant individuals that hatched before experiencing prolonged drying would emerge into a habitat where they would have a high probability of being eaten before reproduction would be possible.

4.5.2 Insects

Insects are important in both terrestrial and aquatic habitats. There have been no comprehensive surveys of vernal pool insects, but it is safe to assert that their impact on vernal pool functioning is considerable in their roles as herbivores, predators, parasites, and pollinators. In the dry stages of vernal pools the insects are presumably drawn from the surrounding vegetation. But insects often have distinct species or races associated with particular plant species, and it is possible that some of the endemic plants support a unique insect fauna.

Aquatic insects. Although the information on aquatic insects specific to vernal pools is scanty, there is little doubt that they are of major importance in structuring the ecosystem of the aquatic phase as grazers and especially as predators. They in turn are preyed upon by birds, mammals, and amphibians.

Information on vernal pool insects is sparse, but Dehoney and LaVigne (1984) collected aquatic insects from pools on Otay Mesa, and David Faulkner of the San Diego Natural History Museum has compiled a list of vernal pool species from the Museum's collection. These two sources of information have been combined (Table 10) to give a minimal list of aquatic insects for at least one area of pools. The total list for all pools would certainly be many times longer.

All of the insects of Table 10 disperse by flight, and because of this, it is not possible to know to what extent their populations are permanent in the vernal pools. Wiggins et al. (1980) found that in temporary waters in eastern North America some insects go through their entire life cycles in the pools, aestivating as larvae or eggs. Others disperse to temporary pools where they lay eggs and in some cases also feed. Any adults of these species that emerge from the pools disperse before the pools dry, seeking summer and winter habitats in more permanent bodies of water. Such species are opportunists, using the pools when they are available and abandoning them when they become unsuitable. Since they lack the behavior and physiology which would allow them to aestivate in a dry habitat, they cannot depend exclusively on vernal pools. Most of the insects of California vernal pools probably are of this type.

Table 10. Aquatic insects collected from or known to be associated with vernal pools based on specimens at the San Diego Natural History Museum or the 1984 published list of Dehoney and LaVigne (single asterisk). Species or other taxa based on both sources are indicated by double asterisks.

Order Odonata (dragonflies)
Family Aeshnidae
Anax junius (green darner)

Order Coleoptera (beetles)
Family Dytiscidae
**_Agabus_ sp. (predaceous water beetle)
Copelatus chevrolati
*_Deronectes striatellus_ (Lec.)
Family Haliplidae
*_Peltodytes_ sp. (crawling water beetles)
Family Hydrophilidae
*_Berosus punctatissimus_ (water scavenger beetle)
Tropisternus lateralis

Order Diptera
Family Anthomyiidae
Family Chironomidae
Family Culicidae
Chaoborus
*_Culiseta_ sp. (mosquitoes)
*_Culex sp._ (mosquitoes)
Family Tipulidae
**_Tipula_ sp. (crane flies)

Order Ephemeroptera
Family Baetidae
Callibatus sp. (small mayfly)

Order Hemiptera
Family Belostomatidae
*_Abedus indentatus_ (Hald.) (giant water bug)
Family Corixidae
*_Trichocorixa_ sp. (water boatman)
Sigara sp.
Family Gerridae
*_Gerris_ sp. (water striders)
Family Notonectidae
*_Notonecta_ sp. (back swimmers)

Dragonfly nymphs (Order: Odonata) are among the largest insects to be found in vernal pools. Mature dragonflies are aerial predators feeding on flying insects, while the nymphal stages are aquatic and prey on aquatic insects, small crustaceans, and other small animals. Dragonfly nymphs are known for their voraciousness, and no doubt they exert a significant influence in the ponds where they occur. Crump (1981) included them as predators on tropical *Hyla* of temporary pools, and they probably take *H. regilla* in vernal pools.

Because of the relatively long period that dragonflies nymphs require to mature, there is some question as to how many actually manage to survive to the adult stage in vernal pools. Corbet (1983) gave times to maturity for a number of species which suggest that in warm water (ca. 29 degrees C) the time from hatching to emergence may be as short as 40-60 days. Larger vernal pools have durations this long in most years, but water temperatures would be considerably below the optimum for much of this time. Unless dragonflies found in vernal pools have an unusually rapid development, it may be doubted if many nymphs survive to maturity. The single species for which there is definite identification (Dehoney and LaVigne 1984) is cosmopolitan and unlikely to have a specialized local race. The nymphs observed in vernal pools may largely be the offspring of dragonflies that emerged from larger, more permanent bodies of water. Dragonflies are able to fly considerable distances from water (it is not unusual to see them in creosote-bush desert miles from the nearest water) so that the dragonflies that lay eggs in the pools may come from other freshwater habitats.

The hemipterans, or true bugs (Order: Hemiptera) include a considerable number of species adapted to life in or on water. At least two groups commonly occur in vernal pools. The notonectids, or back swimmers, are often abundant and easily identified by their habit of swimming on their back, moving through the water by means of powerful "oarlike strokes" (Pennak 1978). Though they feed entirely in water, with the proper stimulus they will readily fly in search of new habitat. Although aquatic, they breathe air, rising to the surface to capture a bubble with special rows of hairs. When the oxygen is exhausted, they are forced to return to the surface. They are carnivorous, feeding on zooplankton when in the nymphal stages, and on insects and tadpoles (Crump 1981) when larger. Very probably they also prey upon fairy shrimp when these are present.

The corixids, or water boatmen, are similar to the notonectids but do not swim on their backs. They breathe air, but are able to stay submerged for long periods in well oxygenated water (Pennak 1978). They feed on detritus, very small animals such as Protozoans, and algae. Like the back-swimmers, water boatmen are strong fliers and are able to disperse considerable distances to locate suitable pools. Their presence in vernal pools may not mean that large numbers of adults emerge from the pools, though in at least the larger, longer-duration pools this is undoubtedly the case.

Predaceous diving beetles (Family: Dytiscidae) are common in many kinds of aquatic habitats and are also characteristic of vernal pools, probably occurring in most that have reasonably long duration (Figures 44, 45). They are black beetles about 1 cm long and with an oval body outline. Like the notonectids, the adults are air breathers that entrap air bubbles, but store the bubble in a chamber that

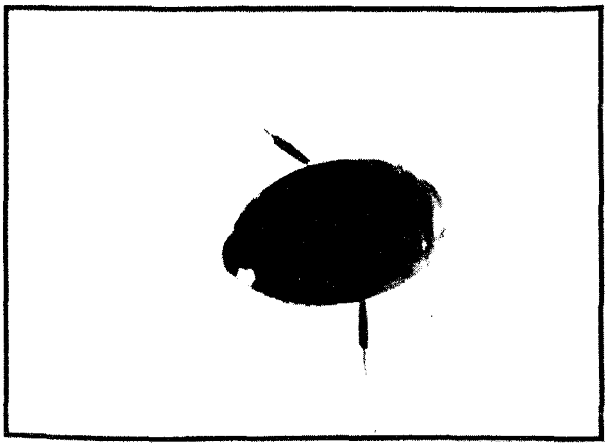

Figure 45. A predacious diving beetle at the surface of the water.

lies below the wing covers (elytra), though a small bubble can usually be seen protruding from the posterior. The larvae, however, are completely aquatic, crawling about the vegetation and pool bottom in search of prey. Both the larvae and adults of the family are predators, and along with the dragonfly nymphs and notonectids they constitute the top of the food chain in the aquatic phase of the vernal pool. The adults are strong fliers that can move many miles from water and are often attracted to lights (Pennak 1978). As with the dragonflies and notonectids it is not clear to what extent the immature are the offspring of adults that matured in more permanent waters and dispersed to the vernal pools to lay eggs, as opposed to being the descendants of resident populations.

The order Diptera is vast and includes mosquitoes, crane flies, and midges, all groups with many aquatic species. Representatives of these groups are certainly at least accidental in vernal pools. Definite records are known for crane flies and mosquitoes (Table 10).

That dipterans are capable of adaptation to temporary pools is shown by the the Australian chironomid Polypedelium vanderplankii. This midge lives in rock pools, and the larvae are capable of recovering from complete dehydration. While dehydrated, the larvae have been shown to withstand immersion in liquid helium and heat over 100 degrees C (Hinton 1960, cited in Bayly and Williams 1973). Perhaps species with similar life histories exist in California vernal pools.

Terrestrial insects. There can be no doubt that nonaquatic insects also play a role in vernal pools as plant herbivores and parasites, as pollinators, and in their interactions with other insects and animals. Their role as pollinators has been studied by Thorp (1976). He observed pollinators of Blennosperma, Lasthenia, Limnanthes, and Downingia in vernal pools of Solana County. Thorp found that host-specific (oligolectic) native bees of the Adrenidae family were particulary important as pollinators, though he also observed visits by generalists -- other native bees, syrphid flies, bee flies, and beetles. Thorp's observations raise interesting questions about the potential importance of pollinators in the maintenance of populations of vernal pool plants, especially the rare endemics. Of greatest concern is the possibility that a rare plant like Pogogyne abramsii depends on a pollinator that in turn depends on some environmental feature that lies outside the immediate vicinity of vernal pools. For example, a bee may nest preferentially on sunny south-facing slopes. In such a case, preservation of vernal pool plants may require preservation of non-pool habitat essential to plant pollinators. It is by no means certain, however, that the plants require specific pollinators to set seed.

Preliminary studies by Jim Mills (Department of Biology, San Diego State University, Calif.; unpubl. rep.) on pollination of Pogogyne abramsii at four sites in San Diego County have shown that the introduced honeybee Apis mellifera is now the most important pollinator of this species. There was also a large suite of native pollinators of which two species of anthophorid bees were most frequent and halictid bees, megachilid bees, and syrphid flies common. At one site there were a large number of visits by bombyliid flies, but Mills has evidence that these are ineffective pollinators that may be more of a drain than a benefit to Pogogyne.

Competition for pollinator visits among plants, which has been well documented in some situations (Rathcke 1983), could perhaps also cause a decline in seed set of native species in certain circumstances. If a vernal pool preserve were very small and if there were near to it large plantings of abundant nectar-producing plants that flowered at the same time as native species, the pollinator populations might be drawn from the relatively scant native populations to the denser more productive artificial plantings. However, one would not expect competition to absolutely prevent pollination, nor would its effect be very strong if preserves were large or far from large plantings.

Terrestrial insects may also be very important in their role as herbivores, feeding on the higher plants of the pools. It would be interesting to know if the insect faunas associated with the rare and restricted plants of the vernal pools, such as Eryngium and Pogogyne, are equally unusual.

4.5.3 Other Invertebrates

In addition to the groups discussed above, we may be certain that there are many other species of invertebrates associated with vernal pools even though there is little published about them. In and around vernal pools, the following groups are certainly present: nematodes (hair worms or round worms), annelid worms (at least in the terrestrial areas), spiders, and mites (Scott 1971). Other groups such as sponges and isopods may also be present. No doubt, careful study would reveal that these groups and others not listed play a significant role in vernal pool landscapes.

Mollusks. Though snails are not usually thought of as organisms of arid regions, many species occur there. Survival in vernal pools, despite the prolonged dry season, is therefore well within the range of adaptability of the group. I have collected the genus Lymnaea in San Diego County vernal pools, and Taylor (1981) reported that another genus, Bachylymnaea, is very desiccation tolerant and may be present in vernal pools north of Santa Barbara.

The genus Lymnaea is widespread in many aquatic habitats. The vernal pool species are small, less than 1 cm long, and light to dark brown. Like other snails they feed by scraping the surface of plants and the substrate. When the pools dry the snails seal their shells with a mucilaginous substance that protects them from desiccation. On Kearny Mesa snails seem to oversummer beneath cobbles in the pool bottoms.

Taylor (1981) indicated that two species of clams in the family Sphaeridae (Musculium raymondi and Pisidium casertanum) are reported from seasonally dry wetlands, and this may include some vernal pools. In eastern North America there are clams that occur in temporary pools and appear to possess a high degree of adaptation to this environment (McKee and Mackie 1981).

A flatworm--Bothromosostoma. Flatworms are widely distributed in nature, both as parasites and free-living forms. The free-living flatworms are usually well hidden beneath rocks or debris. Bothromesostoma, a genus of Rhabdocoel flatworms, is an interesting exception to this generality, since species in this group are conspicuous on the surface of vernal pools (Figure 26). According to W. Hazen (SDSU Biology Department; pers. comm.) there are two species in vernal pools, B. personatum and B. americanum. Other species are found in woodland pools of the eastern United States, and there are species widely distributed elsewhere in the world.

Bothromesostoma individuals appear to be floating, but they are actually moving in the surface film of water. This makes them, in the terminology applied to small aquatic organisms, hyponeustonic. They are incapable of swimming, but they are occasionally found on plants or the pool bottom (W. Hazen, pers. comm.) Like fish and many other aquatic animals, they are counter-colored (light on the bottom, darker on the top) to reduce their visibility from above and below. The cryptic system breaks down in disturbed pools made cloudy with suspended clay, when Bothromesostoma are very obvious against the light background (Figure 26). This may not be too serious, however, since flatworms generally are not highly favored prey items, probably because of the presence of chemical defenses. Bothromesostoma are strictly carnivorous and seem to feed on insects and other small creatures that get trapped on the water surface. In small aquatic habitats which would naturally have a large shore-to-water surface ratio, this input of terrestrial insects may be quite significant and represent a major source of high-protein detritus. Sometimes small groups of Bothromesostoma will encircle a single insect like hyaenas gorging on a water buffalo.

The life cycle of Bothromesostoma is similar to that of other vernal pool animals. They survive the dry season as eggs that are stimulated to hatch when the pools fill. The individuals are hermaphroditic with well-developed copulatory organ systems, so it is reasonable to suppose that egg production is strictly sexual. In any case, two kinds of eggs are produced. One type develops immediately and hatches within the oviduct (ovovivipary). It is probably only later in the season that the dormant "dauereier" (resting eggs) are produced. These over-summer and provide the start of the next winter's population.

4.6 VERTEBRATES

There are no vertebrate species restricted to vernal pools. But there are vertebrates that are characteristic of vernal pools and important in vernal pool ecosystems.

4.6.1 Amphibians--Frogs, Toads, and Salamanders

Frogs and toads are by far the most obvious and typical vernal pool vertebrates. Two species are predominant: Hyla regilla, the Pacific tree frog; and Scaphiopus hammondi, the western spadefoot toad. Both of these are small anurans that have developed the behavior necessary to cope with a long dry season.

The Pacific tree frog is the more common of the two species. It probably occurs in every area of vernal pools, and in a majority of the larger pools within a given set. The species is widespread in the Far West from British Columbia to Baja California, Mexico, and east to Idaho and Nevada (Stebbins 1966). Despite its name, it is primarily to be found in grass and low vegetation and is associated with all sorts of bodies of water, natural and artificial. Adults are about 1.5 to 5 cm long, with a distinctive black eye stripe (Figure 46). Two color morphs are known, a more or less uniform bright green and a mottled brown, with considerable variation in details of the pattern. Although the two-color morphs are genetically determined, both have the ability to lighten or darken within minutes to adjust to their background (Stebbins 1966).

The Pacific tree frog, in common with other members of its family (Hylidae), is a chorus frog, and its communal "kreck-ek" is one of the characteristic sounds of southern California evenings near vernal pools. The choruses are made up of males that move to water and call to attract females. In the competition among males for females the "first-callers" and "solo-callers" have the highest probability of successful mating (Moore 1979). After mating takes place, the eggs are laid in gelatinous masses in the pool (Figure 47). It is thought that the female leaves the vicinity of the pool after egg laying (Jameson 1956). After hatching, the tadpoles feed on algae and detritus (Figure 48). When they grow legs and

Figure 46. The Pacific tree frog *(Hyla regilla)*. Photo by Ellen Bauder.

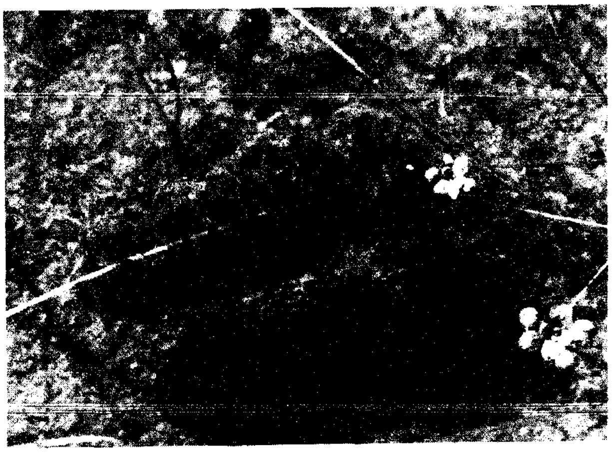

Figure 47. Egg mass of the Pacific tree frog.

