5-1962

Ecology of Spring Fed Salt-Marshes

Eric George Bolen

Utah State University

Recommended Citation

Bolen, Eric George, "Ecology of Spring Fed Salt-Marshes" (1962). *All Graduate Theses and Dissertations*. 6257.
https://digitalcommons.usu.edu/etd/6257

ECOLOGY OF SPRING FED SALT-MARSHES

by

Eric George Bolen

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1962

Man has perceived the ideal that natural phenomena fall easily into neat and orderly classes of knowledge and that that knowledge can in turn be rendered into unbending and noteworthy fact. One has but to venture to a salt-marsh lying deep within an arid desert to realize that a waving tule, a marky soil, and the rushing of water from mineral springs can quickly confound such lofty thoughts of orderliness.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the assistance and insight provided by others in the development and completion of this thesis. To ascribe my thanks in the few words which follow is but a token of my indebtedness to these persons.

To Dr. J. B. Low, who served as both academic and project advisor, I offer my sincerest gratitude. The tempered patience of Dr. Low prevented the clouding of my perspective on many occasions throughout my studies. Thanks are also due Dr. A. W. Stokes for providing the initial thoughts in the research program. Dr. T. W. Box generously gave of his time in the development and treatment of the project during the formative stages. I am indebted to Prof. A. H. Holmgren for his capable assistance in identification of plant materials and in preparation of the checklist for the study area. Prof. Holmgren and his staff also provided the necessary talent for inking the transect diagrams and compiling the reference herbaria. To all these men, I am grateful for constructive and critical review of the manuscript.

Gratitude is due the Branch of Refuges, Region II, U. S. Fish and Wildlife Service for financial and logistical support of the study. I am particularly indebted to Mr. L. A. Greenwalt, Refuge Manager, Fish Springs National Wildlife Refuge. His assistance and interest played no little part in the successful completion of field work. The gracious hospitality rendered by Mr. Greenwalt and his family made the desolate life at Fish Springs most enjoyable. Were it not for the able guidance of Mr. J. P.

Harrison, I should have missed many interesting features of the study area.

Use of the unique soil sampler developed by Mr. N. F. Nelson, Refuge Manager, Ogden Bay Refuge, was greatly appreciated. Some nostalgia was added to the drudgery of collecting soil samples with the knowledge that this was the same instrument used by Mr. Nelson during his original and classic studies at Ogden Bay. Dr. S. A. Taylor generously supplied the use of several soil tensiometers. The staff of the Soils Laboratory, Utah State University, offered their facilities for handling the great number of soil samples. Especial thanks are due Mr. J. P. Thorne, Director, for advice and instruction in use of soils equipment. Considerable attention was given by Dr. N. R. Bohidar to the tedious task of checking the statistical analyses. Figures 2, 15, 16, and 17 are the fine artwork of John W. Canary, Jr.

The financial aid of the Society of the Sigma Xi greatly assisted in compiling the material under one cover. I am grateful for the Society's help in the completion of this thesis.

Without the constant and unyielding support, interest, and patient understanding of my parents, Mr. and Mrs. W. F. Bolen, the opportunity for graduate study would not have been possible. To my mother and father this thesis is dedicated.

Eric George Bolen

TABLE OF CONTENTS

Page

Introduction 1

Review of Literature 3

  Tidal-marshes 3
  Inland salt-marshes 4

The Fish Springs Study Area 5

  Location 5
  Topography 6
  Springs 6
  Weather 9

    Temperature 10
    Precipitation 10
    Wind 10
    Climate 12

  History 12

Methods and Materials 20

The Vegetation 23

  Desert Upland Communities 23
  Distichlis Communities 25
  Juncus Border and Juncus Meadow Communities 28
  Phragmites Communities 35
  Eleocharis Meadows 37
  Emergent-marsh Communities 39
  Submersed Communities 43
  Phenological Observations 47
  Indications of Community Succession and Development . . 52

The Soil Factor 60

  Soil Salinity 60

    General Considerations 60
    Community Tolerances 66
    Seasonal and Long Term Changes 73
    Aspects of Plant Competition 76

Page

Soil Moisture 77
Soil pH 81
Soil Organic Matter 86

The Water Factor 92

Water Chemistry 92
Water Fluctuations 95

Effects on Vegetation 97

Summary and Conclusions 100

Literature Cited 103

Appendixes 108

Appendix A. Study Transects 109
Appendix B. Checklist of Collected Plants from the Fish Springs Study Area 120

LIST OF TABLES

Table Page

1. Flowage rates and aspect for six charted springs, Fish Springs National Wildlife Refuge 8

2. Temperature data for Fish Springs National Wildlife Refuge, 1949 to 1955, inclusive (after Shearer, 1956) 11

3. Precipitation data for Fish Springs National Wildlife Refuge, 1949 to 1955, inclusive (after Shearer, 1956) . 11

4. Community characteristics of Distichlis Meadows based on 22 randomly located plots, Fish Springs National Wildlife Refuge, 1960 25

5. Community characteristics of codominant *Distichlis* communities based on 72 randomly located plots, Fish Springs National Wildlife Refuge, 1960 26

6. Community characteristics of Juncus Meadows based on 18 randomly located plots, Fish Springs National Wildlife Refuge, 1960 32

7. Community characteristics of Juncus Borders based on 12 randomly located plots, Fish Springs National Wildlife Refuge, 1960 33

8. Community characteristics of *Phragmites* based on 18 randomly located plots, Fish Springs National Wildlife Refuge, 1960 37

9. Community characteristics of Eleocharis Meadows based on 10 randomly located plots, Fish Springs National Wildlife Refuge, 1960 38

10. Community characteristics of emergent marsh vegetation based on 73 randomly located plots, Fish Springs National Wildlife Refuge, 1960 41

11. Phenological observations of initial growth and anthesis of selected plant species, Fish Springs National Wildlife Refuge, 1960 50

12. Conductivity ranges and plant responses based upon the data of Scofield (1942) for agricultural crops . . . 61

Table Page

13. Mean conductivities in millimhos from 1:5 soil suspensions for three depths of emersed or submersed soils. Sample size in parenthesis 62

14. Analysis of variance of 1:5 soil suspension conductivities to study the effects and interaction of soil depth and water coverage upon soil salinity. Analysis based upon 750 soil samples 64

15. Mean conductivities in millimhos from 1:5 soil suspensions for four emersed and six submersed-soil marsh communities . 67

16. Comparison of mean salinity values from Table 15 for plant communities studied at Fish Springs. Values shown are the highest level of statistical significance above .50 confidence level as determined by "t" test. Calculated "t" values appear in parenthesis. Salinity values for *Chara-Ruppia* communities not compared 68

17. Fluctuations of mean soil salinity with changes in time as determined by increases or decreases in conductivities of 1:5 soil suspensions from Transects Numbers 1 and 2, April and August, 1960. All figures are millimhos of conductivity based on 300 soil samples 75

18. Mean soil moisture tensions for the first 6 inches of soil in emersed soil communities 78

19. Maximum, median, and minimum pH readings for four emersed and six submersed-soil marsh communities at three soil depths 85

20. Soil organic matter, expressed in percentage organic carbon, occurring in the first 6 inches of soil for four emersed and six submersed-soil plant communities 88

21. Water analyses for three major springs, Fish Springs National Wildlife Refuge, 1959. Data shown in parts per million and equivalent parts per million for each ion 93

22. Water level fluctuations based upon data representative of each type of drainage habitat. Slough A located nearer water source than slough B. Maximum fluctuation data are qualified (see text). All figures are inches and are plus unless otherwise indicated by a minus sign 96

23. Checklist of collected plants from the Fish Springs study area 121

LIST OF FIGURES

Figure Page

1. Aerial view of North Spring drainage showing twisting sloughs running east from mountain base. Snow capped peaks to rear are the Deep Creek Range, those nearest are the Fish Springs Mountains. Open marsh area lies further to right and out of photo. Photo courtesy U. S. Fish and Wildlife Service 7

2. Temperature-precipitation climograph for Fish Springs National Wildlife Refuge. Data compiled from Shearer (1956) 13

3. Distichlis Meadow panorama showing pronounced changes with the incidence of *Sporobolus airoides* at upper right. Both plant types were designated Distichlis Complex vegetation but structural differences appear in text. Vegetation in foreground is a pure stand of *Distichlis stricta* 27

4. *Tamarix pentandra* surrounding abandoned ranch buildings (obscured). This stand is believed to have served as parent stock for those individuals found along ditches elsewhere throughout the study area. Photo courtesy U. S. Fish and Wildlife Service 29

5. Panne of Juncus Meadow. Surrounding vegetation is Distichlis Complex, mostly *Distichlis-Sporobolus*. Foothill to right shows typical upland desert community of *Atriplex confertifolia* and associated species. View is looking southwest at the Fish Springs Mountains 30

6. Twisting depression of Juncus Meadow. Surrounding vegetation is Distichlis Complex, mostly *Distichlis-Sporobolus*. Dark line near horizon is the expansion of the depression into a panne formation 31

7. Juncus Border along slough edge. Vegetation of the Border includes individuals of *Sporobolus airoides*. Emergent-marsh lies to left while Distichlis Complex, mostly *Distichlis-Sporobolus* and *Distichlis-Salicornia* is shown at right. Note *Phragmites* invasion of the Border at right-rear and transect marker in foreground 34

8. *Phragmites* development in Distichlis Complex vegetation. Stems are less than 4 feet tall and thinly dispersed. For more typical *Phragmites* growth along marsh edges, see Figure 7 36

9. Aerial view of marsh mosaic. Light areas are plateaus, dark spots are open water. Vegetation is predominately *Scirpus olneyi*. Photo courtesy U. S. Fish and Wildlife Service . . 40

Figure Page

10. Small communities of *Scirpus acutus* (left) and *Typha* (right). *S. acutus* usually occupied a zone to the water side of other emergent-marsh species but several exceptions made this distinction unreliable. Vegetation to extreme left (background) is *S. olneyi* 44

11. Singular community of *Scirpus paludosus* on both sides of isolated slough. Dark line of vegetation along slough edge is Juncus Border. Small patches of *S. acutus* occupy shallow slough habitat to right and left-center (faint). Trees in distance are shown in more detail in Figure 4. Note ancient lake shores marked on mountain sides . . 45

12. *Chara*-*Ruppia* community in slough bottom. Water has receeded slightly (note gauge in slough near clump at left-center) exposing submersed vegetation. Vegetation along slough banks is *Scirpus olneyi*. Tall stand of *Phragmites* rises behind *S. olneyi* growth to right-center of photo . 46

13. Beginnings of *Najas marina* blockage near South Spring outlet. Water passage became increasingly hindered as these mats enlarged. Dark vegetation on horizon is *Scirpus olneyi*. Note water clarity 48

14. South Spring. Clear water shows submersed vegetation of *Ceratophyllum demersum*, *Utricularia vulgaris*, and *Chara-Ruppia*. Shrubby plants along spring edge are *Tamarix* (note flowers on individual in right-corner at bottom) . 49

15. Linear relationship of 1:5 soil suspension conductivities to saturation extract conductivities and percentage soluble salt in air dry soil. The broken line shows that 5 millimhos of conductivity from a 1:5 soil suspension equals 44.5 saturation extract millimhos and 1.5 percent salt. Inset shows conversion of percent to parts per million. Data compiled from Nelson (1954) and Richards (1954) . . . 63

16. Relationship of 1:5 soil suspension conductivities to osmotic pressures of soil solution. Averages of 0-6 inch and 7-12 inch conductivities from Table 15 for each of the plant communities studied have been superimposed upon the plot to show the osmotic limitations confronting the communities 80

17. Median (darkened areas) and range of pH for 750 soil samples from three sampling depths. Emersed soils (hatched) show slightly more alkaline medians than submersed soils. Ranges show a reciprocal trend with depth of sampling; ranges of emersed soils decrease while submersed ranges increase as soils deepen 84

Figure Page

18. Transect No. 1: plant communities and edaphic data . . 110

19. Transect No. 2: plant communities and edaphic data . . 111

20. Transect No. 3: plant communities and edaphic data . . 112

21. Transect No. 4: plant communities and edaphic data . . 113

22. Transect No. 5: plant communities and edaphic data . . 114

23. Transect No. 6: plant communities and edaphic data . . 115

24. Transect No. 7: plant communities and edaphic data . . 116

25. Transect No. 8: plant communities and edaphic data . . 117

26. Transect No. 9: plant communities and edaphic data . . 118

27. Transect No. 10: plant communities and edaphic data . . 119

INTRODUCTION

Any marsh is a distinctive land-form of varied interest. To the agriculturist it is wasteland to be reclaimed; to the naturalist, a habitat of aesthetic value. To the ecologist, however, a marsh represents a complexity of vegetation under the influences of many and often inseparable factors. It becomes a place of challenging study.

There exists a notable lack of information treating the ecology of inland salt-marshes. Still less known are the ecological conditions imposed upon plant life in marshes arising from saline springs. The presence of such a wetland in western Utah afforded the opportunity to study salt-marsh vegetation in a highly specialized habitat.

The study had two phases. First was a study of the vegetation. Data were secured from collections and study plots within each of the major marsh communities. General descriptions of other plant life were additionally compiled.

It is not within the scope of this paper to discuss or rigidly define the requirements embraced in the use of "community" as a unit of vegetation. Sufficient references are available for those who wish to pursue the point. In this study, a community is a congregation of plants exhibiting differences in appearance and species composition from other plant congregations.

Secondly, studies were directed to the influences of soil and water on the ecology of each community. Transects were used to investigate many of these relationships. Transition zones between communities were narrow and usually sharply delineated. Transects intersected ecotones of this sort; environmental differences which may have occurred in the few broader ecotones were assumed to be of equal magnitude but of more gradual rate of change. Relatively short transects thus adequately represented each community yet allowed collection of intensive data.

Information and data were collected during a 5-week period in August and September 1959 and a 6-month period beginning in March 1960.

REVIEW OF LITERATURE

The subject of plant ecology, whether of marshes, forests, or prairies, encompasses a vast wealth of published material. A comprehensive review of these many works would add little to the present considerations of salt-marsh ecology. Failure, however, to acknowledge the textbook treatments of plant ecology by Weaver and Clements (1938), Dansereau (1957), Oosting (1958), and Daubenmire (1959) would be remiss. Their approach to this highly complex subject covered not a few of the many factors which affect plant life of all forms. A more specific review of literature dealing with the ecology of salt-marshes follows.

Tidal-marshes

Plant ecologists have paid considerable attention to the coastal marshlands of the eastern seaboard. Miller and Egler (1950), in their analysis of tidal-marsh communities, included a reference bibliography covering the more important studies to that time. Penfound and Hathaway (1938) aptly described gulf coast marshes and included considerations of salt-marsh phenology and salt tolerance. Gillham (1957) investigated the relationships of salinity and soil reaction to tidal vegetation along the English coast. Purer (1942) studied the ecology of California marshlands.

Chapman (1938, 1939, 1940b) treated the patterns of plant succession on New England salt-marshes. He demonstrated that coastal vegetation may follow several routes to maximum expression. Other studies (Chapman, 1940) concerned environmental effects on tidal-marsh vegetation. Over 20 years of salt-marsh research resulted in Chapman's (1960) treatise on the subject. His volume, covering salt-marsh vegetation the world over, primarily considered coastal ecology but also reported inland salt-marsh conditions.

Taylor's (1939) investigations revealed differences in growth between laboratory and field conditions for many tidal-marsh species. Bourn and Cottam (1950) studied the biological aftermaths of mosquito-ditching in tideland areas. Wherry (1920) believed soil acidity and alkalinity had much to do with the separation and zonation of coastal vegetation. Davis (1895, 1911) studied the flora and habitat correlations of tidal-marshes.

Inland Salt-marshes

In contrast to coastal marshes, little is known of inland salt-marshes. Jensen (1939) underscored the importance of edaphic relationships in the distribution of aquatic plants. McMillian (1959) investigated the salt tolerance within a Typha community. Ellis (1955) made preliminary studies on the correlation between alkalinity and the distribution of several aquatic species. Evans (1953) and Rawson and Moore (1944) treated the ecology of vegetation surrounding saline lakes. Keith (1955, 1958, 1961) related soil salinity changes to waterfowl habitat.

Nelson's (1954) work at Ogden Bay Refuge was the most rewarding publication reviewed. His study reported the ecological changes which occurred with the addition of fresh water to salt-marsh and saline wastelands. No literature treating the ecology of marshlands arising from saline springs was found.

THE FISH SPRINGS STUDY AREA

In the arid regions of western Utah, a valley of lush green breaks the monotony of barren mountains and endless tracts of desert vegetation. Here a series of springs flows forth from the base of a rugged mountain range. For millennia, these waters have drained into the broad valley creating thousands of acres of saline marshland. These are the Fish Springs marshes.

Location

Located some 35 miles east of the Nevada border, Fish Springs is situated on the northern boundary of Juab County, 140 miles southwest of Salt Lake City. The sparcity of settlement in western Juab County is readily apparent from a map of the area. Towns are widely separated and are but clusters of ranch buildings. Such is Callao, a town of five families, which lies 23 miles west of Fish Springs. Eighty miles to the south, in adjoining Millard County, is Delta, Utah. Dugway Proving Ground, an Army Chemical Corps installation, is 66 miles to the east. North from the marshes, the wastes of the Great Salt Lake Desert form an uninhabitable alkali blanket.

The Callao-Tooele Road, an improved gravel roadway, provides the only access to Fish Springs. From this road several unmaintained dirt roads serve as connections to the outlying sections of the marshes. Along these crude lanes are the sloughs and ponds that form a labyrinth of waterways within the study area.

Topography

The marshes lie in a basin bordered by the Fish Springs Mountains to the west and by rolling dunes along their other perimeters. Inundation is confined to an area about 6 miles long and 3 miles wide. The basin floor slopes gently north and eastward and is underlain with an impermeable layer of hardpan. Elevations within the basin decrease to the north from 4,302 feet to 4,287 feet above mean sea level for an average decrease of 2.6 feet per mile. Eastward, the basin slopes at a rate of 6.6 feet per mile from 4,310 feet to 4,290 feet above mean sea level.

Moraine-like ridges winding along the foot of the Fish Springs Range bear mute evidence to the shoreline washes of ancient Lake Bonneville. Etched deep into these banks are gullies cut by the periodic run-offs from the slopes above. Following intense rain, these rills continue their way to the basin floor and flow into the marshes along the western rim.

Twisting depressions within the basin form shallow sloughs (Figure 1). Where slight increases in elevation occur, these sloughs have backed up to create expanses of marsh. In these regions, many islands or plateaus, varying in size from a few square feet to several acres, rise above the water level to increase further the ratio of edge to surface area.

Man has attempted to exert his influence upon the marshes. Early land owners constructed dikes near the springs and channeled a myriad of ditches in efforts to control the water for irrigation. These attempts largely resulted in rerouting water near the springs but have not materially altered the outlying marshlands.

Springs

With their source hidden in the mountains to the west, the springs

Figure 1. Aerial view of North Spring drainage showing twisting sloughs running east from mountain base. Snow capped peaks to rear are the Deep Creek Range, those nearest are the Fish Springs Mountains. Open marsh area lies further to right and out of photo. Photo courtesy U. S. Fish and Wildlife Service.

of the study area lie in a linear fashion at the foot of the Fish Springs Range. Three major springs and a number of lesser springs supply the marshes with water. `The six springs which have been charted (Table 1) contribute a combined total of 43.5 second-feet of water to the basin (McBride, 1939). Considering, however, the many uncharted smaller springs, 45 to 50 second-feet would be a more probable estimate for the total flow into the marshes.

Table 1. Flowage rates and aspect for six charted springs, Fish Springs National Wildlife Refuge

Spring	Flow in second-feet (McBride, 1939)	Aspect
North Spring	5.0	Large diked pond; pipe flume
Walter's Spring	0.5	Shallow pool; undeveloped
House Springs	7.0	Several deep springs connected by natural channels; some with control structures
Middle Spring (Frog Pond)	12.7	Large diked pond; pipe flume
Scott's Spring	2.5	Crater-like spring; undeveloped
South Spring	15.8	Large diked pond; headwaters for irrigation ditch leading to other spring areas
Total measured flow	43.5	

The springs vary in appearance (Table 1). As a result of intense efforts by former residents to control and divert the waters, the larger springs were enclosed on one or more sides by dikes. In some cases, two or more adjacent spring orifices were collectively diked, today lending the appearance of a single large spring. Pipe flumes within the earthen dikes convey the water to ditches in rushing streams. Thus, the original depth and aspect of these springs have been considerably altered. Others remain untouched. Scott's Spring, for example, emerges from a vertical-sided crater some 15 feet in depth. Here the only evidence of water movement comes from the gentle motion of filamentous green algae which line the steep walls. In contrast, Walter's Spring is but a small pool in a shallow depression, its silty bottom overlain with less than a foot of water.

Common to all the springs are the schools of fish. While only *Gila atraria* Girard (Utah chub) have been positively identified (Woodbury, 1957), it has been suggested that *Gambusia* spp. (mosquitofish) may also be present. The former are thought to be remnants of Lake Bonneville fauna and the latter an introduced species.

Away from the marshes, to the northwest, several hot springs cleave the barren salt flats. One of these has served as a "health spring" for the arthritic for many years; the others, which approach near-boiling temperatures, are far too hot for bathing. As the springs of the study area are warm, about 80 F, it would seem likely that the hot springs are a link in the aquifer which leads to Fish Springs from the west.

Weather

Vegetation depends upon prevailing climate for its development. Temperature, precipitation, and wind are the climatic factors which combine to influence the biota of an area (Dansereau, 1957). A summary of these conditions was compiled from existing records from Dugway Proving Ground (Shearer, 1956). Dugway lies 42.5 air miles to the east and is partitioned from Fish Springs by the Dugway Mountains.

Temperature

Temperatures for Fish Springs appear in Table 2. The mean annual temperature was 51.3 F with an average annual maximum of 65.3 F and an average annual minimum of 37.6 F. January and July were the coldest and warmest months, respectively. The annual range of average temperatures was 50.8 F. The extremes, 109 to -15 F, showed a range of 124 F. Shearer (1956) cited these temperature conditions as the continental type.

Precipitation

The precipitation at Fish Springs depends upon migratory cyclonic disturbances and summer thundershowers. Table 3 shows that only 12.9 percent of the annual average of 7.13 inches fell during the months of July, August, and September.

In addition, Table 3 presents the average monthly snowfall. The high of 7.2 inches for March has been exaggerated by a record 19.2 inches of snowfall in 1952. The average annual snowfall accounted for approximately 2 inches of the total annual precipitation and indicated a snow to water ratio of nearly 10 to 1.

Wind

Wind is due either to differences in atmospheric pressures or the presence of a temperature gradient. At Fish Springs, winds result from both these factors; namely, (a) regional winds associated with poly-directional pressure systems which are migratory, and (b) local winds, northwesterly and southwesterly in direction, which are created by inter-basinal temperature differences. Fish Springs lies in a pathway of

Table 2. Temperature data for Fish Springs National Wildlife Refuge, 1949 to 1955, inclusive (after Shearer, 1956)

Month	Degrees F				
	Average	Average maximum	Average minimum	Maximum	Minimum
January	27.3	38.7	16.9	66	-15
February	34.0	45.4	23.0	71	- 3
March	37.6	49.4	25.6	74	- 7
April	49.1	62.3	34.9	83	14
May	59.9	73.9	44.8	94	29
June	66.8	81.9	50.7	107	33
July	78.1	94.4	61.2	109	41
August	76.1	91.7	60.0	104	38
September	65.7	82.6	48.3	101	26
October	53.8	69.8	37.8	87	20
November	38.6	54.0	26.6	73	- 9
December	29.4	39.3	21.2	55	- 1
Mean[a]	51.3	65.3	37.6	-	-

[a] Mean values have been supplied by the writer.

Table 3. Precipitation data for Fish Springs National Wildlife Refuge, 1949 to 1955, inclusive (after Shearer, 1956)

Month	Inches	
	Total precipitation	Snowfall
January	0.56	3.80
February	0.29	1.58
March	1.45[a]	7.30[a]
April	0.91	Trace
May	0.48	Trace
June	0.85	0.06
July	0.34	0.00
August	0.29	0.00
September	0.27	0.00
October	0.50	2.40
November	0.60	2.00
December	0.59	2.60
Annual total	7.13	19.74

[a] Influenced by a record snowfall of 19.2 inches in 1952.

airmass exchange between the Sevier Basin and the Great Salt Lake Desert.

Climate

Dansereau (1957) defined a half-desert as an area in which the annual rainfall, expressed in centimeters, is more than the annual mean temperature in degrees C, but less than twice that value. By this conversion (from Tables 2 and 3), the Fish Springs study area falls within the half-desert classification. Koppen (in Dansereau, 1957) described a half-desert as a steppe or semi-arid climate with a summer dry season. This description fits well with the data of Table 3. Under these conditions, evaporation exceeds precipitation, and water storage is accomplished during the winter due to low but frequent precipitation and a reduction in evaporation.

A popular method of portraying the climatology of a region is the climograph (Ball, 1910). Plotting of temperature-precipitation values is widely accepted for comparative purposes. Data appearing in Tables 2 and 3 are summarized in Figure 2.

History

That Fish Springs was long a focal point of life for the Indian and pioneer may be appreciated by its isolated supply of water. Watering areas were widely separated and the many miles of desert surrounding the springs precluded further passage without pause. It was upon the abundant waters of this remote area that the historical role of Fish Springs was founded.

