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Title CONTRIBUTIONS TO THE PLANT ECOLOGY OF THE OREGON COASTAL SAND DUNES

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Sand dunes are found along the coasts of most of the large land masses of the world. Because of their proximity to man and his activities, the maritime sand dunes of Europe, particularly Germany, France, Holland and Scandinavia, have the longest history of stabilization activities and botanical investigation. There are coastal dune areas, some of great extent, in Africa, tropical Asia, Australia, and South America. In general, little published information is available concerning these areas. Ecological studies of coastal dune vegetation and environment have been most extensive in Great Britain, and to a lesser extent, in North America.

Of the North American coastal dunes, those of the east coast have received considerable attention while those of the west coast have been largely neglected. Along the Oregon coast are found some of the most extensive and best developed coastal sand dune areas in North America. Occurring on some 225 km. of the state's 500 km.

of ocean facing coastline, these areas are made up of a great variety of dune landscape features and present unique conditions for the development and maintenance of vegetation.

There are many places in this dune area where the strong, constant winds have eroded the sand surface to or near the water table resulting in a stabilized surface—the deflation plain—which provides an excellent starting point for the development of vegetation. After preliminary ground and air reconnaissance, 11 deflation plains were selected for detailed study, ranging in location from Sand Lake on the north to Tahkenitch Creek on the south. These deflation plains and their location are described in detail.

Vegetation data (species and cover) were taken on a total of 134 sampling stands, each consisting of five meter-square quadrats for herbaceous vegetation, and one 6 x 6 meter quadrat for shrub and forest vegetation. The species and stand data were arranged on comparative charts so as to bring together stands with mutually occurring species. This resulted in the delineation of seven communities with definite successional relationships. Primary succession begins with one of four herbaceous communities: dry meadow, meadow, rush meadow or marsh. Succession then proceeds to low shrub, tall shrub and finally forest.

The dry meadow is dominated by three species: *Lupinus littoralis*, *Ammophila arenaria* and *Poa macrantha*. The site is dry with no standing water at any time. Sand deposition and deflation occur in varying degrees. The important species of the meadow are Festuca rubra, Aira praecox, Hypochaeris radicata and Fragaria chiloensis. The surface is dry except for short periods of standing water during the winter months. There is no sand deposition. The rush meadow is characterized by its dense growth of Trifolium willdenovii and Juncus phaeocephalus. The site is low and moist, with water standing on the surface during the winter months. The marsh is found on areas which are quite damp—water stands on the surface for around six months of the year, and is just below the surface for the remainder of the time. It is made up of dense stands of Carex obnupta and Potentilla anserina.

The low shrub community is an open stand of Salix hookeriana, Gaultheria shallon, Vaccinium ovatum and Myrica californica. This develops into a tall shrub stage which is frequently an impenetrable thicket with increasing dominance of seedlings of Pinus contorta and Picea sitchensis. Development of a forest of Pinus and Picea is very rapid. If the area is free from disturbance long enough, the shorter lived Pinus dies out, leaving a forest of Picea.

The deflation plains represent only part of the many aspects of the total dune landscape still awaiting investigation. The increasing importance of the Oregon coastal dunes to industry and recreation make imperative the initiation of long term ecological studies.

CONTRIBUTIONS TO THE PLANT ECOLOGY OF THE OREGON COASTAL SAND DUNES

by

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CONTRIBUTIONS TO THE PLANT ECOLOGY
OF THE OREGON COASTAL SAND DUNES

I. INTRODUCTION

There are many areas in the world where sand dunes are a dominant feature of the landscape. These areas range in size from the very large, extremely dry interior deserts of the continental land masses to the smaller, relatively narrow strips of sand along the shores of the oceans and large lakes. While the latter are not always located in areas of low precipitation, all of the sand dune areas are characterized by unique geomorphological features and an environment that has definite, and often extreme, effects on the existing flora and fauna.

Because of their unique characteristics, these areas have drawn the attention of workers from a wide range of scientific disciplines. Engineers and agriculturists seek to control the active, shifting dunes. Geologists are interested in the sources of the sand and the principles involved in dune formation and movement. Zoologists study the adaptations of animals to environmental conditions that are very unfavorable to the existence of life.

But it is probably the botanist, and more particularly the plant ecologist, who has been most attracted to the sand dune habitat. Though specific environmental factors vary widely throughout the world, the sand dunes are easily recognizable as distinct habitats with similar effects on plant growth. The dune environment exerts a very definite influence on the individual plant and on communities of plants. In an opposite sense, plants exert a definite influence on the dune environment. The influencing factors are readily apparent and their effects can be easily observed, often over short periods of time.

In spite of these similarities, however, the geographical location and overall climatic conditions of the interior deserts and the coastal dune regions have resulted in the development of more or less separate fields of study for these two general areas. The study of coastal, or maritime, sand dunes has been most intense in Great Britain, while in most of the rest of the world such interest has yet to manifest itself.

The extensive coastal dune areas of the United States have not been studied to any great extent. This is particularly true of the dunes along the west coast, some of which are among the most impressive in the world. Along the coast of Oregon, sand dunes are found on more than two-fifths of the state's ocean facing coastline, yet only a very small number of studies have been made on them.

It is the express purpose of this thesis to initiate an orderly, and, hopefully, continuing investigation into the many ecological, and possibly economic, aspects of the Oregon coastal sand dunes. This study takes the form, first of all, of a review of the existing world literature on the botanical and ecological aspects of the coastal, or maritime, sand dunes. This review indicates the extent of such work in other parts of the world; it discusses the terminology used by the many investigators in the field; and it shows the similarities and differences among the various coastal dune regions of the world.

The study then takes up a specific feature of the Oregon dunes, the deflation plains, and describes them and their vegetation in detail. The deflation plains—low, moist areas in the active sand areas—are particularly well suited to ecological study because of their distinct characteristics and relatively good conditions for plant growth. Because they are subjected to the ever present hazard of burial by moving dunes, all stages of vegetation succession can be found on these areas. The increasing importance of the sand dune areas to industry, real estate development and recreation make a written and photographic record of these deflation plains a most important part of the thesis.

The coastal sand dunes of Oregon represent an important and interesting part of our natural landscape. It is hoped that this study will contribute to a better understanding of them, and also stimulate interest in further studies of their many and varied features.

II. MARITIME SAND DUNES

Introduction

The sand dunes of the world represent areas of great physiographic and ecological interest. They can be found wherever the proper combinations of wind and sand supply occur—along seacoasts, lakeshores and in the continental interiors far from any body of water. Both shore dunes and inland dunes are found on all the major land masses and under all climatic regimes from the Arctic in the north to the tropics and to the most southerly land masses.

Located in the horse latitudes both north and south of the equator are the great inland desert regions of the world: the Sahara in North Africa, the Sonoran in Mexico, the Kalahari in South Africa and the vast areas of central Australia. Primitive man has long been associated with these areas, but active interest in them from an ecological viewpoint is still relatively recent.

Of equal significance are the coastal dunes bordering the shores of the northern hemisphere's continental land masses. It was with these dune areas that man first became involved—both in a practical sense and as objects of scientific inquiry. Man has been associated with the great subtropical deserts mentioned above since history began, but it was an equilibrium association: man did not attempt to extend his control over these areas; he needed to know only enough to get along with his environment—to survive.

But in the north, in the temperate zone of Europe, man and his civilization were expanding—building towns and tilling farms right onto the sandy seacoasts themselves. And where the pressure of civilization was the greatest, the destructive nature of the wind and sand interaction was forcibly brought to the attention of the people. The first recorded use of sand stilling vegetation was in 1307 on the coast of the North Sea. In 1567 sand dune reclamation was directed by the government of Holland, and by the 1700's major dune reclamation and conservation work was in progress along the coasts of France, Germany, Holland and Denmark.

Very good summaries of the history of sand dune use and conservation are given by Gerhardt (1900) for Germany, Boerboom et al. (1958) for Holland and Buffault (1942) for France. Olsson-Seffer (1910) presents a historical summary of research and conservation activity on European dunes, and his work is one of the first of its kind written in English. In it, he briefly reviews the major literature pertaining to both coastal and inland dunes of the world. It is not surprising that the greatest part of this work was accomplished by German and French investigators all through the last half of the 19th century. Most of it dealt with stabilization or descriptions of plants or plant communities. Very little of this European literature is available in this country.

Olsson-Seffer also gives brief descriptions of sand dune areas he personally visited during several years of travel. These include dunes on the east and south coasts of Sweden, the west coast of Russia, the Gulf of Finland, islands in the Baltic Sea, the north coast of Germany, the west coast of Denmark, small areas in Holland, Scotland and England, and the extensive dunes of the west coast of France. He mentioned briefly the dunes of the western and southern coasts of Australia, and of New Zealand, Hawaii, Guatemala, Mexico and the west coast of the United States (Santa Barbara, Monterey, San Francisco). Vegetation of these areas is described only as a listing of the plants he collected.

In another paper, however, Olsson-Seffer (1909) describes the conditions for plant life in these areas in terms of atmospheric, hydrodynamic, edaphic, topographic and historical factors. He was impressed with the similarity of conditions and vegetation of coastal sand areas, sharing with Warming (1909, p. 272) the conclusion that "shifting dunes in all lands show a strong general likeness, and that similar sand-fixing plants always occur."

Although Warming was speaking primarily of areas with which he was well acquainted (coasts of northern Europe, Greenland, Iceland), his general conclusions can be applied to all the temperate zones of the world. It would also probably hold for the maritime dunes within the tropical and sub-tropical zones with their distinct vegetation on active sand areas.

The term, maritime dunes, will be used in this review in referring to areas of active and stabilized sand along seacoasts. The sand is deposited on the shore by ocean current and wave action and is then blown inland by the prevailing winds. These areas will, of necessity, be confined to a relatively narrow strip along the immediate shoreline, and are considered distinct from inland or continental dunes which had their origins in much earlier geologic time and from different sources.

Examples of these latter include the alluvial dunes of the Hungarian lowlands of Europe, the great continental deserts that owe their origins to wind erosion of rock in dry climates, the sand hills of North Dakota and Minnesota laid down by ancient Lake Agassiz, and the extensive dune areas along the shores of Lake Michigan. These types of dune areas will be referred to only briefly in the following discussion.

This discussion will be a brief characterization of maritime sand dune regions and their vegetation as reflected in a review of the botanical and ecological research literature of approximately the last 65 years. It will attempt to sketch in a representative manner the extensive history and findings of European dune research; and give a picture of the location, importance and research status of maritime dune areas in the tropics, Asia, Oceania, and South America. The review for North America, essentially the United States, will be fairly complete, and will provide the introductory background for the main study of this dissertation: the Oregon coastal dunes.

Dune Forms and Terminology

It would be very difficult to describe dune systems and their vegetation without some understanding of the terminology used by workers in the various countries in referring to the physiographic features of the dune landscape. This terminology becomes confusing at times because of the various ways it is used, and a summary would be helpful.[1] Figure 1 is a diagrammatic presentation of this summary. Three general features are readily apparent: the beach, the areas of active sand and the dunes stabilized by vegetation.

The beach is the relatively narrow strip lying between the water's edge and the uppermost line of effective wave or tide action. Cowles (1899) divides it into lower, middle, and upper beach, the boundaries being determined by tides, wave action and vegetation. In some areas there is considerable vegetation on the middle and upper beaches, in others, very little. The lower beach is usually bare of plants except for algae. This strip is also known as the

[1] Discussion of the dune terminology will be developed around the excellent work on dune forms by Briquet (1923). A number of other sources were consulted: Behmann, 1930; Cooper, 1958; Ellenberg, 1963; Gerhardt, 1900, Harlé and Harlé, 1920; Kearney, 1901; Lemberg, 1933; Ringuelet, 1949; Salisbury, 1952; Warming, 1909; and Willis et al., 1959a.

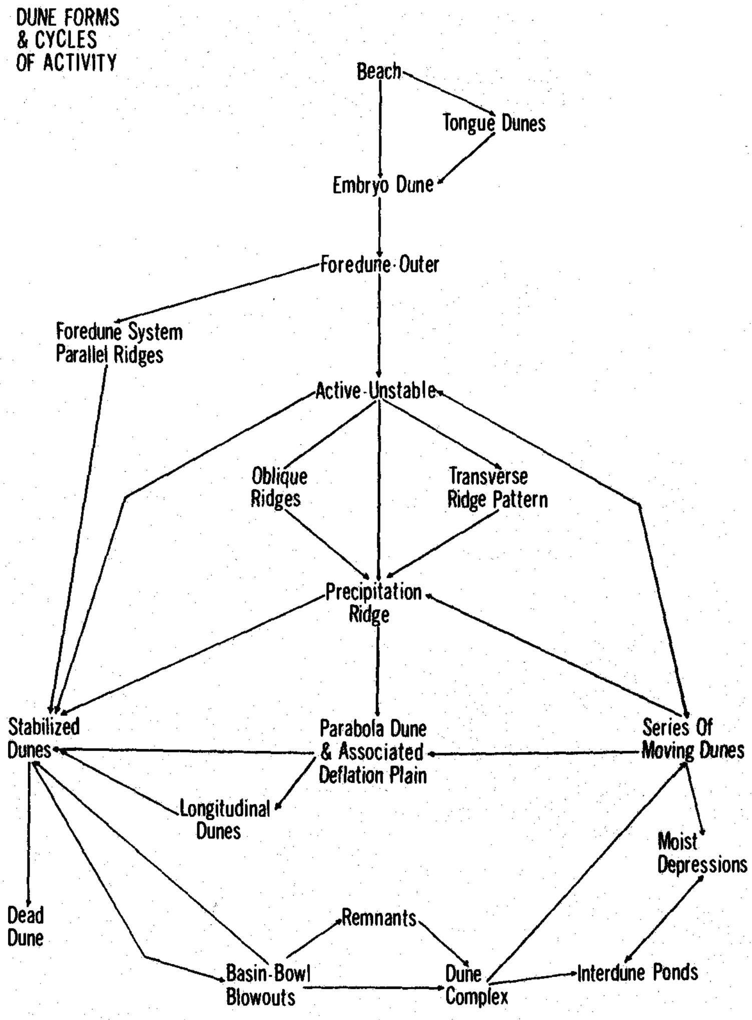

Figure 1. Dune forms and cycles of activity.
See text for explanation.

strand, sand strand, or littoral strip. In German it is the Strand, Spülsaum, Ufer or Küste; in French, littoral, plage or côte; in Spanish, playa maritima. A beach is always associated with a maritime dune system, but not necessarily restricted to it.

The initial dune forms are the small transitory tongues of sand formed on the beach when windborne sand is deposited around obstacles such as rocks, debris and annual plants (Zungenhügel, amas linguiformes).

Although usually relatively temporary, these tongue dunes could continue to accumulate sand around pioneer perennial plants. These embryo dunes (Embryonaldüne, dune embryonnaire) are located at or beyond the upper limits of wave action, forming the basis for the foredune (Primardüne, Vordüne, dune bordière), which results from the coalescence and building up of the embryo dunes along the shore beyond the reach of water action. With classic French imagination, Briquet (1923, p. 386) describes this line of dunes as "un cordon mamelonné."

These foredunes can develop into a successional series of parallel ridges (parallel ridge system, Vordünesystem, complex de dunes bordières), and are particularly typical of prograding shorelines. In regions of strong on-shore winds, these dunes slowly move inland, the rate and distance a function of many variables of vegetation, topography and climate. Such active dunes are given a variety of names in the literature, based either on their activity or on their color (mobile dunes, unstable dunes, white dunes, yellow dunes, weissen Dünen, Grasdünen, Wanderdünen, dunes blanches, dunes vivantes, dunes en vague and dunas vivas). The vegetation cover will vary from practically nothing on very active dunes to considerable amounts on those of less activity. The common European terms of "white dune" or "yellow dune" are based on appearance as determined at least partly by the amount and kind of vegetation. Lemberg (1933, p. 43) states:

> Als "weisse" Dünen werden in der pflanzengeographischen Dünenliterature Dünen definiert, deren Vegetation, hauptsächlich aus Psammophyten bestehend, licht genug ist, um den hellen Dünensand hervortretenzulassen and der Düne so ihr Farbengepräge zugeben.

As this vegetative cover becomes more dense, and as the pioneer plant species give way to the more permanent vegetation, sand activity ceases, and the dune is fixed or stabilized (grey dunes, festliegende Dunen, Graudunen, dunes fixees, dunes gris and dunas fijas). The grey dune is occasionally defined in terms of the developing soil layer under the permanent vegetation, but more frequently it refers to the general color of the vegetation cover—the heath—which is so common over northern Europe. Lembert (1933, p. 73) defines them precisely as dunes

> ...deren Pflanzendecke, aus gewissen Phanerogamen nebst Moosen and Flechten bestehend, so dicht ist, dass der Dünensand nicht mehr durchschimmert, und die so die "graue" Farbe der Düne hervorruft.

Under certain conditions of climate and vegetation, an iron pan (alios, Ortstein) forms under the developing dune soil, and the dune then becomes a dead dune (dune morte). More commonly, however, the next stage is rejuvenation or renewal of sand activity due to disturbance of the surface cover.

The activity begins with a very small break in the protective cover (Windriss) which is gradually enlarged. If there is no single dominating wind direction, this blowout becomes a more or less bowl-shaped hollow (Windmulde, cuvette d'erosion éolienne, caoudeyre). Under strong, unidirectional winds, these hollows become elongated basins (Windgraben). Where very many of these blowouts occur, there will develop high mounds or remnants (peaked dunes, Kupsten, crocs), and the entire area becomes a dune complex (aufgelöste Dünenlandschaft, dune confuse).

Under the influence of strong winds, these blowouts may join, resulting in a series of dunes moving with the wind. In between these dunes are low areas--ponds (lettes) if there is water standing on the surface; moist depressions (slacks, pannes) if free water is not on the surface, but the water table lies close to the surface.

Partial stabilization of these moving dunes, particularly along the two ends where sand activity is the least, brings about the formation of a parabola dune (Parabeldüne, dune parabolique). In this situation there is a differential movement of sand such that the center of the dune continues to move at a relatively rapid rate with the wind, the dune itself then tapering back as two arms in a rough parabolic arc to the points where the process began. The area between the arms and at the foot of the moving center is usually a low, flat moist plain (deflation plain, Erosionmulde). If movement continues until the sand supply is exhausted, all of the sand goes into the arms, the center disappears, and a pair of roughly parallel longitudinal dunes results (Strichdunen, dunes en trainees).

Where large quantities of moving sand, driven by strong, unidirectional winds, come up against a large, relatively uniform mass of vegetation (a forest), a dune builds up to windward of the obstruction. After the sand reaches a certain height, it begins to spill over the leeward face of the dune into the vegetation below, initiating dune advance and invasion of the vegetation. Such a dune is called a precipitation ridge.

Parabola dunes may also result directly from a break in established vegetation. If there is a strong unidirectional wind and a large supply of sand—a precipitation ridge—to windward of the vegetation, a break or weak point in the vegetation front may bring about the differential movement of the precipitation ridge which eventually broadens into a head and two arms with a parabolic shape as described above. A deflation plain also develops at the windward base of the dune. Thus two contrasting actions bring about parabola dune formation: in the one case partial vegetative stabilization brings about the formation of the dune; in the other, partial destruction of the vegetation initiates the process. (See also page 85 and Figure 5.)

The features most frequently mentioned with regard to the vegetation are the strand, the foredune, the active dunes, the fixed or stabilized dunes and the moist depressions. The foregoing discussion should help in understanding the relationships among these features of the dune landscape.

Europe

It is fitting to begin this discussion with the area where dune research began early and has been most extensive. Germany, France and Holland all share this distinction. The Dutch were probably the earliest to begin work on the dunes, the Germans the most productive as regards published literature and the French the most ambitious in actual dune work. A considerable amount of literature exists on the Scandinavian coastal dunes, all published in German and Swedish. The English have been the most recent to recognize the value of dune research. Their work appears to be of high quality and is increasing in scope. Figure 2 is a map of Europe showing the location of some of the sand dune areas referred to in this section.

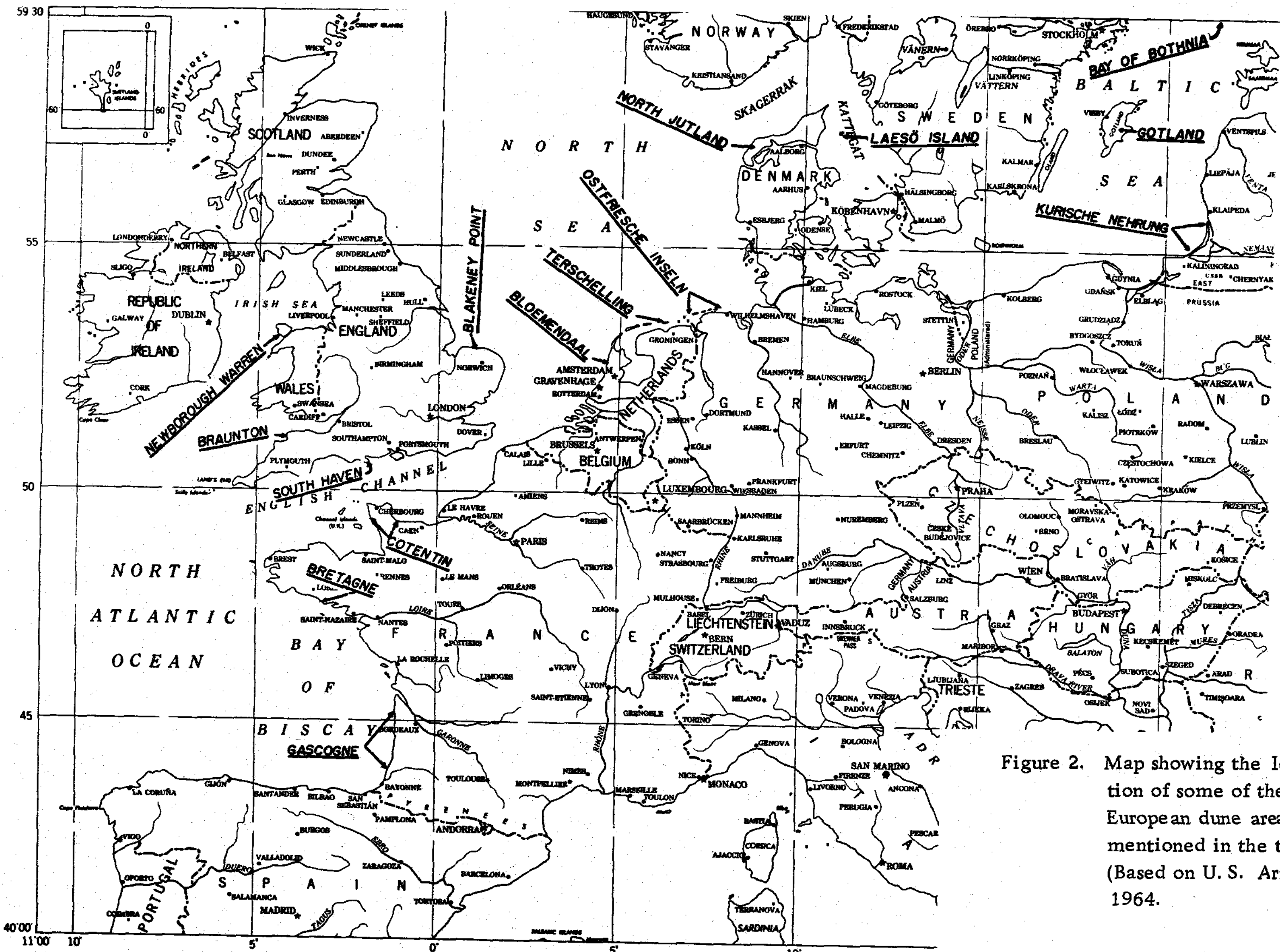

Figure 2. Map showing the location of some of the European dune areas mentioned in the text. (Based on U. S. Army, 1964.

Germany

Probably one of the most intensively studied dune areas in Europe up to 1900 was the "Kurische Nehrung"--the long (80 km.) narrow spit with large moving dunes located on the Baltic Sea in north Germany (Lat. 55° to 55° 30'N.) near Königsberg (Kaliningrad). This is considered the largest moving sand dune region in Europe and Gerhardt's (1900) important and comprehensive book is based to a large extent on knowledge and experience gained in this area. Only one-third of the book is devoted to a discussion of the dunes themselves: distribution, dune materials, dune forms, coastal currents, movement of dunes, and cultivated and native flora of the dunes. The remainder is given over to the "Dünenbau"—literally the management of the dune areas—and covers every method known up to that time of conserving, stabilizing, reclaiming, and cultivating sand dunes and sea shores. The history, morphology and vegetation of the dunes of the Kurische Nehrung have been described in detail by Paul (1944, 1953). He was able to trace dune activity and reclamation work (afforestation) back to 1675, and he constructed a series of maps showing changes in the landscape since that time.

A description of the plant communities[2] on the north German

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[2]In naming component species of a dune community, only the most characteristic (as indicated by the author) will be used. The

coast and islands of the North Sea (East Frisian Islands) is given by Ellenberg (1963). The strands is characterized by species[3] of Atriplex, Cakile maritima Scop., and Salsola kali L.; the foredune by an Agropyron junceum (L.) P. B./Honckenya peploides L. community; and the active dunes by a community of Elymus arenarius L., Ammophila arenaria (L.) Lk. and Festuca rubra L. The grey dunes are essentially stabilized and support a rich flora. Although including species of the previous types, they are predominantly characterized by Corynephorus canescens (L.) P. B., Carex arenaria L., Hypochoeris radicata L. and Tortula ruralis plus species of Viola, Hieracium, Lotus, Cerastium and many mosses. As was noted earlier, it is the cryptogamic vegetation that gives these dunes their greyish-green color from which their name derives. If these dunes are disturbed by wind erosion, a heather type (Braundünen) develops which is characterized first by Empetrum nigrum L. and then by Calluna vulgaris (L.) Hull.

The active dunes can develop directly into shrub communities (Buschdünen) of Hippophaë rhamnoides L. and Salix repens L. With

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names of the various vegetation units used in the complex taxonomic heirarchy of Braun-Blanquet (1932) are omitted since they would be useful only to one thoroughly familiar with this system.

[3]Authority for species names will be indicated in this and the following chapter where they were included in the cited author's work. Frequently the epithet authority was not included nor was any reference made to a flora which might have been used as the basis for naming the species of plants encountered in the study.

further development these can become dune forests (Dünenwälder), Quercus spp. occurring on the drier sites and Pinus silvestris L. on the more mesic. The latter species has become established mostly as the result of planting operations, but natural stands are found.

The dune valleys (Dünentäler) are the moist depressions between the dunes and usually have a very rich flora. Species of Juncus, Carex, Lycopus, Ranunculus and Drosera are among those characteristic of these locations.

The development of the coastal dunes as reflected in soil formation was studied by Hollstein (1931). He was able to determine a definite relationship between the degree of soil formation and the type of vegetation present, and he used this information as a basis for postulating the age of the dune systems as being between eight and ten thousand years old. Most of these sands and the soils developing from them are acid in reaction (pH 5. 0 to 3. 2).

Although the recent German literature on the sand dunes by no means approaches in quantity that of the last half of the 19th century, there is a considerable number of good papers in print, many of which are unavailable in this country. What is available is widely scattered and often difficult to obtain.

France

This unavailability is also true of the French literature, but to a lesser degree. The coastal dune areas of France are more extensive than those of Germany. Economic and scientific interest began about the same time in both countries, but the French have been much more active in the current century.

There are small dune areas along the Mediterranean coast of southern France (about Lat. 43° 30'N.), but these are not very important. More significant dunes extend along the English Channel from the Belgian coast in the north down to and including both west and east sides of the Cotentin Peninsula (Lat. 49° 30'N.), and then again on the southern coast of Brittany. The most extensive dunes are those bordering the Bay of Gascogne and extending far inland as a sandy plain known as "Les Landes" (Lat. 44° to 45° 30'N.).

These dunes rival the Kurische Nehrung in magnitude and importance, and much has been written of them including a very thorough history by Buffault (1942). In it is discussed the geologic origins of the area, stabilization programs, management practices by the government and natural history. The area is divided into "ancient" and "modern" dunes. The former are inland dunes of prehistoric origin, well stabilized with forests of pine. The latter include the bare, moving dunes extending in a strip for 240 km. along the coast with dunes up to 100 m. high. This belt varied in width from four to eight km. during the height of its activity in the 17th and 18th centuries. In 1787 the French government initiated a program of stabilization which was completed in 1864. The area is now managed by the government for recreation and the harvest of forest products such as resin, lumber and firewood.

Harlé and Harlé say of these dunes (1920, p. 56):

> L'aspect intérieur des dunes, vues de l'un des sommets de la châine orientale, et en regardant vers la mer, offre l'image du chaos et d'un inexprimable désorde... C'est un des plus beaux et des plus étonnants spectacles qu'il soit donné a l'homme d'admirer!

They discuss the morphology and origin of the Gascogne complex and also describe "Les Étangs", the chain of large, dune formed lakes along the inner margin of the dunes.

The vegetation on the dunes in Brittany is typical of the dunes over most of France (Berghen, 1958). The strand is characterized by Salsoli kali, Agropyron junceum, and Atriplex spp. while the foredunes have a varying stand of Ephedra distachya, Euphorbia paralias, Agropyron junceum and Ammophila arenaria. This last plus other species such as Festuca rubra and Carex arenaria are found on the mobile dunes. The grey or fixed dunes have a 80 to 100 percent cover of cryptograms—a "tapis muscinal fermé"—consisting of species of Camptothecium (most abundant), Barbula, Tortula and

Cladonia. There are also many grasses (but no Ammophila arenaria) and herbs.

Most existing forests are the result of plantings, particularly the Pinus pinaster stands of Gascogne and Brittany. In drier areas, various species of Quercus are dominant, and in moist depressions there are Populus, Ulmus and Alder. On the dunes of the island of Oléron, Duchaufour (1948) describes a forest succession beginning with Salix and Ulmus and culminating in Quercus. Shrub undergrowth, which is very dense where it is not cleared away for fire prevention purposes, consists of such species as Sarothamnus scoparius, Erica scoparia and species of Daphne, Lonicera, and Ligustrum. Erica is one of the few heather species found on the French dunes.

The vegetation of the pannes (moist depressions) usually terminates in a stand of Hippophaë rhamnoides and Salix repens (DuVigneaud, 1947), although there are many variations such as dense thickets of Ulex europaeus and Sarothamnus scoparius.

In spite of the geographical spread of France's dune areas, Turmel (1952) found them remarkably similar with respect to vegetation and soil. Studying three general habitats—beach, mobile dunes and fixed dunes—on each of five dune areas (including the Mediterranean coast), he found that all were calcareous (13 to 44 percent calcium carbonate), pH ranged from 7. 6 to 8. 4, and little or no organic matter had accumulated. Certain groups of plants are somewhat sensitive to high alkalinity and will show variations in species present (such as in lichens and mosses) or may almost disappear (as the heather species). Calcareous dunes and their vegetation are further discussed in the section on the dunes of Great Britain.

There are dune areas along the Belgian coast, but these are usually considered as being continuous with the French dunes, both in dune morphology and vegetation. This similarity is noted by Briquet (1923, p. 388) who also cites a very early work, published in 1908, treating only the Belgian coastal flora.

Harlé and Harlé (1920, p. 133-135) makes some comparisons between the dunes of Gascogne and those of other locations in Europe. In Portugal, between Ovar and Nazareth, there is a belt of dunes 160 km. long and three to nine km. wide, and not as high as the French dunes. In Spain, on the south Atlantic coast, between Rio Tinto and Guadalquivir, there is a belt of low dunes perched on a substratum which rises above sea level. Little has been written on dunes in these areas, and it is not possible to ascertain their full extent.

Holland

Although the Dutch have been more involved with their dune areas over a longer period of time than other countries, their published literature for the most part seems to be rather recent. The Dutch first began work on their dunes in the 1300's. Since that time the dunes have become increasingly important in the lives of the people. One of the earliest published references to these dunes is Braun's (1911) study of the developmental history of the coasts and dunes of the Low Countries. A geomorphological analysis of the dune landscape of one of the West Frisian islands, Terschelling, was made by Van Dieren (1934) who also included a study of the vegetation.

Boerboom, et al. (1958) have put together a comprehensive study of the coastal dune areas of Holland including a detailed study of the 1600 ha. of dunes that make up the watershed of The Hague (Lat. 52° 7'N.). The effect of both past and future stabilization plantings was analyzed with respect to protection of the coast, watershed (these dunes are a water source for The Hague, a city of over one million population), recreation, fauna and flora and forest products. The plant associations were mapped at a scale of 1:5000. Also included was a history of laws and practices used for dune stabilization and wild life conservation from the 14th century to the present.

Exhaustive plant inventories made on this watershed at the time water pumping began in the early 1920's were compared by Boerboom (1958a) to surveys he had made in the early 1950's. As a result of the dropping water table, species of wet habitats (such as drainage courses) gradually disappeared.

When the water table of the area was raised in 1955 by the infiltration of water from the Rhine River, Boerboom (1958b) was able to follow the corresponding disappearance of certain dry habitat species and the reappearance of a more hydrophytic vegetation.

Many ecological studies of the Dutch dunes are characterized by the delimitation of vegetation zones which generally run parallel to the shore and the successive rows of dune ridges.[4] Kraft (1958) designated the zones on the calcareous dunes at Bloemendaal according to the associations of plants characterizing them:

Aa - Littoral strip of beach and foredune: _Ammophila arenaris_ and _Elymus arenarius_. _Berberis vulgaris_ comes in on the sheltered inner side of the foredune.

R - Blowout (erosion) area of severe relief: _Rubus caesius_ with _Festuca rubra_, _Ononis repens_.

Rr - Small dune valleys: _Salix repens_, _Ligustrum vulgare_.

Rs - Large, low flat areas: Species of _Taraxacum_, _Galium_.

Hh - Long dune ridges further inland: _Hippophaë rhamnoides_ and _Calamagrostis epigeios_. Has

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[4] Parallel dune ridge systems are characteristic of prograding shorelines. Dunes are also found on relatively stable and eroding shorelines. In the latter case parallel dune ridge systems are not common. See page 82.

intervening valleys of Betula and Populus, Sambucus niger, Ligustrum and very poor herbaceous layer.

Hb - Flat, large interior valleys: Hippophaë rhamnoides, Berberis. The thickest vegetation of the dune area. Soil development begins.

Kb - High dune ridge of inner edge of the dune complex: Koeleria albescentis, Berberis, scattered trees, shrubs.

A series of ten more or less well defined zones was described by Boerboom (1957) on the dune landscape near The Hague. These zones run parallel to the shore and inland for 3200 meters. Very generally described, they are: (1) First row of dunes, Ammophila, 0-35 m; (2) Depression between first and second row of dunes, Sambucus niger, 35-35 m. ; (3) Second row of dunes, extremely variable vegetation, 45-140 m. ; (4) Zone of Ligustrum, 140-260 m. ; (5) Zone Eryngium, maritimum, 200-330 m. ; (6) Zone of Gentiana, 330-1000 m. ; (7) Thicket of Rhamnus, 1000-1500 m. ; (8) Zone of Populus nigra, 1500-1800 m. ; (9) Zone of Rhamnus and Populus tremula, 1800-2250 m. ; (10) Zone of Populus canescens, 2250-3200 m.

Sand dunes are very prominent features of the Dutch coast line, and the vegetation is essentially similar on all of them. Published ecological accounts are recent (mostly since 1950) and reflect the work of only a few individuals.

Scandinavia

Almost all of the lands bordering on the North Sea and the Baltic Sea, including the islands in these bodies of water have, to some extent, sand dunes along their coasts. Investigations of these areas were carried out mostly by German and Swedish botanists and range from very general to very detailed and comprehensive. Very few are written in English and most are not readily available in this country.

Studies of dune areas on the coasts of North Jutland (Denmark) are not numerous, and usually are part of other, more extensive works. Böcher, *et al.* (1946) have analyzed the plant communities on the older calcareous dune deposits in Himmerland, on the north coast of Jutland. They also discuss the autecology of the various plant species they feel are indicators of the calcareous habitat.

As part of his comprehensive work on the ecology and geography of Danish vegetation, Böcher (1941) has made a detailed study of the dunes and lichenheath of Laesö Island, located in the North Sea off the east coast of Denmark (Lat. 57° 15' N.). The cryptogamic vegetation is well developed on this island, and the following communities or zones were distinguished:

1. Strand: Cakile maritima, Salsola kali
2. Primary dune (embryo dune): Agropyron junceum. No lichen. pH 7. 3.
3. Coastal dune (foredune): Elymus arenarius, Ammophila arenaria with Festuca rubra. No lichen. pH 7. 3
4. Dune valley: F. rubra, Ammophila with Viola tricolor, Hypochoeris radicata, Sonchus arvensis, Honckenya peploides, Hieracium spp., Corynephorus conescens. No lichen. pH 6. 7
5. Second (older) dune series (white or moving dunes): Ammophila, F. rubra, spots of Hypnum, Tortula, Brachythecium, few Cretaria. pH 6. 6
6. Dune valley: Less F. rubra, more Corynephorus, Sedum spp. , Hieracium, Brachythecium, Cladonia rangiformis. pH 6. 3
7. Third dune series (lower, grey dunes): Corynephorus, Cladonia, Cretaria. pH 5. 6 to 6. 0
8. Festuca ovina - Hypnum cupressiforme
9. Dune heath (Düneheide): Empetrum, Calluna. pH 4. 2 to 6. 0
10. Blowouts (Windbrüchen): Lichens, then Empetrum.
11. Dwarf shrub heath (Zwergstrauchheiden): Heath with

small Alnus, Populus, and Betula.

These dunes have initially only slight amounts of calcium carbonate, and this is quickly leached out, creating a favorable soil habitat for the lichenheath community.

On another island, Gotland, in the Baltic Sea, 100 km. south of Stockholm (Lat. 57° 30' N.), Englund (1942) studied the distribution of plants along the shore. This work is very detailed, having taken some 14 years to complete, and includes distribution maps for each of 165 species. He distinguishes five shore types: rock, gravel, sand, meadow and seaweed. These are divided into zones from the sea toward the interior. The zones in the sand type, with their associated vegetation, are:

1. Hydrolittoral (lowest limits of exposure): Occasional algae.
2. Hygrolittoral (area between normal low tide and extreme upper limit of tide action):
    a. Lower: Ephemeral phanerogams such as Cakile and Salsola.
    b. Upper: Agropyron junceum (halophilic), some Elymus arenarius. Ammophila at upper limits, beginning of heath vegetation.
3. Supralittoral (above highest tides): Heath vegetation.
4. Inland (beyond influence of the sea): Pine forest.

The information is summarized in a table listing 189 species, including for each frequency data for shore and inland locations; relationship to cultivation (whether tame, escaped, dependent on man for dissemination, etc.) on the shore and inland; occurrence in the various shore types and influence of the environmental factors of salt, water and sea-weed fertilization. Also included is a discussion of the role of habitat factors, cultivation and natural dissemination in the distribution patterns of the species included in the table.

Although primarily interested in the dipterous fauna of the marine shore dune ecosystem, Ardö (1957) used transects and quadrats to make vegetation maps of dune areas in western Norway, southwest Sweden, and the west coast of Jutland. He particularly emphasized the importance of the "subsoil green algal, cyanophycean and bacterial vegetation" (p. 36) on the high beach environment. The descriptions of plant communities are similar to those already presented.

The active sand areas of the Finnish coast were studied in great detail by Lemburg (1933, 1934, 1935). The first part of this study (1933) describes the various topographic features encountered in the dunes, and the vegetation succession which takes place on them, considerable emphasis being placed on the role of cryptogams in the succession sequence. Also noted was the similarity of the vegetation of these dunes to those of other parts of Europe, the chief difference being a smaller number of species. Many of the plant species occurring on the dunes are discussed in detail: their anatomy, habitat requirements, growth forms, dissemination, distribution, competition, and so on.

The usual dune formations are found in these areas, and their vegetation is summarized as follows:

1. Beach and embryo dunes: _Salsola kali_ L., _Carex goodenowii_ L., _Agrostis stolonifera_ L., _Hockenya peploides_ Ehrih., _Agropyron repens_ PB.
2. Mobile dunes:
   a. Primary: _Ammophila arenaria_ Lk., _Elymus arenarius_ L., _Festuca rubra_ v. _arenaria_ Osbecki, _F. polesica_ Zopal.
   b. Secondary: _Festuca ovina_ L., _Calamagrostis epigejos_ Roth, _Carex arenaria_ L.
   c. Later entrants: _Rumex acteosella_ L., _Viola canina_ L., _Achillea millefolium_ L., _Leontodon autumnalis_ L., _Hieracium umbellatum_ v. _dunense_ Reyn.
3. Fixed dunes:
   a. Mosses: _Ceratodon purpureus_ (L.) Brid., _Polytrichum piliferum_ Schreb., _Rhacomitrium canescens_ (Timm) Brid.

b. Lichens: Cretaria spp., Cladonia spp.

c. Phanerogams: Initially most from the mobile dunes, which gradually disappear as a complete, thick cover of cryptogams becomes dominant. Scattered clumps or individuals of Pinus silvestris, Alnus incana Moench, and Empetrum nigrum L. may be seen.

4. Shrub dunes: Salix repens L., Ledum palustre L., Empetrum nigrum, Arctostaphylos uva-ursi Spr., Juniperus communis L., Alnus glutinosa Gaertn., A. incana.

5. Depressions: Algae, Bryum spp., Carex spp., Juncus spp., Equisetum arvense, Agrostis stolonifera, Festuca rubra L., Salix repens, and Alnus, these species varying in their occurrence according to moisture conditions.

The second part of the study (1934) records the general features of the marginal dunes (Randdünen), which result from a series of small moving dunes coelescing at the inner margins of the dune areas and becoming vegetated. Successive dunes can be formed, creating a series of ridges parallel to the shore. Forest develops on the oldest of these (innermost) and commonly consists of Alnus incana, a tree which can withstand burial by sand. Betula, Populus and Salix also occur, as do Pinus silvestris and Picea abies. The ground layer is usually moss and lichen and a few phanerogamic species.