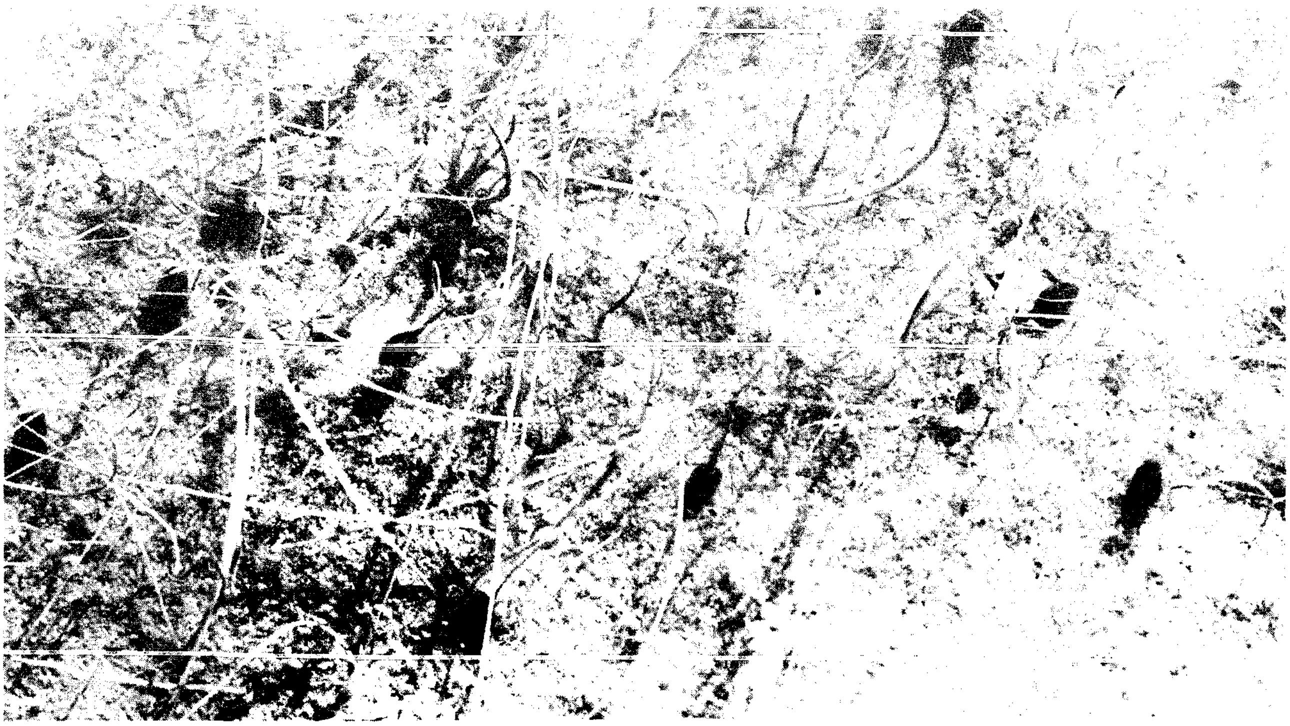

Figure 48. Pacific tree frog tadpoles on the bottom of a vernal pool with *Callitriche longipedunculata* and *Lilaea scilloides*. The tadpoles have stirred up the bottom sediments.

are able to move on the land, they disperse away from the pool, some apparently for hundreds of meters, and with the onset of the summer drought aestivate in old logs, meadow mouse burrows, crevices between rocks, and other similar places that will protect them against heat and dryness (Brattstrom and Warren 1955). The adults feed above water, eating beetles, midges, flies, leaf hoppers, and other insects (Brattstrom and Warren 1955).

The Pacific tree frog has a remarkable homing ability. Jameson (1956, 1957) conducted experiments in Oregon in which he removed males from ponds, marked them, and placed them in other ponds at some distance. He found that the transplanted frogs quickly left the new ponds to return to their former habitat. In one experiment he moved 83 frogs 300 yd, and, in another, 414 frogs 1000 yd. In the first case 56 frogs were recovered, 43 from the original pond. In the second case, after 1 month, none was present in the transplant pond, and five had managed to make their way back to the original pond.

Tadpoles of the Pacific tree frog can reach very high densities, 50 or 100 per square meter of pool bottom being common. Since they are relatively large and quite active, they must have a substantial impact on the limnology of the pools, probably primarily by turning over the surface algal-detrital layer of the pool bottom both by ingesting material and by the physical disturbance of their swimming. Both tadpoles and adults are important items in the diet of some of the vertebrates of vernal pool landscapes.

The spadefoot toad, <u>Scaphiopus hammondi</u>, belongs to a widely distributed group. A mature western spadefoot toad is 3-6 cm long, mottled green, grey, and olive with orange spots. Their name comes from a small black appendage on the hind legs which is used in digging (Stebbins 1966) (Figure 49). Their life history is similar to the Pacific tree frog. Adults become active with winter rains and the males call from pools with a voice "resembling the sound made by stroking the teeth of a pocket comb" (Stebbins 1966). Eggs are laid in gelatinous masses. Food

Figure 49. Spade-foot toad *(Scaphiopus hammondi)*. The toads may over-summer in cracks in the heavy clay soils. Photo by Ellen Bauder.

habits are probably similar to those of the Pacific tree frog, with the tadpoles feeding on algae and organic detritus. Tadpoles are able to metamorphose into adults in as little as a month, this rapid development being an excellent adaptation to life in vernal pools (Stebbins 1966).

The Pacific coast populations of S. hammondi are disjunct by several hundred kilometers from the most closely related populations to the east which were formerly included in the same species. Reproduction in the California S. hammondi is keyed to winter rains, whereas the more eastern Scaphiopus typically breed in response to summer storms. Brown (1976) reported that the range of temperature tolerance for embryonic development is significantly lower in the California populations, suggesting that there has been selection in the Mediterranean environment for cool-season development.

The ability of spadefoot toads to dig is an important aspect of their adaptation to a dry climate. Related populations in Arizona survive dry periods by excavating burrows as deep as 90 cm. While in the burrows they are protected from extremes of temperature and maintain body water by absorbing water from the soil (Ruibal et al. 1969). These observations were made in sandy soils, where digging would be relatively easy. It is difficult to imagine that the toads could burrow to great depth in the rocky clay-rich soils of the coastal mesas, but perhaps they seek out special microhabitats where this is possible. I have seen newly metamorphosed spadefoot toads in the deep cracks that form at the surface on Kearny Mesa. By moving down such cracks and excavating a short distance deeper they may be able to find sufficient protection without the need to burrow through half a meter of dense clay.

Arnold and Wassersug (1978) studied the predation of garter snakes (Thamnophis elegans and T. sirtalis) on anurans including Hyla regilla in Lassen County, California. By examining stomach contents, they established that garter snakes mainly preyed upon newly metamorphosed anurans, and only rarely on tadpoles, even though the snakes foraged in the water as well as on land. They argue that the newly metamorphosed animals are less able to evade the garter snakes than either tadpoles or the older postmetamorphic forms. They reason that the vulnerability of the metamorphosing anurans may account for the aggregations observed in some genera, including spadefoot toads. They believe that the aggregations may represent "selfish herds" formed because individuals have a better chance of surviving when they are in a group.

Some salamanders have an aquatic stage in their life cycle while others do not, and both kinds are found within the range of the coastal vernal pools. Of the pool and pond breeders, the tiger salamander (Ambystoma tigrinum) is reported from large rain pools and therefore occurs in some vernal pools in Santa Cruz County (Luckenbach 1973). They are large (8-16 cm) salamanders with a striking black background color with cream or yellow blotches. Adults spend most of their time underground and are active on the surface only after heavy rains, when they move about to locate breeding sites. Kaplan (1984) proposed that random variability in egg size in salamanders may be an adaptation to the high variability in temporary pool and stream habitats.

4.6.2. Reptiles

No reptiles are thought to be limited to or particularly characteristic of vernal pools or vernal pool landscapes. The usual assemblage of grassland, woodland, and chaparral species is present, and many of these must at least occasionally utilize the resources of vernal pools. The case of garter snake predation on tadpoles is discussed above. On the anecdotal level there is the feeling among workers in San Diego County that snakes of all kinds, including rattlesnakes, are unusually abundant around vernal pools. Possibly this is because of the extra food provided by the amphibians, since many snakes will prey on them when available.

4.6.3 Birds

As for reptiles, there are no birds that are restricted to vernal pool habitats. However, the impact of birds on pools is probably substantial in both the aquatic and terrestrial stages. While filled, vernal pools are visited by a variety of species that forage in the water and along the pool margins, probably eating insects, tadpoles, and perhaps aquatic plants. Some of the species that are believed to occur commonly in the San Diego pools are listed in Table 11. The ducks and coots would obviously be most frequent in the larger and deeper vernal pools. Mallards have become resident in an artificially enlarged pool that persists into the summer on Kearny Mesa. The other species are common in the region and must occasionally stop to feed when pools are filled. One of the commonest species that forages along pool margins is the killdeer, whose piercing cry lends a note of wildness even in areas surrounded by highways and buildings. Quail are also often seen.

As discussed in this chapter, birds are probably a major means by which propagules too large to move by wind are carried long distances. In the case of small isolated habitats like vernal pools the transfer can be even more effective if the birds, on leaving a patch of habitat, fly in search of similar habitat, thus maximizing the probability that any propagules being transferred will establish. While it is difficult to estimate actual rates of transfer, the widespread occurrence in isolated habitats of species with propagules too large to disperse far with wind is indirect evidence of bird dispersal. If it is true that birds effect a continual stream of cross introductions among pools, they would be a significant influence on both genetic and species diversity.

In accordance with the basic tenet of quantitative island biogeography, a higher rate of dispersal of species among pools would, on the assumption that extinctions for at least some species are frequent, lead to a greater average number of species per pool. For populations that persist for long periods, frequent introductions would reduce genetic divergence between vernal pools. Changes in bird abundance, species, local movements, and migration patterns might therefore have profound long term effects on vernal pool biotas.

4.6.4 Mammals

No mammals are restricted to vernal pools, but many mammals are evident in vernal pool areas, especially those that are grassland dominated. One study specific to vernal pools was conducted by Winfield et al. (1984) on Otay Mesa in southern San Diego County. They established a 15-m grid of 152 small-mammal live traps centered on a large (0.91 ha) vernal pool, trapping in 5-day blocks six times in 1980 from March, when the pool was full, to October. Outside the pool the area included open coastal sage scrub and chaparral vegetation. Small mammals live-trapped included:

Audubon cottontail
San Diego pocket mouse
Pacific kangaroo rat
Deer mouse
Western harvest mouse
Dusky-footed wood rat
California meadow mouse

Common names follow Burt and Grossenheider (1964).

Despite the fact that over half of the traps were in the coastal sage scrub, they made few captures there, most of the animals being recovered from the chaparral or the vernal pool basin. Of the species captured, only the western harvest mouse seemed to show a preference for the vernal pool habitat, and then only in the later

Table 11. Partial list of birds known or expected to feed in or be common in the vicinity of vernal pools. A complete list of birds found near vernal pools would probably be a majority of the species of non-marine birds of coastal California. The San Diego County list was provided by J. Zimmer (Department of Biology, SDSU) with additions by G. Cox and P. Garrett (Department of Biology, SDSU) and the personal observations of the author. Robert Holland provided the list of birds seen in other vernal pool areas. Names follow *A Field Guide to the Western Birds* (Peterson 1961).

San Diego County	Other vernal pool areas
Ducks or shore birds:	
American coot	Avocets
Bufflehead	Black-bellied plover
Cinnamon teal	Black-necked stilt
Common snipe	California gull
Greater yellowlegs	Canada goose
Green-winged teal	Common egret
Killdeer	Great blue heron
Long-billed dowitcher	Green heron
Mallard	Lesser yellowlegs
Ruddy duck	Peeps (a variety)
Shoveler	Pied-billed grebe
Spotted sandpiper	Pintail
	Ross' gull
	Sandhill crane
	Whistling swan
	Willet
	Wood duck
Species of grassland, marsh or open areas:	
California quail	Bank swallow
Grasshopper sparrow	Barn swallow
Horned lark	Black phoebe
Lark sparrow	Rough-winged swallow
Mourning dove	Water pipet
Red-winged blackbird	
Western meadowlark	
Species of brushlands:	
Bewick's wren	
Brown towhee	
Bushtit	
California thrasher	
Roadrunner	
Sage sparrow	
Scrub jay	
Wrentit	

spring and summer months. Winfield et al. speculated that the harvest mouse may have been attracted to the vernal pool because of higher populations of insects, on which it is known to feed.

The conclusion of the Winfield et al. (1984) study is that vernal pools are not heavily utilized by small mammals. This is surprising, considering that vernal pools often have green herbage later in the season and contain at least some succulent plants. Rabbit droppings are certainly a conspicuous feature of many vernal pools, suggesting rather heavier use than that reported by Winfield et al. (Figure 50). As they point out, more work is needed before firm conclusions are possible.

The trapping techniques used by Winfield et al. would not, of course, have captured the larger mammals, nor the burrowing species not attracted to an above ground trap. Some of these species, which may also impinge on vernal pools are listed in Table 12.

If the hypothesis of Dalquest and Sheffer (1942) is correct, the pocket gopher must be ranked as the most important mammal in the vernal pool ecosystem. As explained in Chapter 2, this hypothesis holds that Mima mound topography is the long-term result of the tunnelling behavior of pocket gophers. In view of its potential importance, the natural history of pocket gophers merits some discussion.

Valley pocket gophers (<u>Thomomys bottae</u>) are small rodents 16 to 29 cm in total length with tiny ears, a short tail, large exposed incisor teeth, and external fur-lined cheek pouches (Ingles 1965). They spend nearly their entire lives below ground, and are rarely seen on the surface. They dig tunnels through the soil, feeding on the roots, bulbs, and rhizomes

Figure 50. Small mammal use of vernal pools. Note rabbit droppings. Rabbit grazing may be an important influence on pools. The most obvious plant is *Psilocarphus brevissimus*. A dried algal crust is evident just above and to the left of the droppings.

Table 12. Partial list of other mammals common in the vicinity of vernal pools and which might be expected to exploit plants and animals found in vernal pool basins. An even wider range of animals might use vernal pools as watering holes. Names according to Burt and Grossenheider (1964). Possible organisms fed upon are based on Burt and Grossenheider (1964) and Ingles (1965).

Species	Possible food items
Opossum (introduced to California)	Insects, tadpoles
Raccoon	Small animals
Striped skunk, spotted skunk	Insects?
Badger (probably locally extinct in many places)	Pocket gophers
California ground squirrel	Bulbs, seeds
Valley pocket gopher	Roots, bulbs, herbage
Black-tailed jackrabbit	Herbage
Audubon cottontail	Herbage
Brush rabbit	Herbage
Elk ? (extinct in region of coastal vernal pools)	Shrubs, herbage
Mule deer	Shrubs, herbage
Pronghorn ? (extinct in region of coastal vernal pools but formerly abundant)	Shrubs, herbage
Grey fox	Insects, rodents, other small animals
Coyote	Similar to fox

they encounter. They will also pull green plants down into their burrows. Food is sometimes stored in special chambers within the tunnel complex (G. Cox, pers. comm.) Males are territorial, an important element in the theory of mound formation by gophers, since it explains why mounds should be evenly spaced.

The tunnel system consists of a nesting chamber from which foraging tunnels radiate outward. The gophers clear the tunnel system from time to time by pushing small mounds of soil to the surface, similar to molehills except that gopher mounds are thrown up by the gopher by pushing the dirt from an opening to the surface (Figure 51). After the clearing operation is completed, a plug is placed in the tunnel opening, presumably to discourage predators (Ingles 1965).

Like other rodents, pocket gophers have a potentially high rate of population growth. Litter size is usually five or six, and there may be multiple litters per year. If pocket gophers are similar to some other territorial rodents, they may be especially vulnerable to predation as young adults, when they are most likely to be dispersing in search of unoccupied habitat.

Figure 51. A soil heap pushed to the surface by a pocket gopher. The entrance to the tunnel is always carefully closed unless the animal is actively working.

