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THESES AND BOOKS (Introductory pages only.)


Estimation of Optimum Plot Size and Shape for Safflower Yield Trials

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SYNOPSIS. Optimum plot size and shape for safflower yield trials were estimated to be 8 times the basic unit or 3.67 feet wide by 20 feet long. Drastic and sudden changes in soil uniformity can lead to an abnormal calculated value of b.

ONE big problem encountered in experimental yield trials of field crops is variation in yield estimates regardless of how the trial is handled with respect to variety or treatment. This variation in yield fluctuates according to size and shape of plots and is different for each field crop. Determining optimum plot size and shape takes into account both minimum variance and minimum cost of handling the plot. Determining optimum plot size and shape for safflower yield trials was the purpose of this study.

REVIEW OF LITERATURE

The effect of environmental factors such as soil heterogeneity upon experimental field crop trials has been recognized for some time. In an early study to determine experimental error of field trials, Mercer and Hall (4), working with mangel, used the concept of probable error to analyze variation in field experiments. They determined optimum plot size on the basis of a curve relating plot size and percent deviation. Most later workers used this type of study to determine optimum plot size. Federer (2), however, pointed out that this method has a weakness in that point of maximum curvature is not independent of the smallest unit selected or of the scale of measurement used.

A different method of determining optimum plot size was proposed by Smith (5). Using a regression coefficient “b”, computed from variance and plot size data of a uniformity trial with wheat and two cost factors relating number of plots in a test area and the size of the test area, he developed a formula which estimated optimum plot size in terms of basic plot size. Wasson and Kalton (6) and Brim and Mason (1) used this method to determine optimum plot size for bromegrass and soybean yield trials, respectively.

In another approach, Keller (3), working with hops, used the comparable variance method of determining optimum plot size. Variance between basic plots was assumed to contribute 100% information. Between plot variance for each of a number of combinations of plots was calculated and compared with the basic plot variance. Keller found that comparable variance increases and relative information decreases as size of the plot increases.
In the only study dealing with safflower, Draper\textsuperscript{a} used basic plots of two sizes: 4-foot and 5-foot single rows. On the basis of comparable variance, without regard to cost factors, optimum plot size was 3.33 by 18 feet for the 5-foot basic plots and 3.33 by 12 feet for the 4-foot basic plot. Calculating cost factors and utilizing the formula of Smith (5), Draper found optimum plot size for safflower to be 3.33 by 25 feet.

**EXPERIMENTAL PROCEDURE**

**Agronomic Data**

US-10 variety was planted at Utah State University Field Station, Farmington, Utah, on April 6, 1960, on a plot of land approximately ½ acre in size. The soil in the field was variable, with high amounts of clay in the northern third of the field and a slightly sandy condition in the other two-thirds. No fertilizer was applied and the field was thoroughly watered by furrow irrigation five times during the growing season.

Dimensions of the field were 114 feet wide and 189 feet long. Rows were spaced 22 inches apart with a 4-row sugar beet planter adapted for use with safflower seed. Rate of seeding was 15 pounds per acre and a uniform stand was obtained. A total of 62 rows resulted which ran in the long dimension of the field in an east-west direction.

The field was harvested as a series of 5-foot, 1-row plots. As the plants were cut, they were carried to a stationary plot thresher where the seed from each 5-foot section of row was threshed, weighed, and recorded separately. Yield was recorded to the nearest gram.

**Comparable Variance**

This procedure yielded 1782 one-row, 5-foot plots which were considered the basic plots for this study. Contiguous plots were then combined in a total of 32 different combinations; and among plot variances of these different combinations were computed. These among-plot variances were designated \( V_{ab} \). Among-plot variances were then divided by the number of basic units per plot to give comparable variance, designated as \( V \).

Comparable variances were in turn divided by the number of basic units per plot \( x \) to give the variance of yield per unit area. This was designated \( V_x \). Combined with the previous method for finding comparable variance, \( V_x \) can be computed directly by the following relation:

\[
V_x = V_{ab}/x^2 \tag{1}
\]

Variance of the yield per unit area \( (V_x) \) is used in the next section to compute regression coefficients for number of basic units on variance of yield per unit area.

To obtain a measure of relative information, comparable variances for all plot sizes were compared with the plot size having the smallest comparable variance. This method has been used by several investigators including Keller (3) and Wasson and Kalton (6).

**Regression Coefficient and Cost Factors**

Optimum plot size also was determined by considering measures of soil heterogeneity and relative costs. In deriving this method, Smith (5) showed that an empirical relation existed between plot size and plot variance. He characterized this relation by the equation:

\[
V_x = V / x^b \tag{2}
\]

Where \( V_x \) is variance of yield per unit area among plots which are x units in size, \( V_i \) is variability among basic units, and b is regression coefficient between plot size and variance per unit area among plots x units in size providing a measurement of soil heterogeneity. The regression coefficient will vary between zero and plus or minus infinity. A value close to zero indicates a very uniform field while a value near one would indicate a field very heterogeneous in soil fertility. A regression coefficient of 0.5 indicates that the 50% of the time the yield of any given crop on any given field, but it will vary from crop to crop and from year to year.

When equation (2) is expressed in logarithmic form, it becomes:

\[
\log V_x = \log V_i - b \log x \tag{3}
\]

and "b" can be estimated from this relationship. The mean of the regression coefficients for all plot sizes was calculated to obtain a value of "b" for the field. To use "b" in conjunction with relative costs to estimate optimum plot size, two cost factors, \( K_b \) and \( K_x \) must be determined. \( K_b \) is cost proportional to number of plots in test area; and \( K_x \) is cost proportional to total test area. These costs, which were determined from information supplied by individuals experienced in working with safflower, represent estimates of costs for the methods commonly used in safflower yield trials.

Optimum size of plot in number of basic units was then calculated by substituting calculated values of \( b \), \( K_b \), and \( K_x \) into the formula derived by Smith (5):

\[
x = b K_b / (1 - b K_x) \tag{4}
\]

The resulting calculated value of \( x \) gave optimum plot size in number of basic units without regard to shape of plot. Optimum shape was then determined by comparison of variances of same plot sizes that could be made up with that number of basic units and by a consideration of convenience with which each of the variously shaped plots could be handled.

**RESULTS AND DISCUSSION**

The basic plots were added together to produce 32 different combinations of row by range. Six rows, or 11 feet, was the maximum width used, while 11 ranges, or 55 feet, was the maximum length used. Except for single-row plots, only combinations using 2, 4, or 6 rows were used, since only plots of this width could be conveniently handled with the planting and harvesting equipment available.

**Abnormal "b" Value**

The basic plots varied considerably in productivity in that about 1/3 of the rows on the north end of the field had an average production twice that of the other rows. This increased yield might be explained by a higher clay content of this section of the field, which in turn probably resulted in a higher water and nutrient retention than the rest of the field. Productivity of the field from east to west (direction of irrigation water flow) was relatively uniform as measured by the total yield of each range.

As a result of this yield differential, a remarkable inconsistency developed as the data were analyzed. The regression coefficient, b, which is a measure of soil heterogeneity, was calculated as being -0.1 for this field. This would seem to indicate a field with uniform soil. At the same time, the coefficient of variation for basic plots was computed as 39.5%. This is high when compared to an expected value of 12 to 15% for yield trials. Even on maximum sized plots, the coefficient of variation was reduced by only 10%.

The effect of this disproportionate yield between the sides of the field was to increase variance per unit area by a large amount. At the same time this variance decreased only very slowly with increasing plot size, the net result being a very small regression coefficient in spite of obvious differences in the field's productive potential. This is shown in Figure 1, the regression of the logarithm of the variance of yield per unit area on the logarithm of size of plot. This figure also shows a separation of the data into 2 groups, the lower group being those plot sizes 4 rows wide and 3 or more ranges long.

Difference in yields so inflated the variance per unit area that an estimate of "b" was not meaningful and caused the unusually high coefficient of variation. With this in mind, the northern third of the field was excluded from the analysis. This left a total of 36 rows, or 1188 basic plots to

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Table 1—Number of basic units (1), shape (2), among plot variance (3), comparable variance (4), variance per unit area (5), relative information (6), coefficient of variation (7), and regression coefficient (8) for the 32 combinations of plot size and shape of 1188 basic units.

<table>
<thead>
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<th>x</th>
<th>Row x range</th>
<th>V (x)</th>
<th>V</th>
<th>V*</th>
<th>%</th>
<th>%</th>
<th>b</th>
</tr>
</thead>
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<td>(3)</td>
<td>(4)</td>
<td>(5)</td>
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<td>(7)</td>
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<td>9</td>
<td>9.5</td>
<td>0.43</td>
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</table>

Figure 1—Regression of logarithm of variance of yield per unit area on logarithm of size of plot for 1782 basic units.