Preceding exploration by white man, Fish Springs was known only to the Indian. Here the Goshutes, a tribal relation of the Piutes, had encamped near the springs and in the caves of nearby mountains. Today, evidence of Goshute life remains in the bits of rush matting, pottery

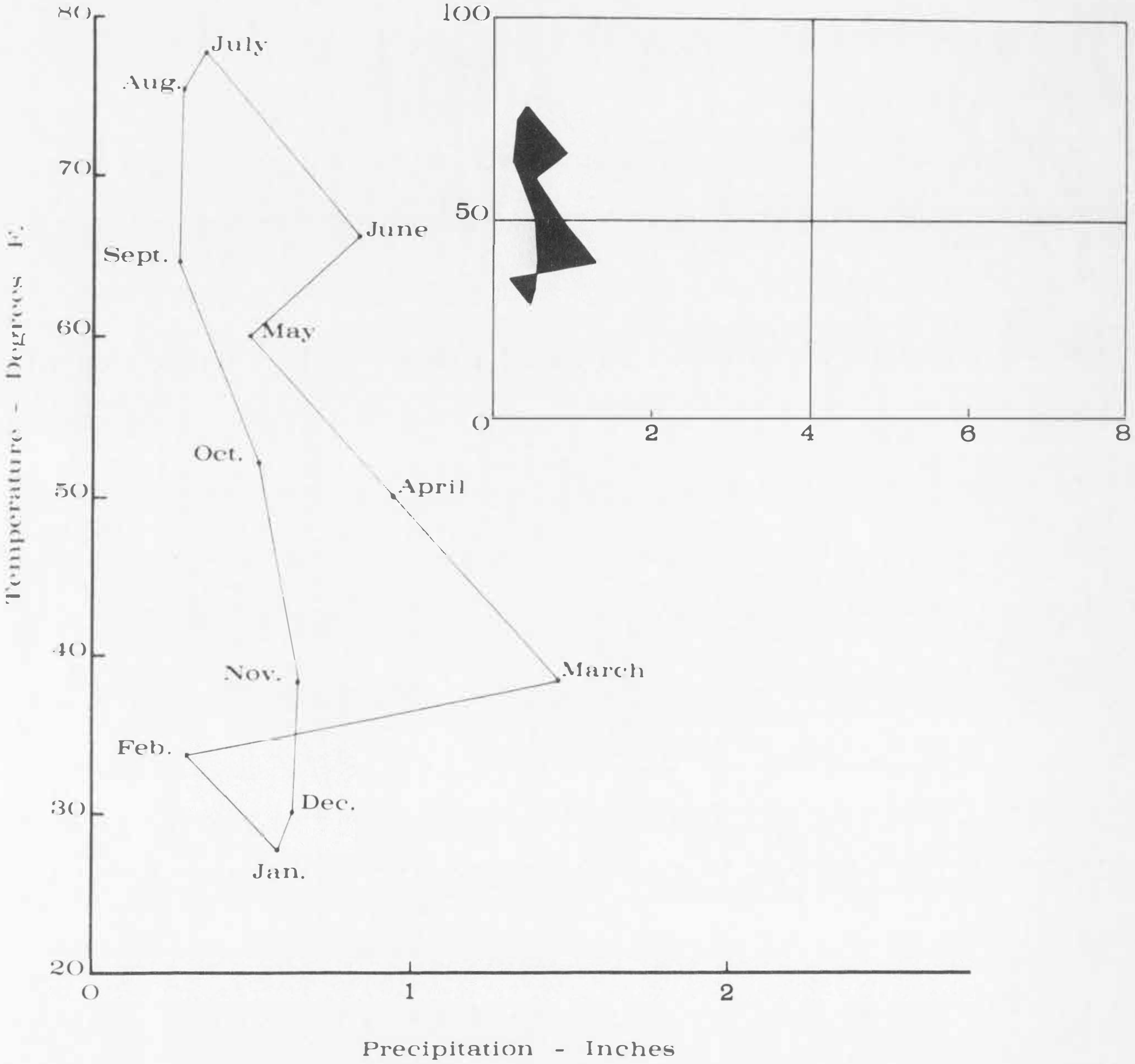

Figure 2. Temperature-precipitation climograph for Fish Springs National Wildlife Refuge. Data compiled from Shearer (1956).

shards, and chips of arrowpoints scattered throughout the study area. From the Indians, the word "Juab", meaning flat, has been taken for the name of the county in which Fish Springs now lies.

Much of western Utah remained unknown, save for the nomadic wanderings of trappers and prospectors, until Captain J. H. Simpson of the Army's Corps of Topographical Engineers began his explorations in 1859. His journals (Simpson, 1876), published as "Report of Explorations Across the Great Basin of the Territory of Utah for a Direct Wagon-Route from Camp Floyd to Genoa, in Carson Valley," makes mention of the Fish Springs area.

Simpson and his party camped at Fish Springs (Camp No. 5) on May 6-7, 1859, while on their westward march. His journal for that day contains the following entry (Pg. 50):

> There is a mail-station at these springs, where we are encamped. At present the only shelter is a thatched shed. The mail-agent reports that it is perfectly impracticable to shorten the route by striking across the valley to this station, on account of the alkaline flat, which will scarcely allow animals with packs to cross. The springs are large and copious, very clear, the bottom presenting a whitish appearance, with a hue of green. An innumerable quantity of fish are to be seen sporting in the water. We have caught some specimens. They are about 6 inches long, have darkish, speckled scales, and seem to be a kind of chub. They are very inferior for the table. The water is slightly brackish and lukewarm, but when allowed to cool is palatable.

Simpson (1876, Pg. 151) summarized his findings in a table entitled "Itinerary of the more northern or outward wagon-route from Camp Floyd, Utah, to Genoa, in Carson Valley." In the table, a suggested sequence of stops were briefly described and located in respect to the distance from the route's origin. Fish Springs was the fifth stop on the proposed trail and was characterized as a campsite 92.8 miles from Camp Floyd with a mail station, saline grass, palatable water and greasewood fuel. A footnote cautioned, however, that "In order to cross the desert between

Simpson's Spring and Fish Springs...with comfort, water kegs should be provided the persons of the party, and at least two grain-feeds for the drought-animals..."

During the same year as Simpson's expedition, the Overland Stage and Freight Company established its western route. The stage line made use of Fish Springs as a watering stop for the stock animals before encountering the desert ahead. Prior to Simpson's visit the line had used mules to continue the journey from Simpson's Spring to the Humbolt River in Nevada. However, on May 8, 1859, the road to Ruby Valley had been sufficiently completed to allow the "mail-stage" to "run the next trip as far as the station in that valley from Camp Floyd" (Simpson, 1876).

Following the route of the stage line, the Central Overland and Pike's Peak Express Company, popularly known as the Pony Express or Pony, was granted a governmental charter to carry mail between St. Joseph, Missouri, and Sacramento, California. Fish Springs afforded a convenient location for a relay station and during the early months of the venture, a stone building was constructed near House Springs.

The first rider to make the 80-mile trip from Deep Creek (now Ibapah, Utah) to Camp Floyd, and hence through Fish Springs, was one George Thatcher (Carter, 1952). Not all of the riders completed their runs, however. Near the Fish Springs station, the unmarked graves of two riders confirm the journey's many hazards.

When the telegraph lines between Fort Churchill and Salt Lake City were connected in 1861, the first transcontinental system of direct communication had been completed. The poles carrying the lines numbered 25 to 30 per mile and averaged 22 feet in length (Browne, 1868). Several salt-encrusted stumps of these poles are still to be found emerging from the salt flats near the southern edge of the Fish Springs marshes.

The Pony Express became history with the completion of the telegraph line. With its passing, the stone relay station was abandoned and later dismantled for use as core material in the dike enclosing South Spring (J. P. Harrison, in per. comm.). Still remaining, however, is the building's foundation surrounding the packed earthen floor.

Much later, in the present century, the route of the express and telegraph lines became a section of the first road to cross the country. The Lincoln Highway followed the southern edge of the study area then abruptly swung northward along the foot of the Fish Springs Range. The Firestone Rubber Company later constructed the "Firestone Cutoff" which deleted this section of roadway from use.

Recorded history left Fish Springs unknown from the close of the Pony Express until 1883, when Mrs. Hilda Ericson, presently of Grantsville, Utah, traveled en route from Deep Creek to Salt Lake City. Mrs. Ericson, then a young girl, periodically made this trip by horse and wagon to secure goods for a store her family operated in Deep Creek. In conversation with the writer on September 7, 1959, she recalled Fish Springs as a slick, muddy area on the route and that passage near the springs was most difficult. During this period, Mrs. Ericson remembered that a family by the name of Smith resided near House Springs. No further information of these early residents was available.

On the western slopes of the Fish Springs Mountains, the decaying ghost town of Fish Springs stands near the once productive Utah Mine. While Leech (1891) mentions a "falling off" of silver production in Juab County, he later cited (1892) that Fish Springs "about doubled its output" during the second year as a mining district. The mine's main shaft later filled with water and was abandoned.

On a rocky hill near the town lie the mounds of eight graves. Seven of these are marked with wooden crosses reading "Unknown" or "Unknown Child." The eighth grave is indicated by a polished stone which reads: "Andrew Pearson, A Native of Scandinavia, Died January 9, 1904." Unsubstantiated rumors attribute these deaths to an epidemic of smallpox.

Long time residents of the area recalled that Arthur Stewart, of Lehi, Utah, settled at Fish Springs in the 1890's and that a relative of his, John Thomas, soon followed (Harold Parker of Trout Creek, Utah, in per. comm.). Utah Land Office records show that Thomas bought land at Fish Springs in 1902. He was the first person known to have raised cattle there, though grazing undoubtedly existed before that time. The only building of this period still standing was built of telegraph poles by Thomas. Succeeding residents have since enlarged the single room structure with several additions.

After successive ownership by a man named Everett and a Dr. Davis of Tooele, Utah, the land passed into the hands of Tass A. Claridge of Trout Creek and James P. Harrison, who presently lives as a trapper at Fish Springs.

In 1926 Claridge and Harrison filed water claims with the State Engineer of Utah. It is interesting to note that these men recognized the refuge possibilities for wildlife on the Fish Springs marshes. Excerpts from these filings, numbered Ms 9921 and Ms 9922, read in part as follows:

> [To build] ditches, laterals, flumes, pipes, excavations, channels, dams, embankments, etc., designed and constructed to impound the water in ponds, and a series of ponds, lagoons, etc. [Thus] creating, maintaining, and operating a habitat for breeding, raising, and cultivation of various adaptable fur bearing animals, muskrats, otter, beaver, etc., or other animals or stock of susceptibility; together

> with propagation of requisite or any aquatic vegetation and plants, and piscicultural developments of the impounded waters formed into said lakes, ponds, lagoons, etc., so far as may be expedient and practicable. And also for the creation, so far as possible, of a refuge for wild and domesticated waterfowl.

Harrison later bought Claridge's interest in the area and, in addition to the trapping business, operated the Fish Springs Ranch Company. The cattle, however, did poorly on the marginal range and the enterprise failed during the severe winter of 1948-49.

Bull frogs were introduced to Fish Springs during the early residence of Harrison. Joseph Scriber of Ogden, Utah, under lease, later utilized 100 acres of marsh near Middle Spring for the commercial production of frogs. War surplus landing barges were hauled to the area for use as rearing pools. Middle Springs was diked and its waters diverted into the barges and a nearby series of bulldozed ponds. Additional breeding stock was imported from commercial hatcheries. While the venture has become largely inoperative, the residual frog population at Fish Springs constitute one of the few in Utah of consequence (Walker, 1953).

An unusual water filing was registered on March 22, 1956, by Stanford Mahoney of Salt Lake City. Water use, as designated in a file numbered I 27965 was for "industrial purposes in the processing of peat moss." A pit was later opened near House Springs and a quantity of the material removed for drying. No further operations were carred on up to the completion of the present study in August of 1960.

Wildlife potentialities of Fish Springs had been recognized by the U. S. Fish and Wildlife Service for many years (Wilson, 1938; Williams, 1938; and Janson, 1941). Land acquisition commenced in March of 1959 with the purchase of 3,775 acres of private and state holdings. Subsequently, 14,097 acres of public domain were withdrawn on August 14, 1959, by the

Department of the Interior for the creation of Fish Springs National Wildlife Refuge.

METHODS AND MATERIALS

Plants collected on the study area are filed in two reference herbaria: the Intermountain Herbarium, Utah State University and Refuge Headquarters, Fish Springs National Wildlife Refuge.

Randomly selected 6 by 24 inch plots were used to sample the structure of the vegetation. Number of plots was estimated statistically at the .05 confidence level and to an accuracy not less than 15 percent of the sample mean. Data are presented in the form cited by Weaver and Clements (1938) as the list or census method. Upland desert communities and submersed vegetation were not quantitatively studied.

Ten transects were established at selected ecotones throughout the marshes (see Appendix A). Each was located with pipe markers and numbered with punched aluminum tags. Contours were determined with a line level at stations 1 foot apart and were measured to the nearest inch.

Soil samples were collected with a core-type sampler. A wooden plunger was fitted with a gasket and inserted within the sampler tube. This created a simple suction mechanism whereby soft marsh soils could be retrieved in an unbroken core some 3 feet long and 1 inch in diameter. Samples to be analyzed for total soluble salts and pH were collected at three soil depths: 0-6, 7-12, and 13-24 inches, respectively. Each sample was assigned a texture class by tactile inspection, numbered, and placed in a plastic freezer bag.

Upon air drying, 50 grams of each sample were mixed with 250 grams of distilled water in quart jars and thoroughly shaken. Electrodes of a Soil Tester solubridge and a Beckman pH meter were then inserted in the suspension. The solubridge readings gave total soluble salt content in millimhos of conductivity. Similar procedures were used by Nelson (1954) in his studies at Ogden Bay.

Organic matter samples were collected from the first 6 inches of surface soil and were analyzed for organic carbon content by the Soils Laboratory at Utah State University. The determinations were made following the methods of Walkley (1935 and 1947). Direct conversion of organic carbon to organic matter was not possible in that the more organic soil materials differed greatly from that of amorphous humus. Thus, organic matter percentages from samples of a different nature would not be comparable (J. P. Thorne, in correspondence).

Soil-moisture relationships within the belts of vegetation were studied with tensiometers. These instruments, commercially known as Irrometers, were inserted in the soil to a depth of 6 inches. Only areas which were 6 inches or more above the water table were studied with tensiometers; soils less than 6 inches above the water table or submersed were assumed not to be limited in water content. Daily readings were taken at each station for a minimum period of 7 days. Rainfall was negligible during the study period, but when precipitation did occur, the following day's data were discarded. The influence of solar radiation on the tensiometers was reduced by covering the instruments with paper bags. Distilled water was added to each instrument as needed. Following each reading the meter was reset at zero by releasing the tension within the water column.

Water levels were recorded weekly at 16 stations throughout the spring and marsh areas. Readings were recorded at the nearest .125 inch.

Water quality was studied with a pH meter and solubridge. At the three larger springs, North Middle, and South, samples were taken and analyzed for calcium, magnesium, sodium, potassium, chloride, sulfate, carbonate, bicarbonate, and nitrate ions. Standard analytical techniques employed at the Soils Laboratory were used to determine the presence and quantity of these ions.

THE VEGETATION

Mason (1957) characterized salt-marshes as having a flora distinctly dissimilar from that of freshwater wetlands. The saline conditions which predominate at Fish Springs have thus contributed to the development of plant communities which differ from those of other areas. While some species, such as members of the Typhaceae, are found in most aquatic habitats, plants belonging to the Juncaginaceae, Characeae, Chenopodiaceae, and, in part, Gramineae and Cyperaceae families are usually associated with saline conditions.

The following sections treat first the Desert Upland communities surrounding the basin. Secondly, the four emersed-soil marsh communities, including (a) _Distichlis_ communities forming broad plains on the basin floor, (b) Juncus Meadows, (c) Juncus Borders, and (d) _Phragmites_ communities found widely scattered throughout the entire area.

Thirdly, six submersed-soil communities are described. These include (a) Eleocharis Meadows found on the peat soils near watercourses, (b) the major emergent community of _Scirpus olneyi_ and lesser emergent stands of (c) _Typha angustifolia_, (d) _Scirpus acutus_, and (e) _S. paludosus_, and finally, (f) the submersed communities of _Chara_ and _Ruppia_.

Desert Upland Communities

The vegetation of the mountain slopes and gravelly uplands at Fish Springs is typical cold-desert climax described by Oosting (1958) as the _Atriplex_ association. Commonly associated with _Atriplex confertifolia_

(Torr. & Frem.) S. Wats. (shadscale)[1] are *Chrysothamnus nauseosus* (Pall.) Britt. and *C. stenophyllus* (A. Gray) Greene (rabbitbrush). Occasional plants of *Ephedra nevadensis* S. Wats. (joint Fir), *Tetradymia spinosa* H. & A. (spiny horsebrush), *T. canescens* DC. (spineless horsebrush), and *Lycium andersoni* A. Gray (wolfberry) complete the shrubby aspect of the uplands. At higher elevations, *Juniperus osteosperma* (Torr.) Little (Utah juniper) is found along the steeper slopes.

Interspersed among these woody species are many herbaceous annuals and perennials common to xeric regions. *Descurainia incisa* (Engelm.) Britt. and *D. sophia* (L.) Webb (tansy-mustard) are frequent plants of the stony desert soils. *Allium nevadense* S. Wats. (wild onion) and *Sphaeralcea coccinea* (Pursh.) Rydb. (globe mallow) occur on the more level areas as does *Helianthus annuus* L. (sunflower), *Lomatium grayi* C. & R. (desert parsley), *Oenothera caesitosa* Nutt., var. *marginata* (Nutt.) Munz. (evening primrose), and *Malacothrix sonchoides* (Nutt.) Torr. & Gray (Malacothrix). Individuals of *Opuntia rhodantha* Schum. (prickly pear) are scattered throughout the community. Disturbed soils bear *Malcolmia africana* (L.) R. Br. (Malcolmia), *Lygodesmia exigua* A. Gray (Lygodesmia), and the introduced noxious weed, *Halogeton glomeratus* (Bieb.) Mey. (Halogeton).

Several grasses flourish on the dry slopes. Of these *Hilaria jamesii* (Torr.) Benth. (galleta), *Oryzopsis hymenoides* (Roem. & Schult.) Ricker (Indian ricegrass), and *Sitanion hystrix* (Nutt.) J. G. Smith (squirreltail) are common. The diminutive *Blepharidachne kingii* (S. Wats.) Hack. (Blepharidachne) occurs less frequently. Much of the upland area, traversed by seasonal sheep drives, contains *Bromus tectorum* L. (cheat grass).

As the topography levels to meet the basin floor, the gravelly desert pavement changes to loosely packed loams. Resulting differences

[1] A complete checklist of collected species and taxonomic references appears in Appendix B.

in plant life are evident. Sarcobatus vermiculatus (Hook.) Torr. (greasewood) and Kochia vestita (S. Wats.) Rydb. (green molly) are associated with the proximity of the water table in these areas. Cleared spaces have regrown with Iva axillaris Pursh (poverty weed) and spreading stands of Bassia hyssopifolia (Pall.) Kuntze (Bassia). Dwarfed individuals of Phragmites communis Trin. (common reed) intermingle thinly with Sarcobatus in the lower fringes of the uplands.

Distichlis Communities

Near the marshes, between the Desert Uplands and the aquatic communities, are broad meadows of Distichlis stricta (Torr.) Rydb. (desert saltgrass). The meadows appear as dense carpets covering the flat plains of the basin floor but do not enter the numerous depressions or extend up the low table-top rises that sometimes occur. The Distichlis Meadow is all but mono-specific; incidence of other species is slight (Table 4). Cordylanthus canescans A. Gray (Cordylanthus) and Suaeda intermedia S. Wats. (seepweed) are the only subordinate plants in this community.

Table 4. Community characteristics of Distichlis Meadows based on 22 randomly located plots, Fish Springs National Wildlife Refuge, 1960

Species	Density per square foot	Percentage frequency
Distichlis stricta	58.9	100
Cordylanthus canescans	(Observed but not in plots)	
Suaeda intermedia	(Observed but not in plots)	

Two halophytes frequently share certain sites with Distichlis. Salicornia utahensis Tidest. (samphire) and Allenrolfea occidentalis

(S. Wats.) Kuntze (pickleweed) becomes members of the plain vegetation in areas lying just above the water table. A tussock community of *Sporobolus airoides* (Torr.) Torr. (alkali sacaton) also combines with *Distichlis* on slight rises within the plains. This vegetation was separated for community structure (Table 5) but is grouped with Distichlis Meadows for treatment in following sections. The term Distichlis Compex is applied to these communities collectively.

Table 5. Community characteristics of codominant *Distichlis* communities based on 72 randomly located plots, Fish Springs National Wildlife Refuge, 1960

	Codominant *Distichlis* community					
Species	Sporobolus		Allenrolfea		Salicornia	
	Den.[a]	Freq.[b]	Den.	Freq.	Den.	Freq.
Distichlis stricta	4.5	45	15.1	100	36.0	100
Sporobolus airoides	9.5	80	0.5	6	0.2	10
Allenrolfea occidentalis	c	c	5.5	81	-	-
Salicornia utahensis	-	-	-	-	34.6	100
Juncus balticus	1.8	20	-	-	-	-

[a] Density per square foot

[b] Percentage frequency

[c] Observed but not in plots

The codominant segments of the Distichlis Complex, (a) *Distichlis-Salicornia*, (b) *Distichlis-Allenrolfea*, and (c) *Distichlis-Sporobolus*, show some overlap in composition (Table 5). *Distichlis*, of course, is omnipresent in all, though its density and frequency drop considerably in the *Sporobolus* stands. This results in discernable changes in the plain panorama (Figure 3). *Sporobolus* is found in varying degrees within the codominant communities; it is sparse in the halophytic segments but

Figure 3. Distichlis Meadow panorama showing pronounced changes with the incidence of Sporobolus airoides at upper right. Both plant types were designated Distichlis Complex vegetation but structural differences appear in text. Vegetation in foreground is a pure stand of Distichlis stricta.

clumped and common in its own segment. *Juncus balticus* Willd. var. *montanus* Engelm. (wire rush), however, occurs only in the *Distichlis-Sporobolus* community. Even so, its presence there reflects marginal location. *Juncus* in these areas is spindly and lacks the sod-forming growth found elsewhere. *Salicornia* and *Allenrolfea* generally remain separate though some intermixing with other Complex communities likely occurs.

Numerous ditches, some dry, intersect the plains. The water-filled ditches have contrasting plant life along their banks. *Spartina gracilis* Trin. (alkali cordgrass), *Polypogon monspeliensis* (L.) Desf. (rabbitfoot grass), and *Muhlenbergia asperfolia* (Nees & Mey.) Parodi (scratchgrass) associate with *Distichlis* at these sites. Nevertheless, the characteristic plant of ditch edges is *Tamarix pentandra* Pall. (salt cedar). A hedge-like growth of this species often follows ditch channels to their ends. Tamarix, the only woody plant to enter the marshes, likely spread from parent stock introduced for windbreaks near the ranch buildings (Figure 4).

Juncus Meadow and Juncus Border Communities

The sweeping landscape of the plains occasionally dips to form pannes and twisting depressions. These physical features interrupt the Distichlis Complex with pockets of dissimilar vegetation (Figures 5 and 6). Meadow communities of *Juncus balticus* dominate these low and irregular areas.

The Juncus Meadow appears as a dense community lacking associated species and separated from adjacent vegetation by knife-like edges. Floristically, however, it contains all of the major components of the Distichlis Complex (Table 6). *Distichlis* and *Sporobolus* are common in

Figure 4. <u>Tamarix pentandra</u> surrounding abandoned ranch buildings (obscured). This stand is believed to have served as parent stock for those individuals found along ditches elsewhere throughout the study area. Photo courtesy U. S. Fish and Wildlife Service.

Figure 5. Panne of Juncus Meadow. Surrounding vegetation is Distichlis Complex, mostly Distichlis-Sporobolus. Foothill to right shows typical upland desert community of Atriplex confertifolia and associated species. View is looking southwest at the Fish Springs Mountains.

Figure 6. Twisting depression of Juncus Meadow. Surrounding vegetation is Distichlis Complex, mostly Distichlis-Sporobolus. Dark line near horizon is the expansion of the depression into a panne formation.

Juncus Meadows but remain completely subordinate to Juncus in density. The presence of Salicornia and Allenrolfea in Juncus Meadows aroused some early speculation about differences in soil salt content between these and other Juncus communities. Although pannes may be sites of forb abundance, only two, Crepis runcinata T. & G. subsp. hispidulosa (Howell) Babc. & Stebb. (Hawksbeard) and Aster pauciflorus Nutt. (Aster) are occasionally present.

Table 6. Community characteristics of Juncus Meadows based on 18 randomly located plots, Fish Springs National Wildlife Refuge, 1960

Species	Density per square foot	Percentage frequency
Juncus balticus	23.2	100
Distichlis stricta	5.8	66
Sporobolus airoides	3.4	66
Salicornia utahensis	2.7	27
Allenrolfea occidentalis	0.4	17
Crepis runcinata	0.2	11
Aster pauciflorus	(Observed but not in plots)	

Juncus balticus also predominates in strips of vegetation bordering the winding shorelines of many sloughs. It appears as a dark band separating the Distichlis Complex from slough vegetation (see Figure 11). The width of Juncus Borders varies from a few inches to several feet but its presence along watercourses and marsh edges is nearly universal.

Table 7 shows the characteristics of the Juncus Border. The rise in Distichlis density from that in Juncus Meadows is attributable to the adjacency of Complex vegetation to the strips of Juncus. Rhizome infiltration is prevalent in these areas. In the larger Juncus Meadows, also bounded by Complex communities, Distichlis infiltration decreases inward from the Meadow periphery and thus, plots taken well within a Juncus Meadow show a corresponding reduction of _Distichlis_ density. _Sporobolus_ is sometimes locally important and augments the otherwise bristled appearance of the Borders with a plummed phase (Figure 7). _Asclepias speciosa_ Torr. (milkweed) is the only forb of the Juncus Border.

Table 7. Community characteristics of Juncus Borders based on 12 randomly located plots, Fish Springs National Wildlife Refuge, 1960

Species	Density per square foot	Percentage frequency
Juncus balticus	37.2	100
Distichlis stricta	22.5	75
Sporobolus airoides	2.2	66
Asclepias speciosa	0.5	25
Phragmites communis	0.3	25

Phragmites is a noteworthy addition to the Border composition. In some cases, particularly where _Phragmites_ grows densely, the conformation of the Border is altered. _Phragmites_ development in these areas ranges from occasional stems (Table 7) to complete dominance of the Border.