The final part of the study (1935) is a description of the location, size and vegetation of 39 individual dune areas, ranging from Lat. 59° 49' N. to Lat. 65° 40' N. Lemberg realized the value of such precise descriptions to future study for he specifically states (1935, p. 5): "Die Bedeutung des dritten Teils dieser Studien liegt also darin, dass sie eine Unterlage für Künftige Untersuchungen der Flugsandgebiet darstellt." Even today, few investigators of sand dune phenomena have this attitude.

The most northerly dune area described by Lemberg, that at Turonhiekka at the north end of the Bay of Bothnia (65° 40' N. Lat.), showed the following zonation (from the shore inland):

1. Strand and embryo dunes (0 to 10 m.): Honckenya peploides, Elymus arenarius, Festuca rubra.
2. Mobile dunes (10 to 60 m.): Active dune formation by Elymus and other species of the first zone; also Empetrum, Tanacetum, and small mats of Polytrichum, Ceratodon and Rhacomitrium.
3. Dune heather, fixed dunes (60 to 230 m.): Complete cover of mosses and lichens of species already noted. Scattered individuals of previous zones and small

shrubs of Salix, Betula and Sorbus.

It is apparent from the foregoing discussion that the Scandinavian dune areas are all fairly similar, primarily characterized by the extensive development of the heath and lichen communities typical of acid soils in northern climates. The dunes of the north German coast also appear to fit into this category. Although some area are permanently calcareous (where underlain by a limestone substratum such as the one at Himmerland, Denmark, described by Böcher, *et al.*, 1946), alkalinity plays at most only a small part, and then only in the initial stages on fresh beach sand. The dune soils rapidly become acidic in reaction.

This is in strong contrast to the dunes of France and Holland where high concentrations of calcium carbonate are built up through the accumulation of the shells of marine organisms. An alkaline reaction is maintained in the soil for great lengths of time. Although it appears that these two types of dune systems—acid and alkaline—are separated geographically, it is not a rigid separation, since they are both found in the British Islands.

Great Britain

Although there are a great number of dune areas in the British Islands, some of them quite striking, it appears they were largely ignored prior to 1900, the literature at least indicating this being so. However this situation changed early in the twentieth century. As Tansley notes (1947, p. 130): "The development of modern ecology in Britain coincides almost exactly with the present century, though the pioneer work was begun in the closing decade of the last." Tansley goes on to attribute this upsurge of interest, and its development in terms of emphasis on successional studies, to Clements of the United States who "had a considerable effect on British work", and whose book, Plant Succession, "...probably influenced British ecology more than any other publication since the foundation works of Warming and Schimper." (p. 133, 137). Admiration for the work of Cowles (1899), another American, is evident in many writings, and dune research naturally shared in this rise of ecological interest.

The change began with a trickle of studies on widely separate dune areas, and has gradually built up to an almost continuous stream of information dealing not only with the many separate dune areas of the islands, but also with intensive studies of single areas. Because of the amount of material available, only the most important and representative will be discussed.

The first general description of British dune areas is contained in Tansley's (1939) book on the vegetation of the British Islands. This description is relatively brief. A more comprehensive treatment is presented by Salisbury (1952), taking in the dune habitat, plant communities and descriptions of individual plant species. He also gives a table (p. 285) listing 30 major dune areas and selected climatic and physical characteristics of each.

The features of the dune landscape are similar to those already discussed. The following description is a general one which can be considered characteristic of the British Islands (Lat. 50°-55°N.) as a whole (Salisbury, 1952).

Strand and embryo dunes. Here are found the typical seashore plants: *Salsola kali* L., *Cakile maritima* Scop., *Atriplex* spp., and *Agropyron junceum* (L.) Beauv. —all tolerant of ground water salinity and the severe climatic conditions of the habitat. Above high tide line, they form the small embryo dunes and beginnings of the foredune system.

Foredune. *Agropyron* and *Ammophila arenaria* (L.) Link. are the dune builders here, the latter abundant where salinity is very low or absent. Also present are *Elymus arenarius* L. and *Euphorbia peplis* L.

Yellow (or white) mobile dunes. These represent later stages of development. Vertical accretion of sand has slowed and the climatic conditions are less severe. Most abundant still is *Ammophila*, but such plants as *Festuca rubra*, *Senecio jacobea* L., *Galium* spp. *Leontodon* spp., *Hypochaeris glabra* L and many others, as well as lichens and mosses, begin to appear. Salisbury (1952, p. 244) lists 73 species of phanerogams for these dunes.

Grey fixed dunes. This stage is characterized by the gradual disappearance of Ammophila and the corresponding increase in the lichen and moss cover. Mosses such as Tortula, Brachythecium, Ceratodon, Hypnum and Bryum usually are more abundant initially, the lichens, mostly of the genus Cladonia, becoming more numerous later. Peltigera appears very late. The habitat becomes so modified that the specialized dune plants become unimportant, while a rich flora of more common species develops. Salisbury (1952, p. 249-255) lists over 250 species of phanerogams from this habitat.

Moist depressions. These interdune areas may start and end with a variety of community types. The initial species are usually Salix repens, Juncus balticus, J. acutus, Plantago coronopus and others. In some areas a sort of wet meadow develops consisting of species of Aira, Drosera, Trifolium, Rumex, Ranunculus, Juncus and many others (Good, 1935). If sand accumulates, the site becomes drier and more grasses enter, giving rise to a grassland of Agrostis stolonifera, Festuca rubra, Carex arenaria, Prunella, Hypochaeris and mosses such as Dicranum (Tansley, 1939). Occasionally Pteridium will invade these dune pastures (Gimingham, 1951). It is also possible that a wet heath-scrub community dominated by Erica tetralix may arise. Betula pubescens, Carex arenaria, Potentilla, Juncus and Spagnum are associated with this community

(Steers and Jensen, 1953).

Dune heath. Both the grey dunes and the wet sites can develop into a dune heath of *Calluna vulgaris* Salisb. and *Erica tetralix* L. In some places a dune scrub of *Ulex europaeus* L. develops, and will replace the ericoids once it is successfully established. The *Calluna* heath appears to be the ultimate vegetation of the British dunes, although Ranwell (1960a) is of the opinion that *Calluna* is a sub-climax due to grazing and wildlife influence. Apparently forests existed on these areas centuries ago.

Forests. Tansley (1939, p. 852) states that natural forest communities do not occur on the fixed dunes due either to the severe winds or to lack of seed parents. Plantations of *Pinus silvestris* and *P. pinaster* have been made and are successful; and in some places these trees have begun to spread naturally.

Calcareous dunes. The reaction of the soil on the dunes is determined first of all by the type of parent material of the sand, and secondly by the addition (or absence) of calcareous material such as sea shells, and finally by the processes of soil development (build-up of organic matter, leaching, etc.). The most common situation is one in which there is a slight accumulation of calcareous animal remains on the beach and foredune, and a resultant pH value slightly above neutral. With time and soil development, this drops rapidly into the acid range. Occasionally no sea shells are deposited on the beaches, and the sands are acid (Salisbury, 1952, p. 285; Hepburn, 1945). Salisbury (1925) estimated that it took about 300 years for all the calcium to be depleted. By working out a rate of depletion he attempted to estimate the ages of the various dune ridges at Southport, Lancashire.

Sometimes conditions of wind and ocean current supply great amounts of calcareous materials. The Isle of Harris in the Outer Hebrides has a highly calcareous sand (48 to 70 percent calcium carbonate) consisting mostly of finely comminuted shell fragments. And because of constant resupply by high winds, this proportion does not decrease very much with time (Gimingham, Gemmel and Greig-Smith, 1948). Hepburn (1945) feels that the high pH (8.0 to 8.5) of the sand of a dune area on the Camel Estuary, North Cornwall, was the result of an abnormally high population of snails. On the beach at Blakeney Point, Norfolk, Salisbury (1922) noted a drift line accumulation zone which was nine inches deep and over a foot wide of the shells of the mollusc Paludestrina stagnalis.

The dunes at Braunton, North Devon, have sands formed from limestone parent material averaging about 15 percent calcium carbonate. These dune soils are permanently alkaline (Willis, et al., 1959a).

The vegetation of calcareous dunes differs somewhat from that of non-calcareous dunes. The acid soil preferring ericoids are absent and different species of phanerogams and cryptogams appear. Instead of changing to grey, fixed dune and then heath, the calcareous yellow dune will develop into a dune scrub of Rubius caesius, Ligustrum vulgare, Ononis repens and Rhamnus sp. —species already noted on the calcareous dunes of Holland (Willis, et al., 1959b). Mosses are usually more abundant than the acid-favoring lichens, though one moss, Brachythecium, is totally absent, its place being taken by Camptothecium, a moss restricted to calcareous soils (Gimingham, 1951). In her unique study of the effects of dune maturation on the fungal population of the soil, Brown (1958) found that the acid and alkaline environments had distinct microfloras.

Brown's study on soil fungi is somewhat typical of many of the types of work done by British ecologists on their sand dune areas. Even the earliest studies emphasize the environment and its relationship to vegetation succession. For example, in an early study on the dunes at Kenfig, South Wales, Orr (1912) records the principle plant communities in relation to their habitats on sand deposited in relatively recent times. Hartley and Wheldon (1914) describe the vegetation zones on the Isle of Manx, taking note of the extreme aridity of the area. Soil analysis and detailed vegetation maps accompany the study of Marsh (1915) on vegetation succession of the maritime regions of Holme-next-the-Sea, Norfolk. Using maps and records dating back to 1797, he was able to reconstruct a historical picture of shoreline, dune and vegetation features.

On some areas, study began early and continued to the present. Blakeney Point in Norfolk, comprising sand dunes, salt marshes and shingle banks, was set aside as a Nature Reserve around 1913. Oliver and Salisbury (1913) published a handbook summarizing the vegetative, topographic and historic features of the area. It was also described by Oliver (1913) and Rowen (1913), both of whom noted the damage to the dune vegetation by feeding rabbits. The ecology of the lichens and bryophytes of Blakeney Point was first studied by McLean (1915) and later by Richards (1929). The soil of the area was described by Salisbury (1922) who related development to plant succession, and also set up a field laboratory in the area. More recently, White (1961) noted changes in the vegetation that had taken place following a reduction of the rabbit population in 1954.

Rabbits had been raised by the farmers for centuries and they were frequently grazed on the dune vegetation. When their economic importance waned, they became wild and increased greatly in numbers. In early 1953 an epidemic of myxomatosis, a disease fatal to the rabbits, started in northern Britain, and by 1954 had spread over the entire country, virtually wiping out the rabbit population. At Newborough Warren, Anglesey, a dune area that carries its association with rabbits in its name,[5] Ranwell (1960b) noted that previous to the epidemic some 14, 000 animals a year were being killed without damage to the population. In the years following 1954, the year the disease struck at Newborough Warren, only 30 to 50 animals were being killed annually. Ranwell had anticipated the effects of the disease in carrying out "pre-disease" vegetation surveys which he continued to study in the following years.

Other studies on the Newborough Warren dunes include the movement of vegetated sand dunes (Ranwell, 1958); the dune system, habitats and soil development (Ranwell, 1959); and the plant communities and succession cycles of the dune vegetation (Ranwell, 1960a).

Another well-studied area is the dune system at Braunton, North Devon. It was first noted by Watson (1918) who emphasized the cryptogamic vegetation. Not until much later were detailed studies undertaken. Willis, et al. (1959a) first described the topography, soils, climate, water table and drainage and methods of vegetation research. The next step was a detailed study (Willis, et al., 1959b) of the plant communities and their place in a postulated successional cycle. Willis and Yem (1961) analyzed the mineral nutrient status of the dune soils and how it affects plant growth.

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[5]Warren: an area especially of uncultivated ground for the breeding of rabbits. Or, a place privileged by prescription or grant from the king for keeping any of various animals (as hares, conies, partridges or pheasants). (Gove, 1961)

This study was extended when Willis (1963) observed the results of adding fertilizers to these soils. Very detailed investigations of the differences in water relations of dune slopes and moist depressions was carried out in this area by Willis and Jefferies (1963). Three physiological plant conditions—water deficit, transpiration rate and stomatal aperture—and five environmental factors—soil water content, air temperature, air humidity, light intensity and rate of evaporation—were measured every hour from dawn to sunset in mid-June. They attempted to relate these differences in water relations to the ecological distribution of the plants.

Studies on South Haven Peninsula, Studland Heath, Dorset, include historical physiography with maps from 1607 to the present (Diver, 1933); survey of the plants and animals (Diver and Diver, 1933; Good, 1935); lichen ecology (Alvin, 1960); and dune soil development (Wilson, 1960). Sand erosion and vegetation development have been studied on the dunes at Breckland (Farrow, 1919; Watt, 1938); and Wright (1955, 1956) noted soil profile development in the sand dune soils of Culbin Forest, Morayshire, an area subjected to stabilization work for many years.

Although the foregoing account of the British sand dunes is lengthy, it serves to show how ecological interest in one specific area—the sand dunes in this case—began with essentially simple floristic studies and advanced and branched out to very detailed investigations. Moreover, there was no urgent need here for stabilization and reclamation, the driving forces for the initial interest in dunes on the Continent. Thus the interest becomes one of pure knowledge: the idea of studying something simply to extend knowledge, practical considerations and applications being of secondary importance.

Furthermore, as will become apparent, maritime dune research has had its longest history and most extensive development in Europe. Much of what has been done in other parts of the world, except North America, has either been carried out by European botanists or has been directly influenced by them.

Africa

The vast interior deserts of this continent, particularly the Sahara of the north, have attracted considerable attention. Walter (1962) presents an excellent discussion of these areas, as well as the other desert regions of the tropical and subtropical zones of the world.

Information on shore dune systems, however, is scarce, probably because of a lack of interest in these areas. They are not as spectacular as those in Europe, and, for the most part, pose no serious threats to the people or economy of the land. The dune vegetation of the south Mediterranean coast is not unlike that further north, although shifts toward species of hotter and drier climates are apparent.

On the Sahel de Sousse, on the east coast of Tunisia (Lat. 35 to 36° N.), the most important beach plant is Salsola kali, while initial dune formation is brought about by Agropyron junceum and Sporobolus pungens. Ammophila arenaria is also present on the foredunes along with species of Imperata and Aristida. Development is toward a prairie vegetation of Vulpia uniglumis, apparently with no shrub or forest stage in this region of hot, dry summers and annual precipitation of only 400 mm. (Burollet, 1927).

This change in species composition is more marked on the eastern Mediterranean dunes. Zohary and Fahn (1952) studied the mobile sands along the coast of Israel and Egypt, an area of winter rains and total annual precipitation of 350 to 800 m. The soil is calcareous, increasing from 2 percent calcium carbonate in the north to 11 percent in the south. The general vegetation zonation included:

1. Beach belt: Ipomaea littoralis, Salsola kali L.
2. "Frontal" foredunes (embryo dunes): Sporobolus arenarius, Lotus creticus.
3. Foredune: Ammophila arenaria, Cyperus conglomeratus Rottb. (in north). As go south, Ammophila is replaced by species of Panicum and Aristida.

4. Rear dunes (moving dunes): Artemisia monosperma Del., Cyperus mucronata.

No mention is made of fixed dunes, the whole area apparently being in a state of high mobility.

A tropical dune area in Ghana (Gold Coast, Lat. 5°N.) is described by Morton (1957). The mobile dunes are vegetated by Scaevola plumiera Vahl. and Sporobolus virginicus Kunth. and the fixed dunes are planted to coconut palms. Morton explains the small size and area of these dunes by stating: "The binding action of salt, deposited after evaporation of sea water, normally prevents the movement of sand on tropical shores..." (p. 497).

An extensive coastal dune system, the Namib Desert, extends along the west coast of Africa from Angola to the Orange River (Lat. 15° to 28°S.). Walter (1962, pp. 342-380) presents a brief description of this very dry (average annual precipitation less than 10 mm.), almost vegetationless region.

By contrast, the coast belt vegetation of Zululand on the north-east coast of Africa (Lat. 26° to 29°S.) is rich and varied (Bayer, 1938, pp. 390 to 414). Annual precipitation averages over 1000 mm. with wet summers and dry winters. This coastal belt consists of coarse sand 20 to 25 m. deep, and up to 65 km. wide, with dunes up to 60 m. high. The vegetation is composed of species for the most part unfamiliar to many temperate zone ecologists.

The strand plants and dune formers include Scaevola plumeri, Ipomaea biloba, and Digitaria eriantha. From here, vegetation development usually proceeds toward a "coastal dune scrub" of primarily Mimusops caffra, growing in very dense stands up to two m. tall. This develops into a "dune bush" of the same species, only taller (6 to 9 m.), much more open and farther back from the sea. On the very high dunes there are thorn forests of Acacia karro.

In some places, development is towards a coastal grassland, initiated by Imperata cylindrica and ten species of Eragrostis, and climaxing in stands of Themeda triandra and Hyparrhenia hirta up to 1.5 m. high. This grassland is maintained by fire, since where fire is excluded, a "coast evergreen scrub" begins to develop. However, these shrubs, mainly Myrica conifera and Parinarium mobola, grow only 0.5 m. high, though they are capable, in other environments, of growing as trees up to 12 m. high. Reasons given for this phenomenon include wind, lack of moisture and extreme limits of distribution for the species.

The climax vegetation in this area is the "evergreen subtropical forest", very dense and complex and consisting of many species of hardwoods and lianas. Conspicuous, though not abundant, is the valuable timber conifer, Podocarpus falcatus, growing 25 m. tall and up to 1.5 m. in diameter.

Similar vegetation and climate is recorded by Macnae and

Kalk (1958) for Inhaca Island, Mocambique (Lat. 26° S.). There is also an interesting discussion of the mangrove swamps of this island (Macnae and Kalk, 1962) in which species succession is very marked from *Avicennia*, requiring areas of standing water, to *Rhizophora*, which grows only on the comparatively dry, low dunes.

Asia

Very little literature is available on maritime dunes of countries east of Europe and Africa. Nothing was noted concerning the maritime dunes along the west and east coasts of India, and only a preliminary study is available of vegetation on the inland dunes of Pilani, a very warm, dry area of scant vegetation (Joshi, 1958).

In his early book on plant geography, Schimper (1903, pp. 387-410) briefly discusses tropical littoral formations, including the littoral woodlands which develop on low dunes. More recently, Richards (1957, pp. 296-299) has reviewed the literature of tropical sandy shores, and compared the vegetation of eastern and western tropical areas, and of tropical and temperate zones. A typical eastern tropical sandy shore (Malaysia) would have an *Ipomaea*/*Canavalia* association on the beach. This is very open near the sea, and becomes closed further inland. From this is developed a *Barringtonia* woodland, at first open, with *Scaevola*, *Tournefortia* and *Pandanus*, and then eventually closed, with *Hibiscus* and *Casaurina*.

Casaurina, characterized by its equisetumlike jointed branches and whorled minute leaves, is considered by some as the most primitive of the dicots (Lawrence, 1951, p. 443). It is well adapted to the dune environment and has been used in stabilization plantings (Macnae and Kalk, 1958, p. 13). A photograph of a _Casaurina_ forest advancing over the coastal dunes of Pahang, Malaya, is given by Corner (1964, Pl. 35)

A significant dune complex in Indonesia, on the south coast of Java, near Poeger, was studied by Booberg (1928). He described two principal associations: a _Spinifex/Ipomaea_ on the young dunes, and a _Pandanus_ on the older dunes. The _Pandanus_ is unique, however, in that two sub-associations are recognized. One is the open, male _Pandanus_ with an understory of many shrubs, herbs and grasses; and the other is the female _Pandanus_, closed, with a very dense cover of _Pandanus_ seedlings and practically no other species. Also included are detailed vegetation maps and transect profiles of the entire dune area.

Of dunes in the temperate zones of Asia, particularly the coast of China, nothing was found. Only in Japan is there a considerable amount of activity taking place, and much of this work is unavailable to American readers, both because of language barriers and because of the distribution of the literature. Japan is the only country other than Britain in which dune soil microflora studies were being carried out. Saitô (1955), working on the Pacific coast in Miyagi Prefecture (Lat. 38° N.), relates the soil microflora to the succession of plant communities much as did Brown (1958) in Britain. His general description of the dune communities shows Elymus mollis, Carex kobomugi and Lathyrus maritimus as the pioneer vegetation. On older dunes, there are pine woods with varying types of undergrowth and associated vegetation.

In another study, Tazaki (1960) worked on two dune areas near Tokyo—Shônan, 50 km. southwest of Tokyo, and Arai, 250 km. southwest of Tokyo (Lat. 34 to 35° N.)—investigating the growth of pine seedlings. Pinus thunbergii appears to play an important part in the Japanese dune vegetation, being present on both low, moist sites (associated with Carex kobomugi and Lathyrus maritimus); and on high more dry sites (associated with an Imperata/Lespedeza community).

Oceania

Australia and New Zealand, encompassing both sub-tropical and temperate climatic zones, stand somewhat apart from the rest of Asia. Australia is, of course, largely desert, and there are extensive sand dune areas along the coast, many of which can be considered part of the inland deserts. This is the case particularly in western Australia. On the coastal plain near Cape Keraudren on the Indian Ocean, the transition between marine sands and the dark red sands of the interior is very abrupt, as is the change in vegetation on the two areas. Spinifex and Triodia dominate on the coastal sands, while tussock grasses such as Plectrachne schinzii dominate on the red desert. Species of Acacia are found in both areas (Burbidge, 1944).

The mobile dunes at Perth, West Australia (Lat. 32°S.) are described by Smith (1957). He gives a taxonomic key to the important sand dune plants, and describes each. He notes the presence of Ammophila arenaria and Cakile maritima.

An early general study of the dunes in Victoria, southeastern Australia, was made by Patton (1934), but more recently, an area at Corner Inlet, Victoria (Lat. 38°S.), was described in detail. Turner, Carr, and Bird (1962) list the zonation of vegetation in primary succession:

1. Embryonic dune: Festuca littoralis
2. Foredune: Spinifex hirsutus
3. Dune scrub on stable ridges: Acacia longifolia, Olearia axillaris
4. Scrub woodland: Leptospermum laevigatum, Banksia integrifolia
5. Dune woodland: Eucalyptus viminalis, Banksia serrata

Sand dunes are the most common coastal land form in New

Zealand, covering some 127,000 hectares of land and extending inland in places up to 12 km. The land forms and plant communities are well summarized by Cockayne (1928, pp. 60-115). On the beaches are Festuca littoralis Labill., Salsola kali L. and Atriplex crystallina Hook. Sand grass dunes consist of Spinifex hirsutus Lab. and Desmoschoenus spiralis (A. Rich.) Hook. (a sand-binding sedge). Several species of Cassinia, an erect, bushy ericoid shrub, and Coprosma acerosa A. Cunn. (a low, wiry shrub) make up the fixed dune shrub. Fixed dunes also are grassland (Danthonia, Microlaena, Zoysia) and fern heath (Pteridium). The dune forest, which is very rare, usually is made up of species of Podocarpus.

The moist hollows and sand plains are colonized by Gunnera arenaria Cheesem. (a creeping rooting herb forming small patches of rosettes). Then appear typical wetland species such as Scirpus, Ranunculus, Epilobium, and Lilaeopsis. A final herbaceous stage may be a complete cover of the rush-like Leptocarpus simplex A. Rich. Progression is eventually to either a heath of Leptospermum scoparium J. R., et G. Forst., or with sand accumulation, a Spinifex grassland.

More recently, Williamson (1953) discussed the environmental factors operating in dune communities and their effect upon the development of the vegetation.

Of the islands of the Pacific Ocean, apparently nothing has been written about dune systems except for Olssen-Seffer's (1910) observations in the Hawaiian Islands.

South America

Most prominent on this continent are the vast coastal deserts of the west slopes of the Andes. Bowman (p. 110-147, 1916) gives a general description of this area which extends for hundreds of kilometers along the coast from Chile north through Peru and into Ecuador. These sands are blown up from the shore by the prevailing southwest winds and move inland 19 to 24 km. over mountains as high as 300 m. The most active dune areas seem to be correlated with the major rivers draining the western slopes of the Andes. They are strikingly developed between Lima and Trujillo in Peru (Rich, 1942, pp. 179-181; 218; Plates 220; 271-274). Except where fogs are a dominant climatic factor, these deserts are bare of vegetation, an important reason for the extensive movement of the sand.

Walter (1962, pp. 381-392) discusses the sparse vegetation of this region: the "Loma-Vegetation" which depends almost exclusively on the moisture laden fogs. In particular, he deals with the various species of Tillandsia (T. werdermanii, T. latifolia, T. purpurea, T. straminea) which constitute the entire vegetative cover in the extremely arid areas, and which are completely dependent for their water upon the fogs, absorbing moisture through leaf trichomes.

There are numerous dune areas along the east and north coasts of the continent, only a few of which have been studied. Ringuelet (1949) lists zones and communities of the littoral dunes of Monte Hermoso, province of Buenos Aires, Argentina (Lat. 35°S.):

1. Littoral plain: Spartina ciliata Brongn. (a bunch grass of very sparse cover).
2. Active dunes: Panicum urvilleanum Kunth. and Plazia argentea (Don) O. K. (a shrub).
3. Fixed dunes: Sporobolus rigens (Trin.) Desv. and Plazia.
4. Humid depressions: Scirpus americanus Pers., Juncus acutus L., Lilaeopsis attenuata (Hook et Arn.) Fernald. Gnaphalium spp., Solidago chilensis Weyen, Baccharis spp., Centaurea spp., Senecio spp.

These dunes are quite calcareous (8 to 13 percent calcium carbonate) in a region of 600 mm. annual precipitation.

Along the coast of Rio Grand do Sul, the southernmost state of Brazil (Lat. 27° to 33°S.) are belts of high, moving dunes separated from the mainland by coastal lakes. Attempts at stabilization center around the planting of Ricinus to provide initial shelter for the native Acacia or Tamarix (Schultz, 1957).

The plant communities of the sandy coastal plain (restingas) of the state of Rio de Janeiro, southeast Brazil (Lat. 21° to 23°S.)

were described by Ormond (1960) in terms of physiognomy, structural formula (layering), shape and size of the area, aggressiveness, floristic composition and physico-chemical conditions of the substratum.

About 120 km. north-northeast of Sao Luiz (Lat. 2° 27' S.) is a great belt of dunes which stretches continuously along the coast for 64 km. and then with interruptions for at least 97 km. further. Sand is blown inland in the form of crescent shaped dunes many kilometers by strong northeast winds. According to Rich (1942, p. 30, Plate 39) who describes these dunes, "the most striking feature is the remarkable herringbone pattern visible on the grassy flats between the dunes ... (which) probably represents the truncated edges of the steeply inclined fore-set beds of dunes that have migrated to new positions." The photograph shows this pattern very clearly.

Eleven regions in Venezuela are listed by Tamayo (1952) as being areas where moving dunes are a problem: six are along the coast and five are interior. He also lists plant species suited for stabilization work in each area. The only known reference to central American dunes is again by Olssen-Seffer (1910) who studies a few areas in Guatemala and Mexico. It would appear that a considerable amount of work is waiting to be accomplished in the initial location and description of coastal dune areas in South and Central America.

North America

Sand dunes are prominent physiographic features of the North American landscape, both in the interior and along the coasts. Of the coastal dunes, those of the west coast are the most extensive and striking, partly because of the dominance of westerly winds which aid in the onshore accumulation of sand. Dunes also lie along most of the east coast, but are not nearly so high nor extensive, as is also true of the Gulf Coast, the Florida Keys and the West Indies. There are dramatic dunes on the shores of the Great Lakes, particularly Lake Michigan, and also on the former shores and beds of ancient glacial lakes such as Lake Agassiz in North Dakota and Minnesota. In other interior areas, there are extensive dune deposits which result from the weathering of native rock.

The beginnings of scientific interest in the sand dunes of the United States coincides almost exactly with the publication in 1899 of Cowles' paper on the Lake Michigan dunes. Many of the early dune papers were floristic studies, the plant communities being described only very generally. Also, many papers were the result of brief visits to the dune areas, usually in conjunction with other activities. However, they are of value because they represent a historical record, frequently of locations which today have been completely altered by the activities of man.

East Coast

Characteristic of many of the areas along the east coast are the low dune ridges running parallel to the ocean shore with moist inter-ridge depressions. Some of these dune systems result from the successive formation of off-shore sand bars which gradually increase in height. Eventually the area between the shore and the bar is cut off from the ocean and begins to fill in with sand. Other areas result from the periodic formation of beach ridges (page 82 also Cooper, 1958, pp. 68-69; 123-126). Both processes are associated with prograding shorelines, much of the Atlantic coastal plain being a sand mantle left by the receding ocean. The dominant winds are mainly north in summer and south-southwest in winter, so that sand movement and accumulation from the beach does not play as prominent a role in dune formation as in other areas, though, of course, it is important in shaping the various local physiographic patterns.

Based on climate and vegetation, the Atlantic coastal dunes fall into three loosely defined regions. The northern part extends from Nova Scotia south to the tip of New Jersey (Lat. 39° N.). The southern part includes the coast from New Jersey down to about central Florida (Lat. 28° N.); and the third, the subtropical, includes the rest of Florida, the Gulf coast of the United States and the islands of the Caribbean (down to about Lat. 15° N.). Moisture is abundant and fairly well distributed throughout the year. In most cases the fresh beach sands are slightly calcareous but rapidly become acidic, this holding true for almost the entire coast line.

In the north, a true maritime climate does not prevail, but it is not as severe as the continental climate further inland. The earliest work concerning this area is that of Harshberger (1900, 1902) who studied the strand and adjacent dune flora of Ocean County, New Jersey. Later (1914) he described the dune heathland at Nantucket, Rhode Island. Snow (1902, 1913) worked on the dunes at Cape Henlopen on the Delaware coast, noting changes in vegetation and dune topography over a ten year period. Much later, Amos (1959, 1965) described the animal life of the Cape Henlopen dunes. He also attempted to explain the apparent recent origin of this dune area.

Other studies of the northern coastal region include a dune area on Cape Breton Island, Nova Scotia (Lat. 47° N.) (Harvey, 1919); the coastal dunes at Ipswich, Massachusetts (Townsend, 1925); the coastal areas of Connecticut (Nichols, 1920) and Maryland (Chrysler, 1910); the vegetation of Long Island (Taylor, 1923; Conard, 1935); and a recent detailed study of Island Beach State Park, New Jersey, by Martin (1959). The object of this last study was a complete inventory and mapping of the vegetation communities, as well as an attempt to clarify the vegetation-environment system which Martin felt was controlled almost entirely by the topographical features.

The vegetation is generally similar throughout the area with most of the workers recognizing more or less distinct types or zones. The beach community is that found to a lesser or greater extent on just about every sand strand in the world: Cakile, Arenaria (Honckenya), Salsola, Atriplex. The active dunes, with their pioneer species of Ammophila breviligulata Fern. A. arenaria (L.) Link. Lathyrus maritimus (L.) Bigel. and others gradually increase in vegetative cover. The species of the fixed dune heath increase in prominence as the pioneers disappear. The main species of this heath—Hudsonia, Rhus, Solidago, Arctostaphylos, Cladonia and Ceratodon—present an appearance not unlike the dune heaths of northern Europe. An alternative, or at times succeeding, stage is the dune brush community of Ilex, Myrica, Vaccinium, Quercus, and Juniperus, leading in turn to a conifer forest of Pinus rigida Mill. with ericacious species, Cladonia and Polytrichum as understory. In some cases, a hardwood forest of several species of Quercus is a final stage in the succession.

The dune area in Nova Scotia (Harvey, 1910) is of interest because Ammophila is relatively unimportant as a dune pioneer, its place being taken by Poa compressa L. Also, the forest is composed of Picea canadensis (Mill.) B. S. P. and Abies balsamea (L.) Mill., both of which can withstand sand covering by developing adventitious roots on the trunk.

One of the most obvious differences between the north and south parts of the east coast dunes is the replacement of Ammophila by Uniola paniculata L. as the pioneer species of the active dunes. This transition occurs in North Carolina, and from here southward new species begin to appear. The climate becomes more moderate as indicated by the presence on the strand and foredunes of sub-tropical species such as Ipomaea stolonifera (Yrill.) Poic. and Andropogon maritimus Chapm., both at the northern limits of their distribution, Yucca, Inodes and others. Pinus rigida is gradually replaced by P. taeda L. in the conifer forests, and a climax forest of Quercus virginiana Mill. and Juniperus virginiana L. attains its best development in this region.

Early investigations include Johnson's (1900) notes on the flora of the banks and sounds at Beaufort, North Carolina; a description of the plant cover of Ocracoke Island, southwest of Cape Hatteras (Kearney, 1900); the plant communities of the dunes at Cape Henry, near Albemarle Sound (Kearney, 1901) and Coker's (1905) observations on the flora of the Isle of Palms, South Carolina.

More recent work has been concerned with the vegetation of the southeast coastal region and its relationship to factors of the environment such as soil, wind, physiography and, most particularly, salt spray (Wells, 1939, 1942; Oosting and Billings, 1942; Boyce, 1954). Oosting (1954) has reviewed the literature pertaining to the coastal dunes of this area and discusses some of the ecological processes involved in the structure of the plant communities.

Along the Florida and Gulf coasts, the appearance of more tropical species (Scaevola, Agave, Xolisma) reflects the warmer climate. This was noticed quite early, both by Webber (1898) in his observations on the Florida dunes, and by Lloyd and Tracy (1901) in their flora of the coasts and sand islands of Mississippi and Louisiana. East and south-east winds dominate in this region, giving rise to the "even-crested sand ridges paralleling each other and the shore" noted by Kurz (1942, p. 16) in his detailed geological and ecological study of the Florida dunes.

With a view toward initiating a long time study, Davis (1942) made detailed vegetation maps of 30 islands of the Florida sand keys lying west of Key West. Formed of limestone outcroppings, the sands of these islands are coarse and calcareous, and support a generally tropical vegetation. Although annual precipitation on the Keys is lower than the rest of Florida, vegetation is similar except that more tropical species are present, including the "hammocks" or tropical climax forests of Smilax, Serenoa, Magnolia and others.

The West Indies have an actual maritime climate, the average annual temperature range being only about 1.5° C., and can be considered truly tropical. Gooding (1947) describes several vegetation zones on Barbados, but noted no forests on the heavily populated island. Ipomaea pes-caprae, restricted to tropical shores, is found here, along with other tropical species.

West Coast

The range of climate and vegetation evident on the east coast is not so apparent on the west coast of the continent, although two definite regions can be discerned. The southern part corresponds roughly to the coast of California and southward (roughly south of Lat. 42° N.); the northern to the coasts of Oregon and Washington, again based both on climate and vegetation. Climate differs markedly from the east coast. The annual temperature range is less, rainfall is very unevenly distributed and the dominant winds blow off the ocean. This, along with an abundant supply of sand, produces extensive dune areas which reach their best development in the extensive dunes along the coast of Oregon. The dunes of Oregon and Washington will be reviewed later in this study.

Very little information is available concerning the California dunes. Early observations were made by Couch (1914) on the dunes between Redondo and Venice, California; and by Ramaley (1918) on an area south of Golden Gate State Park, San Francisco.

The first serious ecological study was by Cooper (1919, 1920, 1922) who set up permanent quadrats and mapped the vegetation on a dune area at Monterey. Later (1936) he published a geobotanical essay on the strand and dune flora of the Pacific coast, and currently he is working on a comprehensive geological and ecological treatment of the California coastal dunes which is scheduled for publication in 1966 (Cooper, 1965).

Cooper's geobotanical essay (1936) is currently the best source of information on the vegetation of the California dunes. The actual strand vegetation in this area is poor, Cakile edentula (Bigel.) Hook. being the most prominent species. On the foredune, except where Ammophila arenaria (L.) Link. has become established, grasses are rare. The dune builders include Franseria chamissonis Less., Abronia latifolia Eschsch. and Mesembryanthemum spp. On the mobile dunes further inland are Oenothera cheiranthifolia Hornem., Anaphalis margaritacea (L.) B. and H. and Glehnia leiocarpa Mathias. This gradually develops into a fixed dune shrub community of Lupinus chamissonis Eschsch., Haplopappus ericoides (Less.) H. and A. and Eriogonum parviflorum Sm. Climax vegetation can develop three ways: (1) To the extensive coastal chaparral of Ceanothus and Arctostapylos in central and southern California; (2) To a coastal sagebrush of Eriogonum fasiculatum Benth., Salvia mellifera Greene and Artemisia californica Less.; or (3) In the more moist areas (especially in the north) to a forest of various species of Pinus.

Other information on the California dunes include two lengthy studies on the autecology of coastal plants (Martin and Clements, 1939; Purer, 1936); a description of the flora and fauna of dunes near Los Angeles (Pierce and Pool, 1938); and a short study by Prat (1949) who stated that fogs were a principle source of water for dune plants during the summer months.[6]

Inland dunes. Aside from the great deserts of Mexico and southwest United States, several inland dune areas are worth noting. Of most pertinent interest are the sand dunes of the Great Lakes. The classic work on the Lake Michigan dunes by Cowles (1899) shows how very similar their vegetation is to that of coastal dune areas, an observation specifically made by Stomps (1915) who compared the coastal dunes of Holland with those of Lake Michigan.

Along the beach of these lake dunes are the familiar *Cakile* and *Lathyrus*, the foredunes and active sand support *Ammophila breviligulata* Fern., *Agropyron dasystachum* (Hook.) Scribn., and others, developing into either a shrub community of *Prunus*, *Salix*, *Solidago* and *Calamagrostis*, or into an *Arctostaphylos*-*Juniperus* heath which goes finally to a heath forest of *Pinus banksiana* Lamb., *Gaultheria*, *Vaccinium*, *Cladonia* and *Polytrichum*.

More recently, Olson (1958) has studied in considerable detail the vegetation succession and soil development on the Lake Michigan

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[6] "Sur la côte californienne, un facteur écologique dominant est constitué par les brouillards, seule ressource en eau de la végétation pendant les six mois que dure la saison sèche." (Prat, 1949, p. 113).

dunes in northern Indiana. Another dune area on Lake Michigan in northern Wisconsin was the object of a detailed ecological analysis by Van Denack (1961) who set up permanent transects from shore to forest to study vegetation changes on the open, active dunes. Eifert (1963, pp. 54-73) describes another lake dune area in northern Wisconsin; and Shelford (1963, p. 139; 200) discusses sand succession on Isle Royal in Lake Superior and at Churchill, Manitoba, on Hudson Bay.

In other areas, seasonal changes in dune vegetation were described by Clute (1931) on the site of ancient Lake Morris southwest of Chicago. Pool (1914) made an extensive study of the Nebraska sand hills vegetation. The sand of this area of almost 50, 000 square kilometers was derived from the weathering of rock. The highest dunes in the United States are also derived from weathered rock. Piled up in ridges up to 200 m. high, they lie in an area 16 km. long at the foot of the Sangre de Cristo Mountains in south central Colorado. Teale (1960) writes of the vegetation of these dunes, which consists mostly of species of Psoralea, a plant that can survive readily on this very active sand.

Conclusions

It becomes evident from a review of this type that a considerable variation exists in the location, climate and vegetation of maritime sand dune regions. Yet a line of continuity can be traced through all—in the physiography of the dune system as well as in the plant communities supported by the corresponding environments.

The principle dune forms—strand, foredune, moving dune, fixed dune and moist depression—are recognizable in all areas. The plant communities—beach, active sand, shrub, heath, meadow, forest—can be found in many or all places in one form or another. Many species are widely distributed. Cakile on the beach is world wide; Ammophila is a sand binder on all temperate zone dunes; Ipomaea is a bare sand pioneer on the beaches and dunes of the tropics and sub-tropics; and Pinus is characteristic of dune forests over much of the world. Yet striking differences can exist—differences due to location and climate. These vary widely—from the uniformly wet and hot tropics to the dry and warm Mediterranean climates to the cool and wet northern maritime zones. Probably no other natural biologic-physiographic feature of the earth's surface can be so precisely delimited in so many places.

This review is not exhaustive nor all inclusive, but it is intended to give a general picture of the location of maritime dune systems, what sort of vegetation they support and a summary of the published literature concerning them. Even sketchy information is lacking from much of South America, Africa, and Asia. The Russian language imposes a formidable barrier to knowledge of the extensive sand dune research activities being carried out in that country. The European dune literature is well accounted for in the several publications cited in this review, though, as has been noted, a great deal of it is unavailable in this country.

Finally, this review serves as a background for the discussion to follow on the coastal sand dunes of Oregon—a very diverse, interesting and practically unknown segment of our landscape.

III. THE OREGON COASTAL DUNES

Introduction

Sand dunes are found along the entire west coast of North America from Alaska to Lower California. They attain their greatest development along the coast of Oregon and the southern coast of Washington. Of some 500 km. of ocean-facing shore line in Oregon, there are dunes on 225 km. or 45 percent of the total. The Washington dunes, extending 90 km. north of the mouth of the Columbia River, can be considered a part of the Oregon dunes system.

Several prominent physiographic features characterize the Oregon coastline. Most spectacular are the high, steep sea cliffs and promontories composed of erosion resistant igneous rock. These alternate with low, narrow coastal plains on which the dune systems develop. Both are joined to the Coast Range mountains at their inner margins. All of the streams and rivers flowing into the ocean show evidence of "drowning"—a result of a relatively recent rise in level of the ocean. The former streambeds of some of the larger rivers such as the Columbia and Coos can be traced across the continental shelf for a considerable distance.

Although all of the present dunes are more or less active, there are a number of locations where very old, semi-consolidated dunes have been exposed (mostly through construction activities). Strikingly different in color and soil development, they suggest a very ancient development of dune systems.

The sand dune areas along the coast can be readily subdivided into three regions.[7] This subdivision is a function both of shoreline features and the form of the dunes themselves, and corresponds quite closely to various shoreline processes to be outlined later.

The first is that associated with the mouth of the Columbia River and is a continuous belt of dunes extending 90 km. north in Washington and 30 km. south in Oregon to Tillamook Head. It is the result of the deposition of erosion sediments from the Columbia River which have created a prograding shoreline. Chiefly characteristic of this dune area are the series of sand ridges running parallel to the shore. This is the only place where the parallel ridge system occurs on the Oregon coast, although it is common, as previously noted, on the east coast of the United States and in Europe.

