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Title: THE RELATION OF TIME AND THE WATER TABLE TO PLANT DISTRIBUTION ON DEFLATION PLAINS ALONG THE CENTRAL OREGON COAST

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Large areas of the Oregon coast that were bare sand 30 years ago now support vegetation varying from meadows and marshes on the more recently vegetated areas to impenetrable thickets of shrubs and trees on older sites. This change was initiated by the planting of *Ammophila arenaria* (L.) Link for dune stabilization and its subsequent spread along the coast to produce a foredune. The effect of this foredune is to trap sand moving in from the beach so that, in the area behind the foredune, sand is removed by the wind until the moist sand near the water table is eventually reached, forming a deflation plain. It is on this deflation plain that these rapid changes in vegetation have been observed.

One of the more striking freatures which is observed on field trips to the deflation plains is the zonation of vegetation with small changes in elevation. Similar zonation has been observed in England,

and related to depth from the soil surface to the water table.

This thesis describes the methods and results of a study of the relation of plant distribution on recently created deflation plains to the two factors: (1) time since succession was initiated on the deflation plain and (2) depth from the soil surface to the water table.

Using stratified random sampling, quadrat data was collected on species presence and absence, depth to the water table, and location on the deflation plain. Aerial photos taken in 1952, 1961, 1968 and 1972 were used to assign each quadrat to an "age class" based on the time since succession was initiated in that location on the deflation plain.

This data was used to characterize the vegetation at various times since succession was initiated, and at various depths to the water table. The "niche" of each of 27 species was described in terms of the probability of occurrence of the species in the two-dimensional space of depth to the water table and age class. A method was developed for predicting depth to the water table based on the species present in a quadrat. This prediction was extremely accurate: for 96% of the quadrats, water table depth was predicted to within 10 cm.; for 73% of the quadrats it was predicted to within 5 cm. The analysis of the errors of prediction in terms of age class, depth to the water table, and number of species present in a quadrat suggests that the method of prediction could be refined to produce even greater accuracy. The accuracy of the prediction provides strong support to the belief that water table depth is one of the most important factors correlated with species distribution on the deflation plains.

The Relation of Time and the Water Table to Plant Distribution on Deflation Plains Along the Central Oregon Coast

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THE RELATION OF TIME AND THE WATER TABLE TO PLANT DISTRIBUTION ON DEFLATION PLAINS ALONG THE CENTRAL OREGON COAST

INTRODUCTION

This thesis describes the methods and results of a study of the relation of plant distribution on recently created deflation plains to the two factors: (1) time since succession was initiated on the deflation plain and (2) depth from the soil surface to the water table.

Time

Wiedemann (1966) documents the dramatic rapid changes that have taken place since the 1930's and 1940's in the vegetation of the Oregon coastal sands. Additional convincing evidence of rapid change may be observed in sets of aerial photographs taken during the Second World War and at about 5-year intervals since then (Figures 1 to 4). Large areas of the Oregon coast that were bare sand 30 years ago now support vegetation varying from meadows and marshes on the more recently vegetated areas to impenetrable thickets of shrubs and trees on older sites. New change was initiated by the planting of *Ammophila arenaria* (L.) Link for dune stabilization and its subsequent spread along the coast to produce a foredune. The effect of this foredune is to trap sand moving in from the beach so that, in the area behind the foredune, sand is removed by the wind until the moist sand

Figure 1. Aerial photo of study area in 1952. Scale 1:20000.

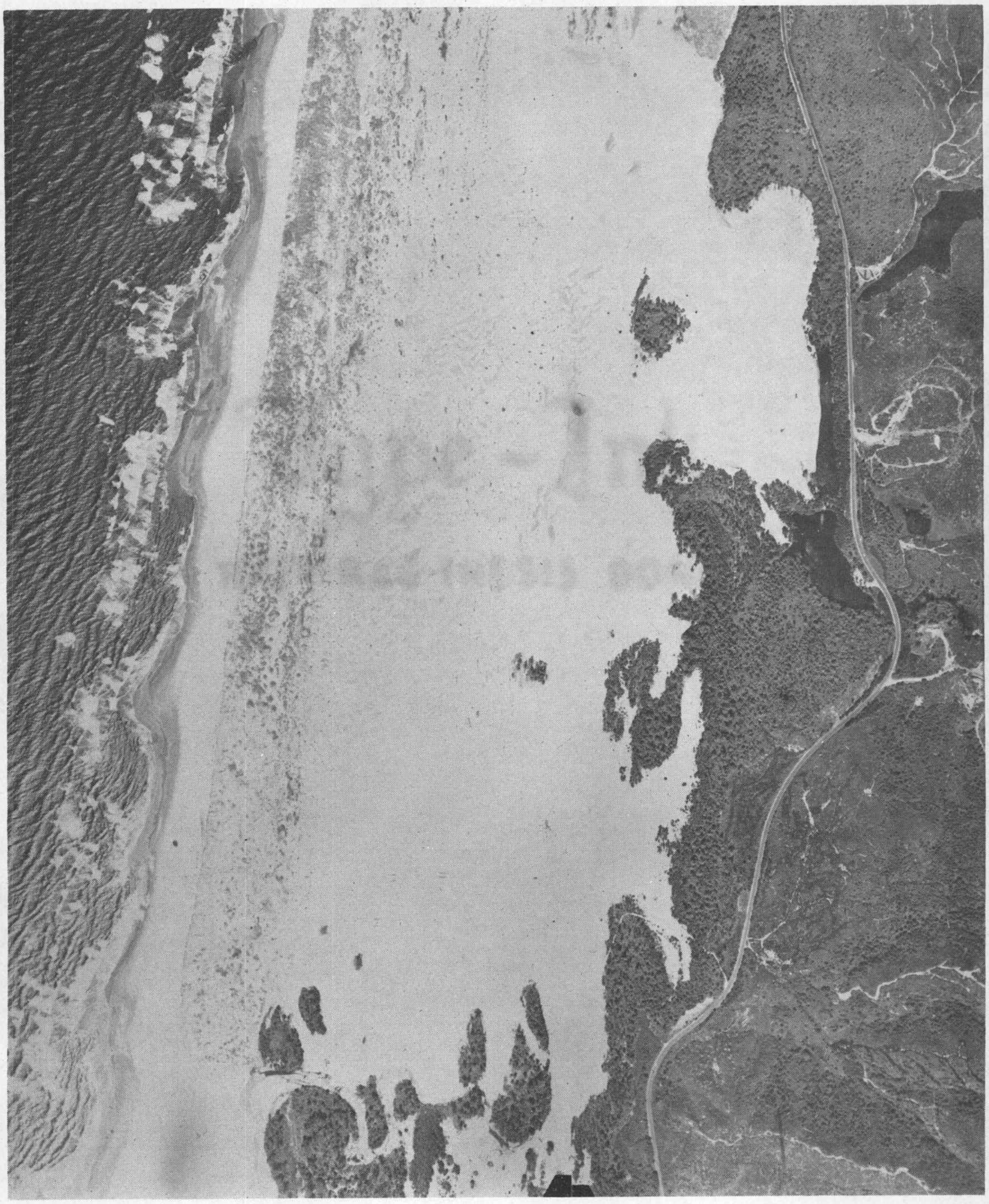

Figure 2. Aerial photo of study area in 1961. Scale 1:12000.

Figure 3. Aerial photo of study area in 1968. Scale 1:15840.

Figure 4. Aerial photo of study area in 1972. Scale 1:15840. (The three straight lines indicate the location of the transects.)

near the water table is eventually reached, forming a deflation plain. It is on this deflation plain that these rapid changes in vegetation have been observed (Figure 5).

The spread of this deflation plain has been continuing with time so that new areas of bare sand are continuing to be exposed for plant colonization. This fact, combined with the rapidity of succession, makes this an ideal location for the study of succession by observing changes in permanent plots over time. An additional approach to the study of succession could use the photographic records of the extension of the deflation plain during the last 30 years to select for study plots of vegetation of various ages but with all other independent variables relatively constant. This approach to the study of succession was used by Olson (1958a) in his study of succession on the Southern Lake Michigan sand dunes. He studied changes that had occurred in dune vegetation over a period of 12,000 years; and thus permanent plot studies were impossible. Because of constraints on the time available for research, the latter approach was used in my research (although the time scale is considerably reduced). It is suggested that research on the rapidly-developing vegetation of the Oregon coast deflation plains can provide an evaluation of the method of studying succession exemplified by Olson's work by comparing the results of such a study to permanent plot studies.