The frequent matting and wind-swept appearance of tidal-marsh _Juncus_ prompted Miller and Egler (1950) to liken these distinctive spots to "cowlicks." No evidence of ill effects was found upon vegetation thus affected. _Juncus_ communities at Fish Springs likewise exhibit this striking formation; otherwise upright and regimented stems are found in irregular swirls of varying extent. Juncus Meadows are usually the only communities of sufficient size to allow cowlick formation but they are sometimes seen in the larger Border communities.

Figure 7. Juncus Border along slough edge. Vegetation of the Border includes individuals of *Sporobolus airoides.* Emergent-marsh lies to left while Distichlis Complex, mostly *Distichlis-Sporobolus* and *Distichlis-Salicornia* is shown at right. Note *Phragmites* invasion of the Border at right-rear and transect marker in foreground.

Phragmites Communities

Phragmites communis occupies many habitats within the study area and typifies its classification by Dansereau (1957) as a cosmopolitan species. It is found in both the lower edges of the Desert Uplands and the marsh interior. A distinctive growth form is associated with each of these areas.

A dwarfed Phragmites community, widely spread but exceptionally thin, is sometimes found in the ecotone regions between the Sarcobatus fringes and Distichlis Compex communities (Figure 8). In this situation, it is of minor importance and cannot be considered a competitor for the habitat. Rhizome production is limited and propagation is presumably the result of infrequent seed germination.

Upon reaching the marshes proper, however, Phragmites growth becomes profuse; dense and compacted stands of tall, thrifty plants dot many slough shores and marsh edges. Its dominance is often absolute, much to the exclusion of other marsh species. Sowls (1955) described extensive communities of a similar nature as "Phragmites jungles."

The community structure of Phragmites was studied as a member of the terrestrial marsh. While pronounced growth can and does occur where water covers its roots (Love and Love, 1954; Bird, 1961; and others), the Phragmites communities at Fish Springs are primarily limited to sites along but not in watercourses. Rhizomes, often many feet long, sometimes expand "mother" communities into nearby vegetation. Phragmites study plots consequently show associated terrestrial and aquatic vegetation (Table 8).

The understory vegetation within an established Phragmites stand is sparce. Bare ground rather than lesser plants occupy much of the surface area in many of the denser communities; canopy closure is exceptional in such instances. A previous section described Phragmites

Figure 8. *Phragmites* development in Distichlis Complex vegetation. Stems are less than 4 feet tall and thinly dispersed. For more typical *Phragmites* growth along marsh edges, see Figure 7.

Table 8. Community characteristics of Phragmites based on 18 randomly located plots, Fish Springs National Wildlife Refuge, 1960

Species	Density per square foot	Percentage frequency
Phragmites communis	8.5	100
Scirpus olneyi	0.6	22
Muhlenbergia asperifolia	2.1	22
Distichlis stricta	1.6	16
Suaeda sp.	0.8	11
Juncus balticus	0.6	11

and Juncus Border relationships but the data for Juncus (Table 8) well reflect the remnants of invaded Border communities. The abrupt decrease of Distichlis incidence is noteworthy. Muhlenbergia and Suaeda are occasional species in the Phragmites understory. The presence of an emergent-marsh species in the study plots was explained earlier.

Eleocharis Meadows

Meadows boggy with the peat of undecomposed plant materials are found near some of the marsh edges. Inundation is littoral; the gradual slope of the basin floor so gently meets the water table that the meadows appear dry. Under foot, however, their saturation quickly becomes known. Eleocharis rostellata Torr. (spike rush) is found in these meadows as an entangled and distinctive community.

Many of the Eleocharis plants are sterile. New plants are established by proliferation and render an aspect of countless green hoops to the meadow profile. Passage through this vegetation is often difficult when plants thus rooted are encountered.

Eleocharis growth is intense. It averaged no less than 160 individuals per square foot of meadow (Table 9). Competition within a habitat so densely covered by the community dominant must be keen although several secondary species are also present. *Berula erecta* (Huds.) Cov. (water parsnip) and *Triglochin maritima* L. (seaside arrowgrass) are occasionally noted. *Triglochin* is especially found on patches of shallow soil which have accumulated over the peat substratum. These are small areas, usually less than a few square feet in size, and are irregularly located in the meadows. Other associates, *Centaurium exaltatum* (Griseb.) Wright (centaury) and *Castilleja exilis* A. Nels. (Indian paint brush) sometimes add a touch of color to the verdant meadows.

Table 9. Community characteristics of Eleocharis Meadows based on 10 randomly located plots, Fish Springs National Wildlife Refuge, 1960

Species	Density per square foot	Percentage frequency
Eleocharis rostellata	160.3	100
Distichlis stricta	9.3	90
Scirpus olneyi	1.1	40
Triglochin maritima	(Observed but not in plots)	
Berula erecta	(Observed but not in plots)	
Castilleja exilis	(Observed but not in plots)	
Centaurium exaltatum	(Observed but not in plots)	

The adaptability of *Distichlis* to varied habitats is exemplified by its frequent appearance in the Meadows; it occurred in 90 percent of the sampled vegetation (Table 9). In addition to the highly organic and acid nature of the meadow strata, appreciation must be given to their saturation. An edaphic comparison of these conditions with those of the more typical Distichlis Complex soils would result in some misgivings in assigning rigid species requirements to *Distichlis*. In community form, however, *Distichlis* tolerance is considerably narrower and relatively predictable.

The appearance of Scirpus olneyi A. Gray (Olney's bulrush) in Eleocharis Meadows marks the beginnings of emergent-marsh vegetation. Scattered plants, reduced in stature, are found on the drier sites but they increase in size and density as the Meadow waters deepen.

Emergent-marsh Communities

At their height of seasonal development, the marshes at Fish Springs are literally a sea of waving vegetation. Tall emergents dwarf the smaller plants and all but obscure the sight of water. Acres of marsh, unbroken save for the exposed plateaus, stretch across the basin floor in luxuriant verdancy.

If a single species were to be designated as descriptive of the marshes it would be Scirpus olneyi. Expanses of this species cover the marshes with rank growth. It also fringes sloughs in a fence-like manner which, when viewed from a distance, outlines the drainage patterns of the meandering waterways. Figure 9 shows a mosaic of plateaus, open water, and S. olneyi communities viewed from the air.

The extensive distribution of Scirpus olneyi throughout the study area allows considerable influx of adjacent vegetation due to edge exposure. The smallest of ponds and sloughs, for example, are sites of substantial communities. Study plots taken at these places would be misleading in obtaining an accurate picture of S. olneyi dominance; plots taken well within the larger areas of marsh show that no other emergent species are able to penetrate this tall community (Table 10). Associated species, Berula and Distichlis, are of minor understory importance. Berula is found only sporadically while Distichlis is somewhat more prevalent.

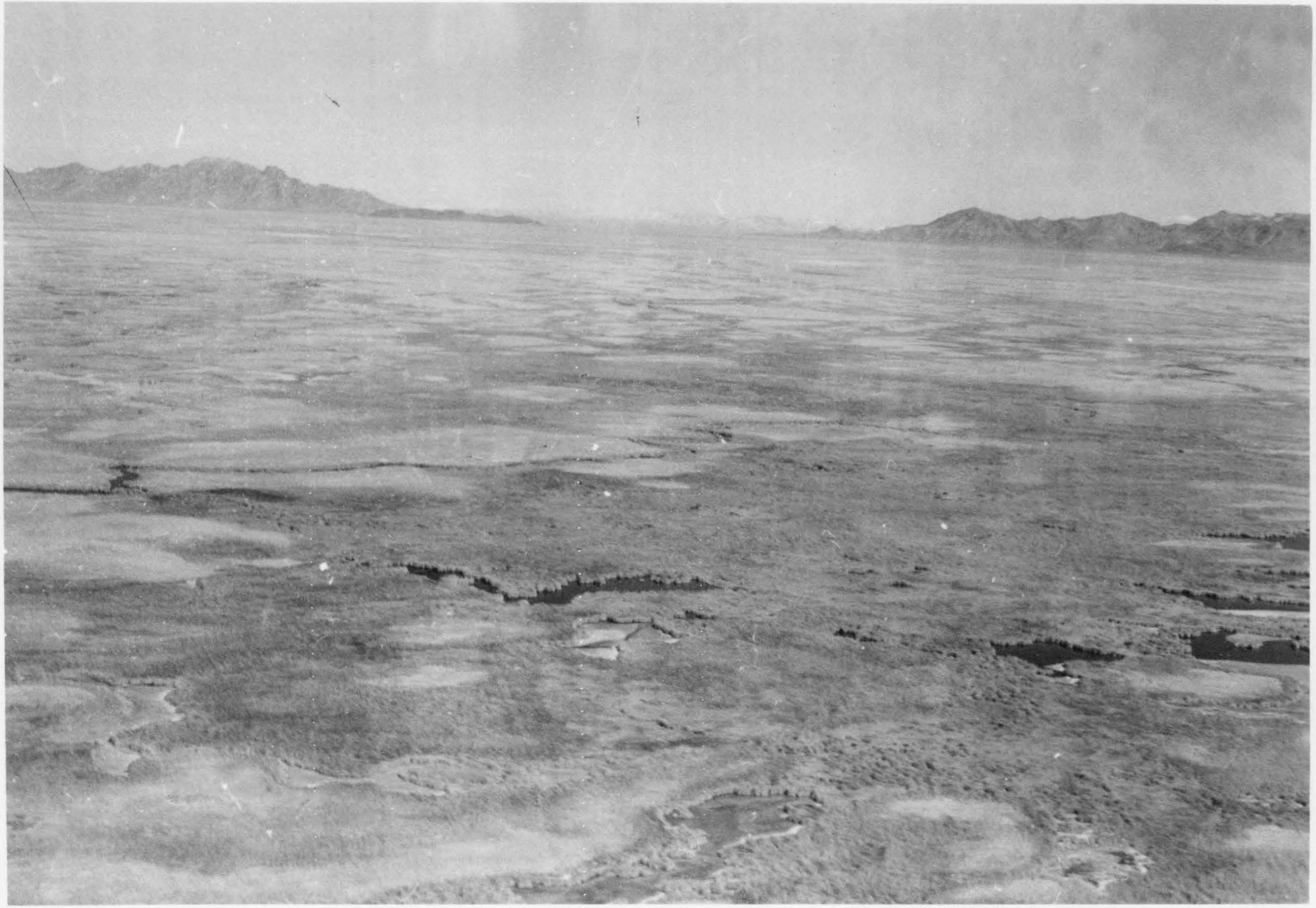

Figure 9. Aerial view of marsh mosaic. Light areas are plateaus, dark spots are open water. Vegetation is predominately *Scirpus olneyi.* Photo courtesy U. S. Fish and Wildlife Service.

Table 10. Community characteristics of emergent-marsh vegetation based upon 73 randomly located plots, Fish Springs National Wildlife Refuge, 1960

Community	Species	Density per square foot	Percentage frequency
Scirpus olneyi	*Scirpus olneyi*	24.5	100
	Distichlis stricta	6.4	23
	Berula erecta	0.3	9
	Glaux maritima	(Observed but not in plots)	
Scirpus acutus	*Scirpus acutus*	15.6	100
	Scirpus paludosus	7.8	25
	Scirpus olneyi	4.4	37
Scirpus paludosus	*Scirpus paludosus*	18.3	100
	Scirpus olneyi	5.3	50
	Scirpus acutus	0.8	11
	Distichlis stricta	8.0	66
	Eleocharis rostellata	(Observed but not in plots)	
Typha	*Typha angustifolia*	4.9	100
	Scirpus olneyi	0.9	22
	Phragmites communis	0.3	5

This is especially true in shallow areas, but even in deeper water, the omnipresent Distichlis survives on matted platforms of S. olneyi roots. Small openings in the emergent-marsh are sometimes blanketed with patches of Glaux maritima L. (saltwort). S. americanus Pers. (shorerush) is locally important along some of the slough edges.

Scirpus olneyi communities contain no other marsh species of comparable status and are considered to represent closed stands of vegetation. Its adaptation to the habitat appears complete and competition by other communities and/or species was not observed.

It becomes something of a speculative nature to issue community status to the remaining emergent-marsh vegetation at Fish Springs. The loose and rather nonrestrictive community definition previously noted, however, permits the inclusion of three other vegetational units in the analysis and description of the emergent-marsh structure. But any comparison of these units with Scirpus olneyi communities should be acknowledged by their small extent, relative unimportance, and failure to exclude S. olneyi from their composition; they are in no way similar to the community form expressed by S. olneyi.

Typha angustifolia L. (narrowleaf cattail) predominates the ditch vegetation and a limited number of other areas. Typha stands are often dense but it does not form the large communities often found elsewhere. The Typha characteristics (Table 10) are based on plots taken within marsh habitats and do not represent ditch vegetation. No evidence for the limitation of Typha communities to a particular water depth was found; stands occur on both sloping marsh edges and in the deeper sloughs.

Small communities of Scirpus acutus Muhl. (tule) are widely scattered throughout the marshes. Circular stands, usually 10 feet or less in diameter, are present in both deep and shallow water situations. When found in the deeper portions of the marshes, S. acutus usually occupies a zone to the water side of other emergent vegetation (Figure 10). Stands thus located tend to exclude other species and infer that such sites are more suitable for the "true" expression of its community form. The lack of deep-water habitats at Fish Springs may be of importance to this and other emergent-marsh species. Data in Table 10 reflect the increased incidence of other plants at the shallower S. acutus locations.

The moist banks and shallow portions of some sloughs would ordinarily provide excellent locations for Scirpus paludosus A. Nels. (alkali bulrush). This was not the case. A single stand worthy of measurement was found on the shoreline of an isolated slough (Figure 11). Further search for S. paludosus disclosed only individual plants in other shoreline communities. Characteristics are thus based on plots taken within the singular occurrence of this community (Table 10). Even within this solitary stand, homogeneity was lacking. Species which dominated other sites freely invaded and presumably will eliminate this solitary stand with the passage of time.

Submersed Communities

The clear waters of the marshes reveal an abundance of plant life beneath their surfaces. However, only two species, Ruppia maritima L. (widgeongrass) and the algae, Chara spp. (muskgrass) constitute the submersed vegetation within the marshes. These plants exhibit no discernable habitat separation and freely intermingle with one another (Figure 12). Their combination in this manner led to their singular treatment as Chara-Ruppia in following discussions.

Figure 10. Small communities of Scirpus acutus (left) and Typha (right). S. acutus usually occupied the zone to the water side of other emergent-marsh species but several exceptions made this distinction unreliable. Vegetation to extreme left (background) is S. olneyi.

Figure 11. Singular community of *Scirpus paludosus* on both sides of isolated slough. Dark line of vegetation along slough edge is Juncus Border. Small patches of *S. acutus* occupy shallow slough habitat to right and left-center (faint). Trees in distance are shown in more detail in Figure 4. Note ancient lake shores marked on mountain side.

Figure 12. *Chara-Ruppia* community in slough bottom. Water has receeded slightly (note gauge in slough near clump at left-center) exposing submersed vegetation. Vegetation along banks is *Scirpus olneyi.* Tall stand of *Phragmites* rises behind *S. olneyi* growth to right center of photo.

It is unfortunate that Chara collections were not identified by species as several forms may have been found. Ooagonia characteristics are necessary for positive species identification. Wood (1950) has pointed out that the genus Chara shows extremely variable ecological traits. Some forms are transitory and vanish soon after establishment while others persist for over half a century. No study of Chara life cycle(s) was undertaken at Fish Springs though the ecological implications of species differences would have made interesting research.

In addition to the Chara-Ruppia communities of the open marshes, spring areas contain rank stands of Najas marina L. (spiny najad). Its distribution is irregular and largely limited to the deeper portions of the springs and immediate channels. Where profuse, Najas chokes water passage with entangled mats of vegetation (Figure 13). Infrequent and scattered individuals of Utricularia vulgaris L. (bladderwort) and Ceratophyllum demersum L. (coontail) are also limited to the springs and nearby drainages (Figure 14). Filamentous algae are present in many of the marsh and spring areas but they were neither collected nor identified.

Phenological Observations

With the coming of spring the vegetation responds in its annual cycle of renewed growth. The sombre colors of winter's dormancy are gradually replaced with hues of green in an ever-increasing radius from the pools of warm water. The contrast of this striking progression was recorded with cursory phenological observations within the plant communities of the marshes.

Observations are recorded under two main headings (Table 11): date of initial growth, e.g., first appearance of green shoots, and date of

Figure 13. Beginnings of *Najas marina* blockage near South Spring outlet. Water passage became increasingly hindered as these mats enlarged. Dark vegetation on horizon is *Scirpus olneyi*. Note water clarity.

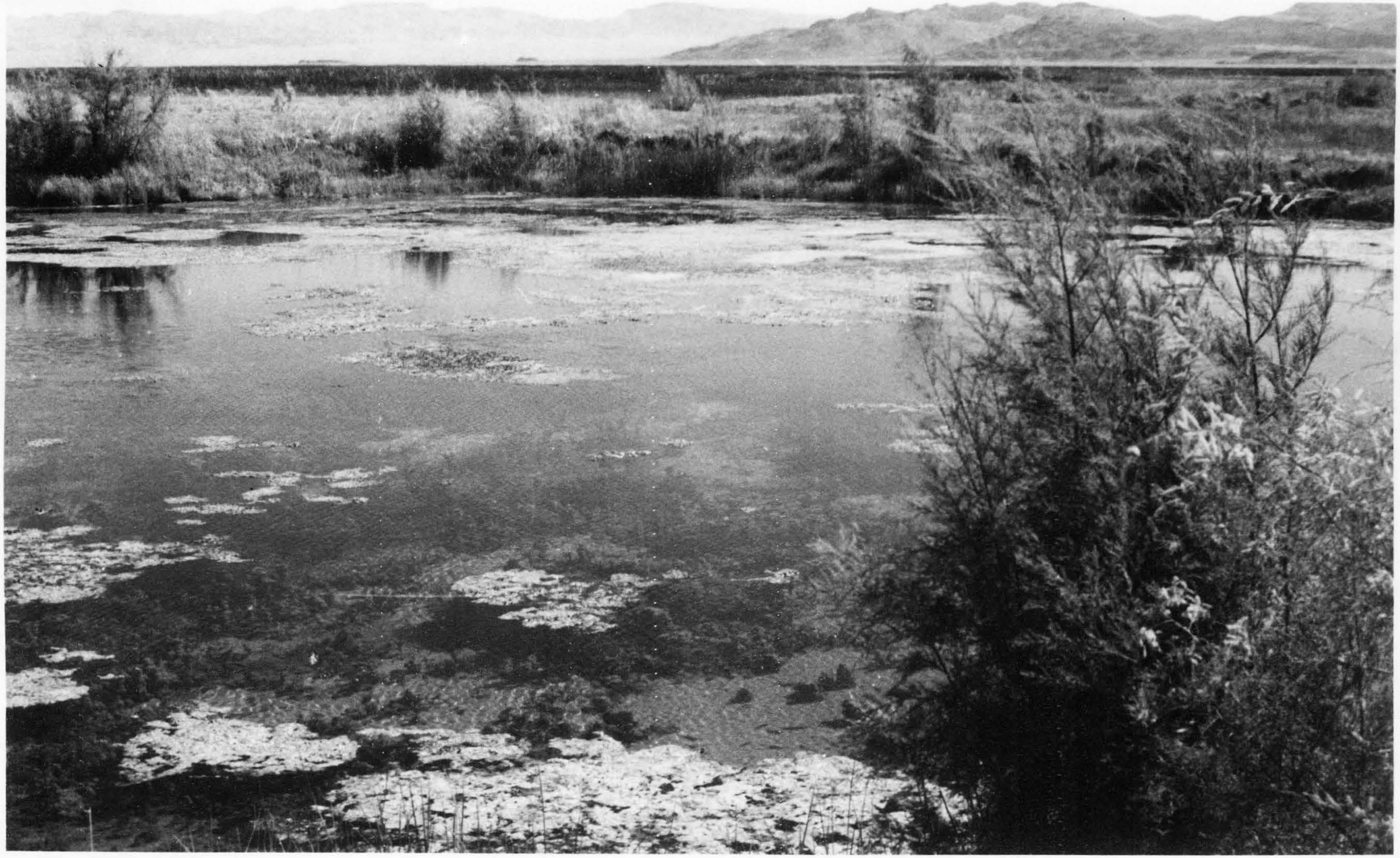

Figure 14. South Spring. Clear water shows submersed vegetation of Ceratophyllum demersum, Utricularia vulgaris, and Chara-Ruppia. Shrubby plants along spring edge are Tamarix (note flowers on individual in right-corner at bottom).

Table 11. Phenological observations of initial growth and anthesis of selected plant species, Fish Springs National Wildlife Refuge, 1960

Species	Date of initial growth			Date of anthesis		
	Warm	"Normal"	Lag (Days)	Warm	"Normal"	Lag (Days)
Ascelepias speciosa	No data	April 4	-	May 11	May 23	12
Chara spp.	Apparently green all year		-	No data	June 27[b]	-
Distichlis stricta	April 2	April 14	12	May 30	June 10	11
Eleocharis rostellata	a	April 29	-	a	May 11	-
Juncus balticus	March 27	April 14	18	April 29	May 5	6
Najas marina	Apparently green all year		-	No data	No data	-
Phragmites communis	April 2	April 14	12	July 15	No data	-
Ruppia maritima	Apparently green all year		-	June 6[c]	June 6	-
Salicornia utahensis	a	April 15	-	a	June 8	-
Scirpus acutus	a	April 12	-	a	May 9	-
Scirpus americanus	a	April 14	-	a	May 4	-
Scirpus olneyi	March 27	April 14	18	April 29	May 5	6
Scirpus paludosus	a	April 11	-	a	May 1	-
Sporobolus airoides	a	May 16	-	a	June 10	-
Tamarix pentandra	April 2	April 17	15	May 11	May 23	12
Triglochin maritima	a	April 29	-	a	June 12	-
Typha angustifolia	March 31	April 17	17	June 27	July 8	11

a = Not found near warm water or apparently not under influence of warm water.
b = Sporangia present.
c = Seed present.

anthesis, e.g., first observed bud or flower development. Further subdivision into classes of warm and "normal" was necessary to discount the influence of the warm spring water upon vernal activity. Outlying sections of marsh, not affected by the water temperature of the springs, were designated "normal" for comparative purposes. The data collected were, of course, dependent upon the weather conditions which prevailed during the study period. They should therefore not be interpreted as fixed dates of annual plant response but rather as an indication of the vegetational phenology at Fish Springs.

Halophytic or semi-halophytic species, among them Distichlis, Salicornia, Sporobolus, and Triglochin produced reproductive structures at dates somewhat later than nonhalophytes. Penfound and Hathaway (1938) noted similar postponement in seasonal development for salt-marsh species. Typha and Phragmites, nonhalophytes, were also delayed in floral development. Data for Juncus response by Border and Meadow forms and Distichlis in any of the Complex communities were not separated and thus lack any phenological distinction in Table 11.

The submersed species, Chara, Ruppia, and Najas, do not exhibit any discernable commencement of growth in either warm or "normal" sites. This led to their designation in Table 11 as green all year. Further and more intensive observation might have disclosed that where the water freezes from surface to bottom, as in many shallow sections of the marshes, these plants would have succumbed during winter. No correlation between the lag periods for initial growth and that of anthesis between warm and "normal" habitats was found. Juncus, for example, lagged 18 days in initial development but only 6 days between dates of anthesis. The lag periods for Distichlis, however, were in near agreement (Table 11). The sketchy data perhaps accounts for these inconsistencies. Nevertheless, the influence of the warm spring waters hastened plant development in all cases.

The phenological data represent the general pattern of plant response in a warm spring salt-marsh environment with contrasting data for areas of "normal" water temperatures. While no comparative data for similar species in nonsaline marshes are utilized, the later development of halophytic plants generally paralleled that in coastal wetlands (Penfound and Hathaway, 1938).

Indications of Community Succession and Development

Fish Springs lies in a region of halophytic and xeric vegetation extending westward from Great Salt Lake. Plant succession in this extensive inland drainage follows a course of descending tolerance to saline conditions and adaptation to desert environments. In the salt wastelands near the lake grow only the most halophytic of plants such as *Salicornia* and *Allenrolfea* (Nelson, 1955). Soil salinity decreases with rises in elevation away from the lake basin. The vegetation changes in pronounced belts as the salinity declines (Kearney et al., 1914) until the edaphic climax of *Sarcobatus*-*Atriplex* is reached (Flowers, 1934).

The wetland habitat at Fish Springs has altered the regional pattern of succession with local trends. Regional climax communities cover the upland areas surrounding the marshes but the Distichlis Complex communities are clearly the point of separation between the desert and marsh vegetation. Chapman (1960) similarly designated *Distichlis* communities as terminal xeric vegetation of inland salt-marshes.

Juncus Borders are closely bound to slough shorelines and are believed to be wholly dependent upon the meanderings of the sloughs for their placement. There is little evidence for natural changes in the course of these waterways; the "oxbow" conditions common to sluggish sloughs and streams elsewhere are absent. Phragmites is the only species able to invade the Borders with enough tenacity to establish a new community. However, succession by Phragmites is enhanced by its unusual propagative potentialities. Its role in the pattern of community development is discussed in following sections.

Juncus Meadows are likewise confined by topographical features. The Meadow vegetation is normally homogeneous but some clues of its successional placement were noted in and near the depressions and pannes. Where strong, continual desert winds have deposited sufficient soil about the perimeter of the Meadows to fill in these edges, Juncus retreated in favor of Distichlis Complex vegetation. Isolated, retarded clumps of Juncus a few feet from the present edge of the depressions indicated the remnants of the former Meadow boundary. Rootstalks of Distichlis commonly trail into the edges of Juncus Meadows, though few of these plants are able to establish new Distichlis communities within the Meadow interiors. It is suggested that Juncus Meadows are permanent communities, limited to depressions, and give way to Distichlis communities only when the depressions become filled.