Figure 2—Regression of logarithm of variance of yield per unit area on logarithm of size of plots for 1188 basic units.

The variance of basic units was assumed to contribute 100% relative information, and therefore the basic plot size contributes the greatest relative information. As plot size increased, relative information decreased, as did variance of yield per unit area. The decrease in relative information was most rapid up to a plot size of about 8 to 10 basic units and changed only a relatively small amount after this point.

In conjunction with this, the variance of yield per unit area, which was very high for basic plots, decreased rapidly up to a plot size of about 8 to 10 units, and then decreased more slowly. This information indicates that a plot size of about eight times the basic unit might be optimum when both the decrease in relative information and decreased variance are considered. While increased plot size would reduce the variance still further, the amount of land required would make the information so obtained more costly.

Soil Heterogeneity and Relative Costs

An estimate of optimum plot size was made using Smith’s (5) regression-coefficient-relative cost relation. The value of the regression coefficient, b = 0.43, is the average of the "b" values for the 32 plot sizes. This value, a measure of the soil’s heterogeneity, indicated a field a little above average in uniformity, if the range from 0.4 to 0.7 is considered to be a common one. This value for "b" would hold only for that portion of the field that comprised the 1188 basic plots. Regression of the logarithm of variance of yield per unit area on the logarithm of size of plot is found in Figure 2, and is quite different from that found in Figure 1.
Table 2—Estimated cost factors, $K_1$ and $K_2$, for this experiment when conventional plot equipment is used.

<table>
<thead>
<tr>
<th>Operation</th>
<th>Man-hours</th>
<th>% of total</th>
<th>$K_1$</th>
<th>$K_2$</th>
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<td>Land preparation</td>
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<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Seed preparation</td>
<td>40</td>
<td>10.7</td>
<td>1.0</td>
<td>1.0</td>
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<tr>
<td>Planting plan</td>
<td>8</td>
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<td>2.1</td>
<td>2.1</td>
</tr>
<tr>
<td>Planting</td>
<td>9</td>
<td>2.4</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>Care of plots</td>
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<td>23.9</td>
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<tr>
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<td>1.6</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>Harvesting</td>
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<td>32.7</td>
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<td>0.4</td>
</tr>
<tr>
<td>Analyzing data</td>
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<td>5.3</td>
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<tr>
<td><strong>Totals</strong></td>
<td><strong>375</strong></td>
<td><strong>100.0</strong></td>
<td><strong>74.1</strong></td>
<td><strong>25.9</strong></td>
</tr>
</tbody>
</table>

In addition to the regression coefficient, two cost factors, $K_1$ and $K_2$, were estimated by considering total cost in man-hours for the following operations: land preparation, seed preparation, preparing planting plan, planting, care of plots, note taking, harvesting, and statistical analysis (Table 2). Percent of total cost was computed for each of these operations and then this proportion was further divided into cost proportional to number of plots in test area ($K_1$) and that proportional to total size of test area ($K_2$).

Calculated values for $K_1$ and $K_2$ apply particularly to this study, but might be also considered representative of safflower yield trials using the same general procedure and equipment. The 3 values, $b = -0.43$, $K_1 = 74.1\%$, and $K_2 = 25.9\%$, were then substituted into formula [4] to obtain an estimate of optimum plot size. The computed value is 2.2 times the basic unit, a value considerably smaller than that arrived at by considering variance alone. Smith indicates, however, that actual plot size could fluctuate both above and below this value without losing what might be considered optimum plot size. It is evident that as cost proportional to number of plots increases, and as the field becomes more heterogeneous, optimum plot size in basic units increases considerably.

**Plot Shape**

It was the opinion of Smith (5) that plot shape generally had no consistent effect on variance. Values in columns 2 and 5 of Table 2 show the effect of number of rows (plot width) on variance of yield per unit area for plots of different lengths. The greatest reduction in variance occurred in 1-row plots, and considerable, but less in 2-row plots. Four- and 6-row plots, even though their variances were lower, did not decrease the variance as much as did the other two. Increased size of plots could be considered as the main reason for decrease in variance. A comparison of the variances ($V_s$) of yield per unit area in long, narrow plots and in the corresponding short, wide plots readily shows very little difference in variance due to shape of plot. For example, the 1-row by 6-range plots had a variance of 576, while the corresponding 6-row by 1-range plots had a variance of 543.

In considering plot shape, it is important to consider convenience in handling plots. A self-propelled plot combine used in harvesting yield trials cuts 2 rows at a time and can be used on a 1-row plot only with difficulty. Four- and 6-row plots would be undesirable with this type of harvesting equipment. With this in mind, plus the fact that variance is only slightly affected by plot shape, plots two rows wide are recommended.

**CONCLUSIONS**

Of 2 methods used to estimate optimum plot size, 1 indicated that about 8 times the basic unit would give the information desired. The other, relating soil heterogeneity and relative costs, gave an optimum plot size of about two times the basic unit. As can be seen from Table 2, variance of yield per unit area for plot sizes using 2 basic units is rather high, particularly as compared with 8 unit plots.

However, as Smith (5) pointed out, plot size calculated from his formula could be as much as four times the calculated value and still be considered an optimum plot size. Plot size calculated by use of relative information fell within this limit.

When all factors are considered, optimum plot size for safflower yield tests were estimated to be eight times the basic unit used in this experiment. Taking into account recommendations concerning plot shape, cost factors, soil heterogeneity, reduction in variance due to increased plot size, and information desired from safflower yield tests, a plot 2 rows wide by 4 ranges long, or 3.67 feet wide by 20 feet long, is suggested as optimum. This is only slightly smaller than the 3.33 by 25 foot plot size recommended by Draper from his study on safflower.

Since many of the results involve use of the regression coefficient "b" in their calculation, a fluctuation of this value could easily cause differences in optimum plot size. As was shown earlier, "b" can be misleading if changes in soil heterogeneity are sudden and drastic in character. Another approach to the problem would be to compute optimum plot sizes for a number of different areas and conditions. Recommendations based on this study cannot be considered as definite since, technically, they pertain only to the field and crop used for this experiment. They can, however, serve as a guide to future studies.

**SUMMARY**

Optimum plot size and shape for safflower yield trials were calculated by using data from a safflower uniformity trial located at Farmington, Utah, in 1960. The area used was harvested as 1782 one-row by 5-foot basic plots, of which 1188 were used in this study. The reduced number was due to a high yield differential between 1/2 of the field and the other 1/2 caused by a supposedly uneven moisture retention of the soil.

Optimum plot size was calculated in two ways. Using comparable variances, plot size was estimated to be eight times the basic unit. Taking into account soil heterogeneity and relative costs, two basic units was estimated to be optimum.

Plot shape had little effect on variance; therefore, a width of two rows was indicated so that plots might be most efficiently handled.

All considerations evaluated, the optimum plot size and shape for safflower yield trials were considered to be 8 times the basic unit, or 3.67 feet wide by 20 feet long.

**LITERATURE CITED**

CONSERVATION IN MALAYSIA

(pg 49-53)

by

A.M. WIEDEMANN

CONSERVATION IN MALAYSIA

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A strict interpretation of the word "conservation" implies preservation or maintenance in an original condition. If this is expanded to "conservation of natural resources", further explanation is necessary because what comes to mind depends upon the individual's background: national parks, soil conservation, bird watchers, nature lovers, impractical ideas, and, perhaps too frequently, nothing at all. What then is meant by natural resources? And can these natural resources be maintained and preserved in an original condition?

Essentially everything that is a part of man's environmental life support system is a natural resource: the soil that is the basis for the provision of his food and fiber, the water he drinks, the air he breathes, the forests and mines that provide the raw materials for his necessities and luxuries and the amazing variety of flora and fauna, which, beyond their biological role in making the earth as an ecosystem "go", provide food, knowledge and beauty. In addition, one of the most important factors of man's environment is man himself, and in this sense he becomes a natural resource of great importance.

It is obvious that the idea of "preservation" cannot apply to all of these resources. The more general meaning has come to be one of "wise use" of resources: preventing the rapid depletion of those in limited supply (minerals), and the careful utilization of those which are renewable (forests, wildlife). Preservation becomes important only when certain components of the earth's biological spectrum are threatened with extinction due to the activities of man, when it becomes necessary to recognize that some resources are important even though they may have no apparent economic or survival value for man. It involves a certain willingness to be concerned with the problems of humanity beyond our own personalities and lifetimes.

