ECOLOGICAL STUDY OF VERNAL POOLS, SAN DIEGO COUNTY 1

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Vernal pools occur in heavy soil in areas of scanty rains on mesas and terraces north and east of San Diego and in other localities, chiefly in the cismontane region of southern California. The pool bottoms exist as a highly specialized and unique plant habitat and support a flora distinct from that of the surrounding areas. North and east of the city of San Diego is the Lindavista mesa located in the foggy-desert belt of Russell ('31). A nearly level terrace, it is cut in a few places by gullies, but only where the mesa is flat and where there is no stream development are vernal pools present. This area, during the rainy season, presents thousands of these pools filling the small depressions of the mesa, intercepted throughout by low, rounded hummocks. Ellis ('19) states that the formation of the hummocks is due "to the action of the wind as it sweeps through the sparse desert vegetation and blows away the loose soil except where it is held by plant roots." Barnes (1879) attributes the formation of hummocks to water and wind action, and, to some extent to gophers, as well as to the absence of forests. Excavations made into the soil of pool bottoms show no stratification. As water in the pools is from the mesa-top only it carries little sediment, consequently, the pools are not being filled with silt. During the wet season when the hills and mesas are green with herbage, wind cannot reach the surface to pick up soil particles. Only during the dry summer and early autumn months can the fine particles be picked up from the pool bottoms and deposited against the bases of the shrubs on the hummocks, thus making them higher.

Som

The mesa is covered with reddish-brown or light-red to red loam with well-rounded particles of hard, resistant rocks, mainly quartzitic. Holmes ('18) states, "The surface soil usually gives way at a depth of about eight to eighteen inches to a thin layer of exceedingly compact clay loam or clay, which bakes hard and checks upon exposure during dry periods." Below this layer is reddish or brownish hardpan.

Most of the soil is fine, but, scattered here and there are bottoms with a surface largely of rounded stones and small boulders. The loss of water

¹ Presented before the annual meeting of the Ecological Society of America at Denver, Colorado, June, 1937.

downward into this type of soil is slight due to the water-holding character of the soil. These pool bottoms form a peculiar habitat, distinct from ponds where sediment is deposited in quantities.

WATER

The water of the pools is obtained directly from precipitation and from the run-off of the mesa immediately adjacent to them, and not from distant elevations. Precipitation is meager, averaging 9.8 inches per year, the greater part coming during the months from October to April.² The depressions fill

TABLE I. Monthly totals of precipitation

1934	Sept.	.18	
	Oct.	.42	
	Nov.	1.95	
	Dec.	3.38	depressions with water
1935	Jan.	2.15	ocpressions with mater
1903	Feb.	4.54	
	March	1.42	many depressions dry
	April	1.02	all depressions dry
	May	.02	an depressions dry
		02	
	June Tulo	Ť	
	July		
	August	.18	
	Sept.	.01	
	Oct.	.05	
	Nov.	.07	
4047	Dес.	.74	
1936	Jan.	.75	
	Feb.	5.18	depressions with water
	March	.92	depressions dry
	April	. <u>48</u>	
	May	T	
	June	.01	
	July	.01	
	August	.28	
	Sept.	.04	
	Oct.	1.86	
	Nov.	.44	
	Dec.	4.45	all depressions with water
1937	Jan.	1.52	frost
	Feb.	4.22	
	March	2.65	
	April	.13	most depressions dry
	May	.32	all depressions dry by end of month
	June	.01	
	July	.16	
	August	0	
	Sept.	Ť	
	Oct.	Τ̈́	
	Nov.	.02	
	Dec.	1.06	depressions with water for brief time
1938	Ian.	0.89	many depressions dry
	Feb.	3.26	depressions with water
	March	3.73	debigging with water
	Apríl	0.44	most depressions dry
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² Report of U. S. D. A. Weather Bureau, San Diego.

with the first heavy rain, usually retaining some water until March or April, while the soil may remain moist until May in some of the deeper sections. In 1934–5 the first precipitation sufficient to fill the pools was in December, 1934; water did not fill the depressions again until February of 1936; in the succeeding season, pools filled in December of 1936, while in 1937 the pools obtained some water in December, sufficient amounts did not follow to keep the pools filled. Table I gives the monthly totals of precipitation with notations when depressions were filled with water or were dry.