The second region extends from Tillamook Head south some 200 km. to Heceta Head. There are many capes and headlands along the north and central coast so that the dune areas tend to be isolated and quite variable in size and form. Of 14 locations with significant

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[7] Although they are natural and obvious, Cooper (1958) is to be credited with their original delineation. He includes a fourth, that extending from the Coquille River south to the California border.

dunes, eight are associated with bays or estuaries. Just about all are characterized by a large parabola dune or parabola dune complex which has developed as a result of peculiar vegetation-wind interactions. Marine erosion has left these parabola dunes in various states of degradation (truncation of their seaward ends) from nearly complete systems to mere remnants.

The most extensive and impressive dunes are in the third region: the coast between Heceta Head and Coos Bay, a distance of 86 km. The dunes are continuous except where two major rivers, the Siuslaw and Umpqua, and several smaller streams cross them. They rest on the broad, low mantle of a terrace which slopes gently below sea level and extends inland up to four km. Cooper calls it the "Coos Bay dune sheet" and attributes its significance to the fact that "the great extent and continuity of receptive shore backed by terrain favorable to dune migration give ample opportunity for development of materials and forces." (1958, p. 88).

There are a few dune areas south of Cape Arago, the most notable extending north and south of the Coquille River for a total distance of about 20 km. They are very low and extend inland about two km. Smaller areas occur at various locations south to California. Cooper (1958) described in some detail 30 dune locations along the coast of Washington and Oregon (subdividing the Coos Bay dune sheet into five sub-regions for convenience). Through comparative ground and aerial observations he was able to postulate a developmental history more or less common to most of these dune locations.

Figure 3 is an adaptation from Cooper's Plate I showing the distribution and location of the sand dune areas and physiographic features along the Oregon coast. Topography, geologic processes, climate and vegetation have all combined to create the existing landscape, which has a diverse and complex developmental history.

Geology

The geologic history of the Oregon coast is not yet thoroughly understood, and even a general account must rely on several sources.[8] The entire coast falls into two rather distinct divisions separated by the Coquille River. To the south are the Pre-Tertiary formations of metamorphic rock, and to the north are Tertiary and Pleistocene sedimentary depositions and igneous intrusions.

The sedimentary formations had their origin in the early Eocene (sixty million years ago) when a eugeosyncline occupied the area from the Klamath Mountains north to Vancouver Island and east to the Cascade Mountains. The initial deposits were volcanic in origin, but by middle Eocene, uplift activity to the south and

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[8]Tertiary events are based on Snavely and Wagner (1963), a very informative and well-organized account. For the remainder, the following sources were consulted: Baldwin, 1959, pp. 1-36; Cooper, 1958, pp. 128-138; Fenneman, 1931, pp. 458-465; Smith, 1933.

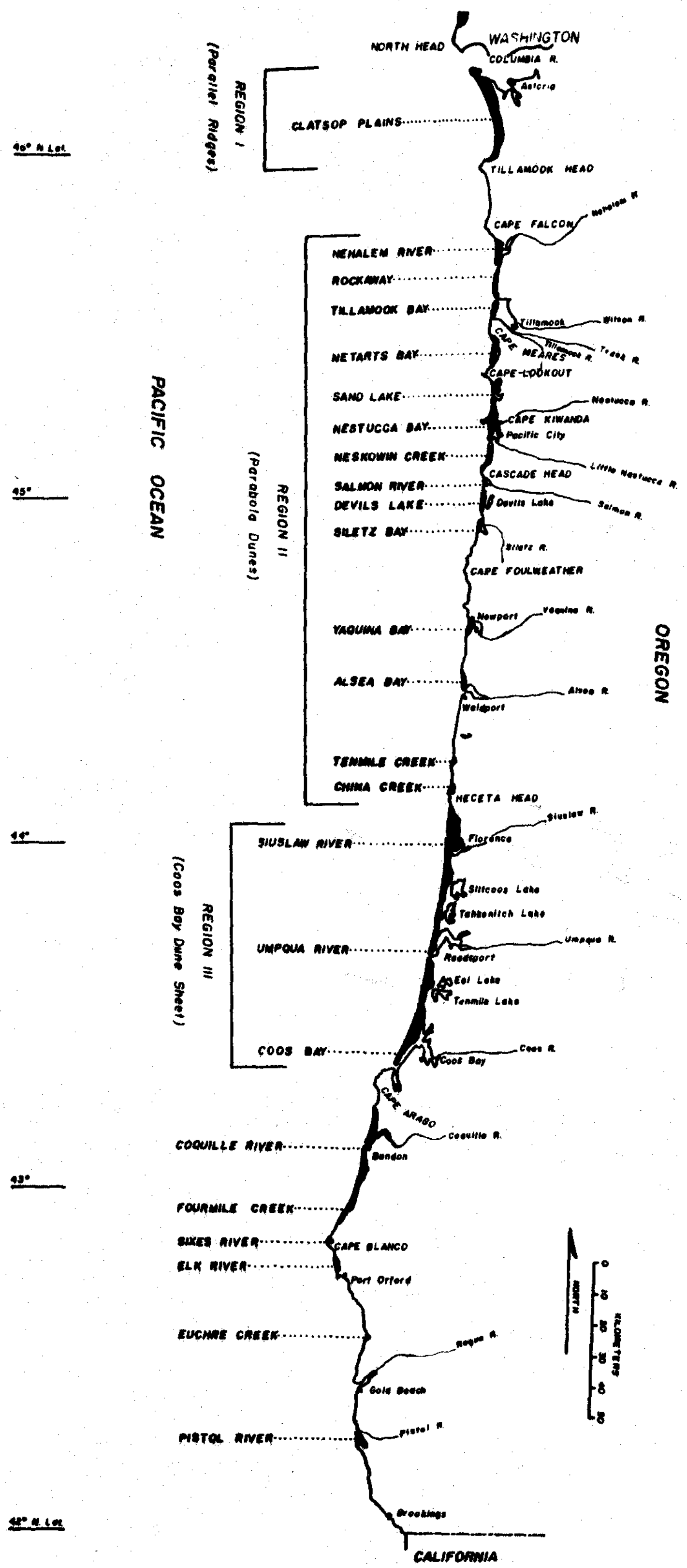


Figure 3. Map of the Oregon coast showing dune areas and regions, physiographic and geographic features. (Adapted from Plate I, Cooper, 1958.)

subsequent erosion contributed arkosic sands as marine deposits for a considerable distance northward. Volcanic activity persisted throughout the Eocene so that igneous materials are frequently interbedded with the sedimentary layers. By late Eocene tuffaceous silts and clays, rich in organic matter, began to be deposited by the streams and rivers flowing from the surrounding highlands.

This deposition continued and increased considerably during the Oligocene (beginning forty million years ago), and into the Miocene (twenty-eight million years), when arkosic sands and silts were also laid down in great amounts. Cape Kiwanda on the north coast near Pacific City is an example of Miocene sandstone and siltstone resting on Oligocene mudstone.

During middle Miocene, vigorous volcanic activity formed many of the basaltic intrusions and headlands which remain today as erosional remnants (Yaquina Point, Cape Lookout, the numerous "sea stacks", Saddle Mountain). Toward the end of the Miocene, uplift began which was to form the Coast mountains. This reached its maximum height during Pliocene (twelve million years), and peneplanation began. The record becomes a little more complex here, since "the coast shows the effect of multiple eustatic sea level changes superimposed on a slowly rising coastline" (Baldwin, 1959, p. 31).

During late Pliocene and early Pleistocene (one million years ago) occurred a period of extreme submergence, indicated by wave-cut terraces found as high as 457 m. above the present sea level. Subsequent uplift lowered the shore line about 91 m. below present sea level, and it is during this period that the rivers and streams cut their trenches across the Continental shelf. Resubmergence to about 49 m. above present sea level saw the beginning of Pleistocene sand dune activity. The location of these "ancient eolian sediments" (Cooper, 1958, p. 128) corresponds roughly to present day activity, but appears to have been much more extensive. Mostly destroyed at maximum submergence, they are found today only at the higher elevations not reached by sea action. They can be distinguished by their red and yellow staining, frequent cross-bedding, coarse, well worn grains and semi-consolidated nature.

A period of relative stability followed by a slight emergence in late Pleistocene resulted in the formation of a terrace that today is situated at an average distance of 45 m. above sea level, though varying from below sea level to some 64 m. above sea level due to warping of the crust. This is the "30-meter terrace" of Cooper, and it is overlain with unconsolidated marine sediments. This terrace and its mantle is quite distinct along the south coast. It is less so in the north, but some evidence can be found of its existence.

Eustatic activity since late Pleistocene is associated with the cycles of glaciation; and the last major lowering of the shore line—to

137 m. below present sea level—coincides with the maximum of the last, or Wisconsin, glaciation. According to a discussion by Hansen (1947, pp. 33-35), this was 70,000 years ago in the east and 20,000 years in the west. Fairbridge (1960) places the Wisconsin maximum at 17,000 years ago, and the lowering of shore line at 100 m. As the glaciers melted, submergence again took place, creating the general features of the present coastline. With resubmergence sand dune activity began again, the sand moving inland ahead of the advancing sea, reaching its maximum development at the end of the period of submergence, about 6,000 years ago (Cooper, 1958, pp. 134, 135; Fairbridge, 1960).

As a result of this submergence, the coastal rivers and streams are characterized by drowned mouths and valleys. On the Columbia, this drowning (indicated by the limits of tide action) extends 225 km. upstream; on the Umpqua, 40 km. Where rivers have kept pace with the "drowning" by depositing alluvial materials, extensive, fertile plains have resulted. The Tillamook area is an example of this. Bays and estuaries result where deposition has not been sufficient, such as Alsea, Yaquina, and Sand Lake.

A special situation exists where small streams not only could not fill their drowned valleys with sediments, but also were at least partially blocked by sand dunes moving inland. Large, fresh water lakes were thus formed with their surfaces above sea level. Siltcoos, Tahkenitch, Clear and Eel Lakes are among those formed in this manner.

In the period since maximum submergence, the sand dunes have undergone a varying cycle of stabilization and rejuvenation, depending upon vegetation, disturbance, and shoreline processes. During these approximately six thousand years, the shoreline has been in a state of relative stability, though not without activity. Along the north coast, on both sides of the mouth of the Columbia River, there is a prograding shoreline, a result of the tremendous loads of sediments carried by the river. Slight to severe erosion characterizes the central Oregon coastline. The beach between Heceta Head and Coos Bay is the most stable part of the coast, with no progradation or erosion (Dicken, 1961, p. 47). Emergence appears to be taking place at one location near Cape Meares (Allen and Van Alta, 1964, p. 24).

Climate

Climate plays no small part in the development and appearance of dune areas, both with regard to its effect on the vegetation, which in turn is very important in dune processes; and through the basic factors of temperature, precipitation and wind. Cooper's discussion of the coastal climate is detailed (1958, pp. 11-20) and it need only be reviewed here.

The various systems of climate classification place the Oregon coast in a general category of mild temperatures and abundant precipitation with little or no seasonal deficiency. In his most recent classification, Thornthwaite (1948) characterizes the climate as $AB_1'ra'$ where A is perhumid (surplus moisture); B_1' is mesothermal; r is no seasonal deficiency, and a' is low summer concentration of thermal efficiency (less than 48 percent of the total potential evapotranspiration occurs during the summer).

Precipitation and temperature data is presented for six stations between Astoria and Brookings in Tables 1 and 2. Latitudinal variation of temperature and precipitation is relatively slight along the entire coast. Annual mean temperature is particularly uniform, ranging only between 10.7° C. and 11.6° C. (between the most northerly and most southerly stations, respectively). Annual precipitation varies somewhat more, the greatest amounts occurring at the north and south ends of the coast.

Fluctuation of mean temperature between the warmest and coldest months is also relatively small, ranging between 7.1° C. difference at Bandon, and 11.9° C. at Astoria. Precipitation is very different, however, showing a very marked seasonal fluctuation. The percent of the total annual precipitation falling during the summer months of June to September is low, varying from 7.0 percent at Astoria to 4.0 percent at North Bend.

TABLE 1. Average monthly and annual temperatures (C°) for six stations on the Oregon coast.

STATION	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual	Length of record
Astoria	4.5	5.9	7.4	9.7	11.9	14.2	16.0	16.4	15.3	12.2	8.4	5.8	10.7	96
Cloverdale (near Sand Lake)	5.7	7.4	7.6	9.4	11.8	13.9	15.7	15.7	14.9	12.4	9.0	7.1	10.9	23
Newport	6.4	7.2	7.8	9.4	11.1	13.0	14.0	14.2	13.6	11.9	9.5	7.4	10.8	67
North Bend	6.8	7.7	8.6	9.8	11.6	13.6	15.2	15.6	14.5	12.3	9.8	7.2	11.1	50
Bandon	7.4	8.2	8.3	9.7	11.4	13.5	14.4	14.5	13.6	11.8	9.8	8.5	10.9	50
Brookings	8.0	8.7	9.3	10.5	12.0	13.8	14.7	15.1	14.9	13.1	10.7	8.7	11.6	41

TABLE 2. Average monthly and annual precipitation (mm) for six stations on the Oregon coast.

STATION	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual	Jun-Aug % total	Length of record
Astoria	287	235	213	133	93	71	28	35	82	163	269	322	1930	7.0	105
Cloverdale (near Sand Lake)	301	269	250	147	102	88	27	37	82	214	292	323	2139	7.1	23
Newport	241	207	194	115	84	62	21	21	66	139	246	274	1679	6.2	68
North Bend	277	226	192	126	82	43	13	10	61	104	253	249	1628	4.0	51
Bandon	271	211	189	122	87	41	12	13	54	142	212	260	1603	4.1	46
Brookings	309	243	218	149	90	61	16	15	65	159	286	317	1928	4.8	43

Humidity, cloud and fog data are very incomplete, but Cooper (1958, p. 13) indicates that these factors contribute significantly to the overall climatic effect of the region. Decker (1961, pp. 34, 35) published data on average daily solar radiation and average percent of possible sunshine for each month of the year for several locations in Oregon. Both sets of data show considerable increases for the southern third of the coast (as compared to the northern two-thirds) for the low precipitation months of June to August. This information is useful in assessing potential evapotranspiration and its effect on the vegetation.

Wind plays an important part both in its influence on the climate and as an active agent in dune processes. Actual measurements of directional frequency and velocity are scarce. On the basis of nearly 12, 000 observations made at three stations (North Head, Newport and North Bend) by the U. S. Coast Guard between 1937 and 1942, Cooper (1958, p. 17) summarizes the seasonal wind regime as follows:

> In summer, onshore winds greatly predominate, and most of these are confined to the sector N. -NW. ; they cover about one octant seaward from the trend of the coast. Winds within this sector have the greatest average velocity. Fall conditions are transitional; winds of the winter type appear in alternation with those of the summer type. In winter, offshore winds are most frequent but have low velocity, except for the gorge winds of the Columbia River. Onshore winds from south to southwest are relatively infrequent but have by far the greatest velocity; they are parallel to the coast or strike it at an acute angle. Spring conditions are again transitional: N. -NW.

> winds reappear, alternating with the gentle offshore breezes and high-velocity S. -SW. winds of winter.

As will be brought out shortly, these seasonal wind patterns are very influential in the shaping of the dune landscape.

The Dune Landscape

Sand supply, shore topography, the climatic regime and vegetation are the four interrelated factors involved in determining the location and features of the sand dunes. The locations have been noted. There are a number of topographic features which constitute the basis of the various dune systems. These are the foredune, the parallel-ridge system, the precipitation ridge, the deflation plain, the transverse ridge, the oblique ridge and the parabola dune. Each will be described briefly, drawing heavily upon Cooper (1958) since some of these features are quite extensively treated in his book.

Sand Supply

The ocean is the great reservoir of sand that has built and maintained the present dune areas. The ultimate source of these sands are the sediment loads of the rivers and streams, and the coastal Tertiary and Pleistocene formations undergoing marine erosion. Offshore ocean currents distribute this sand, depositing it in places and under conditions not yet clearly understood. The offshore currents flow northward in winter and southward in summer under the influence of the annual wind patterns. Mouths of streams and headlands provide obstacles to this flow such that some of the sand load would be deposited and moved up onto the adjoining shore by wave action. The localized dune systems of the central coast, the spits, and the sand fills behind jetties all find their origin in this process. But it does not explain the immense Coos Bay dune sheet.

Twenhofel (1946, p. 8) theorizes that the bulk of the present dunes are made of material from more southerly points deposited prior to the last maximum submergence. This appears to be based on the observation that the black minerals found in the sand have their source mostly south of the Coquille River. Certainly some period of accelerated sand deposition must have occurred to account for the vast amounts of sand now present.

The present day coastal rivers probably contribute considerably to the sand supply. Particularly outstanding is the Columbia River, which, according to Cooper (1958, p. 27) has a water discharge of 5519 cubic meters per second. By contrast, the Umpqua, the largest river between the Columbia and Cape Blanco, discharges only 203 cubic meters per second. Much more sand is delivered by the Columbia than the offshore currents can possibly carry away, resulting in the very extensive parallel-ridge system and prograding shore of this area. The same is also probably true of the Siuslaw and Umpqua Rivers, and may account for some of the sand in the massive dunes of this area.

The Foredune

A comparatively recent phenomenon along the Oregon coast is the foredune, the high (up to 9 m.) ridge of sand paralleling the shore immediately above high tide line. According to Cooper (1965) the foredune has developed mostly since the 1930's. It is strictly a product of vegetation, and of one plant in particular: *Ammophila arenaria* (L.) Link (European beach grass). This grass, introduced in the late 1800's from Europe where it has been used for centuries in dune control work, has spread and been planted all along the Oregon coast. It attains maximum growth and vigor where sand deposition by wind is greatest—the immediate shore area; and the effect is to drastically reduce the amount of sand moving inland off the beach.

The ultimate height and breadth of this dune is not known, nor has it been investigated in this country as far as is known. (See Figure 64 for a cross section of the foredune on the Oregon coast). Ranwell (1960a) studied the formation and possible fate of the foredune at Newborough Warren, England. Several early German books give detailed instructions on the construction and maintenance of the foredune (Gerhardt, 1900; Braun, 1911; Van Dieren, 1934).

The Parallel-Ridge System

The parallel-ridge system is essentially a foredune system, but formed on a prograding shore. Although native plants can initiate such a system, they do not control it as does *Ammophila*. Once started, a large supply of sand builds the ridge rapidly. As the shore extends seaward, the wind deposits sand along a new line of vegetation at the high tide level, less and less being carried inland to the older ridge. Over a long period of time, a considerable number of such ridges will develop (nine on the north coast at the mouth of the Columbia River). They are generally 4.5 to 12 m. high, though they reach 22 m. in places. Figure 4 is a diagrammatic representation of a parallel-ridge system based on the dunes around the mouth of the Columbia River (See also p. 56).

The Precipitation Ridge

In the absence of the foredune, or where there is a sufficient sand supply behind this dune, sand is moved inland by the driving force of the seasonal winds. If an area of vegetation is encountered, sand begins to accumulate as a ridge normal to the direction of dominant wind action because the wind is deflected upward, loses velocity,

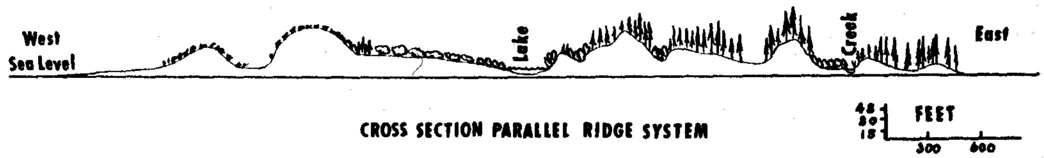


Figure 4. Cross section of the parallel ridge system on the northern Oregon coast. (Adapted from Plate 6, Cooper, 1958.)

and drops its load of sand. This ridge will grow in height, depending upon the height of the vegetation. The lee side becomes very steep, and after a certain angle is reached (about 33° according to many investigators), sand slips down this face, effectively initiating forward movement of the dune and invading the vegetation, usually a forest. This is the precipitation ridge.

The Deflation Plain

The windward slope of the precipitation ridge is very gradual, and as sand removal continues, the moist sand near the water table is eventually reached. At this point, effective sand movement ceases. This is a deflation surface, or, where the area is large, a deflation plain. Deflation to substratum can also stop sand movement. The damp deflation plain then becomes a favorable habitat for the initiation of vegetation. The occurrence and vegetation of the deflation plain is studied in greater detail later.

The Transverse Ridges

Where an extensive area with abundant sand supply and no vegetation occurs, a transverse ridge pattern develops in which the dune crests are oriented generally at right angles to the northwest winds of summer. The ridges average about two m. in height, with slopes steep (33°) on the lee side and gentle (3° to 12°) on the windward side (See Figure 44). Intercrest distances vary from 23 to 46 m. and crest length is highly variable. The pattern is partly destroyed in winter and develops again the following summer. Cooper studied the formative aspects of these dunes very thoroughly and discusses the requirements for their origin and maintenance (1958, pp. 27-49): unidirectional airflow, dry surface sand, sufficient sand depth, and a supply of new materials. He also studied wind current behavior with smoke and motion pictures.

The Oblique Ridge

The oblique ridges, named and studied by Cooper (pp. 49-64) are unique in that they seem to have no counterparts in other dune areas of the world, occurring only on the Coos Bay dune sheet of the Oregon coast. They are so designated because their crests are oriented obliquely to both the northwest and southwest winds. The crest behaves as a transverse ridge with a slipface developing on alternating sides as the wind regime goes through its cycle. These dunes occur in a parallel series, averaging some 168 m. from crest to crest. They rise as high as 50 m. above their base, which often is near the water table and may have developing vegetation. Average length is 1100 m. with extremes up to 1500 m. At their high, inner ends, they are joined by a precipitation ridge which is actively invading what is left of the original dune forest. Their outer, or seaward, ends taper down to an area of transverse ridges, which in turn usually joins the vegetated deflation plain just inside the foredune.

According to Cooper, these dunes are long-lived, and move slowly inland. Observations of the author indicate a net northerly movement under the influence of the strong winter winds. The method of formation of these ridges is unclear, but Cooper postulates (p. 57) that "existing systems of oblique ridges originated in precipitation ridges close to the shore and extra-large masses (built around vegetative barriers) served as nuclei for development of oblique ridges." The mass develops into a high dune as the lower precipitation ridge continues to move inland.

The Parabola Dunes

This dune can only develop on a large sand mass previously stabilized by vegetation. A break occurs in the vegetative cover, a blowout develops, and if there is a differential resistance of the vegetation to sand movement such that it can progress more rapidly in one particular place, a mass of sand, variable in height according to the vegetation it is overwhelming, begins to move inland parallel to a unidirectional wind force. Lateral widening of the break occurs also, creating a ridge somewhat similar in shape to a parabolic curve. The area between the lateral arms may blow down to water table, creating a deflation plain (Also see p.

Almost all of the dunes between Tillamook Head and Heceta Head (Region II) are parabola systems developed by the southwest winds. There are indications that many of these have been truncated at their seaward ends by marine erosion, only remnants being left. The parabola system at Sand Lake is large and well developed. It is shown in its entirety in Figure 5, a vertical aerial photograph. South of Heceta Head, a very high series or parabola dunes occur between the Siltcoos and Umpqua Rivers. Of the four near Tahkenitch Creek, three are formed by northwest winds and the other by southwest winds.

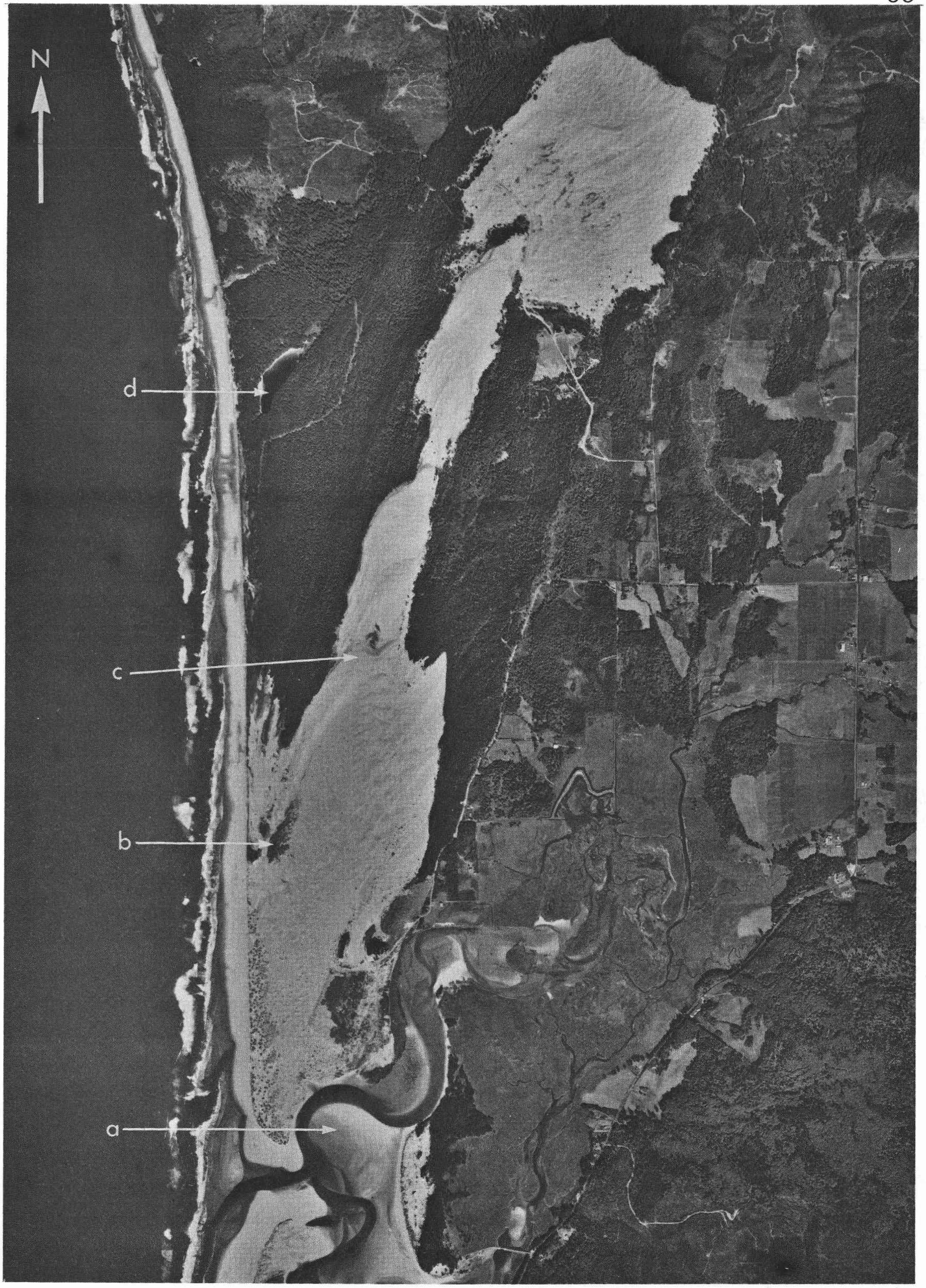
Sand Activity

Attempts to reconstruct the history of sand activity and vegetation development and destruction tend to be highly speculative. By comparing dune ridge patterns as revealed on aerial photographs, Cooper (1958, pp. 131-138) developed his concept of cyclic episodes. Episode I is generally a stabilized precipitation ridge and its windward deflation plain at the inner margins of the present dune areas. Episode II is a secondary precipitation ridge which has moved inland, in some cases stopping short of the first, in others, completely overwhelming and covering it. The precipitation ridge of Episode III is currently active, with vegetation stabilization beginning on the windward deflation plains. A corresponding cyclic pattern is noted for

Figure 5. Vertical aerial photograph of sand dunes at Sand Lake showing extensive development of the parabola dune system.

- a. Sand Lake
- b. deflation plain (SL)
- c. most recent parabola dune advancing in northeasterly direction, covering deflation plain just above it (SL-2)
- d. Chamberlain Lake.

The outermost dune ridge forms the eastern shore of this lake. There are two currently active parabola dunes northeast of c. The rectangular vegetated area south and east of b, on the west shore of Sand Lake, is a beachgrass (*Ammophila arenaria*) nursery planted by the Civilian Conservation Corps in the late 1930's. Just to the north of the nursery, across the beach access road, are two forested remnants which are being slowly eroded away. Scale 1:36000.


N
d
c
b
a

the parabola dunes. These episodes are difficult to date, but presumably Episode I represents the greatest extent of sand activity, occurring as maximum submergence was reached about 6,000 years ago.

The studies of Hansen (1943, 1944, 1947) on postglacial forest succession corroborate the idea of continual sand activity. He feels that there has been little permanent stabilization of the sand dunes along the ocean shore in the past four to seven thousand years, this being indicated by the presence of sand particles throughout peat profiles from the sand dune areas (1943, p. 339).

Since Pinus contorta Loud. (lodgepole pine) is the pioneer forest tree on the sand dunes, both on the ridges and in the wet sites and bogs, the proportion of pollen of this species in the peat profile can tell something of sand movement, a predominance of pine indicating accelerated movement of sand and destruction of the climax forest. Climate along the coast has apparently had little effect on vegetation succession. Pollen profiles indicate a relatively constant postglacial climate with no warm, dry periods as occurred farther inland. The climax spruce (Picea sitchensis (Borg.) Carr. and Tsuga heterophylla (Raf.) Sarg. (western hemlock) were never replaced by xerophytic species (Hansen, 1947, p. 95).

Hansen concludes (1947, p. 98) that "periods of accelerated sand movement, as reflected by pollen profiles, may have been synchronous with climatic fluctuations further inland, but do not seem to be systematically indicated by the recorded trends of forest succession." These climatic changes might have brought about "increased wind velocity for periods of time sufficient to cause considerable shifting of sand" (Hansen, 1944, p. 636).

Concurrent with sand movement, the vegetation has been greatly affected by fire. Fire is one of the causes of renewed sand activity, a fact frequently made evident when old stabilized forest surfaces are exposed by eroding sand. Usually they have charcoal and burned bits of wood in their upper layers and on the surface. Hansen (1944) notes profiles in which charred peat layers occur in conjunction with maximum representation of lodgepole pine pollen.

Cooper (1958, p. 93) discusses fire history in the area around Florence where lodgepole pine, a fire tree, grows in almost pure stands. He sees these forests as resulting from two fires in about 1833 and 1853. The Indians around Florence recalled to early settlers that at the time of one of the fires, "the sun was dark for ten days, and nearly all this part of the coast area was burned." (Knowles, 1952, p. 11). The pioneers themselves described "the big dead trees, an endless horde," the result of fire many years previously (Erlandson, 1947, p. 17). In his descriptions of the Oregon coast, Davidson (1889, p. 431) repeatedly emphasizes the burned over appearance of the coastal country, concluding: "the whole country has been burned over...and bristles with enormous standing trunks of whitened trees."

According to Dicken (1961), man caused fires were of widespread occurrence during the initial years of settlement from 1845 to 1850. Since then, however, fire has probably been less important as an instrument of change than the new activities of man. Logging, grazing, cultivation, mining and the construction of jetties and breakwaters all have helped to alter erosion and deposition patterns along the shore. In his study, Dicken relates these various disturbance factors to physical changes of the shore in the past one hundred years of white settlement.

Vegetation

The present vegetation of the sand dunes, then, is a result of recurrent sand movement, fires, and most importantly, the influence of man. It is difficult to reconstruct the native vegetation landscape of pre-settlement days, except as the obviously introduced species are eliminated. Early pioneers, who used the beaches extensively for travel, made practically no mention of the vegetation, except, perhaps, as it related to the progress of their journey.

Hanneson (1962) used a historical approach to trace changes in the dune vegetation. These changes were of two types: (1) changes in floristic composition through the introduction of exotic species;

and (2) changes in the areal distribution of the major surface cover types. Working mostly around Bandon in the south, and the Clatsop area in the north, he concluded that most changes were due to disturbance and subsequent stabilization.

Early explorers described the Clatsop spit area south of the Columbia River, and gave some clues as to the native vegetation present. This original vegetation, mostly of a prairie type (Agrostis, Festuca, Carex, Trifolium) and some trees (Tsuga, Picea) was practically destroyed by sand activity initiated by grazing and cultivation (U. S. Soil Conservation Service, 1940, p. 2). The present vegetation is the result of stabilization work that began in 1935 (McLaughlin and Brown, 1942).

The spread of Ammophila is, of course, a dramatic example of change through introduction of new species. Equally impressive is the spread of Ulex europaeus L. (gorse) since its introduction as an ornamental in the late 1800's. Covering more than 10,000 ha. in Curry, Coos and western Lane Counties, it has effectively resisted most efforts aimed at its eradication (Hill, 1949).

None of the tree species originally introduced for sand stabilization work have become securely established, and so they have not changed the composition of the original forests. The entire coast is included in the Cedar-Hemlock Forest of Weaver and Clements (1938, p. 501) in which Tsuga heterophylla (western hemlock)

Thuja plicata D. Don (western red cedar) and Picea sitchensis (Sitka spruce) are the characteristic species of the climax forest. Shelford (1963, p. 211) includes the dunes of the Oregon coast in his "Hemlock-Red Cedar-Wapiti Association" of the "Rainy Western Hemlock Forest Biome".

The earliest published accounts of the vegetation of the Oregon coastal dunes are those of House (1914a, 1914b). He noted the extensive forests of Pinus contorta with a thick undergrowth of Gaultheria shallon Pursh., Vaccinium ovatum Pursh. and Rhododendron macrophyllum G. Don. A discussion of environmental factors and the species encountered is included in Byrd's (1950) study of vegetation zones on the dunes at Waldport. These dunes are presently all in private ownership, and are slowly being subdivided and built into communities and resorts.

Egler (1934) describes the plant communities on the Coos Bay dunes. These communities can be divided into those beginning development on the sand plains (low, moist areas) and on the sandhills (active sand areas and dunes). Picea sitchensis (Sitka spruce) is found along the immediate shore and on moist sites farther inland, while Pseudotsuga menzeisii (Mirb.) Franco. (Douglas fir) is found on drier sites. The regional climax species, Tsuga heterophylla (western hemlock) and Thuja plicata (red cedar), are found on the dunes in areas which presumably have been free from disturbance for some time. Their occurrence, however, is not common.

A general discussion of climate, dune forms, and dune communities is included by Reardon (1959) in his study of the mammalian fauna of the wooded dunes of the middle Oregon coast. His primary study on the deer mouse (Peromyscus maniculatus rubidus) was conducted on a forested "sand island" directly west of Cleawox Lake. It is thought to be a remnant of the forest standing on these dunes prior to the present period of activity. The forest presently is a mixed stand of conifers: Pinus contorta, Tsuga heterophylla, Picea sitchensis and Pseudotsuga menziesii with the usual dense ericaceous understory.

In the first known study of Oregon coastal dune vegetation to use quantitative data, Kumler (1963) used an ordination technique to describe plant succession on active sand areas. He also included physiological studies of certain adaptative features of the native dune plants. The recent study of Green (1965) traces the development of vegetation on stabilization plantings of Ammophila arenaria, Cytisus scoparius (L.) Link. and Pinus contorta on the area between the Siuslaw and Siltcoos Rivers. She studied plantings of these species made in 1937 and in each of the years between 1951 and 1963.

Because of the dynamic nature of the dune landscape, the vegetation is in constant change and can easily be found in many stages of development. The most obvious places for development to begin are the moist deflation plains. A number of these deflation plains, in various stages of vegetation development, will be used to study the communities and successional sequences found in these particular habitats.

IV. DEFLATION PLAINS

Introduction

The sand which forms the large moving dunes of the Oregon coast (the oblique and parabola dunes) is blown by the wind, first from the beaches, and then, as the dune moves further inland, from the sand supply at the windward base of the dune. If the rate of movement is faster than the rate of resupply from the beach; or, if the supply from the beach is materially reduced (by the building of a foredune), a situation can arise in which sand removal at the windward base of the dune is reduced or stopped. When this occurs, the sand is said to have reached a "deflation base" (Cooper, 1958, p.55). One of two situations set this deflation base: either all of the sand has been removed and substratum is exposed; or, more commonly, the surface nears or reaches the water table, resulting in wet sand which is not easily blown away.

Throughout his book, Cooper (1958) calls these areas on the Oregon coast "deflation plains". In practically every case their deflation bases are set by the water table. The only other place that an approximate equivalent of this term is used is in Lemberg's work (1933, p. 102) where "Deflationsflächen" are described as dry, shallow depressions with an exposed moraine substratum and very poor vegetation. Low, moist depressions set by the water table and supporting luxuriant vegetation are called "Erosionsmulden" by Lemberg. These terms are also used by Gerhardt (1900) and other German authors.

Another type of moist dune habitat is the inter-dune depression, perhaps best typified by the parallel ridge system of alternating dunes and valleys, but also found anywhere that interdune depressions reach the water table. These are the "pannes" of the French (DuVigneaud, 1947), the "Dünentäler" of the Germans (Gerhardt, 1900), the "slacks" of the British (Ranwell, 1959) and the swales of the Americans (Kurz, 1942). They are frequently characterized by standing water for a good part of the year, and, of course, a hydrophytic vegetation. They differ from the deflation plains in size, location, and amount and duration of standing water.

Along the Oregon coast, deflation plains are associated with both parabola dune systems and oblique dunes, in both cases near their windward bases. They are located fairly close to the shore, usually no more than half a kilometer, are variable in size (20 to 40 ha.) and generally have water standing in parts of them for varying periods during the year. Rather than being totally flat, the surface usually is low and quite wet in the middle and at the lower (windward) edge, then slopes upward toward the sides and base of the dune, providing successively drier habitats.

This stabilized sand surface provides an excellent starting point for vegetation. Pioneer species quickly become established and development takes place at a rapid rate. Because of the dynamic character of the dune landscape, deflation plains are continually being formed, colonized by plants, and destroyed by new moving dunes at various places in the dune system, thus making possible the observation and study of many phases of deflation plain history at one time. The similarity of formation and of habitat from one deflation plain to the next makes them easily recognizable and useful in studying vegetation and plant succession.

The specific study of these particular dune habitats seems to have been largely neglected. Gerhardt (1900) lists the species found in the "Dünentäler" of the German coast, and Lemberg (1933) mentions the rich flora of the Finnish "Erosionsmulden". The pioneer plants of the "pannes" near Dunkerque, France, were listed by DuVigneaud (1947). He notes particularly the occurrence of communities in relation to moisture conditions. Steers and Jensen (1953) studied the ericaceous slacks along the east coast of England, and Willis, et al. (1959b) discussed the correlation between species distribution and the number of months in a year that water stood in the slacks at Braunton Burrows. A brief discussion of the slack environment is also given by Chapman (1964) in his book on English coastal vegetation.

In the United States, Harshberger (1902, p. 642) termed the vegetation of the depressions of the New Jersey dunes a "xerophytic marsh association" with species common to wetlands rather than characteristic of dunes. Kurz (1942) observed an acid swale with vegetation distinctly different from the surrounding dunes, and with many familiar marsh species. On the Oregon coast, House (1914a) noted only that meadows started in the moist hollows. Egler (1934) showed the "sand plain" as an initial phase in the succession of vegetation on the dunes, and gave a general description of the plant groupings present on these sand plains.

It was apparent that a thorough study of the vegetation of the deflation plains along the Oregon coast would not only be interesting and informative, but would also be a necessary contribution toward a fuller understanding of the Oregon coastal dune landscape. The general objectives of such a study were: (1) to list the plant species found on these areas and to determine the occurrence, if any, of more or less well defined plant communities; (2) to speculate about plant succession on deflation plains and the part it plays in the overall dynamics of dune vegetation; and (3) to describe certain of these areas, both for present information and as a record for future study and reference.

Method of Study

Reconnaissance and Selection of Study Areas

Before an ecological study of this type can be outlined in terms of definite objectives and procedures, the investigator must become thoroughly familiar with the landscape he will be later studying in detail. This is logically accomplished both through the literature and by travels in the field.

Since literature was scarce for this particular study, the author had to depend mostly on field observations. These were made during the summer and autumn of 1963, and involved some 8000 km. of travel along the Oregon coast. Foot travel was considerable since very few roads passable to ordinary vehicles provide access to the dune areas. A very important adjunct to the travel was the use of aerial photographs. Just about all of the dune areas have been covered by at least one government agency and these photographs are readily available. They are almost indispensable to any kind of understanding of the dynamics of dune processes, as well as for locating certain dune features—deflation plains, in this case. An added bonus to the discovery of the usefulness of aerial photographs was the fact that often the same area had been photographed many years apart, and comparisons of vegetation development could be made.

The final part of the formal reconnaissance phase was an aerial flight over the dune areas. This is very useful in that the investigator can photograph specific areas, and, more importantly, get a "feel" for the area by seeing great portions of it at once. It should be emphasized, however, that reconnaissance is never completed. Only continuous observation, even when working on smaller scale, specific projects, can lead to the ultimate understanding of, and familiarity with, the landscape that is the mark of a successful ecologist.

As a result of this reconnaissance, it was decided to make detailed studies on six representative deflation plains (primary study sites) that showed a wide range in vegetation, but which were otherwise similar with respect to size, distance from the ocean, formative processes and so on. The farthest north of these is at Sand Lake, about 32 km. southwest of Tillamook. The next is on the south side of the mouth of the Yaquina River at Newport. Two, Sutton Creek and Lily Lake, are located on the Coos Bay dune sheet north of Florence; the other two are south of Florence: Cleawox Lake between the Siuslaw and Siltcoos Rivers; and Carter Lake Transect a little to the south of the Siltcoos River.

In addition, five other areas (secondary study sites) were sampled, but not considered representative because of size, location, or other unusual features. They will be only briefly described. Table 3 lists these 11 areas, along with their study site code symbols and specific location. Figure 6 is a composite Geological Survey map showing the location of the areas situated between Heceta Head and Tahkenitch Creek. See the map of the Oregon coast, Figure 3, for the other areas. The deflation plains north of Florence are also marked on Figure 40, an oblique aerial photograph.