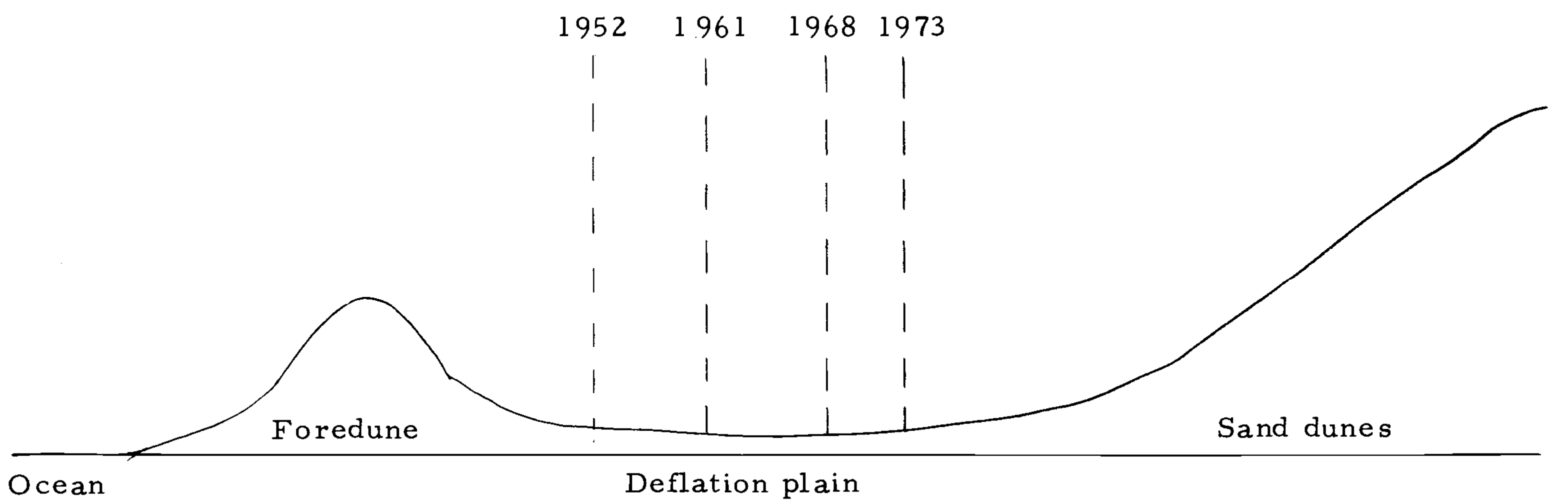

Figure 5. Diagram showing relative position of deflation plain, and the spread of vegetation through time. The dates indicate the location of the boundary between vegetation and bare sand in those years. (Not to scale.)

Besides the obvious scientific value of a study of succession under these ideal circumstances, a study of time changes in vegetation on the deflation plains would be of great value to the managers of the newly-established Oregon Dunes National Recreation Area. The results of such a study would be useful not only in helping them make management decisions but also for interpretive purposes since these deflation plains offer such dramatic examples of succession.

The most thorough work on these deflation plains has been by Wiedemann (1966). He provides a successional flow chart based on his observations of a wide variety of deflation plains, but admits that it is only "speculative." The rapid rate of succession at some locations is referred to, but no detailed study of changes in vegetation with time was made. Kumler (1969) studied plant succession on the crests of parabola dunes on the Oregon coast, but specifically avoided studying the deflation plains because "a variable water table was a complicating factor."

The Water Table

One of the more striking features which is observed on field trips to the deflation plains is the zonation of vegetation with small changes in elevation. Willis *et al*. (1959), in their study of some English "slacks" (hollows between the dunes where the water table is near the sand surface), stated that:

> It was apparent at an early stage of the investigation that the marked zonation of vegetation closely reflects differences in shelter and accessibility of ground water. In general, the height above ground water may be taken as a useful index of these factors.

Exactly the same statement could be applied to the deflation plains of the Oregon coast. Based on an examination of vegetation at 270 sites, Willis and his co-workers developed histograms of percent occurrence as a function of elevation above the water table for about 30 of the chief species. These data show that, particularly at low levels, small differences (about 1 foot) in depth to ground water are of critical importance in determining the distribution of many species. In a separate study of other English slacks, Ranwell (1959, 1960) measured the height of the soil surface above ground water at 17 sites where vegetation was sampled and he was also impressed by the effects of ground water near the soil surface on plant distribution. More recent research at the same location by Onyekwelu (1972) supported Ranwell's research. In a recent ordination of the vegetation of this same location by Onyekwelu (1972), it was found that the first axis of variation of the ordination was well correlated with the trend in water table depth. Wiedemann (1966, 1969) recognized the importance of small changes in elevation on plant distribution on the deflation plains of the Oregon coast; however, he only took one measurement of water table depth in each of the four herbaceous communities he described. More of these measurements would be desirable to obtain a clearer picture of the relationship between plant distribution and depth to the water table.

This readily observed zonation of vegetation with the environment could be used as the basis of an interesting story interpreting the relationship between plants and the environment to visitors to the Oregon Dunes National Recreation Area. A combined study of plant distribution as a function of the water table depth and time could provide the basis for an even more interesting interpretation.

Wiedemann (1966) refers to wells drilled in the dunes just north of Coos Bay, Oregon, by the Pacific Power and Light Company. These wells are intended to provide 8 to 10 million gallons of water a day; but nothing is being done to study the effect on the vegetation of this loss of water. A detailed study of the variation of vegetation with time and water-table-depth would be of value in predicting and assessing the effect of these wells.

METHODS

Selection of Study Area

The study area was selected on the basis of reconnaissance on foot in the summer of 1972 and spring of 1973, assisted by the examination of aerial photos. Criteria considered in selection of the area were:

(1) A "young" deflation plain, since the physical environment currently measured would be expected to correlate better with the vegetation of a "young" area that with an older area in which the environment has probably changed more since the vegetation was established, and in which species interactions would be more developed.

(2) Within this "young" area, the existence of a significant range of times since succession was initiated, so that the direction of succession might be observed.

(3) The ability to use aerial photos to clearly identify the time since succession was initiated as a function of position on the deflation plain.

(4) Easy accessibility combined with low visitor use.

An area satisfying these criteria was chosen within the Oregon dunes NRA between Carter Lake and Tahkenitch Creek. This location is identified on the map of the Oregon coast, Figure 6, and is more

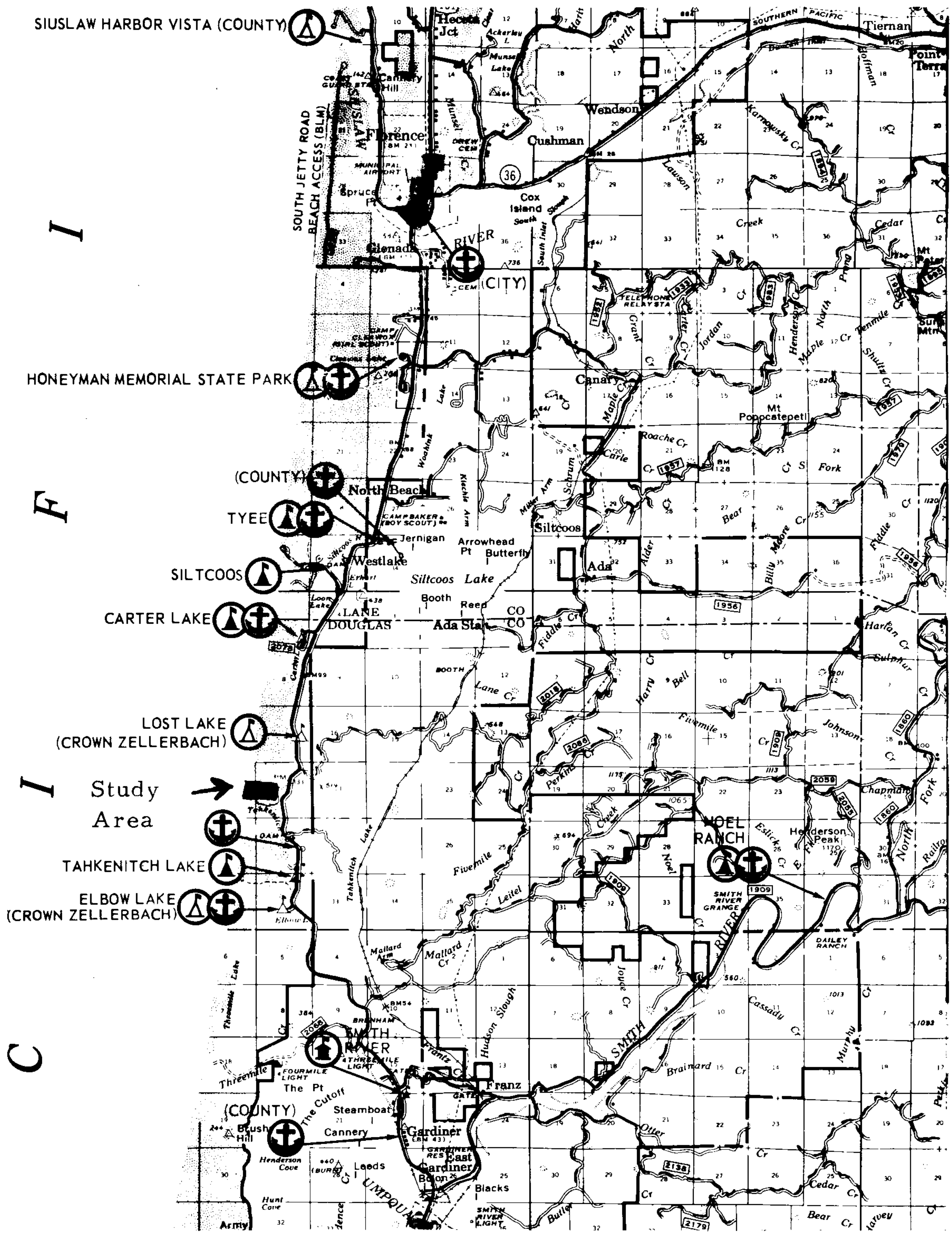

Figure 6. Map showing location of study area.

precisely shown on the 1972 aerial photo, Figure 4.

Collection of Data

Within the study area, three transects perpendicular to the shore were randomly selected (I. E. using a table of random numbers). The location of these transects is indicated on the 1972 aerial photos, Figure 4. Figures 7 to 9 provide photographs of each of the transects looking from west to east.

Figure 7. View from west to east on transect 1.

Sampling of each transect extended from open sand on the east to the dry hummocks behind the foredone on the west. A 2X5 dm. quadrat was used for sampling, because is was evident from the

Figure 8. View from west to east of transect 2.

Figure 9. View from west to east on transect 3.

reconnaissance study that small changes in location were often accompanied by significant changes in vegetation. In June, 1973, samples were chosen along each transect using stratified random sampling with inclusion probabilities varying from 1/4 to 1/100. The reason for this variable inclusion probability is that strata were chosen so as to be essentially homogeneous with respect to species present and topography; thus some strata were much larger than others.