CHAPTER 5. VERNAL POOLS AS ECOSYSTEMS

5.1 ECOSYSTEM FUNCTION

An ecosystem is a piece of the biosphere delimited for study. To predict how an ecosystem will change, it is necessary to understand not only its internal interactions and functioning, but also to consider the external influences acting on it. Therefore, although the vernal pool ecosystem can be said to end at or slightly above the high-water mark of a basin, it is necessary to look beyond these boundaries to the larger system of which the pool is a part.

Many of the organisms important in vernal pools are wide ranging, and interactions among pools and between pools and the surrounding vegetation can be significant (Figure 52). For example, dragonflies may disperse from nearby permanent water; some plant and animal species may regularly disappear from a pool and be reintroduced from nearby pools where their populations are more permanent. Pools isolated by roads or housing developments may lack pollinators essential to seed production of some species. The landscapes in which pools are found also are

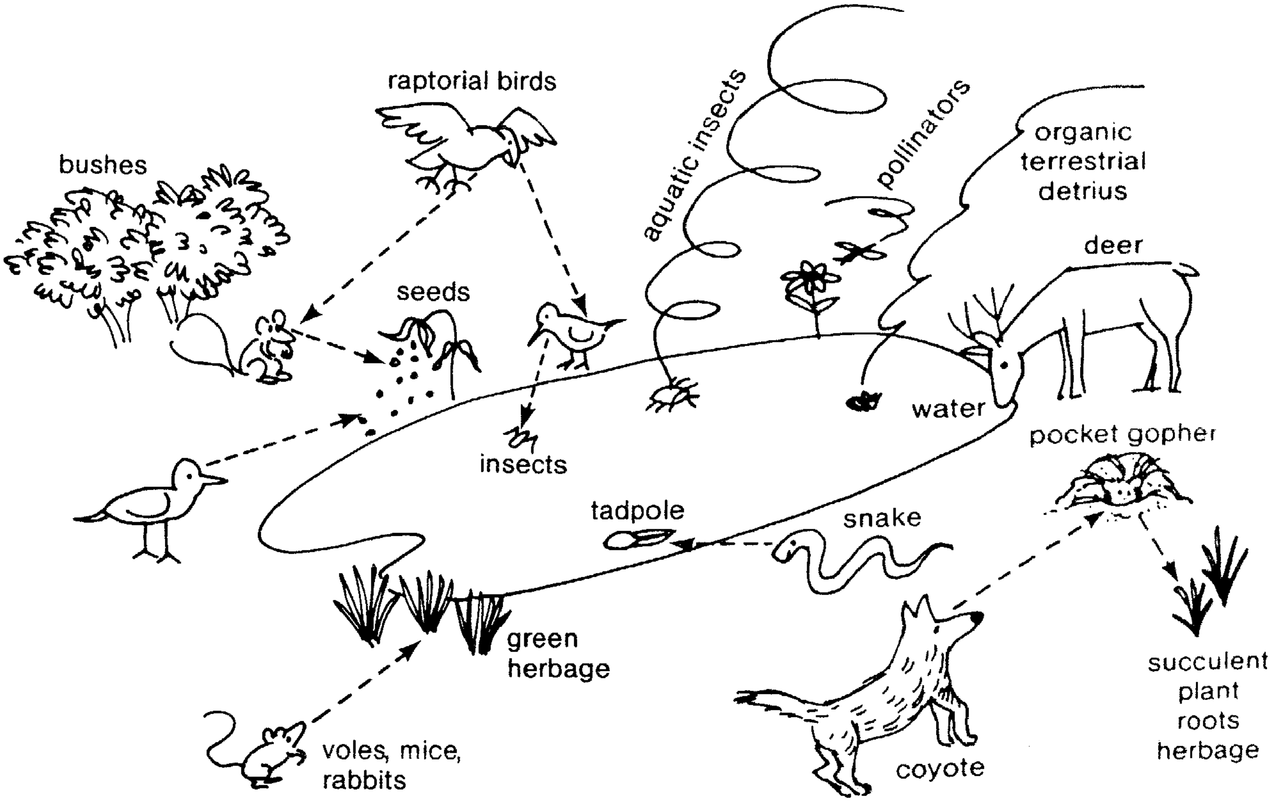

Figure 52. Some of the interactions between a vernal pool and its terrestrial surroundings.

changed by the presence of the pools. Vernal pools are not merely isolated ecosystems but elements in complex systems that include humans.

5.1.1 The Vernal Pool in Its Terrestrial Context

In an arid region, the presence of standing water for even a brief period represents a dramatic change in resources available to animal populations. For some birds and larger mammals the location of water is a major determinant of the patterns of movement. An increase in the supply of surface water means an increase in the freedom and range of movement. Vernal pool areas should support more mammals and birds than comparable areas without vernal pools.

Because of the brief periods of high productivity of the aquatic and amphibious plants and animals, the vernal pools probably also are a significant source of forage and prey. The dense aggregations of frog and toad tadpoles must be important in the diet of a wide variety of animals such as snakes and small mammals which in turn provide prey for larger, more widely ranging predators like coyotes and raptorial birds. After amphibians mature, they disperse away from the pools, feeding on insects and other small animals in other vegetation areas, providing food for predators at some distance from the pools.

There are few studies of vertebrate or nonaquatic invertebrate utilization of vernal pools. A study of mammal use of a vernal pool (Winfield et al. 1984) was discussed in Chapter 4. Some idea of the importance of pools to birds may be gleaned from a study by Browning (1959) of the food habits of the mourning dove (*Zenaidura macroura*), one of the most abundant species in coastal California and an important game species. Browning's study site was about 15 km east of Sacramento and consisted mostly of annual grassland and abandoned orchard, with a small area of vernal pools. Despite the fact that vernal pools were not the most abundant habitat, at least 8 out of 74 plant species taken by the doves were from vernal pools. Included among the 8 was *Plagiobothrys* (*Allocarya*) *stipitata*, whose seeds were among the 11 most important food items for the doves. Equally detailed study of other species of animals would probably reveal that vernal pools represent a significant source of energy to many other bird, small mammal, and reptile populations.

Fire is common in California shrublands and grasslands, and vernal pool landscapes have certainly burned repeatedly over the past thousands of years. The effect of fire on vernal pools has never been carefully studied. But Collins and Uno (1983) reported significant fire effects on the vegetation of buffalo-wallow pools in Oklahoma, and it is reasonable to suppose that fire has influenced California pools as well. Many pools have enough dead vegetation to carry a fire, and for these the effects of fire may be direct. For example, the large pools on the Santa Rosa Plateau have areas of dense *Eleocharis* that could easily carry fire. Pools that did burn could lose much of the previous year's seed production of genera like *Pogogyne* and *Eryngium* that retain seeds on the dried plant. If loss of seed crop were coupled with a dry year, a population crash, though probably not local extinction, could result.

For all pools there would be indirect effects of fire, chiefly the fertilizing effect of ash. After a fire, ash moves readily by wind and water and generally accumulates in depressions. Plant ash is high in potassium and calcium salts and is strongly alkaline. Phosphorus may be present in small amounts if the fire is of low intensity, though nitrogen is almost completely volatilized. The addition of ash to pool basins should raise the pH and increase the supply of available phosphorous. In pools such as those on Kearny Mesa that tend to be acidic, the ash may thus stimulate nitrogen fixation and nitrogen cycling. Increased runoff may also bring nutrients to the basins along with soil and plant litter.

In vernal-pool landscapes in which shrubs are dominant, such as Kearny Mesa in San Diego County and Burton Mesa in changed by the presence of the pools. Vernal pools are not merely isolated ecosystems but elements in complex systems that include humans.

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Santa Barbara County, the removal of brush cover by fire may have several indirect effects. The water use by the shrub canopies may fall significantly, and this plus the increased runoff from reduced crown interception and litter cover may mean that vernal pools in a burned area receive more water and hold it longer after a burn than before. Because plant cover is likely to be greater in the pools than the surrounding vegetation, herbivory may be more intense in the pools in the first year or two after the fire. A smaller scale effect, but one that might have an even greater impact on small pools, might result from the elimination of shading. In the dry winter of 1983-84 in San Diego Ellen Bauder noted that the vegetation of the south side of pools surrounded by heavy brush stayed green longer and was less affected by drought than that on the north side, presumably because it benefitted from the shade provided by shrubs. If this effect is general, removal of protective canopies might cause at least temporary reshuffling of species.

Some of these expected fire effects were noted on Burton Mesa in Santa Barbara County, where pools in an area of dense coastal chaparral burned in a fairly intense controlled fire in 1983. Though no measurements were made, the pool basins seemed to be particularly lush in the winter following the burn, indicating both minimal harm from the fire and a fertilizer effect. Since the soils of this mesa are predominantly nutrient-deficient Pleistocene sands, the effect of nutrient addition may have been particularly pronounced.

5.1.2 The Vernal Pool as an Aquatic System

While pool basins are filled with water, they function as miniature lake ecosystems. A vernal pool may exist for only a brief time, but the structure of community it supports is still very complex (Figure 53). In fact, the number of species and their population densities, on a per-unit-volume basis, probably greatly exceed those of most lakes.

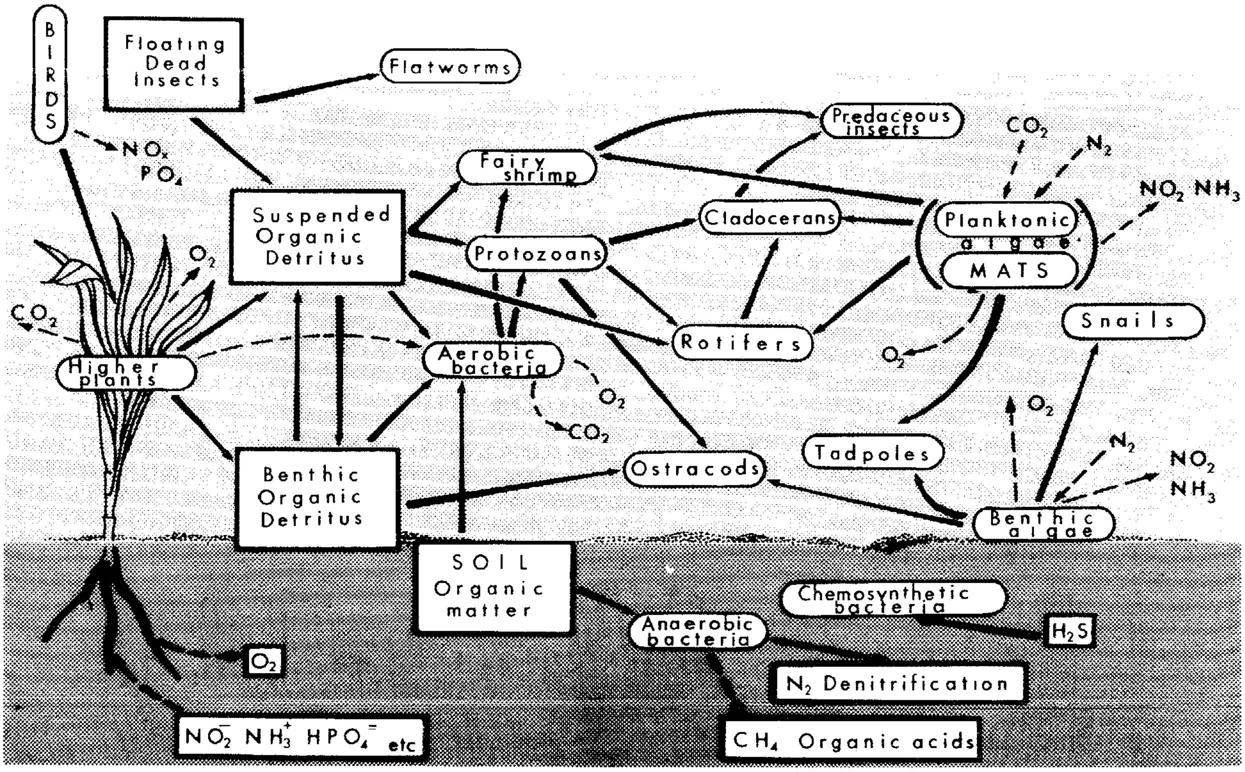

Figure 53. A simplified aquatic food web for a vernal pool in the late aquatic stage.

The richness of aquatic life in a vernal pool may be attributed to three primary causes: the favorable temperatures, low to moderate salinity and alkalinity, and the large amounts of energy available to the pool ecosystem. Just how large these amounts are cannot be specified, because there have been no studies of vernal pool primary productivity or energy flow. But it is possible to outline the major pathways or energy and material transfers, and speculate how important each of these might be.

During the late summer and autumn the vernal pool ecosystem is almost completely dormant. There may be some foraging for seeds by birds, limited grazing by rabbits or other herbivores, and a few scattered plants of late-developing species such as dove weed that are still photosynthetically active. Most of the dried remains of the previous season's plants have broken up and fallen, but many also remain more or less intact. Organic debris from the surrounding grasslands and shrublands tends to collect in the pool depressions. The few summer showers and the first fall rains beat down and hasten the breaking up of the old plant stalks, and running water may transport additional amounts of debris into the basins.

When the pools first fill, they contain decomposing vegetation seasoned with accumulated animal droppings. If the water stands for several days, a rapid proliferation of microscopic decomposers must follow, providing a food source for microscopic predators--protozoans, rotifers, and others. In this early stage of the aquatic phase a vernal pool is a detritus-based system, driven primarily by the energy of decomposition. Hutchinson et al. (1932) attributed the early peak in abundance of the aquatic fauna in South African temporary waters to the initial bloom of bacteria and saprophytic flagellates. They speculated that the species richness of temporary waters generally may be due to the "sudden influx of nutritive matter as soon as the basins (are) filled."

The resting stages of the green and blue-green algae also respond quickly to water, probably even to the earliest rains that merely wet the soil. Bare soils often turn distinctly green with a coating of algae. The rapid mobilization of the algae and the growth of the inundation-tolerant higher plants make the purely detrital phase of vernal pools short.

The response of the higher plants will depend to a large degree on the seed reserve present and the pattern of rain prior to filling. In most years germination will be stimulated by the earliest rains, so that there will be some green herbage present in the pool when it fills. But if rains have been scanty, the cover will be sparse, and many of the seedlings will be of nonpool species that have dispersed into the pool basins. On the average, the effect of inundation is probably mostly negative on the plants that have grown before inundation. However, filling the pool seems to stimulate some species such as *Elatine* spp., to germinate, thus adding to the total pool primary productivity.

If the pool stays continuously wet for several weeks, the aquatic system matures. While the detrital energy pathways will always be important, algal productivity in vernal pools is high, and many of the animal populations must derive their energy from it. Frogs and toads move to the ponds, and tadpoles hatch and begin to forage across the bottom of pools, probably aiding decomposition by stirring the bottom sediments and thus increasing oxygenation. Tadpoles probably have at least as much impact on vernal pools as they do on the much larger ponds studied by Seale (1980). She found that tadpoles significantly reduced the biomass of suspended algae, and that they also had a pronounced effect on the cycling of nitrogen and phosphorus within the pond.

The soil also responds to pool filling. The oxygen is depleted in the deeper layers as bacteria break down the organic material from the previous season. A steep oxygenation gradient from supersaturated at times at the surface to anaerobic a few millimeters or centimeters down may be present and should produce a corresponding series of microbial communities. The growth of roots of the large plants changes the soil environment; aquatic-adapted species with provision for oxygen diffusion through the plant probably have a net aerating effect, while others deplete oxygen levels.

As in other aquatic systems, the productivity of vernal pools must be limited by resources. The high biological demand for phosphorus, its relatively low abundance in the lithosphere, and its low rate of movement from its main reservoirs in the mineral sediments and soils into the water column often limit productivity (Wetzel 1983). Vernal pools, because of their small size, have a much higher ratio of mineral substrate to water volume and should have more phosphorus moving from the soil into the water. But the soils associated with most vernal pools are not especially rich in nutrients, and some are notably deficient; it would not be surprising if vernal pool productivity were phosphorus limited.

Nitrogen, needed by organisms in even larger amounts than phosphorus, is less often the major limiting factor because of significant atmospheric inputs and biological nitrogen fixation. Nitrogen fixing algae and bacteria and the feces of terrestrial animals are probably also significant inputs. Thus one would expect that nitrogen would stimulate productivity of vernal pools less than addition of phosphorus. But saturated soils, because of their low oxygen content, also favor denitrification, in which nitrogen escapes from the biological cycle in gaseous form. This loss may be important in vernal pools.