The temperature of the water varies, the minimum occurring in January of 1935, 1937 and 1938 and February of 1936. Ice formed on the pools during several nights of January, 1937, while the highest recorded temperature, 34° C. was in April. Daily temperatures also vary considerably, the water being decidedly warm to the touch in the afternoons due to the shallowness of the pools.

Acidity was tested weekly in twenty-five pools during one season. Both the Quinhydrone-calomel electrode assembly with a Leeds and Northrup potentiometer ³ and the La Motte set were used. There were variations from pH 5.6 early in March to 7.18 in April, with the majority of the readings between pH 6.13 and 6.55. Since there is practically no run-off there is a tendency for the pools to be acid, due to the accumulation of organic matter.

With the first heavy rains the pools are filled with water and more or less interconnect. After the first run-off from the mesa the pools, almost continuous between the hummocks, soon become reduced in size, the water being retained in what is often referred to as "hog-wallow" depressions, or vernal pools. These vernal pools consequently have an origin and physical character very different from other low, wet areas, such as small ponds or mudholes filled by streams, springs or seepage.

The areas are more or less oval in shape, with the long axis of the pool usually in a north-south direction, but there are many exceptions. In one hundred pools measured there was found a variation in area of from 22 by 35 meters to one less than a square meter. A large number measured between 10 by 15 meters and 3 by 5 meters. The deepest portion of the pools is usually their center where water in the larger pools stands at 25 to 30 centimeters for the first weeks after a rain, to 8 or 10 centimeters in smaller pools.

VEGETATION

The first information regarding the plants in these pools was briefly recorded by Orcutt in 1885 and again in 1887. The pool areas attract attention not only because they are a seasonal feature of the mesa-country but also because of their floristic specialization. Even in very dry years when the rainfall is much below normal, the pools remain delimited in the mesa vegetation and ruderals do not obliterate or greatly trespass their margins. Occasionally

³ Tests made through the courtesy of Kyle F. Williamson, San Diego.

these latter plants may invade though they never establish themselves. The pools, it seems likely, are filled with water at the time that these common species of the mesa are beginning to grow on the surrounding areas, and, hence are too wet a habitat for them. The pool areas support a dense population of specialized plants whose seeds are well soaked before they sprout, whose roots are tolerant to water, slight acidity, water soaked ground and small oxygen supply, whose upper parts are not shade tolerant for the most part and whose period of growth to reach maturity is relatively short.

The following plants are commonly present in the vegetation of the vernal pools.4 Intruders able to grow in this specialized habitat but not restricted to it are marked *: Pilularia americana A. Br., Isoetes howellii Engelm. var. minima (A. A. Eaton) Pfeiffer, I. orcuttii A. A. Eaton, Lilaea subulata Humb. & Bonpl., Phalaris lemmonii Vasey, Alopecurus saccatus Vasey, Deschampsia danthonioides (Trin.) Munro var. gracilis (Vasey) Munz, Eleocharis mamillata Lindb. fil., *Juncus bufonius L., J. triformis Engelm., J. dubius Engelm., *Brodiaea synandra (Heller) Jeps., *B. orcuttii (Greene) Baker, Myosurus minimus L. var. apus Greene, M. minimus L. var. filiformis Greene, *Lepidium nitidum Nutt., Sedum variegatum Wats., Tillaea aquatica L., T. drummondii T. & G., Callitriche marginata Torr. var. longipedunculata (Morong) Jeps., Elatine brachysperma Gray, E. californica Gray, Lythrum hyssopifolia L., Eryngium parishii C. & R., Centunculus minimus L., *Gilia hamata (Greene) Munz, Plagiobothrys acanthocarpus (Piper) Jtn., P. leptocladus (Greene) Jtn., P. undulatus (Piper) Jtn., P. reticulatus (Piper) Jtn. var. rossianorum Jtn., P. bracteatus (Howell) Jtn., P. purerae Jtn., Acanthomintha ilicifolia Gray, Pogogyne nudiuscula Gray, P. abramsii J. T. Howell, Veronica peregrina L. var. xalapensis (H. B. K.) Pennell, *Plantago hookeriana F. & M. var. californica (Greene) Poe, P. heterophylla Nutt., Downingia immaculata Munz & Jtn., Aplopappus venetus (H. B. K.) Blake var. decumbens (Greene) Munz, Psilocarphus tenellus Nutt., P. globiferus (Bert.) Nutt., *Hemizonia fasciculatum (DC.) T. & G., *Baeria chrysostoma F. & M. var. gracilis (DC.) Hall, and Cotula coronopifolia L.