Collection of the Data

Two basic problems face every community ecologist as he goes into the field to obtain quantitative data on the vegetation he is studying: how to sample, and where to take the samples. On the deflation plains two things further complicate the problem. First, not only are there differences between deflation plains; but there are also differences within them, as for example, vegetation ranging from pioneer herbaceous sites to mature forest on a single area. Secondly, while the herbaceous vegetation is easily sampled, the thick shrub and dense forest vegetation is frequently all but impenetrable. To handle both of these situations frequent improvisations of established routines must be made.

TABLE 3. Primary and secondary study sites. Symbol, name and legal and geographic location.

Study site symbol	Name	Location: Legal	Location: Geographic
Primary Study Sites:			
S L	Sand Lake	T3S, R10W, Sec. 19 SW$\frac{1}{4}$	Tillamook County, 29 km. SW of Tillamook, 3.5 km W of Sandlake on north side of Galloway Road.
N	Newport	T11S, R11W, Sec 17 SW$\frac{1}{4}$; Sec 18, SE$\frac{1}{4}$; Sec 19, NE$\frac{1}{4}$	Lincoln County, 1.5 km. S of Newport, immediately adjacent to south jetty, Yaquina Bay.
L L	Lily Lake	T17S, R12W, Sec 22, W$\frac{1}{2}$	Lane County, 13 km. N of Florence, 1 km. W on county road.
S C	Sutton Creek	T17S, R12W, Sec 27, W$\frac{1}{2}$ of SW$\frac{1}{4}$	Lane County, 9 km. N of Florence, 2.5 km. NW on private road along Sutton Creek.
G P	Cleawox Lake	T19S, R12W, Sec 9, S$\frac{1}{2}$; Sec 16, NW$\frac{1}{4}$	Lane County, 5 km. S of Florence, 1.5 km. W of Cleawox Lake.
C L X	Carter Lake Transect	T20S, R12W, Sec 5, S$\frac{1}{2}$	Douglas County, 13 km. S of Florence, 0.5 km. NW of end of trail from Carter Lake Campground.
Secondary Study Sites:			
S L 2	Sand Lake - 2	T3S, R10W, Sec 19, W$\frac{1}{2}$ of NE$\frac{1}{4}$	0.5 km. NE from SL.
S C 2	Sutton Creek - 2	T17S, R12W, Sec 27, SW$\frac{1}{4}$ of NW$\frac{1}{4}$	0.8 km. SE of south end of LL.
H B	Heceta Beach	T17S, R12W, Sec 34, W$\frac{1}{2}$ of SW$\frac{1}{4}$, Sec 33, E$\frac{1}{2}$ of SE$\frac{1}{4}$	0.8 km. S of SC.
C L	Carter Lake	T20S, R12W, Sec 5, SW$\frac{1}{4}$ of SE$\frac{1}{4}$	At west end of Carter Lake Campground trail.
T	Tahkenitch Creek	T20S, R12W, Sec. 29, W$\frac{1}{2}$ of W$\frac{1}{2}$ Sec 30, E$\frac{1}{2}$ of E$\frac{1}{2}$	Douglas County, 21 km. S of Florence, 1 km. W of Tahkenitch Lake Campground.

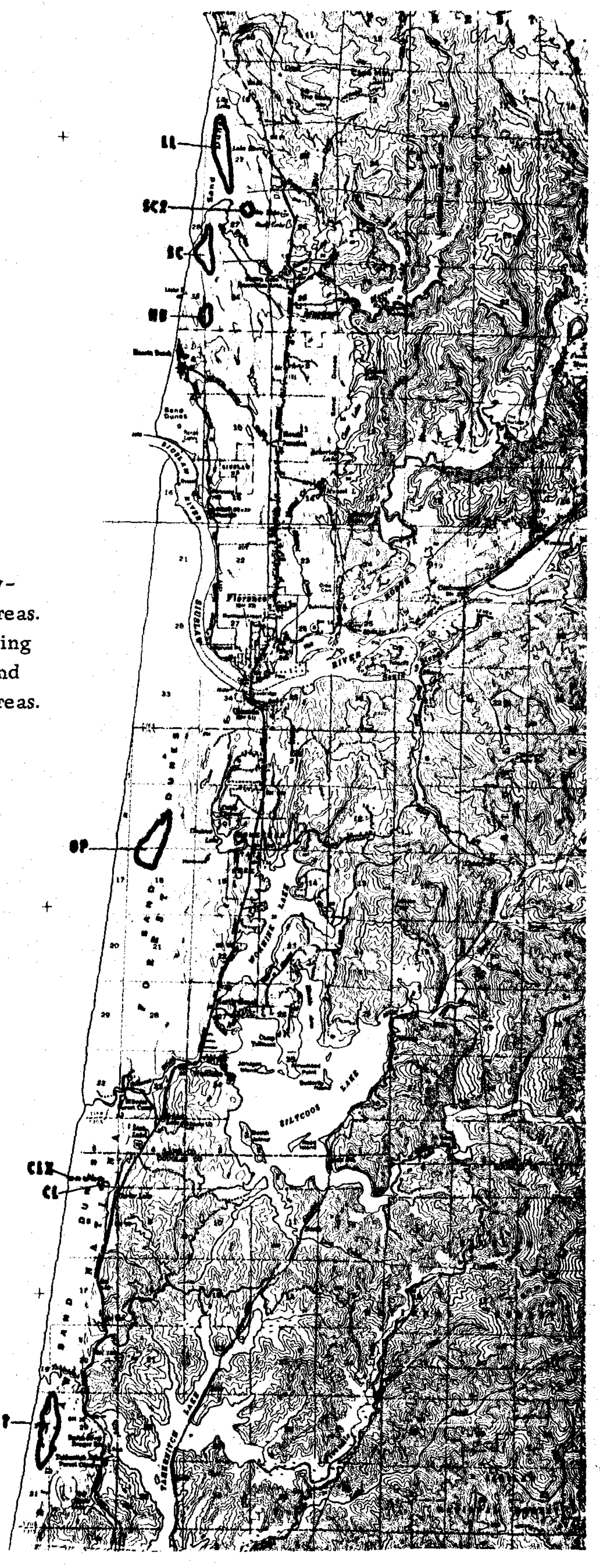
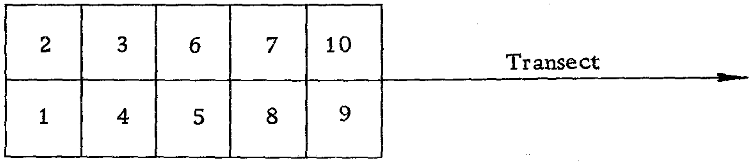


Figure 6. Map of Oregon coast from Heceta Head to Tahkenitch Creek showing location of study areas. See Table 10 for meaning of study site symbols and location of all study areas.

Plot Size and Number. The most frequently used quadrat size for herbaceous vegetation is the square yard or square meter. The latter was arbitrarily chosen for this study. Subsequent experience, however, led to the speculation that the smaller quadrats (two square feet) used by Poulton and Tisdale (1961) on range vegetation, and by Thilenius (1964) on the understory of white oak forests would have served just as well. More detailed studies utilizing a species-area curve would be needed to confirm this.

The shrubs and tree seedlings (up to about one m. in height) were sampled with the meter square quadrat. Beyond this height, they usually grew as a thicket such that quantitative assessment could be accomplished only by walking around the thicket or by looking down on it from a high point. As the trees matured, the understory cleared a little, and occasionally it was possible to lay out a six meter square quadrat. This was about maximum manageable size under these conditions, and several times smaller quadrats were used.

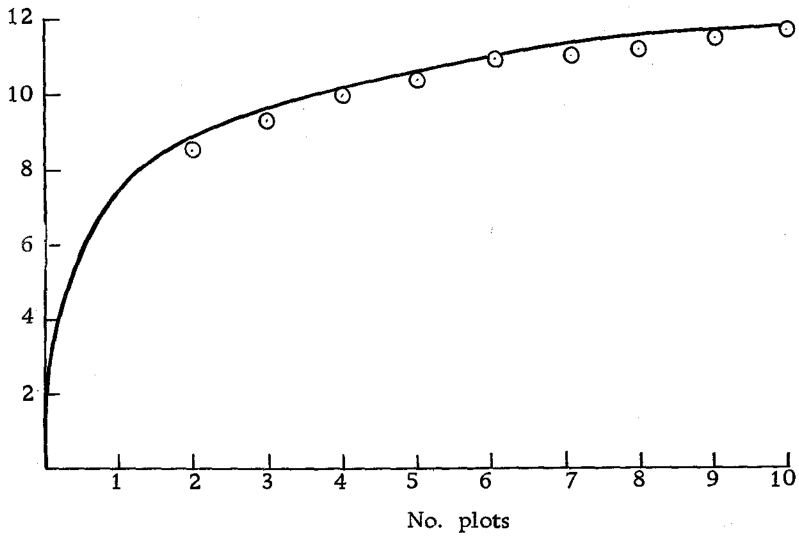
The number of meter-square quadrats to use for sampling the herbaceous vegetation of a single site was based both on time and effort requirements; and on the species-area curve. This latter gives information that will assist in determining the smallest number of quadrats that will yield satisfactory data (Cain and Castro, 1959, p. 167-172). Figure 7 shows the results of plotting number of quadrats against increasing totals of listed species for a series of ten



a. Arrangement of quadrats

No. of quadrats	1	2	3	4	5	6	7	8	9	10
Accumulative total of listed species (Aug)	7.8	8.5	9.4	10.0	10.6	10.9	11.2	11.4	11.6	11.8
Percent of total species	66	72	80	85	90	92	95	97	98	100

b. Species-quadrat data used in plotting curve



c. The species-area curve

Figure 7. The species - area curve.

adjacent quadrats on a number of herbaceous vegetation sites. On the average, 66 percent of the species were listed in the first quadrat, and 90 percent were listed by the fifth, the point where the curve is just about level. Five adjacent quadrats were thus used, three on one side and two on the other side of the transect in the manner shown in Figure 8. The tall shrub and forest vegetation was sampled as frequently as possible by the methods discussed above.

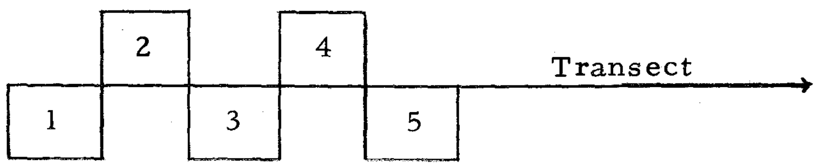


Figure 8. Layout of quadrats for each herbaceous sampling stand.

Sampling Locations. Each group of five quadrats and each tall shrub and forest sample was designated a "stand", and represents an area of vegetation generally uniform with respect to species composition, elevation, moisture, and exposure. The herbaceous stands were located at 15 m. intervals along transects which were located so as to best sample the variation existing on the deflation plain. If the stand fell on an obvious ecotone between two vegetation types, or communities, it was shifted laterally if possible, or forward or backward, to avoid the ecotone. This is an application of the technique of stratification, or recognition of homogeneous vegetation units, as outlined by Poulton and Tisdale (1961, p. 15). Following a transect through the thicket and forest was generally not feasible so in these situations stands were sampled whenever it was possible to do so.

This method of sampling is quite subjective, finding no small support in the Braun-Blanquet school of community classification (Whittaker, 1962, p. 129-130):

> Samples are in general, though not always, chosen to represent community-types; and sample choice is affected by subjective factors including the phytosociologist's preliminary interpretations of the vegetation, his conceptions of units as influenced by both precedent and the desire to recognize new community-types, his judgements of typical or representative vs. atypical and mixed stands, of stable vs. unstable ones, etc. Randomization is not used for sample choice; samples are chosen to represent the range of variation in the vegetation studied. . . The choice generally is, and should be, frankly subjective.

The objectives of this study, the type of vegetation being studied, and the intended analysis of the data favored this type of approach.

Data Recorded. A listing of the species[9] and the percent cover contributed by each was recorded for each of the five quadrats of the stand. Proportion of bare ground and litter was also noted. No attempt was made to determine density "since so many of the dune species reproduce from rhizomes it was impractical to tally the number of individual plants. Therefore percentage of cover was used as the criterion of dominance." (Boyce, 1954, p. 33).

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[9] A complete list of species names, authorities, and common names is given in Appendix Table I. Except as noted in the Appendix names are based on Peck, 1961.

For simplicity, percent cover was recorded as "cover classes", but because of the many species which were present in only small amounts, the usual breakdown of ten equal cover class units from one to ten (e.g., cover class one represents one to ten percent cover; two represents 11 to 20 percent cover; and so on) proved to be impractical and misleading. Instead, the eight coverage classes listed by Poulton (1962, p. 12) were used (See Table 4). More emphasis is placed on the lower class ranges in which most of the deflation plain species fall. As Poulton notes: "When making these estimates, extreme care should be exercised to estimate each species as though its canopies, in normal form and spread, were just touching from plant to plant and thus to estimate the percent of ground surface that would be covered. These estimates, for all species, may well total over 100 per cent. . . "

For shrubs and tree seedlings occurring within each quadrat, the above information as well as average height was noted. Species composition, average cover and height was recorded as well as possible for the impenetrable thickets. Where plots could be laid out in the forests, species, number, cover, trunk diameter, and height were recorded for the trees; and species, cover and height for the understory vegetation.

TABLE 4. Coverage classes (Poulton, 1962, p. 12).

Class	Class range (%)	Midpoint
1	0+ - 1	0.5
2	1+ - 5	3.0
3	5+ - 10	7.5
4	10+ - 25	17.5
5	25+ - 50	37.5
6	50+ - 75	62.5
7	75+ - 95	85.0
8	95+ - 100	97.5

Other Data. Obtaining a visual record of the vegetation was considered an important part of the study. Both color and black and white photographs were taken of as many different vegetation types as possible. These photographs were numbered and catalogued, and will remain on file for future reference.

Two permanent transects were established. On the Carter Lake Transect, vegetation data was obtained by laying down a meter-square quadrat every three m. along a 550 m. transect running from high tide line, across the foredune, and through the deflation plain behind the foredune. In addition a topographic profile was obtained (using a range pole and hand Abney level); and soil samples were taken at various locations along the transect and analyzed for pH, organic matter and total salts.[10] At Sand Lake, a transect was established at right angles to the long axis of the deflation plain. Vegetation data was taken by laying down meter-square quadrats every three m. A sketch was made showing relative elevations and roughly outlining the topographic profile.

To facilitate data taking and movement to and from the study area, the author designed a lightweight, open end, folding meter-square quadrat that incorporates a combination vertical measuring rod and carrying handle. It was fabricated by the Oregon State University Physical Plant from aluminum and weighs about 1.3 kg. The open end is a very necessary feature when working in dense

[10]Soil analysis by Oregon State University Soil Testing Laboratory.

or high vegetation. Figure 9 shows the quadrat and details of its construction.

Analysis of the Data

The analytic principles used for the basic arrangement of the field data were essentially those of the Braun-Blanquet school of community classification as outlined by Ellenberg (1956, p. 45-57). The first step was the transfer of the stand information (average cover for the stand and frequency[11]) from the data cards to a preliminary organization table. Based on experience gained in the field, and on the data in the table, the species were then rearranged into rough groupings according to their mutual occurrence. In the sorting process species which showed no affinity for a particular grouping or which occurred so infrequently as to preclude their assignment to a specific grouping were designated "non-significant species". When this grouping process was accomplished, the stands were then rearranged along two gradients; dry to wet sites, and herbaceous to forest vegetation. In these tables, the

[11] Frequency here refers to the proportion of quadrats of a stand in which the species occurred.

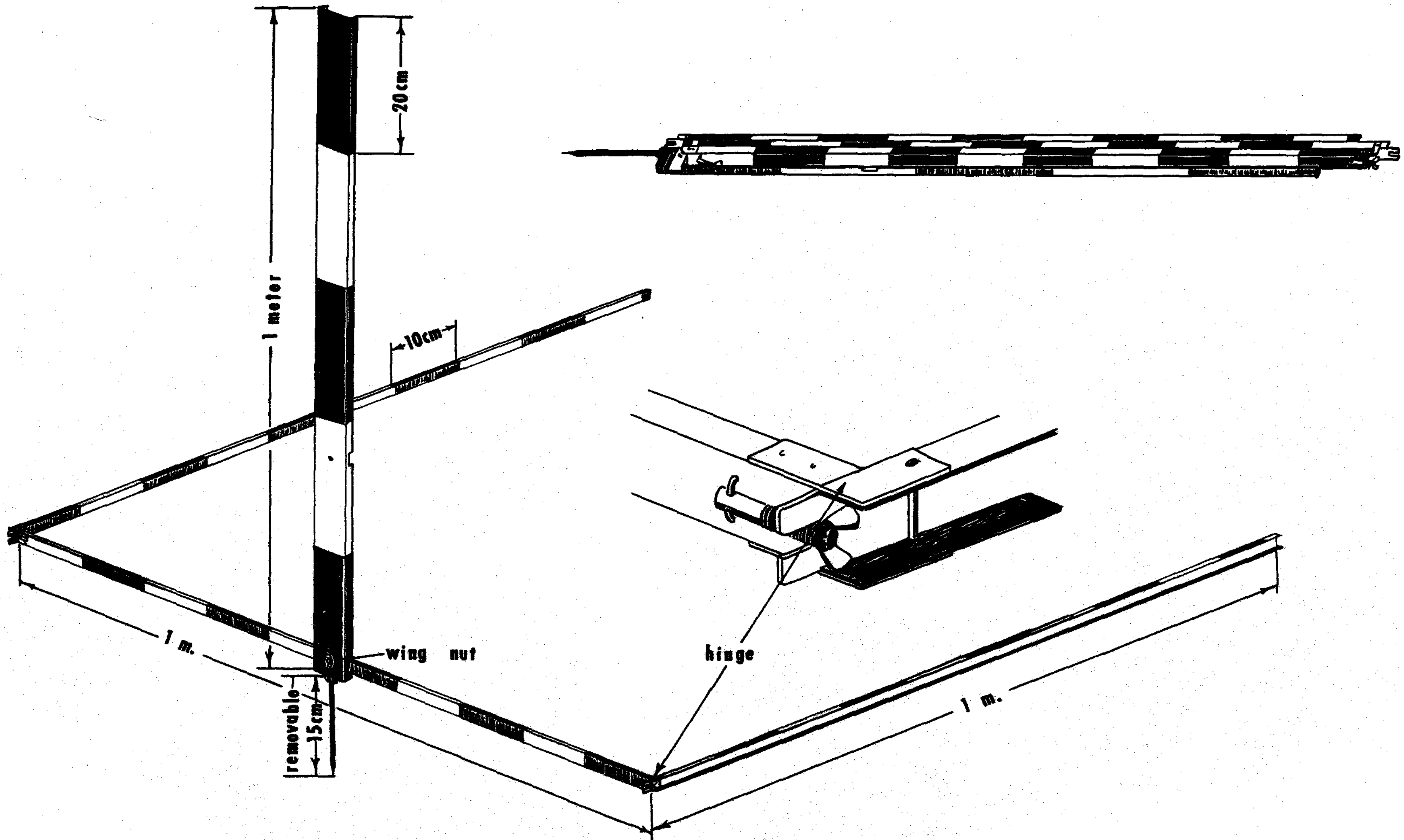

Figure 9. Folding quadrat used in sampling herbaceous vegetation.

the stands were arranged without regard to the deflation plains from which they were taken.

By this time, certain "differential-species"[12] began to stand out, and the species and stands were rearranged in additional organization tables to bring together the species of differential groups and the stands characterized by them, the objective being to obtain "groups of samples (stands) which are relatively homogeneous and relatively distinct from other groups and which can be characterized by diagnostic species." (Whittaker, 1962, p. 131). These "homogenous groupings" are the plant communities of the deflation plains.

From the completed "differential-table", the following values were calculated for each species within each community: (1) constancy (percentage of stands of each community in which the species occurred); (2) average cover (cover class of each species as an average of the community stands in which it occurred); (3) constancy-cover value (constancy multiplied by average cover to give a measure of the species' importance within the community); and (4) frequency (percentage of total quadrats of each community in which the species occurred). In the tall shrub and forest communities, where each sample was designated a stand, constancy and frequency are identical.

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[12]"Species present in the samples (stands) of one grouping, and absent or less important in those of another, closely related grouping" (Whittaker, 1962, p. 131).

The four classes of information were then organized into a survey table showing the relationship of each species within each community. The further arrangement of this community data into a hierarchy of lower or higher units was not an objective of this study.

Various data from the survey table and other field notes were arranged into figures and tables to provide descriptive information concerning the vegetation of the various deflation plains.

The data on the permanent transect at Carter Lake was plotted along the topographic profile to show the relative importance of each community along the transect. To show both cover and occurrence of the species, the cover values of the species of each community at each sampling point were totaled and these community values were then plotted along separate profiles above the topographic profile to provide a comparison between community occurrence and topography, elevation, and certain soil conditions.

Vegetation and Succession on Deflation Plains

During the summer of 1964, six deflation plains designated "primary study sites" and five designated "secondary study sites" were sampled according to the methods outlined in the previous section. No set number of stands was taken in each deflation plain, but effort was concentrated on the primary study sites to sample as completely as possible the different types of vegetation occurring on them. The secondary sites were sampled to provide a wider range of conditions as well as additional information.

Of the 134 stands sampled for this study, 100, or 75 percent, were taken on the six primary sites. The remaining 34 were taken on the secondary sites. A total of 522 quadrats were used (including the tall shrub and tree plots).

In Appendix III is shown a photographic reduction of the differential table that was the result of repeated re-arrangements of the initial organization tables. Both cover and frequency values are shown for all of the species encountered in the 134 sampling stands. Four herbaceous communities based on a moisture gradient from dry to very wet were first delineated on the table; then a successional gradient is presented with the first four herbaceous communities representing the initial stage, then grading to low shrub, tall shrub and finally forest communities.

Of the 91 species encountered in the sampling of the deflation plains, 41 were finally included as significant species in the community groupings. Fifty species plus the mosses were relegated to the non-significant group (bottom half of the chart). One species, *Juncus lesueurii*, had the highest constancy and frequency (occurrence in total quadrats) of any on the chart, and clearly showed no marked affinity for any community. Casual field observation would probably fail to detect this ubiquitous character because of the plant's generally inconspicuous growth form. Mosses were also included in the non-significant group because only limited information was available concerning individual species' names and distribution.

The differential table shows, then, seven clearly recognizable communities occuring on the deflation plains. Four are herbaceous communities distinguished by species composition and moisture conditions: the dry meadow, the meadow, the rush meadow and the marsh. Two are characterized by shrubs and one by trees, moisture and species differences playing a lesser role: the low shrub, the tall shrub, and the forest.

The survey table (Table 5) summarizes various characteristics for each community: frequency, constancy, average cover, and constancy-cover value (CCV). The constancy-cover value is taken as the measure of a species' relative importance in the various communities. The average CCV for each species group within each community (Table 6) is a measure of how the species group fits into the pattern of communities. These tables are discussed further below. A diagrammatic comparison of the importance of nine species in the four herbaceous communities is given in Figure 10. Included are the two most important species of each community and the ubiquitous _J. lesueurii_.

TABLE 5. Community survey table. Frequency (FRE), constancy (CON), cover (COV) and constancy-cover value (CCV) for each of the 41 species characterizing the seven deflation plain communities. Frequency is percent occurrence in the total quadrats taken in the community; constancy is percent occurrence in the stands of the community. Average values for each species group within each community are also indicated.

COMMUNITY	DRY MEADOW				MEADOW				RUSH MEADOW				MARSH				LOW SHRUB				TALL SHRUB				FOREST			
No. stands	27				30				24				17				14				8				14			
Total no. quadrats	135				138				112				53				62				8				14			
Avg. no. spp. / stand	8				14				16				10				17				11				5			
Ground water depth (Aug)(cm.)	> 90				90				45				15				--				--				--			
Avg. bare ground	6.0				4.4				3.8				2.8				2.9				none				none			
	FRE	CON	COV	CCV	FRE	CON	COV	CCV	FRE	CON	COV	CCV	FRE	CON	COV	CCV	FRE	CON	COV	CCV	FRE	CON	COV	CCV	FRE	CON	COV	CCV
DRY MEADOW GROUP:																												
Lupinus littoralis	78	93	3.0	298	82	93	2.6	242	25	29	1.6	46					3	14	1.0	14								
Ammophila arenaria	48	70	2.0	140	17	40	1.0	40	12	25	1.3	33					8	21	1.0	21								
Poa macrantha	59	89	1.3	116	12	30	1.0	30	6	17	1.0	17																
Polygonum paronchyia	34	63	1.4	88	17	27	1.3	35	4	8	1.0	8																
Glehnia leiocarpa	41	63	1.3	82	1	3	1.0	3																				
Lathyrus littoralis	16	30	1.6	48																								
Agoseris apargioides	7	19	1.0	19																								
Cardionema ramosissima	7	7	2.5	18																								
Convolvulus soldanella	4	15	1.0	15																								
(Average values)	33	50	1.7	92	16	24	1.6	43	5	10	1.2	12					1	4	1.0	17								
MEADOW GROUP:																												
Festuca rubra	10	22	1.3	29	48	63	2.7	170	8	17	1.3	22	2	6	1.0	6	50	57	1.9	108								
Aira praecox	13	22	1.5	33	67	80	2.1	168	54	71	1.5	107	8	6	3.0	18	27	36	1.2	43								
Hypochaeris radicata	21	37	1.1	41	76	90	1.6	144	74	79	1.3	103	19	18	1.0	18	58	64	1.1	70	13	13	1.0	13				
Fragaria chiloensis	22	41	1.3	53	62	77	1.7	131	53	75	1.8	135	17	18	2.0	36	60	71	1.4	99	25	25	1.5	38				
Agrostis pallens	10	11	2.3	25	27	40	2.2	88	19	25	1.2	30					21	36	1.0	36								
Anaphalis margaritacea	7	26	1.1	29	20	43	1.4	60	7	17	1.3	22					13	21	1.0	21								
Lotus purshianus					21	23	2.4	55	4	8	1.0	8					35	36	1.4	50								
Tanacetum camphoratum	10	33	1.3	43	18	40	1.3	52	18	29	1.0	29					5	14	1.0	14								
Achillea millefolium	2	7	1.0	7	20	27	1.4	38	1	4	1.0	4					2	7	1.0	7								
(Average values)	11	25	1.4	29	40	54	1.9	101	26	36	1.3	51	5	5	1.6	9	30	38	1.2	50	4	4	1.0	6				
RUSH MEADOW GROUP:																												
Juncus phaeocephalus	24	41	1.1	45	40	50	1.6	80	94	96	3.1	298	62	76	2.7	205	82	93	2.2	204	63	63	2.6	164				
Trifolium willdenovii	1	7	1.0	7	17	30	1.4	42	74	79	2.9	229	38	53	1.4	74	60	64	1.8	115	25	25	1.0	25				
Aster subspicatus					14	30	1.0	30	57	79	1.4	111	47	53	2.0	106	81	93	1.3	121	25	25	1.0	25				
Sisyrinchium californicum					2	7	1.0	7	42	71	1.5	107	30	35	2.3	81	37	64	1.0	64	38	38	1.3	49				
Juncus falcatus					33	60	1.0	60	49	71	1.0	71	40	41	1.7	70	45	71	1.2	85	38	38	1.0	38				
Agrostis palustris					5	10	1.3	13	22	25	2.5	63	28	29	2.4	70					13	13	1.0	13				
Epilobium franciscanum					6	23	1.0	23	19	38	1.0	38	6	12	1.0	12	10	29	1.0	29								
Centaurium umbellatum					4	10	1.0	10	9	17	1.8	31	2	6	1.1	7	3	7	1.0	7	13	13	1.0	13				
Holcus lanatus					4	7	2.0	14	12	21	1.4	29	4	12	3.0	36	3	14	3.5	49								
Mimulus guttatus					1	3	1.0	3	9	29	1.0	29																
(Average values)	5	8	1.1	9	12	22	1.3	27	39	53	1.8	100	27	33	2.1	70	33	44	1.7	69	23	22	1.5	38				
MARSH GROUP:																												
Carex obnupta					2	3	1.0	3	12	21	1.2	25	79	82	4.1	336	15	29	3.5	101	38	38	5.0	190	43	43	4.7	202
Potentilla anserina					1	3	1.0	3	32	50	1.8	90	55	53	3.4	180	5	7	1.0	7	50	50	2.0	100				
Hypericum anagalloides									13	21	1.6	34	23	41	2.1	86	16	36	2.0	72	13	13	1.0	13				
Ranunculus flammula									12	21	1.4	29	25	41	1.7	70	13	36	1.2	43	50	50	1.0	50				
Lilaeopsis occidentalis									8	21	1.0	21	30	29	2.0	58	5	7	1.0	7	13	13	1.0	13				
Carex hindsii									12	29	1.0	29	11	18	2.7	47	15	21	1.3	27	25	25	2.5	63				
Lycopus uniflorus									8	13	1.7	22	6	18	1.3	23	8	14	1.0	14	38	38	3.0	114				
(Average values)					1	2	1.0	2	13	23	1.5	36	31	39	2.2	109	9	21	1.5	36	31	32	2.0	70	6	6	1.0	30
SHRUB GROUP:																												
Salix hookeriana					5	13	1.0	13	23	38	1.7	65	32	59	1.8	106	63	79	3.3	261	100	100	3.9	390	43	43	4.0	172
Gaultheria shallon					6	13	1.0	13	13	25	1.8	45	4	12	1.0	12	56	100	1.9	190	88	88	3.3	290	57	57	2.8	160
Vaccinium ovatum	1	4	1.0	4	13	20	1.2	24	4	8	1.0	8	9	18	1.0	18	34	57	2.4	137	38	38	2.0	76	57	57	3.0	171
Myrica californica					1	3	1.0	3	1	4	1.0	4	4	3	1.0	3	27	57	2.0	114	100	100	5.4	540	71	71	3.6	256
(Average values)	1	1	1.0	1	6	12	1.1	13	10	18	1.4	31	12	23	1.2	34	45	73	2.4	176	82	82	3.7	324	57	57	3.4	190
FOREST GROUP:																												
Pinus contorta	1	4	1.0	4	16	30	1.6	48	5	17	1.0	17	2	3	1.0	3	24	64	1.8	115	38	38	3.7	141	93	93	6.1	567
Picea sitchensis					1	3	1.0	3	1	4	1.0	4					5	14	1.0	14	13	13	1.0	13	64	64	4.0	256
(Average values)	1	1	1.0	2	8	17	1.3	25	3	10	1.0	10	1	2	1.0	2	15	39	1.4	65	25	25	2.4	77	79	79	5.2	412

TABLE 6. Constancy-cover values for the various species groupings within the seven deflation plain communities.

Species group	Communities: Dry meadow	Meadow	Rush meadow	Marsh	Low shrub	Tall shrub	Forest
Dry meadow	92	43	12	--	17	--	--
Meadow	29	101	51	9	50	6	--
Rush meadow	9	27	100	70	69	38	--
Marsh	--	2	36	109	36	70	30
Shrub	1	13	31	35	176	324	190
Forest	2	25	10	2	65	77	412

Plant Communities of the Deflation Plains

The Dry Meadow Community. Situated at the driest end of the community sequence, the dry meadow is almost exclusively dominated by three species: *Lupinus littoralis*, *Ammophila arenaria*, and *Poa macrantha*, the first being more important than the other two put together (based on CCV's of 298 for *Lupinus* and 140 and 116 for *Ammophila* and *Poa* respectively). Also characteristic of this community (CCV in parenthes): *Polygonum paronchyia* (88), *Glehnia leiocarpa* (82), *Lathyrus littoralis* (48), and *Agoseris apargioides* (19). Two species are important only in local areas: *Cardionema ramosissima* (18) and *Convolvulus soldanella* (15). *Lathyrus* and *Convolvulus* were restricted to this community; *Cardionema*, *Glehnia*, and *Agoseris* were noticed outside the community only very occasionally (Table 5).

Lupinus, on the other hand, is almost equally important in the meadow community (Figure 10), but observation of the species in the field and its higher CCV in the dry meadow clearly put it into this community. *Ammophila* (Figure 10) and *Poa* are both well adapted to sites where active sand deposition is taking place, but also persist in the more moist, stable communities. The remaining species all tolerate sand deposition in varying amounts. This community is illustrated in Figures 11 and 12.

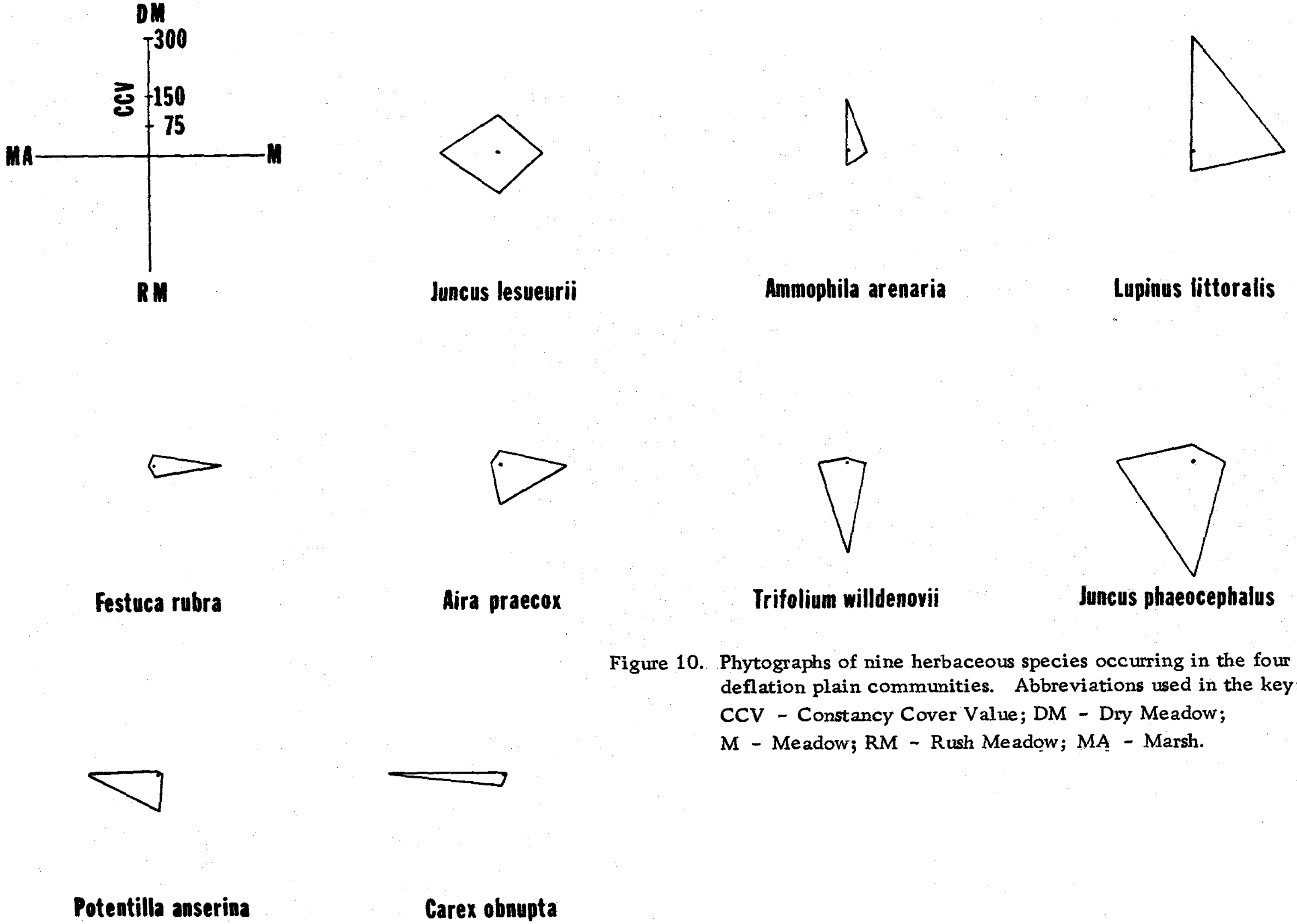


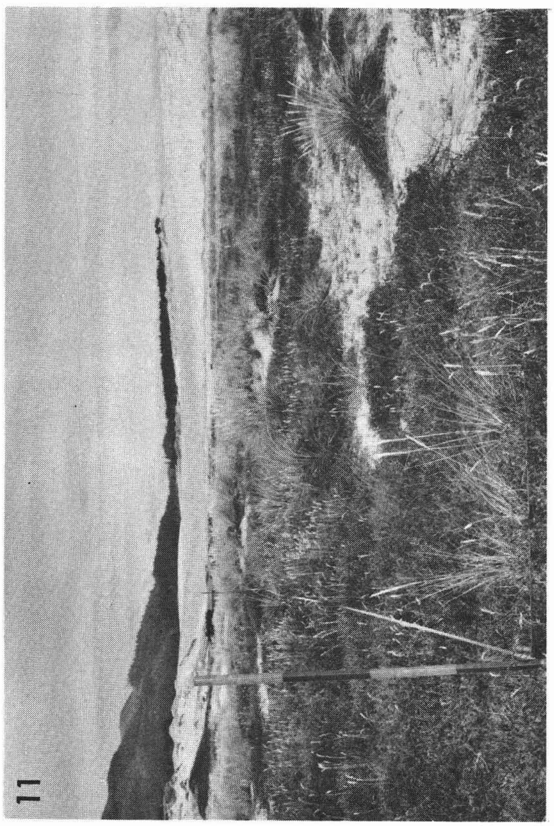
Figure 10. Phytographs of nine herbaceous species occurring in the four deflation plain communities. Abbreviations used in the key: CCV - Constancy Cover Value; DM - Dry Meadow; M - Meadow; RM - Rush Meadow; MA - Marsh.

Figure 11. Dry Meadow. Closed stand of Ammophila arenaria with low growth of Lupinus littoralis. July. Sand Lake.

Figure 12. Dry Meadow. Open stand of Poa macrantha, Glehnia leiocarpa and Lathyrus littoralis. September. Sand Lake.

Figure 13. Dunes formed by sand accumulating in thick stands of Juncus lesueurii. Just northwest of Sutton Creek-2.

Figure 14. Meadow. Luxuriant growth of Lupinus littoralis with Hypochaeris radicata as an "understory". June. Sand Lake.



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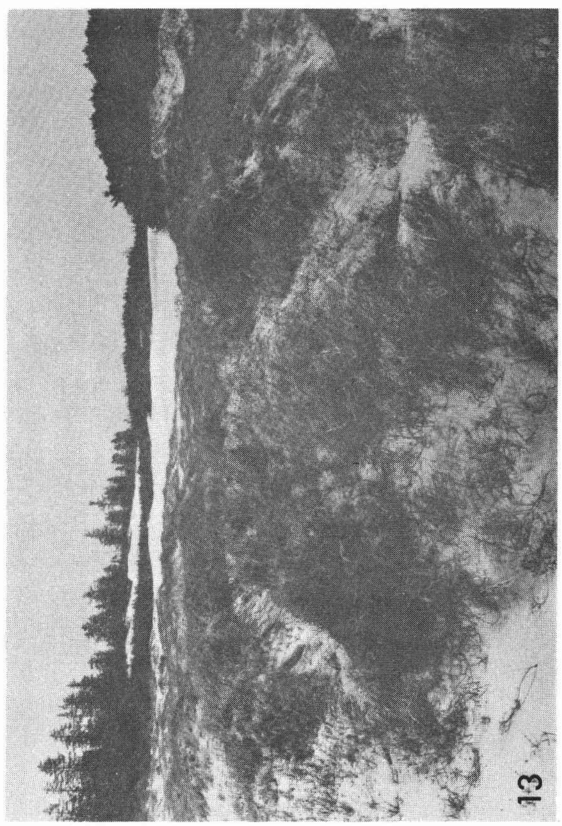

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14

The community site is dry, and is hummocky where _Ammophila_ clumps have collected sand. It is usually open (average bare ground-litter cover class is 6, or 50 to 75 percent), and has the least number of species (average, eight) of all the communities. It occurs on raised areas on the deflation plain, around the higher edges, and very typically behind the foredune, where it grades into a pure _Ammophila_ community seaward as sand deposition increases. Sand deposition in the dry meadow varies from almost none where _Lupinus_ dominates in dense stands, to considerable amounts in open stands of _Poa_, _Glehnia_, _Lathyrus_, or _Convolvulus_. There is no evidence of soil development.

Phenologically, the community reaches its peak in late spring—May and early June—when most of the species are growing vigorously and are in full bloom. Particularly striking is _Lupinus_ which begins growth as early as December, is in full bloom by May, and generally is completely dried up by the end of August. _Polygonum_, on the other hand, has inconspicuous flowers during the entire year.

The average CCV for all of the species of this community is 92. It drops to 43 in the meadow, 12 in the rush meadow, and the species group is absent in the marsh (Table 6). Thus, except possibly for _Lupinus_, all the species can be considered characteristic of this community. Of the other species groups, only that of the meadow contributes any significant amount of vegetation to this community, and this is comparatively small (CCV 29). Marsh, shrub and forest species are insignificant.

Species from the non-significant group include J. lesueurii (CCV 84), Erechtites prenanthoides, and Solidago spathulata (One percent constancy[13] each). The presence of J. lesueurii indicates that the water table is, or at one time was, near the surface. This species tolerates considerable sand deposition, and will even form dunes if there is a sufficient amount growing in one place (Figure 13).

The Meadow Community. Average number of species increases in this community to 14, while bare ground—litter cover decreases to 4.4 (about 17 percent). The dominant species in terms of constancy and cover are Festuca rubra and Aira praecox (CCV 170 and 168 respectively). Decreasing constancy and cover values in the other communities (Figure 10 and Table 5) make these fairly characteristic species. Less characteristic, but almost as important are Hypochaeris radicata (144) and Fragaria chiloensis (131), these two also being important in the rush-meadow, and to a lesser extent, in the marsh.

The remaining five species show much less importance in the other communities. Agrostis pallens (88), Anaphalis margaritacea (60), Lotus purshianus (55), Tanacetum camphoratum (52) and

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[13] Occurring in the stands of the community.