Data recorded for each quadrat included: location, depth to the water table, percent coverage by bare sand, inclusion probability, presence or absence of 27 species and miscellaneous information which might explain anomalies in species distribution, ex., unusual topography, or a nearby large shrub. Data were recorded for a total of 332 quadrats.

Depth to the water-table was recorded directly for quadrats at the lower elevation by drilling a hole to the water table with a soil augur, and measuring depth with a ruler. For adjacent higher elevations, depth to the water-table was estimated by using an Abney level to estimate the difference in elevation with respect to a nearby "low-elevation" sample. For purposes of analysis, all depths were corrected to correspond to the date June 5, 1973, by adjusting for changes in water-table depth recorded between then and the date the sample was collected. There was no measurable change in water table depth with tidal fluctuations, so no correction was required on that account.

Aerial photographs of the study area (Figures 1 to 4) taken in 1952, 1961, 1968, and 1972 were obtained from the U.S. Forest Service. By stereoscopic examination of these while walking in the study area, it was possible to deduce the segments of each transect which were vegetated prior to 1952, between 1952 and 1961, between 1961 and 1968, and since 1968, respectively. Thus, the information on the location of a quadrat allowed it to be assigned to one of four "age classes" (Figure 5).

Analysis of Data

The data were analyzed in various ways in order to illuminate the relationship between species presence or absence and the two variables: (1) depth from the soil surface to the water table, and (2) time since the beginning of succession. For simplicity of discussion, these variables will subsequently be referred to as "depth" and "age class," respectively.

A weight was computed for each quadrat by dividing the inverse of the inclusion probability by 4. Thus the most intensively sampled areas had quadrats with weight 1; whereas, quadrats in less intensively sampled areas had larger weights, proportional to the larger areas represented by these quadrats.

Some algebraic notations are used in the following paragraphs in the hope that they will clarify the distinction between two kinds of proportions. Let n_{ijk} be the total weighted number of occurrences of species i at depth j in age class k, and let N_{jk} be the total weighted number of quadrats at depth j in age class k. These quantities are computed simply by summing over the data: i.e., n_{ijk} is the sum of weights of all quadrats at depth j in age class k containing species i. Further summing produces: $N_{j.} = \sum_k N_{jk}$, the total weighted number of quadrats at depth j; and $N_{.k} = \sum_j N_{jk}$, the total weighted number of quadrats in age class k; and $N_{..} = \sum_j N_{j.} = \sum_k N_{.k}$, the grand total weighted number of quadrats; and, with corresponding definition, $n_{ij.}$, $n_{i.k}$ and $n_{i..}$.

Actually, the summation over age classes is presented only for the three age classes prior to 1968, since, as will be apparent from the results and later discussion, the most recent age class differs so drastically from the earlier ones that merging it with the others would lead to confusion. This difference was obvious in the field in terms of large amounts of drifting sand in the most recent age class compared to almost continuous vegetation in the older classes. Also, because of the free sand movement, measurements of depth to the water table are less meaningful in this most recent class. (Refer to Figures 10 and 11 for views of the area on either side of the boundary between the most recent age class and the other age classes.)

Figure 10. View of the most recent age class from its boundary with the other age classes.

Figure 11. View of the other age classes from this boundary.

By taking ratios of the sums, various proportions were computed; for example,

$$S_{ijk} = \frac{n_{ijk}}{N_{jk}} ,$$

the (weighted) proportion of occurrences of species i in quadrats at depth j and age class k, and

$$d_{ijk} = \frac{n_{ijk}}{n_{i \cdot k}} ,$$

the (weighted) proportion of occurrences of depth j in quadrats containing species i in age class k.

It is important to understand the difference in the significance of these two proportions defined above. As Kershaw (1964, p. 31-32) points out:

> . . . numerous studied have been made relating the distribution of a given species to pH by taking a soil sample at each site examined where the species was growing. This in fact is a sample of the variation of soil pH in a given area and the resultant data relates to the frequency distribution of pH in that particular area. Such data offers no real proof of an interrelationship between species and pH . . .

The data he is referring to corresponds to the "d" proportions defined above. He then gives an example which shows that the "S" proportions are needed to depict the distribution of a species with respect to an environmental variable. However, for the purpose of predicting depth to the water table the probabilities d_{ijk} should be more useful since they take into account the actual distribution of depth on the deflation plain. Accordingly, these two types of proportions are used in different ways: the "S_{ijk}" type of proportion is used to provide a picture for each species of its niche in terms of depth and age class; whereas, the "d_{ijk}" type of proportion is used in the prediction of depth to the water-table given a list of species present in a quadrat.

The method of prediction is based on the intersection of the ranges or "percentiles of ranges" of the species present in a quadrat. This range data is provided in Table 39. The 100% range simply consists of the set of depths over which the species was found. The 90% range class excludes from this 10% of the depths at which the species was found. The "d probabilities" are used to exclude 5% of the occurrences at each end of the range at which the species was found. The other "percentiles of ranges" are constructed in a similar way by exclusion of an equal proportion of occurrences at each end of the species range.

With a table of ranges and percentiles of ranges available, the method of prediction is very simple and may be best understood by an example. Suppose you observe on the deflation plain a quadrat containing _Juncus phaecocephalus_ Engelm., _Lupinus littoralis_ Dougl., and _Aira praecox_ L. For convenience, part of Table 39 corresponding to these species is reproduced below.

Percent of Range of Depths to Water Table (in cm.)	100	90	80	70
Juncus ph.	44,71	41,69	43,66	45,61
Lupinus	44,71	49,71	51,71	53,71
Aira	51,71	58,71	61,71	63,71

From the first column of this table, the range of possible depths is 51 to 71 cm. To narrow this range down to a prediction of a particular depth, occurrences at the ends of the ranges of each species are progressively eliminated. Thus, excluding 10% of the occurrences of each species, reduces the predicted depth to between 58 and 69 cm. Note that 58 is the maximum for the species present of the minimums under "percent 90," while 69 is the corresponding minimum of the maximums. Excluding 20% of the occurrences of each species, reduces the predicted depth to between 61 and 66 cm. Excluding 30% of the occurrences of each species implies a minimum depth of 63 cm. and a maximum of 61. This reversal tells you that to arrive at a point prediction of depth, less than 30% of the occurrences should be excluded. Linear interpolation between the cases of 20% exclusion and 30% exclusion is used to arrive at a point prediction of 62.

In practice, it is not necessary to successively examine all of the columns of Table 39. Instead, just skip across until you encounter the first column where the lower bound of the prediction is greater than or equal to the upper bound, and interpolate using the preceeding column if necessary.

Depth was predicted for all of the sample quadrats in the three age classes prior to 1968, and a summary was made of the prediction error in terms of the mean, standard deviation, mean absolute value and distribution for the complete set of quadrats and for subsets corresponding to different age classes, predicted and actual depths, and numbers of species present.

Fortran IV computer programs were written and used on the CDC 3300 computer at OSU to perform the computations described above.

RESULTS

The Twenty-Seven Species

The 27 most common species in the study area are listed in Table 1 in order of increasing median depth to the water table. There is a number preceding each species name, since it is intended that this list be referred to as a key in order that results may be presented in a compact form. An extra separate copy of this page has been included to make its use easier. Where possible, the nomenclature used follows Wiedemann, Dennis and Smith (1969), so that their book may be used as a companion to this thesis to provide descriptions, pictures and identifications of species referred to here. For the three species marked with an asterisk (*) the nomenclature used follows Hitchcock and Cronquist (1973). At the time of the year sampling was done, the various species of Agrostis could not be distinguished although the genus could be recognized and was fairly common. Thus, "species 20" actually refers to a genus. After each species is recorded the plant community (if any) of which Wiedemann (1966) considered that species to be a characteristic species. Wiedemann believed that the most significant environmental difference among these communities was increasing depth to the water table as one goes from marsh to rush meadow to meadow to dry meadow. The ordered list of species agrees with his work with three exceptions:

Table 1. The 27 species in order of increasing median depth to the water table.

1.	Carex viridula Michx.	
2.	Mimulus guttatus DC.	rush meadow
3.	Carex obnupta Bailey	marsh
*4.	Lilaeopsis occidentalis Coult. and Rose.	marsh
5.	Potentilla pacifica Howell	marsh
6.	Ranunculus flammula L.	marsh
7.	Epilobium franciscanum Barb.	rush meadow
8.	Sisyrinchium californicum (Ker.) Dryand.	rush meadow
9.	Spiranthes romanzoffiana Cham.	
10.	Juncus falcatus E. Meyer	rush meadow
11.	Juncus phaecocephalus Engelm.	rush meadow
12.	Juncus leseurii Boland	
13.	Tanacetum camphoratum Less.	meadow
14.	Trifolium wormskjoldii Lehm.	rush meadow
*15.	Aster subspicatus Nees.	rush meadow
16.	Orthocarpus castillejoides Benth.	
17.	Gnaphalium purpureum L.	
18.	Festuca rubra L.	meadow
19.	Hypochaeris radicata L.	meadow
20.	Agrostis spp.	meadow and rush meadow
21.	Centaurium umbellatum Gilib.	rush meadow
22.	Fragaria chiloensis (L.) Duch.	meadow
23.	Lupinus littoralis Dougl.	dry meadow
24.	Anaphalis margaritacea (L.) B. and H.	meadow
25.	Ammophila arenaria (L.) Link.	dry meadow
26.	Aira praecox L.	meadow
*27.	Rumex acetosella L.	