All the species are herbs, with the exception of one decumbent shrub, most of them are fragile and delicate, rarely reaching 15 centimeters in height. All those not starred are usually restricted to the pool bottoms except a few, as Isoetes, Juncus, etc., which may be present in ditches or other hydric locations close by. Certain species are found only in pools which hold water for long periods. No area has one dominant species, although a pool bottom may appear to have but one kind of plant, as Downingia, due to the density of its stand. With the passing of its maturity, however, other plants, as Eryngium, which have been in the seedling stage beneath the Downingia will grow and flower in the same space a few weeks later.

Perennials as *Juncus* and *Cotula* are found in the deeper portions of the larger pools. Annuals are largest in that portion where the water remains

⁴ Nomenclature as given in Munz's Manual of Southern California Botany, 1935.

the longest, those at the shallow edges frequently do not mature sufficiently to produce flowers.

A number of species present in pools on the Lindavista Mesa are also present in desiccating pools on mesas elsewhere in the county. Parish's ('17) list of vegetation of the Red Hill Pools, Riverside County, gives some of the same species as those in San Diego County. Orcutt (1887) states that he found "on the high mesa lands among the hills between the old missions of Santo Tomas and San Vicente, in Lower California, the same species of Pilularia, Elatine, Isoetes, Tillaea and Callitriche that I had previously collected on the mesas back of San Diego City." The author found these and other vernal pool species in pools near Ensenada, Lower California. In South America some of these species also appear in ephemeral pools on the highlands of Chile (Jaffuel, '32).

No comparative studies can be made of the vegetation of the vernal pools with that of ponds, for the mesas on which the pools are found do not have ponds or lakes. The plants present in ponds are species of Salix, Populus, Baccharis and other woody plants, Polygonum and other water plants. No vernal pool plants appear in any stages of the pond life. There is therefore in the vernal pool area a unique habitat with distinctly different plants from those encountered in pond studies.

Variation in the seasonal aspect is so noticeable that it is difficult from week to week to recognize a given depression. This is especially true in a season of small rainfall. In early spring, especially when there is an abundance of water, the algal population is considerable, and as the pools dry and the water level decreases, the seed plants push their way through a mass of algal filaments. Among the more abundant genera of algae are Spirogyra, Zygnema, Microspora and Nostoc. In addition, the ground is covered with liverworts, frequently submerged for a few weeks after heavy rains.

Callitriche is early found floating on the surface and as the water evaporates spreads out on the soil. Isoetes and Pilularia appear early in the season, and as they reach maturity plants of Downingia, Plagiobothrys, Veronica, etc., often growing below the water level, now develop leaves and flowers above the water surface. While Plagiobothrys is flowering, seedlings of Pogogyne begin to mature with its flowering season following that of Plagiobothrys, usually when the soil is dry. Meanwhile, the late flowering plants, as Eryngium have been spreading over the surface and when most of the other plants have withered, it matures on the hard, cracked soil, completing the growing season of the vernal pools. This is a simple explanation of a complicated succession of plants for temperatures of soil and water, amounts of water and other factors vary the conditions from season to season as well as in individual pools throughout the area.

In years that the rainfall is abundant the pools are luxurious with flowers; in dry years there is a paucity both in the kinds and numbers of plants. As most of the year the pool bottoms are dry the wind is able to blow the loose





Fig. 1. Aspect of vernal pools in winter (a) and in late spring (b).

soil particles and scatter the seeds of the pool plants. In addition, birds may play a part in seed distribution as they are frequently seen. Although the seeds of the pool plants are scattered beyond the confines of the pools, they do not grow on the mesa beyond the limits of the pool margins. As has been mentioned the water requirements of the pool plants are not found outside the pool areas.