One further, though man induced, example of Juncus Meadow succession was observed in a shallow slough purposely drained some time ago. The slough, edged with the abandoned dens and runs of muskrats, had become lined with Juncus Meadow after drainage. Later, Distichlis Complex vegetation successfully invaded the site. Now the only evidence of Juncus occupancy are clumps of decaying Juncus hummocks which "checkerboard" the field of *Distichlis*. The reason that this particular slough advanced to *Distichlis* while other depressions remain in Juncus Meadow may possibly lie in changes in water table depth and soil salinity due to its drainage.

Observations of Juncus communities indicate that *Juncus*, in either the Border or Meadow form, is a major mesic stage between purely hydric and xeric vegetation.

Phragmites is a highly competitive species possessing tremendous growth and encroachment properties. Less competitive communities are often successfully invaded by its rhizomes. *Phragmites* also represents a definite seral stage in the vegetational development of many marshes known as the reed-swamp stage (Weaver and Clements, 1938). Thus a *Phragmites* stand may be that which has come about by (a) invasion of any seral stage, regardless of successional rank, or (b) that which has occurred as one of the theoretical steps of vegetational development from pioneer to climax.

The reed-swamp stage, as usually defined, includes the major emergent species in its composition and lies one step prior to the development of meadow vegetation. However, at Fish Springs, the preponderance of *Phragmites* communities on soils above the water table did not permit their inclusion in the emergent-marsh vegetation, but rather as communities of the dry marsh edges. The remaining choice of *Phragmites* establishment by invasion must therefore be accepted. If so, *Phragmites* communities at Fish Springs represent unique units of vegetation, not encumbered by the presence of other terrestrial communities, and only limited in distribution by soil and other habitat restrictions. Adaptation following invasion appears complete and there is no evidence for its replacement by other vegetation.

The establishment of Eleocharis upon peat soils somewhat confounds successional analysis of this species. Had extensive Eleocharis growth been found on soil types more typical of other marsh areas, further knowledge about its successional status might have been obtained. Miller and Egler (1950) found that blocks of peat, when displaced and transported elsewhere by tides, continued to bear the same vegetation as before, even though presently located in a different community zone and subjected to different habitat conditions. Vegetation at Fish Springs generally follows a Juncus Border to Scirpus olneyi sequence without an intervening Eleocharis zone where peat is absent. When peat is present, Eleocharis occupies a zone between Juncus and S. olneyi. Hence, these communities are of an intermediate status but, because of their specialized locale, are extremely stable and of little importance to the overall trends of the study area.

The singular occurrence of Scirpus paludosus in community form warrants especial mention. S. paludosus is usually considered an emergent-marsh pioneer species (Nelson, 1954 and 1955) but often persists until saline levels are reduced and/or other salt-tolerant species dominate its habitat. Presence of this relict community suggests that S. paludosus may have at one time existed in extensive communities at Fish Springs but that it presently has been all but superseded by other vegetation. On the other hand, this stand might be the beginning of new S. paludosus communities not yet widely distributed within the marshes. Evidence presented in following sections, indicates that the former opinion is more plausible. Be that as it may, S. paludosus cannot presently be regarded as a prominent step in the plant succession at Fish Springs. Creation of new habitat by flooding salty dryland areas with shallow waters would undoubtedly result in expansion of this community though succession to S. olneyi may rapidly follow.

Emergent-marsh species are often assigned a successional status in respect to their zonation with water depth. Wells (1942) noted that "A prevalent concept in aquatic ecology is that water depth is primarily in control of the communities, with these zoned in a simple sequence from shore outward." But conflicting and overlapping tolerances to water depth for emergent-marsh species have been reported by Kadlec (1960). Thus the specific limitations of water depth upon emergent plant distribution and succession have not been resolved.

The overwhelming occurrence of Scirpus olneyi at Fish Springs left little doubt that these communities represent terminal emergent-marsh vegetation. While water depth likely created the zonal features of these and other emergent-marsh communities from open water areas, no pronounced effects of water depth were observed between or among them. Thus, it is not possible to make definite statements about S. acutus or Typha angustifolia in regards to their successional roles on the study area.. Both are considered marsh dominants in many areas and may represent terminal emergent-marsh vegetation in such places. Possibly the limitations of soil salinity and shallow water together with the biological limitations of S. olneyi competition are not favorable for maximum expression of either S. acutus or Typha at Fish Springs.

The Chara-Ruppia communities are the only submersed communities within the greater portion of the study area. Because of this, they obviously represent the most hydric stage of succession at Fish Springs. Because of their habit of becoming encrusted with carbonate compounds, some successional importance has been attached to the Characeae in the formation of marl and filling in of aquatic environments. However, Wood (1950) has cautioned that only a few species are able to accumulate sufficient deposits to produce these habitat changes. An earlier study (Wood, 1950) reported that *Chara* may occur "above, amid, or below" the zones occupied by other submersed species. The shallow waters at Fish Springs dictate that *Chara* be found in a single depth zone and that this zone be shared with *Ruppia*.

Some evidence of a cyclic pattern of development within *Chara*-*Ruppia* communities has been advanced by Bourn (G. W. Barclay, in corresp.). The cycle depends upon the amount of dissolved solids present in the water surrounding the vegetation. According to Bourn's observations, *Chara* absorbs dissolved solids in amounts large enough to appreciably decrease the salinity of the water. Laden with these incrustations, the plants then fall to the marsh bottom. *Ruppia*, favoring "sweeter" (Barclay, *op*. *cit*.) or less saline water than *Chara* (Nelson, 1955), replaces *Chara* until the salt content of the water again rises. The cycle then repeats with the regrowth of *Chara*. When present, *Zannichellia* *palustris* L. (horned pondweed) and *Potamogeton* *pectinatus* L. (sago pondweed) are incorporated into the cycle between the *Chara* and *Ruppia* stages.

It is doubtful that such a cycle of *Chara*-*Ruppia* development prevails throughout the study area, though in ponds separated from the consistent influx of spring waters, this pattern may occur. *Chara*-*Ruppia* communities observed during the study period were confronted with a continual influx of saline water from the springs. Neither species show enough dominance over the other to warrant their separation and an intermixed community is the rule rather than the exception. Future studies in isolated bodies of saline water may provide further insight upon *Chara* and *Ruppia* relationships. Certainly, identification of the Characeae by species is required before an interpretation of their ecology can be adequately undertaken (Wood, 1950).

In hydroseres, or as more correctly applied to Fish Springs, haloseres, Weaver and Clements (1938) have designated submerged (submersed of the present writer), floating leaf, reed-swamp, sedge-meadow, and upland vegetation, usually woodlands, as stages in marsh succession. All but one of these, the floating leaf stage, are present at Fish Springs. This omission has been observed in other salt-marshes. Penfound (1952) noted that reed-swamp vegetation dominated southern salt water habitats to the exclusion of floating leaved species. Floating-leaved plants were either lacking or of no consequence to succession at Ogden Bay (Nelson, 1954).

To summarize these stages in the halosere concept, (a) Chara-Ruppia communities represent the submersed stage, (b) Scirpus olneyi as reed-swamp, (c) Eleocharis as sedge-meadow communities when peat was present but more commonly seen as Juncus Borders and Meadows, and (d) the upland or xeric stage represented by Distichlis Complex vegetation.

One important aspect of succession and development of the vegetation at Fish Springs became acutely apparent during the study period, namely the stability and static nature of the communities. With the exceptions of Phragmites and Scirpus paludosus, evidence for community stability is as follows:

(a) Ecotones are, for the most part, sharply defined by knifelike edges. Active succession is indicated by broader transition zones.

(b) No pioneer communities are present. Annual vegetation is so thinly distributed within other communities, if at all present, that they could have only been the result of local disturbances and not remnants of a prior successional stage.

(c) The few species within each community suggested that each zone had reached a level of stability favorable to the community dominant.

(d) Many of the physical influences affecting succession in marshes are absent at Fish Springs. Among these are large water fluctuations, tidal effects, silting, flooding, and water quality changes resulting from drainage, erosion, or influx of fresh water from nearby streams.

(e) The dominance of Scirpus olneyi. Regarding this species, Nelson (1955) stated that the predominance of Scirpus olneyi indicated old marshes that have had stabilized growing conditions for some period of time. He characterized this plant as forming dense sods which crowd out other marsh plants and that this formation takes many years to expand into dominating communities. Scirpus olneyi so dominates the greater portion of the Fish Springs marshes that, in light of the above observations, expansion of other marsh vegetation is unlikely.

(f) The treatment of soil salt stability will be found in a succeeding section, but where such conditions prevail, Chapman (1960) has concluded that each community zone is an edaphic climax with little chance for further development. He proposed the term sereclimax be used to designate terminal plant zones in these circumstances.

THE SOIL FACTOR

The soil stratum is the assembly point for most plant life and contains many of the factors which determine plant distribution. In addition to the mechanical function of supplying an anchorage medium, the physical and chemical attributes of a soil may offer a habitat suitable only to certain plant communities. The following sections deal with the soil factors studied on the salt-marshes at Fish Springs and with their implications upon the vegetation.

Soil Salinity

General considerations

Excess soluble salts in the soil media may limit plant growth and development in three ways (Hayward and Bernstein, 1958). First, the accumulation of specific ions may decrease the absorption of an essential nutrient or may inhibit growth by their direct toxic effects. Secondly, excessive salts in the soil solution may sufficiently increase the osmotic gradient to prevent adequate water uptake by a plant. Finally, a combination of the above factors may limit plant growth. Hayward and Wadleigh (1949) believe that osmotic effects of soluble salts are the most detrimental factor to vegetation in saline areas.

Germination of crop species in saline areas has been investigated by Ayers and Hayward (1948) and Ayers (1952) while the writer (unpublished) studied similar relationships for eight species of grasses. They found that excessive concentrations of salts markedly reduced germination percentages but that salt tolerance during germination could not be correlated with tolerances during later stages of plant development.

Plant responses to soil salinity were studied by Schofield (1942). A summary of his findings for agricultural crops is presented in Table 12. Crops generally failed to thrive when a 1:5 soil suspension conductivity of 0.90 millimhos was exceeded and survival was limited at 1.68 millimhos.

Table 12. Conductivity ranges and plant responses based upon the data of Schofield (1942) for agricultural crops

Plant response	1:5 soil suspension conductivities millimhos
All crops thrive. No evidence of salt injury.	0.00-0.49
Sensitive crops do not thrive. Tolerant crops may do well.	0.50-0.90
Crop growth restricted. Yields usually poor.	0.91-1.68
Only a few species survive.	1.69-

Most literature dealing with salinity studies present data in millimhos of conductivity based upon saturation extracts or upon the weight basis of parts per million or percent. The saturation extract method has been cited by Richards (1954) as the best manner of predicting the effects of salt concentrations upon plant growth. However, because of the expense of determining conductivities from saturation extracts, Nelson (1954) at Ogden Bay and the present writer at Fish Springs employed a 1:5 soil suspension technique for the hundreds of samples analyzed. A close linear relationship exists between the two methods; saturation extracts yielded conductivities on the average 8.9 times larger than the 1:5 soil suspension data (Nelson, 1954). Calculation of percentage salt in air dry soil at Fish Springs was determined by the formulae of Richards (1954) and may be approximated by taking three tenths of the 1:5 suspension conductivities and expressing the results as a percentage. Thus a 1:5 conductivity reading of 10 millimhos is about equal to 3 percent salt in an air dry soil sample. These relationships are graphically shown in Figure 15 for comparison with other studies using either the saturation extract method or percentage salt in an air dry sample.

The mean conductivities of soil samples collected at Fish Springs (Table 13), when segregated into classes of emersed and submersed soils, show the effect of inundation upon the salt content of marsh soils.

Table 13. Mean conductivities in millimhos from 1:5 soil suspensions for three depths of emersed or submersed soils. Sample size in parenthesis

Soil depth (inches)	Classification		All samples
	Emersed	Submersed	
0-6	5.41 (103)	1.11 (147)	2.88 (250)
7-12	1.68 (103)	0.97 (147)	1.26 (250)
13-24	0.96 (103)	0.80 (147)	0.87 (250)

Differences in salt content for the classified data are about four times greater in favor of the emersed soils in the upper 6 inches and about twice as great for the 6-12 inch sampling level. The lowest level sampled, 13-24 inches, shows only small differences in salt content. Comparisons between the conductivities at each level for all samples with those of the classified data show the emersed soils to have higher conductivities while lower values are found for submersed soils.

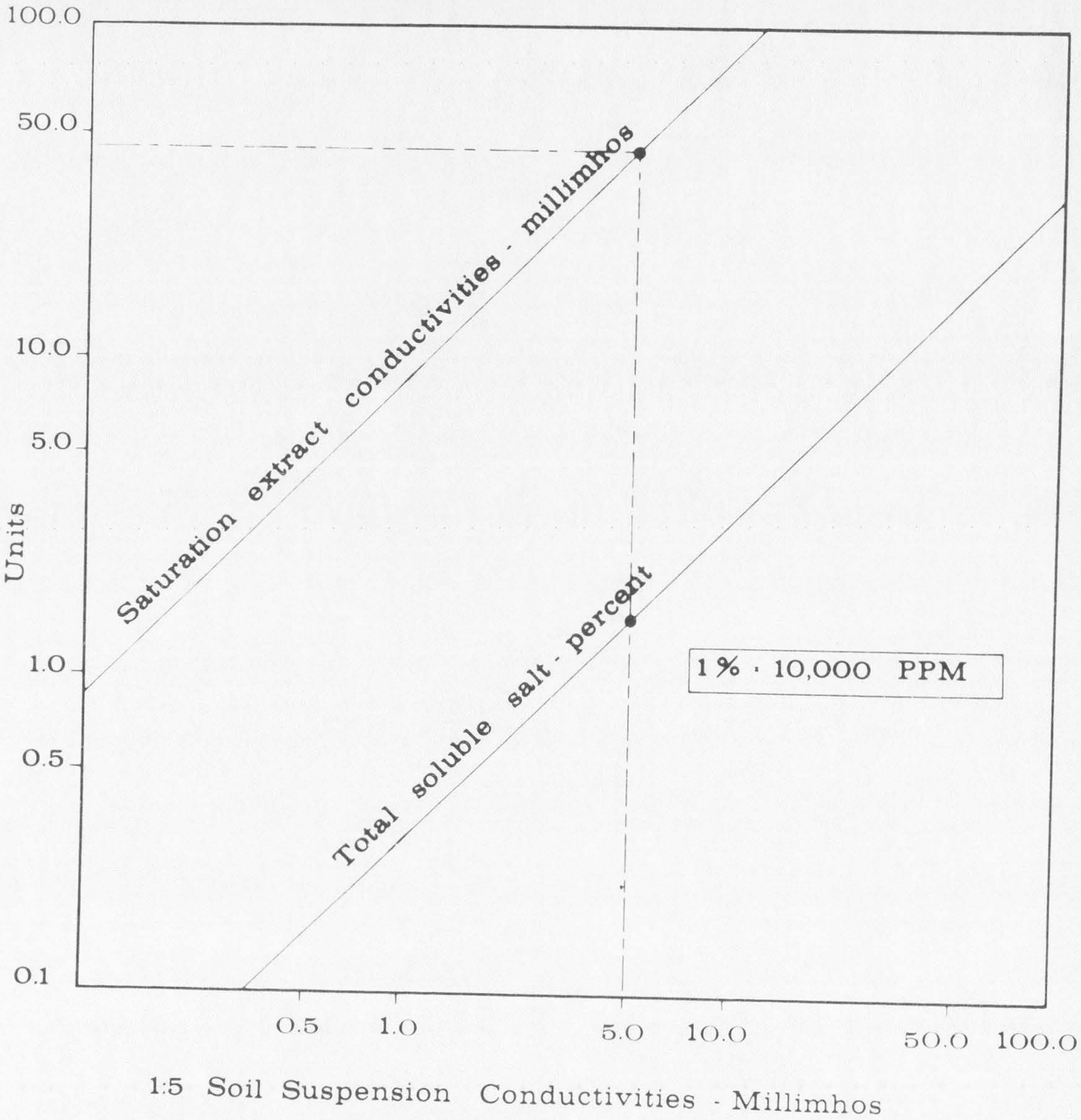

Figure 15. Linear relationship of 1:5 soil suspension conductivities to saturation extract conductivities and percentage soluble salt in air dry soil. The broken line shows that 5 millimhos of conductivity from a 1:5 soil suspension equals 1:5 percent salt and 44.5 saturation extract millimhos. Inset shows conversion of percent to parts per million. Data compiled from Nelson (1954) and Richards (1954).

Testing by analysis of variance (Table 14) reveals the significance of soil depth and inundation upon the salt content of the marsh soils at Fish Springs. Very significant "F" values are obtained for each of these criteria. In addition, the interaction between depth and water coverage yields a strong test of significance.

Table 14. Analysis of variance of 1:5 soil suspension conductivities to study the effects and interaction of soil depth and water coverage upon soil salinity. Analysis based upon 750 soil samples.

Source of variation	Degrees of freedom	Sum of squares	Mean square	"F"
Between emersed and submersed soil samples	1	540.08	540.08	142.35[a]
Between soil depths	2	568.44	284.22	74.91[a]
Interaction	2	611.72	305.86	80.61[a]
Residual	744	2822.72	3.79	
Total	749	4542.96		

[a] Highly significant at the .01 confidence level.

The salinity differences shown in Table 14 between inundated and emersed soils may be the result of simple dilution and washing of the soil. Evaporational losses of soil water from emersed soils leave concentrations of salt within the soil profile. Strong concentrations such as these are not found in submersed soils because of their dilution by the water above them. Hence the presence or absence of permanent water above a soil determines the strength of the saline conditions within the soil.

Salinity differences in different soil depths may be explained as follows: Final passage of soil moisture into the atmosphere takes place at the soil surface and therefore leaves at this point the largest amounts of salt. The separation of salt from the soil water takes place in lesser amounts at subsequently lower depths from the soil surface. A decreasing gradient of soil salt or salt profile is accordingly established from surface to substrata.

The highly significant interaction between soil depth and water coverage upon soil salt content may be accounted for by water table levels. Where the water table is near the soil surface, the dissolved salts are readily deposited at the surface by evaporation. Low water tables reduce the amount of surface deposition. Krammer (1949) pointed out that there is little capillary movement of water to the soil surface where the water table is more than 3 or 4 feet deep. Kearney (1911) stated that conditions which favor evaporation from the soil surface also favor the accumulation of salt on or near the surface. A reduction of "alkali" content in Great Basin soils was found by Flowers (1934) to be proportional to the depth of the water table below the soil surface. These findings indicate that the salt content of a soil sample is relative to both the presence of the water table and depth from which the sample is taken.

Some difficulty arises in attaching specific ecological importance to a soil depth at which salinity becomes critical to plant life. The arbitrary sampling depths of this study offered only a mechanical means for understanding the salt profile at Fish Springs. It is at once apparent, however, that salt concentrations at the soil surface are those which largely inhibit germination. The saline conditions of surface samples should therefore have some ecological bearing upon community distribution. Those plants which reproduce vegetatively need not be dependent upon surface conditions for reproductive purposes but may well be limited in distribution by salt occurring in their root zones.

While data regarding root depth were not obtained at Fish Springs, some deductions may be made. Aside from physically supporting a plant, the primary function of roots is to absorb nutrients and moisture from the soil solution. Because the water table in any marsh is shallow or exposed, it follows that marsh plants are not of necessity deeply rooted. Chapman (1940a) observed that the bulk of roots for eastern tidal marsh species were 3 to 9 inches below the soil surface. Krammer (1949) noted that deep root penetration does not occur where shallow water tables exist while Russell (1947) stated that only the upper 6 or 8 inches of soil is suited to plant life where heavy soils are found.

It therefore seems justifiable to assume that salinity determinations taken at (a) the soil surface and (b) at some point within the first foot of the soil profile are of especial ecological merit to community zonation at Fish Springs.

Community tolerances

The effects of individual salts upon plants are many and vary in degree. However, the overall effects of excessive salinity are largely osmotic, for equal concentrations of different salts may yield equal reductions in plant growth (Daubenmire, 1959). Mean concentrations of soil salts are shown in Table 15 for each of the plant communities studied at Fish Springs. These values are not necessarily maximal or minimal tolerances of individual species but represent relative salinity differences between the communities.

Distichlis communities are the most tolerant to saline habitats among

Table 15. Mean conductivities in millimhos from 1:5 soil suspensions for four emersed and six submersed-soil marsh communities

Community	Soil depth (inches) 0-6	7-12	13-24
		Emersed soils	
Distichlis Complex	6.96	1.92	1.01
Juncus Border	2.73	0.92	0.70
Juncus Meadow	4.23	1.69	0.99
Phragmites	2.92	1.50	1.02
		Submersed soils	
Scirpus olneyi	1.30	1.16	1.04
Scirpus paludosus	0.75	0.40	0.21
Scirpus acutus	0.80	0.62	0.48
Eleocharis Meadow	1.64	1.28	1.12
Typha	0.74	0.75	0.60
Chara-Ruppia	0.92	0.94	0.72

the four emersed-soil communities examined. Soils bearing Distichlis are often seen with encrusted layers of salt at their surfaces. The high tolerance of Distichlis Complexes to salt is reflected in the marked separations (Figure 6) often noted between these and other emersed-soil communities. Statistical comparisons of conductivity means for each of the four terrestrial communities (Table 16) show that soil salt differences are highly significant between the Distichlis complexes and both Phragmites and Juncus Border communities at the upper level of sampling. A less significant difference is shown for Juncus Meadow communities. Significance between salt concentrations between Distichlis Complex and Juncus Border communities occurs at the second sampling level and to a lesser degree at the third.

Following in community salt tolerance are Juncus Meadows, Phragmites, and Juncus Borders (Table 15). The interjection of Phragmites communities between the two Juncus groups in relative salt tolerance is of particular interest. While, as implied, the two communities consist of the same

Table 16. Comparison of mean salinity values from Table 15 for plant communities studied at Fish Springs. Values shown are the highest level of statistical significance above .50 confidence level as determined by "t" test. Calculated "t" values appear in parenthesis. Salinity values for *Chara*-*Ruppia* communities not compared

Community	Community compared	D.F. at each soil depth	Soil depth (inches)		
			0-6	7-12	13-14
		Emersed soils			
Distichlis Complex	Juncus Border	73	.01(2.860)[b]	.05(2.538)[a]	.20(1.504)
	Juncus Meadow	70	.20(1.571)	-(0.521)	-(0.087)
	Phragmites	74	.01(2.865)[b]	-(0.347)	-(0.050)
Juncus Border	Juncus Meadow	25	.05(2.242)[a]	.01(3.130)[b]	.05(2.230)[a]
	Phragmites	29	-(0.237)	.05(2.636)[a]	.05(2.500)[a]
Juncus Meadow	*Phragmites*	26	.10(1.741)	.50(0.778)	-(0.236)
		Submersed soils			
Scirpus olneyi	*Scirpus paludosus*	51	.01(3.107)[b]	.01(3.584)[b]	.01(3.143)[b]
	Scirpus acutus	52	.01(2.840)[b]	.05(2.660)[a]	.05(2.187)[a]
	Typha	61	.01(3.943)[b]	.05(2.356)[a]	.05(2.156)[a]
	Eleocharis Meadow	65	.05(2.377)[a]	.50(0.800)	-(0.441)
Scirpus paludosus	*Scirpus acutus*	21	-(0.373)	.10(1.732)	.10(1.914)
	Typha	30	-(0.070)	.10(1.813)	.05(2.349)[a]
	Eleocharis Meadow	34	.01(4.917)[b]	.01(6.432)[b]	.01(7.109)[b]
Scirpus acutus	*Typha*	31	.50(0.382)	.50(0.687)	-(0.677)
	Eleocharis Meadow	35	.10(4.590)[b]	.10(4.817)[b]	.01(4.539)[b]
Typha	Eleocharis Meadow	44	.01(5.882)[b]	.01(3.509)[b]	.01(3.823)[b]

[a] Significant

[b] Highly significant

dominant, Juncus balticus, they occupy completely different ecological niches in respect to zonation. The Borders follow the slough banks while the Meadows occur in numerous depressions in the Distichlis plains. Large differences between the mean soil salt content for these communities are reported in Table 15. The strength of these data for Juncus is supported in the statistically significant differences found at all sampling depths; mean conductivity readings between the soils of the two Juncus communities are sharply delineated by high confidence levels. The range and strong differences in the mean conductivity data suggest that J. balticus has a wide tolerance to soil salinity and therefore the distribution of Juncus communities at Fish Springs is dependent upon a factor, or factors, of greater influence than salt alone.

Phragmites fails to show significant community differences to soil salinity at the surface when compared to Juncus Borders. Significant differences do occur, however, at lower soil depths. Figure 7 shows a Phragmites stand successfully crowding out a Juncus Border. Such domination reflects the competitive nature of Phragmites to invade other terrestrial communities of equal or near equal saline conditions. Comparisons between Phragmites and Juncus Meadows suggests that here salt conditions truly exceed Phragmites tolerance and that invasion by this grass would not successfully take place in the depressions occupied by Juncus Meadows. The somewhat lower-than-standard confidence level of .10, accepted as a significant difference in this comparison, is bolstered by the lack of Phragmites as a sampled member of the Juncus Meadow communities (Table 8).

Mean conductivity readings and their statistical comparisons for submersed-soil communities also appear, respectively, in Tables 15 and 16. The submersed-soil communities which exhibit the highest tolerance to soil salinity at all sampled soil depths are Eleocharis Meadows. The high incidence of *Eleocharis* establishment upon peat soils probably accounts for the values recorded. Soil salinity is often excessive in peat areas because of their low topography and poor drainage (Campbell and Richards, 1950). Only where soil texture or elevations sharply change within an Eleocharis Meadow does the vegetation appreciably differ. Further substantiation lies in the statistical tests which separate the mean salt content of these Meadow soils from all other communities of submersed-soil habitats. Lack of significance is found only at the two lower levels in comparison with *Scirpus olneyi* stands. As noted previously, peat soils at Fish Springs are actually semi-submersed and are therefore subjected to the evaporational concentrations of surface salt. This condition was not noted for the other submersed-soil communities present.