Note: Species 22 through 27 all had a median depth to the water table of greater than 70 cm. which was the upper limit for which precise depth measurements were made. That is, depths greater than 70 cm. were recorded merely as depths greater than 70 cm.

(1) Mimulus guttatus which he assigned to the rush meadow community has a median depth corresponding to marsh species; (2) Tanacetum camphoratum which he assigned to the meadow community had a median depth corresponding to rush meadow species; (3) Centaurium umbellatum which he assigned to rush meadow community has a median depth corresponding to meadow species. With respect to Mimulus guttatus and Tanacetum camphoratum their occurrence in pioneer communities with much open sand might mislead a person into thinking the water table was further below the surface than it actually is. Thus Wiedemann's classification could probably be improved by separate defintion of two or more pioneer communities. It would be interesting to apply to my data the information statistic classification program of Lance and Williams (1968) which was successfully applied in a similar situation on the English coast (P.D. Moore, 1971), and compare the results to Wiedemann's classification. Three of the species in Table 1, were included in the 30 species for which Willet et al. (1959) developed histograms of percent occurrence as a function of depth above the water table. These three species (Ammophila arenaria, Festuca rubra, and Ranunculus flammula) occupy a position in my ordered set of species similar to that in theirs.

Age Classes

For each of the four age classes, and for the combination of the oldest three age classes, Tables 2 to 6 present the results on: (a) the number of occurrences of each species as a function of depth, (b) the percent occurrence of species at given depths (corresponding to the "S" proportion described in the methods), and (c) the percent occurrence of depths for given species (corresponding to the "d" proportion described in the methods).

A great deal of information is summarized in these tables, and although a further summary will later be given of the most common species in each age class, the tables have been made as compact as possible to encourage people to look at them. Accordingly, the depths have been grouped into four classes: ≤ 50 cm., > 50 cm. but ≤ 60 cm., > 60 cm. but ≤ 70 cm., and > 70 cm. These depth classes are indicated in the tables by their upper limits, with "1000" indicating depths to the water table of greater than 70 cm.

The next column gives the total weighted number of quadrats at that depth or the percent of the total quadrats which occur at that depth, as appropriate to the table. The remaining 27 columns provide the information for each species. For the "percent occurrence" tables, the "total" now gives the percent of the total quadrats in that age class in which each species occurs. Table 7 was constructed

Table 2. Species occurrence in '68 to '73 age class.

NUMBER OF OCCURENCES

DEPTH		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	15	0	15	0	0	0	0	0	0	0	0	15	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	72	0	20	0	0	0	0	13	0	0	15	27	17	8	0	0	0	1	0	0	19	0	0	9	0	0	0	0
70	31	0	10	0	0	0	0	3	0	0	2	2	2	0	0	0	0	0	0	0	2	0	0	3	0	9	2	0
1000	79	0	6	0	0	0	0	3	0	0	0	3	10	0	0	0	0	3	0	0	0	0	0	3	0	17	0	0
TOTAL	197	0	51	0	0	0	0	19	0	0	17	47	44	8	0	0	0	4	0	0	21	0	0	15	0	26	2	0

PERCENT OCCURENCE OF SPECIES AT GIVEN DEPTHS

DEPTH		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	8	0	100	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	37	0	28	0	0	0	0	18	0	0	21	38	24	11	0	0	0	1	0	0	26	0	0	13	0	0	0	0
70	16	0	32	0	0	0	0	10	0	0	6	6	6	0	0	0	0	0	0	0	6	0	0	10	0	29	6	0
1000	40	0	8	0	0	0	0	4	0	0	0	4	13	0	0	0	0	4	0	0	0	0	0	4	0	22	0	0
TOTAL	100	0	26	0	0	0	0	10	0	0	9	24	22	4	0	0	0	2	0	0	11	0	0	8	0	13	1	0

PERCENT OCCURENCE OF DEPTHS FOR GIVEN SPECIES

DEPTH		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	8	0	29	0	0	0	0	0	0	0	0	32	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	37	0	39	0	0	0	0	68	0	0	88	57	39	100	0	0	0	25	0	0	90	0	0	60	0	0	0	0
70	16	0	20	0	0	0	0	16	0	0	12	4	5	0	0	0	0	0	0	0	10	0	0	20	0	35	100	0
1000	40	0	12	0	0	0	0	16	0	0	0	6	23	0	0	0	0	75	0	0	0	0	0	20	0	65	0	0
TOTAL	100	0	26	0	0	0	0	10	0	0	9	24	22	4	0	0	0	2	0	0	11	0	0	8	0	13	1	0

Table 3. Species occurrence in '61 to '68 age class.

NUMBER OF OCCURENCES

SPECIES

DEPTH		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	93	20	16	0	36	17	34	14	19	3	60	81	32	3	0	7	4	0	0	11	4	0	4	13	1	1	1	0
60	31	0	2	0	1	1	2	4	0	6	19	25	15	10	0	2	0	2	6	8	4	0	1	13	0	0	9	0
70	34	0	0	0	0	0	0	6	0	0	23	26	8	1	0	0	3	8	5	10	17	0	0	28	0	5	17	0
1000	49	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	3	24	37	0	20	49	7	12	25	0
TOTAL	207	20	18	0	37	18	36	24	19	9	102	132	57	14	0	9	7	10	14	53	62	0	25	103	8	18	52	0

PERCENT OCCURENCE OF SPECIES AT GIVEN DEPTHS

SPECIES

DEPTH		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	45	22	17	0	39	18	37	15	20	3	65	87	34	3	0	8	4	0	0	12	4	0	4	14	1	1	1	0
60	15	0	6	0	3	3	6	13	0	19	61	81	48	32	0	6	0	6	19	26	13	0	3	42	0	0	29	0
70	16	0	0	0	0	0	0	18	0	0	68	76	24	3	0	0	9	24	15	29	50	0	0	82	0	15	50	0
1000	24	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	6	49	76	0	41	100	14	24	51	0
TOTAL	100	10	9	0	18	9	17	12	9	4	49	64	28	7	0	4	3	5	7	26	30	0	12	50	4	9	25	0

PERCENT OCCURENCE OF DEPTHS FOR GIVEN SPECIES

SPECIES

DEPTH		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	45	100	89	0	97	94	94	58	100	33	59	61	56	21	0	78	57	0	0	21	6	0	16	13	13	6	2	0
60	15	0	11	0	3	6	6	17	0	67	19	19	26	71	0	22	0	20	43	15	6	0	4	13	0	0	17	0
70	16	0	0	0	0	0	0	25	0	0	23	20	14	7	0	0	43	80	36	19	27	0	0	27	0	28	33	0
1000	24	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	21	45	60	0	80	48	88	67	48	0
TOTAL	100	10	9	0	18	9	17	12	9	4	49	64	28	7	0	4	3	5	7	26	30	0	12	50	4	9	25	0

Table 4. Species occurrence in '51 to '61 age class.

NUMBER OF OCCURENCES

DEPTH		SPECIES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	44	4	0	9	20	16	31	0	22	7	38	41	25	3	0	4	4	0	2	2	3	0	3	7	0	0	0	0
60	82	0	0	0	13	8	21	1	15	6	40	70	60	13	1	9	9	2	6	16	25	4	14	45	1	0	2	0
70	52	0	0	0	0	0	1	0	0	0	8	35	31	2	0	13	6	1	22	25	14	8	11	48	6	4	26	0
1000	82	0	0	0	0	0	0	0	0	0	0	0	38	13	0	0	0	0	6	37	20	11	29	81	12	13	64	0
TOTAL	260	4	0	9	33	24	53	1	37	13	86	146	154	31	1	26	19	3	36	80	62	23	57	181	19	17	92	0

PERCENT OCCURENCE OF SPECIES AT GIVEN DEPTHS

DEPTH		SPECIES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	17	9	0	20	45	36	70	0	50	16	86	93	57	7	0	9	9	0	5	5	7	0	7	16	0	0	0	0
60	32	0	0	0	16	10	26	1	18	7	49	85	73	16	1	11	11	2	7	20	30	5	17	55	1	0	2	0
70	20	0	0	0	0	0	2	0	0	0	15	67	60	4	0	25	12	2	42	48	27	15	21	92	12	8	50	0
1000	32	0	0	0	0	0	0	0	0	0	0	0	46	16	0	0	0	0	7	45	24	13	35	99	15	16	78	0
TOTAL	100	2	0	3	13	9	20	0	14	5	33	56	59	12	0	10	7	1	14	31	24	9	22	70	7	7	35	0

PERCENT OCCURENCE OF DEPTHS FOR GIVEN SPECIES

DEPTH		SPECIES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	17	100	0	100	61	67	58	0	59	54	44	28	16	10	0	15	21	0	6	3	5	0	5	4	0	0	0	0
60	32	0	0	0	39	33	40	100	41	46	47	48	39	42	100	35	47	67	17	20	40	17	25	25	5	0	2	0
70	20	0	0	0	0	0	2	0	0	0	9	24	20	6	0	50	32	33	61	31	23	35	19	27	32	24	28	0
1000	32	0	0	0	0	0	0	0	0	0	0	0	25	42	0	0	0	0	17	46	32	48	51	45	63	76	70	0
TOTAL	100	2	0	3	13	9	20	0	14	5	33	56	59	12	0	10	7	1	14	31	24	9	22	70	7	7	35	0

Table 5. Species occurrence in pre-'51 age class.