Barclay and Knight (1984) studied the physical and chemical features and algal composition and productivity in Olcott Pond in the Jepson Prairie Preserve near Dixon in the Central Valley. This pool is highly turbid because of suspended clay and therefore somewhat atypical. The light diminishes so rapidly with depth that no photosynthesis is possible below 2 cm from the surface. The concentration of dissolved phosphorus is high relative to that of dissolved nitrate and ammonium nitrogen. The highest nitrogen:phosphorus ratio they observed was 2:1. Since optimum ratios for phytoplankton productivity are considered to range from 16:1 to 30:1, the authors believe that the algae in this pool (mostly diatoms) are probably nitrogen rather than phosphorus limited. It remains to be seen how general this conclusion is, but the fact that most of the coastal vernal pools are neither alkaline nor extremely turbid suggests that they have rather different properties than this relatively large Central Valley pool.

Despite the large input of detritus, the aquatic plants may also be carbon limited. This is the basis of Keeley's hypothesis (see Chapter 4) for the advantage of CAM metabolism in *Isoetes*. Rapidly growing algae in the brightly lit pools may take up carbon dioxide faster than it is produced by the respiration of decomposing bacteria and other organisms.

Whatever the controls on pool productivity, it seems unlikely that the vernal pool aquatic system could ever equilibrate. Neither the physical nor the biotic environment ceases changing during the course of its existence. A pool forms initially because rainfall exceeds evaporation, but eventually day length and temperature increase, favoring increased photosynthesis. But these changes, along with decreasing rainfall, also make water levels more unstable. Stability is also directly related to size. Smaller pools generally fill and dry one or more times during the course of a single season, and the margins of the largest pools are repeatedly inundated. Particular pools, and all pools in unusual years, will go through this cycle many times. Balko and Ebert (1984) speculated on the small-scale biogeographic consequences of this pattern, and discussed the life histories of organisms adapted to it.

Pools vary from place to place and from time to time, but the basic ecological groupings and their roles in aquatic ecosystem function are probably fairly consistent, and cautious generalization is possible. The food web of Figure 53 is for a small vernal pool at the stage where it has held water for some weeks. In southern California this would usually be from early February to mid-March. The pool at this stage has a good development of the inundation-tolerant aquatic plants, as well as large populations of the other important aquatic groups.

Figure 53 emphasizes the energy flow among the various elements of the aquatic system in a simplified way. With the exceptions of the fairy shrimp, tadpoles, and snails, each functional group consists of several to many distinct species, each with their own specializations and patterns of population growth and resource use. Much of the structure of such interacting networks of species is a result of the balance between predators and their prey, and small aquatic systems are probably especially sensitive to such interactions. The distribution and time of arrival of larger aquatic predators such as corixid beetles and dragonfly nymphs may be important factors affecting spatial and temporal variability of vernal pool organisms. It is apparent that many organisms, for example fairy shrimp, are present in vernal pools precisely because it is a habitat free of large predators.

Work with experimental microcosms and observations in special natural situations suggest what would happen if the predatory insects were excluded from pools. The larger predators tend to remove organisms that are feeding on the organic debris or the microplankton. When they are abundant they can reduce the herbivores to such low levels that algae, previously removed at high rates, accumulate in the water column, turning the water conspicuously green. Excluding predators allows the herbivores to reach maximum population size, which reduces the algal standing crop so that the water clears. Because there is a significant lag between the appearance of pools and the dispersal of the larger predators into pools, seasonal succession of the community may be influenced as much by changes in the structure of the food web as by changes in temperature and day length.

In contrast, the filamentous algae, once well established, cannot effectively be controlled by the organisms filtering the water column. Algal blooms are thus possible even without the release from predation afforded by low predator populations. Since filamentous algae can flourish even in the presence of large populations of filter feeders, one might expect filamentous blooms to be universal in pools. As this is not the case, some other factor, most likely macronutrient levels, might explain the differences in abundance of filamentous algae. Tadpole grazing may also play a role in changing algal composition.

5.1.3 The Vernal Pool System in the Drying and Drought Phases

Before filling, between fillings, and after drying, vernal pools are terrestrial systems, subject to the influences of organisms from neighboring plant communities. They are grazed by herbivores from the surrounding vegetation, and seeds and other plant and animal propagules disperse into them. Foraging columns of ants extend over the pools and the seeds of some of the vernal pool species are collected in great numbers. Pocket gophers extend their foraging tunnels into the pools.

In the give and take between terrestial and aquatic organisms that characterizes vernal pools, the long dry season belongs to the organisms of dry land. With the return of the winter rains, these incursions will mostly be repulsed. But in extended droughts the pools may be heavily invaded and substantially changed. This process will be examined in more detail for the plants in the next section.

5.2 VEGETATION STRUCTURE AND DYNAMICS

When viewed on a larger scale, as in Figure 15, a vernal pool landscape is a continuously varying complex of soils and vegetation, in which vernal pools are patches of habitat approaching an extreme along the soil-moisture gradient. The distribution of the plants in this landscape is fundamentally controlled by the physical environment, but the interactions among the species are also important in shaping vegetation patterns.

These vegetation patterns are not static. The physical environment varies from year to year, largely in response to changing climate, which in turn sets in motion shifts in species distributions across the landscape. In the case of extreme events, such as fire, flood, severe drought, earthquakes, or human disturbance, these changes can be very great, and it may take decades or even longer for the landscape to settle back to a condition in which year-to-year change is minor and responsive mostly to varying climate. There has probably never been a true equilibrium in vernal pool vegetation, but at best a quasi-equilibrium in which the composition of pool biotas drifted around a long-term average.

Because vernal pools owe their unique features to standing water and the high levels of soil moisture that occur before and after inundation, they are especially sensitive to varying rainfall. Over millenia, extended drier and wetter periods cause contraction and expansion of vernal pools and probably some pool "mortality" and "rebirth." Over the shorter time periods that humans experience, pools are unlikely to appear or disappear, but their margins enlarge and shrink from one year to the next. In dry years many pools may not form at all, and in wet years smaller pools merge to form interconnecting chains.

Obviously the change in the biota of vernal pools at all scales in time and space is complex, and existing knowledge is inadequate to understand it fully. Here an attempt will be made to simplify the complexity by first assuming that the pool landscape can be divided into pools and nonpools. In the following section the structure of vegetation found within pools from pool margin to the deepest point will be discussed. Next, the effect of climatic variability on pools will be considered. In a third section larger scale patterns, and especially the role of pool-to-pool dispersal of organisms and how this relates to the persistence of pools in human-dominated landscapes, will be discussed.

5.2.1 Within-Pool Gradients

Just as at the landscape level there are habitats that are intermediate between vernal pools and upland areas never affected by ponded water, so within a pool there is a more or less continuous gradation from the deepest parts of the pool with long durations to the surrounding nonpool vegetation (Holland and Jain 1977). The physical environment changes over this distance (Lathrop 1976; Rosario 1979), and plant species composition and relative abundance change with it (Table 13). The distribution of species along this gradient is controlled ultimately by the physical environment, but this in turn causes changes in the biological components and in the biological interactions among species (Table 13). The change in species abundances is a consequence of the combined effect of physical and biological influences.

The response of plants to the varying environmental conditions along the center-to-edge gradient is most evident at the time of flowering, when successive bands of color show the replacement of one species by another from the edge to the pool bottom. It is not surprising then that several workers have characterized pools as consisting of concentric zones (e.g., Lin 1970; Kopecko and Lathrop 1975). Holland and Jain (1977) discussed several of these zonal classifications. Though they differ in detail, all recognize the existence of higher zones dominated by annual grassland species such as soft chess (Bromus mollis), fescue (Vulpia megalura), and tarweed (Hemizonia spp.); an intermediate zone or zones dominated by species tolerant of or requiring some inundation--toad rush, (Juncus bufonius), veronica, (Veronica peregrina), and hair grass (Deschampsia danthonioides); and a deep zone with the most water-tolerant or water-requiring species like quillwort (Isoetes spp.), Downingia spp., and coyote thistle (Eryngium spp.).

The problem with a zonal approach is that species distributions overlap and the peaks of abundance in general do not coincide. Detailed study of a single pool shows that while there is a tendency for each species to have a more or less clear peak in abundance along the gradient, every species is also patchy in its occurrence within elevational bands. Species are usually present well outside the zone in which they are most apparent to casual observation. A further complication is that small species (e.g., Pilularia americana) are most obvious in places where the cover of other species is sparse even though they may be equally abundant elsewhere. Finally, there is no good reason to suppose that the physical-chemical gradient from pool bottom to dry mound top has sharp discontinuities that would produce distinct zones. Even the level of highest water, though often clearly evident by a change in vegetation height or density, is rarely the absolute upper limit of pool species or the lower limit of nonpool species.

Both the tendency to zonation and the considerable overlap of species distributions were demonstrated in a study conducted in 1979 on the vernal pools of Kearny Mesa (Zedler et al. 1979) in which the occurrence of species from pool bottoms to surrounding nonpool vegetation was

Table 13. Factors important to plant growth that differ from the center to the margin of pools.

Factor	Center	Margin
Water duration	Long (> 30 days)	None
Soil texture	Usually finer (clay, clay loam)	Usually coarse
Soil structure	Usually puddled when wet, massive when dry	Soil aggregates present, more voids for air, water movement
Soil surface characteristics	Generally more complex, e.g. layer of cobbles, large drying cracks, microridges and depressions	More uniform, but shrubs, plants causing heterogeneity
Soil moisture sufficient for germination	Earlier in the season	Later in season
Soil moisture during growing season	More reliable, deep moisture through growing season, concentration of runoff from small rains	Less reliable, short periods of drought during growing season
Soil moisture depletion to permanent wilting	Occurs later	Occurs earlier
Macronutrients	Higher because of runon, algal N-fixation, litter?	Lower?
Salinity, alkalinity	Higher (much higher in some vernal pools) because of evaporative concentration of salts	Lower, but may be minimal in pools with subsurface drainage
Soil oxygen	Essentially none for extended periods	Usually high
Herbivory	May be more intense early because of early greening, germination, then probably lower, then higher again because of extended growing season	Intense at times especially when grazed by livestock

recorded in 1-dm^2 quadrats placed along transects in 26 pools. The water levels in the pools were monitored and the elevation of each quadrat along the transect measured. With these data it was possible to express the occurrence of species relative to the depth of the pool, and more important, to the length of time that a quadrat was under water during the study year. Since the length of time under water was felt to be a better predictor than depth in the pool, the occurrence of species at each water duration in the combined set of data was calculated, allowing graphs of percentage of occurrence as function of length of time water stood to be plotted (Figure 54). Zedler (1984) may be consulted for a more complete discussion of how these graphs were obtained.

Examination of graphs for representative species of the three zones discussed above shows that all occur over a broad range of inundation conditions. Peaks are evident in some of the graphs (e.g., Anagallis) but rather obscure in others (e.g., Pogogyne), and combining the graphs for all species produces an almost continuous series of peaks in accord with the continuum concept of species distribution. The species of vernal pools differ significantly in traits that allow them to exploit the vernal pool habitat, but do not form distinct groupings corresponding to zones.

This point can be made in another way, by calculating the weighted average water duration class (Zedler et al. 1979). Plotting the results for the more abundant species shows that the mean values of water duration class for the species are well distributed along the entire gradient (Figure 55).

Holland and Jain (1984) gave the results of a similar ordination of species along a margin-to-center gradient for data from pools in the Central Valley. The tendency apparent in Figure 55 for more species to have their average peak occurrence at the drier end of the gradient is also true for their data. They argued that this may be because the geometry of pools insures that more area is available at the higher elevations, stating that "the number of taxa specialized for a given depth (is) proportional to the availability of habitat at this depth."

The evidence from these two studies is consistent with the idea that the flora of vernal pools is made up of species that collectively exploit the full range of water and soil conditions along the bottom-to-edge gradient. While there is substantial overlap in distributions, the data suggest that each species differs enough from others to have some part of the vernal pool basin in which it is able to outperform other species.

Such an arrangement of species is unlikely to arise by chance. It is probable that in undisturbed pools the collection of plants is the end product of a long period of selection of species or genotypes. The species are fitted together to make a working whole--a dynamic mosaic. A mosaic can be assembled by searching through a stockpile of pieces until one that fits is found, or each piece may be specially shaped to fit. In the same way, at the extremes, vernal pool ecosystems may have been constructed of taxa that evolved in other systems, or they may be made up of populations that have been specially molded to the vernal pool habitat.

Vernal pool biotas have probably been built up by both processes. Even the cursory survey of a few of the vernal pool plants (Chapter 4) showed that some are highly restricted and occur only in pools while others are found in many other habitats. But it is also true a majority of vernal pool species are not pool restricted. Thus at the level of species we may conclude that a few pieces in the vernal pool ecological mosaic have been specially shaped but most have probably been incorporated more-or-less as found.

But the analysis must go below the level of species. Research on genetic diversity of plant populations in natural habitats has shown that there are large amounts of within-species variability. Plants often show adaptation to local environmental conditions. Since even nearby vernal pools can differ dramatically in soil, hydrology, and other important features, we may expect genetic differentiation among pool populations.

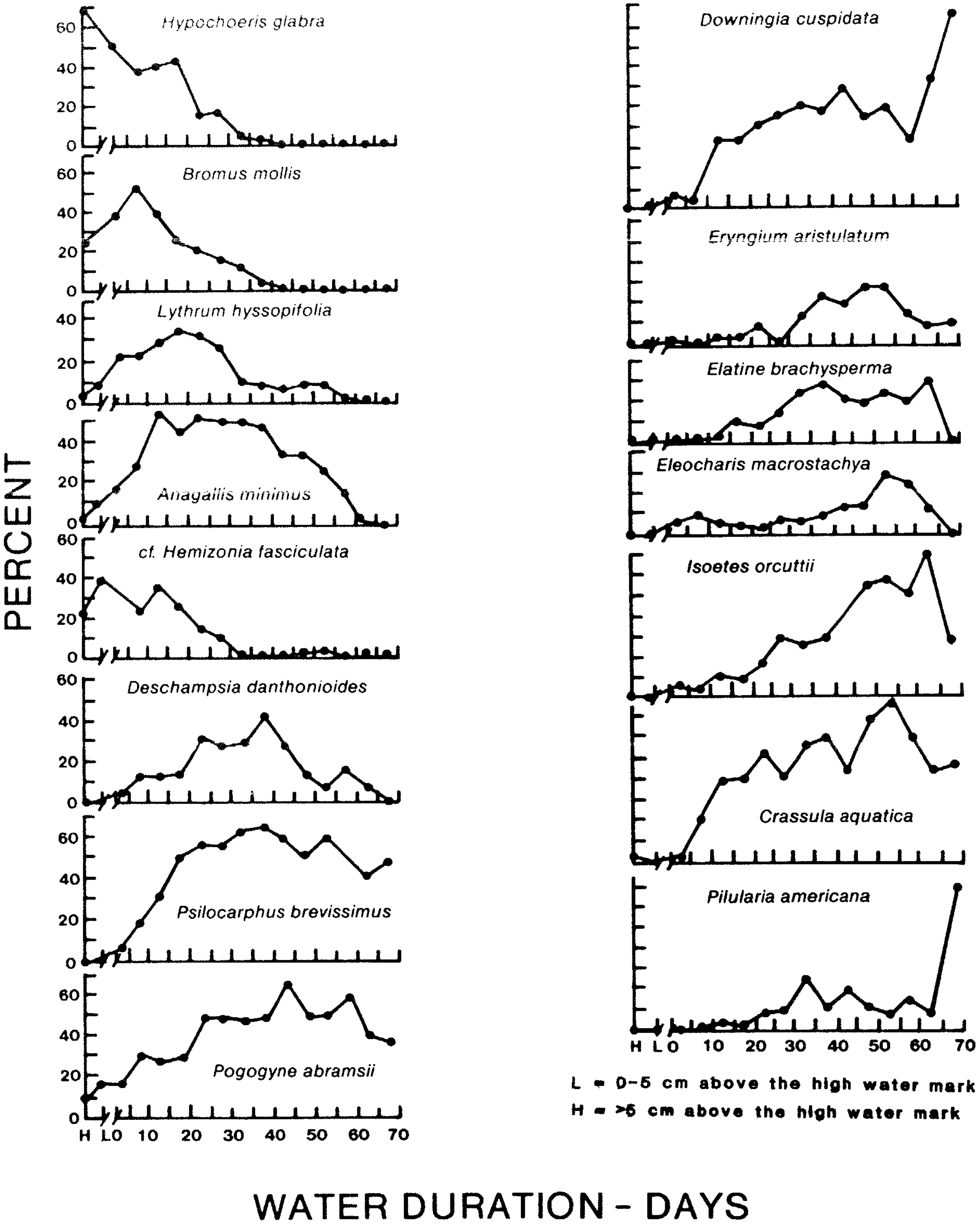

Figure 54. The relative occurrence of species across the water duration gradient for pools on Kearny Mesa, San Diego County. The data are combined from many pools. Although there is very broad overlap, the peaks in abundance are fairly well distributed.