Conservation can be considered at three inter-related levels, all of which have relevance for Malaysia. The first is that of conservation of the economically important natural resources by their utilization on a long-term, sustained yield basis. Mineral and forest resources can be exploited rapidly over a relatively short period of time, providing immediate economic benefits, but leaving nothing for the future. Lack of care for the soil and water resources can eventually create conditions unfavourable to agriculture. Such economic aspects of conservation can be quantified and programmed in definite terms.

At another level is the conservation of nature, a slightly nebulous concept involving economic values which may be negligible or even negative. Here is considered the preservation of flora and fauna in various kinds of parks and game reserves because of their scientific and aesthetic value. Sensible utilization is often a part of such preservation, especially with regard to larger game animals, but where species or types of ecosystems (the rhinoceros, lowland rain forest) are threatened with extinction, protection must become absolute if there is to be survival for the interest and study of future generations.

At the third level, the conservation of man, it becomes even more difficult to define objectives and assign values. The problems involve man's relationship with himself and with other human beings, as well as his understanding and appreciation of the environment in which he lives and functions. One reason for creating parks is to allow increasingly urbanized man to "get back to nature" — to get away from
crowds of people and to satisfy his desire for knowledge and appreciation of his surroundings. Even more important is the increasing pollution of air and water, a direct result of man’s economic activities which makes these resources unfit for use, creates hazards to health and well-being and results in the degradation of the environment to the point of unpleasantness. Still largely unknown is the eventual effect on man of the ever-increasing size and density of the world’s large cities. More and more of the world's geometrically increasing population is being concentrated in an urban environment. At what point does space become a natural resource in urgent need of conservation?

One of the most important aspects of resource conservation in Malaysia is that of climate. It is well-known theory that the deserts of North Africa were once covered by forest and had a much more equable climate which changed considerably with the wholesale destruction of the vegetation by man. While the general climates of North Africa and Malaysia are very different, how much is really known about the effect of great masses of vegetation on the climatic regime of an area? Could water ever become a limiting factor in this country? It has been shown that in a year's time, potential evaporation of water and precipitation are closely balanced. With no vegetation a much higher proportion of the intense solar radiation could strike the ground, causing a possibly marked change in the moisture balance of the climate.

A lack of vegetation could also have drastic effects on the soil resource. While soil erosion may not yet be a serious problem in Malaysia, it is occurring, and severely enough to silt up rivers which then flood during heavy rains. Is the flooding becoming more frequent? To see how fast erosion can occur, one has only to look at unprotected bare hillsides: the amount of soil washing down in even a moderate rainfall reaches staggering proportions.

The vegetation itself is a resource. Moist tropical climates are capable of growing enormous, but not inexhaustible, amounts of timber. If timber lands are to be continually productive they must be managed in terms of ecologically sound and locally oriented silvicultural and harvesting practices. In Malaysia, the federal government owns no timber lands and the Federal Forest Department serves mainly in an advisory capacity to the various state forest departments. The extent and overall quality of forest conservation varies greatly from state to state. Furthermore, although each state has created forest reserves (for the management of timber on a sustained yield basis) and jungle reserves (for the preservation of original habitat types), the boundaries of these reserves are not permanent. Economic pressure based on immediate needs can and does result in the loss or gradual attrition of these reserves by action at the state level. It would be very desirable, for the long-term benefit of the country, to expand existing forest reserves and to put their overall management into the hands of a single, well-trained forest department.

While forests must be managed, and thus altered, for optimum production, there is also a need for preserving in unchanged form various examples of natural vegetation types and their associated animals. There is much yet to be learned about our natural world — its evolution, its composition and its functioning. Once destroyed beyond reproduction, wild animals, plants and ecosystems become mysteries of the past. It is also essential that future generations of people in Malaysia have some way of knowing what the original landscape of the country was like.

Some of this need is met in the existing national parks of the country: Taman Negara, Templer Park, Bako National Park and Kinabalu National Park. Only the first is under direct control of the federal government; the others are actually state parks. A current study by the Federal Game Department is defining various areas of the country which should be given national park status. Criteria of selection include: unique habitat or vegetation type; educational and scientific interest; and potential value for recreation. A further objective of the study is the formulation of a unified national parks law putting all national parks under direct federal control thus insuring the integrity of the parks as well as maintaining a high standard of management.

The potential national parks defined thus far include:
1. Tasek Bera National Park, 46,000 acres in central Pahang, southeast of Temerloh, a large inland "black water" swamp with many restricted species of plants and animals.

2. Mersing National Park, 4,000 acres on the southeast coast in Johore, an area of beach and freshwater swamp, scientifically important because of the presence of plant species characteristic of Borneo.

3. Sigari National Park, 3,800 acres in Perak on the west coast north of Pangkor, an area of beach forest and important nesting site for green turtles.

4. Limestone Hills National Park, 3,400 acres in Perak, about 15 miles south of Ipoh, an extensive area of limestone outcrops with characteristic vegetation and abundant wildlife.

5. Batu Caves National Monument, 640 acres, a massive limestone outcrop six miles north of Kuala Lumpur containing an extensive series of caves with a unique cave fauna.

There are also game reserves in the various states established to preserve the habitats and ranges of special types of animals,12 but the same situation exists here as with the forest reserves and national parks. These game reserves are under state control and under economic pressure many of these areas are slowly diminishing in size. The establishment of a Federal Game Law which would provide jurisdiction over all wildlife conservation efforts in the country is currently under consideration.

To be really effective, any such legislation requires both public understanding of, and basic research into, the habits and habitats of the animals involved. Elephants, though decreasing in number, are coming into increasing contact with man, resulting in demands for their destruction. The Sumatran rhinoceros is on the verge of extinction, not only because of their relentless slaughter, but also because of the gradual restriction of their habitats. An encouraging sign is the money and effort being spent on green and leathery turtle conservation in this country.9 But even this has been prompted not so much by the desire to save a unique form of life for posterity as much as by the possible economic loss should the species die out and provide no more eggs for collection.

It is this economic factor which governs every aspect of conservation thinking. Each particular society reacts to its natural environment in a way which is governed to a large extent by its level of economic existence and degree of social stability. The development of a society to an optimum level of existence is more and more becoming a function of conserving the human resource — of creating conditions of human life conducive to action and thought beyond the scope of immediate need.

Western nations are finding that problems of water and air pollution are not only increasing rapidly, but that they are very difficult to control or eliminate. Developing countries see vast amounts of human resource expended in the struggle to support burgeoning populations. Although neither of these problems has yet developed to any serious extent in this country, the potential is there. For example, the indiscriminate and wide-spread use of pesticides in plantation management has received scant attention.1 Yet evidence exists that their use can cause far more problems than they solve, including the contamination of the human environment.

Optimum, long-term development of a society should be accompanied by the wise use of the resources which are contributing to its growth: climate, water, soil, forests, the landscape, its people. To what extent will these various aspects and needs of resource conservation find response in this country? This will depend, in the end, on the building of an effective conservation attitude among those most concerned with the problem: the leaders and educators of the country, and through them, the people.

It is possible to trace out three more or less distinct lines of thought with regard to conservation and nature, based on the developmental patterns of human societies. In the largely industrialized countries conservation has become very important. Having created an "artificial ecology" through science and technology, the people of these
lands have begun to realize that however advanced man may become technologically, he is still basically tied to his natural environment. This is reflected in concern over air and water pollution, in the over-crowding of cities, in the need for man to 'get back to nature'.

Many developing countries are largely devoid of natural resources because of continued exploitation by man back into pre-historic times. In the countries of North Africa and the middle-east, the original forest vegetation is just tradition in ancient folk-lore. With the forests went much of the soil and control of the water supply. In these areas, emphasis is on development through afforestation, soil erosion control and water catchment: attempts to replenish the needed natural resources.

In developing countries with ample natural resources, such as South America and many countries of south-east Asia, the emphasis is on the use of these resources for rapid economic and technological growth. In these areas, concepts of sustained yield forests, preservation of wildlife and vegetation and the provision of areas for outdoor recreation are difficult to grasp by the majority of the people. Economic advance is the important thing, and while this cannot be argued against, what will be the end result of unrestrained resource exploitation? What is needed is a "conservation attitude" that strives for the greatest good for the most people over the longest possible period of time.