(a) NUMBER OF CCCURENCES

DEPTH													SPECIES															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	16	1	0	1	4	16	7	0	13	0	13	15	15	0	14	1	0	0	0	0	1	0	0	0	0	0	0	0
60	68	0	0	6	31	24	10	0	38	5	40	58	57	0	36	20	3	3	0	10	10	2	5	9	0	0	1	1
70	11	0	0	0	0	0	0	0	0	0	1	4	5	1	4	5	1	2	0	2	4	2	4	9	0	0	6	2
1000	76	0	0	0	0	0	0	0	0	0	0	8	1	0	1	0	0	0	0	8	1	1	58	76	0	42	59	10
TOTAL	171	1	0	7	35	40	17	0	51	5	54	85	78	1	55	26	4	5	0	20	16	5	67	94	0	42	66	13

(b) PERCENT OCCURENCE OF SPECIES AT GIVEN DEPTHS

DEPTH													SPECIES															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	9	6	0	6	25	100	44	0	81	0	81	94	94	0	88	6	0	0	0	0	6	0	0	0	0	0	0	0
60	40	0	0	9	46	35	15	0	56	7	59	85	84	0	53	29	4	4	0	15	15	3	7	13	0	0	0	0
70	6	0	0	0	0	0	0	0	0	0	9	36	45	9	36	45	9	18	0	18	36	18	36	82	0	0	55	18
1000	44	0	0	0	0	0	0	0	0	0	0	11	1	0	1	0	0	0	0	11	1	1	76	100	0	55	78	13
TOTAL	100	1	0	4	20	23	10	0	30	3	32	50	46	1	32	15	2	3	0	12	9	3	39	55	0	25	39	8

(c) PERCENT OCCURENCE OF DEPTHS FOR GIVEN SPECIES

DEPTH													SPECIES															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	9	100	0	14	11	40	41	0	25	0	24	18	19	0	25	4	0	0	0	0	6	0	0	0	0	0	0	0
60	40	0	0	86	89	60	59	0	75	100	74	68	73	0	65	77	75	60	0	50	63	40	7	10	0	0	0	0
70	6	0	0	0	0	0	0	0	0	0	2	5	6	100	7	19	25	40	0	10	25	40	5	10	0	0	2	8
1000	44	0	0	0	0	0	0	0	0	0	0	9	1	0	2	0	0	0	0	40	6	20	87	81	0	100	89	77
TOTAL	100	1	0	4	20	23	10	0	30	3	32	50	46	1	32	15	2	3	0	12	9	3	39	55	0	25	39	8

Table 6. Species occurrence in the combination of the three oldest age classes.

NUMBER OF OCCURENCES

DEPTH		SPECIES																										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	153	25	16	10	60	49	72	14	54	10	111	137	72	6	14	12	8	0	2	13	8	0	7	20	1	1	1	0
60	181	0	2	6	45	33	33	5	53	17	99	153	132	23	37	31	12	7	12	34	39	6	20	67	1	0	12	1
70	97	0	0	0	0	0	1	6	0	0	32	65	44	4	4	18	10	11	27	37	35	10	15	85	6	9	49	2
1000	207	0	0	0	0	0	0	0	0	0	0	8	41	13	1	0	0	0	9	69	58	12	107	206	19	67	148	10
TOTAL	638	25	18	16	105	82	106	25	107	27	242	363	289	46	56	61	30	18	50	153	140	28	149	378	27	77	210	13

PERCENT OCCURENCE OF SPECIES AT GIVEN DEPTHS

DEPTH		SPECIES																										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	24	16	10	7	39	32	47	9	35	7	73	90	47	4	9	8	5	0	1	8	5	0	5	13	1	1	1	0
60	28	0	1	3	25	18	18	3	29	9	55	85	73	13	20	17	7	4	7	19	22	3	11	37	1	0	7	1
70	15	0	0	0	0	0	1	6	0	0	33	67	45	4	4	19	10	11	28	38	36	10	15	88	6	9	51	2
1000	32	0	0	0	0	0	0	0	0	0	0	4	20	6	0	0	0	0	4	33	28	6	52	100	9	32	71	5
TOTAL	100	4	3	3	16	13	17	4	17	4	38	57	45	7	9	10	5	3	8	24	22	4	23	59	4	12	33	2

PERCENT OCCURENCE OF DEPTHS FOR GIVEN SPECIES

DEPTH		SPECIES																										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
50	24	100	89	63	57	60	68	56	50	37	46	38	25	13	25	20	27	0	4	8	6	0	5	5	4	1	0	0
60	28	0	11	38	43	40	31	20	50	63	41	42	46	50	66	51	40	39	24	22	28	21	13	18	4	0	6	8
70	15	0	0	0	0	0	1	24	0	0	13	18	15	9	7	30	33	61	54	24	25	36	10	22	22	12	23	15
1000	32	0	0	0	0	0	0	0	0	0	0	2	14	28	2	0	0	0	18	45	41	43	72	54	70	87	70	77
TOTAL	100	4	3	3	16	13	17	4	17	4	38	57	45	7	9	10	5	3	8	24	22	4	23	59	4	12	33	2

based on this row, to emphasize the more common species in each age class.

Table 7. Most common species in each age class.

Age Class	Species with Frequency of 25% or Greater											
'68 to '73	2,											
'61 to '68			10,	11,	12,		19,	20,		23,		26
'52 to '61			10,	11,	12,		19,			23,		26
prior to '52		8,	10,	11,	12,	14,			22,	23,	25,	26

The most striking feature of Table 7 is the difference between the most recent age class and the three older classes. This difference has been already referred to in the methods section as the reason for not pooling the data of the most recent class with that of the others for the study of the relation between vegetation and water table depth. Species 20 barely misses the '52 to '61 class list since it occurs with frequency 24% in the class; otherwise, the species listed in Table 7 are the same for the '52 to '61 and the '61 to '68 age classes. The oldest age class has many of the same common species but 19 and 20 are replaced by 8, 14, 22, and 25 in the list of frequent species. This change may be explained by the position of the oldest age class on the deflation plain. It could be considered as a transition between the rest of the deflation plain and the dry hummocks at the rear of the foredune. Also, it can be seen from comparison of Tables 5(a) and 6(a) that the depths in this age class were greater than those in the sum of the three oldest age classes; thus the differences in observed species frequencies could be attributed to depth differences as well as to succession.

Besides species 2, other "pioneer" species in the most recent age class may be seen in Table 2. These are: 7, 10, 11, 12, 17, 20, 23, 25, and 26. Notice that many of these pioneers are among the more frequent species at later stages of succession.

Depths

Table 8. Most common species in each depth class.

Upper Limit of Depth Class (cm.)	Species with Frequency of 25% or Greater
50	4, 5, 6, 8, 10, 11, 12
60	4, 8, 10, 11, 12, 23
70	10, 11, 12, 18, 19, 20, 23, 26
> 70	19, 20, 22, 23, 25, 26

An overview of how each species behaves with regard to increasing depth to the water table may be obtained by examination of Table 6, which refers to the sum of the three older age classes. From this table, one can extract the information necessary to construct Table 8 which corresponds to Table 7 presented in the section on age classes. These tables show, not surprisingly, some species with narrow ranges of occurrence in terms of high, low, or intermediate depths to the water table, and some with quite broad ranges. In agreement with Wiedemann (1966), species 12 (*Juncus leseurii*) was found to have the broadest range, although species 23 (Lupinus littoralis) occupied a surprisingly broad range in view of Wiedemann's use of this species to characterize his extreme "dry meadow" community.

Age Class and Depth

Table 9. Species with frequency 50% or greater in combined depth and age classes.

	Age Classes			
Depth (cm.)	'73	'68	'61	'52
50	2, 11, 12	10, 11	6, 8, 10, 11, 12	5, 8, 10, 11, 12, 14
60	none	10, 11	11, 12, 23	8, 10, 11, 12, 14
70	none	10, 11, 20, 23, 26	11, 12, 23, 26	23, 26
> 70	none	20, 23, 26	23, 26	22, 23, 25, 26

Table 9 gives an interesting two-dimensional view of the deflation plain in terms of the combination of succession and water table depth, and is much more meaningful than either Table 7 or 8 since the effects of water table depth and succession are separated out. Recall that in examining Table 7 there was uncertainty as to whether the changes in species frequency in the oldest class compared to the intermediate age classes might merely result from the different distribution of depths corresponding to the oldest age class. Table 9 shows that with depth held constant there are significant changes in the list of most frequent species between the oldest and next oldest age class. However, one should still be cautious in using the vegetation of the pre'52 age class as a prediction of the future vegetation of the other age classes because of its "transitional" location between the rest of the deflation plain and the dry hummocks behind the foredune.

The difference between the two intermediate age classes is more apparent in Table 9 than it was in Table 7. The older of these shows a greater variety of high frequency species.

Table 9 again emphasizes the great difference between the youngest age class and all others. It also reveals that succession begins mainly at the lower depths.

Niches

As Whittaker, Levin and Root (1973) point out, the use of the word "niche" is very confused. In this paper, niche is used in the sense of the probability of occurrence of a species in an n-dimensional space of environmental variables. Specifically, this section presents the niche of each species in terms of the two dimensions of depth to the water table and age class.

The general form of the tables is illustrated by Table 10 which shows how the observations were distributed in terms of depth and age class. The rows correspond to depths, while the columns correspond to age classes:

Case 1 -- '68 to '73
2 -- '61 to '68
3 -- '52 to '61
4 -- prior to '52
5 -- combination of cases 2, 3, 4.

Table 10. Number of samples in each combination of depth and age class.

	Cases				
Depth	1	2	3	4	5
50	15	93	44	16	153
60	72	31	82	68	181
70	31	34	52	11	97
1000	79	49	82	76	207
Total	197	207	260	171	638

Table 10 records the number of samples in each combination of depth and age class; whereas, the tables which follow for each species give the percent frequency of occurrence of the species. If this percent frequency of occurrence is regarded as an estimate of the probability of occurrence of the species for the particular combination of depth and age class, then there will be more confidence in the estimate for those combinations with more observations. To take this into account, and assist the reader in determining whether numbers in these tables are significantly different, 90% confidence intervals were constructed using the normal approximation to the binomial (Kurtz, 1963, p. 133) and these are displayed to the right of each frequency table.