Achillea millefolium (38) are all characteristic of this community and habitat (Table 5). The average CCV for the community species group is 101, dropping to 29 in the dry meadow, 51 in the rush meadow and an insignificant nine in the marsh (Table 6). The relatively high CCV of the dry meadow group in this community (43) is due mainly to Lupinus, which forms an important part of the vegetation. Species of the shrub and forest group also show some importance here, seedlings of Pinus contorta being most numerous.

The habitat is generally level, more moist than the previous community, and there is essentially no sand deposition. There is no specific zone of occurrence within the deflation plain, the distance to water table apparently being the chief factor. The water table at one location, Sand Lake, was at 90 cm. in July. There is no apparent soil development, but frequently there is up to three cm. of dry or decaying organic matter under the dense cover of lupine and grasses.

The characteristic vegetative appearance of the community is contributed chiefly by Fescue, Agrostis, and Lupine. Aira is a very inconspicuous annual that is usually dried up by early summer. Fragaria is also inconspicuous except where it dominates an area, as it occasionally does. In mid-summer, the showy flowers of Hypochaeris, Tanacetum, Anaphalis and Achillea present a striking aspect. Figures 14, 19 and 20 illustrate this community.

The data for Hypochaeris radicata is complicated by the fact that it frequently includes the data for Leontodon nudicaulis which grows in close association with the former. Except in the flowering stage, the two species are very difficult to differentiate, so they were both included under Hypochaeris which appeared to be the more abundant species. In dense stands, they exist as more or less inconspicuous rosettes under the grass and lupine cover.

J. lesueurii occurs in 93 percent of the community stands and has a high CCV of 112, which is consistent with its widespread distribution. Other species found in this community are (percent constancy in parenthesis): Gnaphalium purpureum (40), Rumex acetosella (37), Festuca myuros (20), Poa confinis (13), Aira caryophyllea (79), Plantago lanceolata (7), Abronia latifolia (3), Lotus formosissimus (3), Rumex crispus (3), Senecio jacobea (3), and Orthocarpus pusillus (3). Mosses occurred in 27 percent of the stands with a CCV of 35. Species identified from this group include: Ceratodon purpureus, Polytrichum juniperinum, Campylium hispidulum, and Brachythecium spp.

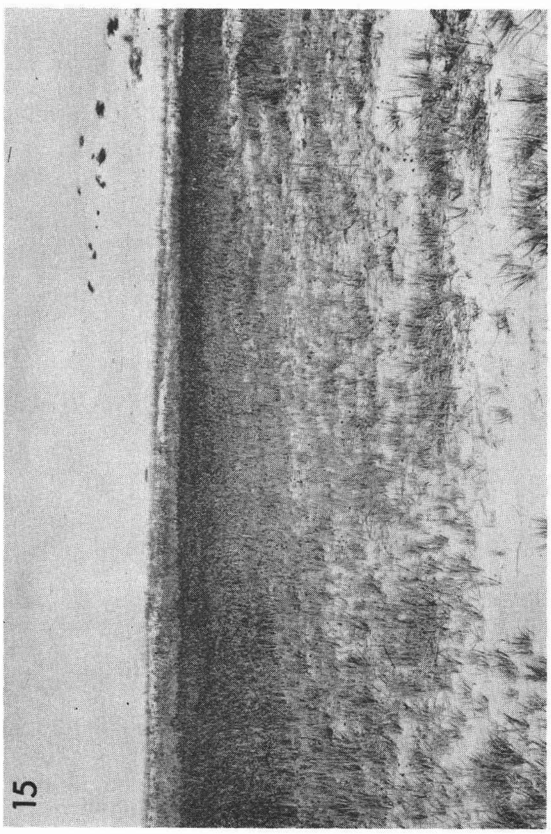
The Rush Meadow Community. This community is impressive for its dense, low growth of Trifolium willdenovii (CVV 229), and thick stands of Juncus phaeocephalus (298)(Figures 15, 16). The latter, however, is more extensively distributed in the other communities (Figure 10). Average number of species goes up to 16 and the bare

Figure 15. Rush Meadow. *Agrostis palustris* foreground; *Juncus phaeocephalus*, *J. falcatus* dark band in center. July. Sand Lake-2.

Figure 16. Rush Meadow. Dense stand of *Juncus phaeocephalus*. *Trifolium willdenovii* forms a low "understory". *Potentilla anserina* also present. In background isolated clumps of *Ammophila arenaria*. August. Carter Lake Transect.

Figure 17. Marsh. Almost pure stand of *Carex obnupta*, 45 to 75 cm. tall. *Potentilla anserina* forms a rather sparse understory. Shrubs are *Salix hookeriana*. August. Just west of ponds, Tahkenitch Creek.

Figure 18. Tall Shrub. Road cut through extremely thick stand of *Myrica californica* and *Salix hookeriana*. Note *Picea sitchensis* growing through dense cover. August. Northwest corner Cleawox Lake (GP).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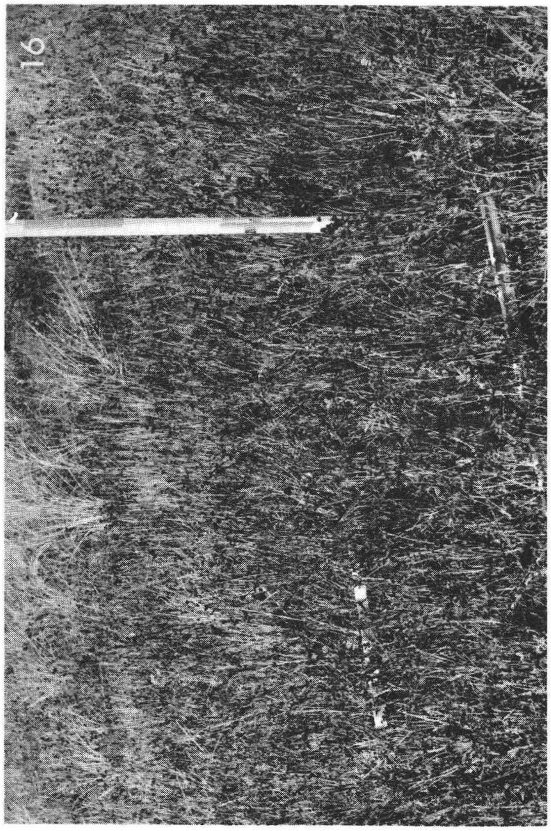
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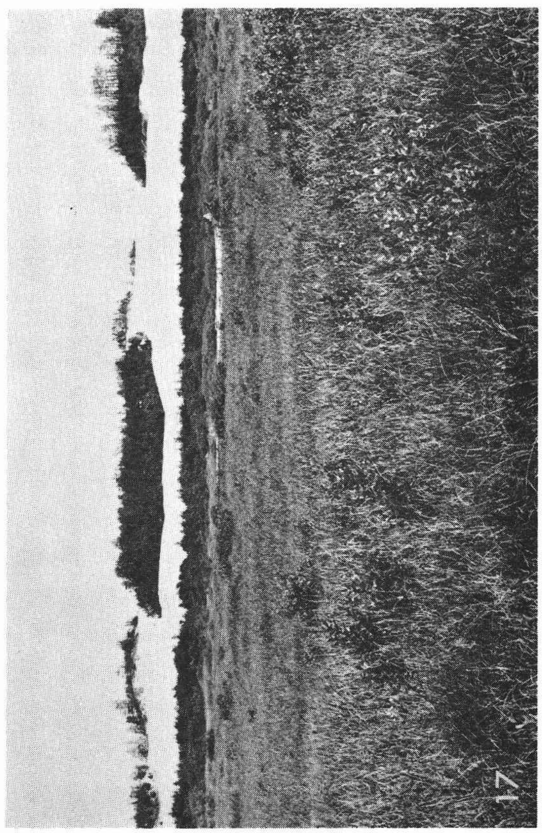
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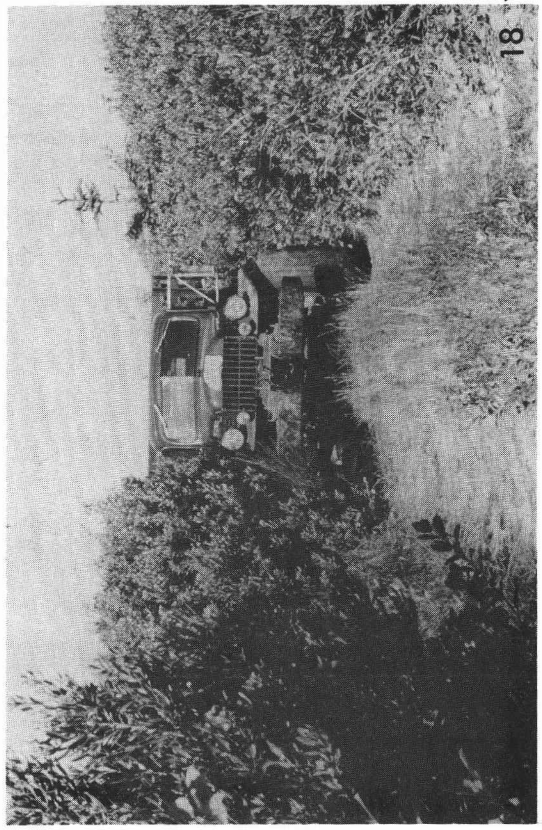
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ground—litter cover class is down to 3.8 (about eight percent). Other important characteristic species (CCV's in parenthesis) are *Aster subspicatus* (111), *Sisyrinchium californicum* (107), *Juncus falcatus* (71—also fairly widely distributed), and *Agrostis palustris* (63). The remaining species, *Epilobium franciscanum* (38), *Centaurium umbellatum* (31), *Holcus lanatus* (29) and *Mimulus guttatus* (29) are less important, but quite closely restricted to this community (Table 5).

The species group CCV for this community is 100. It is quite high in the marsh community (70), but considerably lower in the meadow and dry meadow (Table 6). The meadow group, however, is the highest (51) in the rush meadow. The shrub and forest groups show about the same relative importance except that seedlings of *Salix hookeriana* are more numerous than any of the other species.

The community occurs on lower ground than the previous. Sometimes as little as 15 cm. vertical difference will separate them. The water table at Lily Lake, measured in July, was about 45 cm. below the surface. There is a thin layer of raw organic matter on the surface, followed by up to two cm. of a rusty colored peat-like substance, below which, in the pure sand, is a very dense root layer about four cm. thick. Several centimeters of water stand on these sites for several months during the winter.

In the spring, the huge, pink flowers of *Trifolium* are the first to appear. Where Mimulus is abundant (only a few places, notably Lily Lake), there is a very showy display of the brown-spotted yellow flowers during early summer. Sisyrinchium, Epilobium and Centaurium flower most of the summer, the dark blue flowers of Aster being the last to appear.

Of the non-significant group, J. lesueurii is present in 83 percent of the stands (CCV 106), and the mosses in 33 percent. This latter includes the species already listed plus others that could not be readily identified. Also of highest constancy in this community are (percent constancy in parenthesis) Spiranthes romanzoffiana (33), Orthocarpus castillejoides (29), Sagina procumbens (21), the fern, Botrychium silaifolium (17), Sagina crassicaulis (13), Elymus mollis (8—very accidental on this site), Epipactis gigantea (8), the insectivorous Drosera rotundifolia (8), Hypericum perforatum (8), Carex viridula (8), Cerastium holosteoides (8) and Juncus bufonius (4).

The Marsh Community. These sites are marshy in the sense that they are quite wet most of the year. At one location (Cleawox Lake) water table was only 15 cm. below the surface in August, and on most stands, kneeling or standing in one spot would produce moisture (except in the very driest periods). Obviously these are the lowest areas, in which free water stands the longest. Average species number per stand drops to ten and bare ground-litter to 2.8

(about five percent).

The most characteristic species of this community is Carex obnupta with an impressive CCV of 336 (Figure 17; Table 5) almost entirely restricted to these very wet sites. Another good indicator species is Potentilla anserina (CCV 180). Figure 10 shows graphically their rather restricted ranges. The other five species also prefer wet sites such as these. They include (CCV in parenthesis) Hypericum anagalloides (86), the low, creeping Ranunculus flammula (70), the tiny, weird Lilaeopsis occidentalis (58), Carex hindsii (47) and Lycopus uniflorus (23). The yellow flowers of Potentilla and Ranunculus provide the principal color in this community, while the drooping spikes of C. obnupta and jointed leaves of Lilaeopsis add their distinctive appearances.

The species group CCV for the marsh is 114 (Table 6). In the rush meadow it is 36, and is reduced to practically nothing in the remaining two. As would be expected, the rush meadow species group is the only other one of importance in the marsh. Shrubs, particularly Salix, are present, but the forest group is insignificant.

The ever present J. lesueurii occurs in 71 percent of the stands (CCV 150), and the mosses reach their greatest development in this community with a CCV of 123. Additional species found to a large degree in this community (non-significant species) include (percent constancy in parenthesis): Galium triflorum (18), Veronica scutellata (18), Agrostis ampla (18) Eleocharis palustris (12), Plantago subnuda (12), Stellaria calycantha (12), the club moss, Lycopodium inundatum (6), Galium trifidum (6), Juncus acuminatus (6) and Scirpus americanus (6).

The Low Shrub Community. The stands making up this community were chosen only on the basis of the high occurrence within the stand of shrubs and tree seedlings less than 120 cm. tall. The presence of species of the four herbaceous communities was not considered. As a result, each community species group, except the dry meadow, has generally the same importance (CCV) in this community. The significance of this is brought out later.

The most important shrub here is Salix hookeriana (CCV 261) with Gaultheria shallon (190) close behind, although the latter has the highest constancy (100 percent). Vaccinium ovatum (137) and Myrica californica (114) also are part of this group, as are seedlings of Pinus contorta (115). Picea sitchensis has a very low value (14) (Table 5). The combined CCV's of the shrub and forest group is 241, considerably higher than the remainder of the species groups represented in the community (Table 6).

Mosses occurred in 43 percent of the stands. J. lesueurii in all of them; and Spirea douglasii and Alnus rubra each in seven percent. Average number of species per stand was 17, and bare ground-litter, 2.9 (five percent).

To convey some idea of the density and size class distribution of the shrub species of this community, three 1.5 by 50 m. plots were laid out and sampled by counting six size classes of eight species of shrubs and tree seedlings present in the plots. These plots were located in a well-developed low shrub community at two ends of the Lily Lake deflation plain.

Table 7 shows that 336 individuals were counted, of which 32.4 percent were Gaultheria and 27.3 percent were Salix. The most numerous size class was 15 to 30 cm. (29.4 percent), and most of the Salix and Gaultheria were less than 30 cm. tall. The tallest were the two tree species, Alnus and Pinus. Average density over the three plots was 1.3 plants per square meter. The range around the average was slight.

The chief difference between the data of this table and that for the low shrub community in general is in the high proportion of Alnus. It is a wet site species, but is usually not found on sand, and Lily Lake is the only deflation plain where Alnus is present in large amounts. The community is illustrated in Figures 42 and 57.

The Tall Shrub Community. This community is very similar to the preceding except that the species making up the shrub layer are taller—from 1.2 to about 3 m. (Figure 18). It is also more of a thicket, in some cases being impenetrable. Herbaceous species decrease—on the tallest and thickest stands they occur only on the

TABLE 7. Composition of a low shrub community (LL). Distribution by size class of eight shrub and tree species on three 1.5 by 50 m. plots.

Species	Size class (height in centimeters)						Total ind. ea. species	Percent of total inds.
	< 15	15-30	30-60	60-90	90-120	> 120		
Gaultheria shallon	34	54	14	7	-	-	109	32.4
Salix hookeriana	27	16	22	20	7	-	92	27.3
Alnus rubra	3	2	12	17	6	1	41	12.2
Pinus contorta	6	8	9	14	2	1	40	11.9
Vaccinium ovatum	7	11	8	1	-	-	27	8.0
Picea sitchensis	2	5	11	2	-	-	20	5.9
Myrica californica	-	3	2	1	-	-	6	1.7
Ledum columbianum	-	-	1	-	-	-	1	0.2
Total ea. class	79	99	79	62	15	2	336	
Percent of total of all classes	23.5	29.4	23.5	18.4	4.4	0.5		100.0

fringes. The most important of the herbaceous species belong to the marsh group (CCV 78). The ground under the shrub thickets is devoid of plant life. There is only a layer of plant debris and leaves which varies considerably in depth.

The wet character of the sites is further shown by the predominance of Myrica (540) and Salix (390), both present in 100 percent of the stands (Table 5). Gaultheria (290) and Vaccinium (76) are usually associated with Myrica on slightly drier sites than those on which Salix occurs, and constitute the main species of the wind formed shrub stands close to the ocean shore. A series of five meter square quadrats taken at random in such a stand at Sutton Creek showed the following average percent composition: Myrica, 25; Pinus, 20; Gaultheria, 20; Vaccinium, 15; Salix, 10; Picea, 5; Lonicera involucratum, 3; and Ledum columbianum, 2. Myrica also is associated with Salix, and this accounts for its high importance in the community.

Pinus (CCV 114) is frequently a part of this community, usually growing just a little taller than its associated shrubs. In a few cases, Pinus was the only species, representing a young forest. A six by six m. plot was laid out with great difficulty in one such stand at Tahkenitch Creek. Cover was 100 percent Pinus at an even three meters tall. The following numbers in each size class (diameter at the ground) were recorded: less than 2.5 cm., 13; 2.5 to 5 cm., 20;

5 to 10 cm., 7; over 10 cm., 1. This last one, about 18 cm., was probably older than the rest of the individuals (it was also considerably taller). Density was one tree per square meter, the intervening space being taken up completely by wide-spreading branches down to ground level. Basal area was 25 square meters per hectare.

The very scattered Picea (CCV 13) usually can be readily recognized by the way their crowns extend as much as a meter above the surrounding vegetation (Figures 18, 57, 60). The combined shrub-forest group CCV is 401, twice that in the low shrub community (Table 6).

Moss is less important in this community (13 percent constancy), and even J. lesueurii drops to 38 percent. Other species found, particularly around the edges of the tall shrubs (percent constancy in parenthesis), were the blue flowered Gentiana sceptrum (13), a fern, Struthiopteris spicant (13), and the low growing shrubs, Vaccinium uliginosum (13) and Arctostaphylos uva-ursi (13). Mixed in with the taller shrubs was Ledum columbianum (38) and Lonicera involucrata (13).

The composition of a five by six m. shrub plot laid out at Sutton Creek (Table 8) shows Pinus contributing 75 percent of the tree cover; Salix, Gaultheria, and Vaccinium in the understory, and a minor herbaceous layer.

The tall shrub community varies considerably, and the data reported here is primarily useful in obtaining at best a rough idea of its appearance and composition.

TABLE 8. Composition of a tall shrub stand (SC). (5 by 6 m. plot).

Species	% Cover	Height (m.)	No. ind.	Base dia. (cm.)
Trees:				
Pinus contorta	75	3	12	7.5
Shrubs:				
Myrica californica	5	2		
Salix hookeriana	15	1		
Gaultheria shallon	10	0.8		
Vaccinium ovatum	10	0.5		
Herbs:				
Juncus phaeocephalus	10			
Juncus lesueurii	2			
Fragaria chiloensis	8			
Mosses:	50			
Litter:	30			

The Forest Community. Again a variable type, the forest can range from the impenetrable young *Pinus*-*Salix* forest, to open *Pinus* on marshy ground and thick *C. obnupta* understory, to the dark, open *Picea* forest with only a thick layer of mosses on the ground. Combined shrub-tree CCV for this community is 602, 200 more again than the previous (Table 6). It is dominated by *Pinus* (567), while Picea (256) varies from none to almost pure stands. *Gaultheria* (160) and *Vaccinium* (171) are usually a sparse, high shrub understory, while *Salix* (172) and *Myrica* (256) can vary from tall shrubs to trees a little shorter than the dominants (Table 5).

Carex obnupta occurred in open *Pinus* forests on marshy ground (43 percent of the stands). It grows in dense stands up to one m. tall on these sites. It is the only herbaceous species noted in the forest community. In the damp, dark forests, mosses grow thickly on the ground. These were chiefly *Eurhynchium oreganum* and *Mnium punctatum*. A liverwort, *Porella navicularis*, was picked up in one stand.

The litter-duff layer in the older forests was up to 15 cm. deep. The thick network of tree roots in and under the litter made it extremely difficult to determine the extent of soil development. However, a definite, darkening of the upper layers was apparent.

Data for five forest stands is presented in Table 9, showing percent cover, average diameter, height, and number of individuals for each tree species. In all of the stands where *Pinus* and *Picea* occur together, the latter are generally a little larger and taller. No seedlings of any species were found, and there were very few

TABLE 9. Analysis of five forest stands showing percent cover, average diameter, average height and number of individuals for each species (6 by 6 m. plots).

Table stand no.	1				2				3				4				5			
Location (study site)	Heceta Beach				Cleawox Lake				Sand Lake				Cleawox Lake				Cleawox Lake			
Species	% Cover	Ave. dia. (cm.)	Ht. (m.)	No. ind.	% Cover	Ave. dia. (cm.)	Ht. (m.)	No. ind.	% Cover	Ave. dia. (cm.)	Ht. (m.)	No. ind.	% Cover	Ave. dia. (cm.)	Ht. (m.)	No. ind.	% Cover	Ave. dia. (cm.)	Ht. (m.)	No. ind.
Tree																				
Pinus contorta	90	10.1	9.1	33	65	12.7	9.0	12	40	35.5	14	4	25	15.2	7.6	5				
Picea sitchensis					25	17.8	9.0	4	50	30.5	15	4	65	25.4	10.6	2	100	25.0	12.0	11
Shrub																				
Salix hookeriana	10	3.8	7.6	4													10	3.8	4.5	3
Myrica californica					5	2.5	3.0	2	5	7.6	3.6	7					10	7.6	3.6	4
Gaultheria shallon	10		3.0						1		0.3		30	2.5	3.0	7	3		2.4	
Vaccinium ovatum					15		1.5						10		1.5		2		2.4	
Herbaceous																				
Carex obnupta	70		0.9		25		0.9						15							
Moss					10				10				15							
Litter					65				90				70				100			
Diameter range (cm.)/ no. trees 5 cm. or less																				
Pinus contorta	5 to 20/6				3 to 20 /1				5 to 45/1				5 to 30/2				----------			
Picea sitchensis	----------				10 to 30/0				10to 45/0				20 to 30/0				5 to 30/1			

trees under 5 cm. in diameter, except in Stand 1, which was pure _Pinus_ of small size. Stand 3 had the largest trees, two of each species measuring 45 cm. diameter at breast height. Forests of this type are rare on the dunes, the range of the other four stands being most common. Figure 21 shows a dense growth of young _Pinus_ with some shrub understory. Figure 22 is an old stand of _Picea sitchensis_ with a few small _Pinus_ and essentially no understory. Figure 23 is an open stand of _Pinus_ on a very damp site with a thick ground cover of _Carex obnupta_.

Succession

The plant community has been variously, but similarly, defined as "...an aggregation of living organisms having mutual relationships among themselves and to their environment" (Oosting, 1956, p. 17); as "...an organized complex having a typical composition and structure that result from interactions through time" (Cain and Castro, 1959, p. 288); as "an abstract vegetation unit distinguished by physiognomic, structural, floristic, ecological or syndynamical criteria, or by any combination of these criteria" (Becking, 1957, p. 428); or "as a naturally occurring, stable combination of specific plant species which are in biological balance with each other and with their environment" (Walter, 1962, p. 4).[14]

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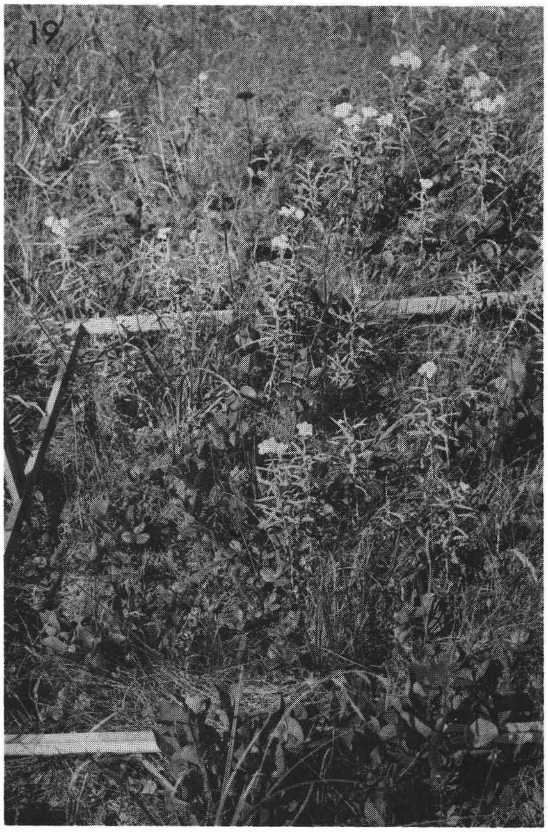
[14] "Unter einer Pflanzengemeinschaft verstehen wir eine in

Figure 19. Meadow. Fragaria chiloensis and Tanacetum camphoratum in Festuca rubra. A small Gaultheria shallon immediate foreground. August. Plot 5, Permanent Transect SLT-1, Sand Lake.

Figure 20. Meadow. Turf-like stand of Festuca rubra. Typical occurrence of Juncus lesueurii. August. Plot 4, Permanet Transect SLT-1, Sand Lake.

Figure 21. Forest. Dense stand of young Pinus contorta about 9 m. high, 5 to 10 cm. diameter. Note extensive lichen growth on tree trunks. Undergrowth is mainly Gaultheria shallon with some Vaccinium ovatum. July. Heceta Beach (HB).

Figure 22. Forest. Stand of old Picea sitchensis on low damp site, 15 to 20 m. high, 30 to 35 cm. diameter. Smaller trees are Pinus contorta. Few scattered shrubs, Gaultheria shallon. Ground covered with thick layer of organic material and mosses, chiefly Eurhynchium oreganum, some Mnium punctatum. Sand Lake.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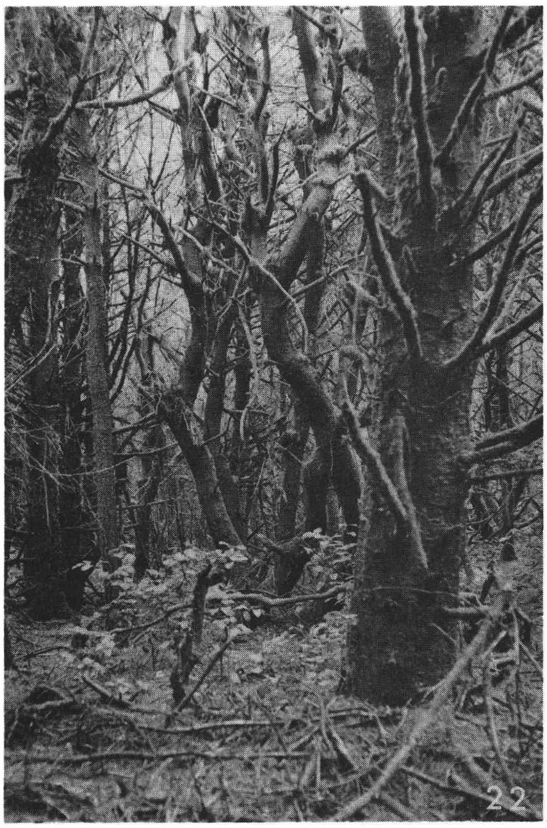
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Figure 23. Forest. Open stand of Pinus contorta, 7 to 10 m. high, 25 to 30 cm. diameter. Ground cover is Carex obnupta, up to 1 m. tall. August. Carter Lake.

Figure 24. Ecotone between rush meadow (right) and meadow (left). Vertical difference about 15 cm. August. Plot 57. Carter Lake Transect.

Figure 25. Mound of Ammophila arenaria on low, wet site. Species present from base upwards: Trifolium willdenovii, Juncus phaeocephalus, J. lesueurii, Epilobium franciscanum, Hypochaeris radicata, Lupinus littoralis, A. arenaria. Mound about 1 m. diameter, 0.5 m. tall. July. Sand Lake.

Figure 26. Permanent rush meadow stand. Area of deep standing water during winter and spring. Open cover of Juncus phaeocephalus, J. falcatus, J. lesueurii. Surrounded by Salix hookeriana up to 1 m. tall. August. Near Plot 12, Carter Lake Transect.


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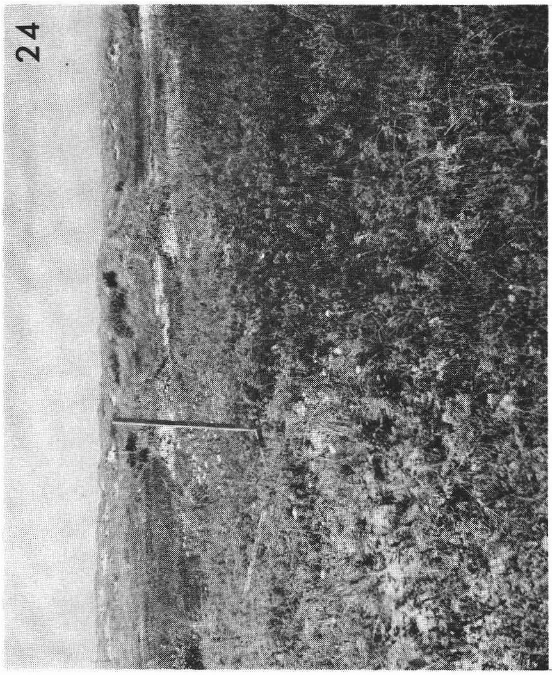
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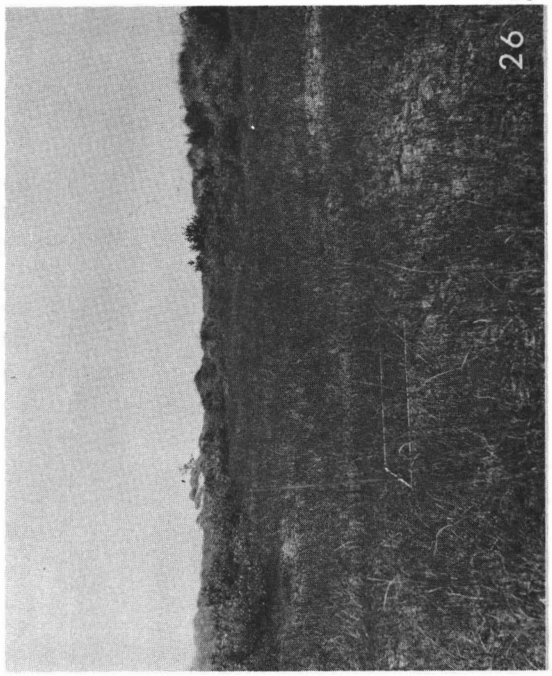
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In this study, the term "community" is used to designate an assemblage of species growing together <u>either</u> in a certain habitat (dry meadow, meadow, rush meadow, marsh); <u>or</u> as a grouping of species occurring at arbitrarily defined stages of development (herbaceous, low shrub, forest). Since few species are confined to specific habitats or stages of development, their relative importance in these situations becomes important both to define the limits of the community and to recognize ecotone stands, or stands which show conditions obviously not a part of the usual community pattern. No implication is made that the community is either fixed as concerns species and habitat conditions, or that it must of necessity proceed to a higher level of succession.

Although succession through a series of seral communities to a climax or self-maintaining community can be considered a "normal" occurrence in nature, it should be kept in mind that many biological and environmental factors can slow or prevent the process. On the sand dunes this is particularly noticeable. Oosting (1954), for instance, doubts that herbaceous vegetation patterns (zonation) are invariably indicators of successional change. He feels that topography as it influences wind, salt spray, moisture, and other environmental forces is the controlling factor in determining succession,

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der Natur vorkommende, mehr oder weniger stabile Kombination von bestimmten Pflanzenarten, die sich in einem ökologischen Gleichgewicht miteinander und mit ihrer Umwelt befinden."

and that the plants themselves have little to do with it (except that once a shrub stage is initiated, succession to forest is possible and probable). Martin (1959) concurs in this concept of topographic and environmental control.

This type of "polyclimax" situation can be found both on the low, wet sites of the deflation plains, and on the higher dunes with their more severe environmental conditions. The dry meadow is the result of only one process: the gradual slowing of sand deposition on a previously active area. This occurs behind the foredune, and here the community can be a succeeding stage to the pure *Ammophila* foredune community; and it occurs as a pioneer stage on parabola dunes or precipitation ridges when the supply of sand is reduced or cut off (by formation of a deflation plain). Succession would proceed to a meadow community similar to that of this study as cover increased, but many of the moist habitat species would be absent. It is possible, however, that sand deposition could maintain this community indefinitely, mostly by restricting the development of *Lupinus*, which is limited in its tolerance to sand burial. If succession occurs, eventually shrub and forest communities would develop (Kumler, 1963).

Succession on the bare sand of the deflation plain can begin with either of the three communities (meadow, rush meadow, marsh), depending upon moisture conditions. Probably the first species to become established are the rushes: *Juncus lesueurii, J. phaeocephalus* and *J. falcata*. *Trifolium willdenovii* and *Mimulus guttatus* are also pioneers. Shrub seedlings of *Myrica* and *Salix* establish quickly. The pattern of development then is generally toward the rush-meadow. On extremely wet sites, *Carex obnupta, Potentilla anserina* and their companions dominate. On the higher sites, species of the meadow become established, chiefly *Hypochaeris radicata, Fragaria chiloensis, Festuca rubra, Aira praecox*, and, of course, *Lupinus*.

The meadow can also develop from the marsh or the rush meadow through a successional sequence if dry sand is blown across the deflation plain and deposited on areas of thick vegetation. Unless there were a permanent rise in the water table, it would be almost impossible for succession to proceed the other way, that is from meadow to rush meadow to marsh. Very little increase in elevation is needed to change community types, as has been noted by several workers (Kurz, 1943; Willis *et al.*, 1959b). Examples of the effect of slight elevation differences are shown in Figures 24 and 25, the first showing the distinct line between a rush-meadow and a meadow stand; the second showing distribution of species on a 50 cm. high *Ammophila* mound located on a low, wet site.

The topographic and plant community profiles of the Carter Lake Transect (Figure 64, show no zonation or progression along a successional gradient. Instead the distribution of the communities is correlated with elevation, or distance from water table. And here, elevation is mostly a matter of sand deposition in vegetation, generally clumps of Ammophila. The establishment and survival of Ammophila on these low areas is a matter of chance so that there is little possibility for the development of any regular pattern. On these areas—the deflation plains behind the foredune—the vegetation advances inland as the sand is eroded to water table, but the type of community that is established depends upon mounds, drainage patterns, initial colonizers and so forth.

Usually the rapid establishment of Salix and Myrica and other shrubs initiates a successional sequence. But a community can be relatively permanent as is shown by the rush-meadow stand of Figure 26. This small depression is surrounded by Salix shrubs up to one meter high. Water stands in it up to 60 cm. deep all winter and spring, but it becomes quite dry in summer and fall. This situation occurs frequently, and in all cases, neither Salix seedlings nor marsh species become established. A long-time study of such an area would be very useful.

It is interesting to compare studies on European wet sand communities. In France, DuVigneaud (1947) divided the communities into xerosere and hydrosere as follows:

Xerosere

Transient *Ammophila arenaria*

Tortula/*Camptothecium*/*Galium verum*

Rosa spinossisma/*Ranunculus bulbosa*

Hippophaë rhamnoides/*Salix repens*

Calamagrostis epigeios/*Juncus obtusifolius*

Carex trinervis/*Salix repens*/*Ranunculus flammula*

Eleocharis palustris

Hydrosere

The succession of communities is frequently brought on by sand deposition on the wet site vegetation. Forest did not develop on these areas.

Willis, *et al*. (1959b) studied the slacks and hollows at Braunton Burrows in England, and distinguished the following communities, although noting that they had no sharp limits: (1) *Plantago*/*Leontodon* (shallow flooding one to five months of the year, no summer drying); (2) damp pasture (complex, depending on flooding, mostly grasses and sedges); (3) *Festuca rubra*/*Agrostis stolonifera* (driest community); (4) rush communities. They emphasized the apparent slight, but definite differences in moisture requirements and tolerance to flooding. Except for that initiated by sand movement, succession did not take place. As in much of the British dune landscape, forest did not occur.

On the deflation plains of the Oregon coast, however, forest development is almost inevitable. It can be seen from Tables 5 and 6 that the CCV's for the species groups within their respective communities are all around 100. The CCV for the shrub-forest group is 251 in the low shrub, 401 in the high shrub and 602 in the forest. This suggests that the first four communities are distinct, without definite seral relationships. They may develop as outlined previously, or they may not. The increasing CCV of the other three communities, on the other hand, confirms a successional progression in which each community succeeds a previous one. If this were carried to its theoretical end, a value of about 800 would be reached—a closed forest of 100 percent constancy and cover class eight (95 to 100 percent cover). Such a forest of Picea occurs just north of Cape Kiwanda, but it is on Pleistocene sand just adjacent to the recent dunes (note Egler's statement below).

The CCV for the shrub-forest species in the three communities—meadow, rush meadow, marsh—indicate, however, that development toward forest is almost without exception and can begin in any of the three communities. The presence of the three herbaceous species groups in the low shrub community also bear this out.

In the tall shrub community most of the herbaceous species of drier sites have dropped out, probably due to the fact that on the wet sites, the shrub and tree stands are more open, thus allowing these species to persist, while on the drier sites, growth is too dense to allow much understory growth. In the forest, everything is gone except for _C. obnupta_, which grows luxuriantly in the open, wet _Pinus_ stands. As is shown in Table 9, and it appears to be the general case, there is no reproduction of pine or spruce occurring within these forests.

Picea usually becomes established along with _Pinus_, or just a little later, apparently requiring a degree of protection from ocean winds as a seedling. Usually, however, by the time the pines are about two meters tall, the spruce will be half a meter or so taller, and from then on maintains this dominance. Mixtures of the types in Stands 2, 3, and 4, Table 9, are most common. Pure pine or spruce forest can be found. The forests around Florence are mostly even aged stands of pure pine, with no indications of succession to a spruce forest. Similarly the pure spruce forests probably began as pure stands or at most only with very low numbers of pine. At any rate, the classical concept of succession whereby a mature forest is replaced by another growing up through it is not completely valid for the sand dune pine and spruce forests.

However, where spruce and pine occur together, the former usually becomes the dominant tree, and probably over very long periods of time the pine dies out. Thus it appears that _Picea_ is the climax species on these low, wet sites near the shore. However, there are indications that a forest of Thuja plicata, one of the regional climax species, could develop if the area remained stable long enough and/or there were sufficient protection from the ocean winds. Scattered cedars, from saplings to trees 25 cm. in diameter occur in hollows near the shore on the Sand Lake dunes. A considerable stand can be found in and near Darlingtonia State Park north of Florence, an interesting bog area of Thuja, Ledum, the pitcher plant, Darlingtonia californica, Lysichitum americanum, Struthiopteris spicant and Spagnum sp.

Egler (1934, p. 39), on the other hand, states that Picea is a subclimax forest maintained by wind:

> Successive windfalls through many centuries favor the spruce because of prolific reproduction, so that eventually, if physiographic forces are inactive, an Aeolian Subclimax forest of spruce may cover the dunes as it now covers the Pleistocene formations.

Most of the extensive pine forest around Florence developed on deflation plains (Cooper, 1958, p. 88-93). This old (over 100 years), mostly mature, forest was extensively damaged by the Columbus Day, 1962, windstorm, and it would be interesting to observe vegetation changes occurring as a result of this opening up of the forest. As far as can be determined at the present time, there is nothing to indicate that Picea is going to succeed Pinus as the dominant species on the wet sites around Florence.

Wind, then, is the most important factor in initiating changes in the dune vegetation, both in the case of blowdown, and in the important effects of sand activity. It is frequently possible to see the remains of previous forests on present day deflation plains, indicating a definite cycle of sand movement in certain locations (Figure 45). As indicated earlier, fire has also been important, but usually this led to renewed sand activity, the effect in the end being again that of the wind and moving sand.

The successional relationships discussed in this section are presented diagramatically in Figure 27. The significant species of each community are also listed. It should be kept in mind that renewed sand activity—a new parabola dune or precipitation ridge crossing the deflation plain—would shunt the whole sequence back to bare sand.