How can this be accomplished? Basically by education, which will have to begin in the universities where the future leaders and teachers of the country are being trained. There needs to be developed a desire to provide for the wise and orderly use of all resources in the development of the country. There needs to be recognition of the difficulties encountered in so much of the world because of lack of regard for resource conservation, and a willingness to try to avoid these same problems in this country.

Finally, there is needed the development of a public consciousness about conservation that will not make it seem illogical to want to protect the seladang or the rhinoceros or a stand of dipterocarps simply because they have a right to exist, and there is aesthetic value in their mere presence apart from all other considerations of scientific or economic usefulness. How long it will take for such a conservation attitude to develop will depend entirely on the extent to which institutions of higher learning provide leadership in environmental education, and on the enthusiasm and effectiveness of individuals and organizations which are deeply interested and involved in the conservation of the country's natural resources.

REFERENCES

ACKNOWLEDGEMENT

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9. J.A. Bullock, School of Biological Sciences, University of Malaya.
10. Lord Medway, School of Biological Sciences, University of Malaya.
11. Mok Sian Tuan, Deputy Conservator of Forests, Forest Research Institute, Kepong.
12. W.E. Stevens, Federal Game Department, Seremban.
13. B.C. Stone, School of Biological Sciences, University of Malaya.
A quadrat in the Ulu Gombak Jungle Reserve

ALFRED M. WIEDEMANN

The Forest Reserves of Malaysia are managed by silvicultural methods that attempt to create a continuously yielding natural resource. However, these methods drastically alter the natural (original) floristic composition of the forests, and can result not only in the upset of ecological balance, but also in the disappearance of individual species or characteristic groupings of species or plant communities (Wyatt-Smith, 1958). The situation is even more serious in the total exploitation of non-reserved forest lands, including the alienation of forests for land development schemes.

To prevent the total extinction of particular types of natural vegetation and rare species of plants, the Forest Department, West Malaysia, has provided for the establishment of Jungle Reserves. Aside from their value in conservation, these Reserves are also useful for biological studies and serve as controls for the managed forests. They are formed either within existing Forest Reserves or created from other lands under the Land Code. It is required that they be above a certain minimum size in area and that the forests be generally undisturbed (no timber extraction). Full details of the objectives and criteria for selection of Jungle Reserves can be found in Malayan Forest Records 23, 1963.

The Ulu Gombak Jungle Reserve is one of a number of such reserves in the state of Selangor (Figure 1). It comprises 1183 acres and was formed from Compartment 22 (1108 acres) and part of Compartment 23 (75 acres) of the Ulu Gombak Forest Reserve in 1959. It is located on the north side of the Kuala Lumpur—Bentong road at Mile 22. The road forms one boundary of the reserve, the Selangor-Pahang state line another, and Compartment 21 of the Ulu Gombak Forest Reserve the third. The headwaters of the Sungei Gombak lie within the reserve, which varies in elevation from 1500 to 3750 feet a.s.l. The topography is rough, mostly steep hillsides and narrow valley bottoms. The vegetation in the main is a good example of primary hill dipterocarp forest, replaced at higher elevations by upper dipterocarp forest (See Symington, 1943, for definition of forest types). Disturbance has been minimal. In Compartment 22 there is no history of timber felling, and only a slight amount of pole (small tree) extraction took place in 1947–49; in Compartment 23 there was selective felling of timber in 1944–49, and pole extraction in 1948–49. However, the portion of Compartment 23 in the Jungle Reserve shows little evidence of disturbance.

1 CSIRO, Division of Land Research, Canberra, Australia. Formerly Fulbright Professor, School of Biological Sciences, University of Malaya, Kuala Lumpur.
Figure 1. Map of the Ulu Gombak Jungle Reserve showing location of the forest quadrat. (Based on a map of the Selangor Forest Department, Kuala Lumpur.)

In an attempt to initiate detailed, long-term ecological study of this forest, located only seven miles from the University of Malaya’s Ulu Gombak Field Studies Centre, a permanent forest quadrat was established in 1967–68. The quadrat is located in the area where Dr Elliott McClure and Lord Medway have made regular phenological observations since 1961 (McClure, 1966). Dr M.E.D. Poore also worked in this area in 1964, identifying and marking about 80 trees, which were subsequently identified by K.M. Kochummen of the Forest Research Institute, Kepong. This previous activity made it a logical place to try to organise a long-term study.

The quadrat measures three chains on each side (198 ft) and is subdivided into nine one-chain square subplots (0.1 acre each) for a total of 0.9 acre. The corners of the quadrat and subplots are marked by numbered stakes. It is located on a steep, north-facing hillside, and is accessible by a path from the lay-by at the 22nd mile of the Bentong road. Within each
### Table 1
Size class distribution of trees on the Ulu Gombak Jungle Reserve forest quadrat.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Number of Individuals</th>
<th>Per Cent. of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 to 2 ft (3.5 to 6.9 in.)</td>
<td>86</td>
<td>51.2</td>
</tr>
<tr>
<td>2 to 3 ft (7.0 to 10.4 in.)</td>
<td>39</td>
<td>23.2</td>
</tr>
<tr>
<td>3 to 4 ft (10.5 to 13.9 in.)</td>
<td>17</td>
<td>10.1</td>
</tr>
<tr>
<td>4 to 6 ft (14.0 to 20.9 in.)</td>
<td>13</td>
<td>7.7</td>
</tr>
<tr>
<td>6 to 10 ft (21.0 to 34.9 in.)</td>
<td>8</td>
<td>4.8</td>
</tr>
<tr>
<td>10 to 20 ft (35.0 to 69.9 in.)</td>
<td>4</td>
<td>2.4</td>
</tr>
<tr>
<td>Over 20 ft (Over 70.0 in.)</td>
<td>1</td>
<td>0.6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>168</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Although only a small proportion of the 168 trees recorded have been identified so far, some interesting information can be derived from available data. The size class distribution of the trees is given in Table 1. Over half the individuals have a girth of less than 2 ft, and almost half the remainder are less than 3 ft in girth, with an average for the entire quadrat of 2 ft 10 in. (10 in. in diameter). Only five trees are over 10 ft in girth (about 3 ft diameter): 11 ft 9 in., 14 ft, 12 ft 2 in., 18 ft 4 in., and 23 ft 3 in. A size class distribution of this type is considered characteristic of the tropical rain forest elsewhere in Malaysia (Richards, 1964: p. 3). Similar results were obtained by Wyatt-Smith (1949) in a study of lowland tropical rainforest in Malaysia. In one of his plots (adjusting his figures to the 0.9 acre quadrat size) he listed a total of 163 trees with the following size class distribution: 4 to 8 in. diameter, 100 trees; 8 to 16 in. diameter, 49; over 16 in. diameter, 14.

### Table 2
Comparison of the nine 0.1 acre subplots of the Ulu Gombak Jungle Reserve forest quadrat with respect to total number of trees, their average girth and basal area.

<table>
<thead>
<tr>
<th>Subplot</th>
<th>No. of Trees</th>
<th>Average Girth</th>
<th>Total Basal Area (Sq. ft.)</th>
<th>Basal Area Less Trees 10ft Girth</th>
<th>Largest Tree Girth</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>32</td>
<td>2 ft 5 in.</td>
<td>17.7</td>
<td>17.7</td>
<td>7 ft 5 in.</td>
</tr>
<tr>
<td>B</td>
<td>23</td>
<td>2 ft 9 in.</td>
<td>25.0</td>
<td>10.6</td>
<td>14 ft 0 in.</td>
</tr>
<tr>
<td>C</td>
<td>21</td>
<td>3 ft 6 in.</td>
<td>37.0</td>
<td>10.2</td>
<td>15 ft 2 in.</td>
</tr>
<tr>
<td>D</td>
<td>20</td>
<td>2 ft 6 in.</td>
<td>14.6</td>
<td>14.6</td>
<td>6 ft 10 in.</td>
</tr>
<tr>
<td>E</td>
<td>18</td>
<td>2 ft 4 in.</td>
<td>10.8</td>
<td>10.8</td>
<td>7 ft 3 in.</td>
</tr>
<tr>
<td>F</td>
<td>15</td>
<td>4 ft 1 in.</td>
<td>50.1</td>
<td>10.6</td>
<td>23 ft 3 in.</td>
</tr>
<tr>
<td>G</td>
<td>16</td>
<td>2 ft 8 in.</td>
<td>13.1</td>
<td>13.1</td>
<td>8 ft 8 in.</td>
</tr>
<tr>
<td>H</td>
<td>17</td>
<td>3 ft 1 in.</td>
<td>31.8</td>
<td>7.2</td>
<td>18 ft 4 in.</td>
</tr>
<tr>
<td>J</td>
<td>6</td>
<td>2 ft 4 in.</td>
<td>2.6</td>
<td>2.6</td>
<td>3 ft 10 in.</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>168</td>
<td>2 ft 10 in.</td>
<td>202.7</td>
<td>97.4</td>
<td></td>
</tr>
</tbody>
</table>