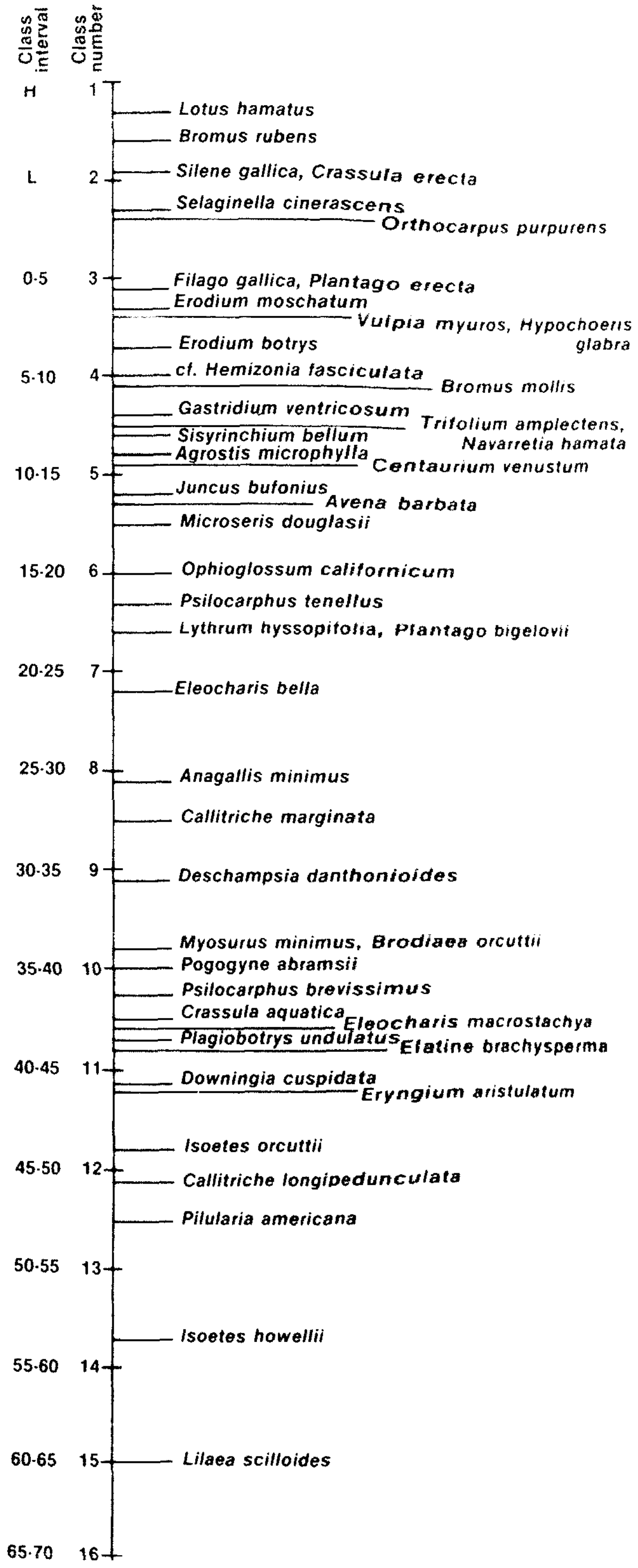

Figure 55. The average water duration class of common vernal pool species for Kearny Mesa.

This expectation is confirmed by the studies of Jain and his students on the genus Limnanthes, common in the vernal pools of the Central Valley (Jain 1978, 1984). They found considerable genetic diversity within species, but usually substantially less within local populations than in the taxon as a whole. Local populations differ, and some part of this variation is probably a result of local specialization.

The presence of genetic differences is not in itself proof that vernal pool species have been shaped by unique pool conditions. Differences may result from random variation. Work by Linhart (1972, 1974, in press) on Veronica peregrina provided evidence that there is "fine-tuning" of plants to the vernal pool habitat. He has been able to show that populations of this species that occur at the deepest part of pools are genetically different from those near the edge. Furthermore he has argued that the differences in the populations are attributable to gradients in nutrients and competition (Linhart, in press). In the deeper parts of the pool a Veronica plant typically is subjected to competition from another Veronica plant, while near the edge it is more likely to be surrounded by grasses. Plants grown from seed collected from the margin and centers of pools differed in the manner expected when they were grown experimentally in the two situations. The central populations were less sensitive to intraspecific competition than the marginal populations (Linhart, in press).

Linhart's observations support the idea that the vernal pool flora is more than a jumble of chance immigrants. If populations of plants can be narrowly adapted to specific parts of a single pool, then it would be surprising if they were not also evolved to particular pools and climatic regions. As Linhart's results show, other species are an important part of a plant's habitat. Thus the assemblage of plants in a particular pool may be coevolved to some extent. The hypothesis that vernal pool plant communities are assembled at least in part by the shaping of species to fit the unique aspects of pools and local habitats seems likely to prove true.

Another way to view the within-pool gradient is to measure the change in the number of species with increasing inundation. For the set of data from the 1979 Kearny Mesa study (Zedler 1984), species richness (expressed as the average number of species per square decimeter in each water-duration class) peaks in the higher elevations of the pool and then declines steadily toward the deeper parts of the pool (Figure 56). A dm^2 quadrat deep in a pool will usually have two to three fewer species that one place near the edge.

This pattern may simply be a reflection of the tendency, noted above, for more species to have peak occurrences higher in the pools (Holland and Jain 1984). Arguing against this is the fact, evident in Figure 56, that most pool plants occur over nearly the entire gradient, and that the diversity of nonpool plants at the "H" position is lower than that of the pool plants, even though there is much more area at this position. More probably the strong diversity gradient is because the margins of the pool are a zone of intermixing of nonpool and pool elements where species of either type plus a few specialists can exist. Competitive exclusion may fail in this zone because of year to year variability.

5.2.2 Effects of Climatic Variability

The highly variable rainfall characteristic of southern California (Chapter 2) must be a major factor affecting plant communities centered on temporary bodies of water. Though close study of many pools (and related habitats) over many years would be needed to understand all the effects of climatic variability, enough is known to offer some preliminary ideas.

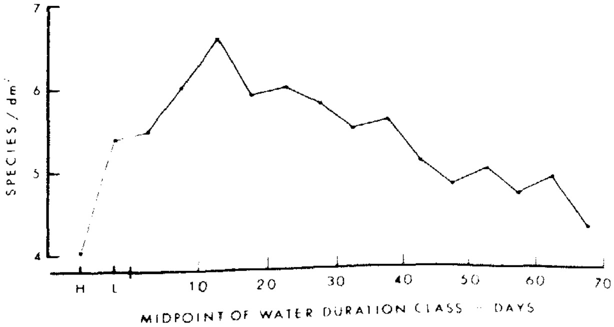

Figure 56. The average number of species per square decimeter at various points along the water duration gradient. Data for Kearny Mesa.

A first point, discussed above, is that the number of basins holding water for a given amount of time must vary over time. In years of extreme rainfall standing water is perhaps almost everywhere on mesas with impermeable soils, while in the driest years only the deepest and largest basins hold water for more than a few hours or days. Where soils do not saturate in most years one would not expect vernal pool plants (Zedler 1984). Vernal pools should occur only where the perched water table forms in all but the driest years. In very wet years there should be evidence of mortality of nonpool plants in basins that normally do not hold water for extended periods. No data can be produced to support these contentions.

However, there are data on change in the distribution of vernal pool plants over several years. Holland and Jain (1984) reported the changes in species richness for Central Valley pools in four areas over 3 years during which the driest and wettest years had rainfall differing by a factor of two. For three of the four areas the average number of species per pool was greatest in the wettest year. The exception, Pixley, is an area of alkaline soils and relatively low species diversity.

Zedler and his students resampled a small number of transects established in the 1978-79 growing season 2 years later. The rainfall for the 3 years was above average in the first 2 years (39.5 and 39.9 cm) but only 21 cm in 1980-81. Despite this, the changes in the abundance and distribution of the species were generally small. One of the clearest patterns was an increase in nonpool, marginal species such as tarweed (Hemizonia spp.) and their occurrence deeper in the pool basin. This is reasonable because the reduction in standing water should have allowed nonadapted plants whose seeds could disperse into the pool to do better in the dry year. Less easily explained were increases noted in some vernal pool plants (Pogogyne abramsii, Psilocarphus brevissimus). It was hypothesized that the larger populations were present because of high seed production in the previous 2 years. This suggests that the sequence of wet and dry years may be important. Three wet years followed by three dry years would have a very different impact on populations than 6 years of alternating wet and dry years.

Ellen Bauder has continued the monitoring of the 1979 transects on Kearny Mesa, and now has data for 4 years on some pools. Her results to date show a surprising degree of stability in the distribution of vernal pool plants, effectively refuting Zedler's contention (1984) that the populations of at least the annual plants should show major shifts along the bottom-to-edge gradient in response to varying rainfall. Two examples illustrate this (Figure 57). Psilocarphus brevissimus, the diminutive composite, varied in abundance in the 4 years, but its distribution along the gradient differed only slightly. Bromus mollis, an annual grass common around pool margins but intolerant of prolonged inundation, was excluded from the deeper parts of pools in the wettest years.

Our current understanding of change in vernal pool plant populations, based largely on Bauder's work, can be summarized graphically (Figure 58) for a hypothetical annual nonpool plant (e.g., Bromus mollis, Hemizonia fasciculata) and a hypothetical pool plant (e.g., Pogogyne abramsii, Psilocarphus brevissimus), starting in a wet year occurring after several previous wet years. In the following dry year (year 2) seed reserves of the pool plant are present along the entire gradient, whereas the seeds of the nonpool plant have to disperse into the pool basin. The pool plants are able to grow and survive in the dryer upper margins of the pool as long as competition is not too severe from the nonpool species. Since this will be the case in the first dry year, the result is seed production by the pool plant along the entire gradient, but at reduced levels. In the second dry year (year 3) the upper margin of the pool has larger populations of nonpool plants, and the seed production of pool plants in the upper edges of the

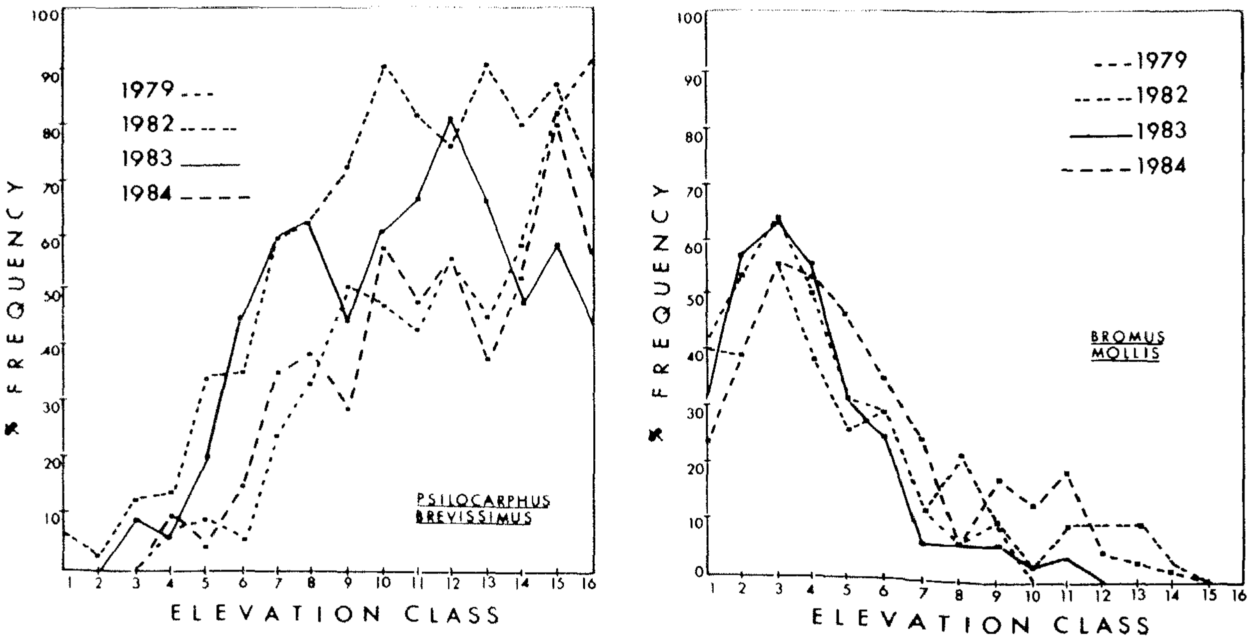

Figure 57. The occurrence of *Psilocarphus brevissimus* and *Bromus mollis* along the water duration gradient for several years. Despite considerable variation in rainfall from year to year, the distributions are relatively stable. Unpublished data of Ellen Bauder from Kearny Mesa.

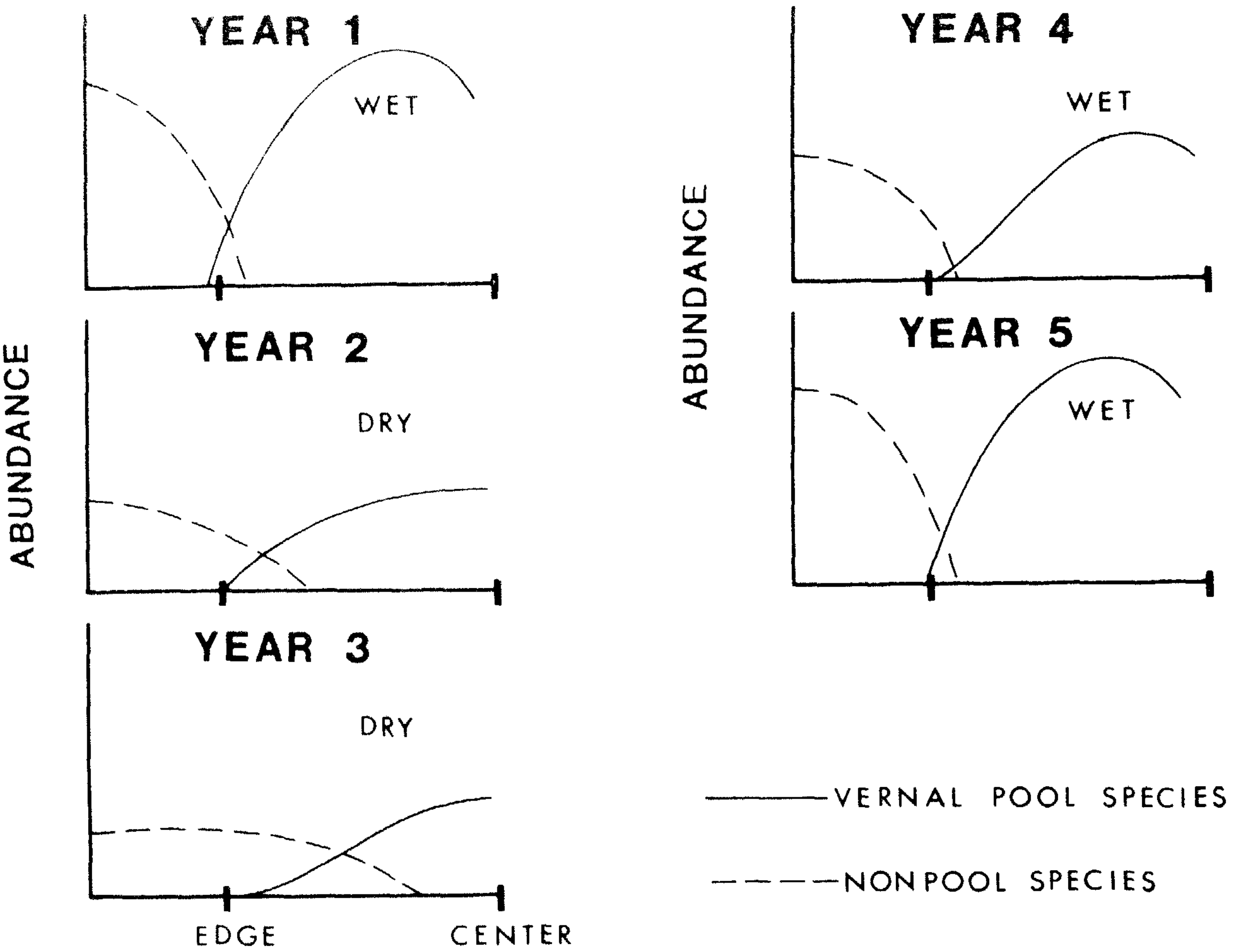

Figure 58. Hypothesized shift in species along the pool-nonpool boundary. As the pool retreats, nonpool species increase in abundance. As the pool expands, pool species will again dominate the boundary.

basin is greatly reduced, though perhaps not reduced to zero. If a wet year follows (year 4), the nonpool plant is excluded because of high mortality caused by inundation and saturated soil, but the pool plant does not recapture all of the upper pool habitat immediately because of low seed reserves at these higher levels. If a second wet year follows, the original pattern can be reestablished.