A final point worthy of note is that the species of the deflation plains are not so characteristic of sand dune habitats as much as they are of wetland sites. The exception, of course, are the dry meadow species and others with adaptations for survival in habitats of shifting sand. Many, such as *Pinus contorta* and the introduced ruderals, are very widely distributed in both wet and dry habitats. Many of the remainder occur over a wide range in the western United States, some over the world. Thus while the habitat (the deflation plain) is unique and unusual, the vegetation that covers it is not

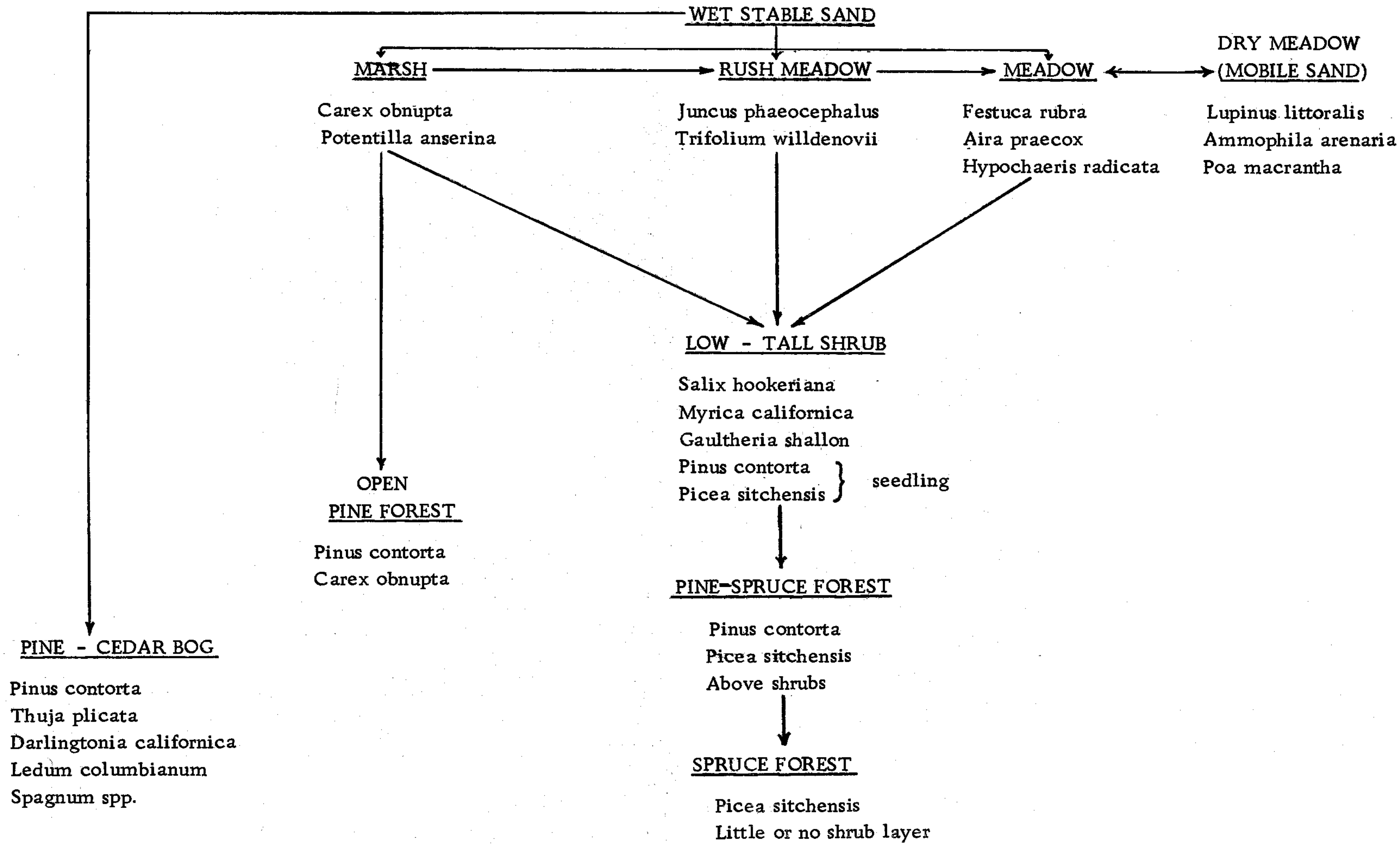


Figure 27. Successional relationships on sand dune deflation plains.

particularly so.

This does not, however, make the deflation plains any less interesting. As will be seen in the following section, they are areas of rapid change—change that can be reckoned in years instead of decades or centuries. For this reason, if for no other, they are worthy of study and description.

Description of the Deflation Plains

The purpose of this section is to provide a descriptive record of the deflation plains that were included in this study. This will include both a general description of the vegetation and features and photographs. Particularly useful are the aerial photographs taken several years apart, showing vegetation development.

All six of the primary sites will be described—the secondary only where interesting or unusual features warrant their mention. Table 3 lists these areas with their study site symbol, and geographical and legal location. Table 10 shows the distribution of sampling stands (by community) for each deflation plain.

Sand Lake

The deflation plain at Sand Lake has developed at the windward base of a large moving dune that is part of an extensive parabola system. The dune is the most recent of a series of at least four

TABLE 10. Number of sampling stands of each community on each study site.

Study site symbol	Dry Meadow	Meadow	Rush Meadow	Marsh	Low Shrub	High Shrub	Forest	Total
SL	14	7	4	-	-	-	1	26
N	2	3	1	5	-	-	1	12
LL	-	-	7	4	1	-	-	12
SC	-	4	2	2	6	2	-	16
GP	-	-	3	2	4	4	5	18
CLX	8	4	6	-	1	-	-	19
SL2	2	1	1	-	-	-	-	4
SC2	-	1	-	-	1	-	1	3
HB	-	2	-	-	1	-	3	6
CL	1	4	-	1	-	-	3	9
T	-	4	-	3	-	2	-	9
Total	27	28	24	18	14	8	14	134

dunes to move inland under the driving force of the southerly winds of the winter season. Figure 5 is a vertical aerial photograph showing the entire Sand Lake dune complex. The deflation plain and dune components are indicated.

This deflation plain and its vegetation is of recent origin. Figure 28 is a pair of aerial photographs taken 22 years apart. The bottom one shows only damp sand on the lower portion where the one on the top shows the most extensive vegetation development. Local residents confirm that this was a bare sand area just 20 years ago.

Figure 29 is a winter photo of the deflation plain looking southwest from the parabola dune. Figure 31 is a pair of photographs looking across the deflation plain from a high dune on the east side. Both photographs were taken from approximately the same location as evidenced by the snag in the left side of the photographs. The upper one was taken in about 1925, the lower in 1965. Note the absence of Ammophila in the early photograph and the extensive development of the grass in the recent. This pioneer species did not become widespread in this area until the early 1940's. It has since spread extensively, building high mounds on the low areas. This mound building takes place both by the deposition of sand on the clumps of grass, and by intermound erosion as the deflation plain develops.

A long narrow belt of Alnus and Salix, about 1.5 m. high, has

Figure 28. Sand Lake (SL). Aerial photographs showing vegetation development.

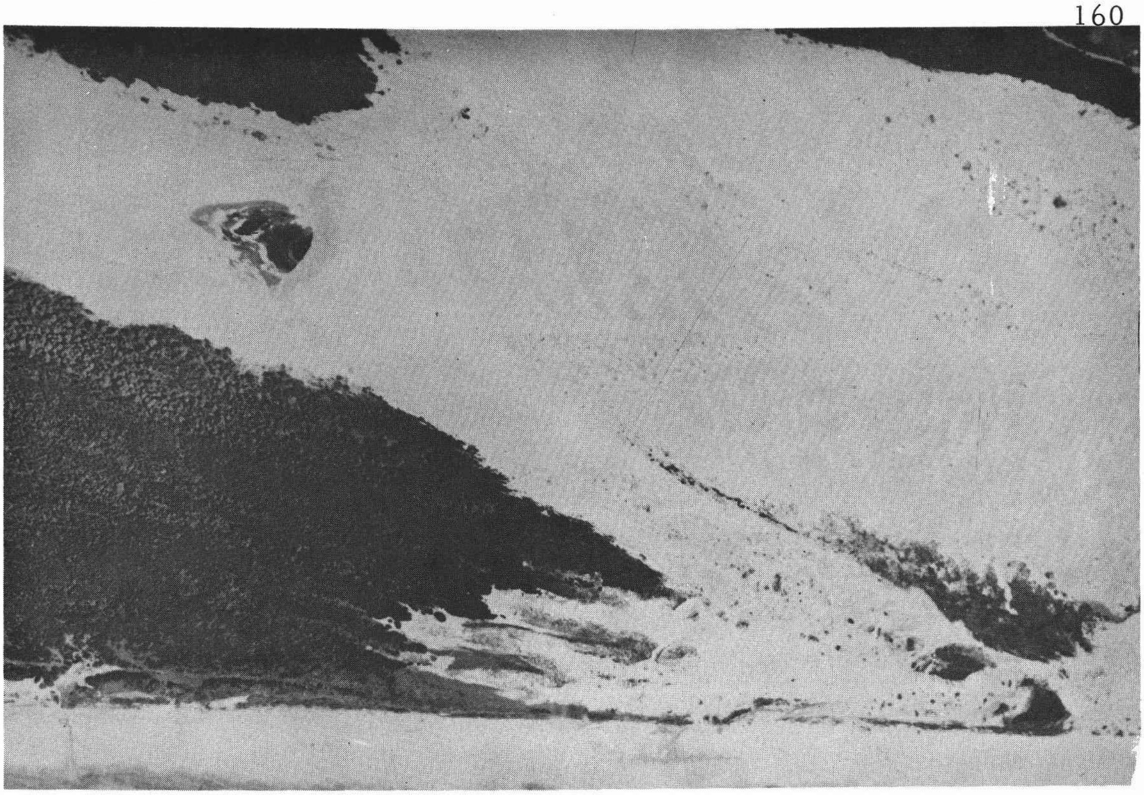
BOTTOM - 1939

TOP - 1961

Deflation plain right, center both photographs. Recent vegetation development lower right, TOP. Upper left both photographs shows most recent active parabola dune advancing over previously vegetated deflation plain (SL-2).

North to left.

Scale approximately 1:10,000.

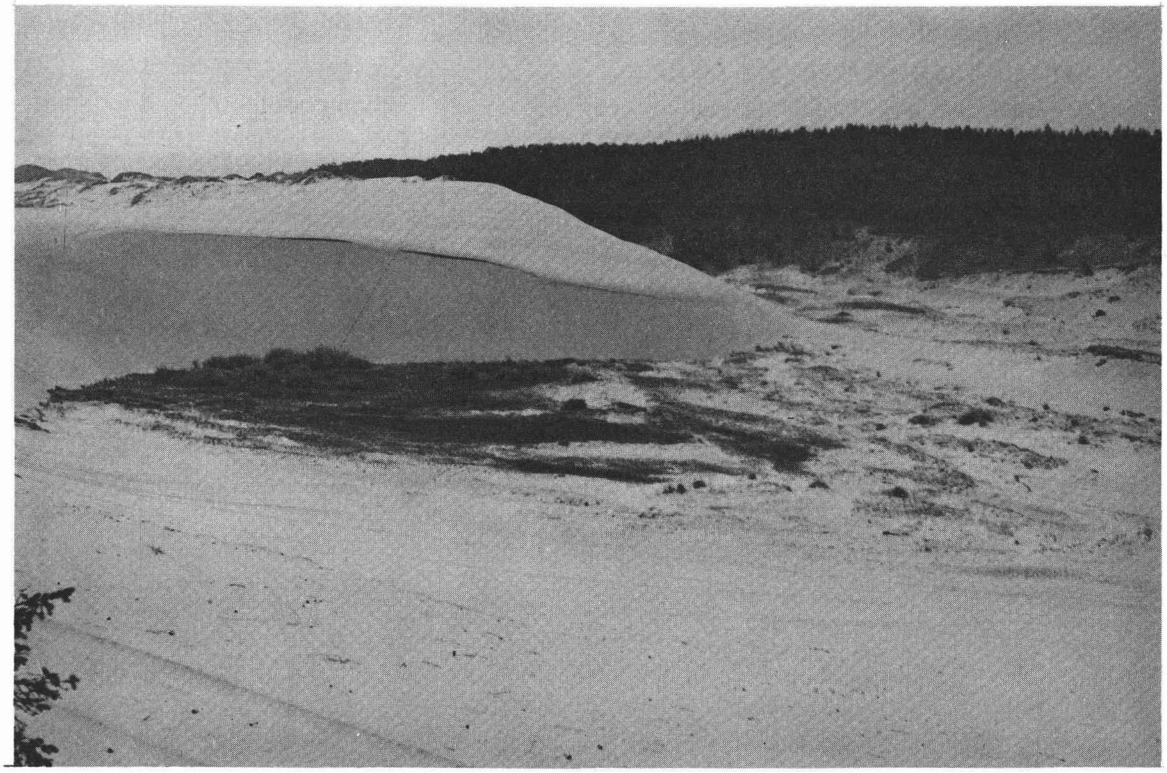


TOP

Figure 29. Sand Lake (SL). Deflation plain looking southwest from most recent parabola dune. Haystack Rock (lies off Cape Kiwanda) in the distance. Dead tree trunks in right foreground are remnants of vegetation that developed prior to current dune activity. December, 1964. (Compare with Figure 28, TOP)

BOTTOM

Figure 30. Sand Lake-2 (SL-2). View of the deflation plain from high dune ridge to the east. Active parabola dune (about 30 m. high) covering vegetation, mostly rush meadow. Shrubs are *Salix hookeriana* up to 2 m. tall. This dune is the site for studies of rate of dune movement. September, 1964.



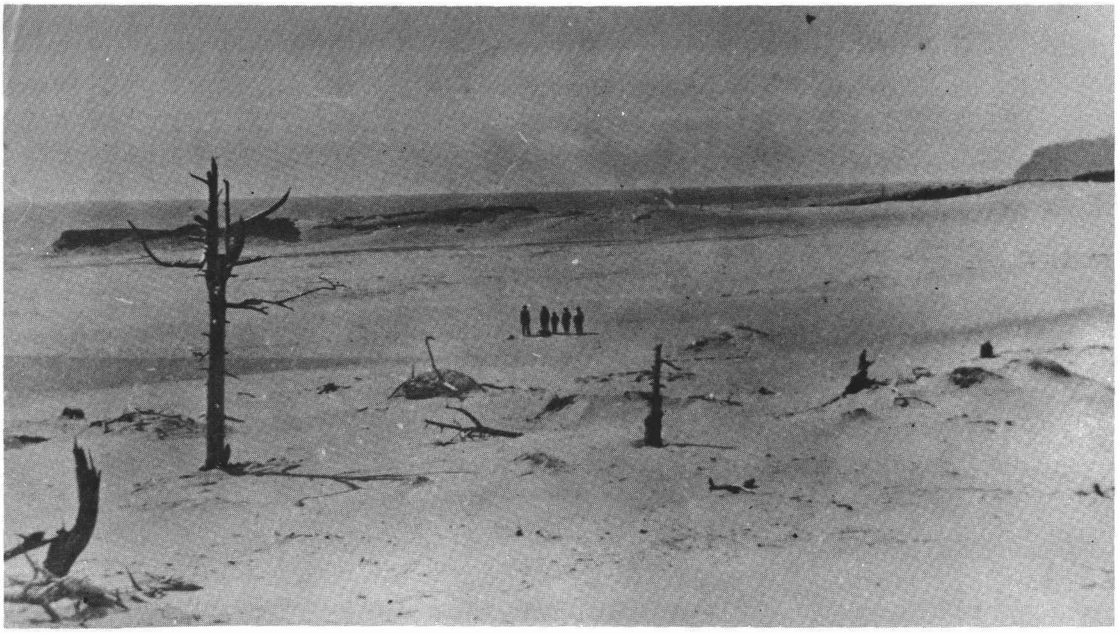


Figure 31. Comparative photographs of vegetation development at Sand Lake. Looking west across the deflation plain from the high dune ridge which extends northeast from the forested remnants near end of Galloway Road. (See Figure 5). Most development due to Ammophila arenaria. Note mounds on deflation plain. Upper: Taken about 1925 (Furnished by Mrs. Otis Edwards, Tillamook, Oregon). Lower: Taken January, 1965. Wet sand shows as dark areas on deflation plain.

developed along the drainage course at the upper end of the deflation plain. Seedlings of Pinus, about five years old, have become established through the central part of the area (Figure 32), and there is a scattering of Vaccinium and Gaultheria on the more moist sites. The pine and shrub seedlings are confined to the meadow and rush-meadow communities. The preponderance of drier sites (Table 10) is probably due to the well-developed drainage pattern which prevents extensive areas of flooding during the winter.

At the extreme upper end of the deflation plain, where considerable water collects, the first plants are Juncus phaeocephalus and J. lesueurii (Figure 33). Ammophila becomes established in scattered locations and mound formation begins. The beach annual, Cakile edentula, occurs along the extreme lower slope of the dune.

Two transects were established on this deflation plain. SLT-1 runs approximately across the middle, widest part, and was sampled from west to east with meter-square quadrats laid down every three m. Both ends were marked, and in addition, the eastern end was marked 30 m. out on the bare sand. There is complete photographic documentation. Figure 34 is a view along the transect from west to east.

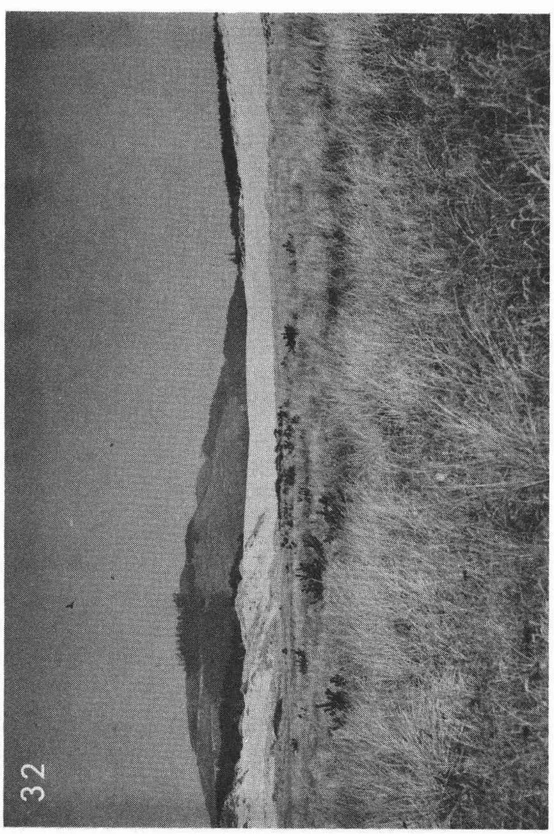
The other transect, SLT-2, located at the upper, narrow end of the deflation plain, is actually a series of three staked plots, each one by three meters in size. These have been photographed, and

Figure 32. Sand Lake (SL). View to northeast from about center of deflation plain. Scattered seedlings of _Pinus contorta_, 0.5 to 1 m. tall. Grass is mostly _Ammophila arenaria_. September, 1964.

Figure 33. Sand Lake (SL). Initiation of primary succession. Colonization by _Juncus phaeocephalus_ and _J. lesueurii_ at windward base of parabola dune. _Ammophila_ mounds in background. July, 1964.

Figure 34. Sand Lake (SL). View from west to east along permanent transect SLT-1. Marker stake is on transect. August, 1964.

Figure 35. Sand Lake (SL). View from west to east along permanent transect SLT-2. Stake in foreground marks first plot; stake in background marks third plot. Shrubs are _Salix hookeriana_; tree seedlings, _Pinus contorta_. Stake divisions 30 cm. September, 1964.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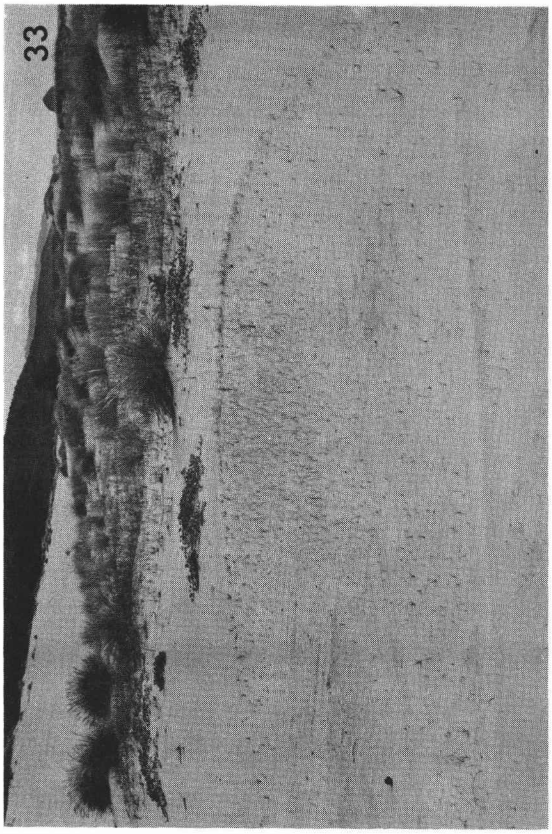
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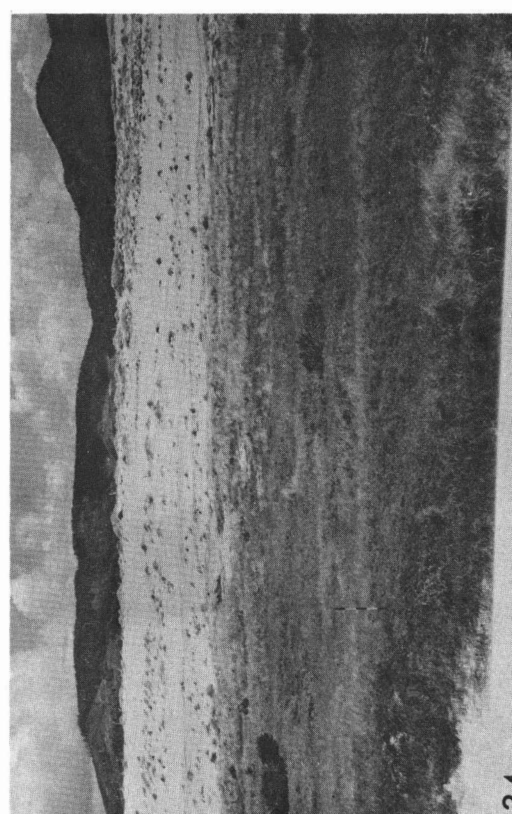
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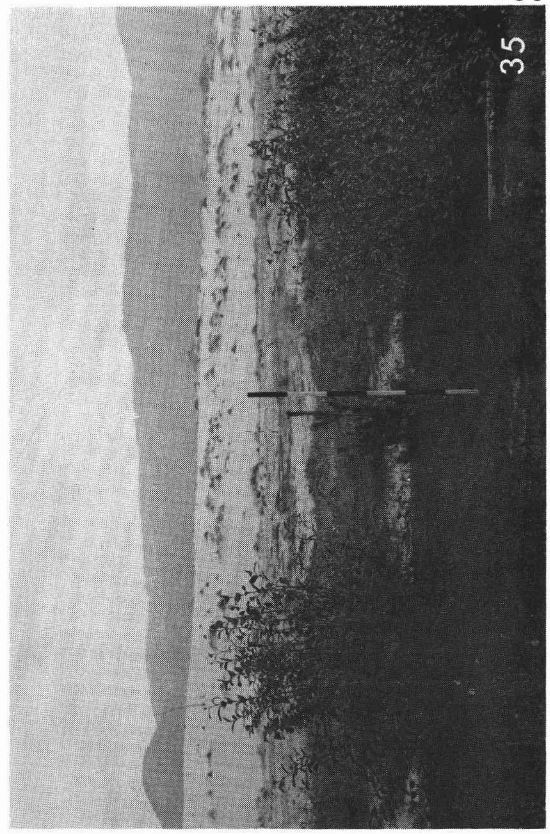
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species occurrence and cover documented. Figure 35 is a view along this transect.

This deflation plain will probably develop directly into a forest of Pinus with Salix and Alnus along the water course. No seedlings of Picea are present, but this may be a matter of seed supply, since there are no mature trees nearby. Shrubs are poorly developed, and the shrub stages may be by-passed.

An interesting aspect of this area is the recent increase in the population of Citellus beechyii, the California ground squirrel (Ward, 1964). These animals dig burrows in Ammophila mounds and in the hillsides where Festuca rubra is established, the root systems of these plants apparently holding the sand together well enough to permit this activity. This habitat preference was also noted by Reardon (1959) in his study of Peromyscus on the dunes south of Florence. Even more important, the squirrels feed on the seeds of Ammophila—in the fall of the year, practically every Ammophila clump looks as though a giant mower had cut off all the spikes.

There are a great number of these animals in the area, providing an ideal opportunity to study a plant-animal ecosystem. The work of Ranwell (1960) and other British ecologists on the rabbit-vegetation relationships on the English sand dunes lends support to this idea.

Part of this deflation plain is owned by the U. S. Forest

Service, and the rest by Tillamook County. As far as could be determined, the county is not holding this area for park or recreation purposes, but is hoping for some type of real estate development. However, no definite plans appear to have been made.

Sand Lake - 2

This deflation plain is being covered by the latest advancing parabola dune of the Sand Lake system (Figure 5). A number of small, dead pine seedlings indicate that the area has become increasingly wet in recent years. Water stands up to 60 cm. deep in winter, apparently draining into the lower deflation plain. Two young trees still survive on a raised mound. The *Salix* shrubs, at present about two meters tall, are rapidly being covered. The study of the rate of movement of the dune is being set up as a long term project. Most of the area is a rather open stand of *J. phaeocephalus*, *J. falcata*, *J. lesueurii* and *Agrostis pallens*. On the very wet sites, the main species are *Salix* seedlings, *Eleocharis palustris* and *Ranunculus flammula*. Figure 30 is a view of this deflation plain from a high point on the east side showing the advancing dune.

Newport

The deflation plain south of the mouth of the Yaquina River at Newport owes its existence to the jetty built in the late 1800's.

According to Cooper (1958, p. 82) the dunes upon which Newport is built are a remnant of a more extensive parabola system. Both Cooper and Baldwin (1950) believe that the mouth of the Yaquina River probably flowed into the ocean southwest along the bluff on the south side of the river. As the mouth shifted northward, northwest winds built a dune area on the old riverbed that eventually reached a width of almost two km. An early map of the area (U.S. Coast and Geodetic Survey, 1863) shows the sharply incurving shore line. After the jetty was constructed, sand began to fill in behind it so that by the early 1940's it appeared as in Figure 36, bottom, an aerial photo showing a large flat expanse of bare sand to the south of the jetty. Presumably shore line progradation is continuing.

Another aerial photograph taken in 1958 (Figure 36, top), shows that considerable vegetation has developed. Figure 37 is a view looking north from a high mound at the south end. The trees are growing in two more or less parallel rows, each row about six m. wide, and with high ground on both sides and in between the rows. Pinus predominates, averaging three m. in height; Salix is present to about ten percent and is 2.5 m. high, and a single Picea was observed. The trees are all very bushy and thickly branched to the base. Their stems are from eight to ten cm. in diameter at the base, and they are about ten years old. Figure 38 looks across this tree belt along one of the transects used to locate stands. This area

Figure 36. Newport (N). Aerial photographs showing vegetation development.

BOTTOM, about 1940.

TOP, 1958.

Upper right both photographs Highway US 101; lower left, channel and jetties of Yaquina River. Forested area was surveyed and roads built for resort development, but only a few houses were built and most of these are abandoned.

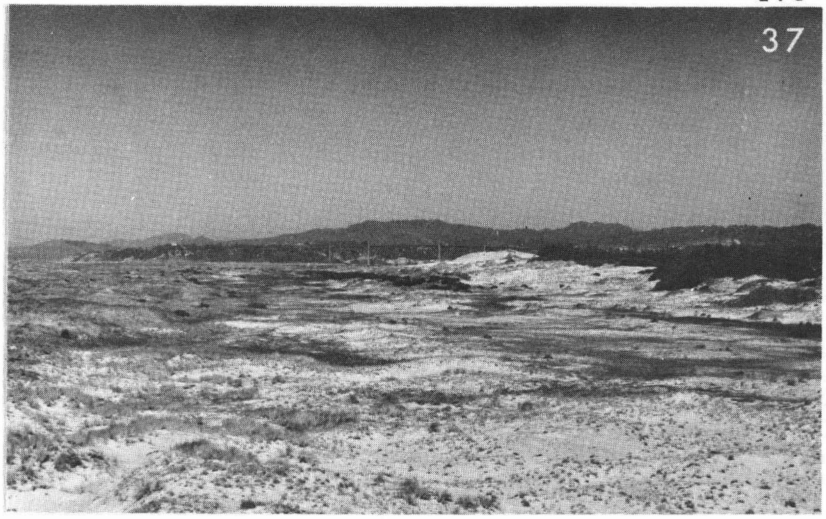
North to left.

Scale approximately 1:34, 000.

Figure 37. Newport (N). View of deflation plain from high mound near south end. Foreground is low, flat area of *Juncus* spp. The two rows of tree vegetation, *Pinus contorta*, are in the center of the photograph. Highway US 101 bridge over Yaquina Bay in background. July, 1964.

Figure 38. Newport (N). View (east to west) across tree (3 to 5 m. tall) vegetation belts along sampling transect. Light shrubs are *Salix hookeriana*, darker trees, *Pinus contorta*. Surface rises on far side toward foredune with vegetation mostly *Ammophila arenaria*. July, 1964.

Figure 39. Newport (N). Area of exposed smooth rocks and pebbles probably representing former beach line. Located toward south end of deflation plain. Vegetation is *Lupinus littoralis*, *Agrostis palustris*, *Juncus lesueurii*, *Agoseris apargioides*. July, 1964.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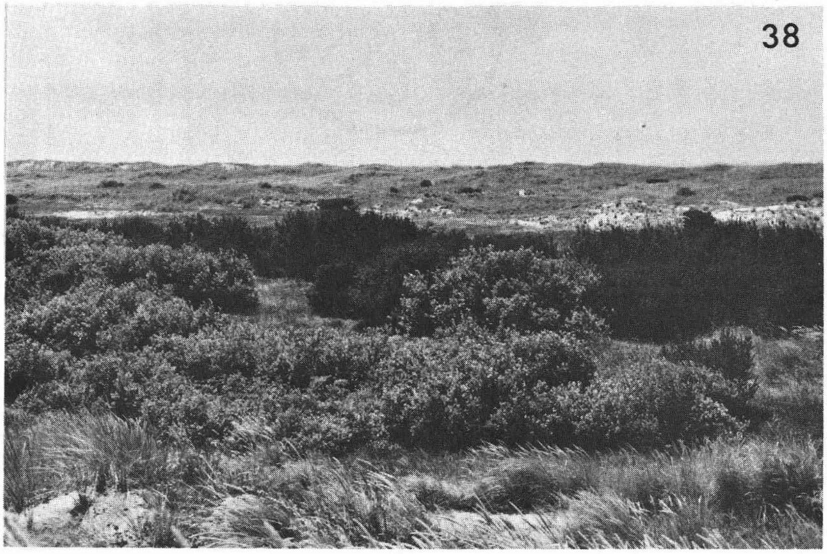
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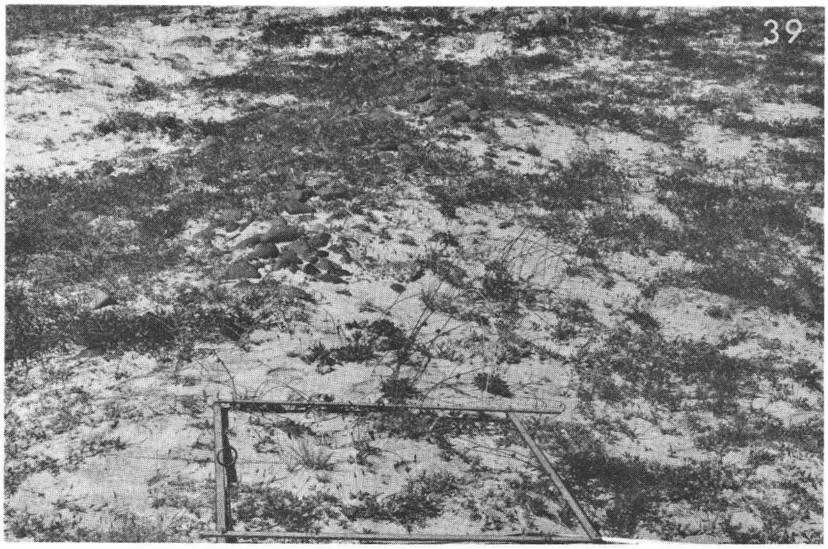
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is very uneven, both as regards vegetation and topography. Toward the south end a scattered shrub stage of Vaccinium and Gaultheria is developing, while the extreme south end is a low area of standing water and rush meadows.

A unique feature was the presence on the deflation plain of large areas of pebbles and smooth rocks up to 15 cm. in diameter suggesting the former beach line. The vegetation is sparse on these areas which were found at the south end, and a little to the west, of the tree line. The predominant vegetation in Figure 39 which shows such a stony area is Lupinus and Agrostis palustris.

About 8 ha. of this dune area was planted to Ammophila in the early 1930's, and a well developed foredune complex has developed. The high area behind the foredune is as large as the deflation plain itself, and its hummocky surface supports a very dense stand (100 percent cover) of Ammophila, Lathyrus japonicus, Lupinus littoralis, Aira praecox, Poa macrantha, Elymus mollis and Lathyrus littoralis (in about that order of importance). The top and leeside of the main foredune has a thick cover of Ammophila, L. japonicus and Elymus.

Lily Lake

Several deflation plains find their origin in the vigorous rejuvenation of sand activity in this area between Heceta Head and Florence—all under the influence of the northwest winds. Figure 6 is a map outlining the deflation plains of this study that lie between Heceta Head and Tahkenitch Creek. Several can also be seen in the oblique aerial photograph of Figure 40.

The development of vegetation on the Lily Lake deflation plain is remarkably documented by the two aerial photographs of Figure 41 taken in 1945 and 1961. Sutton Creek has been an effective barrier to invasion of the forest by sand. Vegetation on the deflation plain apparently developed around a drainageway, which is now the site of a long, narrow belt of trees 1.5 to 2 m. high, and composed of _Pinus_ (50 percent), _Alnus_ (25 percent) and _Salix_ (25 percent).

The vegetation appears uniform over the entire area, suggesting that development began over the entire area at once. Shrub sampling plots taken at both ends showed no differences in species composition or distribution of height classes except for _Pinus_ and _Picea_, both of which were younger at the south end. Figure 42 shows a shrub area in the center of the deflation plain.

As can be seen from the aerial photographs (Figures 40 and 41), the area is subjected to the severe unidirectional action of the northwest winds. Instead of a normal foredune developing along the beach, a series of high (six m.) _Ammophila_ ridges have developed, with intervening wind swept valleys, parallel to the wind direction. Figure 43 is a ground view of this pattern. Some idea of these severe winds can also be obtained from Figure 44, showing the formation of

Figure 40. Oblique aerial photograph of area between Heceta Head and the Siuslaw River. View to south from point directly above Heceta Head. Siuslaw River approximately center of photograph. Lily Lake lower left. Highway US 101 is just off left side of photograph. Location of three deflation plains shown by study site symbols.


HB
SC
LT

Figure 41. Lily Lake (LL). Aerial photographs showing vegetation development.

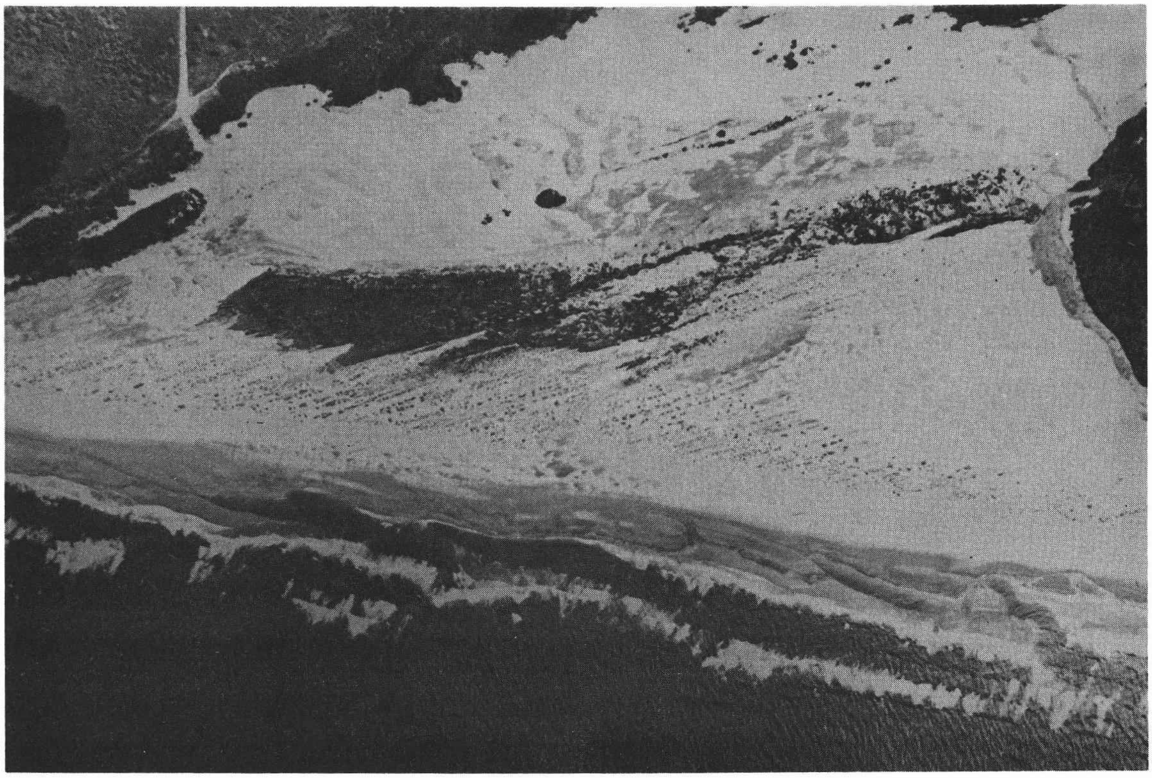
BOTTOM, 1945.

TOP, 1961.

Right center both photographs, Sutton Creek; left center, Lily Lake. Note striated pattern of *Salix* mounds (TOP) oriented parallel to northwest wind direction. An area of well developed transverse dune ridge patterns.

North to left.

Scale approximately 1:16,000.



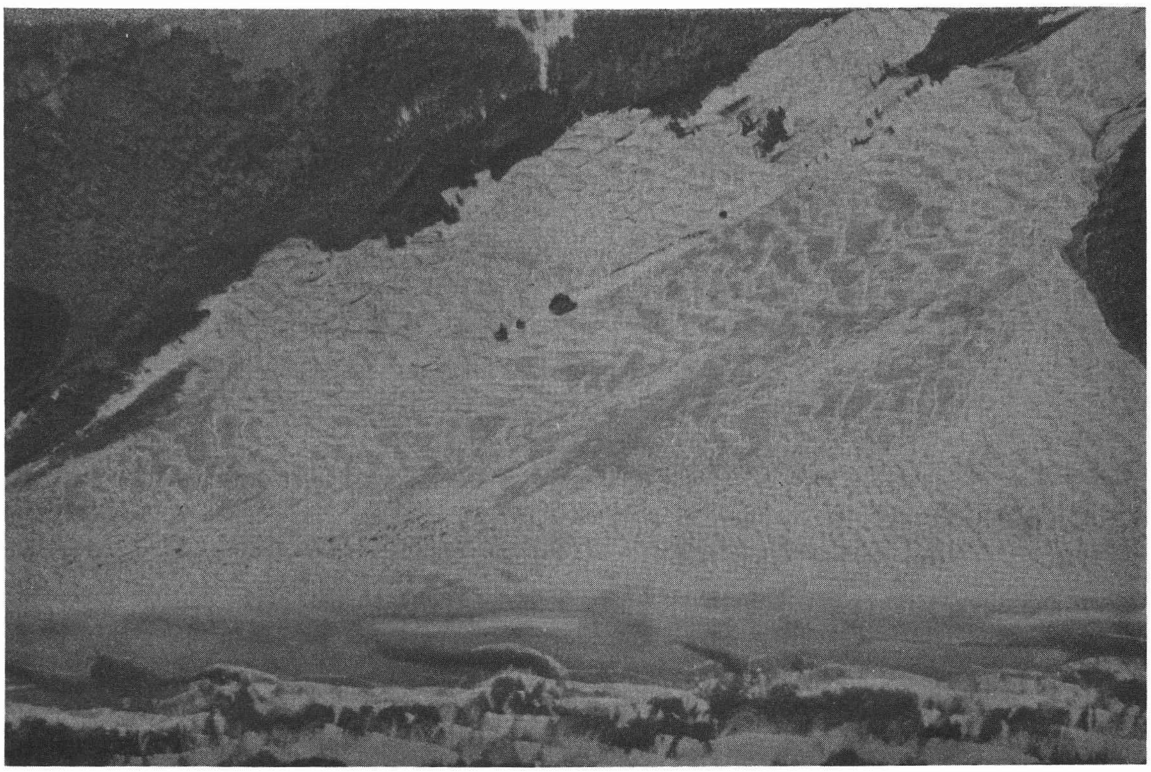
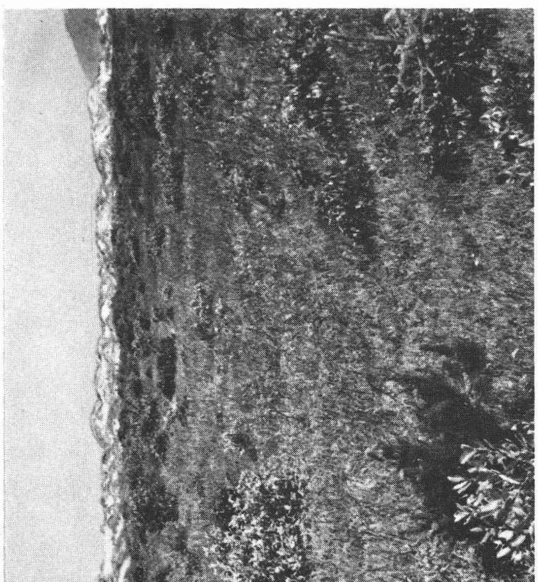


Figure 42. Lily Lake (LL). Low shrub stage in center of deflation plain. View to northwest. Lower right corner: seedling of _Picea sitchensis_; lower center, seedlings of _Pinus contorta_ and _Alnus rubra_; center background, mostly _Salix hookeriana_. Shrubs up to 1 m. tall. Herbaceous vegetation mostly rush meadow. July, 1964.

Figure 43. Lily Lake (LL). Ground view of dune ridges oriented parallel to the direction of the dominant summer winds (northwest). Mounds about 6 m. high, formed by _Ammophila arenaria_. July, 1964. (Compare with Figure 40 and 41, TOP)

Figure 44. Lily Lake (LL). Active sand of the transverse dunes. Strong northwest winds. Note mounds of _Ammophila arenaria_. July, 1964.