Scirpus olneyi communities follow in salt tolerance. These stands occupy the greater portion of the marshes and are considered to be the dominant marsh type. Higher mean soil salinity values are shown for *S. olneyi* communities than for the averages of all submersed soils sampled (Table 13). Based on these averages, the soils bearing *S. olneyi* are more saline than those found throughout the remainder of the marshes. Testing the *S. olneyi* data reveals strong significant differences from the salt content of other submersed-soil communities. The exception of Eleocharis Meadows has been discussed.

Communities of *Scirpus acutus*, *S. paludosus*, and *Typha* follow in that order to salt tolerance as shown in the surface salinity data. Subsequently lower samples demonstrated that *Typha* communities tolerate slightly greater saline conditions and that *S. acutus* replaces *S. paludosus* in community tolerance at the lowermost level. The close agreement of the mean conductivity determinations for these communities is reflected in the statistical analyses in Table 16. Few tests of noteworthy significance are found.

The noted lack of significant differences in soil salt content between *Scirpus acutus*, *S. paludosus*, and *Typha* communities is not unduly surprising. Their distribution in the Fish Springs marshes is of a minor nature in comparison with the other communities studied. Patches of *S. acutus* are widely separated and never extensive while *S. paludosus* is limited to the shoreline of a single slough. *Typha* distribution is somewhat more extensive in a few areas. Often small stands of *S. acutus* are found among or immediately adjacent to *Typha* communities. Incidence of *S. acutus* was also found in the *S. paludosus* study plots. The chance that salt conditions dictate this spotty distribution is small and led to the conclusion that soil salinity is not a critical factor in the ecological separation of these emergent plant types from one another.

While the salt tolerance for *Typha angustifolia* at Fish Springs does not exceed the corresponding data for *T. latifolia* reported by Nelson (1954) or McMillian (1959), some regard should be given to the absence of *T. latifolia* from the study area. Laboratory research with supporting field observations of *Typha* communities (McMillian, 1959) revealed that zonational features of *T. latifolia* and *T. angustifolia* were due to the influences of soil salinity. A genetic "intermediate" of these species, *T. glauca* Godr., was observed to occupy a zone of soil salinity midway between the tolerance of its progenitors. The possibility that *T. latifolia* would occur at Fish Springs if suitable conditions prevailed cannot be evaluated here. Suffice it to mention that *T. latifolia* has been found on many brackish marshes in varying degrees of success. One is therefore compelled to explain the absence of this species in terms of an acknowledged limiting factor, soil salinity.

Based on McMillan's (1959) determinations, the salt content of the marsh soils at Fish Springs is not in the range found to affect either seed germination or growth of *Typha latifolia*. He found that seed production for this species, however, was affected. *T. latifolia* propagules were produced in only 2 years of a 4-year study period on saline soils. Penfound and Hathaway (1938) also noticed a definite postponement of anthesis in salt-affected soils. It becomes plausible to imagine that the natural introduction of *T. latifolia* at Fish Springs could have been affected by the above situations and led to the cautious conclusion that the saline soils of the study area were an inhibitive factor in the establishment of this species.

Statistical comparisons for the *Chara*-*Ruppia* salinity data were not feasible for the following reasons: (a) these are the only submersed communities of sufficient extent and distribution to warrant sampling and comparisons of these data with that of nonsubmersed plant types would be of little ecological consequence, (b) they often occur on the same soil sites as do emergent species and would thus exhibit many of the attributes common to all submersed-soil samples regardless of the community where the samples were collected, and (c) no zonational tendencies or distributional preferences are shown among the components of these communities. Reason b, above, was borne out when the mean conductivities for *Chara*-*Ruppia* communities (Table 15) were found to approximate the conductivities shown in Table 13 for all submersed soil samples.

The omnipresence of *Chara*-*Ruppia* throughout the marshes precludes a quantitative ecological relationship with soil salinity based on comparative data. Soil salinity of the marsh bottoms, however, seemingly dictates the establishment of these plants only. Jensen (1940) observed that *Chara* spp. are not dependent upon substrate conditions in the same respect as other plants and that *Ruppia maritima* can withstand soil salt conditions high enough to prevent dominance by another form of community. Save for the minor distribution of *Najas marina* and scatterings of *Ceratophyllum demersum* and *Utricularia vulgaris*, the dense and often unbroken carpets of *Chara*-*Ruppia* allow little chance for the successful establishment of other submersed communities. These observations infer that soil salinity is especially favorable to *Chara*-*Ruppia* and that the preponderance of these species additionally prohibit the potential advancement by other submersed communities.

Seasonal and long term changes

Many studies conducted on saline areas have shown soil salt content to vary throughout the year. Changes corresponded with water table fluctuations and evaporational losses. Nelson (1954), for example, found conductivity measurements to increase sixfold at the same sampling station between early spring and late summer. The importance of salt dynamics, both seasonal and long term, can be found in the investigations of Keith (1955, 1958, and 1961). His earlier studies demonstated a dramatic dieoff within a *Juncus* community when soil salinity increased 0.3 percent during the growing season. Adjacent plants of the same species continued growth in normal fashion. *Typha* was affected by similar changes. The impoundment of water for several years so increased soil salt deposition that major community changes were enforced in surrounding prairie grasslands. Shoreline communities of *Hordeum jubatum* L. (foxtail barley) were replaced by *Distichlis* communities when pothole waters were raised and stabilized.

The stability of soil salt concentrations at Fish Springs was examined by resampling two of the transects some 5 months after initial samples had been collected. Mean conductivities for the plant communities thus sampled show little differences in soil salt content between the April and August sampling periods (Table 17). Total salinity decreases amounted to 2.23 millimhos while increases totaled 1.96 millimhos for a net change of only 0.27 millimhos. The 0-6 inch data for the Juncus community seem somewhat inconsistent with the other statistics and are assumed to be the result of sampling error. These results indicate that the soil salt at Fish Springs is not undergoing any appreciable fluctuation during periods of plant growth.

There are some implications of salt stability upon the ecology at Fish Springs. Variation of soil salt during the growing season would limit the survival of plants within a community if salt tolerances were exceeded. Some degree of establishment by late-starting pioneer halophytes might occur in these areas. Long term salt changes would result in similar invasion of tolerant annuals and terminate with establishment of adaptive serial communities. There is no reason to believe that either of these situations take place at Fish Springs. Seasonal variation has already been acknowledged as nonexistent. Affects on marsh vegetation due to this condition could not have occurred and none were accordingly observed. Results of long term salinity changes, if present, would not have been detected in the scope of present observations. Some insight, however, on this matter may be offered. Chapman's (1960) thoughts on vegetational changes on inland "desert" marshes have already been expressed. Alteration of water table depth would be necessary for pronounced and long term

Table 17. Fluctuations of mean soil salinity with changes in time as determined by increases or decreases in conductivities of 1:5 soil suspensions from Transects Numbers 1 and 2, April and August, 1960. All figures are millimhos of conductivity based on 300 soil samples

Community	Soil depth (inches)	April	August	Increase	Decrease
Distichlis Compex	0-6	6.73	6.66	-	0.07
	7-12	2.39	2.10	-	0.29
	13-24	0.88	0.62	-	0.26
Juncus Border	0-6	1.43	2.56	1.13	-
	7-12	0.56	0.83	0.27	-
	13-24	0.26	0.63	0.37	-
Phragmites	0-6	3.80	3.60	-	0.20
	7-12	1.95	1.61	-	0.34
	13-24	1.38	1.20	-	0.18
Scirpus paludosus	0-6	0.57	0.75	0.18	-
	7-12	0.45	0.40	-	0.05
	13-24	0.20	0.21	0.01	-
Chara-Ruppia	0-6	1.15	0.71	-	0.44
	7-12	0.82	0.65	-	0.17
	13-24	0.81	0.58	-	0.23
			Totals	1.96	2.23
			Net difference	0.27	

salinity changes, either increases or decreases, to occur. The steady and consistent flow of water from the springs allows little chance for permanent changes to be found in the marsh water tables at Fish Springs.

It is concluded that the influences of soil salt upon the vegetation at Fish Springs are of a fixed nature, presently expressing both its maximum and minimum, and that of seasonal and long term salt variation need not be considered.

Aspects of plant competition

The composition of a plant community makes it a separate and unique vegetational structure and it is under separate and unique circumstances that the community flourishes. Ruttner (1953) recognized that the composition of an organic community was greatly affected by the salt content within the community's environment. The differences in soil salinity at Fish Springs have been shown to affect differences in many of the plant components which arise in the marshes. Some thought should be given, however, to plant competition as the purveyor of community distribution in salt marshes.

The data for *Phragmites communis* and *Juncus balticus* offer a suitable example. *Phragmites* shares a soil salinity tolerance with *Juncus* in the Border community and exhibits its contention for that habitat by active invasion. But where *Juncus* dominates pannes and other depressions in Meadow form, *Phragmites* did not enter. Salt concentrations exceeding *Phragmites* tolerance are found in the soils of Juncus Meadows. The implication of these relationships pointed to *Juncus* survival in a habitat of extreme but tolerated salinity while survival under less severe salt conditions was threatened by other communities of a highly competitive nature.

Thus Taylor (1939) warned that the distribution and zonational features of salt marshes are not always due to communities which merely prefer concentrations of soil salt but that they survive in such places only because they must. He supported his statements with demonstrations of salt marsh species which grew more luxuriantly when experimentally placed in less saline situations. These results suggested that the removal of competitive nontolerant species allowed tolerant plants to "emerge into dominance" and abound in salt-marshes.

Soil Moisture

Plants derive the bulk of their moisture requirements from the soil and the soil conditions which control water availability are twofold. Osmotic effects, previously mentioned, are determined by the soluble salts present in the soil while matric suction is dependent upon the surface tension of water held by the soil particles (Richards, 1959). The combined pressures of matric suction and osmotic pressure represent the stress which a plant must overcome to obtain adequate water for growth.

Soil moisture relationships at Fish Springs were separated for study; matric suction data were obtained from tensiometers and osmotic pressures were obtained from knowledge of soil salinity. The nature of tensiometer operation limited their use to emergent soils 6 inches or more above the water table.

Matric suction data are measured in units of atmospheric pressure or centibars, 100 centibars equaling one atmosphere of pressure at sea level. Variability of tensiometer readings in <u>Distichlis</u> communities was quite large, 3.0 to 36.0 centibars, and required a considerable number of determinations before a relatively stable mean could be calculated.

Readings in other emersed soil communities showed less variation and required fewer observations.

Moisture tensions of Distichlis communities average 11.71 centibars (Table 18) and were the highest recorded. Juncus Meadows follow with a mean of 8.35 millibars. Near agreement of tensions in Juncus Borders and Phragmites communities indicate similar moisture stresses from matric suction.

Table 18. Mean soil moisture tensions for the first 6 inches of soil in emersed-soil communities

Community	Number readings	Moisture tension-centibars
Distichlis complex	109	11.71
Juncus Border	46	7.71
Juncus Meadow	54	8.35
Phragmites	21	7.66

Plant physiologists generally agree that 80 centibars represents less than one-tenth the range of soil moisture tensions that plants may endure but that this range corresponds with the greater share of available soil moisture (Taylor, 1958; Richards, 1949 and 1959). The data reported in Table 18 fall well into the lower range of moisture stress from matric suction. This indicates that water availability *per se* is not a factor of significance to emersed-soil communities.

The low tensions in fact suggest a water logged condition. Evans (1953) found that poor root aeration in water logged soils was a factor associated with community zonation. However, the narrow range of tension data within the four plant zones largely rejects the influence of water logging upon zonation at Fish Springs.

Even when adequate soil water is present, osmotic conditions may create a "physiological drought" for many species. Small increases in osmotic pressure can produce large decreases in water absorption according to Krammer (1959).

Campbell et al. (1949) measured osmotic pressures of saline soil solutions and found that these pressures could be estimated from saturation extract conductivities. Their original data were transformed (Figure 15) to 1:5 conductivities for determination of osmotic pressures by the soil suspension method used in this study. Figure 16 shows this relationship and the osmotic pressures to which the plant communities at Fish Springs are subjected.

Use of Figure 16 in assessing osmotic pressures assumes complete saturation of soil salts in the soil solution. Empirically this assumption is not always met; undissolved salts encrust the soil surface at many of the emersed sampling sites and possibly to a lesser extent at subsurface levels. The osmotic pressures estimated by 1:5 conductivities may therefore tend to somewhat exceed those existing for field conditions. Osmotic pressures for the plant communities are accordingly based upon conductivity averages for soil salt occurring at both the 0-6 and 7-12 inch sampling levels to help discount this influence.

Distichlis Complexes thrive at 15 atmospheres of osmotic pressure while Phragmites communities tolerate about half this amount. Juncus ranges from nearly 10 atmospheres in the Meadow form to 6 atmospheres in Border communities. Submersed soil communities are concentrated between osmotic pressures of 1.8 to 4.9 atmospheres.

The array of plant communities along the plot of osmotic pressures in Figure 16 reflects a more accurate picture of community tolerance to

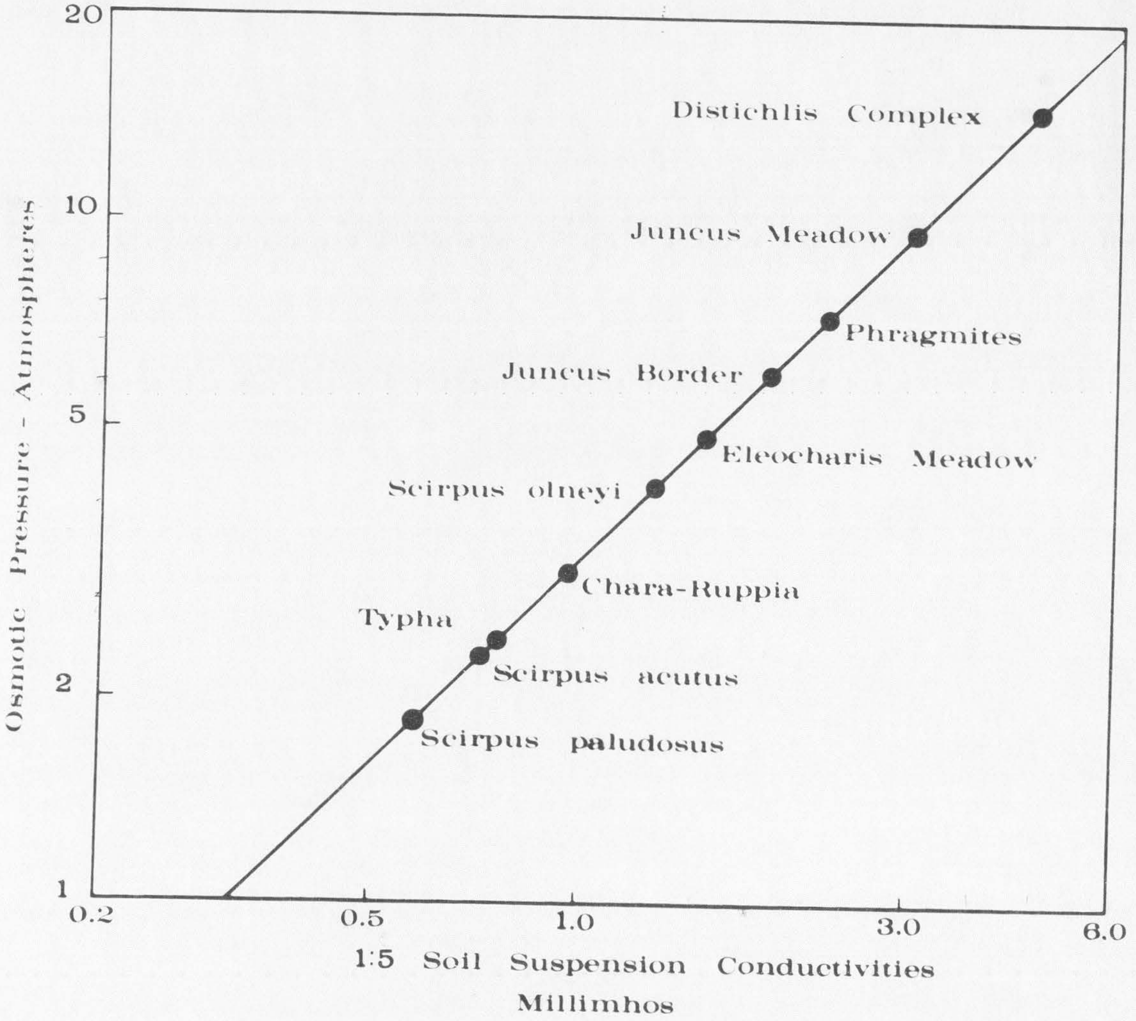

Figure 16. Relationship of 1:5 soil suspension conductivities to osmotic pressures of soil solution. Averages of 0-6 inch and 7-12 inch conductivities from Table 15 for each of the plant communities studied have been superimposed upon the plot to show the osmotic limitations confronting the communities.

soil salinity. While the order of tolerance does not materially change from the tolerances of Table 16, the actual ecological condition of community limitation, osmotic pressures of the soil solutions, can be directly evaluated. Thus osmotic pressures have been correlated with plant succession in some saline habitats (Weaver and Clements, 1938). Community susceptibility to salt toxicity, however, cannot be appraised in this concept. The importance of salt in this respect has yet to receive research attention from marsh ecologists.

Soil pH

The log of the hydrogen ion concentration or pH of a soil indirectly affects plant growth. Extreme pH conditions render essential nutrients, especially iron and calcium, unavailable to plants and may also increase the solubility of other elements to toxic levels (Krammer, 1956). Good plant growth over a pH range of 4 to 9 was obtained by Arron and Johnson (1942) when required nutrients remained available. Excessive acidity or alkalinity are also injurious to plant roots and impede both their growth and functioning (Bonner and Galston, 1952). The corrosive nature of strong acid or base media directly affects plant tissues where found in sufficient concentration. Specific pH levels have been designated by Daubenmire (1959) as the factor inhibiting many soil-borne plant diseases. Plant tolerance to soil pH has received much attention but Small (1946) concluded that most higher forms of plants grow well in a pH range of 5 to 7 with limits lying at pH 3.4 and pH 9.0.

pH conditions of the soil media have been the subject of considerable controversy when related to plant distribution. Data are often conflicting and commonly lead to opposing conclusions. After field and laboratory investigations, Olsen (1924) concluded that soil pH was largely the determining factor in the composition of plant cover. Daubenmire (1959) cited pH as the greatest single soil factor of ecological significance but that this soil attribute may not be as closely correlated with biological phenomena as formerly believed. Nelson (1954) found little effect of pH upon the distribution of plant life in salt-marshes. His studies revealed that principal marsh plants grew equally well in areas of both high and low pH. Soil pH was also found to have little effect upon the distribution of important submersed species (Jensen, 1940).

The pH samples collected at Fish Springs yielded, at best, variable information. pH data, because of their logarithmic character, do not readily lend themselves to statistical analyses, and conversion to absolute hydrogen ion concentrations is both time consuming and tedious. The data were therefore studied by computing median values from frequency distributions.

There is a tendency for surface soils to be more acid than those of the lower levels. Likewise, the second level of sampling proved to be more acid than the third. This pH stratification is attributed to the deposition of organic matter upon the upper layers of the soil profile but seems to remain true even when no difference in soil texture could be detected. The peat soils at Fish Springs, however, show a reversal of this gradient--surface peats are, for the most part, less acid than samples collected from lower levels. Lower pH values were also found in subsurface peat soils from tidal banks in California (Campbell and Richards, 1950) but Waksman et al. (1943) reported a general tendency for peat to become less acid with increased depth of sampling. This periodic inundation of the peat meadows allows for the partial silting out of alkaline soils and probably contributed to the upset of the otherwise uniform pH gradient observed in the marsh soils. Nevertheless, the strong acid reaction of the peat soils at all depths remains unique when one considers their inundation with the alkaline waters of the saline springs.

Surface water seems to affect the pH of underlying soils. When the data are separated into classes of submersed and emersed soils, these differences become more apparent (Figure 17). While the median values for both classes and at all depths fell between pH 8 and 9, the submersed soils show somewhat more acid midpoints than corresponding data for emersed soils. Inundation likewise affects the range of pH. The reciprocal structure of pH ranges is shown in Figure 17; emersed soils diminish in pH range with depth while submersed soils show an increase of pH distribution with progressively deeper sampling levels. Reduction of oxidation rates and the smaller amounts of salt buffers in the water-laden soils are the probable factors contributing to the disparity between the pH values recorded between the two soil classes.

The four terrestrial communities show little difference between median pH values within the three levels of sampling but are generally more alkaline than the typically aquatic communities (Table 19). _Juncus balticus_ exhibits median values which differ only by one-tenth of a pH unit when the Border and Meadow communities of this species are compared. Further comparison among the nonaquatic communities reveals little information of significance.

Surface soils show the widest pH distribution in _Scirpus olneyi_ communities. This community, the marsh dominant, grows in a pH range of 9.0 to 5.9 and most commonly occurs at pH 7.9. Eleocharis Meadows exhibit the widest pH spread at subsurface levels. The acid peat soils account

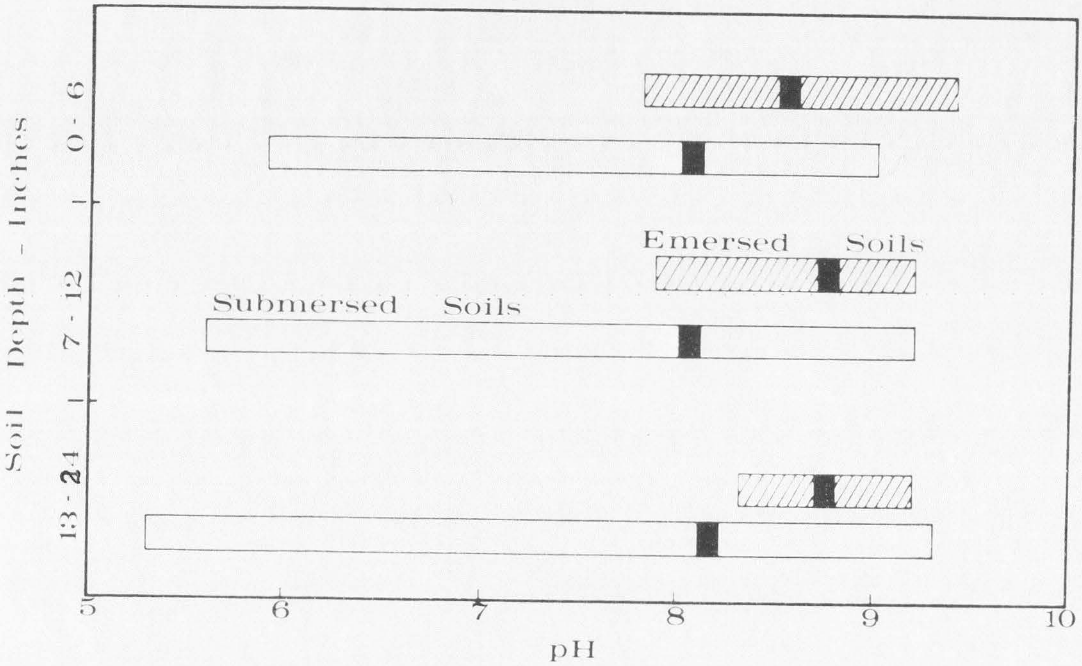

Figure 17. Median (darkened areas) and range of pH for 750 soil samples from three sampling depths. Emersed soils (hatched) show slightly more alkaline medians than submersed soils. Ranges show a reciprocal trend with depth of sampling; ranges of emersed soils decrease while submersed ranges increase as soils deepen.

Table 19. Maximum, median, and minimum pH readings for four emersed and six submersed-soil marsh communities at three soil depths.

Plant community	Statistic	Soil depth (inches)		
		0-6	7-12	13-24
	Emersed soils			
Distichlis Complex	Maximum	9.4	9.1	9.2
	Median	8.7	8.8	8.8
	Minimum	7.9	8.1	8.3
Juncus Border	Maximum	8.9	9.1	9.1
	Median	8.4	8.8	8.9
	Minimum	7.8	7.9	8.5
Juncus Meadow	Maximum	8.9	9.0	9.0
	Median	8.5	8.7	8.8
	Minimum	8.3	8.3	8.5
Phragmites	Maximum	9.2	9.2	9.0
	Median	8.6	8.7	8.7
	Minimum	8.2	8.4	8.3
	Submersed soils			
Scirpus olneyi	Maximum	9.0	9.1	8.9
	Median	7.9	7.7	7.7
	Minimum	5.9	6.3	6.7
Scirpus paludosus	Maximum	8.4	8.8	8.9
	Median	8.2	8.7	8.8
	Minimum	8.0	8.4	8.5
Scirpus acutus	Maximum	8.8	9.2	9.1
	Median	8.5	8.3	8.4
	Minimum	7.8	7.4	7.6
Eleocharis Meadow	Maximum	8.2	8.6	8.7
	Median	7.5	6.9	6.8
	Minimum	6.3	5.6	5.3
Typha	Maximum	9.0	9.1	9.3
	Median	8.5	8.4	8.7
	Minimum	7.4	7.3	6.6
Chara-Ruppia	Maximum	8.8	8.8	9.2
	Median	8.1	7.9	8.2
	Minimum	7.2	7.2	6.8

for these species showing the widest pH range. Were it not for their presence in this soil type, the median pH values for both these communities would be more alkaline than those shown in Table 19.

A comparatively small sample size for <u>Scirpus paludosus</u> accounts for the limited pH range reported for this community. Further sampling of this community would likely extend the narrow range shown. Nelson (1954) found <u>S. paludosus</u> to grow vigorously in areas of considerable pH variation.