Variability from season to season and the dynamic tension between inundation tolerant and intolerant plants may be the explanation for the pattern of decreasing diversity in Figure 56. A completely consistent pattern of rainfall and inundation should lead to the gradual exclusion of intolerant species within the pool basin. In this case, a more or less flat curve of diversity might be expected. But a shifting pool boundary may prevent competitive exclusion and allow coexistence of species in a temporary nonequilibrium mixture. If this view is correct, then putting it together with the model in Figure 58 would lead to the prediction that diversity in the transition zone should be highest in moderately wet years that occur after dry years, when the mixture of species in the seed bank should be near maximum. This may be part of the explanation for the greater diversity of the wet year noted by Holland and Jain (1984).

Although between-season variability may enhance the species diversity of pools, the effect of within-season variability may be quite different. Ebert and Balko (1984) analyzed the plant data for 47 pools from the 1979 Kearny Mesa study and found a negative correlation between the number of times a pool dried in 1979 and the number of pool species present. This suggests that variability within a season makes the pool a more difficult environment and excludes species intolerant of extremes in water conditions.

Perhaps the most important question about seasonal and yearly variation is, "How often do populations crash to local extinction within vernal pools?" Holland and Jain (1981) cited several references that reported the disappearance and reappearance of species, suggesting that there may be considerable turnover. If this is the case, then vernal pool populations may be in a highly dynamic condition, with a continuous flux of species among pools. Observations in San Diego County do not support this view, however. No disappearances of important species have been recorded, and the most dramatic cases of the appearance of species where they were not present before has been the result of purposeful introduction of propagules (e.g., Scheidlinger 1984). A nagging problem in testing any extinction-invasion theory is the extreme difficulty of establishing that an extinction or invasion has taken place. Most vernal pool plants have seeds that can persist in the soil for more than a single season after dispersal. The absence of flowering plants in a particular year, even if this were to be verified by the meticulous search required, is not sufficient evidence of extinction. For example, Bauder (pers. comm.) observed the germination in the second year of *Pogogyne abramsii* seeds set out in experimental clearings. *Orcuttia* (*Tuctoria*) populations in the Central Valley observed for over a decade have been known to go through wild swings in abundance from one year to the next, yet local extinction and reinvasion are almost certainly not involved. From time to time species must go extinct in pools, but the rate is probably very low for all but the casual species that disperse into pools from adjacent nonpool habitats and rarely become abundant.

5.2.3 Between-Pool Dynamics--Pools as Islands

The most startling feature of vernal pools is their strong contrast with the semiarid vegetation surrounding them. It is reasonable that they should be viewed as islands of habitat isolated from one another by greater or lesser stretches of inhospitable habitat. There exists a considerable literature on the biography, ecology, and evolution of "real" islands and several authors (Holland and Jain 1981; Rosario and Lathrop 1984; Ebert and Balko 1984) have attempted to apply the principles and insights from these studies to the island-like situation of vernal pools.

One theory (MacArthur and Wilson 1967) holds that the number of species on an island is predictable from its size and the distance to landmasses from which species can disperse. This theory, applied to vernal pools, would predict that smaller pools would have fewer species than larger pools. A smaller pool presents a smaller target area for dispersing organisms, has fewer subhabitats and has smaller, more extinction-prone populations. Further, a pool near many other pools would have more species than an equal size pool far away from all other vernal pools. For the near pool there would be a greater probability of introduction of new species and of replacement of any locally extinct species by dispersal from other nearby pools. The isolated pools, were they to lose a species, would have to wait a long time for chance dispersal of a propagule to reintroduce the species.

An alternative view, which still considers pools as islands, is that the number of species and the species composition of each pool are highly individual pool properties for which the details of pool morphology, soil chemistry, water movement and persistence, etc., play very important roles. While pool area and location relative to other pools may have something to do with the number of species in a pool, these may be no more important than a number of other variables. Similarly, geographic distance to the nearest pool may be less important than other factors that affect the movement of propagules across the landscape.

But is the assumption that vernal pools are islands justified? Many species of vernal pools also occur in other habitats. For example, pillwort (Pilularia) is widely distributed. Its biogeography and population dynamics cannot be understood solely on the basis of narrowly defined vernal pools. Eryngium aristulatum, which is completely restricted to pool basins on Kearny Mesa, occurs scattered in the grassland on Camp Pendleton. In contrast, Pogogyne abramsii seems to have only accidental occurrences outside of vernal pools, and perhaps for this species vernal pools are truly islands. Thus while most vernal pool species have island-like distributions, vernal pools are only a subset of the total habitat area for many species.

The data published so far do not allow us to see which of these competing ideas comes nearest the truth. It is well established that species number does increase in a statistically significant way with pool size (Holland and Jain 1981; Ebert and Balko 1984; Rosario and Lathrop 1984). However, in all these cases the slope (z) of the double-log relationship:

ln (species number) =
(a constant) + z (ln (pool area))

is lower than that predicted for island situations by MacArthur and Wilson (1967), and the scatter of points about the trend line is great (Ebert and Balko 1984, Figure 59).

Holland and Jain (1981), whose z value of 0.04 is substantially lower than the values in the 0.13-0.17 range for plants reported by the other two papers, were surprised at the discrepancy from theory. They offered the hypothesis that a vernal pool is a demanding habitat which

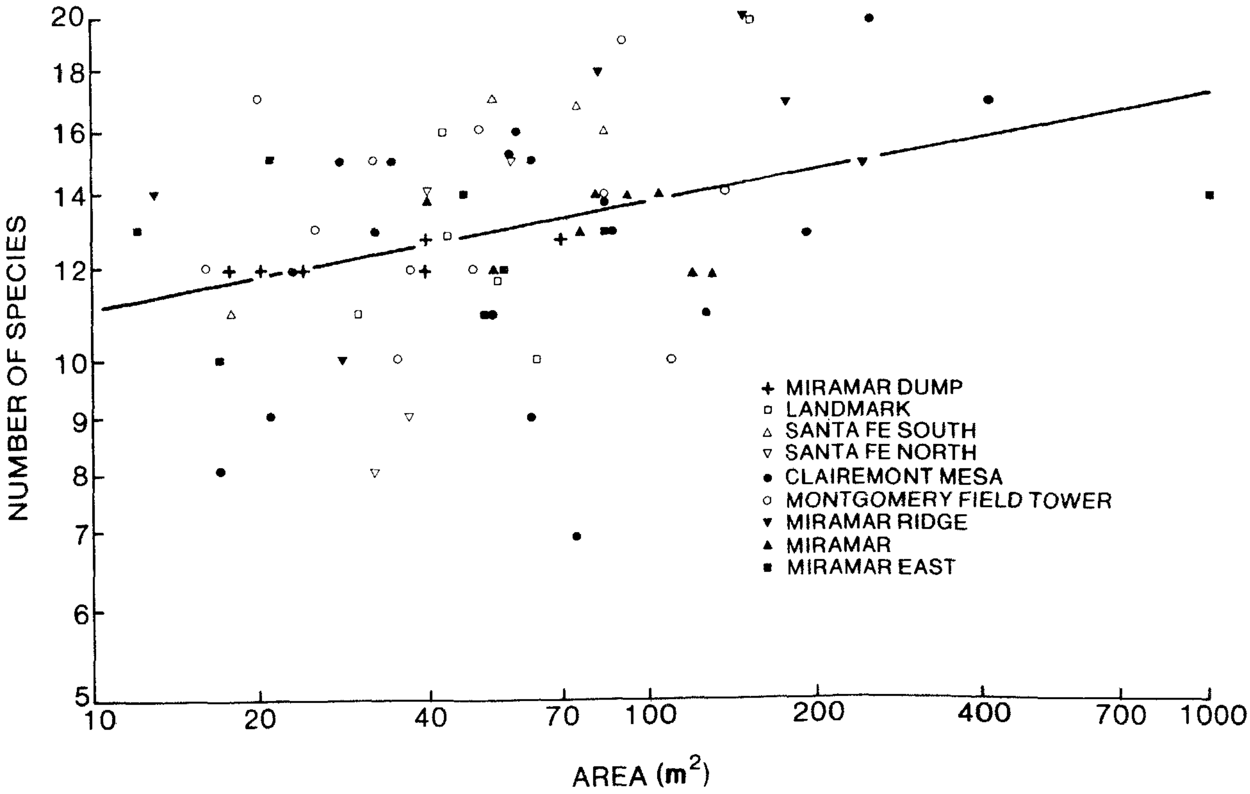

Figure 59. Number of species in Kearny Mesa pools as a function of maximum pool area. The slope of the regression calculated from the double log transformed data is $r = +0.360$; ($S = 8.89A^{0.096}$) is the line on the graph. Based on an analysis by T. Ebert and M. Balko.

relatively few taxa can exploit. Successful taxa tend to radiate geographically so that much of the diversity is over a large geographic scale. Increased area of a pool cannot increase species numbers very much because the total number of species capable of growing in pools is limited within any region.

Ebert and Balko (1984) concluded from their analysis of both plant and animal species data that pool area is a better predictor of species number for plants than it is for invertebrates though the amount of variation explained in both cases is low. Columns two and three below are coefficients of determination (r values squared) for the regressions (ln) (number of species)= a + z (ln (X)) where X was either pool area or the number of times a pool dried in 1979. The fourth column is z values, coefficients of the regression equations where X is pool area. These may be compared to the range 0.2-0.35 expected for island situations. The first three rows of data are from Ebert and Balko (1984), and the fourth row comparable data for plants from Holland and Jain (1981).

Taxonmomic group	Coefficients of determination for X =		
	Times dry	Area	z
Crustaceans	0.66	0.27	0.36
Rotifers	0.27	0.01	NS
Pool plants	0.20	0.27	0.17
All plants	---	0.07	0.04

For invertebrates the variability of the environment measured as the number of times pools dried during the 1979 season was a better predictor of species number than pool area. As might be expected the relation between the number of species and times dry is negative. The more drying episodes, the fewer species were present. Ebert and Balko concluded that habitats, like pools, should be viewed as islands in time as well as islands in space, with islands that appear infrequently and last only a short time having fewer species than those that are frequent and persist for long periods. They also made the point that the different life histories of species make them respond differently to patterns in time and space. This is borne out by the z value for crustaceans (0.35) which is twice that of the plants.

As all of these authors would agree, we must know far more about changes in populations of vernal pool organisms before the role of dispersal among vernal pools can be understood. The drastic reduction in the area of vernal pools and the imposition of urban and agricultural barriers between surviving areas of pools could provide a kind of crude test of some of these ideas. If interpool and interarea dispersal is important in maintaining species diversity in pools, then we should be able to see a gradual impoverishment of the most isolated and smallest groups of remaining pools. For purposes of preserving the unique vernal pool flora and fauna, we must hope that dispersal is not of major importance in short-term population dynamics.

5.2.4 Response of Vernal Pools to Human Disturbance

Until galloping urbanization swept over the coastal mesas of southern California, the predominant use of vernal pool landscapes was for grazing and agriculture. It is doubtful if there is a vernal pool anywhere in the State that is free of the impact of humans or domestic animals. Comparisons of less disturbed with more disturbed pool areas and studies of severely disturbed pools in the process of recovery suggest that vernal pool ecosystems are relatively resistant to continuous light disturbance and even occasional severe disturbance.

Moderate cattle or horse grazing does not seem to pose much of a threat to the persistence of vernal pool plants despite the disruptive effect of trampling. In other situations grazing usually promotes the invasion of weedy introduced species that are less palatable and better able than native plants to exploit the disturbed soil created by animals. The grasslands that often surround vernal pools fit this pattern, because introduced species are usually dominant in them. In contrast, the pools have few introduced species, an these are generally of limited importance (Holland and Jain 1977). The resistance of vernal pools to the invasion of exotics may be attributable to the extreme environment of the pool basin which excludes nonpool species intolerant of inundation (Holland and Jain 1981). So long as the basin hydrology is not disrupted, the pool flora and fauna are relatively immune from the competition of introduced plants and seem to be able to persist and recover rapidly. The microtopography of pools in long-grazed areas no doubt has been altered to some extent, but the overall species composition of natives is probably much the same as it was before the arrival of European land-use practices.

In exceptional circumstances grazing can even help to perpetuate vernal pool plants. On the campus of the University of California at Santa Barbara a horse pasture was maintained for many years in a former vernal pool area. Though hardly pristine pool habitat, many characteristic taxa were present in the heavily grazed pasture. When the horses were removed, the abundance of vernal pool species seemed to decline in proportion to the increase in nonpool species (W. Ferren, pers. comm.). Evidently the hydrology of the former vernal pool area had been modified so that without grazing the introduced species could grow well enough in the basins to exert significant competitive pressure.

Obviously agriculture represents a much more serious threat to vernal pools than grazing, since breaking up of the surface and planting are involved. It appears that vernal pools can recover to some degree even from this drastic a disturbance, because some areas known to have been cultivated have small impoverished pools on them, as at Goleta (D. Smith, Department of Biology, University of California, Santa Barbara; pers. comm.).

In San Diego County the area of vernal pools in the National Landmark on Miramar Naval Air Station appears to be covered with uniform and undisturbed chamise chaparral in a 1928 aerial photograph. Partial clearing, probably by discing, was carried out sometime between then and the 1950's (Figure 60). The area has now regrown to the point where the less disturbed portions once again have a dense shrub cover. The pools have a full complement of species and could not be distinguished from undisturbed pools solely on the basis of their species composition.

Insight into how much disturbance can be sustained by vernal pool ecosystems was provided by a study conducted in San Diego County for the U.S. Environmental Protection Agency (Scheidlinger et al. 1984; Patterson, in prep.). A small parcel on northern Kearny Mesa slated for development and containing good natural vernal pools was ripped with a caterpillar tractor in March 1980, leaving the surface deeply rutted. The recovery of this area was followed for three seasons starting in May 1981. In the summer of 1981 six pools were reshaped with a small tractor to approximate what might have been their natural shape, size, and depth. Half of these were seeded with material collected from an adjacent area to be developed, and half were left unseeded. Six disturbed basins were left unmodified, and half of these were seeded. A nearby set of pools that had not been recently disturbed provided a basis for gauging the recovery of the disturbed pools.

The results of the study showed first that the ripping operation badly disrupted the vernal pools and greatly decreased the cover of vernal pool species in the depressions that remained, but probably did not eliminate any important vernal pool species. Several species (Crassula aquatica, Pogogyne abramsii, Downingia cuspidata) that normally occur only in the inundated portion of a vernal pool basin were found growing on disturbed ground that had never had standing water. This lends support to the hypothesis that vernal pool plants are prevented from growing outside of vernal pools by competition from grassland and shrubland species.