The species are discussed in order of increasing median depth to the water table.

Table 11. Niche of species 1: Carex viridula Michx.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	22	9	6	16	0	20	15	30	3	20	0	27	11	22
60	0	0	0	0	0	0	5	0	11	0	4	0	5	0	2
70	0	0	0	0	0	0	11	0	10	0	7	0	26	0	4
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	10	2	1	4	0	2	7	14	1	4	0	4	3	6

This species was not recorded in the youngest age class, or at depths greater than 50 cm. Examination of the confidence intervals does not show any significant variation in probability of occurrence among the other age classes.

Table 12. Niche of species 2: Mimulus guttatus DC.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	100	17	0	0	10	80	100	11	25	0	8	0	19	6	15
60	28	6	0	0	1	20	38	1	19	0	4	0	5	0	4
70	32	0	0	0	0	19	48	0	10	0	7	0	26	0	4
1000	8	0	0	0	0	4	15	0	7	0	4	0	5	0	2
Total	26	9	0	0	3	21	32	6	13	0	1	0	2	2	4

This species is a pioneer recorded only in the two youngest age classes, and mainly in the youngest. In the youngest class it is present throughout all depth classes, but its frequency significantly decreases with increasing depth. In the next youngest age class it is recorded only at the lower depths.

Table 13. Niche of species 3: Carex obnupta Bail.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	0	20	6	7	0	20	0	4	11	33	0	27	4	12
60	0	0	0	9	3	0	5	0	11	0	4	4	17	1	6
70	0	0	0	0	0	0	11	0	10	0	7	0	26	0	4
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	0	3	4	3	0	2	0	2	2	6	2	8	2	4

This species was recorded only in the two oldest age classes and in the two lower depth classes. There is evidence that it occurs at greater depths in the older age class.

Table 14. Niche of species 4: Lilaeopsis occidentalis Coult. and Rose.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	39	45	25	30	0	20	31	48	32	58	10	49	32	46
60	0	3	16	46	25	0	5	0	15	10	24	36	57	20	31
70	0	0	0	0	0	0	11	0	10	0	7	0	26	0	4
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	18	13	20	16	0	2	14	23	10	17	15	26	14	19

This species was recorded in the two lower depth classes in all but the youngest age class. Again there is evidence that it occurs at greater depths in older age classes, although there is no significant increase in frequency among the three older age classes.

Table 15. Niche of species 5: Potentilla pacifica Howell.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Interval 1		2		3		4		5	
50	0	18	36	100	32	0	20	12	26	24	50	81	100	26	39
60	0	3	10	35	18	0	5	0	15	5	18	26	46	14	23
70	0	0	0	0	0	0	11	0	10	0	7	0	26	0	4
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	9	9	23	13	0	2	6	13	6	13	18	29	11	15

Like the above species, this species was recorded in the two lower depth classes in all but the youngest age class. However, unlike the above species, this species shows a significant increase in frequency with age class, and does not show any significant increase in depth of occurrence with age class. It may be that these two species are illustrating the effect of competition, with the increase in species 5 over time forcing species 4 out of its "preferred" niche into one further from the water table.

Table 16. Niche of species 6: Ranunculus flammula L.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Interval 1		2		3		4		5	
50	0	37	70	44	47	0	20	29	46	57	81	23	67	40	54
60	0	6	26	15	18	0	5	1	19	18	35	9	24	14	23
70	0	0	2	0	1	0	11	0	10	0	10	0	26	0	5
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	17	20	10	17	0	2	13	22	16	25	7	15	15	20

This species is recorded in all but the youngest age class, and shows a peak of abundance in the intermediate '52 to '61 age class. It is confined almost entirely to the two lowest depth classes, occurring with significantly greater frequency in the lowest depth class.

Table 17. Niche of species 7: Epilobium franciscanum Barb.

Depth	Cases 1	Cases 2	Cases 3	Cases 4	Cases 5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	15	0	0	9	0	20	9	23	0	8	0	19	6	14
60	18	13	1	0	3	11	27	5	28	0	6	0	5	1	6
70	10	18	0	0	6	3	24	9	33	0	7	0	26	3	12
1000	4	0	0	0	0	1	10	0	7	0	4	0	5	0	2
Total	10	12	0	0	4	7	14	9	16	0	1	0	2	3	6

This is another pioneer, recorded only once outside of the two youngest age classes. It differs in distribution from species 2 (Mimulus guttatus) in that: (1) it is about equally frequent in the two youngest age classes; (2) it is more frequent at intermediate depths.

Table 18. Niche of species 8: Sisyrinchium californicum (Ker.) Dryand.

Depth	Cases 1	Cases 2	Cases 3	Cases 4	Cases 5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	20	50	81	35	0	20	14	28	37	63	58	94	29	42
60	0	0	18	56	29	0	5	0	11	12	27	45	66	24	35
70	0	0	0	0	0	0	11	0	10	0	7	0	26	0	4
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	9	14	30	17	0	2	6	13	11	18	24	36	15	20

This species is similar in distribution to Potentilla pacifica (species 5), but occurs at slightly greater distances from the water table.

Table 19. Niche of species 9: Spiranthes romanzoffiana Cham.

Depth	Cases					90 Percent Confidence Intervals									
	1	2	3	4	5	1		2		3		4		5	
50	0	3	16	0	7	0	20	1	8	8	28	0	19	4	12
60	0	19	7	7	9	0	5	9	35	3	14	3	15	6	13
70	0	0	0	0	0	0	11	0	10	0	7	0	26	0	4
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	4	5	3	4	0	2	2	7	3	8	1	6	3	6

This species occurs in the three older age classes and the two lower depths. The frequencies are fairly small but erratic with no significant trend.

Table 20. Niche of species 10: Juncus falcatus E. Meyer.

Depth	Cases					90 Percent Confidence Intervals									
	1	2	3	4	5	1		2		3		4		5	
50	0	65	86	81	72	0	20	56	73	74	93	58	94	66	79
60	21	61	49	59	55	14	31	45	75	40	59	48	69	49	61
70	6	68	15	9	33	1	19	52	81	8	26	1	38	25	42
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	9	49	33	32	38	6	13	43	55	28	38	26	38	35	41

This is one of the most widely distributed species, occurring in all age classes and at all depths except the deepest. The lack of records at the lowest depth in the youngest age class could be due to the fact that only 15 observations were made for this combination.

The most significant trend is the decrease in frequency of this species with age class for depths of 60 to 70 cm.

Table 21. Niche of species 11: Juncus phaecocephalus Engelm.

Depth	Cases 1	Cases 2	Cases 3	Cases 4	Cases 5	90 Percent Confidence Intervals 1		2		3		4		5	
50	100	87	93	94	90	80	100	80	92	82	98	73	100	85	94
60	38	81	85	85	85	29	48	65	91	77	91	76	91	80	89
70	6	76	67	36	67	1	19	61	87	55	77	14	64	58	75
1000	4	0	0	11	4	1	10	0	7	0	4	6	19	2	7
Total	24	64	56	50	57	19	30	58	70	51	61	43	57	54	60

This species is even more widely distributed than the preceding, and occurs with a greater frequency over its range. It also shows a decrease in frequency at depths of 60 to 70 cm. with increasing age class, although this effect is not as pronounced as for the preceding species. It occurs in almost all samples with depths less than 60 cm. except that it is not as frequent in the youngest age class at depths of 50 to 60 cm.

Table 22. Niche of species 12: Juncus leseurii Boland.

Depth	Cases 1	Cases 2	Cases 3	Cases 4	Cases 5	90 Percent Confidence Intervals 1		2		3		4		5	
50	100	34	57	94	47	80	100	26	43	44	70	73	100	40	54
60	24	48	73	84	73	16	34	33	64	64	81	75	91	67	78
70	6	24	60	45	45	1	19	13	39	48	71	20	72	36	54
1000	13	4	46	1	20	1	21	1	13	37	56	0	6	16	25
Total	22	28	59	46	45	17	27	23	34	54	64	40	53	42	48

This is the most broadly distributed species of all. It is the first one described here in which the maximum frequency of occurrence is at greater than 50 cm. However, in the youngest age class, it is similar to Juncus phaecocephalus in having much greater frequency at the lowest depths. It appears to reach a peak in frequency of occurrence in the '52 to '61 age class (as did species 6, Ranunculus flammula) mainly due to much more frequent occurrence at depths over 70 cm. in this age class. This could be the result of competition from Ammophila which, as will be seen later, is frequent both as a pioneer and in the pre-'51 age class as a transition from the foredune.

Table 23. Niche of species 13: Tanacetum camphoratum Less.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	3	7	0	4	0	20	1	8	2	18	0	19	2	8
60	11	32	16	0	13	6	19	19	48	10	24	0	5	9	18
70	0	3	4	9	4	0	11	0	14	1	13	1	38	1	9
1000	0	0	16	0	6	0	4	0	7	10	24	0	5	4	10
Total	4	7	12	1	7	2	7	4	11	9	16	0	4	5	9

This species has a wide but erratic distribution. It is present in all age classes and depth classes but not in all combinations of them. The peak of its distribution is at depth 50 to 60 cm. in age class '61 to '68; its distribution broadens considerably in the '52 to '61 age class; and it is scarcely recorded in the pre-'52 age class.

Table 24. Niche of species 14: Trifolium wormskjoldii Lehm.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	0	0	88	9	0	20	0	4	0	8	65	98	6	14
60	0	0	1	53	20	0	5	0	11	0	6	42	63	15	26
70	0	0	0	36	4	0	11	0	10	0	7	14	64	1	9
1000	0	0	0	1	0	0	4	0	7	0	4	0	6	0	2
Total	0	0	0	32	9	0	2	0	2	0	1	26	38	7	11

This species was recorded almost exclusively within the oldest age class. Within this age class there was a decrease in frequency of occurrence with depth, with only one observation over 70 cm.