TABLE II. List quadrats

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per
1	Center of pool; moist April 2, 1937	Tillaea, in flower Psilocarphus Downingia, in bud Pilularia Isoetes Callitriche, in flower Brodiaea	3300 3100 1900 1850 1650 450 90
2	Center; moist April 3, 1937	Tillaea, in flower Psilocarphus Pilularia Downingia, in flower and bud Isoetes Deschampsia, in flower Callitriche, in flower	8500 3800 3200 3100 1800 90 55
3	Center of deep depression; wet April 9, 1937	Myosurus, in flower Baeria, dry spot Scattering of Callitriche	3200 26
4	Shallow; dry; cracked April 9, 1937	Tillaea, in flower Psilacarphus, in flower Lichens Juncus bufanius Plagiobathrys, in flower Callitriche, dried	1100 190 28 16 6
5	Center of pool; damp April 16, 1937	Tillaea, in flower Pilularia Psilocarphus Callitriche, in flower Plagiobothrys, in flower Lythrum Downingia, in flower Isocles Deschampsia Hemizonia, dry corner Eleocharis, in flower	4500 3400 252 110 68 40 32 20 6 2
6	Stony; dry April 16, 1937	Isaeles, dried Tillaea, in flower Downingia, îmmature; depauperate Downingia, in flower Brodiaea orcultii, in bud Deschampsia, in flower	1200 1100 700 360 24 6
7	Water 8 cm. in depth April 17, 1937	Psilocarphus, drier corner Pogogyne Lilaea, in flower Plagiobothrys, in flower; drier corner Rest of quadrat a dense mat of Isoeles, Pilularia, covered with Callitriche and green algae	30 18 16

TABLE II.—Continued

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
8	Pastured; rocky; dry April 17, 1937	Pogogyne Downingia, in flower Deschampsia, in flower Phalaris, in flower Eryngium Hemizonia Weedy grasses (Hordeum and Bro- mus)	850 510 18 5 1 1
9	Just north of burned quadrat No. 24; slightly stony; damp April 19, 1937	Isaetes Psilocarphus, in flower Eleocharis, in flower Downingia, in flower Plagiobathrys, in flower Pogogyne	3110 2880 255 180 80 60
10	Damp; stony April 19, 1937	Pure stand of <i>Pogogyne</i> except for <i>Deschampsia</i> , in flower <i>Brodiaea</i>	8 5
11	Dry; stony April 19, 1937	Pure stand of <i>Pogogyne</i> except for <i>Downingia</i>	2
12	Moist; center of deep depression April 19, 1937	Isoetes Downingia, in flower Psilocarphus, in flower Eleocharis, in flower Deschampsia, in flower Tillaea, in flower Plagiobothrys, in flower Lythrum Cotula, in flower	1600 1500 450 400 110 45 45 10
13	Damp April 20, 1937	Callitriche Isoetes Psilocarphus, in flower Tillaea, in flower Downingia, in flower Brudiaea Eleocharis, in flower Eryngium	900 900 440 310 93 31 29
14	Edge of depression; dry; small stones April 20, 1937	Callitriche Isoetes Myosurus, in flower Psilocarphus, in flower Tillaea, in flower Eryngium Brodiaea Eleocharis, in flower	700 350 200 90 80 17 10 4
15	Edge of depression; dry April 22, 1937	Juncus triformis, in flower Psilocarphus, in flower Downingia, in flower Liverworts Tillaea, in flower Brodiaea Eleacharis, in flower Callitriche, in flower Eryngium	1500 1500 1050 800 450 280 56 55