In the first year of observation (1982) the pools in the disturbed area had values of total plant cover 30%-40% below the 88% recorded in the adjacent undisturbed pool. Among the disturbed pools the lowest cover, as expected, was in the

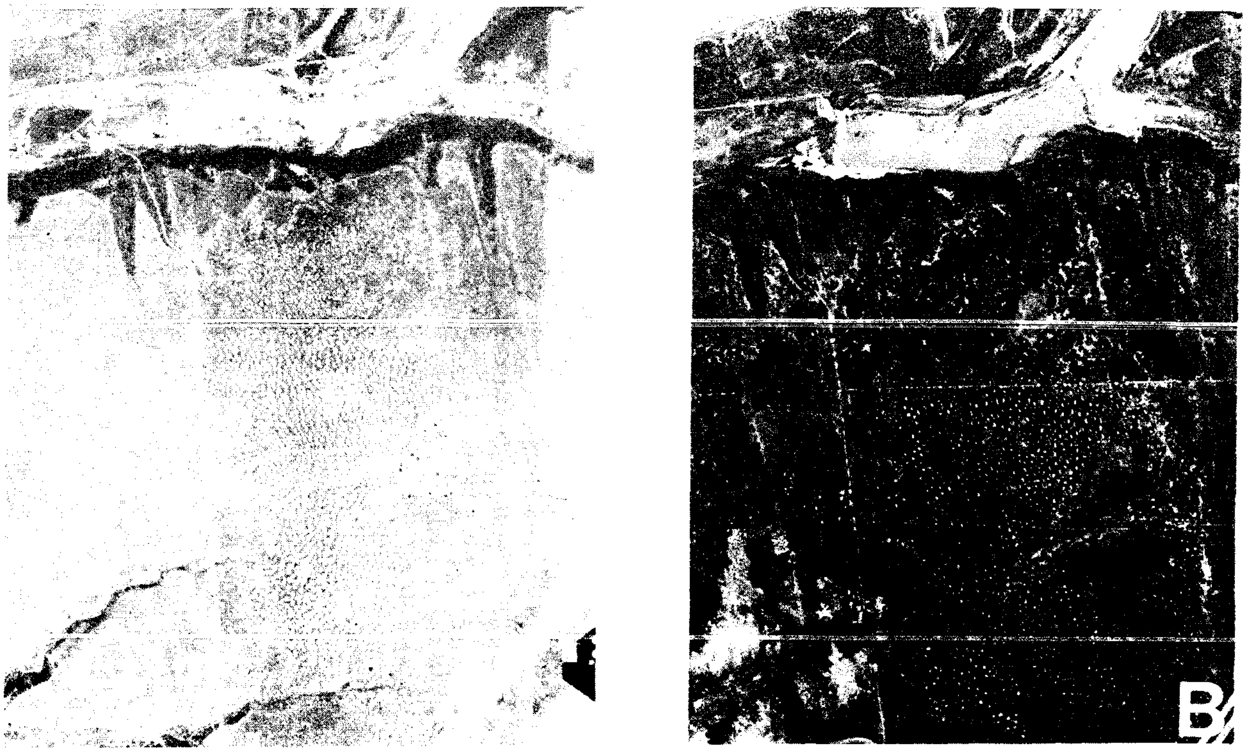

Figure 60. Twenty-six years change in the National Landmark vernal pool area (now Miramar Naval Air Station). Photo A was taken on 31 March 1953 and Photo B on 30 July 1979. The white dots visible in both pictures are the barren tops of mounds. These bare spots are not natural and indicate that the area was brushed or scraped. In 1953 the area was dominated by grass cover and an open-shrub cover in the northeast corner. By 1979 the shrub cover had increased dramatically, although some of the scraped mound tops remained barren. The two canyons visible at lower left in 1953 but absent in 1979 were used for sanitary landfills. Photo courtesy of the California Department of Transportation.

restructured pools that had not been seeded. By 1984, the restructured unseeded pools had developed cover comparable to that observed in the other pools in 1982, and the remaining pools, with some exceptions, were approaching the cover values of undisturbed pools. The increasing cover was largely the result of increased density of vernal pool species, showing that the basins were gradually approaching a near-natural condition.

The soil disturbance, both the original ripping and the restructuring by tractor, caused the pools to be very turbid with suspended clay. While turbidity is normal in some vernal pools (such as those of the Jepson Preserve near Dixon; Barclay and Knight 1984), most undisturbed pools in San Diego County are clear. The turbidity, plus the greater depth of restructured pools, seemed to be the cause of the high plant mortality in the centers of some pools, presumably because of severe light limitation. In the excavated but unseeded pools less than 5% of surface light penetrated to 12 cm, whereas in the natural pools at the same depth 30% light was recorded.

Upon superficial examination one of the most striking features of the restructured pools is the presence, around the basin, of a zone of almost bare soil. It seems that the destruction of the natural soil structure makes mesa soils very inhospitable to plant growth, perhaps because of soil crusting. This bare zone, along with the reduced plant cover in the basins, may be the cause of the high turbidity of the pools.

Leveling transects across disturbed topography showed that filling of ruts in these soils is very slow. In a single year the local relief of 20-cm-deep ruts changed by 1-3 cm. Since the filling process will slow as local relief is reduced, 6 years may be taken as an absolute minimum for the filling of a 20-cm rut, with 10-15 years probably closer to the time it will take for ruts to disappear. This shows how important it is to protect vernal pools against vehicles and emphasizes the critical need to fence vernal pool preserves.

After 4 years of recovery the disturbed area would hardly pass as pristine vernal pool habitat, but all of the plant species seem to have survived and the reseeding, though it speeded the rate of recovery, was probably not necessary. Vernal pool ecosystems show a remarkable ability to reassemble after severe disruption, provided that there is standing water present.

5.3 EVOLUTION OF THE VERNAL POOL ECOSYSTEM

According to current understanding, the modern California flora is the product of a long period of gradually increasing aridity (Raven and Axelrod 1978). In the mid-Tertiary, about 35 million years ago, California already contained many elements of the modern flora: oaks, ceanothus, redwoods, etc., but forests were more prominent and richer in species of broad-leaved trees than they are now. The part of California west of the San Andreas Fault (nearly all of the area in which the coastal vernal pools occur) was far to the south. The portion on the continental plate supported a semi-arid short-tree forest with strong affinities to the subtropical deciduous forests found today in the frost-free climates with both winter and summer rain in western Mexico. Temporary wetlands probably existed at this time, but the major events that followed must have reshuffled the biotas substantially.

In the late Pliocene (3 million - 7 million years ago) several significant events began to reshape the landscape. The Coast and Transverse Ranges emerged, and the Sierra Nevada approached its present height as the seas retreated to form, during the Pleistocene, the coastal terraces that now support most of the coastal vernal pools (Chapter 2). The Central Valley emerged, and although it remained dotted with extensive marshes until historic time, it became available for invasion by terrestrial biotas. These developments account for the distinctiveness of the flora in California. They created a wide variety of habitats including some mild climates, and the high mountains and transmontane deserts isolated California from temperate vegetation to the east. The California biota was enriched by the survival of taxa that went extinct elsewhere in North America (e.g., the redwood) as well as by the proliferation of new species that formed to exploit the diversity of often isolated habitats.

In the Pleistocene the continental glaciers descended across much of North America, but southern California, then as now, was a relative climatic haven where temperatures remained fairly moderate and rainfall increased less drastically. It is thought that it was not until the Pleistocene that the present Mediterranean climate prevailed (Raven and Axelrod 1978), and that before this there was summer as well as winter rain. By the late Pleistocene the state of vegetation in southern California can be gauged very accurately from the macrofossils collected at Rancho La Brea in the Los Angeles Basin. At this time (ca., 25,000 to 40,000 years ago) the vegetation was roughly comparable to that presently found on the Monterey Peninsula, suggesting that glacial activity had shifted the vegetation zones some hundreds of miles to the south along the coast (Warter 1976).

From the late Pleistocene to the present has been a time of great change in both climate and biota. The effect of the glacially influenced climatic variations is illustrated by data from the pluvial (rain-influenced) lakes in the arid west (Figure 61). These data show that the lakes reached their maximum depth and extent from 14,000 to 24,000 years ago, an interval during which the Continental and Cordilleran glaciers reached their maximum size and began to retreat. From 14,000

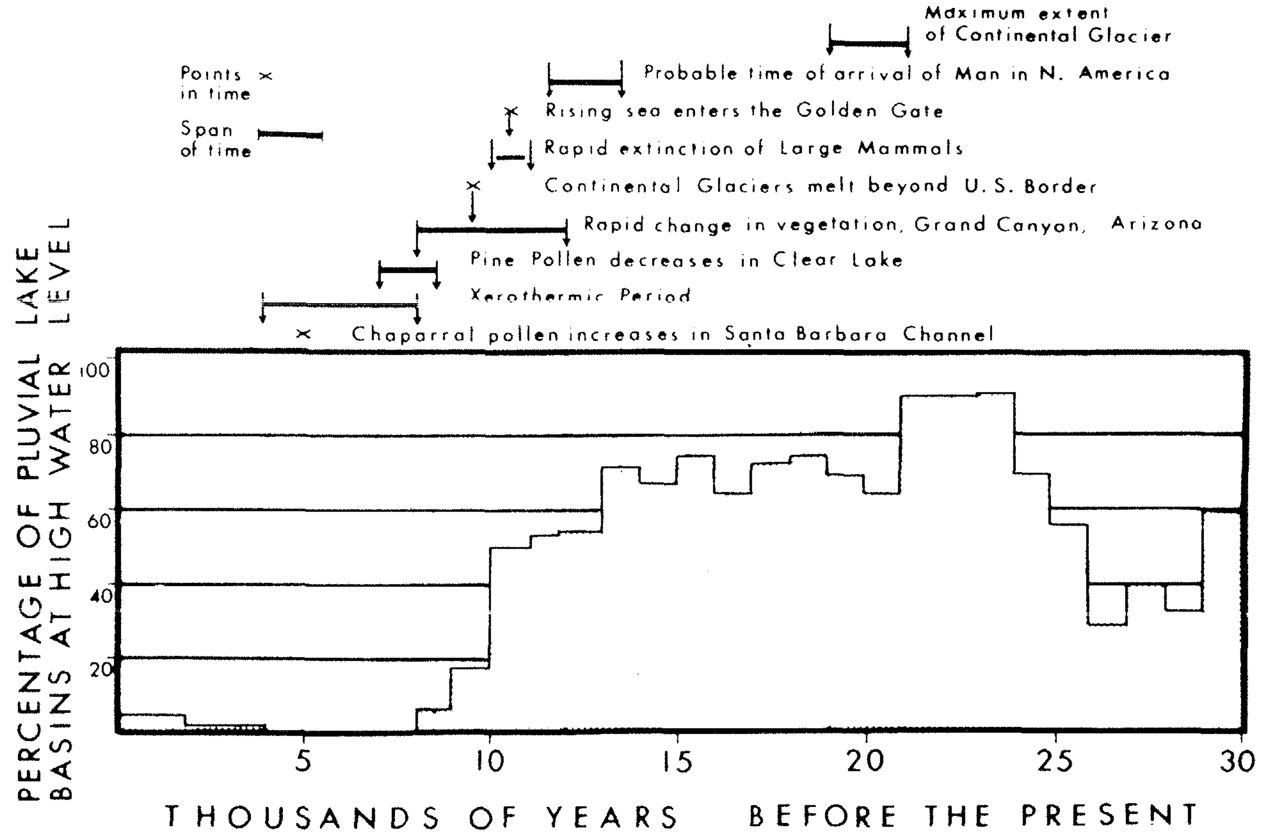

Figure 61. Change in extent of pluvial lakes as indicated by the percentage of lake basins at high levels by 2000-yr intervals and corresponding time of events or processes of importance. Modified from Smith and Street-Perrot (1983).

years ago to about 8000 years ago the lakes rapidly dried, and a period (the Xerothermic) ensued from about 8000-4000 years ago during which the climate was substantially drier than it is today. Axelrod (1966) argued that it was during the Xerothermic that arid vegetation expanded and that the ranges of many moisture-requiring species were contracted and disrupted.

Vernal pool ecosystems probably have been continuously evolving through all this time, but they must have been most strongly influenced by recent (late Pleistocene) climatic variations. Some taxa clearly are very ancient and almost without doubt had close relatives living in temporary water habitats in the Southwest U.S. during the Tertiary. Isoetes and the heterosporous ferns (Marsilea, Pilularia) are widely distributed in the world, usually in aquatic habitats that are temporary or have fluctuating water levels. They must be ancient specialists for temporary water habitats that moved into temporary wetlands of the present landscape as they emerged.

Eryngium is an example of a seed plant genus whose history must also extend back at least to the late Tertiary. This genus also occurs in tropical America, the Mediterranean region, west Asia, and sparingly in Australia and New Zealand. Many of the species occur in marshy or temporarily wet situations including two found in Western Mexico and several in the Eastern and Southeastern United States. Within its family (Apiaceae) it is fairly advanced so that although obviously not a very recent taxon, neither can it be very ancient. All of this suggests that the progenitors of vernal pool Eryngium were almost certainly in the region by at least the late Tertiary and that like Isoetes they moved to these habitats as they became available. This must have occurred well before the last thousands of years, however, because they have differentiated genetically to form new species with a diversity of local populations.

Another similar example is Myosurus, the mousetails. Species in this genus occur in the temperate parts of the Northern and Southern Hemispheres (Stone 1957, 1959), almost always in seasonally wet habitats. The genus belongs to a family usually considered to be primitive within the angiosperms, and therefore it too could be an ancient specialist for temporarily wet habitats. However, unlike Eryngium, the distribution of Myosurus is centered in temperate areas. It may be that the predecessors of the vernal pool mousetail were associated with temperate forests in high-elevation areas or to the north before it migrated to vernal pools. It must have been a part of vernal pool biotas relatively early, however, because it has differentiated within California into a number of taxonomic subunits (Stone 1957).

These examples give the impression that vernal pool biotas may have assembled from a variety of preexisting elements that were ready to exploit vernal pools. But another set of vernal pool plant taxa is unique to California's temporary wetlands, and this is evidence that vernal pools as they exist today are a new ecosystem. At least six genera listed by Raven and Axelrod (1978) as restricted primarily to the California Floristic Province (CFP) are mainly associated with vernal pools: Downingia, Legenere, Limnanthes, Neostapfia, Orcuttia, and Pogogyne. While the possibility that some of these used to be widespread and have survived only in California cannot be absolutely ruled out, the facts fit better with the idea that these groups have differentiated in the CFP relatively recently. In the Limnanthaceae, for example, there are only two genera, Limnanthes and Floerkea. Floerkea is an annual understory plant in rich deciduous forests. It grows for a brief period in the spring in damp microsites. Because in the West such habitats were much more prevalent in the Tertiary than they are today, it is reasonable to suppose that the restricted genus Limnanthes represents an offshoot of an Arcto-Tertiary taxon that has radiated within a semiarid environment. Pogogyne, though probably not derived from forest herbs, may similarly have specialized for vernal pools within the last several million years and differentiated sufficiently to make its connection with more widespread taxa obscure. Genera like Limnanthes and Pogogyne, once specialized for temporary pools, leap-frogged their way across the landscape as vernal pool habitat proliferated on the alluvial landscapes left by retreating seas.

Combining all of this information allows speculation that vernal pool-like communities have existed since at least the late Pliocene. These "Urpools" probably would have had a smaller and less specialized flora than we know today, just as in more humid regions in the Eastern United States the temporary pool habitats support a more generalized flora. With the isolation and increased aridity the tempo of specialization must have quickened. As predominantly forested vegetation gave way to grasslands, shrublands, and open woodlands, and the contrast between wet winters and dry summers sharpened, the stage was set for the development of modern vernal pools. Because California vernal pools can only exist in a semiarid climate, it is probable that their spread and the specialization of their flora were fostered rather than retarded by interglacial dry periods and the more recent Xerothermic period. The pollen record at Clear Lake (Baker 1983) shows a sharp decrease in pines and a corresponding increase in shrubs at the onset of the Xerothermic period. If this decrease in forest cover also occurred on the coastal terraces and inland valleys, the result may have been the opening up of large areas for vernal pool biotas.

The Central Valley is probably the key to the origin of vernal pools. In its original state there was not only more vernal pool habitat than in the rest of the region combined, but also a wide variety of other aquatic habitats. The valley's north-south orientation would have facilitated the migration of species, and might have played a role in allowing the continuing accumulation of biotic diversity through the vicissitudes of glacial times. All of the endemic genera are found in the Central Valley, and it is the only habitat for at least two of them. Most probably vernal pool biotas evolved primarily in the Central Valley and dispersed from there to the south and west as increasing aridity and landscape evolution by weathering or gophers created temporary pools in these areas.

If Dalquest and Scheffer (1942) and Cox (1984a) are correct in believing that pocket gophers formed the microrelief, then the establishment of vernal pools might have followed a somewhat different course. If gophers are the cause of the mounds, there would have been a lag between the appearance of land surfaces and the creation of the pool basins, which might have been quite long in instances where the hardpan is the cause of the shallow soil and therefore of the mounding. But none of the proponents of the gopher theory have suggested that all vernal pool basins were formed by gophers. One possibility is that vernal pool biotas were shaped in larger temporary marshes and pools, and that the mounded topography allegedly formed by gophers merely offered a chance for vernal pool species to expand their ranges.