Figure 45. Sutton Creek-2 (SC-2). "Pine graveyard"—dead forest being uncovered by moving dune which is covering the forest on SC-2. Note thick growth of _Juncus lesueurii_ in foreground. July, 1964.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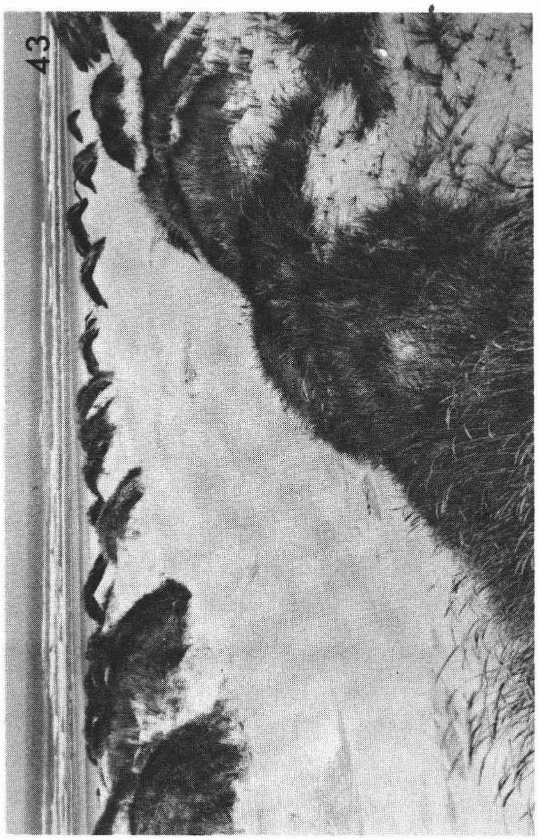
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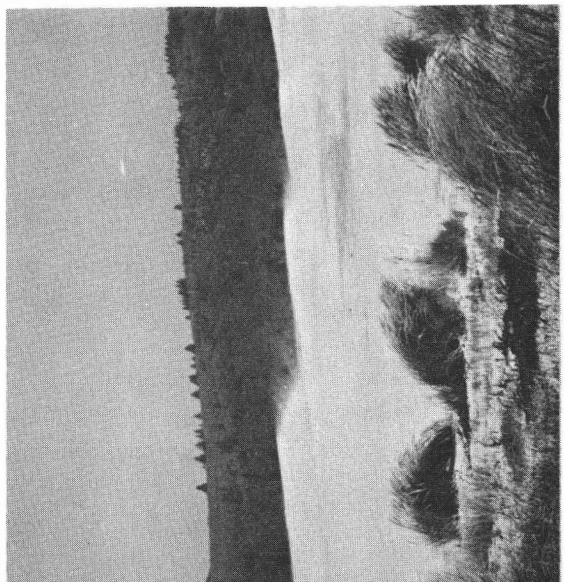
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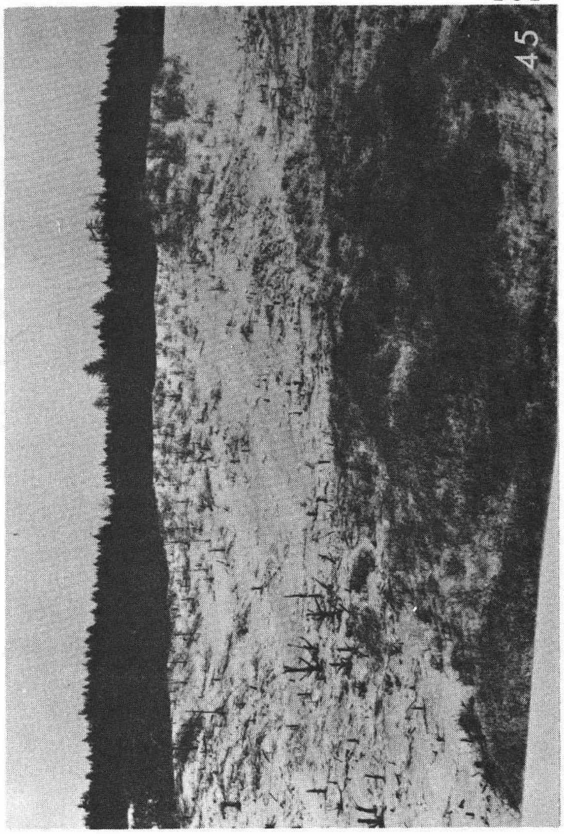
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transverse dunes on the sand east of the deflation plain. The wind here was stronger than at any other point north of Coos Bay.

Sutton Creek-2

This small deflation plain is located a few hundred meters southeast of the previous (Figures 6, 40). It is a marshy forest of 95 percent Pinus, five to ten m. high, the remainder Myrica and Alnus. The only understory is a thick growth of Carex obnupta. It is significant for two reasons: (1) a very dense, impenetrable growth of Ulex europaeus surrounds it on three sides; and (2) it is being invaded from the northwest by a high dune which has already passed over about one-half of the original area. Figure 45 shows the uncovered "pine graveyard" which was part of the original area. The vegetation at the bottom of the picture is a thick growth of J. lesueurii, which forms extensive hummocks in this area.

Sutton Creek

This deflation plain (Figure 6, 40) shows a successional sequence from bare sand (upper or southeast end) to shrub to forest (lower, or northwest end). Figure 46, a pair of aerial photographs, shows the changes in the area over 20 years. Note particularly the change in the outlet of Sutton Creek. Its former course, extending much further to the south, is still discernible in the recent

Figure 46. Sutton Creek (SC). Aerial photographs showing vegetation development.

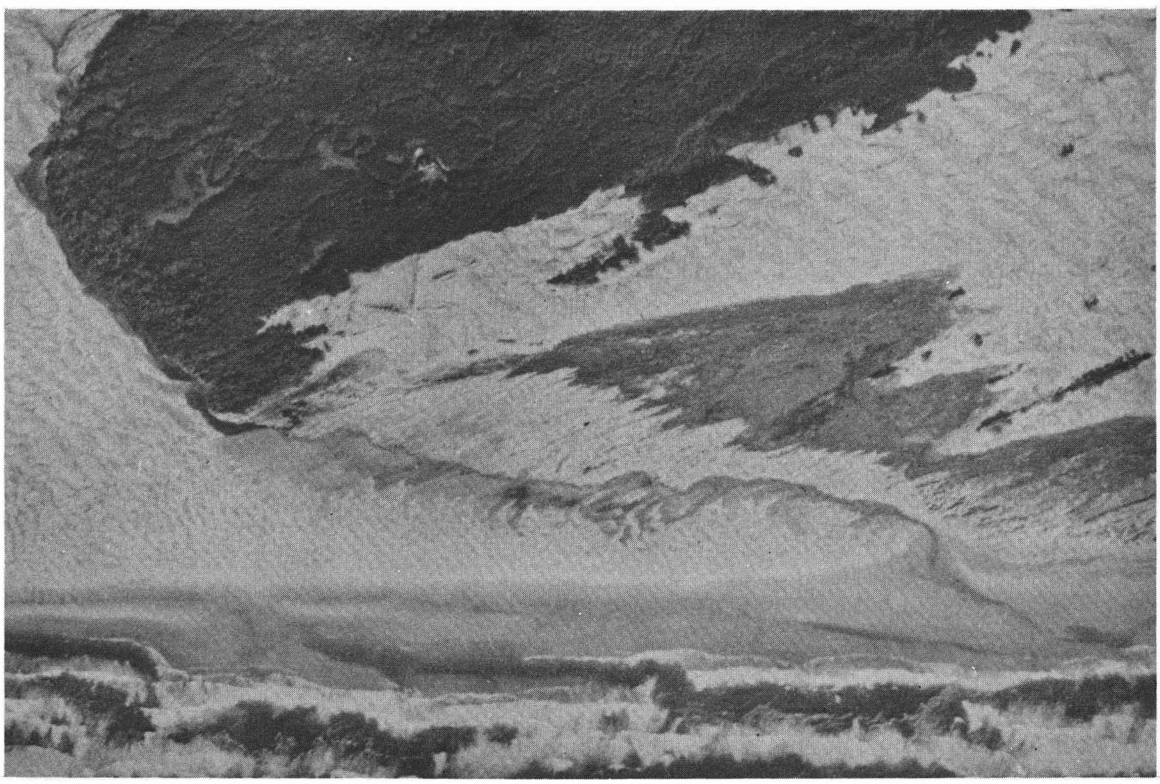
BOTTOM, 1945.

TOP, 1961.

Deflation plain right center both photographs. Forest vegetation was just beginning development in 1945. Note change in course of Sutton Creek—former course still visible in recent photograph. Compare Figure 48. Road (TOP) built into private development which was just beginning in 1945.

North to left.

Scale approximately 1:13, 000.



photograph as a bank and an oblong pond. Figure 47 is an overall view from the southeast end, and Figure 48 is an oblique aerial view from the west. This too has been an area of cyclic activity as evidenced by the many dead tree trunks of many sizes, and also the numerous remnant mounds up to ten m. high. These latter appear to be the result of sand accumulation around tall individuals or clumps of spruce (Figure 49).

The distance from sand thru meadow, rush meadow and low shrub communities to the high shrub was about 180 m. This high shrub is actually mostly (75 percent) Pinus up to three m. tall, the rest being Salix (15 percent), Myrica (5 percent), and Gaultheria and Vaccinium (10 percent) each. A six by six m. plot in the oldest part of the forest had the following distribution of size classes (dbh) of Pinus: 2.5 to 5 cm.-1; 5 to 10 cm.-10; 10 to 15 cm.-11; and 15 to 20 cm.-5. They averaged seven to nine m. high. Gaultheria and Vaccinium occurred as spindly shrubs two m. tall, and there was about eight cm. of litter on the ground. From the high mounds, very scattered spruce could be seen growing above the pines.

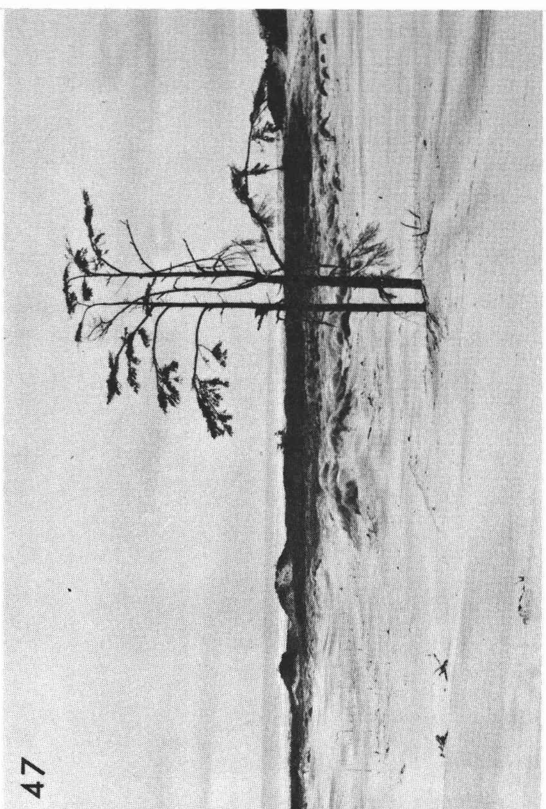
The trees here, as noted elsewhere, tend to grow in belts with low areas in between that support both rush meadow and marsh communities. Tree and shrub seedlings indicate these will eventually fill in. These low meadows appear as light colored patches in Figures 46 and 48. This pattern will be noted and discussed further

Figure 47. Sutton Creek (SC). Ground level view of deflation plain toward northwest. Picea sitchensis in foreground a remnant of a previous forest on the area. Note dead tree stems in sand, left center. July, 1964.

Figure 48. Sutton Creek (SC). Oblique aerial photograph from west. Sand movement toward right. Light patches (lower center) are low, wet meadows. Debris along bottom marks former course of Sutton Creek. July, 1964.

Figure 49. Sutton Creek (SC). Dune landscape in area of sand activity. Large mounds the result of sand accumulation around tall Picea sitchensis which were not killed by dune activity. Small deflation plain in center covered by mounds of Ammophila arenaria—probably will not go through the typical herbaceous stages of other deflation plains, but will build into very "hummocky" terrain. July, 1964.

Figure 50. Heceta Beach (HB). The narrow ecotone between active sand forest. Trees are all Pinus contorta except for few scattered Salix. Herbaceous vegetation in meadow. July, 1964.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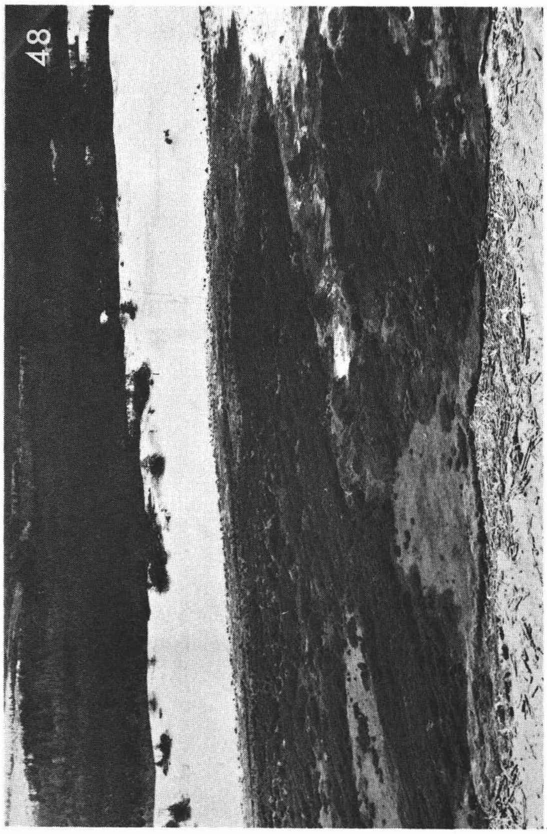
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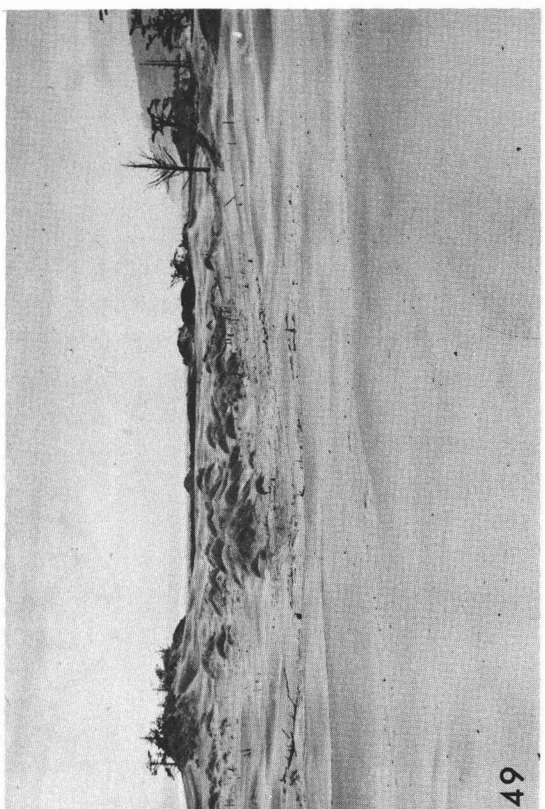
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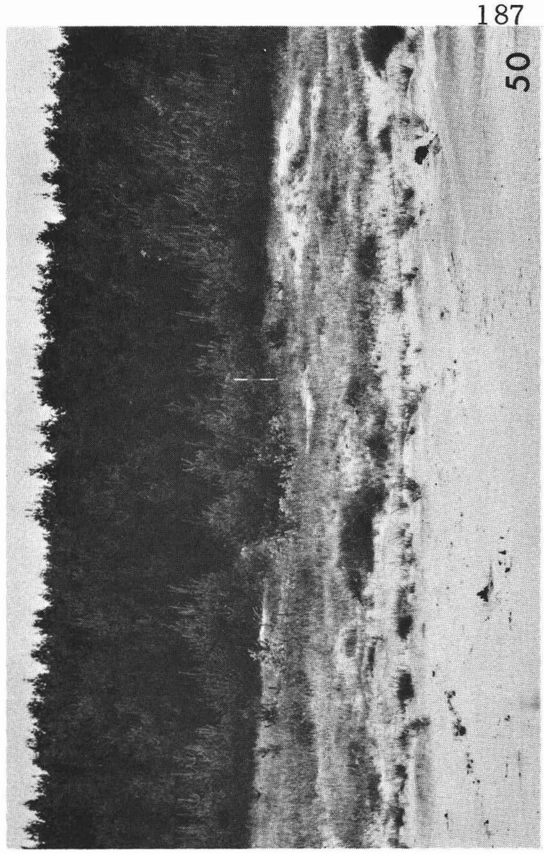
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in connection with the Cleawox Lake deflation plain.

This area is part of the Siuslaw National Forest, and the Forest Service is planning the construction of a campground on part of it within the next year (Lyne, 1964).

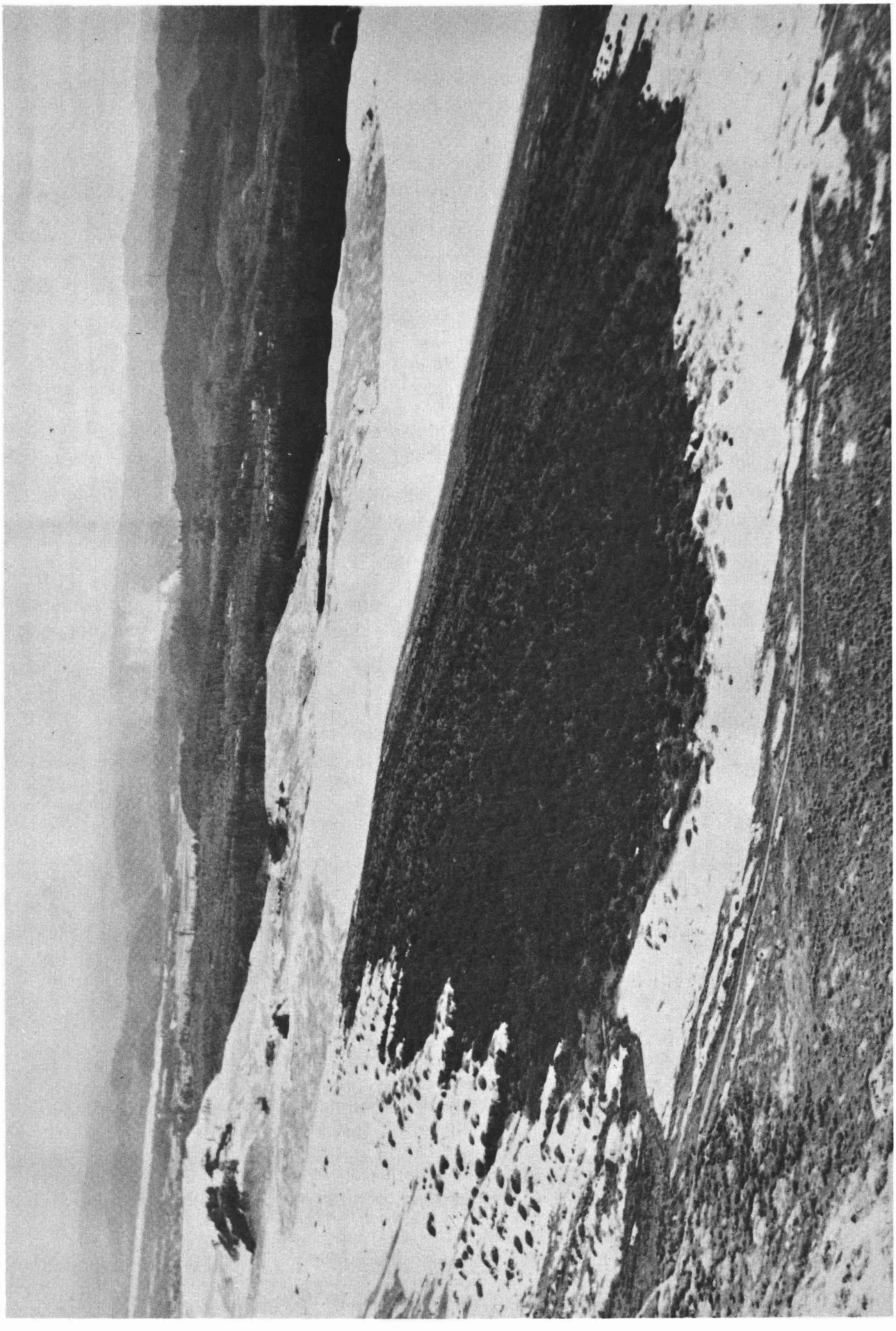
Heceta Beach

This deflation plain is the site of a well-developed forest. Most of the description of the Forest Community is based on it. For location, see Figures 6 and 40. The transition from sand to forest is a very short, narrow belt of meadow and pine seedlings. This is probably due to active lateral sand movement, the ecotone area lying parallel to the dominant wind direction (Figure 50). The forest is entirely *Pinus*, with up to 30 percent *Salix* understory in the marshy areas. *Gaultheria* is almost vine-like, attaining heights of five m. but it is not very abundant, as is also true for *Vaccinium*. No spruce were noted.

Cleawox Lake

This unique deflation plain (Figure 51) provides a classic example of succession on wet sand. Moreover, it lies in an area that will be included in the Oregon Dunes National Seashore (U. S. Congress, 1963), and as such will be available for future study (Figure 6).

Figure 51. Cleawox Lake (GP). Oblique aerial view toward northeast. Cleawox Lake and Honeyman State Park off upper right. Florence and Siuslaw River upper left. Part of foredune lower left. Note sand invading from north (left) and to a lesser extent from the south. Vegetation spots on the active sand are Salix mounds (Compare Figure 54). Vegetation in lower part of photograph is developing behind the foredune and is similar to that described under Carter Lake Transect. June, 1964.



Its origin can be closely traced. According to Hanneson (1962, p. 93), the U.S. Coast and Geodetic Chart of 1887 shows no vegetation in this area. Cooper (1958, p. 109) notes that this is an area of cyclic vegetation growth and destruction, apparently governed by drainage from Cleawox Lake, about 1200 m. to the east. Dead tree trunks and a single live spruce still present in 1941 north of the present area led him to postulate a similar vegetative growth around 1800.

There is no doubt, however, that the present vegetation is recent. Its development is obvious when early and recent aerial photographs are compared (Figure 52). F. L. Mackechnie (1915), a Forest Service worker, described the area as it appeared in 1915:

> This area lies about $\frac{1}{4}$ mile from the ocean beach between the sea-wall and the primary sand dunes... It is probably 10 or 15 feet above the sea level, near the outlet where this low area drains into the ocean, and where the grass, moss, and strawberry plants, etc., have not formed too much sod. Most of the area is kept moist the year round by a sub-drainage from Lake Cleawox about one mile east, which at the present time of the year (April) has a running outlet into this low area and has a portion of it flooded. The extent of the entire grassy tract is about $1\frac{1}{2}$ miles (north and south) by about $\frac{1}{4}$ mile (east and west), and during a short time of the year a few cattle cross the open sands from the lake country to the east, and make their rendezvous till it has been cropped short.

The area was chosen for experimental plantings of *Pinus pinaster*, the pine used so successfully for dune stabilization in

Figure 52. Cleawox Lake (GP). Aerial photographs showing vegetation development.

BOTTOM, 1939.

TOP, 1955.

Pinus pinaster plantings clearly outlined in bottom photograph; just barely visible in upper as a lighter toned patch in same location. Deflation plain about the same length (north-south) in both photographs, but has increased in width in the more recent one. There were very few trees in 1939—vegetation was mostly shrub and herbaceous species. Note ponds and drainage (probably from Cleawox Lake) has changed very little, but development of the foredune and vegetation behind it has been extensive.

North to left.

Scale approximately 1:13, 200.

France. A total of 3.3 acres (1.3 ha.) was planted on two plots in 1915 and 1916. Several rows of Cytisus scoparius were also planted, as was one row each of Eucalyptus gumni and E. globulus (swamp and blue gum, respectively)(Mackechnie, 1915; 1916). Most of these plantings failed, as did the earlier efforts in 1908, when Forest Service personnel "set out thousands of willow, scotch broom, and grass roots in sand west of Cleawox and Siltcoos Lakes." (Knowles, 1951, p. 3).

All that remains of the pines planted by Mackechnie are low (four to six m.) distorted bushy trees that are slowly being covered by the invading sand (Figure 53). Even away from the covering sand, many trees are dying out. The plots can be seen clearly on the 1939 aerial photo, but only close inspection can discern them on the 1955 photo (Figure 52).

The deflation plain was later described by Cooper (1958, p. 110): "In 1941 the area was essentially a meadow, but willow bushes 1-2 m tall were scattered thickly over it, and a few pines and spruces up to 7 years old and even a few hemlock seedlings were present." Today it is a very dense thicket of vegetation that can be traversed from east to west only with great difficulty. It is about 1400 m. along its longest north-south axis, and 600 m. at its widest point. It is being continually shortened by sand invading from both ends, that caused by the northwest winds obviously having the greater effect.

Figure 53. Cleawox Lake (GP). Remnants of _Pinus pinaster_ planted in 1915. _Picea sitchensis_ in background. August, 1964.

Figure 54. Cleawox Lake (GP). Mounds of _Salix hookeriana_ formed as sand invaded north end of deflation plain. _Salix_ survives sand burial, the stems extending down to the former surface and water table. Mounds 5 to 10 m. high. August, 1964.

Figure 55. Cleawox Lake (GP). Pioneer vegetation eastern side of deflation plain. _Juncus phaeocephalus_ and _Agrostis pallens_. August, 1964. (Figures 55 to 60 form a series across the deflation plain from east to west.)

Figure 56. Cleawox Lake (GP). Wildlife planting zone next to pioneer vegetation zone. Grasses mainly _Festuca elatior_ and _Lolium perenne_. Note _Salix hookeriana_ hedges at both edges, but none in planting. August, 1964.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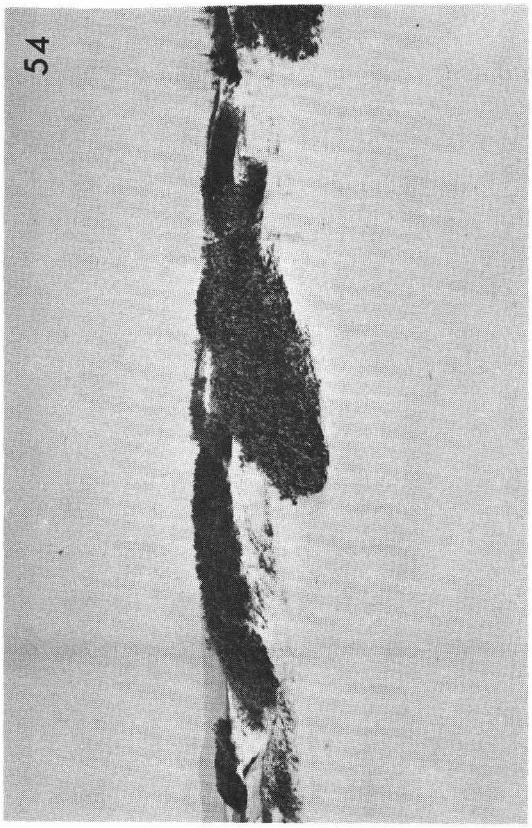
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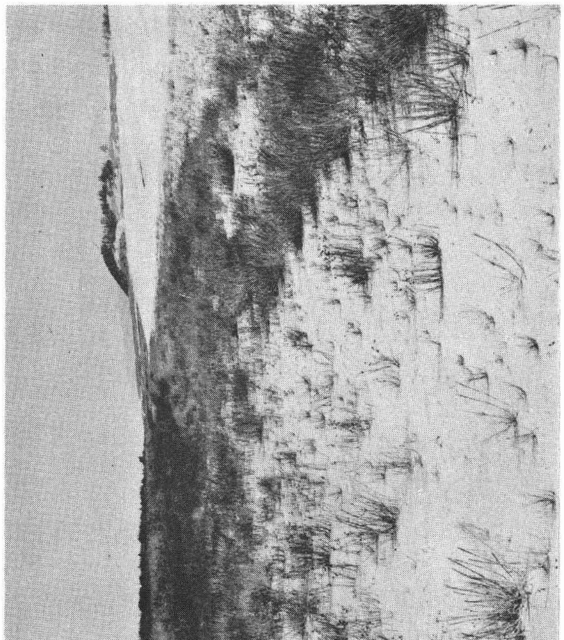
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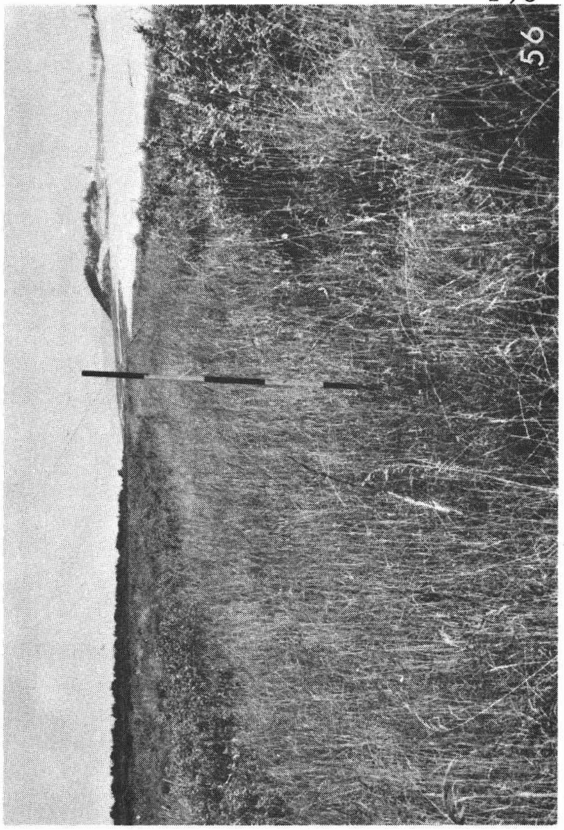
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The pattern of vegetated ridges along the northwest side of the deflation plain is similar to that seen at Lily Lake, except that these are formed by Salix. These plants started at water table, and have kept pace with sand deposition until the mounds now reach five to ten m. in height, and are oriented in rows parallel to the course of the northwest winds (Figure 54).

The same phenomenon occurs at the southern edge, but it is less pronounced. The striated vegetation pattern readily apparent in the aerial photos, particularly along the eastern half of the deflation plain, is due to more or less alternating belts of trees and shrubs, and herbaceous vegetation. This is the result of the successive advances of the vegetation eastward as the active dune sand moves inland. The south to south-west winds probably emphasize the effect in much the same way as the northwest winds do with Salix and Ammophila, though it is not nearly so severe. This belt pattern occurs along the entire width from east to west, but is no longer distinct in the older forest.

The vegetation of the deflation plain, pictured in the oblique aerial photograph of Figure 51 shows a gradual succession of communities from bare sand on the east to spruce forest on the west. The easternmost (most recent) belt of vegetation is about 12 m. wide, and is a pioneer community of J. phaeocephalus and Agrostis pallens (Figure 55). The next zone is six m. wide "wildlife planting" seeded about 1961 to Lotus major, Festuca elatior var. arundinacea and Lolium perenne. Low Salix forms a thick hedge at both edges of the planting, but so far has not invaded it (Figure 56). Adjacent to this is a 15 m. strip that had been similarly seeded several years previously and is now well colonized by Salix about 45 cm. high, and scattered Myrica and Vaccinium (Figure 57).

For about the next 60 m., the shrubs, including increasing amounts of Myrica, become taller, up to two m., and scattered individual pines (0.5 to 2 m. high) appear (Figure 58). The herbaceous vegetation is mostly rush meadow and marsh. The sundew, Drosera rotundifolia is an important part of the vegetation in this area. Beyond this point, following a straight line becomes increasingly difficult as the vegetation becomes more and more dense. About another 210 m. was the limit, at which point the pines were very numerous and ranged up to five m. tall. Numerous scattered spruce were beginning to raise above the surrounding vegetation.

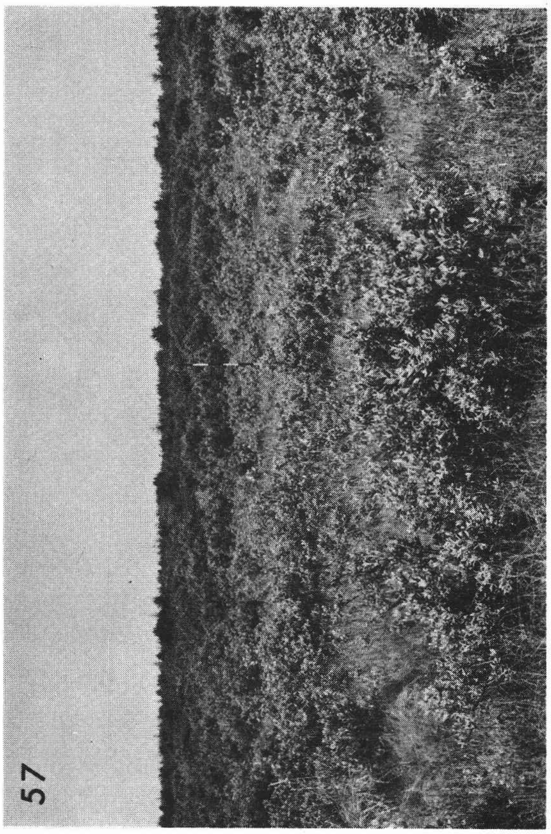
These dense belts of vegetation, oriented generally north and south, usually consist of a row of widely spaced pine, five to eight m. tall and 10 to 20 cm. in diameter, in between which grow thickets of Myrica and Salix 2.5 to 3 m. high. The low intervening "corridors" are very marshy, one to six m. wide, and support a dense growth of C. obnupta. They vary in length from about six to several hundred m. Figure 59 shows one such vegetation belt and corridor

Figure 57. Cleawox Lake (GP). Older planted zone well colonized with low shrubs, chiefly _Salix hookeriana_. Note scattered tall _Picea sitchensis_ in distance. August, 1964.

Figure 58. Cleawox Lake (GP). Tall shrub zone. _Myrica californica_ (right front) and _Salix hookeriana_. Note interspersed low herbaceous areas. Compare Figure 59. August, 1964.

Figure 59. Cleawox Lake (GP). Low areas or "corridors". Shrubs are _Salix_ and _Myrica_, the large trees _Pinus contorta_. Herbaceous vegetation is a mixture of marsh and rush meadow. August, 1964.

Figure 60. Cleawox Lake (GP). Well developed forest on westernmost part of deflation plain. Mostly _Picea sitchensis_. The shorter trees are _Pinus contorta_. Water is a drainage outlet, possibly underground drainage from Cleawox Lake. August, 1964.



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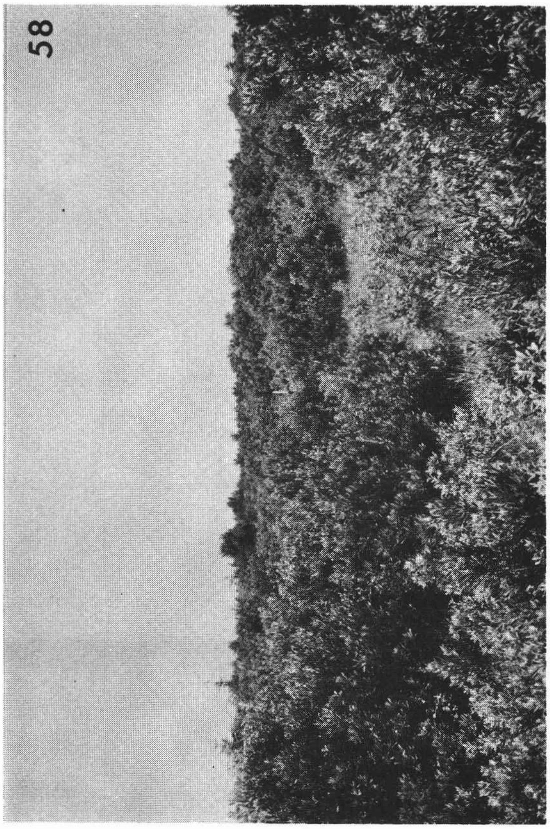

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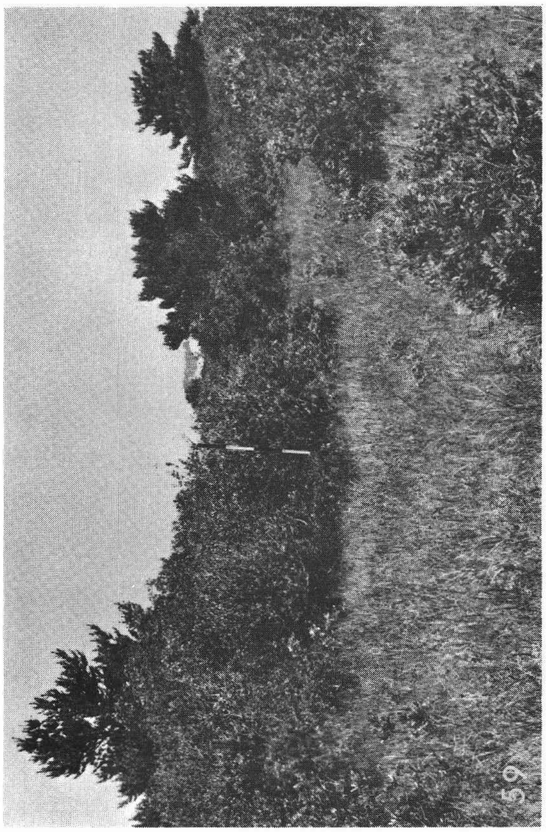

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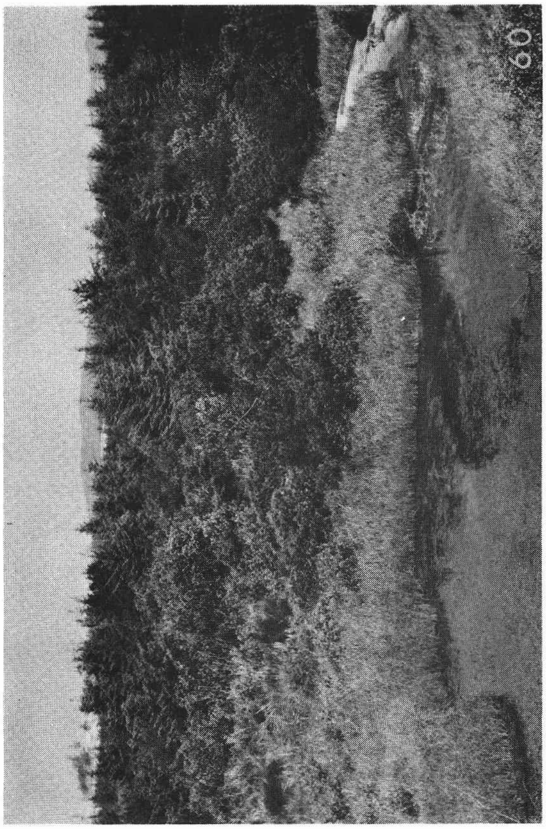

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in a developmental stage.

Many of these have grown into thicket in the older part of the forest. However, there are still numerous small clearings scattered over the older forest area which support rush meadow or marsh communities. They average about nine by 15 m. in size, and usually have scattered shrub and tree seedlings in them. On very wet sites, C. obnupta is dominant. Several hemlock (Tsuga) up to three m. tall were noted at the edge of one of these clearings.

The oldest forest is at the easternmost part of the deflation plain (Figure 60). The pines and spruce here reach diameters of 30 to 35 cm., with heights up to 12 m. If early accounts are correct, none of these trees can be over 50 years old, indicating a very rapid rate of growth. Increment borings were made on several pines about 25 cm. in diameter. Number of rings varied from 28 to 35. The rings were mostly uniform in size and up to three mm. wide.

The general composition of this forest is given by Table 11, which gives percent cover, average height and average diameter for the species found. Basal area and size class distribution are also presented for the tree and high shrub species. Although less in number, the spruce are the more dominant species and eventually a forest of the type in Stand 3, Table 9, a mixture of spruce and pine, will develop. The high proportion of Myrica and C. obnupta reflects the high moisture conditions of the area. The size class distribution,

TABLE 11. Composition of the forest at the west end of the Cleawox Lake deflation plain (GP). (Six 6x6 m. plots).

Species	Average of six plots				Size class distribution (total for all six plots)						
					Size classes (cm.)						
	% Cover	Avg. height (m.)	Avg. dia. (cm.)	Basal area ($m.^2$/ha.)	<2.5	2.5-5	5-10	10-20	20-30	>30	Total
Tree:											
Pinus contorta	43	6.7	8.1	26.2	8	21	30	12	4		75
Picea sitchensis	35	9.1	21.3	37.4			3	4	9	3	19
Shrub:											
Myrica californica	26	3.0	5.0	2.5		2	1				3
Salix hookeriana	2	4.5	3.3	0.2	13	39	2				54
Vaccinium ovatum	10	1.5									
Gaultheria shallon	10	2.1									
Herb:											
Carex obnupta	13	0.9									
Mosses:	7										
Litter:	80										

which shows no spruce reproduction, supports the previous conclusion that these two species, *Picea sitchensis* and *Pinus contorta*, grow up together rather than in a strict successional sequence. The numerous small pines are tall and spindly, and are not young trees.

The "wildlife plantings" made along the edges of the deflation plain and behind the foredune for much of the distance between the Siuslaw and Siltcoos Rivers are intended to promote gamebird populations (Ternyik, 1964). Migrating geese visit the area regularly, giving rise to the term "goosepasture"—as the deflation plain is called by local residents. Beaver were introduced into the deflation plain about 1955, pheasants are regularly stocked, and natural populations of the blacktail deer have increased rapidly in the past few years (Ames, 1964).

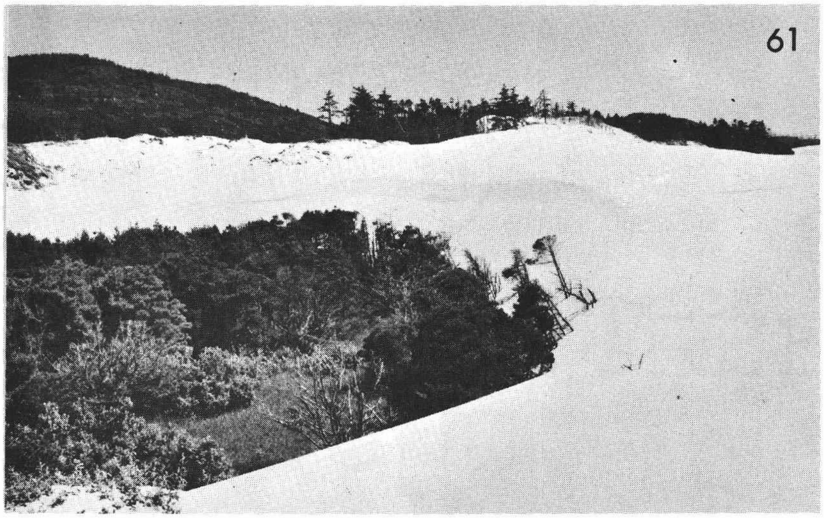
Carter Lake

This small deflation plain (Figure 6) is one of a series that owe their origin to the northward movement of the oblique ridges, and they are destroyed by these same dunes. There are many places where "pine graveyards" are being uncovered. The vegetation here also shows the belt pattern noticed on the other areas. In this case, there are three belts, the oldest and largest trees on the west. Ring counts place their age at about 60 years. Figure 61 shows the south end being invaded by a high dune. The north end is low and wet

Figure 61. Carter Lake (CL). South end of deflation plain being covered by active dune. Trees, _Pinus contorta_, about 8 m. high. August, 1964.