TABLE II .- Continued

Nuniber of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
16	Deep pool; water April 22, 1937	Eryngium Eleocharis Rest a mass of green algae and Callitriche in water with Isoetes in mud	28 9
17	Deep pool; water April 22, 1937	Downingia, in flower Juncus dubius, in flower Rest a floating mass of green algae; some Callitriche; in mud hun- dreds of Isoeles plants	280 18
18	Edge of depression; dry; somewhat stony April 24, 1937	Isoetes (moister corner) withering Tillaea, in flower Psilocarphus, in flower Downingia, in flower Pogogyne, in flower Deschampsia, in flower Veronica, in flower Eleocharis, in flower Eryngium Brodiaea Hemizonia, drier corner	4040 1170 1110 300 270 150 120 58 18 15 2
19	Center; wet April 24, 1937	Isoetes, much withered Pilularia Downingia, in flower Pogogyne, in flower Callitriche Algae	6000 2200 500 280
20	Edge: damp April 24, 1937	Downingia, in flower Pilularia, withering Isocles, withering Deschampsia, in flower Veronica, in flower Callitriche	1200 600 600 40 40

Population Studies

In making a population study, the list, permanent and denuded quadrats were employed. A square meter, divided into smaller squares was used and in some cases where the vegetation was very dense 10, 20 or 50 square decimeters scattered over the square meter were used and the total computed. Difficulty was encountered in determining an individual plant especially in the cases of *Pilularia* and *Callitriche*. Pools were selected in varied portions of the mesa.

Twenty-five permanent quadrats marked with tags were checked during the spring of 1936 and 1937. There was a great increase in the density of the stands in 1937 as compared to 1936 and 1938, the number being frequently double. Hundreds of plants in marked quadrats never matured in 1936. *Isoctes, Pilularia* and the green algae were much more abundant in

TABLE III. Denuded quadrats

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
21	Top soil removed to depth of 5 cm.; damp April 1, 1937	Callitriche	purestand
22	Top soil removed to depth of 5 cm.; damp April 9, 1937	Lythrum Callitriche, rest of quadrat	3
23	Top soil removed to depth of 3 cm.; rather dry April 16, 1937	Downingia, in flower Brodiaea Lythrum 1/3 of quadrat (deep portion) covered with Callitriche	17 8 2
24	Burned previous season; slightly stony; damp; just south of quadrat No. 9 April 19, 1937	Tillaea, in flower Downingia, in flower Psilocarphus, in flower Pagogyne Callitriche, small amount	1440 6 1 1
25	Top soil removed to depth of 5 cm.; damp April 20, 1937	Downingia, in flower Brodiaea Callitriche sparsely scattered on damp soil	8
26	Burned previous season; damp April 26, 1937	Tillaea, in flower Psilocarphus, in flower Brodiaea Hemizonia Downingia, in flower	82 32 18 14 8
27	Top soil removed to depth of 3 cm.; dry April 26, 1937	Tillaea, in flower Psilocarphus, in flower	2600 44
28	Top soil removed to depth of 8 cm.; moist April 26, 1937	Downingia, in flower Brodiaea Scattering of Callitriche	10 2
29	Top soil removed to depth of 3 cm.; dry April 26, 1937	Brodiaea Downingia, in flower Callitriche	16 11
30	Top soil removed to depth of 3 cm.; deep pool; moist April 26, 1937	Brodiaea Lythrum Abundant with Callitriche	8 1
31	Top soil removed to depth of 3 cm.; dry April 26, 1937	Lythrum Catlitriche	18
32	Top soil removed to depth of 5 cm.; dry April 26, 1937	Pure stand of Callitriche	

1937. In pastured areas there was an increase in grasses, especially weedy grasses and non-pool plants. Low plants as *Isoctes* or *Pilularia* were not cropped, but *Dozeningia* and other larger annuals were eaten closely in 1936 as the mesa grasses withered early in the season. In grazed areas in 1936 less than half as many plants appeared as in 1935, but in the same area not pastured in 1937 there was about 40 per cent increase in the number of plants.

Chart quadrats were made of shallow depressions in 1936 but so much vegetation appeared in these same areas in 1937 that the work was too difficult and was not continued.

No two quadrats are alike, either as to the density of the stand or as to the components of the vegetation. In 1937 the stands were much denser than in 1935 or 1936; the plants were taller and many more plants reached maturity. The count is low where large sized plants predominate, where the pool bottom is stony or where the water remains for a very short period.