Table 25. Niche of species 15: Aster subspicatus Nees.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	8	9	6	8	0	20	4	15	3	20	0	27	5	13
60	0	6	11	29	17	0	5	1	19	6	19	20	39	13	22
70	0	0	25	45	19	0	11	0	10	16	37	20	72	13	27
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	4	10	15	10	0	2	2	7	7	14	11	20	8	12

This species is present in all of the three older age classes, but shows an increased frequency with increasing age class, except in the lowest depth class where the frequency is small and essentially constant. This is the first species discussed here which shows its greatest frequency of occurrence between 60 and 70 cm., although the difference in frequency between this depth class and the 50 to 60 cm. class is not significant. It was not recorded over 70 cm.

Table 26. Niche of species 16: Orthocarpus castillejoides Benth.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	4	9	0	5	0	20	1	10	3	20	0	19	3	9
60	0	0	11	4	7	0	5	0	11	6	19	1	11	4	11
70	0	9	12	9	10	0	11	3	22	6	22	1	38	6	17
1000	0	0	0	0	0	0	4	0	7	0	4	0	5	0	2
Total	0	3	7	2	5	0	2	1	6	5	10	1	5	4	7

This species is present at low essentially similar frequencies in all age classes except the youngest and at all depths except the deepest. There is evidence of a greater frequency in the '52 to '61 age class, and at the 60 to 70 cm. depth.

Table 27. Niche of species 17: Gnaphalium purpureum L.

Depth	Cases					90 Percent Confidence Intervals									
	1	2	3	4	5	1		2		3		4		5	
50	0	0	0	0	0	0	20	0	4	0	8	0	19	0	2
60	1	6	2	4	4	0	6	1	19	0	7	1	11	2	7
70	0	24	2	18	11	0	11	13	39	0	10	4	47	6	18
1000	4	0	0	0	0	1	10	0	7	0	4	0	5	0	2
Total	2	5	1	3	3	1	5	3	8	0	3	1	6	2	4

This is another species with wide distribution but generally low and erratic frequency. It occurs in all age classes and all depth classes except the shallowest. There is no significant trend in frequency with age class, but frequency is definitely higher for the 60 to 70 cm. depths. This species differs from previously discussed pioneers in that it occurs at higher elevations as a pioneer than it does at later stages of succession.

Table 28. Niche of species 18: Festuca rubra L.

Depth	Cases					90 Percent Confidence Intervals									
	1	2	3	4	5	1		2		3		4		5	
50	0	0	5	0	1	0	20	0	4	1	15	0	19	0	4
60	0	19	7	0	7	0	5	9	35	3	14	0	5	4	11
70	0	15	42	0	28	0	11	7	29	31	54	0	26	21	37
1000	0	6	7	0	4	0	4	2	16	3	14	0	5	2	7
Total	0	7	14	0	8	0	2	4	11	11	18	0	2	6	10

This species occurs in all depth classes, but only in the intermediate age classes, and it is more frequent at intermediate depths. There is a significant increase in the depth to the water table at which the species occurs as the age class increases.

Table 29. Niche of species 19: Hypochaeris radicata L.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	12	5	0	8	0	20	7	19	1	15	0	19	5	13
60	0	26	20	15	19	0	5	14	42	13	29	9	24	14	25
70	0	29	48	18	38	0	11	17	44	36	60	4	47	30	47
1000	0	49	45	11	33	0	4	37	61	36	55	6	19	28	39
Total	0	26	31	12	24	0	2	21	32	26	36	8	17	21	27

This species was recorded in all but the youngest age class, although there is a significant reduction in frequency in the oldest age class. It was recorded in all depth classes, but with significantly lower frequency in the lowest depth class.

Table 30. Niche of species 20: Agrostis spp.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	4	7	6	5	0	20	1	10	2	18	0	27	3	9
60	26	13	30	15	22	18	36	5	28	22	39	9	24	17	28
70	6	50	27	36	36	1	19	35	65	17	39	14	64	28	45
1000	0	76	24	1	28	0	4	64	85	17	33	0	6	23	34
Total	11	30	24	9	22	8	15	25	36	20	29	6	14	19	25

As might be expected, this "species" which is actually a combination of all species of the genus Agrostis is quite widespread occurring in all age and depth classes. There are significantly lower frequencies of this species at depths less than 50 cm., and there is also a significant decrease in frequency with age class (among the three older classes) at depths greater than 70 cm.

Table 31. Niche of species 21: Centaurium umbellatum Gilib.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	0	0	0	0	0	20	0	4	0	8	0	19	0	2
60	0	0	5	3	3	0	5	0	11	2	11	1	10	1	6
70	0	0	15	18	10	0	11	0	10	8	26	4	47	6	17
1000	0	0	13	1	6	0	4	0	7	8	21	0	6	4	10
Total	0	0	9	3	4	0	2	0	2	6	13	1	6	3	6

This species was recorded only in the two oldest age classes, and only for depths greater than 50 cm. Its peak frequency is between 60 and 70 cm. At depths greater than 70 cm., there is a significant reduction in frequency in the oldest age class.

Table 32. Niche of species 22: Fragaria chiloensis (L.) Duch.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	4	7	0	5	0	20	1	10	2	18	0	19	3	9
60	0	3	17	7	11	0	5	0	15	11	26	3	15	8	16
70	0	0	21	36	15	0	11	0	10	12	33	14	64	10	22
1000	0	41	35	76	52	0	4	29	54	26	45	66	84	46	58
Total	0	12	22	39	23	0	2	0	16	18	27	33	46	20	26

This species occurs in all depth classes, and in all age classes except the youngest. There is a significant increase in frequency with depth and also with age class.

Table 33. Niche of species 23: Lupinus littoralis Dougl.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	14	16	0	13	0	20	9	22	8	28	0	19	9	18
60	13	42	55	13	37	7	22	27	58	45	64	7	22	31	43
70	10	82	92	82	88	3	24	67	91	82	97	53	96	81	93
1000	4	100	99	100	100	1	10	93	100	94	100	95	100	98	100
Total	8	50	70	55	59	5	12	44	56	65	75	48	61	56	62

As noted previously, this is an extremely widespread species. There is a significant increase in frequency with depth, and the species appears to be further from the water table in the pre-'52 age class and closer in the most recent age class. The peak abundance is in the '52 to '61 age class.

Table 34. Niche of species 24: Anaphalis margaritacea (L.) B. & H.

	Cases					90 Percent Confidence Intervals									
Depth	1	2	3	4	5	1		2		3		4		5	
50	0	1	0	0	1	0	20	0	5	0	8	0	19	0	4
60	0	0	1	0	1	0	5	0	11	0	6	0	5	0	4
70	0	0	12	0	6	0	11	0	10	6	22	0	26	3	12
1000	0	14	15	0	9	0	4	7	25	9	24	0	5	6	13
Total	0	4	7	0	4	0	2	2	7	5	10	0	2	3	6

Records of this species are almost completely confined to three "cells:" age class '61 to '68 at depths greater than 70 cm., and age class '52 to '61 at depths greater than 60 cm.

Table 35. Niche of species 25: Ammophila arenaria (L.) Link.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	1	0	0	1	0	20	0	5	0	8	0	19	0	4
60	0	0	0	0	0	0	5	0	11	0	4	0	5	0	2
70	29	15	8	0	9	16	45	7	29	3	18	0	26	5	16
1000	22	24	16	55	32	15	31	15	36	10	24	45	65	27	38
Total	13	9	7	25	12	9	18	6	13	5	10	20	31	10	14

With the exception of one observation, this species was recorded only at depths greater than 60 cm. There is a significant increase in depth of occurrence with age class, as would be expected from its known mound building habit (Wiedemann, 1966). The observation that frequencies are lower at intermediate ages than at the extremes may be explained as follows: The relatively high frequencies in the youngest age class are the result of Ammophila's success as a pioneer in areas of moving sand; whereas, the high frequencies in the oldest age class may be attributed to its position on the deflation plain as a transition to the Ammophila foredune.

Table 36. Niche of species 26: Aira praecox L.

Depth	Cases 1	2	3	4	5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	1	0	0	1	0	20	0	5	0	8	0	19	0	4
60	0	29	2	1	7	0	5	16	45	0	7	0	7	4	11
70	6	50	50	55	51	1	19	35	65	38	62	28	80	42	60
1000	0	51	78	78	71	0	4	39	63	69	85	69	85	65	76
Total	1	25	39	39	33	0	3	20	31	30	40	33	46	30	36

This species occurs mainly in the three older age classes and at depths greater than 50 cm. In the '61 to '68 age class, its frequency distribution is shifted to lower depths.

Table 37. Niche of species 27: Rumex acetosella L.

Depth	Cases 1	Cases 2	Cases 3	Cases 4	Cases 5	90 Percent Confidence Intervals 1		2		3		4		5	
50	0	0	0	0	0	0	20	0	4	0	8	0	19	0	2
60	0	0	0	1	0	0	5	0	11	0	4	0	7	0	4
70	0	0	0	18	2	0	11	0	10	0	7	4	47	0	7
1000	0	0	0	13	5	0	4	0	7	0	4	7	21	3	8
Total	0	0	0	8	2	0	2	0	2	0	1	5	12	1	3

This species occurred with the least frequency of all those listed. It occurred only in the oldest age class and (with one exception) at depths greater than 60 cm.