Figure 62. Carter Lake Transect (CLX). View along the transect from east to west. West end marker is the telephone pole on the foredune just to the right of the large east end marker in the foreground. The east end marker is a short distance west and north of the Carter Lake deflation plain (CL). August, 1964.

Figure 63. Tahkenitch Creek (T). Oblique aerial photograph of the series of high parabola dunes encroaching on forest vegetation east of the deflation plain. Formed by northwest summer winds (dunes on left) and southerly winter winds (right). Highway US 101 runs across photograph. Tahkenitch Lake to right; Elbow Lake to left. June, 1964.



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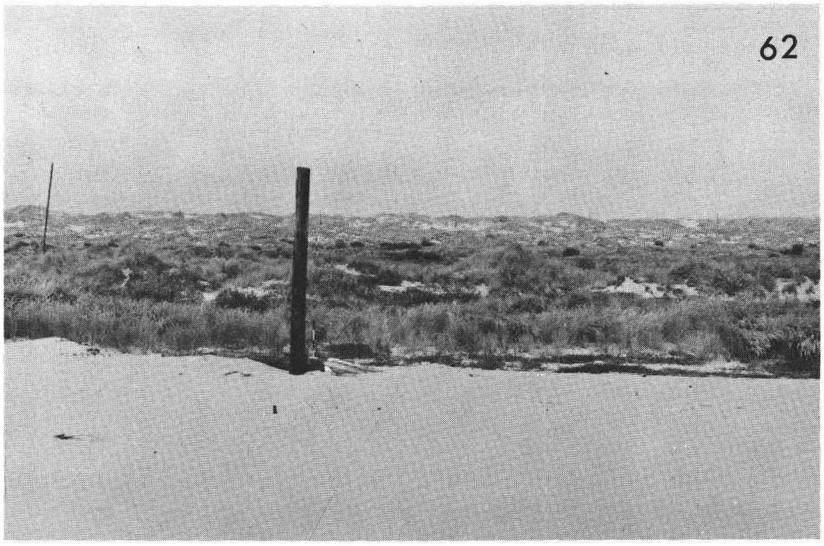

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before the sand rises again in another dune which is invading a similar area about 540 m. to the north. High Salix mounds are scattered around the northwest side.

Carter Lake Transect

This transect was set up to record the vegetation and topography across the deflation plain that is formed on the lee side of the foredune (Figure 6). It is developing along the shore the entire distance between the Siuslaw River and Coos Bay, its width and stage of development a matter of moisture and topography. Around the Cleawox Lake deflation plain, for instance, a Myrica-Salix tall shrub community has developed on low, wet ground. It is very thick and up to three m. high (Figure 18). At Carter Lake it is much less developed. The transect has been marked at both ends, and the vegetation data and photographs will be kept on file for future reference.

Figure 62 is a view along the transect from east to west. Figure 64 presents the data of the transect, based on the topographic profile. There is a general agreement between the dominance of the plant communities and moisture and topographic features. It is particularly interesting to note that the surface of the deflation plain is mostly at or a little above approximate high tide level, the high places all being mounds formed around Ammophila. Total salt

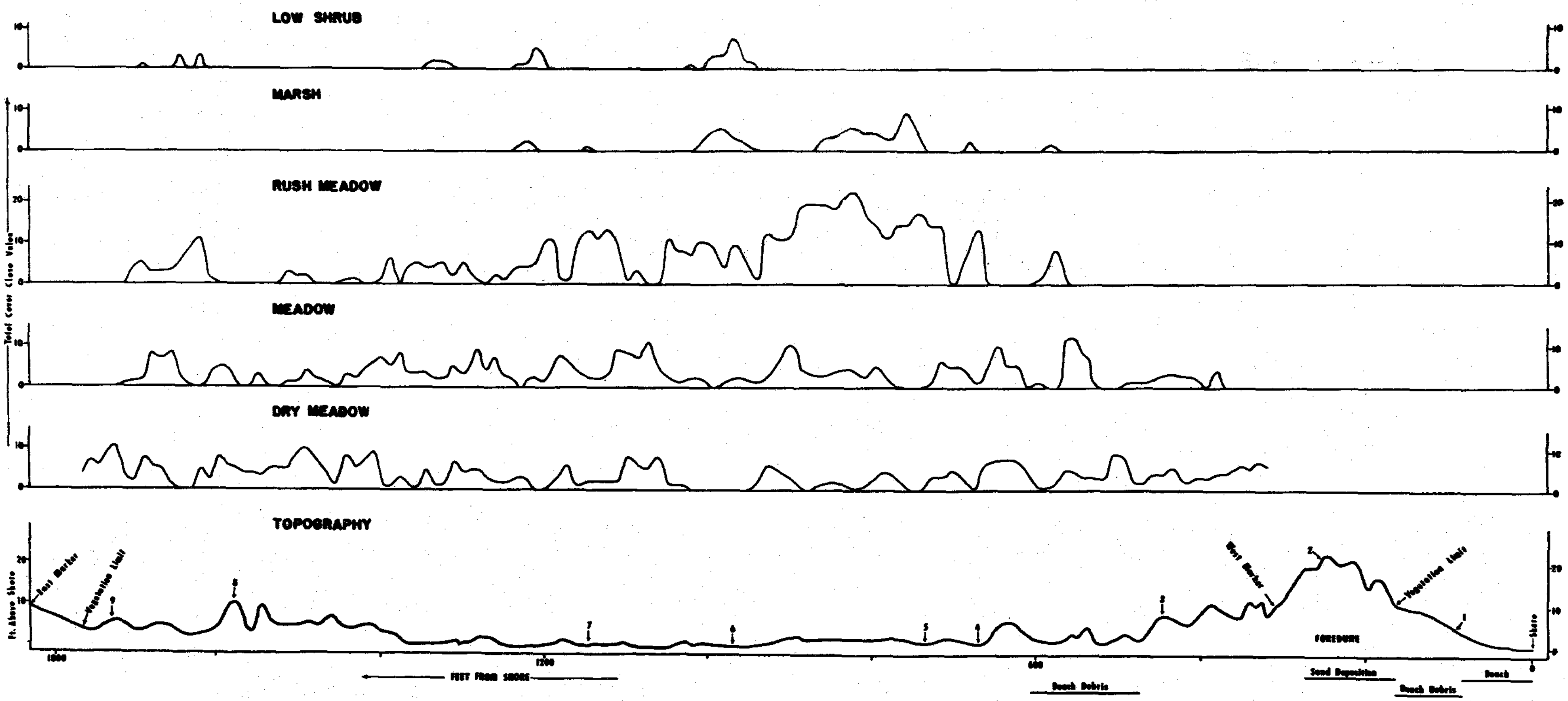

Figure 64. Carter Lake Transect (CLX). Topographic and plant community distribution profiles for the transect. Numbers on topographic profile refer to soil sampling locations. Total cover class value refers to the sum of the cover classes for all the species of a community at each of the sampling points (quadrats) which were spaced 6 m. apart along the transect.

values (mmhos/cm) were 1.63 at the west end of the transect (beach debris line), and ranged from 0.11 to 0.14 for the other sampling locations (numbers along the topography profile). A sample taken further inland (CL) had a value of 0.15, so soil water salt is not a problem for this vegetation.

The beach debris zone to the east of the foredune is good evidence for the relatively recent occurrence of the foredune. The vegetation from the west marker westward across the foredune consists only of Ammophila. The occurrence of the dry meadow community throughout the transect is due mostly to Lupinus, which, as has been seen, ranges widely between this community and the meadow. The rush meadow and marsh communities are more restricted in their occurrence, being located in areas where water stands several months of the year.

The soil samples show no great changes (Table 12). The initially high pH (7.4) is not due to carbonates, but to a sodium saturated exchange complex, which could be expected in sand washed up by the ocean (Moore, 1965). The pH drops to 7.0 atop the foredune and then varies between 5.6 and 6.1. Organic matter ranges from zero (on the beach) to 0.6 percent, the highest values coinciding with the low rush meadows of dense vegetation. The 0.6 percent sample, however, was taken from a thick, well established meadow stand. A sample from the deflation plain further inland (CL) had

TABLE 12. Soils analysis data (pH, organic matter and total salts) for the Carter Lake Transect.

Sample no.	Distance from west end of transect (m.)	pH	Organic matter %	Total salts (mm hos. /cm.)
1.	27	7.4	0	1.63
2.	78	7.0	0.12	0.13
3.	136	5.8	0.36	0.10
4.	204	6.1	0.54	0.14
5.	224	5.9	0.36	0.12
6.	296	5.5	0.18	0.11
7.	349	6.0	0.24	0.11
8.	482	5.9	0.36	0.10
9.	528	5.6	0.60	0.11
10.	CL*	5.2	0.60	0.15

*Sample from area of herbaceous vegetation on Carter Lake deflation plain.

values of 5.2 for pH and 0.6 percent for organic matter, the sample having been taken from the oldest part of the area. All samples were taken at a depth of five cm.

Tahkenitch Creek

This deflation plain is formed around the former course of Tahkenitch Creek (Figure 6, 65), and the activity of the series of parabola dunes to the east (Figure 63). Aerial photographs from 1939 to the present show the mouth of Tahkenitch Creek shifting back and forth. In 1953 it flowed almost directly into the ocean, but has since shifted southward. Davidson notes (1889, p. 405), "Inside the entrance of this creek, the stream runs northward parallel with the coast for one and a quarter miles and only two hundred and fifty yards inside the ocean beach." This easily accounts for the long, narrow ponds present on the area.

There is considerable forest on this deflation plain, much of it spruce. The thick vegetation and standing water make it impossible to cross except along a road. There are several stands of spruce over 50 years old that suggest recurrent sand activity. A 1939 aerial photograph shows only herbaceous vegetation and a few scattered trees, including those just mentioned.

The ponds are shallow, and hydric succession is taking place, the dominant species being _Scirpus validus_, _Polygonum_

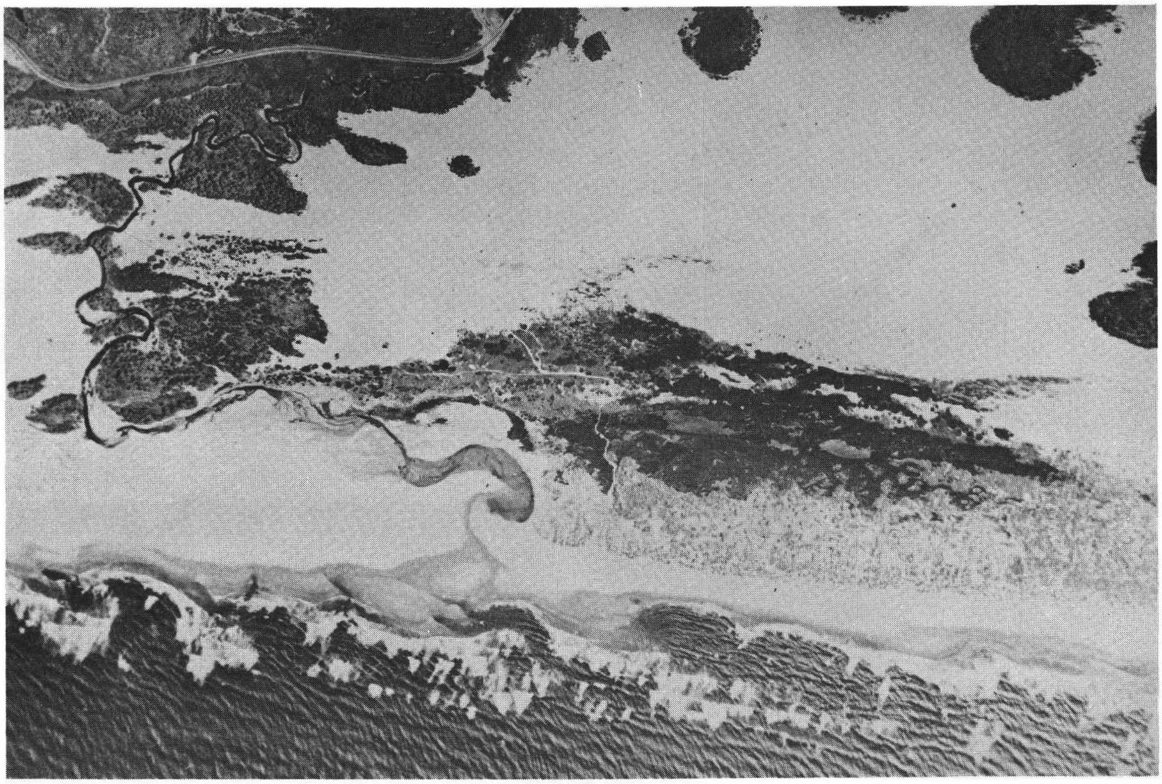

Figure 65. Tahkenitch Creek (T). Aerial photograph of the deflation plain and surrounding area. Highway US 101 top right. Tahkenitch Creek, top. Ponds are oblong, light, smooth textured areas just to left of center-line of deflation plain (porbably represent a former course of Tahkenitch Creek). High parabola dunes (Figure 64) are right and bottom. Top is north. Scale approximately 1:16000.

hydropiperoides, Cicuta douglasii and Potentilla palustris. Most of the ground west of the ponds is very wet with C. obnupta, Potentilla anserina and Eleocharis palustris.

Bandon

A brief survey was made of the vegetation on the sand dunes located both north and south of the Coquille River at Bandon on the southern Oregon coast. These dunes are forested much as the dunes around Florence, but toward the ocean, on the windward side of the active dune ridges, are extensive "sand plains" or meadows: in effect, deflation plains. Most of these have been or are being farmed.

Although the plant communities found here are very similar to those farther north, a number of species were noted which had not been encountered before, some of which do not occur on the coast north of Coos Bay (Peck, 1961). In the marsh community, these included Carex pansa, Mentha arvensis, Armeria maritima, Prunella vulgaris and Sisyrinchium bellum. Only two, Helenium bolanderi[15] and Gnaphalium chilense, were noted for the meadow; while there are four for the dry meadow: Oenothera cheiranthifolia,[15] Artemisia campestris, and Erigeron glaucus. Ceanothus

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[15]Does not occur north of Coos Bay.

thyrsiflora[16] was new among the shrubs; and Arbutus menziesii and Chamaecyparis lawsoniana[16] were important components of the forest vegetation.

An interesting feature of this region is the extensive spread of gorse (Ulex europaeus) since its introduction as an ornamental in the late 1800's. It is very aggressive and rapidly takes over cultivated land and pastures. Because of its high oil content, it burns almost explosively and was in a large measure responsible for the destruction of Bandon by fire in 1936. Eradication is a long time project (Hill, 1950).

[16] Does not occur north of Coos Bay.

V. SAND DUNES—DISCUSSION AND PERSPECTIVES

The unique features of the dune habitat—unstable sand, lack of soil nutrients, strong winds and frequently a lack of moisture—create specialized environments which have special effects on plant community development. As such, these habitats are of great interest to botanists, and more particularly to ecologists, since it is possible to study a wide variety of plant-environment relationships in a relatively small area.

Although early studies of the sand dunes were conducted on a practical basis—the need for stabilization—the vegetation itself, relatively simple in structure and organization, soon became a focal point for investigation. Much of the initial work, both in Europe and North America, centered on the description of the vegetation, frequently a simple listing of the species present. More refined studies listed species in relation to the habitats in which they were found. Finally there came the detailed analysis of the plant cover in which the species were grouped into rather distinct communities of plants—communities which could be recognized in other locations with similar environmental conditions. Much of the early impetus in community classification can be accredited to European ecologists such as Braun-Blanquet.[17]

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[17]A lengthy discussion of the history and ramifications of plant community classification is the subject of a paper by Whittaker, 1962.

The concept of tying this community structure into the various aspects of environment, however, can easily trace a good part of its development to the stimulus of North American ecologists such as Clements and Cowles. Whether in its immediate effect on the existing vegetation, or in its putative effect over time on the ultimate vegetation, environment is closely related to community development and can not be ignored.

As a result, much of the sand dune literature of Great Britain and North America is concerned with the plant communities, their development in relation to factors of the environment, and the changes which take place in these communities with time. The concepts of conservation and preservation—of keeping certain areas of land in a "natural" state—are making possible the planning of long term studies of the plant-environment complex.

Such studies, whether they be conducted on a coastal sand dune area or on an alpine tundra, can provide information over time and space that would be difficult to come by even in the most elaborately equipped laboratories or by the most intense of speculatory projection. Information thus obtained serves two basic purposes, each justifiable in its own right to serve as a basis for work of this type.

First is simply the extension of knowledge into an area of great complexity: basic research into the why, when and how of the plant-environment interaction. On sand dune areas, the plant community structure is relatively simple, the environmental factors obvious and rather certain in their influence. Moreover, in many places on the dunes, the action is compressed into shorter cycles of time, such that the development of vegetation from bare sand to forest to bare sand is possible in the lifetime of a single man. And if this is not sufficient, the constant physical change in the dune landscape makes possible the study of many phases of vegetation development at the same time. All of this contributes to our understanding and awareness of the intensely interesting world around us—of the plant world in our individual role of ecologist; of the world in general as hopefully intelligent human beings in a world confronted with the age-old problems of greed and selfishness, with the new problems of lopsided prosperity and too many people.

These problems contribute in no small way to the importance of the application of this knowledge. To the early European, it was a simple matter of stopping the sand and making the land productive. When the land gave out, the American pioneer simply picked up and moved. But today the situation is more complex. The intelligent management of agricultural lands requires a considerable knowledge of the relationships between plants and their environment, knowledge which becomes of even greater importance as more and more "marginal" lands are put to use producing the increasing food demands of an increasing population.

But the management of food producing lands is only part of the need for applying ecological knowledge. An increasingly prosperous society allows more time for recreation, and increasingly this takes the form of outdoor activities. The demand on state and national parks and forests reaches staggering proportions in some areas. How are such lands to be managed? The concept of leaving certain areas in a "natural state" becomes difficult to apply when everything around the area itself has changed and when the area itself is experiencing the invasion of multitudes of outdoor recreation enthusiasts. In addition, many public lands must bear the demands of industry as well as recreation. Clearly, there must be management, but management based on an intimate knowledge of the workings of nature and not on the immediate, and often selfish, demands of man and his society.

All of which has relevance to the Oregon coastal sand dunes. These dunes are easily the most extensive and impressive in North America. The many dune areas along the east coast and even along the coast of California are being rapidly altered or obliterated by the activities of man. The Oregon dunes, on the other hand, have much potential for long term research and study because most of the area is owned by the U. S. Government and administered by the U. S. Forest Service.

Very little has been accomplished in terms of describing the vegetation of these dunes, and in initiating work with a potential for long term study. The research reported in this thesis represents only a small part of the research needs existing on these dunes. The deflation plains are relatively discrete habitats of dynamic activity and which had not been looked at in detail by anyone. The record of their location and description should prove useful in future study.

Interesting problems exist with regard to the vegetation on the high dunes—both active dunes and those being stabilized by vegetation. Little information seems to be available concerning the ecology and physiology of many of the active dune species such as Ammophila arenaria, Lupinus littoralis, Abronia latifolia, Franseria chamissonis and many others. Successional and community relationships on these sites have not been clearly defined. On the dunes at Sand Lake, there is an interesting situation which should be investigated in greater detail. Here there is a sequence of natural stabilization which seems to begin with a bunchgrass form of Festuca rubra, followed later by a moss, Rhacomitrium canescens, which can survive a limited amount of sand burial. When the moss forms a complete carpet over the sand, the low mat forming shrub, Arctostaphylos uva-ursi, becomes established, providing, in turn, a favorable environment for the development of seedlings of Pinus contorta.

There are other features of Sand Lake which makes the entire area worthy of extensive study. There are three, large parabola dunes which are actively moving in a northeasterly direction. The rate of movement of one of these dunes is currently being studied by the author. Two large forested remnants stand on the southern part of the area near Sand Lake; and near these is an abandoned nursery of Ammophila arenaria, planted in the late 1930's by the Civilian Conservation Corps. This nursery shows interesting developmental features worthy of further study. Over the entire area, covering some five square miles (two ha.), all phases of dune and dune vegetation development are present. Furthermore, there has been relatively little disturbance by man. A number of permanent transects quadrats and photopoints have been located on the area with a view toward long term developmental studies.

Most of these dunes are included in the Siuslaw National Forest, part is owned by the Boy Scouts of America, and a small portion belongs to Tillamook County. There are also a few small private holdings. Some of the stabilized dune ridges within the Forest Service holdings are slated for development as campgrounds in 1966 and 1967 (Anderson, 1964). How this would effect the vegetation of these dunes—forests of Pinus contorta and Pseudotsuga menziesii—is not fully known. This type of development has already taken place in some forested dune areas; and is planned for others (Lyne, 1964). A study of some sort should be initiated to determine what effect the clearing of the undergrowth and the movement of many people will have on these forests and the dunes themselves.

This increasing rate of development of outdoor recreation facilities reflects national concern with this problem. It also has a marked bearing on the future of the Oregon coastal dunes. The dune areas in private ownership are being rapidly converted into resort and residential areas. An example is the very fine parabola complex just north of Waldport which is all but lost to the real estate developers. The Forest Service, which administers most of the remaining coastal dunes, especially the stretch between Florence and Coos Bay, operates under a concept of multiple use which attempts to balance the commercial and recreational utilization of these resources.

This in itself is controversial. Extensive dune stabilization plantings are favored by those who see in the moving sand only a destructive force threatening to fill rivers and cover property. These plantings are anathema to the ecologist, geologist, naturalist and all those who appreciate the opportunity to study and enjoy such unusual natural features.

The drilling of wells in the dunes just north of Coos Bay by the Pacific Power and Light Company is another example of activity which may have considerable effect upon the dunes and their vegetation. These wells supply a million and a half gallons (5,600,000 l.) of water a day to a nearby papermill, and long range planning calls for pumping eight to ten million gallons (37,850,000 l.) a day (U.S. Senate, 1963, pp. 106-127). Although effects on water table and lake levels have been postulated from preliminary studies, nothing is being done to study the effect on the vegetation of this loss of water.

The practically unrestricted use of these dunes by a public which manifests an unhappy degree of personal irresponsibility brings on more difficulty. The ubiquitous, snarling dune buggies roam everywhere, disturbing and destroying vegetation cover, and aiding in the spread of the ever increasing paper, plastic, glass and metal litter of an ever more prosperous society. The establishment of plots and transects is difficult and frustrating because necessary markers are all too often destroyed or removed.

But however disturbing the problems, the fact that these lands are in public ownership is significant. Udall (1963, pp. 188-189) estimates that in 1960 only seven percent of the 21,000 (34,000 km.) miles of ocean shore line in the contiguous 48 states was reserved for public recreation. Even considering the entire coastline, this condition of potential overcrowding makes Huxley's plaintive description of conditions in Great Britain seem rather minor, but no less disturbing (1965, p. 177):

> Recreation and wildlife, natural beauty and unspoiled coasts are especially pressed upon. Britain has a relatively long coastline; yet if every British man, woman and child were to go to the seaside on the same day, they would have little more than one

> yard of coastline apiece. The coasts of all Europe are being speedily filled up by the army of holiday makers.

Since even with public ownership, the natural state or beauty of an area can be drastically altered, there has been an increasing pressure to set aside some of these coastal areas as National Seashores. Four have already been established,[18] and work has been in progress since 1959 to include at least a part of the Oregon dunes into an Oregon Dunes National Seashore (U.S. Congress, 1959; U.S. Senate, 1963).

So far the attempt has been unsuccessful. Most controversy is centered on the amount of private property to be included in the proposed park, and on the methods of acquiring the property, factors which will become increasingly troublesome in future acquisitions of lands for public recreation. Another point of contention is the assertion that almost all recreation on the dunes takes place in the forests and on the sheltered lakes along their inner margins. Few people, it is contended, venture out onto the dunes and beaches which are frequently stormy and windy. This would be even more the case if dune buggies were restricted in their wanderings and walking were necessary.

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[18] Cape Hatteras National Seashore, North Carolina; Cape Cod National Seashore, Massachusetts; Padre Island National Seashore, Texas; and Point Reyes National Seashore, California.

This lack of desire for intimate contact with the forces of nature is probably real, but certainly no excuse to try to change the existing pattern of the dunes to accommodate such a situation. Man would do better to develop more of the spirit of John Muir, who "...wandered through the wood 'enjoying the passionate music of the storm'... sought the most intimate relation to natural forces—to the winds, the storms, the rivers and forests and wild animals... (and) developed his inner ear to catch the nuances of nature." (Udall, 1963, pp. 121-122).

But just as important a reason for maintaining some degree of naturalness in these areas is the opportunity they present to study and observe the many and complex inter-relationships between plants and their dynamic environment. This is not a matter of necessity in terms of stabilization or reclamation of the land for the use of man as was the case in Europe. Rather it is a matter of understanding—for man's own satisfaction and for his intelligent use of the rapidly diminishing natural resources.

In testimony before the Committe on Interior and Insular Affairs (U.S. Congress, 1963, p. 25), Cooper says of the Oregon coastal dunes:

> The area of the proposed Oregon Dunes National Seashore comprises three zones parallel to the shore: beach, dunes, and lakes, each uniquely beautiful. Most spectacular, of course, are the dunes. In magnitude, beauty, and opportunity

> for research they surpass those of any of the four national seashores that have so far been established; they are by far the finest coastal sand dunes in North America, and have few rivals in the world. So far as possible they should be preserved in their natural state.

One of the objectives of the present work was to stimulate interest in this unique resource. It is hoped that the two phases of the work—the review of world literature on coastal sand dunes; and the ecological analysis of the deflation plains—will contribute to this objective as well as to a greater understanding of the general dune habitat.

VI. SUMMARY

Sand dunes are found along the coasts of most of the large land masses of the world. Because of their proximity to man and his activities, the maritime sand dunes of Europe, particularly Germany, France, Holland and Scandinavia, have the longest history of stabilization activities and botanical investigation. There are coastal dune areas, some of great extent, in Africa, tropical Asia, Australia, and South America. In general, little published information is available concerning these areas. Ecological studies of coastal dune vegetation and environment have been most extensive in Great Britain, and to a lesser extent, in North America.

Of the North American coastal dunes, those of the east coast have received considerable attention while those of the west coast have been largely neglected. Along the Oregon coast are found some of the most extensive and best developed coastal sand dune areas in North America. Occurring on some 225 km. of the state's 500 km. of ocean facing coastline, these areas are made up of a great variety of dune landscape features and present unique conditions for the development and maintenance of vegetation.

There are many places in this dune area where the strong, constant winds have eroded the sand surface to or near the water table resulting in a stabilized surface—the deflation plain—which provides an excellent starting point for the development of vegetation. After preliminary ground and air reconnaissance, 11 deflation plains were selected for detailed study, ranging in location from Sand Lake on the north to Tahkenitch Creek on the south. These deflation plains and their location are described in detail.

Vegetation data (species and cover) were taken on a total of 134 sampling stands, each consisting of five meter-square quadrats for herbaceous vegetation, and one 6 x 6 meter quadrat for shrub and forest vegetation. The species and stand data were arranged on comparative charts so as to bring together stands with mutually occurring species. This resulted in the delineation of seven communities with definite successional relationships. Primary succession begins with one of four herbaceous communities: dry meadow, meadow, rush meadow or marsh. Succession then proceeds to low shrub, tall shrub and finally forest.

The dry meadow is dominated by three species: Lupinus littoralis, Ammophila arenaria and Poa macrantha. The site is dry with no standing water at any time. Sand deposition and deflation occur in varying degrees. The important species of the meadow are Festuca rubra, Aira praecox, Hypochaeris radicata and Fragaria chiloensis. The surface is dry except for short periods of standing water during the winter months. There is no sand deposition. The rush meadow is characterized by its dense growth of Trifolium willdenovii and Juncus phaeocephalus. The site is low and moist, with water standing on the surface during the winter months. The marsh is found on areas which are quite damp—water stands on the surface for around six months of the year, and is just below the surface for the remainder of the time. It is made up of dense stands of Carex obnupta and Potentilla anserina.

The low shrub community is an open stand of Salix hookeriana, Gaultheria shallon, Vaccinium ovatum and Myrica californica. This develops into a tall shrub stage which is frequently an impenetrable thicket with increasing dominance of seedlings of Pinus contorta and Picea sitchensis. Development of a forest of Pinus and Picea is very rapid. If the area is free from disturbance long enough, the shorter lived Pinus dies out, leaving a forest of Picea.

The deflation plains represent only part of the many aspects of the total dune landscape still awaiting investigation. The increasing importance of the Oregon coastal dunes to industry and recreation make imperative the initiation of long term ecological studies.

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APPENDICES

APPENDIX I

SPECIES LIST

Species are listed alphabetically by scientific name followed by the common name in parenthesis. The family, and in some cases the tribe, is also given for each species. Except as noted, all names are based on Peck (1961).

* Bryophyte identification was made by Pechanec (1965) and family names are based on Conard (1958).

** Species of Lotus based on Isely (1951).

*** Pinus pinaster based on Dallimore and Jackson (1948).

Abronia latifolia Esch. (Yellow abronia)	Nyctaginaceae
Achillea millefolium L. (Yarrow)	Compositae (Anthemideae)
Agoseris apargioides (Less.) Greene (Seaside agoseris)	Compositae (Cichorieae)
Agrostis ampla Hitch. (Dense flowered bentgrass)	Gramineae (Agrostideae)
Agrostis exarata Trin. (Western bentgrass)	Gramineae (Agrostideae)
Agrostis pallens Trin. (Seashore bentgrass)	Gramineae (Agrostideae)
Agrostis palustris Huds. (Creeping bentgrass)	Gramineae (Agrostideae)
Aira caryophyllea L. (Silvery hairgrass)	Gramineae (Aveneae)
Aira praecox L. (Little hairgrass)	Gramineae (Aveneae)

Alnus oregana Nutt. (Red alder)	Betulaceae
Ammophila arenaria (L.) Link. (Beach grass)	Gramineae (Agrostideae)
Anaphalis margaritacea (L.) B. & H. (Pearly everlasting)	Compositae (Inuleae)
Arbutus menziesii Pursh. (Madrono)	Ericaceae
Arctostaphylos uva-ursi (L.) Spreng. (Kinnikinnick)	Ericaceae
Armeria maritima (Mill.) Willd. var. purpurea (Koch) Lawr. (Thrift)	Plumbaginaceae
Artemisia campestris L. var. scouleriana (Bess) Cron. (Silky field wormwood)	Compositae (Anthemideae)
Aster subspicatus Nees. (Douglas's aster)	Compositae (Astereae)
Botrychium silaifolium Presl. (Leathery grape-fern)	Ophioglossaceae
*Brachythecium spp. (Moss)	Hypnaceae
Cakile edentula (Bigel.) Hook. var. californica (Hel.) Fern. (American sea rocket)	Cruciferae
*Campylium hispidulum (Brid.) Mitt. (Moss)	Hypnaceae
Cardionema ramosissima (Winm.) Nels & Macbr. (Sand mat)	Illecebraceae
Carex hindsii Clarke (Hind's sedge)	Cyperaceae

Carex obnupta Bail. (Slough sedge)	Cyperaceae
Carex pansa Bail. (Sand dune sedge)	Cyperaceae
Carex viridula Michx. (Green sedge)	Cyperaceae
Ceanothus thyrsiflorus Esch. (Blue blossom)	Rhamnaceae
Centaurium umbellatum Gilib. (Centaury)	Gentianaceae
Cerastium holosteoides Fries. (Common mouse-ear)	Caryophyllaceae
*Ceratodon purpureus (Hedw.) Brid.) (Moss)	Ditrichaceae
Chamaecyparis lawsoniana Parl. (Port Orford cedar)	Cupressaceae
Cicuta douglasii (DC.) C. & R. (Western water hemlock)	Umbelliferae
Comarum palustre L. (Marsh cinquefoil)	Rosaceae
Convolvulus soldanella L. (Coast morning glory)	Convolvulaceae
Cytisus scoparius (L.) Link. (Scotch broom)	Leguminosae
Darlingtonia californica Torr. (California pitcher plant)	Sarraceniaceae
Drosera rotundifolia L. (Round leaved sundew)	Droseraceae
Eleocharis palustris (L.) R. & S. (Creeping spike rush)	Cyperaceae

Elymus mollis Trin. (Sea lyme grass)	Gramineae (Hordeae)
Epilobium franciscanum Barb. (Pacific willow-herb)	Onagraceae
Epipactis gigantea Dougl. (Giant helleborine)	Orchidaceae
Erechtites prenanthoides DC. (Australian fireweed)	Compositae (Senecioneae)
Erigeron glaucus Kerr. (Seaside erigeron)	Compositae (Astereae)
**Eurhynchium oreganum* (Sulliv.) Jaeger & Sauerb. (Moss)	Hypnaceae
Festuca elatior L. var. *arundinacea* (Schrad.) Weinm. (Meadow fescue)	Gramineae (Festuceae)
Festuca myuros L. (Rat tail fescue)	Gramineae (Festuceae)
Festuca rubra L. (Red fescue)	Gramineae (Festuceae)
Fragaria chiloensis (L.) Duch. (Coast strawberry)	Rosaceae
Franseria chamissonis Less. (Silver beachweed)	Compositae (Ambrosiae)
Galium trifidum L. (Small bedstraw)	Rubiaceae
Galium triflorum Michx. (Fragrant bedstraw)	Rubiaceae
Gaultheria shallon Pursh. (Salal)	Ericaceae

Gentiana sceptrum Griseb. (Staff gentian)	Gentianaceae
Glehnia leiocarpa Math. (Beach silver top)	Umbelliferae
Gnaphalium chilense Spreng. (Cotton batting plant)	Compositae (Inuleae)
Gnaphalium purpureum L. (Purplish cudweed)	Compositae (Inuleae)
Helenium bolanderi Gray. (Coast sneezeweed)	Compositae (Helenieae)
Holcus lanatus L. (Velvet grass)	Gramineae (Aveneae)
Hypericum anagalloides C. & S. (Bog St. John's wort)	Hypericaceae
Hypericum perforatum L. (Common St. John's wort)	Hypericaceae
Hypochaeris radicata L. (False dandelion)	Compositae (Cichorieae)
Juncus acuminatus Michx. (Sharp-fruited rush)	Juncaceae
Juncus bufonius L. (Toad rush)	Juncaceae
Juncus falcatus E. Mey. (Sickle leaved rush)	Juncaceae
Juncus lesueurii Boland. (Salt rush)	Juncaceae
Juncus phaeocephalus Engelm. var. *glomeratus* Engelm. (Brown headed rush)	Juncaceae
Lathyrus japonicus Willd. var. *glaber* (Ser.) Fern. (Beach pea)	Leguminosae

Lathyrus littoralis (Nutt.) Endl. (Gray beach pea)	Leguminosae
Ledum columbianum Piper. (Pacific labrador tea)	Ericaceae
Leontodon nudicaulis L. (Rough hawkbit)	Compositae (Cichoriae)
Lilaeopsis occidentalis C. & R. (Western lilaeopsis)	Umbelliferae
Lolium perenne L. (Perennial ryegrass)	Gramineae (Hordeae)
Lonicera involucrata (Rich.) Banks. (Black twinberry)	Caprifoliaceae
**Lotus formosissimus Greene (Seaside lotus)	Leguminosae
**Lotus major Scop. (Bird's foot trefoil)	Leguminosae
**Lotus purshianus (Benth.) Clem. & Clem. (Spanish clover)	Leguminosae
Lupinus littoralis Dougl. (Seashore lupine)	Leguminosae
Lycopodium inundatum L. (Bog club moss)	Lycopodiaceae
Lycopus uniflorus Michx. (Bugle weed)	Labiatae
Mentha arvensis L. (Field mint)	Labiatae
Mimulus guttatus DC. var. litoralis Penn. (Common monkey flower)	Scrophulariaceae
*Mnium punctatum Hedw. (Moss)	Mniaceae

Myrica californica C. & S. (Western wax myrtle)	Myricaceae
Oenothera cheiranthifolia Hornem. (Beach evening primrose)	Onagraceae
Orthocarpus castillejoides Benth. (Paintbrush orthocarpus)	Scrophulariaceae
Orthocarpus pusillus Benth. (Dwarf orthocarpus)	Scrophulariaceae
Phacelia argentea Nels. & Macbr. (Silvery phacelia)	Hydrophyllaceae
Picea sitchensis (Bong.) Carr. (Sitka spruce)	Pinaceae
Pinus contorta Loud. (Coast pine, lodgepole pine)	Pinaceae
***Pinus pinaster Aiton. (Maritime pine)	Pinaceae
Plantago lanceolata L. (English plantain)	Plantaginaceae
Plantago subnuda Pilgr. (Tall coast plantain)	Plantaginaceae
Poa confinis Vas. (Dune bluegrass)	Gramineae (Festuceae)
Poa macrantha Vas. (Seashore bluegrass)	Gramineae (Festuceae)
Polygonum hydropiperoides Michx. (Mild water pepper)	Polygonaceae
Polygonum paronchyia C. & S. (Beach knotweed)	Polygonaceae
*Porella navicularis (Lehm. & Lindenb) Linb. (Liverwort)	Porellaceae

Potentilla anserina L. var. concolor Hayne (Silver weed)	Rosaceae
Prunella vulgaris L. (Heal-all)	Labiatae
Pseudotsuga menziesii (Mirb.) Franco. (Douglas fir)	Pinaceae
Ranunculus flammula L. var. ovalis (Bigel.) Bens. (Small creeping buttercup)	Ranunculaceae
*Rhacomitrium canescens Brid. var. ericoides (Brid.) Moenk. (Moss)	Grimmiaceae
Rumex acetosella L. (Red sorrel)	Polygonaceae
Rumex crispus L. (Curly leaved dock)	Polygonaceae
Sagina crassicaulis Wats. (Thick stemmed pearlwort)	Caryophyllaceae
Sagina procumbens L. (Procumbent pearlwort)	Caryophyllaceae
Salix hookeriana Barr. (Coast willow)	Salicaceae
Scirpus americanus Pers. (Three square rush)	Cyperaceae
Scirpus validus Vahl. var. creber Fern. (American great bullrush)	Cyperaceae
Senecio jacobea L. (Tansy ragwort)	Compositae (Senecioneae)
Sisyrinchium bellum Wats. (Western blue eyed grass)	Iridaceae

Sisyrinchium californicum (Ker.) Dryand (Golden eyed grass)	Iridaceae
Solidago spathulata DC. (Sticky goldenrod)	Compositae (Astereae)
*Sphagnum spp. (Moss)	Sphagnaceae
Spiranthes romanzoffiana Cham. (Hooded ladies' tresses)	Orchidaceae
Spirea douglasii Hook. (Western spirea)	Rosaceae
Stellaria calycantha (Ledeb.) Bong. (Northern starwort)	Caryophyllaceae
Struthiopteris spicant (L.) Weis. (Deer fern)	Polypodiaceae
Tanacetum camphoratum Less. (Western tansy)	Compositae (Anthemideae)
Thuja plicata D. Don. (Giant cedar)	Cupressaceae
Trifolium willdenovii Spreng. (Spring bank clover)	Leguminosae
Tsuga heterophylla (Raf.) Sarg. (Western hemlock)	Pinaceae
Ulex europaeus L. (Gorse)	Leguminosae
Vaccinium ovatum Pursh. (Evergreen huckleberry)	Ericaceae
Vaccinium uliginosum L. (Blueberry)	Ericaceae
Veronica scutellata L. (Marsh speedwell)	Scrophulariaceae

APPENDIX II

NOTES ON PHOTOGRAPHS

Except as noted below, all photographs were taken by the author in the course of field work for this study. Copies of these photographs and, wherever feasible, the location of the photopoints, will be kept on file with the Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon.

Figure 5. U.S. Coast and Geodetic Survey photograph. Index 53A, No. 58-S-9304A, September 7, 1958. Washington, D.C.

Figure 6. Composite map from Geological Survey maps: Heceta Head, Oregon, 1956, and Siltcoos Lake, Oregon, 1956. Scale 1:62500.

Figure 28. BOTTOM: Corps of Engineers photograph. No. 5645, 1939. Portland, Oregon. Used by permission.

TOP: U.S. Forest Service photograph. Project Symbol EIJ, No. 6-73, August 20, 1961. Portland, Oregon.

Figure 36. BOTTOM: No source data available. Photograph on file in Supervisor's Office, Siuslaw National Forest, Corvallis, Oregon.

TOP: Corps of Engineers photograph. No. 61-2000, June 7, 1958, Portland, Oregon.

Used by permission.

Figure 41. BOTTOM: No data available. Photograph is numbered 3-LI-367. Obtained from Mr. Don Brackett, U. S. Soil Conservation Service, Florence, Oregon.

TOP: U. S. Forest Service photograph. Project Symbol EIJ, No. 3-41, August 6, 1961. Portland, Oregon.

Figure 46. BOTTOM: No data available. Photograph is numbered 4-LI-367. Obtained from Mr. Don Brackett, U. S. Soil Conservation Service, Florence, Oregon.

TOP: U. S. Forest Service photograph, Project Symbol EIJ, No. 3-43, August 6, 1961. Portland, Oregon.

Figure 52. BOTTOM: Corps of Engineers photograph, No. 2998, 1939. Portland, Oregon. Used by permission.

TOP: U. S. Coast and Geodetic Survey photograph, Index 54A, No. 55-W-1059, October 16, 1955. Washington, D. C.

Figure 65. U. S. Forest Service photograph. Project Symbol EIJ, No. 3-89, August 6, 1961. Portland, Oregon.