13.
The number of trees per 0.1 acre subplot at Ulu Gombak ranges from 6 to 32, averaging 18 (Table 2). Only two subplots, A and J (Figure 1) vary greatly from the mean values. There is evidence in subplot J of an extremely large tree having fallen comparatively recently. The area is covered with a dense growth of vegetation, which may be tree seedlings which have been stimulated by the sudden opening of the canopy or seedlings of shrubs or invading weeds as the plot is near the road, or a combination of these. If the seedlings are those of primary rain forest trees, active forest regeneration could be taking place. Subplot A has the greatest number of trees, but it does not have the largest total basal area. The data shows that over half the trees have a girth of less than 2 ft, there is only one tree

<table>
<thead>
<tr>
<th>TAG NO.</th>
<th>SUBLOT</th>
<th>TREE NAME</th>
</tr>
</thead>
<tbody>
<tr>
<td>11</td>
<td>A</td>
<td>Pentace strychnoides</td>
</tr>
<tr>
<td>12</td>
<td>A</td>
<td>Shorea platyclados*</td>
</tr>
<tr>
<td>14</td>
<td>A</td>
<td>Shorea laevis</td>
</tr>
<tr>
<td>15</td>
<td>A</td>
<td>Shorea leprosula</td>
</tr>
<tr>
<td>16</td>
<td>A</td>
<td>Shorea platyclados</td>
</tr>
<tr>
<td>19</td>
<td>A</td>
<td>Xanthophyllum sp</td>
</tr>
<tr>
<td>20</td>
<td>A</td>
<td>Xanthophyllum sp</td>
</tr>
<tr>
<td>21</td>
<td>A</td>
<td>Garcia sp</td>
</tr>
<tr>
<td>23</td>
<td>A</td>
<td>Shorea curtisii**</td>
</tr>
<tr>
<td>26</td>
<td>A</td>
<td>Oncospermum horridum</td>
</tr>
<tr>
<td>27</td>
<td>A</td>
<td>Gymnaeanthra eugeniifolia</td>
</tr>
<tr>
<td>29</td>
<td>A</td>
<td>Artocarpus sp</td>
</tr>
<tr>
<td>30</td>
<td>A</td>
<td>Melanochyla angustifolia</td>
</tr>
<tr>
<td>32</td>
<td>H</td>
<td>Shorea resina-nigra***</td>
</tr>
<tr>
<td>53</td>
<td>B</td>
<td>Shorea curtisii***</td>
</tr>
<tr>
<td>61</td>
<td>G</td>
<td>Artocarpus sp</td>
</tr>
<tr>
<td>62</td>
<td>G</td>
<td>Eugenia sp</td>
</tr>
<tr>
<td>66</td>
<td>G</td>
<td>Prunus polystachium</td>
</tr>
<tr>
<td>69</td>
<td>G</td>
<td>Diopyros H</td>
</tr>
<tr>
<td>70</td>
<td>G</td>
<td>Dialium patens**</td>
</tr>
<tr>
<td>71</td>
<td>G</td>
<td>Diospyros densifolia</td>
</tr>
<tr>
<td>73</td>
<td>G</td>
<td>Vitex sp</td>
</tr>
<tr>
<td>91</td>
<td>F</td>
<td>Hydnocarpus woodii</td>
</tr>
<tr>
<td>92</td>
<td>F</td>
<td>Garcinia rostrata</td>
</tr>
<tr>
<td>93</td>
<td>F</td>
<td>Xanthophyllum sp</td>
</tr>
<tr>
<td>94</td>
<td>F</td>
<td>Macaranga lowei</td>
</tr>
<tr>
<td>95</td>
<td>F</td>
<td>Santiria rubiginosa*</td>
</tr>
<tr>
<td>96</td>
<td>F</td>
<td>Parkia speciosa**</td>
</tr>
<tr>
<td>97</td>
<td>F</td>
<td>Melanophyla angustifolia*</td>
</tr>
<tr>
<td>99</td>
<td>F</td>
<td>Hydnocarpus woodii</td>
</tr>
<tr>
<td>102</td>
<td>F</td>
<td>Hopea ferrugineae</td>
</tr>
<tr>
<td>103</td>
<td>F</td>
<td>Xanthophyllum sp</td>
</tr>
<tr>
<td>105</td>
<td>F</td>
<td>Anisoptera laevis**</td>
</tr>
<tr>
<td>106</td>
<td>F</td>
<td>Eugenia sp</td>
</tr>
<tr>
<td>116</td>
<td>C</td>
<td>Melanorrhoea inappendiculata***</td>
</tr>
<tr>
<td>118</td>
<td>C</td>
<td>Shorea faguetiana***</td>
</tr>
<tr>
<td>121</td>
<td>E</td>
<td>Artocarpus lanceifolius*</td>
</tr>
<tr>
<td>176</td>
<td>D</td>
<td>Angelesia splendens**</td>
</tr>
</tbody>
</table>

* — 4 to 6 ft girth  
** — 6 to 10 ft girth  
*** — over 10 ft girth

Table 3. List of identified trees, Ulu Gombak Jungle Reserve forest quadrat.
with a girth over 6 ft, and none over 10 ft. There is, then, a high density of relatively small trees, indicating that perhaps here, too, forest regeneration is taking place, but at a more advanced stage than may be occurring in subplot J.

The greatest total basal area is found in those subplots containing trees of over 10 ft girth (B, C, F, H). If the large trees are excluded from the computation, basal area drops to lower values than those subplots without large trees. This may indicate something of the intensive competition occurring in a forest of this type. Of the total quadrat basal area of 202.7 sq. ft, 52 per cent. is contributed by the five trees of over 10 ft girth.

While there are what appear to be interesting relationships between tree number, tree size and subplot basal area, it is not possible to draw firm conclusions from the present scope of the study. Identification of tree species, the collection of data on heigh and maturity and increasing the number of subplots would all be possible because of the relatively permanent nature of the Jungle Reserve.

REFERENCES


VEGETATION STUDIES IN THE SIMPSON DESERT, N.T.

By A. M. Wiedemann*

[Manuscript received July 14, 1970]

Abstract
A transect of contiguous quadrats was used to study the sand dune vegetation of a small area of the Simpson Desert. The study was carried out shortly after a period of abundant precipitation which resulted in optimum winter growth conditions for both ephemeral and perennial species. The frequency data of 54 species were analysed by computer programmes that grouped the 729 quadrats according to similarity of species composition. Seven habitat types could be distinguished: swale hard clayey sand, lower slope clayey sand, mid-slope clayey sand, mid-slope Triodia mound, upper slope loose sand, steep slope loose sand, and crest mobile sand. Rather than sharply defined plant communities corresponding to these habitat types, the species groupings tended to form a continuum from swale to crest. Additional description of the vegetation is provided by studies of two permanent plots and of the size class distributions of eight shrub and tree species. An appendix listing all species collected during the study period is included.

I. Introduction
The Simpson Desert of central Australia is a vast expanse of predominantly red sand dunes oriented in a generally north-south direction and spaced with remarkable uniformity for almost 200 miles in an east-west direction. The active sand ridges extend continuously for as much as 200 miles with little or no lateral movement of sand onto the stabilized dune slopes.

The desert is part of a larger area of sandy and rocky country once known as the Arunta Desert lying west of a line running 700 miles from Tennant Creek in the north to Birdsville in the south (Fletcher 1965). It was recognized and described as a distinct physiographic unit by Madigan (1930, 1936) who gave the area its name in 1929 in honour of A. A. Simpson, then president of the Royal Geographic Society of Australasia.

It is located between latitudes 23 and 27° S. and longitudes 135 and 139° E. The total area of c. 56,000 sq miles lies mainly in the south-eastern part of the Northern Territory with small extensions into Queensland and South Australia (Fig. 1).

The general boundaries of the Simpson Desert have been described by Madigan (1939, 1945). The area of sand ridges begins in the west at the Finke and Macumba Rivers and extends in the south to Lake Eyre. The Mulligan River, Eyre Creek, and Warburton River define the desert margin in the east and south-east, but sand ridges,

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mostly large isolated dunes, can be found in an area extending over 100 miles further to the east, and south to Lake Frome. The Adams Ranges, Marshall River, and MacDonnell Ranges form the northern boundary of the desert, but the sand ridges themselves gradually fade out into the flat sand plains stretching hundreds of miles to the north.