There is some evidence for a daily and seasonal fluctuation in soil pH at the same sampling station. Jensen (1940) recorded higher pH values in marsh soils during periods of intense photosynthetic activity. He attributed these changes to the precipitation of calcium carbonate by plants onto the marsh floor. A rhythmic seasonal fluctuation of pH has been reported by Daubenmire (1959) but was dismissed as unimportant because of the buffers found within the soil. Olsen (1924) found seasonal differences amounting to 0.2 or 0.3 pH units for the same soil. Deviations such as these may well be present at Fish Springs but little importance can be attached to them in terms of plant distribution when the ranges of Table 19 are considered.

The differences of median pH values between the plant communities are not large and are often less than one-tenth of a pH unit. Such near agreement of median values and the extensive overlapping of maxima and minima determinations lead to the conclusion that any correlation between soil pH and the vegetation at Fish Springs is of negligible significance.

Soil Organic Matter

Organic matter incorporated in a soil serves as an indicator of nitrate production. Soil organic matter and nitrate production for marsh soils follow corresponding curves and offer a method of determining production of this important nutrient (Jensen, 1940). As the amount of organic matter in the soil decreases, smaller amounts of it undergo nitrification. Studies in England have indicated that organic matter is important to the distribution and succession of marsh and aquatic plants (Pearsall, 1921; Misra, 1938). Peat soils are known to support characteristic vegetation in many areas though the excessive pH conditions of peat likely contribute to this specialization.

Soil organic matter is expressed (Table 20) in percentage of organic carbon found within the first 6 inches of the soil profile. Direct conversion of these data to percent organic matter is not possible due to differences of organic materials in the samples. However, a factor of 1.72 would approximate percent organic matter when applied to the lower carbon values but would result in increased error when applied to the larger carbon percentages (J. P. Thorne, in correp.).

Submersed soils are generally higher in organic carbon content than emersed soils (Table 20). The increase of organic content in inundated soils from that occurring in emersed soils is typical of wetlands; water coverage greatly reduces the rate of organic oxidation and facilitates the accumulation of organic debris (Kadlec, 1960). Increased retention of organic matter has also been correlated with increases in soil water content on English coastal marshes (Gillham, 1957).

Juncus Border soils are highest in organic carbon content among the emersed-soil communities. The increased carbon in these soils is due to the location of the communities on the slough shorelines where wind and water movement deposit floating materials. Soils of Distichlis Complexes,

Table 20. Soil organic matter, expressed in percentage organic carbon, occurring in the first 6 inches of soil for four emersed and six submersed-soil plant communities.

Community	Number samples	Percentage organic carbon
	Emersed soils	
Distichlis Complex	23	4.03
Juncus Border	5	7.25
Juncus Meadow	5	4.61
Phragmites	7	4.40
	Submersed soils	
Scirpus olneyi	14	12.66
Scirpus paludosus	5	9.04
Scirpus acutus	7	3.36
Eleocharis Meadow	4 (peat excluded)	7.49
Typha	8	5.03
Chara-*Ruppia*	10	5.59

Phragmites, and Juncus Meadows contain similar amounts of organic carbon. These percentages are low, between 4.03 and 4.61 percent, and reflect the high inorganic increment common to soils of arid climates. Mineralization of litter within the emersed-soil communities is undoubtedly rapid and the formation of humus negligible. The influences of surface salt may also play an important part in the transfer of plant material to soil humus.

Three samples are not included in Table 20. These were collected from Distichlis Flood Plains and from a transition zone between a Juncus Border and Scirpus olneyi stand. The Flood Plain samples (2) contained 12.22 and 7.51 percent organic carbon, respectively. Fluctuation of water levels with resultant die-offs of Distichlis and Chara-Ruppia added to the organic matter accumulation on slough shores. Higher organic carbon accordingly resulted in samples from these sites. The single transition zone sample contained 29.75 percent organic carbon. In addition to Juncus and S. olneyi, the ecotone was vegetated with scattered clumps of Sporobolus airoides and some Distichlis. A marked soil change from clay loam to loamy peat accompanied the community transition.

Soil of Scirpus olneyi communities contained 12.66 percent organic carbon; excluding peat samples, these soils are organically the richest of the marshes. A large deposition of fallen stems accompanied by extensive regrowth the following season adds to the accumulation of organic debris in these communities. Additional organic materials are probably entrapped within the dense stem growth and network of roots.

The slough bottom bearing the Scirpus paludosus community contains 9.04 percent of organic carbon. Nelson (1954) found that barren saline soils, upon flooding, were initially vegetated with S. paludosus. The organic matter of these wasteland soils prior to inundation was by no means plentiful. At Fish Springs, the occurrence of S. paludosus on soils of relatively high organic content further suggests that this community presently occupies a habitat and a prolonged serial stage unlike that usually associated with this species.

Excluding peat samples, which may be considered of completely organic nature, soils bearing Eleocharis contain 7.49 percent organic carbon. These data are derived from comparatively inorganic soils which supported isolated patches of Eleocharis throughout the marshes. Eleocharis Meadows, however, seemingly correspond with the distribution of peat and those clumps of this species found elsewhere are not deemed representative of the true Meadow vegetation.

Other submersed soils contain somewhat lesser amounts of organic carbon. Chara-Ruppia soils average 5.59 percent, Typha 5.03 percent, and Scirpus acutus 3.36 percent organic carbon.

The role of organic matter in the ecology of the Fish Springs marshes was not readily determined. In theory, a community may add enough organic matter to a soil to sufficiently inhibit its own welfare which results in succession by another community more adapted to these new conditions. Plant succession and distribution have thus been shown by Misra (1938) to be correlated with the accumulation of organic matter in some aquatic habitats. Jensen (1940) demonstrated that Ruppia occidentalis (or R. maritima) became dominant on nonorganic soils while another submersed species, Potamogeton pectinatus, was limited to organic areas. However, the inert succession of inland saline marshes (Chapman, 1960) and the stability of salt concentrations (Table 18) indicate that the vegetation at Fish Springs undergoes little change. The exceptions of S. paludosus withdrawal and Phragmites encroachment have been previously treated.

It will be recalled that small clumps of _Eleocharis_ are present on soils of 7 percent organic carbon while extensive meadows of _Eleocharis_ coincide with the distribution of highly organic peat. Generally, inorganic soils preceed the formation of organic soils in marshes; furthermore, the organic increment of a soil is largely derived from plant materials deposited from within the community above. The adaptability of _Eleocharis_ growth to both extremes of organic strata thus advocates the origin of these communities on the inorganic sites. It also suggests that _Eleocharis_ has thrived on the accumulated plant materials rather than giving way to a successor community.

The propensity for latent plant successors to adapt, survive, and reproduce on sites of changing organic concentrations may be of importance on nonsaline or tidal marshes. Succession is often active and of definitive course in these areas. However, in salt-marshes of consistent and relatively predictable salinity, succession becomes all but stationary. Here the accumulation of organic matter may be of some importance in the maintenance of community form but evidence for its influence in the encouragement of community dynamics is lacking.

THE WATER FACTOR

Water is necessary for life to all organisms. Without water life either ceases to exist or enters a state of dormancy. For plants, water assumes five important functions, each a requisite of existence (Krammer, 1959). It is a constituent of protoplasm, it is a reagent for most if not all chemical reactions involving life functions, and likewise it is a solvent of universal importance in these and other plant activities. Water also provides the turgidity of cell construction in herbaceous tissues and finally, it is the medium of translocation for plant nutrients. The following sections treat the chemistry and fluctuation of the water providing life for the marsh communities at Fish Springs.

Water Chemistry

North, Middle, and South Springs are each the source of a drainage system terminating in expanses of marshland. Ion analyses of water samples taken from these springs are shown in Table 21. With two exceptions, a striking similarity exists between the data for each spring. North Spring notably differs from the others in its higher sodium and chloride content. Other ion concentrations vary only slightly or not at all. Nitrate determinations, given only in parts per million, may be regarded as traces. Only minute quantities of nitrate, if any at all, are found in unpolluted waters (Reid, 1961). In addition to the similarities of ion abundance, the linear arrangement of the springs and their corresponding water temperatures further indicate that a common aquifer supplies the water to all the springs.

Table 21. Water analysis for three major springs, Fish Springs National Wildlife Refuge, 1959. Data shown in parts per million and equivalent parts per million for each ion.

Ion	North Spring		Middle Spring		South Spring	
	epm	ppm	epm	ppm	epm	ppm
Cations						
Calcium	6.28	126	4.13	83	4.06	81
Magnesium	3.65	44	4.42	53	4.41	53
Sodium	32.10	738	21.30	490	20.60	474
Potassium	1.28	50	1.14	44	1.11	43
Anions						
Chloride	31.85	1129	18.01	639	18.01	639
Sulfate	8.76	421	8.69	418	8.21	394
Carbonate	0	0	0.29	9	0	0
Bicarbonate	4.13	252	3.79	231	2.43	148
Nitrate	-	0.1	-	0.2	-	0.2

The preponderance of sodium and chloride in all the springs leaves little doubt that common table salt, sodium chloride, is the principal compound contributing to the salinity of the marshes. Lesser amounts of sodium likely combine with other anions but the great affinity which exists between sodium and chloride refutes the appreciable combination of other sodium salts. However, as Hutchinson (1957) has pointed out, the salinity of inland waters may be regarded as the concentration of all ions present in those waters. Thus conductivity measurements taken from spring samples show that North Spring, with total dissolved solids equaling 2760 parts per million, has a conductivity of 4.60 millimhos. Dissolved solids total 1870 and 1890 parts per million in South and Middle Springs, respectively, and yield a conductivity of 3.10 millimhos in each case.

The absence of all but traces of carbonate and the presence of considerable bicarbonate have some effects upon the pH of the spring waters. Bicarbonate is the major causative agent in a pH range of 7 to 9 while carbonate gains significance at pH levels above 9 (Hutchinson, 1957). Alkaline conditions are increased within these ranges by higher concentrations of the respective ions. pH determinations taken in the springs correspond well with the ion analyses (Table 21); water from the three springs ranges from pH 7.2 to pH 7.6 with the latter figure being recorded at Middle Spring where a slight concentration of carbonate is found. Calcium bicarbonate along with magnesium bicarbonate undoubtedly are the two salts contributing to the pH factor. Other bicarbonate salts more than likely are formed but, as with sodium and chloride, the affinity between calcium, magnesium, and bicarbonate ions predetermine their combination.

The ecological application of water chemistry to vascular plant life has not been clearly defined. Nutrient availability is rarely a limiting factor to vegetation in salt water habitats (Penfound, 1952). And unless toxic levels are detected in water supplies, the effects of water chemistry must be directed to their influences upon the soils of a marsh.

Water Fluctuations

Water level data were secured during the period generally coinciding with the greater portion of the growing season (see Table 11). Gauges were placed in spring, slough, and marsh areas to determine changes within each of these drainage systems. Obstruction of water movement by vegetation, transpiration, and evaporation contributed to water level variation but no effort was made to attribute the proportion due to each of these factors. Plant obstruction appears to be most effective in sloughs (Figure 13) while transpiration and evaporation presumably are more active in marsh habitats.

Presentation of data for each of the 16 water level stations would be at best bulky and often confusing. A summary of water level information for each of the drainage habitats is therefore given in Table 22. Maximum fluctuations are also given for each habitat although these may have occurred at widely separated stations and in drainages of less important springs.

No fluctuations of water levels were found before the fourth week in May. At that time the growth of submersed vegetation in sloughs nearest the springs began to hinder the rate of water movement. Water levels in sloughs further from the springs had not yet come under this influence. It should be remembered that, although submersed vegetation appeared green

Table 22. Water level fluctuations based upon data representative of each type of drainage habitat. Slough A located nearer water source than slough B. Maximum fluctuation data are qualified (see text). All figures are inches and are plus unless otherwise indicated by minus sign.

Month	Week	Drainage habitat			
		Spring	Slough A	Slough B	Marsh
May	3	-	-	-	-
	4	-	0.250	-	-
June	1	0.375	0.750	0.500	-
	2	0.500	0.750	0.875	-0.750
	3	0.875	1.375	0.375	-1.000
	4	0.875	1.250	0.125	-1.000
July	1	1.250	1.625	0.375	-0.750
	2	1.500	1.875	0.250	-1.125
	3	1.875	2.000	-0.125	-1.125
	4	2.375	2.250	-0.500	-1.375
August	1	2.875	2.500	-0.500	-1.500
Maximum gain		4.625	2.875	1.000	0.500
Maximum loss (-)		1.875	0.250	2.125	4.000

all year, active growth is limited during winter months. Hence those plants nearest the warm spring waters were first to commence growth. A corresponding rise in water levels resulted.

Changes in the spring pools soon followed; as adjacent slough waters were slowed, the backup of water forced an increase in the levels of the spring pools. These rises became even more conspicuous in springs surrounded by dikes and in those partially checked by control structures. The constant effluence of the springs continually added to the increases of both the spring pools and immediate slough drainages.

Water levels of outlying sloughs began to increase at the time spring pools were rising. Submersed vegetation had begun to cause similar blockage as it had further upstream. By the second week in June the water in these sloughs had reached its peak. The obstruction of slough vegetation then began to cause a decline in the water levels of the marshes; marsh levels dropped .750 inches during the first week of the drawdown (Table 22).

Water level trends for the remaining portion of the season were established during the third week of June. The spring pools continued to rise and slightly exceeded the increases found in nearby sloughs. Other sloughs, further from the springs, progressively lost their previous gains until small losses were registered. The marshes steadily receeded under the influence of upstream obstruction and, as the heat of summer commenced, lost additional amounts to evaporation and transpiration. Evapotranspirational losses undoubtedly occur in all water areas but are likely to be greater in marsh habitats where quiescent waters and rank stands of emergent plants are found.

Effects on vegetation

The water level changes at Fish Springs are largely due to the presence and activities of the vegetation. These fluctuations in turn affect the plant life. Vegetation along spring shores and slough banks is flooded while marsh edges and hummucks are exposed. Some slough vegetation is alternately confronted with both situations. However, flooding and exposure varied considerably depending upon the topography of any particular locale under observation.

Despite maximum water fluctuations of more than 4 inches (Table 22), no changes in soil salt concentration due to this influence were found (see Table 17). Ground water supplies presumably are not affected by the temporary fluctuations which took place. Previous sections have treated soil salinity, water tables, and plant responses and no further mention of these relationships to water levels need be made here.

Emergent species seem indifferent to the slight water fluctuations. While flooding can cause a die-off of emergent plants (McDonald, 1955) the severity of kill is related to both the duration and depth of unfavorable inundation. Likewise, prolonged periods of exposure reduce emergent vegetation to dried and decedent marsh. The changes in the water levels at Fish Springs are not of the magnitude to cause either of these adversities.

Submersed vegetation is somewhat affected by reduced water levels in a few areas. These effects, however, are not changes in community composition or distribution but upon individuals or small mats of plants. Vegetation left partially exposed by receeding waters often becomes brown-tipped while those completely exposed quickly wither and die. Flooding in no way influences the welfare of submersed species.

The exposure of marsh edges and some slough banks affords an alteration of the plant life on these sites. Primarily affected are banks and edges of relatively steep inclination where emergent-marsh communities are lacking. The exposed soils bear either desiccated litter of submersed communities or no plants at all. Annual vegetation quickly immigrates and soon establishes temporary communities. *Atriplex patula* L., var. *hastata* A. Grey (spearscale) is the most frequent pioneer species. Leafy stands of this plant rim distant sloughs and ring plateaus by the end of July. Less prominent species are *Suaeda occidentalis* S. Wats. (seepweed), *Ranunculus cymbalaria* Pursh., var. *saximontanus* Fern. (buttercup) and *Chenopodium hybridum* L. (goosefoot). *Distichlis* encroachment often follows but is usually shortlived. Where *Distichlis* becomes more permanent, as on some of the higher banks, the vegetation is designated a Distichlis Flood Plain. Nevertheless, the plant zones affected by water recessions during summer months are transitory habitats, undergoing continual modification and indeterminate vegetative change.

SUMMARY AND CONCLUSIONS

1. Ecological studies were made at Fish Springs National Wildlife Refuge during the summer of 1959 and the spring and summer of 1960. Investigations were directed to the structure and composition of the vegetation and to the environmental factors affecting the vegetation.

2. Fish Springs National Wildlife Refuge consists of about 18,000 acres of marshland in western Utah. Three large springs and a number of lesser springs provide a constant flow of mineral waters to the marshes. Total measured flow is 43.5 second-feet. The springs are warm and have been, for the most part, diked by early land owners for irrigational purposes. Outlying marsh areas, however, are not materially affected by these control structures. Weather records show that Fish Springs is a "half-desert" habitat with a mean annual temperature of 51.3 degrees F. and an annual precipitation of 7.13 inches.

3. The history of Fish Springs is rich with the events of explorations, the Pony Express and Overland Stage lines, and various other enterprises based upon the availability of water in a remote desert region.

4. An analysis of the vegetation describes the surrounding Desert Upland vegetation, four emersed-soil communities, and six submersed-soil communities. The emersed-soil communities include (a) Distichlis Complex communities, (b) Juncus Borders, (c) Juncus Meadows, and (d) *Phragmites* communities. The submersed-soil communities include (e) Eleocharis Meadows, (f) the major emergent community of *Scirpus olneyi* and lesser emergent stands of (g) *Typha angustifolia*, (h) *S. acutus*, (i) *S. paludosus*, and (j) the aquatic *Chara*-*Ruppia* community.

5. The warm spring waters hasten seasonal development for many species while outlying sections of marsh are slower to show vernal response. Halophytic species are later to develop flowering organs than many plants less tolerant to soil salinity.

6. Vegetational zonation generally follows a course dictated by soil salinity and, to a lesser extent, ecological amplitude. Chara-Ruppia to Scirpus olneyi to Juncus to Distichlis is the most common zonational pattern. Intervening stages of Eleocharis and Phragmites are sometimes prevalent while the sole stand of S. paludosus suggests that it represents the tenaceous remnants of a pioneer stage. Several aspects of the vegetation, including (a) knife-like community boundaries, (b) relatively few plant components within each community, and (c) the lack of pioneer communities, indicate that succession is static and not undergoing active progression to terminal vegetation.

7. Soil samples collected at three depths and from both emersed and submersed-soil sites show that (a) salt content decreases with soil depth and (b) that inundation greatly reduces the salt present. Soil salt concentrations are also shown to be different between many plant types and offers an explanation for community zonation. Seasonal and long term soil salinity changes are concluded to be absent and therefore of no influence to the marsh vegetation. Salt and plant competition sometimes exhibit a definite relationship in community distribution within salt-marshes as shown in the data for Juncus and Phragmites.

8. Matric suction measurements of soil moisture indicate that this soil stress is of no consequence to salt-marsh vegetation. The osmotic pressures which result from soil salinity, however, create a wide array of tolerances between the plant communities studied.

9. Organic carbon determinations are higher in submersed-soils than in emersed-soils. While it is suggested that, in some cases, the accumulation of organic materials may be important to plant succession, no significance of this characteristic was found in the ecology at Fish Springs.

10. Soil samples collected at three depth and from both emersed and submersed-soil sites show that pH ranges are affected by (a) soil depth and (b) inundation. However, median pH values for each of the plant communities show little, if any differences between the pH of their soils. Soil pH is of little consequence to the marsh communities at Fish Springs.

11. Sodium chloride is the salt likely responsible for the salinity of the marshes. Calcium bicarbonate and magnesium bicarbonate are believed to be the salts contributing to the recorded pH ranges of 7.2 to 7.6 from the spring waters. The ecological influences of water chemistry are not deemed directly important to plant life but are considered the causative agent for many of the soil characteristics of the study area.

12. Annual vegetation immigrates to newly exposed habitats in some marsh areas. This is the result of slight changes in water levels brought about by plant obstruction, transpiration, and evaporation.

LITERATURE CITED

Arron, D. I., and C. M. Johnson. 1942. Influence of hydrogen ion concentration on the growth of higher plants under controlled conditions. Plant Physiology 17:525-539.

Ayers, A. D. 1952. Seed germination as affected by soil moisture and salinity. Agronomy Journal 44:82-84.

Ayers, A. D., and H. E. Hayward. 1948. A method for measuring the affects of soil salinity on seed germination with observation on several crop plants. Proceedings Soil Science Society of America 13:224-226.

Ball, J. 1910. Climatological diagrams. Cairo Science Journal 4(50).

Bird, R. D. 1961. Ecology of the aspen parkland of western Canada. Contribution No. 27, Canadian Department of Agriculture, Ottawa.

Bonner, J., and A. W. Galston. 1952. Principles of plant physiology. W. H. Freeman and Company, San Francisco.

Bourn, W. S., and C. Cottam. 1950. Some biological effects of ditching tidewater marshes. Research Report No. 19, U. S. Fish and Wildlife Service, Washington.

Browne, J. R. 1868. Report of J. Ross Browne on the mineral resources of the states and territories west of the Rocky Mountains. Government Printing Office, Washington.

Campbell, R. B., C. A. Bower, and L. A. Richards. 1949. Change of electrical conductivity with temperature and the relation of osmotic pressure to electrical conductivity and ion concentration of soil extracts. Soil Science Society of American Proceedings 13:66-69.

Campbell, R. B., and L. A. Richards. 1950. Some moisture and salinity relationships in peat soils. Agronomy Journal 42(12):582-585.

Carter, K. B. 1952. Riders of the pony express. The Pony Express Mid-century Memorial Commission, Salt Lake City.

Chapman, V. J. 1938. Studies in salt-marsh ecology. Sections I-III. Journal of Ecology 26:144-179.

Chapman, V. J. 1939. Studies in salt-marsh ecology. Sections IV-V. Journal of Ecology 27:160-201.

Chapman, V. J. 1940a. Studies in salt-marsh ecology. Journal of Ecology 28:118-152.

Chapman, V. J. 1940b. Succession on the New England salt-marshes. Ecology 21:279-282.

Chapman, V. J. 1960. Salt-marshes and salt-deserts of the world. Plant Science Monographs. Interscience Publishers, Inc., New York.

Dansereau, P. 1957. Biogeography and ecological perspective. The Ronald Press Co., New York.

Daubenmire, R. E. 1959. Plants and environment. John Wiley and Co., New York.

Davis, C. A. 1895. The flora of the salt-marshes. Asa Gray Bulletin 3: 11-12 and 3:23-24.

Davis, C. A. 1911. Salt-marshes, a study in correlation. Association of American Geographers Annual 1:139-143.

Ellis, L. L. 1955. Preliminary notes on the correlation between alkalinity and the distribution of some free floating and submerged aquatic plants. Ecology 36:763-764.

Evans, L. T. 1953. The ecology of halophytic vegetation at Lake Ellesmere, New Zealand. Journal of Ecology 41:106-122.

Flowers, S. 1934. Vegetation of the Great Salt Lake region. Botanical Gazette 95:353-418.

Gillham, M. 1957. Coastal vegetation of Mull and Iona in relation to salinity and soil reaction. Journal of Ecology 45:757-778.

Hayward, H. E., and L. Bernstein. 1958. Plant-growth relationships on salt-affected soils. Botanical Review 24:584-635.

Hayward, H. E., and C. H. Wadleigh. 1949. Plant-growth relations on saline and alkali soils. Advances in Agronomy 1:1-38.

Hutchinson, G. E. 1957. A treatise on limnology, Vol. 1. John Wiley and Sons, Inc., New York.

Jansen, R. 1942. Report on Fish Springs. U. S. Fish and Wildlife Service memorandum (typed).

Jensen, G. H. 1940. The relation of some physical and chemical factors of the soil to the productivity and distribution of certain waterfowl food plants at Bear River Refuge. Unpublished MS thesis, Utah State University Library, Logan.

Kadlec, J. A. 1960. The effect of a drawdown on the ecology of a waterfowl impoundment. Michigan Department of Conservation Report 2276, Lansing.

Kearney, T. H. 1911. The choice of crops for alkali lands. U. S. Department of Agriculture Farmer's Bulletin No. 446, Washington.

Kearney, T. H., L. J. Briggs, H. L. Shantz, J. W. McLane, and R. L. Piemeisel. 1914. Indicator significance of vegetation in Tooele Valley, Utah. Journal of Agricultural Research 1:365-417.

Keith, L. B. 1955. An ecological study of waterfowl on artificial impoundments in southern Alberta. Unpublished MS thesis. University of Alberta Library, Edmonton.

Keith, L. B. 1958. Some effects of increasing soil salinity on plant communities. Canadian Journal of Botany 36(1):79-89.

Keith, L. B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildlife Monographs No. 6.

Krammer, P. J. 1949. Plant and soil water relationships. McGraw-Hill Book Company, Inc., New York.

Krammer, P. J. 1956. Roots as absorbing organs. Encyclopedia of Plant Physiology 3:188-214.

Krammer, P. J. 1959. Transpiration and the water economy of plants. Plant Physiology Vol. 2. Academic Press, New York.

Leech, E. O. 1892. Report of the Director of the Mint upon the production of the precious metals in the United States during the calender year 1891. Government Printing Office, Washington.

Leech, E. O. 1893. Report of the Director of the Mint upon the production of the precious metals in the United States during the calender year 1892. Government Printing Office, Washington.

Love, A., and D. Love. 1954. Vegetation of a prairie marsh. Bulletin of the Torrey Botanical Club 81(1):16-34.

Mason, H. L. 1957. A flora of the marshes of California. University of California Press, Berkeley and Los Angeles.

McBride, B. 1939. Engineering report, Fish Springs area. U. S. Fish and Wildlife Service memorandum (typed).

McDonald, M. E. 1955. Cause and effects of die-off of emergent vegetation. Journal of Wildlife Management 19:24-35.

McMillian, C. 1959. Salt tolerance within a Typha population. American Journal of Botany 46(7):521-526.

Miller, W. R., and F. E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal-marshes. Ecological Monographs 20:143-172.

Misra, R. D. 1938. Edaphic factors in the distribution of aquatic plants in English lakes. Journal of Ecology 26:411-451.

Nelson, N. F. 1954. Factors in the development and restoration of waterfowl habitat at Ogden Bay Refuge. Utah Department of Fish and Game Publication No. 6.