Prediction

The prediction of water table depth based on species present in a quadrat was extremely accurate: for 96% of the quadrats, water table depth was predicted to within 10 cm; for 73% of the quadrats, it was predicted to within 5 cm. The analysis of the errors of prediction in terms of age class, depth, and number of species suggests that the method of prediction could be modified to produce even greater accuracy.

Table 38 summarizes the errors of prediction. The columns give the average error, average of the absolute values of the errors, standard deviation of the errors, the distribution of the errors in terms of the percent of observations with errors less than or equal to

Table 38. Summary of errors of prediction.

	SUMMARY OF ERRORS MEAN	MEANABS	STD DEV	DISTRIBUTION OF ERRORS 5	10	15	20	25	30	RSQ
OVERALL										
	.59	3.54	5.19	73	23	3	1	0	0	.76
AGE										
1	-0.97	1.78	3.16	89	9	1	0	0	0	
2	.18	4.18	5.67	68	26	5	2	0	0	
3	2.40	4.19	5.40	66	31	1	0	0	0	
DEPTH										
40	6.27	6.27	2.80	59	32	9	0	0	0	
45	7.39	7.39	3.98	29	66	2	0	2	0	
50	4.12	4.30	2.89	78	21	1	0	0	0	
55	1.99	2.92	4.42	82	15	0	3	0	0	
60	-1.18	3.50	4.11	71	29	0	0	0	0	
65	-0.24	3.29	4.43	82	16	2	0	0	0	
70	-7.62	8.52	4.83	21	50	29	0	0	0	
75	-1.64	1.64	3.26	84	16	0	0	0	0	
NO. OF SP.										
1	5.44	5.44	6.10	56	38	0	0	6	0	
2	-0.27	4.78	7.38	61	31	2	7	0	0	
3	2.55	3.05	3.98	69	30	0	1	0	0	
4	-0.51	3.07	4.79	75	24	1	0	0	0	
5	-1.14	4.60	6.09	65	17	18	0	0	0	
6	1.15	3.54	4.48	75	25	0	0	0	0	
7	.38	2.91	3.46	91	9	0	0	0	0	
8	1.96	2.71	3.54	92	4	4	0	0	0	
10	4.00	4.00	0	100	0	0	0	0	0	

5 cm., between 5 and 10 cm., etc., and R^2. The R^2 value is included for interest since it is commonly used in regression models; however, it does not provide as good an evaluation of the prediction as does the distribution of errors, since R^2 may be heavily influenced by a small percentage of erratic points.

The rows of the table summarize the errors of prediction overall, and for various age classes, depths and numbers of species (of the 27 species) present in the quadrat for which depth to the water table is being predicted. Ages "1, 2, 3" refer to age classes pre-'52, '52 to '61, and '61 to '68, respectively. The depth numbers listed are upper limits of intervals (in cm.), with 75 being used to indicate the set of depths greater than 70 cm.

Although there is an increase in the error of prediction with age class, this does not appear significant when compared with the standard deviations of the errors. There is, however, a significant over-prediction of depths at low depths, and an underprediction at high depths. This is not unexpected, since a method in which ranges are successively truncated at both ends obviously "favors" intermediate values. This property of the prediction could be reduced by rederiving Table 39 such that for the more extreme species at high and low depths the progressive truncation of their ranges occurred only at the one end of their range at intermediate depths, rather than using a "two-tailed" truncation.

As expected, the errors of prediction are larger when only one species is present than they are when more species are present. It would seem that an improvement could be made in the overall prediction if quadrats with only one species were excluded; however, only 2.5% of the total quadrats fall in the "one species" class so any improvement would be small.

A detailed examination was made of all of the quadrats for which the prediction was in error by more than 10 cm. The only evident feature these had in common was that they were extreme points in the range of some species, and that they would probably "come as surprises" to most methods of prediction.

SUMMARY AND CONCLUSIONS

Using quadrat data on species presence and absence, depth to the water table and location on the deflation plain, the various age classes, depths to the water table, and combinations of these two variables were characterized in terms of percent frequency of occurrence of 27 species. The "niches" of each of the 27 species was then discussed. Finally, the prediction of water table depth based on species presence or absence was evaluated with some suggestions for improvement.

The species "niches" show each one to be an individual with its own quite distinct niche in terms of depth to the water table, and time since initiation of succession. There is, however, evidence of possible interaction where a decrease in the frequency of some species might be explained in terms of competition from other species. The distributions of some species have increasing depth to the water table with age class; whereas, other species decrease their depths to the water table with age class.

The extremely accurate prediction of water table depth based on species present in a quadrat provides strong support to the beliefs of Willis et al. (1959), Ranwell (1959, 1960), Wiedemann (1966, 1969) and Onyekwelu (1972) that water table depth is one of the most important factors correlated with species distribution in those areas of the coastal sands where the water table is relatively close to the surface.

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APPENDIX

APPENDIX

Range Table Used for Prediction

The use of this table has been explained in the methods section. It does not contain any "new" information that is not summarized in another form in the results section.

Table 39. Range table used for prediction.

RANGES OF SPECIES

PERCENT OF RANGE / SPECIES	100	90	80	70	60	50	40	30	20	10	MEDIAN
1	40 48	40 46	40 43	40 43	40 43	40 43	40 43	40 41	40 41	40 41	40
2	40 56	40 56	40 53	40 46	40 46	40 48	40 43	43 46	43 46	44 45	44
3	40 53	39 53	41 51	41 51	41 51	42 51	43 51	43 51	43 48	44 46	45
4	40 56	40 53	40 53	41 53	42 52	43 51	44 51	46 51	47 51	45 48	48
5	40 58	40 57	40 53	40 53	41 51	42 51	43 51	44 51	47 50	45 50	48
6	40 61	40 54	40 53	41 53	42 52	43 51	45 51	46 49	48 48	48 48	48
7	43 64	43 64	43 64	46 64	46 62	46 55	46 53	46 51	45 51	48 48	48
8	40 58	40 56	40 55	41 53	43 53	43 53	46 53	45 52	45 51	45 51	50
9	40 56	40 56	40 55	47 55	48 53	46 52	48 51	48 51	51 51	51 51	51
10	40 69	40 66	41 64	43 56	46 56	46 53	48 53	48 53	48 53	50 51	51
11	40 71	41 69	43 66	45 61	47 60	48 56	48 55	50 53	51 53	51 53	51
12	40 71	43 71	46 71	48 69	48 64	51 61	51 58	51 56	52 55	53 53	53
13	41 71	42 71	48 71	51 71	51 71	51 71	52 64	53 61	53 57	53 53	53
14	46 71	48 69	48 61	48 58	49 57	50 56	51 56	51 55	52 55	53 53	53
15	40 69	43 69	46 69	48 69	50 69	52 65	52 56	53 56	53 55	55 55	55
16	43 69	43 69	46 69	46 65	48 62	50 62	51 61	51 56	52 56	53 55	55
17	52 65	52 65	52 61	53 61	55 61	56 61	56 61	56 61	58 61	61 61	61
18	48 71	51 71	51 71	51 71	54 69	58 69	61 69	61 69	63 69	64 66	65
19	40 71	47 71	52 71	53 71	53 71	56 71	58 71	61 71	61 71	62 71	66
20	41 71	50 71	51 71	51 71	53 71	53 71	56 71	62 71	64 71	66 71	66
21	52 71	53 71	56 71	57 71	58 71	61 71	61 71	61 71	66 71	66 66	66
22	43 71	50 71	53 71	56 71	61 71	61 71	71 71	71 71	71 71	71 71	71
23	44 71	49 71	51 71	53 71	55 71	61 71	62 71	65 71	66 71	69 71	71
24	50 71	55 71	61 71	61 71	61 71	61 71	71 71	71 71	71 71	71 71	71
25	50 71	62 71	62 71	71 71	71 71	71 71	71 71	71 71	71 71	71 71	71
26	51 71	56 71	61 71	63 71	64 71	67 71	71 71	71 71	71 71	71 71	71
27	53 71	53 71	66 71	66 71	69 71	71 71	71 71	71 71	71 71	71 71	71

Table 1. The 27 species in order of increasing median depth to the water table.

1.	Carex viridula Michx.	
2.	Mimulus guttatus DC.	rush meadow
3.	Carex obnupta Bailey	marsh
*4.	Lilaeopsis occidentalis Coult. and Rose.	marsh
5.	Potentilla pacifica Howell	marsh
6.	Ranunculus flammula L.	marsh
7.	Epilobium franciscanum Barb.	rush meadow
8.	Sisyrinchium californicum (Ker.) Dryand.	rush meadow
9.	Spiranthes romanzoffiana Cham.	
10.	Juncus falcatus E. Meyer	rush meadow
11.	Juncus phaecocephalus Engelm.	rush meadow
12.	Juncus leseurii Boland	
13.	Tanacetum camphoratum Less.	meadow
14.	Trifolium wormskjoldii Lehm.	rush meadow
*15.	Aster subspicatus Nees.	rush meadow
16.	Orthocarpus castillejoides Benth.	
17.	Gnaphalium purpureum L.	
18.	Festuca rubra L.	meadow
19.	Hypochaeris radicata L.	meadow
20.	Agrostis spp.	meadow and rush meadow
21.	Centaurium umbellatum Gilib.	rush meadow
22.	Fragaria chiloensis (L.) Duch.	meadow
23.	Lupinus littoralis Dougl.	dry meadow
24.	Anaphalis margaritacea (L.) B. and H.	meadow
25.	Ammaphila arenaria (L.) Link.	dry meadow
26.	Aira praecox L.	meadow
*27.	Rumex acctosella L.	

Note: Species 22 through 27 all had a median depth to the water table of greater than 70 cm. which was the upper limit for which precise depth measurements were made. That is, depths greater than 70 cm. were recorded merely as depths greater than 70 cm.