The elevation of the desert drops from 1100 ft in the north-west to 130 ft on the Mulligan River in the south-east and to sea-level at Lake Eyre in the south. Drainage is to the south-east. The major rivers flowing into the desert—the Finke, Todd, Hale, and Hay—along with smaller streams drain an estimated 500,000 sq miles. Of these rivers, only the Finke has been known to empty its waters into Lake Eyre (Madigan 1939).

According to Madigan (1946a) the sands that form the dunes of the Simpson Desert have accumulated in the Lake Eyre basin since the early Pleistocene, brought in by the rivers eroding and draining the mountain ranges to the east and north. Sand dune formation began as the climate increased in aridity toward the end of the Pleistocene. They take the form of very long continuous ridges with a mean trend of north 26° west. The ridges are very straight and evenly spaced (four to six to the
mile), particularly toward the centre of the desert. This pattern is frequently altered
by the junctions of dune ridges. The dunes vary in height from 30 to 100 ft, and are
asymmetrical in cross section, the western slope averaging 15° and the eastern 25°.
Except for the active dune crests, which are 50–100 ft wide, the dunes are vegetated
and considered stable. The entire dune area appears to be underlain by a fairly level
subaeolian surface. It is alluvial in character, consisting of rounded pebbles of
silcrete, quartz, and porcellanite in poorly graded sand. In places this surface is exposed
in the swales, but usually it is covered by a mantle of sand up to 4 ft deep (Mabbutt
and Sullivan 1968). The geology of the Simpson Desert has been thoroughly studied,
and numerous gravity and seismic surveys undertaken since 1960 (Sprigg 1963).

### Table 1

**CLIMATIC DATA FOR CHARLOTTE WATERS**

Source: “Climatic Averages, Australia” (Bur. Met., Melbourne, 1956)

<table>
<thead>
<tr>
<th></th>
<th>Average Temperatures (°F)</th>
<th>Average R.H. (%)</th>
<th>Average Precipitation (points)*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Max.</td>
<td>Min.</td>
<td>Mean</td>
</tr>
<tr>
<td>Years of record</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>98.7</td>
<td>72.1</td>
<td>85.4</td>
</tr>
<tr>
<td>February</td>
<td>98.1</td>
<td>71.8</td>
<td>85.0</td>
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<tr>
<td>March</td>
<td>92.2</td>
<td>66.2</td>
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<td>April</td>
<td>83.1</td>
<td>57.2</td>
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</tr>
<tr>
<td>May</td>
<td>74.0</td>
<td>48.2</td>
<td>61.1</td>
</tr>
<tr>
<td>June</td>
<td>67.6</td>
<td>43.0</td>
<td>55.3</td>
</tr>
<tr>
<td>July</td>
<td>67.0</td>
<td>40.9</td>
<td>53.9</td>
</tr>
<tr>
<td>August</td>
<td>72.3</td>
<td>44.4</td>
<td>58.4</td>
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<tr>
<td>September</td>
<td>80.0</td>
<td>50.8</td>
<td>65.4</td>
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<tr>
<td>October</td>
<td>88.0</td>
<td>58.6</td>
<td>73.3</td>
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<tr>
<td>November</td>
<td>93.3</td>
<td>65.1</td>
<td>79.2</td>
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<tr>
<td>December</td>
<td>97.5</td>
<td>70.3</td>
<td>83.8</td>
</tr>
<tr>
<td>Annual</td>
<td>84.3</td>
<td>57.4</td>
<td>70.9</td>
</tr>
</tbody>
</table>

* 100 points = 1 inch.

The climate of this part of Australia has been discussed by Slatyer (1962). Located
in one of the driest parts of the continent, the desert is practically enclosed
by the 5-in. isohyet. Although annual distribution of precipitation is fairly even
(with slightly more in summer than in winter) on a long-term average, actual pre-
cipitation is very erratic, both seasonally and annually. At Charlotte Waters, on the
south-western margin of the desert, average annual precipitation was 5·12 in. over
44 years, with monthly means ranging from 0·18 in. (September) to 0·75 in.
(January). Mean annual temperature for a 30 year period of record was 70·9°F,
with a mean maximum of 84·3° and mean minimum of 57·4°. Monthly mean
temperatures ranged from 72·1° (January) to 53·9° (July). The maximum recorded
temperature is 118·8° and the minimum 21·6°. The climatic data are summarized
in Table 1.
There are no permanent surface waters though rain water will stand in the interdune hollows and river flood-out areas for weeks or months. The Great Artesian Basin underlies the entire desert and although no bores have been sunk in the central 40,000 sq miles of the desert (Sprigg 1963), water is generally available around the margins at depths of 300–1000 ft.

Madigan (1930, 1939) reviewed early attempts at exploration of the desert. Sturt was the first to travel a short distance into the desert in 1845. Subsequent exploration was confined mainly to the border areas. Simpson’s announcement in 1928 that the Royal Geographic Society of Australasia would send an expedition to explore this “apparent desert” (Simpson 1928) was the first scientific interest shown in the area. This resulted, in August of 1929, in a 15-day aerial reconnaissance flight over the desert under the leadership of C. T. Madigan (Madigan 1930). In 1936, Colson, a cattleman from Aminga on the south-western margin of the desert, crossed the southern part of the desert approximately along the South Australian border (Colson 1940). Then, in the winter of 1939, a scientific expedition of nine men and 19 camels, financed by A. A. Simpson and led by C. T. Madigan, crossed the desert through the centre (Madigan 1946a). A popular account of the journey was later published (Madigan 1946b) and the scientific results published as a series of reports in the Transactions of the Royal Society of South Australia (Carroll 1944; Hickman 1944; Kinghorn 1945; Madigan 1945, 1946a; Musgrave 1945; Whitley 1945; Crocker 1946; Eardley 1946, 1948).

The Northern Territory part of the Simpson Desert was included in the CSIRO land survey of 1956–57, and was classified with the Simpson land system (Perry et al. 1962).

In its journey across the desert and around the south-eastern and southern margins, the Madigan expedition collected 350 species of plants from 50 families. Of these, 76 species were collected in the desert proper while the sand ridges were being traversed (Eardley 1946).

The vegetation of the Simpson Desert is classified into three edaphic complexes by Crocker (1946): (1) the Triodia basedowii–Zygochloa paradoxa complex (the sands of the crests, slopes, and inter-ridge corridors); (2) the Astrakia pectinata–Atriplex vesicarium–Bassia spp. complex (the brown soils associated with surface gibbers around the margins and on isolated mesas and buttes); (3) the Eucalyptus coolabah–Atriplex nummularium complex (the river floodplains).

Within the sandy soils complex he defines two associations. Zygochloa paradoxa, along with a few associated species, occupies the unstable dune crests. The slopes and hollows of the dunes are occupied by Triodia basedowii. Within the Triodia association he recognizes three vegetation zones (hollow, lower and middle slope, upper slope) on the basis of associated species, but feels they are rarely abundant enough to give a distinct community.

The Triodia inter-crest association gives way in the south near Lake Eyre to a Nitraria schoneri association. Zygochloa is less abundant in this region. These changes were attributed to the high salinity and pH of the soil. A fourth association, on the sand plains at the northern margin of the desert, is characterized by Triodia basedowii plus species of Eucalyptus and Grevillea.
A. octocarpum has environmental significance, these two groups of quadrats should be considered a single subgroup of group C, and will be considered so in this paper.

The situation is different, however, with regard to group C₂. The species predominant in group C₂A are those associated with the Triodia mounds: Calotis hispidula, Pitlotus polystachus, Senecio gregorii, Lepidium rotundum, Calandrinia polyandra, Bassia johnsonii, and the ubiquitous Calocephalus knappii. The other quadrats, group C₂B, are those of the harder clayey sands of the intermound areas. Anguillaria dioica and Haloragis gossei are particularly characteristic here. The grasses, Aristida browniana and Eragrostis spp., are rarely on Triodia mounds, but have greater density near the mounds so were more likely to be included in overlapping mound quadrats. There are abundant seedlings of C. knappii on the intermound areas, but their growth is poor. Only on the Triodia mounds and in the swale does the species develop substantial cover.

The general picture, then, provided by the similarity analysis technique shows two mid-slope groups: the Triodia mound and the intermound; and an upper slope group on sandier soils. Although not all of the original group C quadrats could be used, the results were clear and could be applied to the situation in the field.