Nelson, N. F. 1955. Ecology of Great Salt Lake marshes. Utah Academy Proceedings 32:37-40.

Olsen, C. 1924. Studies on the hydrogen ion concentration of the soil and its significance to the vegetation, especially to the natural distribution of plants. Journal of Ecology 12:139-142.

Oosting, H. J. 1958. The study of plant communities. W. H. Freeman and Company, San Francisco.

Pearsall, W. H. 1921. A suggestion as to factors influencing the distribution of free floating vegetation. Journal of Ecology 9:241-253.

Penfound, W. T. 1952. Southern swamps and marshes. Botanical Review 18: 413-446.

Penfound, W. T., and E. S. Hathaway. 1938. Plant communities in the marshlands of south-eastern Louisiana. Ecological Monographs 8:1-56.

Purer, E. A. 1942. Plant ecology of coastal salt-marshes of San Diego County, California. Ecological Monographs 12:81-111.

Rawson, D. S., and J. E. Moore. 1944. The saline lakes of Saskatchewan. Canadian Journal of Research 22(6):141-201.

Reid, G. K. 1961. Ecology of inland waters and estuaries. Reinhold Publishing Corp., New York.

Richards, L. A. 1949. Methods of measuring soil moisture tension. Soil Science 68(1):95-112.

Richards, L. A. 1954. Diagnosis and improvement of saline and alkali soils. U. S. Agricultural Handbook No. 60, Washington.

Richards, L. A. 1959. Availability of water to crops on saline soil. Agriculture Information Bulletin No. 210, Washington.

Russell, E. J. 1917. Soil conditions and plant growth. Longmans, Green, and Company, Inc., New York.

Ruttner, F. 1953. Fundamentals of Limnology. University of Toronto Press, Toronto.

Scofield, C. S. 1942. The Pecos River joint investigation. Soil salinity investigation. National Resources Planning Board, Part III, Section 6: 263-334.

Shearer, D. L. 1956. Climatological Report No. 2, Dugway Proving Ground. Technical Services, Dugway Proving Ground, Utah.

Simpson, J. H. 1876. Report of explorations across the Great Basin in the territory of Utah for a direct wagon-route from Camp Floyd to Genoa, in Carson Valley. Government Printing Office, Washington.

Small, J. 1946. pH and plants. Van Nostrand Company, Inc., New York.

Sowls, L. K. 1955. Prairie ducks. The Stackpole Company, Harrisburg.

Taylor, N. 1939. Salt tolerance of Long Island salt-marshe plants. New York State Museum Circular 23.

Taylor, S. A. 1958. Measuring soil moisture. Del Centro Internazionale Studi De Irrigazoine A Pioggia-Verona 5(1):20-38. (Italian and English).

Waksman, S. A., H. Schufhoff, C. A. Hickman, T. C. Cordon, and S. C. Stevens. 1943. The peat soils of New Jersey and their utilization, part B: The peat resources of New Jersey. Geological Series, Department of Conservation and Economic Development Bulletin No. 55.

Walker, V. D. 1953. Factors affecting the establishment and spread of the bullfrog, Rana catesbeiana, in Utah and northern Idaho. Unpublished MS thesis, Utah State University Library, Logan.

Walkley, A. 1935. An examination of methods for determining organic carbon and nitrogen in soils. Journal of Agricultural Science 25: 598-609.

Walkley, A. 1947. A critical examination of a rapid method for determining organic carbon in soils--effect of variations in digestion conditions and of inorganic soil constituents. Soil Science 63:251-264.

Weaver, J. E., and F. E. Clements. 1938. Plant ecology. McGraw-Hill Book Company, Inc., New York.

Wells, B. W. 1942. Ecological problems of the southeastern United States coastal plain. Botanical Review 8:533-561.

Wherry, E. T. 1920. Plant distribution around salt-marshes. Ecology 1: 42-48.

Williams, C. S. 1938. Report on observations made at Fish Springs, Utah. U. S. Fish and Wildlife Service memorandum (typed).

Wilson, V. T. 1938. Report on Fish Springs. U. S. Fish and Wildlife Service memorandum (typed).

Wood, R. D. 1950. Stability and zonation of Characeae. Ecology 31(4): 642-647.

Wood, R. D. 1952. The Characeae. Botanical Review 18(5).

Woodbury, A. M. 1956. Ecological check lists, Great Salt Lake Desert series. Ecological Research, Dugway, Utah. University of Utah, Salt Lake City.

APPENDIXES

APPENDIX A

Study Transects

Graphic reproductions of the study transects are shown in the following pages. Much of the data presented in the foregoing discussions have been plotted under the transect cross sections to show trends in the edaphic ecology at Fish Springs. The salinity data have been smoothed by threes to facilitate interpretation; other figures have not been so treated. Note also that the vertical scales of the salinity graphs have been logarithmically condensed. Any of the measurements which were recorded at a particular point within a community may be enumerated by reading the graphs directly below the desired location on the transect.

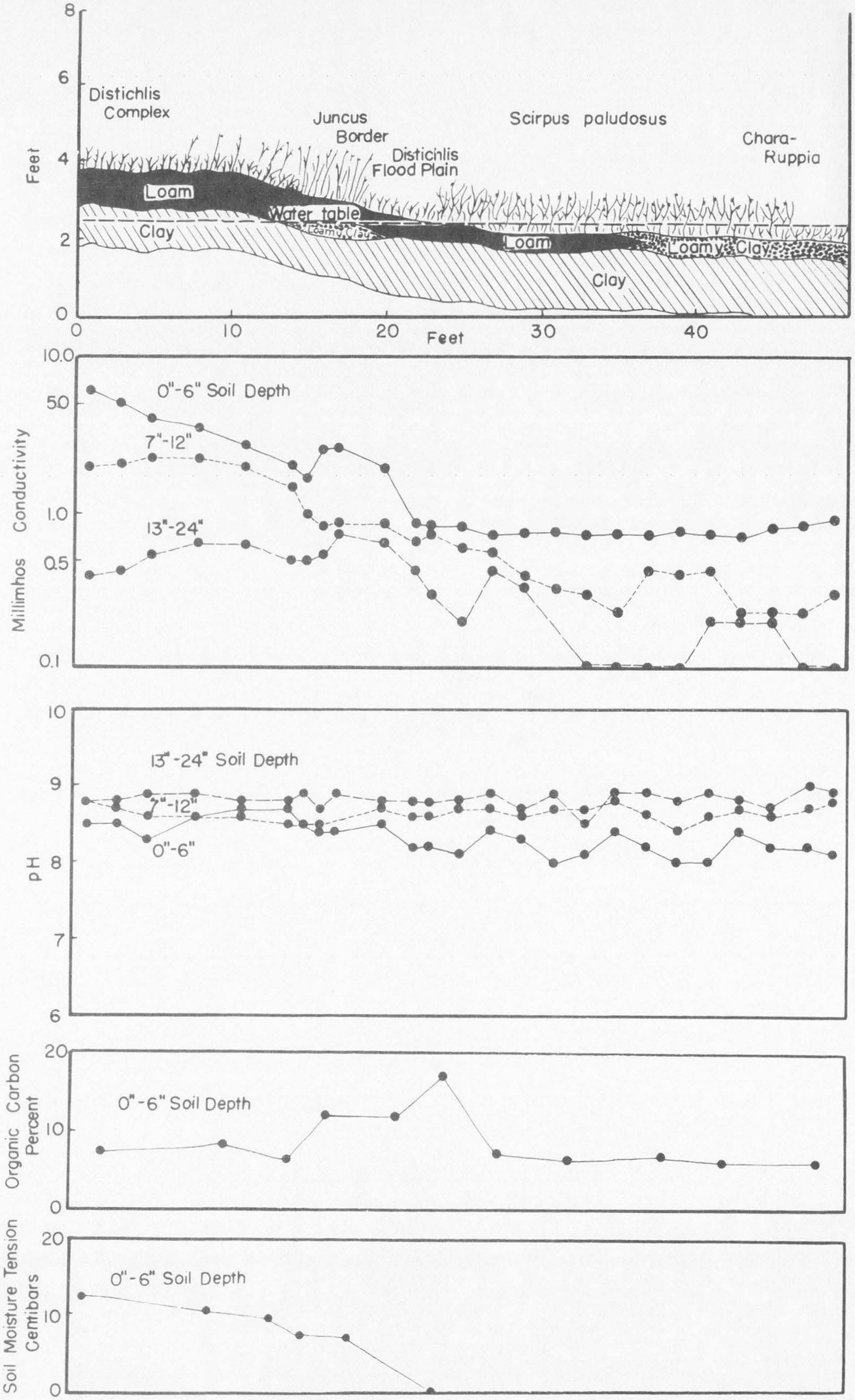

Figure 18. Transect No. 1: plant communities and edaphic data.

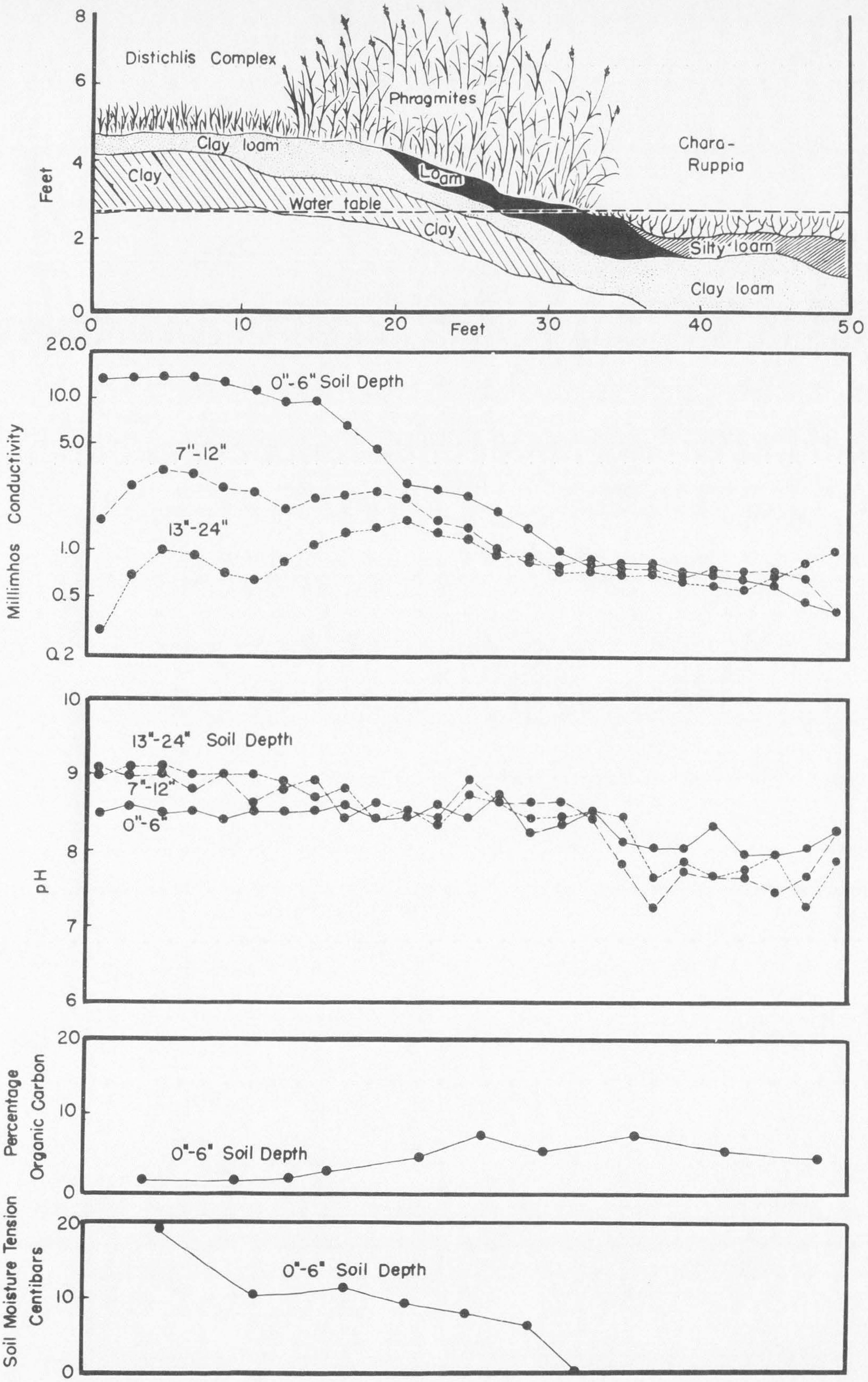

Figure 19. Transect No. 2: plant communities and edaphic data.

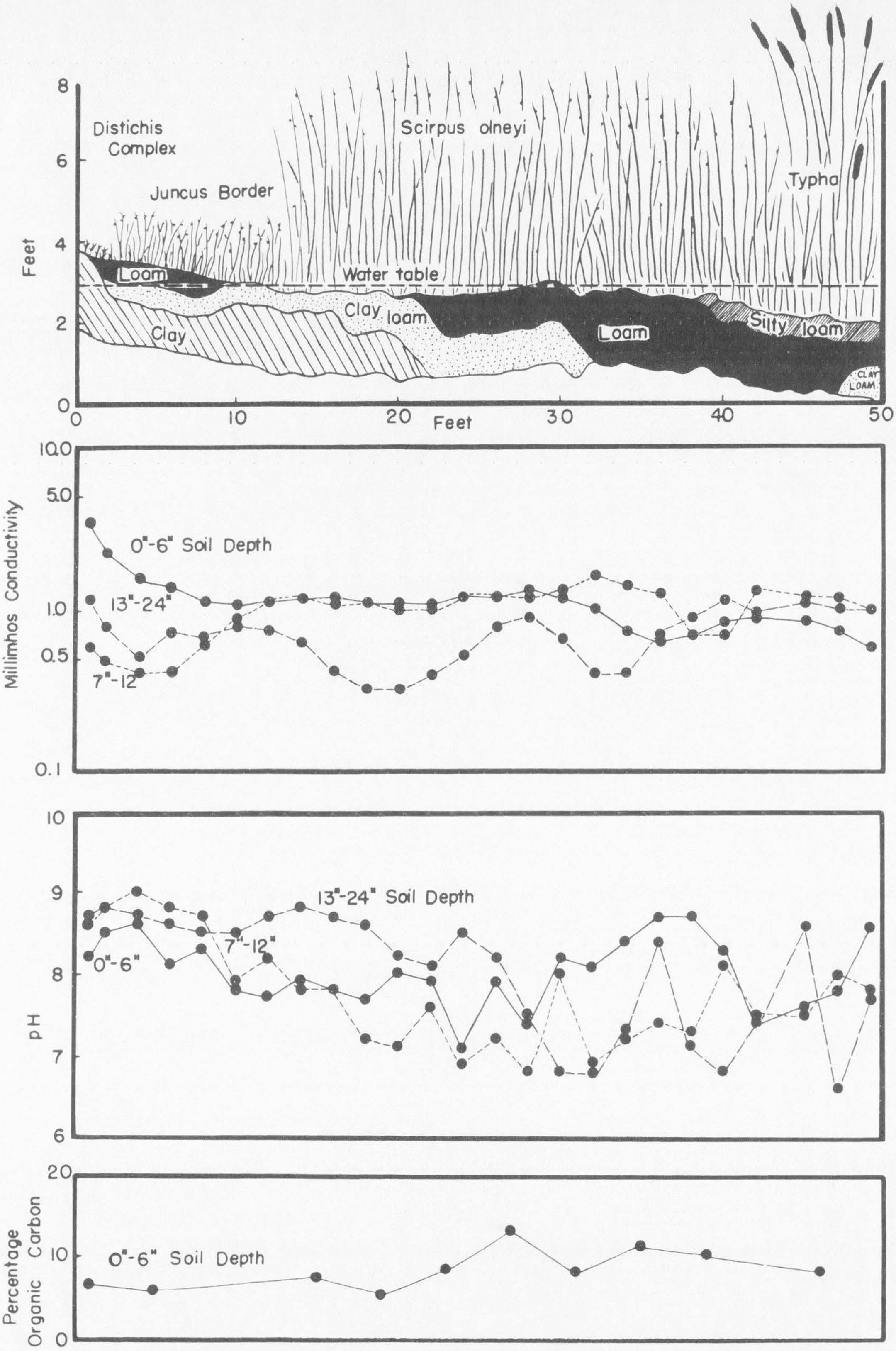

Figure 20. Transect No. 3: plant communities and edaphic data.

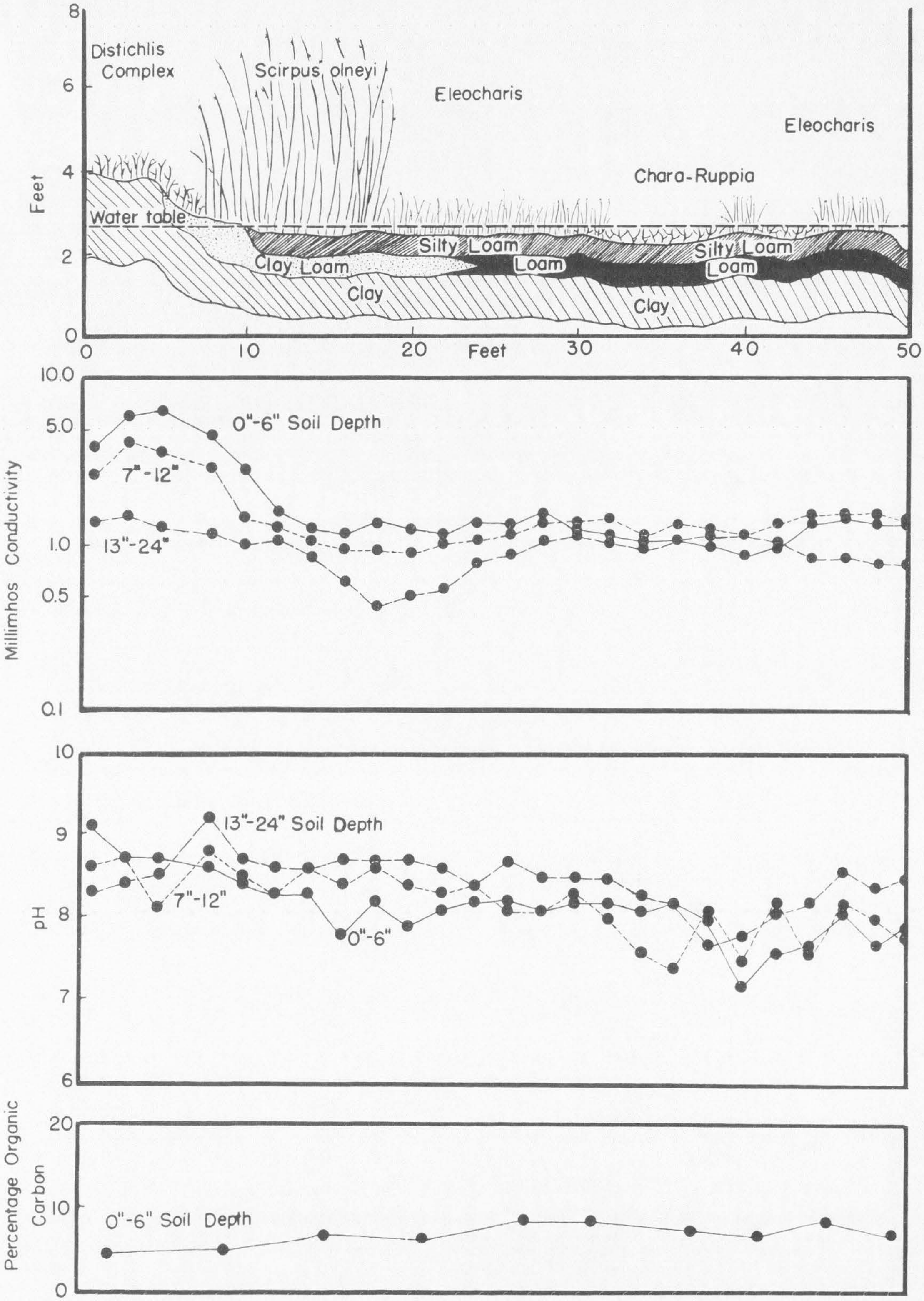

Figure 21. Transect No. 4: plant communities and edaphic data.

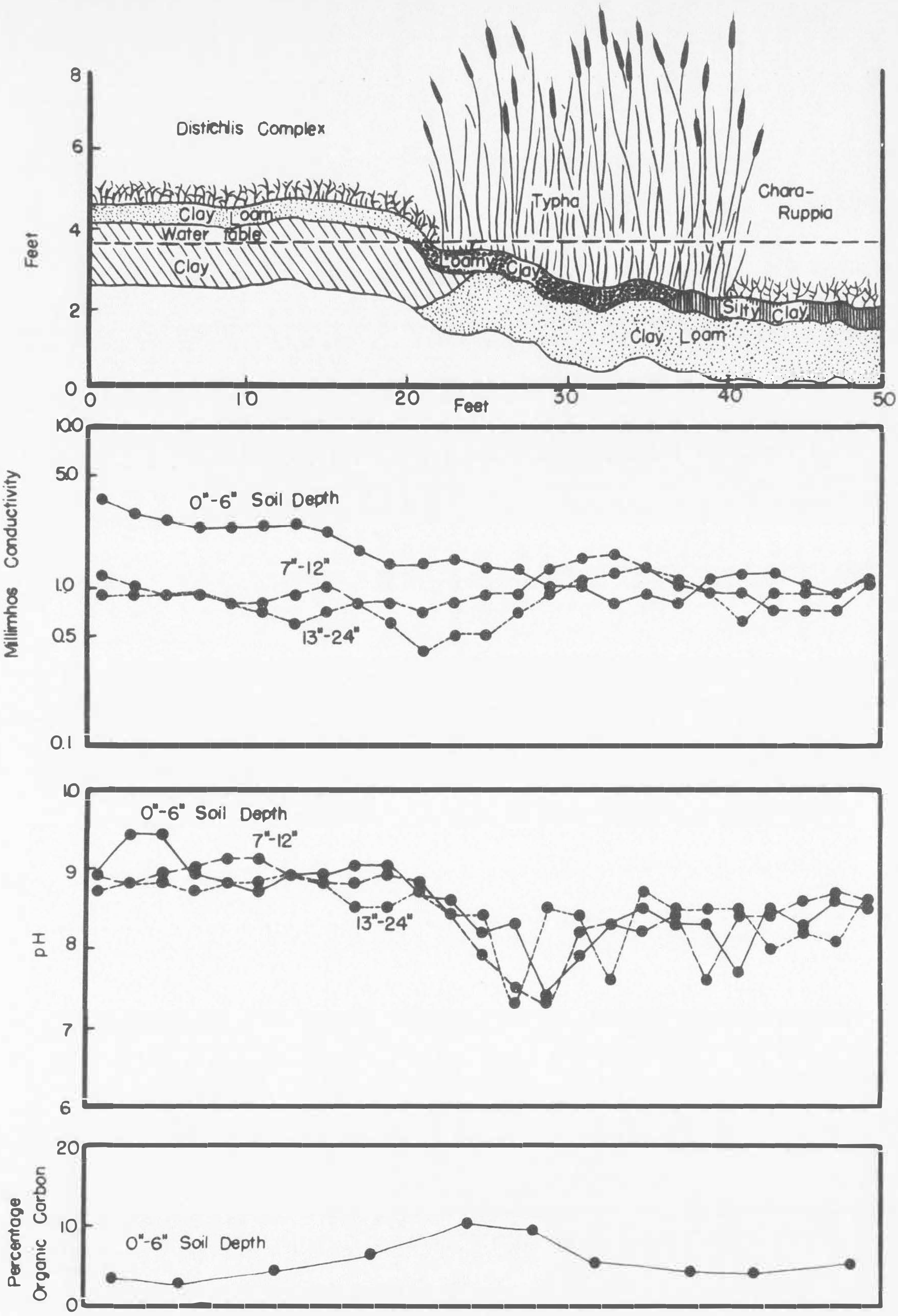

Figure 22. Transect No. 5: plant communities and edaphic data.

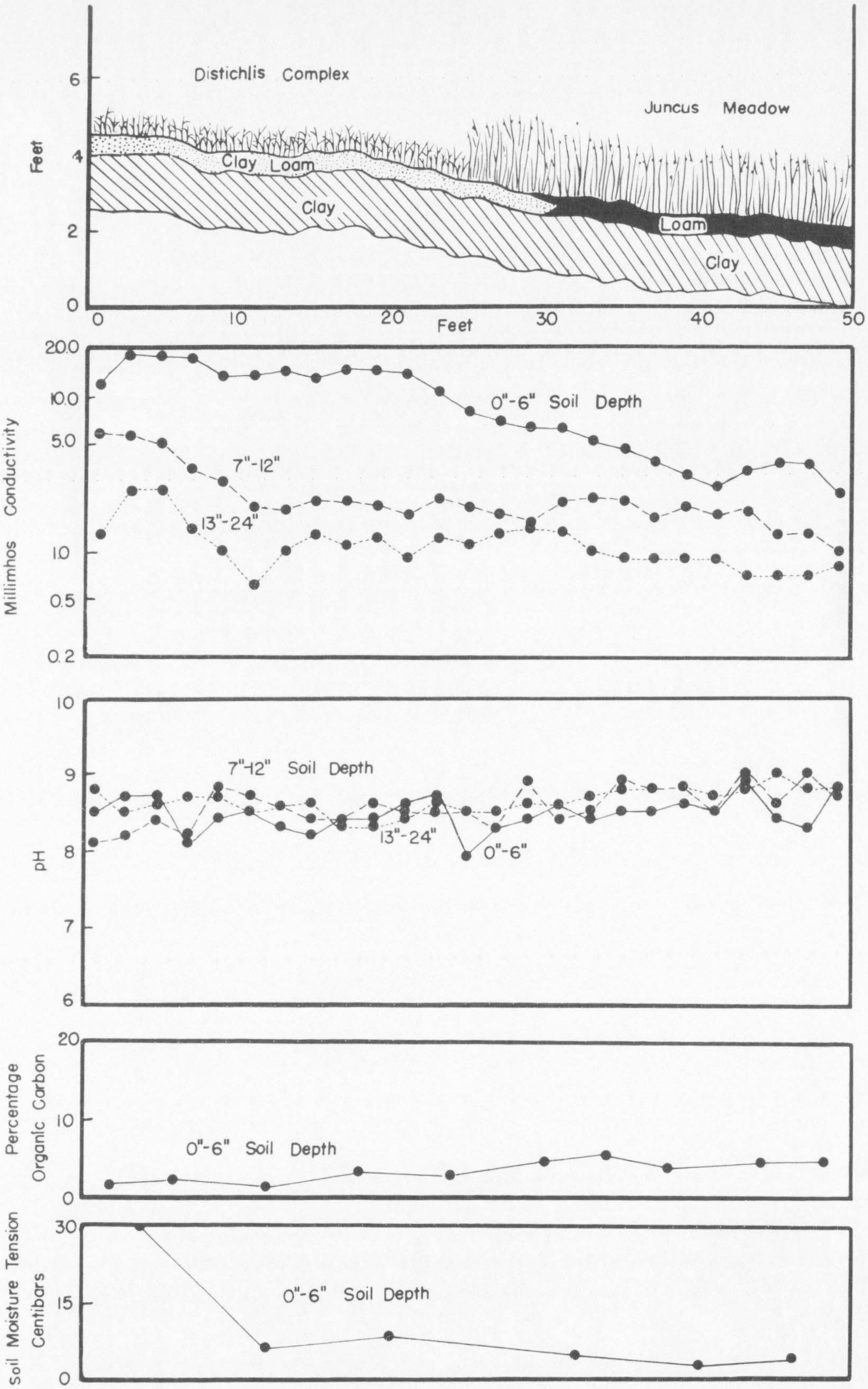

Figure 23. Transect No. 6: plant communities and edaphic data.