The foregoing discussion has emphasized the plants. This is mostly because we know more about them, but partly because what we may surmise about the animal component suggests that it contains fewer unique and endemic species. Only the invertebrates seem to be vernal pool specialists, and most of these are wide ranging species that are really more appropriately called temporary pond specialists. Presumably they trace back for many millions of years. A plankton tow in a temporary pond in the Eocene would probably have yielded a similar complement of rotifers, cladocerans, and anostracans. Studies of brine shrimp however, suggest that wide ranging groups of temporary habitats adapt to local conditions (Dana 1984; Bowen et al. 1984). If this is generally true, the argument made above would predict that the tempo of genetic and ecological change of these ancient groups probably picked up in the late Pliocene.

CHAPTER 6. PRACTICAL PROBLEMS

6.1 PROTECTION OF VERNAL POOLS

Most citizens believe that society should preserve natural ecosystems, for economic reasons and purely for aesthetic enjoyment. There is also strong feeling in favor of preserving species of symbolic importance like the bald eagle and giant sequoia. More surprisingly, there is even considerable support for saving obscure rare species, such as the Furbish lousewort (Kellert 1985).

Vernal pools, which contain rare organisms, are beautiful, and are distinctive to the California region, should be a biological asset that the public deems worthy of preservation. Proof of this is that the Nature Conservancy was able to raise $5 million for purchase of the Santa Rosa Plateau from private sources But the protection and acquisition of pools in other instances have not always been as easily accomplished, in large part because preservation has conflicted with development of valuable real estate. Vernal pools occur on the same level topography favored by housing developers and builders of highways. Most of the southern pools occur in the heavily urbanized coastal strip, where land values have soared in recent decades.

Vernal pools also have what politicians might call an "image problem." They are beautiful, but only for a part of the year. Like many arid ecosystems, during the depths of the dry season they exhibit dormant starkness rather than lush beauty. Even in the growing season much of the interest of vernal pools is at a small scale--they require close attention to be appreciated. Perhaps most important, they are not very well known, and those who seek them out may not be certain what they are looking for. Ironically, it is just as they are coming to be more widely appreciated that the last remnants are rapidly disappearing. Though the options are closing rapidly, there are still some choices to be made on the size and arrangement of vernal pool preserves. Equally important is the interrelated question of how the vernal pool preserves will be managed.

6.2 LEGAL ASPECTS OF VERNAL POOL PRESERVATION

The protection of natural areas everywhere was greatly affected through the 1960's and 1970's by legal developments that grew out of concern over pollution and the loss of open space and biological diversity. One of the broadest of these legal concepts is that public undertakings must be accompanied by an assessment of "environmental impact." This is the idea behind the Federal National Environmental Policy Act (NEPA) and the corresponding California Environmental Quality Act (CEQA) of 1970. The details of these laws are complex, but the guiding philosophy is that government should assess the consequences of its actions on the environment from a broad perspective by weighing both the positive and the negative aspects. While often criticized, in the balance NEPA and CEQA have been credited with improving land use in California. However, they have had little direct impact on vernal pool preservation because they require only that impact be assessed and an effort made to minimize it. In no case did this legislation cause any vernal pools to be preserved that would otherwise have been destroyed.

The passage of the Endangered Species Act of 1973 put into law the obligation of the Federal Government to protect species threatened with extinction. This was a long overdue response to the admonition of conservationist Aldo Leopold in midcentury that society take the preservation of the biological integrity of its landscapes as a moral responsibility. What more obvious sign of biological mismanagement, it was reasoned, than the disappearance of species? Hence the need to insure that the Federal Government managed lands with a kind of ecologist's Hippocratic oath -- to do no harm (as measured by extinction) to the lands over which they had jurisdiction. The concept was to identify species on the edge of extinction, and require that government agencies or those working under their authority or consent consult with the U.S. Fish and Wildlife Service whenever one of these species was likely to be affected.

The Endangered Species Act was a major departure from more narrowly conceived preservation efforts because it encompassed both plants and animals. Furthermore, the criteria for degree of endangerment were not public recognition and interest, but a scientific assessment of the significance of the taxon, the size of its population, and the probability of its imminent extinction. By these criteria many animals and plants thought to be worth saving, such as redwoods and elk, were not endangered, while others that most people had never heard of like the Furbish lousewort and the snail darter were judged to be on the verge of extinction.

The State of California, through the Department of Fish and Game, has also developed programs to recognize rare and endangered species and encourage their preservation. The Endangered Plant Program is most relevant to vernal pools and is described by Cochrane (1984). The Nature Conservancy, a private organization interested in the preservation of natural communities, cooperates with the State in the maintenance of the Natural Diversity Data Base, which keeps track of rare and endangered plants and animals and serves as a central storehouse of information on their range and status (Cochrane and Jensen 1984). However, unlike the Federal laws which in certain instances can halt land development, the State provisions are primarily educational, cautionary, and advisory. State law cannot prevent a private landowner from destroying a State-listed plant or animal. The hope is that by making landowners and others aware of the existence of significant biological resources they will encourage development that minimizes damage to them.

The existence of these laws and government policies have set the stage for vernal pool preservation efforts. In the 1970's, southern California botanists, aware of the rapidly disappearing vernal pool habitat, proposed to the Fish and Wildlife Service that <u>Pogogyne abramsii</u> be listed as endangered. After a suitable review, this was done in October 1978. A further important development for wetlands was the extension of the Rivers and Harbors Act of 1899 to give the U.S. Army Corps of Engineers (USACE) jurisdiction over all wetlands, not just navigable waters in the strict traditional sense (Bartel and Knudsen 1984). This obligated the Corps to regulate the destruction of vernal pools, and required them to prevent filling of vernal pools that contained an endangered species.

These laws have had considerable impact in San Diego County. The California Department of Transportation (CALTRANS), aware of the fact that <u>Pogogyne abramsii</u> lay in the path of the extension of Interstate Highway 15, moved quickly in 1978 and 1979 to deal with the problem that this posed (Rieger 1984). Minor changes in freeway alignments bypassed a few pools, but many remained in the right-of-way. After two consultations with the U.S. Fish and Wildlife Service, the outcome was that CALTRANS acquired two areas of natural pools equivalent in area to the pools to be sacrificed.

CALTRANS had to reopen negotiations for State Route 52, which was scheduled to cross an area of vernal pools on the Miramar Naval Air Station. A proposal to apply the same remedy, by purchasing privately owned pools to replace those destroyed, was rejected by CALTRANS when it was determined that this would cost in the vicinity of $5 million. A compromise was worked out that included purchase of pools and creation of additional artificial habitat. Although the area of pools acquired was approximately the same as the area to be destroyed, they were judged to be of lower quality, especially with regard to their suitability as habitat for the endangered Pogogyne abramsii. Additional parcels of lands were therefore acquired on which it is intended to create artificial pools capable of supporting P. abramsii. Because the creation of artificial habitat for a rare species was a relatively untried and controversial means of preservation, CALTRANS was also required to monitor the success of the project for 5 years.

This resolution of the problem is a classic compromise in that it leaves no one completely happy. The landowners were unwilling sellers, and some remain irate at what they view as the confiscation of their land. Conservation groups question the wisdom of the creation of artificial habitat. If it is a failure, it will be impossible or prohibitively expensive to return to the option of buying more pools. If it is successful, the unjustified assumption may be made that the creation of artificial habitat will work for all species everywhere. Conservationists are also painfully aware that the outcome of all these negotiations has not increased the public holdings of vernal pools, while overall the number of pools continues to shrink as more and more areas are developed.

6.3 HOW BEST TO PRESERVE

Ecologists, realizing that the exploitation of the landscape is certain to increase over the next century, have devoted considerable thought to the question of the best design for systems of nature preserves (e.g., Simberloff and Abele 1976; Frankel and Soule 1981; Harris 1984). Among the questions that have been asked are these: Should there be fewer larger or more smaller preserves? Should preserves be clumped together or widely separated? What is the importance of connecting corridors? What aspect of nature preservation should be stressed, maximum species diversity or maximum preservation of representative ecosystems?

Taking a theoretical view, the following points are relevant to vernal pool preservation:

1) Much of the species diversity of vernal pools exists at a large geographical scale. Each region and area has endemics. Preserving pools in only one place will preserve only a fraction of the interesting species.

2) Much of the genetic diversity within a single species is expressed at a large geographical scale. Preserving one group of pools with species X in it, will probably preserve only a part of the genetic diversity of that species.

3) Pool-to-pool dispersal plays an unknown but possibly important role in the population dynamics of vernal pool plants and animals. The drastic reduction in area of vernal pools over the past 75 years may eventually result in reduced local species diversity and greater probability of invasion by introduced species. Small isolated preserves are much more likely to suffer irreversible change than larger preserves near other preserves.

4) The landscape setting of vernal pools is as interesting and worthy of preserving as the pools themselves. Moreover, in many places, and especially in San Diego County, many rare nonpool plants occur in the same areas as vernal pools.

5) Vernal pools, because they are small and can only be appreciated at close range, pose some special management problems in areas open to public use. Compounding the difficulties is the susceptibility of pools to disturbance in the winter when soils are saturated and very soft.

6) On the average, larger pools contain more species than smaller pools, but the variation is so great that in ranking pools for preservation, area can only be considered after other features have been evaluated.

7) Though species number is only loosely related to pool area, certain rare species (e.g., Orcuttia spp.) tend to occur primarily in larger pools.

8) Pool hydrology is a major determinant of pool biota. Available evidence suggests that at least in southern California the perched water table associated with a particular pool is usually very

local. Pool hydrological regimes can usually be maintained with a watershed that is only one to two times the size of the pool basin area. However, local hydrological conditions vary, and study of each situation is necessary when circumstances dictate that land dedicated to preservation be the minimum possible.

9) No one would say that all species in vernal pools should be weighted equally in evaluating which areas have the highest priority for preservation. This is the concept behind the designation of rare and endangered species. By law such species must be given the highest priority.

Considering these points, would it be possible to preserve nearly all of the biotic diversity present in vernal pools by preserving only a fraction of the pools that still exist? Because of point 2, above, the answer is *no*. There is genetic variation in populations that could be maintained only by preserving the sites in which the particular allele or other genetic variant is advantageous. Even if all species were preserved, some genetic diversity is bound to be lost. In theory, the genetic diversity of species could be maintained in artificial culture, but this is unrealistic except for those taxa (e.g., Limnanthes) that have a prospect of economic use.

Dropping one level, would it be possible to preserve all of the vernal pool species by preserving something less than all the current vernal pool area? To this the answer is probably yes, which leads to the further question of how large a proportion of existing pools should be preserved. Theoretical answers to this could be given by working from existing information on species presence in pools. But point nine, above, is relevant here. Species have been weighted differently in deciding on areas to preserve. It is obviously silly to choose pool A over pool B because A has one more species that is a common weed. Thus the question is really how much area is needed to preserve the "priority" species?

A priority ranking of species that suggests itself in this context is 1) legally recognized rare or endangered species, 2) any undesignated species endemic to the set of pools being considered, 3) local populations of species endemic to vernal pools in California, 4) locally disjunct populations of wide-ranging species, 5) scientifically or aesthetically interesting species regardless of rarity. These five categories would probably encompass one-half to two-thirds of the plant species list of pools. Since the animal component of pools is so poorly studied, it is difficult to say what proportion of the faunal list would be included, but it would probably be smaller, one-tenth to one-fourth. Pools could be ranked for priority of preservation by weighting population sizes of each species by preservation priority and summing to get an overall rank.

Having decided which species to preserve, the population ecology of the species must be considered. At this level the goal of preservation is viewed as the preservation of sufficient habitat to allow the species of highest priority a high probability of survival into the indefinite future. To clarify what this means, Shaffer (1981) suggested that a minimum population size should insure a 99% chance of survival for 1000 years. By adopting this admittedly arbitrary definition, he is not assuming that the required probability will be easily determined. In practice, calculations of this kind would necessarily involve many tenuous assumptions.

Though quantitative predictions are difficult, certain qualitative relations are obvious. Species that live in variable environments and undergo large swings in population abundance will require that larger average populations be preserved. This would usually require larger preserves. Similarly, if a species has a very restricted distribution, the size of local reserves would have to be larger since possible extinctions are less likely to be offset by invasion from other habitats. It is very difficult to deal with the potential effect of catastrophes even qualitatively. But the possibility of unanticipated disasters can only argue for more and larger preserves. The introduction of a foreign and highly virulent disease is a particularly worrisome possibility. No species should be preserved in only a single reserve unless this is unavoidable.

Theoretical background is essential to well conceived plans for nature conservation (Harris 1984), but sadly the press of practical affairs often requires that decisions be made by a seat-of-the-pants approach. Rarely do preservation projects involve the rigorous analysis necessary to achieve optimal solutions. The information needed is rarely available and expensive to obtain. Preservation is of necessity a political process in which scientific data is only one element, regrettably sometimes a minor one.

A theorist may view preservation as the process of selecting reserves out of the set of all possible areas. In practice, circumstances often dictate that at a particular time only one area may be available for preservation. Unless the area is of the highest priority in every conceivable way, a critical decision will have to be made--should this area be preserved even if it is not optimal, or should a move be made to acquire some other better area, recognizing that the attempt may fail with the result that nothing is preserved. Because of all these social, political, and scientific complexities, the best preservation plans have usually been the joint products of scientists working with talented and dedicated private citizens acting as volunteers.

6.4 MANAGEMENT OF VERNAL POOL PRESERVES

For the past decade the flow of events has focused interest on saving vernal pools. There has been less attention to how such preserves will be managed once they have been acquired. Eventually this problem will have to be faced, for vernal pools present some difficult management problems. This is especially true in the urbanized areas of southern California, where it is now clear that some vernal pool areas will ultimately be small parcels in the midst of a vast megalopolis.

The chief problem is that vernal pools, while resilient enough to recover from occasional massive disruption, could not withstand continual high levels of use by large numbers of people. Also, unlike mountainous areas, all of a vernal pool area is readily traversed on foot, and much is open to off-road vehicles. If vernal pool areas of less than several hundred acres are designated but left completely open to all kinds of use, their future survival is doubtful.

Fortunately, there is some precedent. The Torrey Pines State Reserve was established with the primary goal of preserving a single species. The public has accepted more severe limitations on access and use than is general in parklands. Trails are fenced, picnicking is prohibited, etc. This model suggests that vernal pools could be managed similarly. A problem is that unlike Torrey Pines Reserve, in which the spectacular ocean views can be enjoyed by people quite indifferent to Torrey pine, vernal pools have a more subtle appeal. Most coastal vernal pool areas, from a distance, can't be distinguished from other areas of chaparral, except that they are flatter than most.

These considerations lead to the conclusion that preservation of vernal pools should be tied in with a public education effort (C. Scheidlinger; pers. comm.). Most people won't know what is special about vernal pools or what is worth looking at without some information. This could be provided in a program in which guides, possibly volunteers, would guide tours of vernal pool areas. Access at other times would have to be controlled to some extent, especially during the wet season. In the summer there would be no reason to limit entry by pedestrians. At all times of year vehicles would have to be excluded, and in a highly populated urban area this means substantial fencing and a minimum of patrol.

The Santa Rosa Plateau vernal pool preserve, recently established by the Nature Conservancy, has been one of the most important developments in vernal pool preservation in southern California. Located in a beautiful setting in a typically southern California landscape, this reserve preserves not only a fine set of vernal pools, but also excellent examples of the associated grassland, chaparral, and oak woodland communities. A full-time manager lives on the property and is responsible for maintaining the scenic and biological values of the reserve. The value of this reserve in educating southern Californians to the natural heritage of their region will obviously be very great. We may hope that the value of preserving vernal pools in other places will be recognized.

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Author's affiliation: Biology Department
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16. Abstract (Limit: 200 words)

Vernal pools are shallow temporary bodies of water that form in winter and spring in the Mediterranean climate region of the Pacific coast. They occur in a diversity of natural settings, often in association with mounded topography. The origin of this mounded topography is still controversial.

The short duration of pools and the extreme variation from standing water to severe drought favor a unique fauna and flora. The organisms of vernal pools have special life history features that fit them to this environment. Some of the plants and many of the animals have cosmopolitan distribution, and are found in temporary wetlands at widely scattered locations. Others are extremely restricted in distribution and many are endemic to clusters of pools within the California biotic province.

Vernal pools have disappeared at an increasing rate over the past 100 years; because of this, several plant taxa associated with them are listed as rare and endangered by the Federal Government and the State of California.

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Vernal pools, topography, Mima mounds, biotic setting, vascular plants, lower plants, invertebrates, vertebrates, ecosystem function, vegetation structure and dynamics, evolution of vernal pool ecosystems, protection, management.

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