Lying on the still sandier soils of the steep east slope and steepest part of the west slope, group D has many species in common with the upper slope group C₁ quadrats. However, it is characterized by a dense stand of Calandrinia polyandra and C. balonensis, both of which occur to a lesser extent in the Triodia mounds lower on the slopes. Mixed in with the Calandrinia is considerable Senecio gregorii and a lesser amount of Myriocephalus stuartii. During the peak flowering period these upper east slopes present a very colourful picture. From the data at hand it does not appear that there are major differences in the habitat distribution of the two Calandrinia species. Also characteristic of this group are Hibiscus krickauffianus, Dicrastylis costelloi, Eremophila willsii, and Sida cunninghamii. The sand, though very loose, is essentially stabilized in this area except for minor fluctuations in the active sand margin.

It is this active sand margin which, through its effect on the distribution of Calocephalus knappii, sharply defines group E. Certain species are wholly or mostly restricted to the active sand habitat: Zygochloa paradoxa, Pitlotus latifolius, Crotalaria cunninghamii, and Sida virgata. Zygochloa paradoxa is the characteristic species of this group. It grows in large tufts up to 6 ft in diameter and 6 ft high. These tussocks are located mainly along the edges of the dune crest, building mounds as blown sand accumulates in the tussock. Though the grass may influence morphological changes in the dune crest, it is doubtful if it has an important role in the stabilizing of the active ridges since its cover is not continuous. Also, the presence of many degenerating Zygochloa mounds caused by erosion of sand indicates both its ineffectiveness in preventing this erosion and its apparent requirement for sand deposition for optimum growth. In these respects it is similar to Ammophila arenaria (L.) Link of the coastal sand dunes of Europe and North America. Other species which occur here grow in the protection of the larger ammophilous species or in relatively still hollows.

When the quadrats were again positioned along the transect in January, it was found that most of the vegetative cover was due to standing dead material of the previous winter’s vegetation. Of the ephemeral species, only Calandrinia was still
study site received over twice as much precipitation (8·54 in.) as the stony plain site (4·09 in.). Finke, in comparison, received 11·2 in. in this period, probably owing to its higher elevation. Table 2b gives day by day data for the three stations for a wet period at the end of August 1968. It indicates that even on a daily basis, precipitation varies widely within a small distance. In the 3 months preceding the start of the main field work for this study (March 28 to July 4, 1968) 5·4 in. was recorded for the swale site.

**Table 2**

**SHORT-TERM PRECIPITATION DATA (IN.) FOR TWO SIMPSON DESERT SITES AND FINKE, N.T.**

*Sources.*—Dune swale and stony plain: Water Resources Branch, Northern Territory Administration, Alice Springs, N.T. Finke: Commonwealth Bureau of Meteorology, Melbourne, Vic.

(a) Periodic totals for the 13 months
12 September 1967 to 17 October 1968

<table>
<thead>
<tr>
<th></th>
<th>Dune Swale</th>
<th>Stony Plain</th>
<th>Finke</th>
</tr>
</thead>
<tbody>
<tr>
<td>12 Sept. 67–18 Nov. 67</td>
<td>—</td>
<td>—</td>
<td>0·01</td>
</tr>
<tr>
<td>19 Nov. 67–11 Feb. 68</td>
<td>0·45</td>
<td>0·96</td>
<td>2·69</td>
</tr>
<tr>
<td>12 Feb. 68–28 Mar. 68</td>
<td>0·50</td>
<td>1·47</td>
<td>0·14</td>
</tr>
<tr>
<td>29 Mar. 68–29 May 68</td>
<td>3·00</td>
<td>1·34</td>
<td>4·23</td>
</tr>
<tr>
<td>30 May 68–4 July 68</td>
<td>2·40</td>
<td>0·06</td>
<td>2·08</td>
</tr>
<tr>
<td>5 July 68–31 July 68</td>
<td>0·12</td>
<td>0·01</td>
<td>0·22</td>
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<tr>
<td>1 Aug. 68–31 Aug. 68</td>
<td>1·40</td>
<td>0·19</td>
<td>1·19</td>
</tr>
<tr>
<td>1 Sept. 68–30 Sept. 68</td>
<td>—</td>
<td>—</td>
<td>0·09</td>
</tr>
<tr>
<td>1 Oct. 68–17 Oct. 68</td>
<td>0·73</td>
<td>0·06</td>
<td>0·55</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>8·50</strong></td>
<td><strong>4·09</strong></td>
<td><strong>11·20</strong></td>
</tr>
</tbody>
</table>

(b) Daily totals for the period
23 to 29 August 1968

<table>
<thead>
<tr>
<th></th>
<th>Dune Swale</th>
<th>Stony Plain</th>
<th>Finke</th>
</tr>
</thead>
<tbody>
<tr>
<td>23 Aug.</td>
<td>0·06</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>24 Aug.</td>
<td>0·17</td>
<td>0·03</td>
<td>0·32</td>
</tr>
<tr>
<td>25 Aug.</td>
<td>0·10</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>26 Aug.</td>
<td>0·80</td>
<td>0·08</td>
<td>0·46</td>
</tr>
<tr>
<td>27 Aug.</td>
<td>0·01</td>
<td>0·03</td>
<td>0·19</td>
</tr>
<tr>
<td>28 Aug.</td>
<td>0·15</td>
<td>0·05</td>
<td>0·18</td>
</tr>
<tr>
<td>29 Aug.</td>
<td>0·03</td>
<td>—</td>
<td>0·03</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>1·32</strong></td>
<td><strong>0·19</strong></td>
<td><strong>1·18</strong></td>
</tr>
</tbody>
</table>

The vegetation of the site is Crocker’s (1946) *Triodia basedowii–Zygochloa paradoxa* sand complex, with the corresponding crest and slope associations readily apparent. The high late autumn and winter precipitation noted above, however, resulted in an unprecedented growth of vegetation and provided the opportunity for a detailed study of the distribution of plant species in this general habitat.

**III. METHODS**

The detailed study of species distribution on the sand dunes and swales of the study site, and the description of the vegetation was carried out in three ways: continuous transects across part of the area; mapping of the vegetation on permanent plots; and observations, collections, and measurements made over several visits to the site.

(a) *Transects*

A permanent transect was surveyed running from the crest of the sand ridge parallel to the western side of the site, across the swale to the crest of the middle sand ridge, a total distance of 728 m (2378 ft). A second transect, not surveyed and not marked, was run 30 m (98 ft) to the north of and parallel to the first. The transects thus include a short, steep eastern slope and a longer, more gentle, western slope.
Vegetation data were taken by positioning contiguous 1.0 by 0.5 m quadrats the length of both transects, the long side of the quadrat being parallel to the transect. Selection of the small quadrat size was based on general observations of the vegetation and the need to minimize the time involved in taking the data. A quadrat of this general size has been found sufficient for herbaceous dry land vegetation (Poulton and Tisdale 1961). For each quadrat a percentage cover value was estimated for each species present. Wire loops representing 1% and 5% of the quadrat area were used in making the estimates of cover. Data were taken on July 17–23, 1968. A total of 54 species of vascular plants was recorded along the two transects. Of these, 31 species had frequencies of less than 5% and only 11 had frequencies over 20%. In two cases, *Euphorbia* spp. and *Salsola* spp., the data involve two species which could not be differentiated at the time the work was carried out. Since in each case the two species have apparent distributional differences, the data were not used in the analysis. In a third case two species are included under *Eragrostis* spp., but as far as could be ascertained, there was no ecological separation of their distributions. The quadrats were again positioned, on the permanent transect only, on January 20–22, 1969, the same data being recorded.

A profile of the permanent transect was drawn from the survey data. To facilitate analysis and presentation of the data, the quadrats were combined by pairs, the cover values being averaged for each species over the two quadrats. This produced, in effect, a contiguous series of 2.0 by 0.5 m quadrats for each transect. To show the distribution of selected species along the transect area, two histograms, one for each transect, were plotted from the July cover values of each of the species. The histograms of each pair were then superimposed to form a single histogram for each species. This was done to give a clearer indication of the general distributional pattern of these species in this area.

To study the association of species along the transect, the 729 quadrats (with 54 recorded species) resulting from the combination of quadrats described above were analysed by the divisive information analysis* and similarity analysis techniques developed by Lance and Williams (1968) and Williams, Lambert, and Lance (1966) respectively. These techniques have been programmed for use with the Control Data 3600 computer of the CSIRO Division of Computing Research.