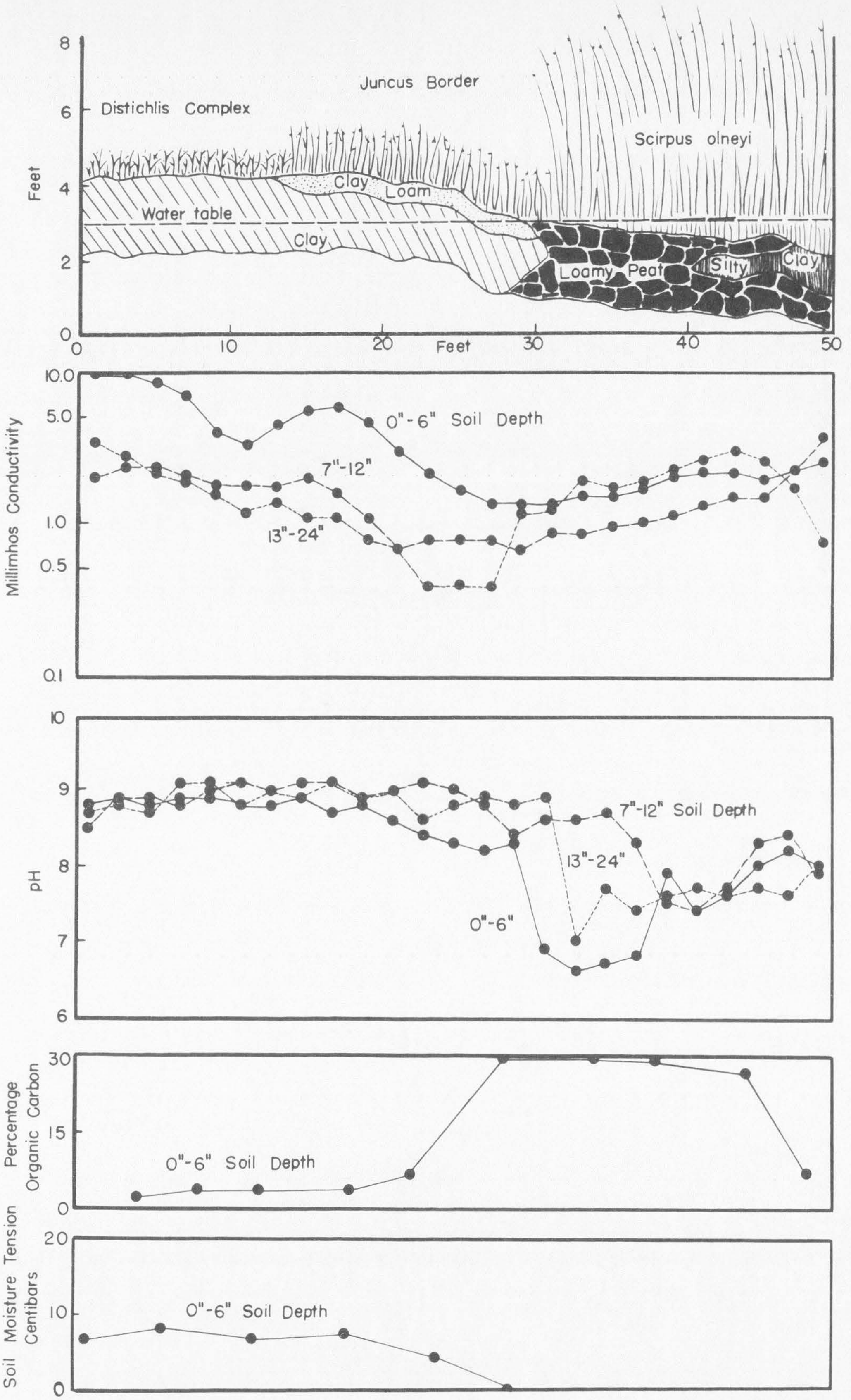

Figure 24. Transect No. 7: plant communities and edaphic data.

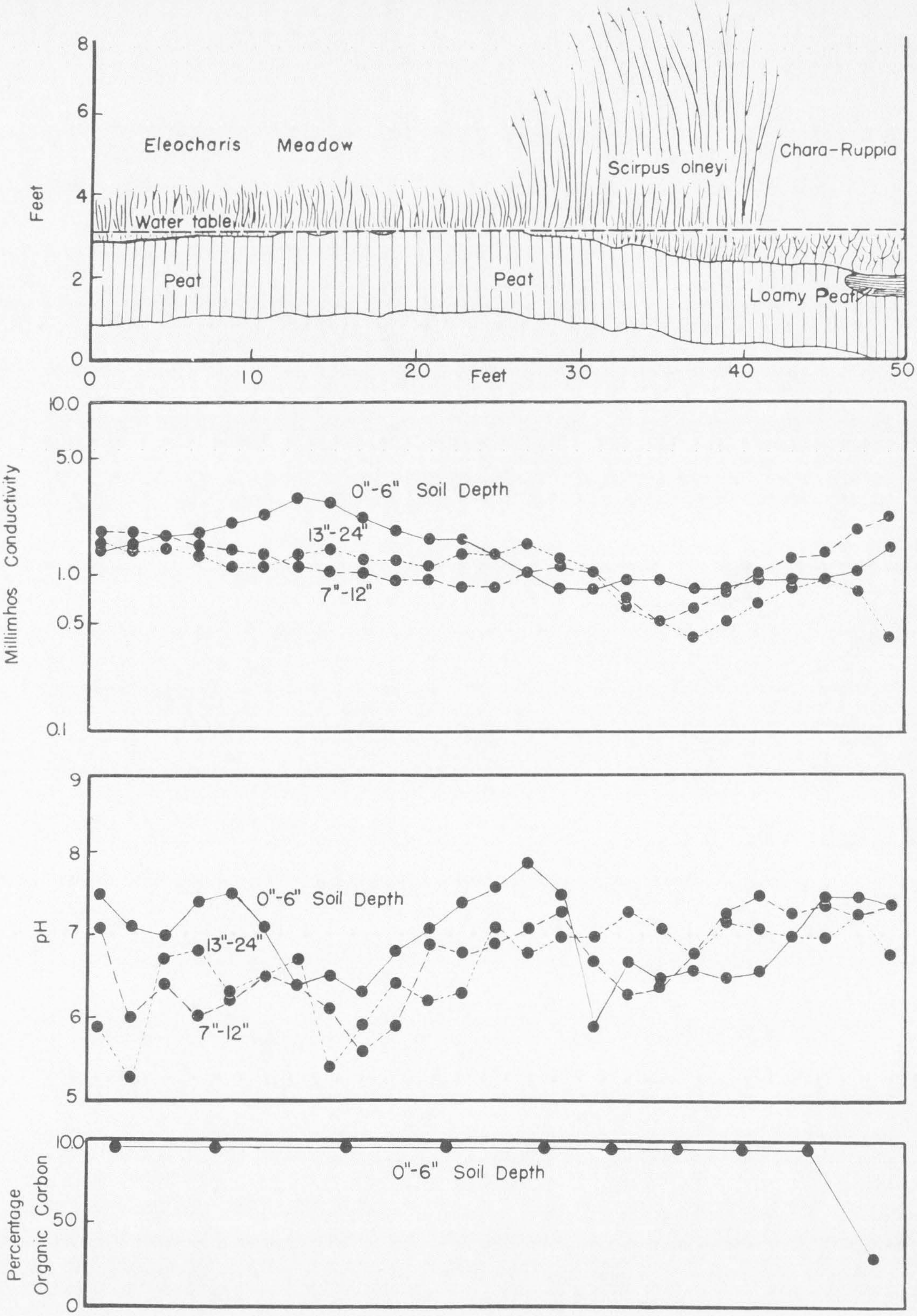

Figure 25. Transect No. 8: plant communities and edaphic data.

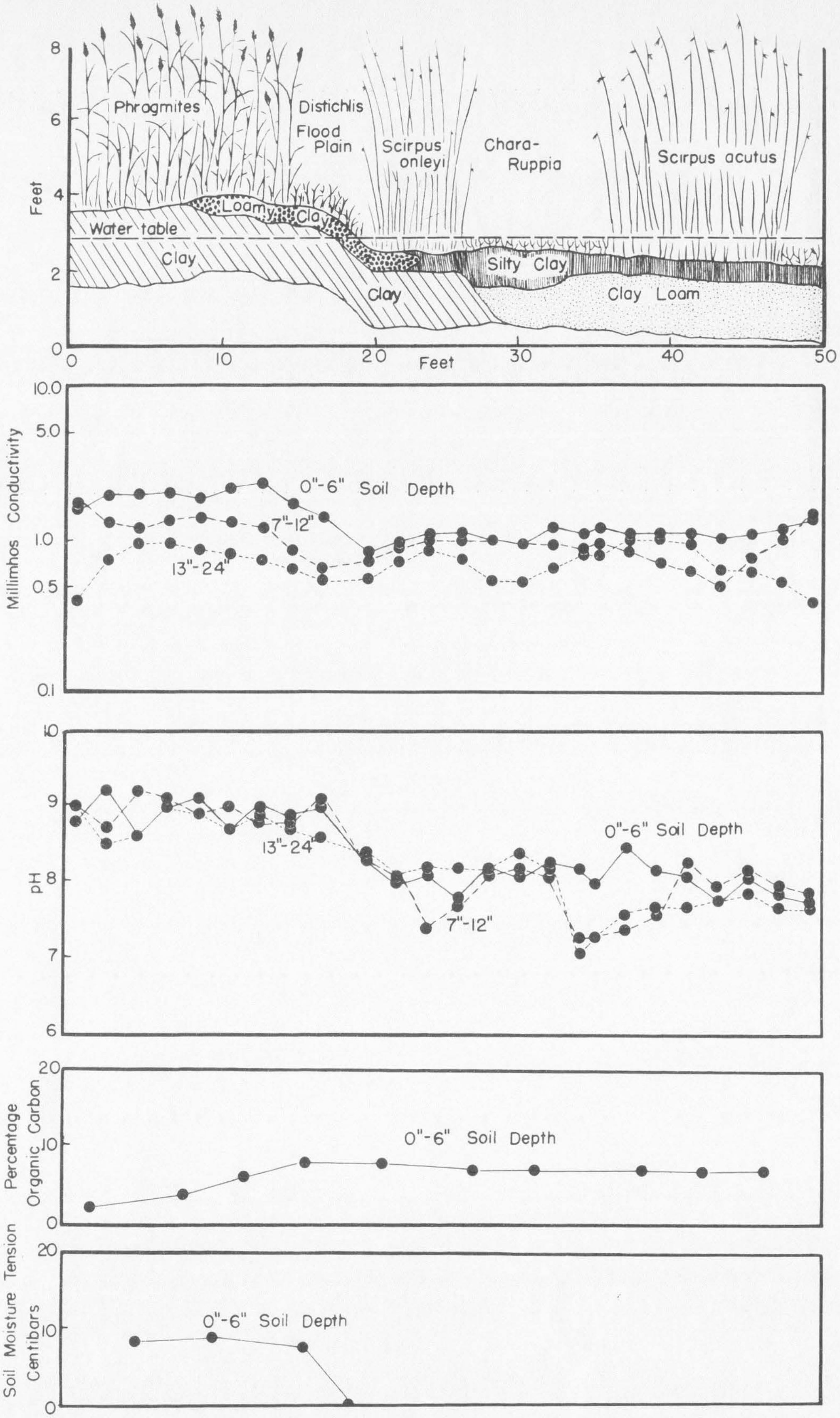

Figure 26. Transect No. 9: plant communities and edaphic data.

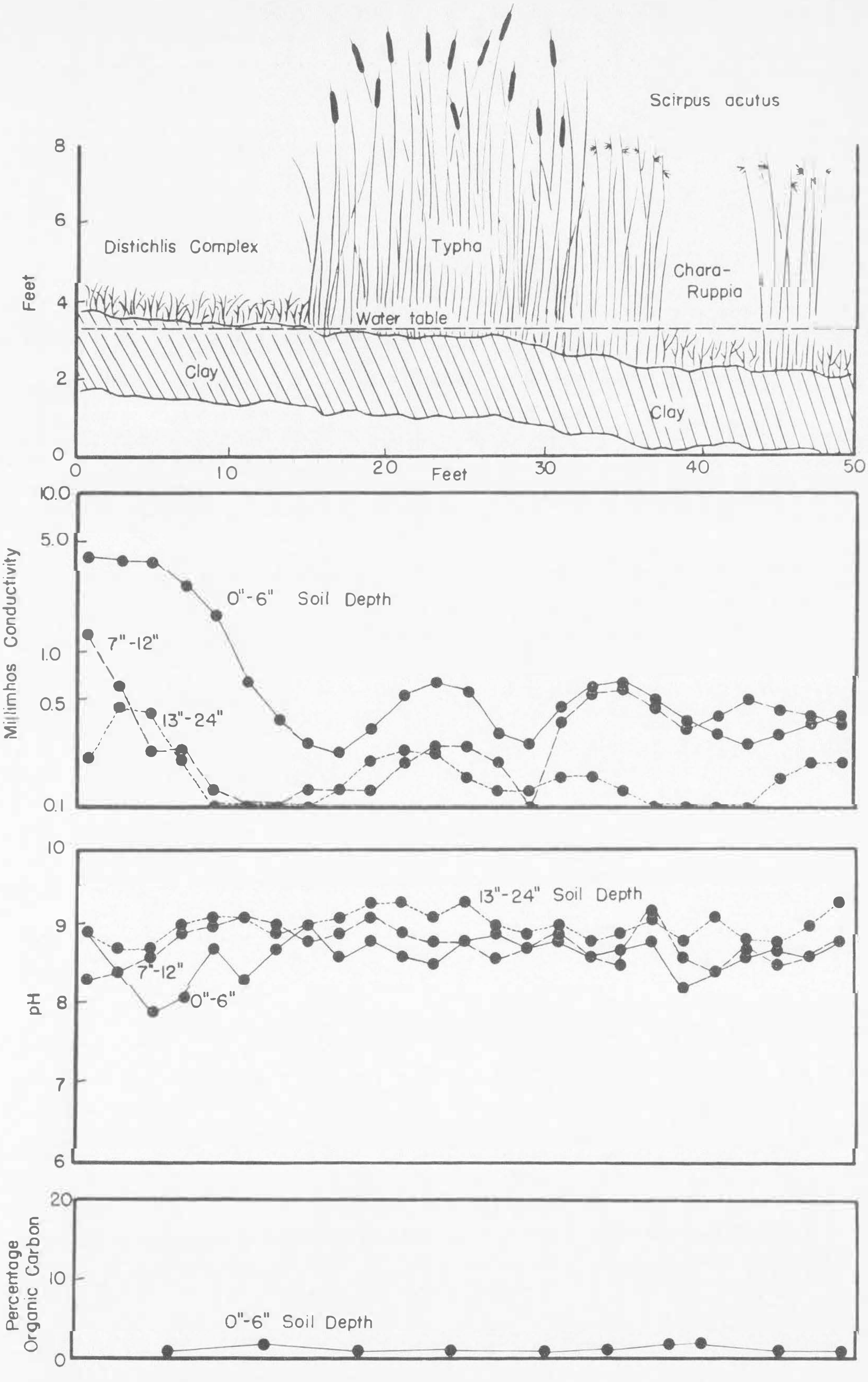

Figure 27. Transect No. 10: plant communities and edaphic data.

APPENDIX B

Checklist of Collected Plants from the Fish Springs Study Area

Thirty-four plant families and 99 species were identified from collections made in the marshes and surrounding upland areas. Filamentous algae were not collected. The checklist includes one family of non-filamentous algae, two gymnosperm families, and 31 angiosperm families of which seven are monocotyledonous and 24 are dicotyledonous. Families are listed in taxonomic order while genera and species are alphabetically arranged (Table 23).

Several botanical references and keys were employed in the identification of the plants and in the preparation of the checklist. These included:

Hitchcock, A. S. 1950. Manual of the grasses of the United States. U. S. Department of Agriculture Miscellaneous Publication 200, Washington.

Holmgren, A. H. 1942. Handbook of the vascular plants of northeastern Nevada. Utah State University, Logan.

Holmgren, A. H. 1959. Handbook of the vascular plants of the northern Wasatch. Lithotype Process Company, San Francisco.

Mason, H. L. 1957. A flora of the marshes of California. University of California Press, Berkeley and Los Angeles.

Tidestrom, I. 1925. Flora of Utah and Nevada. Contribution U. S. National Herbarium 25, Washington.

All plants collected are on permanent file with the Intermountain Herbarium, Utah State University, Logan, Utah. Grateful acknowledgment is offered to Arthur H. Holmgren, Curator, for his generous assistance in compiling the present checklist.

Table 23. Checklist of collected plants from the Fish Springs study area

Species	Family	Common name
	1. CHARACEAE	
Chara spp.		Muskgrass
	2. CUPRESSACEAE	
Juniperus osteosperma (Torr.) Little		Utah juniper
	3. EPHEDRACEAE	
Ephedra nevadensis S. Wats.		Joint fir
	4. TYPHACEAE	
Typha angustifolia L.		Narrowleaf cattail
	5. NAJADACEAE	
Najas marina L.		Spiny najad
Ruppia maritima L.		Widgeongrass
	6. JUNCAGINACEAE	
Triglochin maritima L.		Seaside arrowgrass
	7. GRAMINEAE	
Agropyron elongatum Host		Longspike wheatgrass
Agrostis alba L.		Redtop
Blepharidachne kingii (S. Wats.) Hack.		Blepharidachne
Bromus tectorum L.		Cheat grass
Distichlis stricta (Torr.) Benth.		Desert saltgrass
Elymus triticoides Buckl.		Beardless wildrye
Hilaria jamesii (Torr.) Benth.		Galleta
Hordeum jubatum L.		Foxtail barley
Muhlenbergia asperifolia (Nees & Mey.) Parodi		Scratchgrass
Oryzopsis hymenoides (Roem. & Schult.) Ricker		Indian ricegrass
Phragmites communis Trin.		Common reed
Polypogon monspeliensis (L.) Desf.		Rabbitfoot grass
Sitanion hystrix (Nutt.) J. G. Smith		Squirreltail
Spartina gracilis Trin.		Alkali cordgrass
Sporobolus airoides (Torr.) Torr.		Alkali sacaton

Table 23. Continued

Species	Family	Common name
	8. CYPERACEAE	
Eleocharis rostellata Torr.		Spike rush
Scirpus acutus Muhl.		Tule
Scirpus americanus Pers.		Shorerush
Scirpus nevadensis S. Wats.		Nevada bulrush
Scirpus olneyi A. Gray		Olney's bulrush
Scirpus paludosus A. Nels.		Alkali bulrush
	9. JUNCACEAE	
Juncus balticus Willd., var. *montanus* Engelm.		Wire rush
	10. LILIACEAE	
Allium nevadense S. Wats.		Wild onion
Smilacina stellata (L.) Desf.		False Solomon's seal
	11. SALICACEAE	
Populus alba L.		White poplar
Salix lutea Nutt.		Yellow willow
	12. ULMACEAE	
Ulmus pumila L.		Siberian elm
	13. POLYGONACEAE	
Eriogonum ovalifolium Nutt.		Eriogonum
	14. CHENOPODIACEAE	
Allenrolfea occidentalis (S. Wats.) Kuntze		Pickleweed
Atriplex confertifolia (Torr. & Frem.) S. Wats.		Shadscale
Atriplex patula L., var. *hastata* A. Gray		Spearscale
Bassia hyssopifolia (Pall.) Kuntze		Bassia
Chenopodium hybridum L.		Mapleleaf goosefoot
Halogeton glomeratus (Bieb.) Mey.		Halogeton
Kochia vestita (S. Wats.) Rydb.		Green molly
Nitrophila occidentalis (Nutt.) S. Wats.		Nitrophila
Salicornia utahensis Tidest.		Samphire
Sarcobatus vermiculatus (Hook.) Torr.		Greasewood
Suaeda intermedia S. Wats.		Seepweed
Suaeda occidentalis S. Wats.		Seepweed
	15. CERATOPHYLLACEAE	
Ceratophyllum demersum L.		Coontail
	16. RANUNCULACEAE	
Delphinium andersonii A. Gray		Delphinium
Ranunculus cymbalaria Pursh., var. *saximontanus* Fern.		Buttercup
Ranunculus juniperinus M. E. Jones		Buttercup

Table 23. Continued

Species	Family	Common name
	17. CRUCIFERAE	
Coringia orientalis (L.) Dum.		Hare's ear
Descurainia incisa (Engelm.) Britt.		Tansy-mustard
Descurainia sophia (L.) Webb		Tansy-mustard
Lepidium dictyotum Gray		Peppergrass
Malcolmia africana (L.) R. Br.		Malcolmia
Physaria chambersii Rollins		Double bladder-pot
	18. ROSACEAE	
Rosa woodsii Lindl.		Wild rose
	19. LEGUMINOSAE	
Astragalus utahensis T. & G.		Lady slipper
	20. MALVACEAE	
Sphaeralcea coccinea (Pursh.) Rydb.		Globe mallow
	21. TAMARICAECAE	
Tamarix pentandra Pall.		Salt cedar
	22. CACTACEAE	
Opuntia rhodantha Schum.		Prickly pear
	23. ONAGRACEAE	
Oenothera caespitosa Nutt., var. *marginata* (Nutt.) Munz.		Evening primrose
	24. UMBELLIFERAE	
Apium graveolens L., var. *dulce* DC.		Celery
Berula erecta (Huds.) Cov.		Water parsnip
Cymopterus longipes S. Wats.		Cymopeterus
Lomatium grayi C. & R.		Desert parsley
	25. PRIMULACEAE	
Glaux maritima L.		Saltwort
	26. GENTIANACEAE	
Centaurium exaltatum (Griseb.) Wight		Centaury
	27. APOCYNACEAE	
Apocynum sibiricum Jacq., var. *salignum* (Greene) Fern.		Dogbane
	28. ASCLEPIADACEAE	
Asclepias incarnata L., subsp. *occidentalis* Woodson		Swamp milkweed
Asclepias sepeciosa Torr.		Milkweed
	29. CONVOLVULACEAE	
Cressa truxillensis H.B.K.		Cressa

Table 23. continued

Species	Family	Common name
	30. POLEMONIACEAE	
Gilia sinuata Dougl.		Gilia
Phlox longifolia Nutt.		Phlox
	31. SOLANACEAE	
Lycium andersonii A. Gray		Wolfberry
	32. SCROPHULARIACEAE	
Castilleja chromosa A. Nels.		Indian paint brush
Castilleja exilis A. Nels.		Indian paint brush
Cordylanthus canescans A. Gray		Cordylanthus
Penstemon dolius Jones		Penstemon
	33. LENTIBULARIACEAE	
Utricularia vulgaris L.		Bladderwort
	34. COMPOSITAE	
Aplopappus racemosus (Nutt.) Torr.		Aplopappus
Aster pauciflorus Nutt.		Aster
Chaenactic douglasii H. & A.		Chaenactis
Chrysothamnus nauseosus (Pall.) Britt.		Rabbitbrush
Chrysothamnus stenophyllus (A. Gray) Greene		Rabbitbrush
Cirsium drummondii T. & G.		Thistle
Crepis runcinata T. & G., subsp. *hispidulosa* (Howell) Babc. & Stebb.		Hawksbeard
Enceliopsis nudicaulis (A. Gray) A. Nels.		Enceliopsis
Erigeron pumilus Nutt.		Fleabane
Helianthus annuus L.		Sunflower
Hymenopappus eriopodus A. Nels.		Hynemopappus
Iva axillaris Pursh		Poverty weed
Lygodesmia exigua A. Gray		Lygodesmia
Malacothrix sonchoides (Nutt.) Torr. & Gray		Malacothrix
Psathyrotes annua (Nutt.) A. Gray		Psathyrotes
Senecio uintahensis (A. Nels.) Greenm.		Senecio
Stephanomeria tenuifolia (Torr.) Hall S. myrioclada		Skeletonweed
Tetradymia canescens DC.		Spineless hores horsebrush
Tetradymia spinosa H. & A.		Spiny horsebrush
Townsendia florifer (Hook) A. Gray		Townsendia