First to appear in a pool where previously three to eight centimeters of top soil had been removed is *Callitriche*. There are fewer green algae than in undisturbed pools. The *Callitriche* is soon crowded by *Downingia* and other annuals. Occasionally, plants of *Brodiaea* appear in the shallower pools or at their margins, for their corms buried deeply in the soil were not disturbed when the top soil was removed. In a quadrat denuded by burning the most conspicuous plant is *Tillaea* with a sprinkling of other annuals.

Zonation is varied in that no two pools have the same depth, nor is the depth uniform throughout. Twenty-five pools were tagged and measurements of length, width and depth of the water were taken weekly during one season to check on the zonation, if possible. This was difficult as a heavy rain would increase the depth of the water, inundating plants which ordinarily would not be submerged. The zoning of the pools is not as conspicuous as in poud studies, due to the smallness of the areas treated, the irregularity in amounts of precipitation, the unevenuess in depth of the water and to the smallness of the plants. The zonation is not spacial as in pond studies but rather in this case, temporal, i.e. seasonal. A single species does not, as a rule, form a pure stand, nor are any two or more given pool species found regularly associated together. Then, too, a depression may be moist enough for Isoetes and Pilularia and then dry quickly leaving barely visible plants on the ground, while Downingia and others will be flowering above them. In the deeper sections where water stands to a depth of twenty-five centimeters for a few weeks, we find perennials as Juneus, Cotula, Eryngium and Eleocharis. The water may be clear, but it is usually covered with Callitriche and green algae. In portions slightly shallower there are present Isoctes, Pilularia, Elatine and Myosurus. Psilocarphus, Tillaea, Veronica and Pogogyne are scattered between the deeper portions and the margins. Around the shallow edges are Plagiobothrys and Deschampsia and in the driest portions at the margins are grasses and other mesa plants, invaders from the surrounding areas. Liverworts are abundant in early spring in the moist areas; lichens on some of the dry spots.

GERMINATION STUDIES

From early November to February 1937–8 twenty soil samples from vernal pool bottoms, mesa soil nearby and subsoil were placed in 7 by 10.5 inch trays, covered with two centimeters of water and kept in a sunny location. Temperature ranges were 16° to 33° C. In four days some plants appeared, the maximum number within a month. The highest count was 305 dicotyledons and 40 monocotyledons in one tray. After trays were permitted to dry out thoroughly they were again flooded and the highest count was 145 young plants in the tray just mentioned above. The trays containing soils from the mesa around the pool had but a small percentage of plants and they soon died. Trays with subsoil had as many as 145 dicotyledons and three dicotyledons. Algae appeared in most of the trays, also some liverworts. Undoubtedly, many seeds of mesa plants find in the pools conditions unsuitable for growth. Soil from the surface of the pool bottom had the highest percentage of plants, with *Downingia* predominating.

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SUMMARY

Vernal pools on mesas in various portions of San Diego County are abundant on the Lindavista mesa in the foggy-desert belt, with scant seasonal winter rains. With exposure to full sun, the daily and seasonal fluctuations in the temperature of the water are high as the pools are small and shallow. Within a few months' period the pool bottoms present a rapid change from hydric to extreme xeric conditions.

The flora of the pools is distinct from that of the surrounding areas. No trees or shrubs (except one decumbent one) are present; there are few perennials; annuals are most numerous. The plants are mostly fragile and delicate, less than fifteen centimeters in height.

The seasonal aspect is very noticeable. At first Callitriche and green algae are abundant, then Juncus and Eleocharis become conspicuous along with Pilularia and Isoctes which grow in mud or somewhat submerged. Then Downingia, Plagiobothrys and Psilocarphus appear, then Pogogyne followed by Eryngium growing in the caked dry soil.

List quadrat studies show very dense populations in favorable portions

of a pool and as low as fifty plants per square meter in other portions. Variation depends principally on the amount of water present, on whether the area has been denuded or not, and on the types of plants present. Permanent quadrats show great differences in yearly appearance due to amounts of precipitation and also to grazing.

Zonation is not noticeable. Perennials are present in the deeper portions, while annuals are usually found where it is shallower. Along the margins may be found invaders from the surrounding mesa. Callitriche and green algae frequently cover the surface of the water. Liverworts are abundant on wet soil.

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