The main analysis was accomplished by using the DIVINF programme (Lance and Williams 1965) in which the initial quadrat group is subdivided into successively more homogeneous groupings of quadrats in a descending hierarchy. Subdivision in each case is based on the species that gives the greatest reduction in heterogeneity (i.e. change in information content) of the resulting two groups: one of quadrats containing the species; the other of quadrats in which the species is absent. This heterogeneity is indicated by the *information content*, a value giving a measure of the entropy of the quadrat group. It is derived from the information statistic which uses data only on the presence or absence of species in the quadrats (see Lance and Williams 1966, for a detailed explanation of the information statistic). DIVINF is the only Canberra taxonomic programme that can accept a problem of this size.

* Divisive information analysis is similar to the association analysis discussed by Williams and Lambert (1960).
Fig 2.—Profile of the permanent transect (Tran. 1) with approximate limits of the habitat types. Vertical scale 5 times the horizontal. Top.—Histograms of species distribution and cover. Data from both transects combined for each species histogram. Bottom.—Distribution within the five main quadrat groupings, by transect, of the 729 quadrats.
To further clarify the results of part of the preceding analysis, a group of 150 quadrats was analysed with the CENTCLAS programme (Lance and Williams 1966) in which individual quadrats, and subsequent groupings of quadrats, are combined according to their compositional similarity in an ascending hierarchy. The information statistic was used to measure heterogeneity, combining quadrats and groups of quadrats which resulted in the least increase in information content in the resultant groups. The same information statistic was used in both analyses for the purpose of comparison, but in CENTCLAS fusion is dependent on the overall qualitative composition of the quadrats.

Another programme, GROUPER (Lance, Milne, and Williams 1968), analyses groups of quadrats already defined by other programmes to determine the extent to which each species found in any pair of groups contributes to the difference between these two groups. For the groups defined by the CENTCLAS analysis the difference values were computed from the information statistic. Since DIVINF subdivides the quadrats on the species contributing most to the difference between the groups (either present in all quadrats or absent in all) these groups were not analysed by GROUPER.

(b) Permanent Plots

Two permanent plots were established on the study site. They are located near the permanent transect on the gentle western slope. One plot, located near the margin of the active sand, was placed to include a large mound which had been formed by the growth and degeneration of a Triodia basedowii tussock. The other plot, located further down the slope, was placed to represent the vegetation of the mid-slope inter-mound areas and has dimensions of 6·0 by 4·0 m (19·7 by 13·1 ft). To map the vegetation, 1·0 by 0·5 m contiguous quadrats were laid down in a series of transects across the plots, the area of each species being plotted on gridded data sheets. Total area of each species in each plot was computed from these data sheets. The mapping was carried out on July 19, 1968 and the plots revisited on January 20, 1969 to observe seasonal variations.

(c) Other Data

The research site was visited by the author on three separate occasions: March 26–28, 1968; July 8 to August 16, 1968; January 10–23, 1969. During these periods general observations were made on the character of the vegetation and collections made of plant species found in the research area. In addition, collections were made at the same and other times by the staff of the herbarium of the Arid Zone Research Institute, Alice Springs, who were also responsible for most of the identifications. The results of these collections are incorporated into a general species list for the research site.

A series of height measurements was made of eight of the most important tree and shrub species at the site: Acacia aneura, A. kempeana, A. murrayana, Cassia nemophila, Eucalyptus terminalis, Grevillea stenobotrya, Hakea divaricata, and Thryptomene maisonneuvii. The individuals were measured with an 18-ft surveyor's staff as they were encountered in walking a transect across the research site. Transects were walked until 50 individuals of each species had been measured, except A. kempeana,
for which 60 were measured, and *A. aneur*us, for which only 29 were measured. In the case of *A. kempeana*, a large spreading shrub, crown diameter and the diameter of an associated non-vegetated area were also measured. The mean heights were computed for each species and the size class distribution plotted in graphical form.

IV. RESULTS AND DISCUSSION

(a) Transects

A profile of the permanent transect is shown in Figure 2. The hard red clayey sands are found in the swale and extend up the slopes, gradually grading into the red sands of the upper slope and crest. Patches of the subsurface alluvial soil are exposed in the lowest part of the swale. The *Triodia* mounds, rising as much as 2 ft above the surrounding surface, are distributed mostly along the eastern and western lower and middle slopes. The active sand margins shown are the lower limits of the loose sand of the crest and are essentially the upper limits of stable vegetation. These margins will vary slightly depending upon the effect of the seasonal winds on the mobile sand of the crest, but overall, seem to remain fairly constant in both time and space. The transects at both ends stop at the active sand margin on the opposite sides of the respective crests. The higher margin at the east end of the transect is due to the convergence of the middle and east dunes.

The histograms arranged above the profile in Figure 2 show the general floristic pattern that follows good winter rains. *Calocephalus knappii* is found continuously along the transect between the limits of active sand with the highest cover values in the swale and on the *Triodia* mounds. *Aristida contorta* is largely confined to the swale, but on the lower slope its distribution overlaps that of *A. browniana* which in turn is best developed on the middle slopes. Also characteristic of the middle slopes is *Triodia basedowii* with scattered occurrences of very high cover; and *Abutilon octocarpum*, which tends to be patchy in distribution and can be found as scattered individuals even in the swale. Three of the species are commonly found on the *Triodia* mounds (but not restricted to this habitat): *Pilolus polystachyus* is found on the lower slopes and in the swale; *Trachymene glaucifolia* is absent from the swale, but continuous over the slopes and is found on the mobile sand of the crests; and *Calandrinia polyandra* is characteristic mainly of the upper dune slopes. *Crotalaria dissitiflora* is mainly an upper slope and crest species; and *Pilolus latifolius* is restricted in its distribution to the active sand ridges. It is apparent from these distribution patterns that there is a definite, though gradual change in ecological factors affecting the growth of species in the swale and up the dune slopes. At the active sand margin there is an abrupt change. There is also variation due to the presence of the *Triodia* mounds. These conditions are reflected in the quadrat groupings defined by the various analyses.

(b) Quadrat Groups

The hierarchical subdivision of the 729 quadrats by the *DIVIN*F programme down to the information content level of 800 is shown in Figure 3. At this level five groups, roughly corresponding to those recognized by Crocker (1946), can be distinguished. The distribution of the quadrats of each group along each transect is arranged under the transect profile in Figure 2.
The first subdivision was based on the restricted swale and lower slope distribution of *Aristida contorta*. The group with *A. contorta* was in turn subdivided on the basis of *Trachymene glaucifolia* which is absent from the swale. Further subdivision of these two groups, A and B, resulted in a very scattered distribution of individual quadrats. The quadrat group without *A. contorta* was subdivided on *Calocephalus knappii*, which does not grow on active sand. Group E does not have this species, while the group containing *C. knappii* was further subdivided on *Calandrinia polyandra*, a species of loose, but not active, sand, into groups C and D. Further subdivision of group C on *Ptilotus polystachyus* (indicated by dashed lines in Fig. 3) resulted in a scattered distribution of quadrats that suggested further definable groups. A portion of these group C quadrats was analysed by CENTCLAS as discussed below.

![Diagram](image)

Fig. 3.—The hierarchical subdivision of the 729 transect quadrats by the DIVINF programme down to the five group level. Numbers indicate number of quadrats in each group. Division in each case is on the species indicated into a group without (-) and a group with (+) the species. The dashed lines indicate a further subdivision of group C that was not used.

Although the majority of the quadrats of each of the groups has a fairly continuous distribution along the transects, there is enough scattering of individuals or overlapping of groups to make the placing of boundaries between the groups difficult. The distributions of the species among the groups, shown in Table 3, also makes characterization difficult since very few of the species of major importance (in terms of frequency) are restricted to one or the other of the groups. Rather than distinct units of vegetation, there appears to be a continuum, and the result of the DIVINF analysis was to classify the quadrats of the transects into relatively homogeneous segments.


<table>
<thead>
<tr>
<th>Plant Species</th>
<th>E (Mobile sand)</th>
<th>D (Loose sand)</th>
<th>C (Clayey sand)</th>
<th>B (Hard sand)</th>
<th>A (Total)</th>
</tr>
</thead>
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<td>11.0</td>
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<td>0.2</td>
<td>3.2</td>
<td>7.4</td>
</tr>
<tr>
<td>Zygochloa paradoxa</td>
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<td>0.5</td>
<td>10.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Pilostus latifolius</td>
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<td>0.2</td>
<td>3.2</td>
<td>7.4</td>
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<td>4.1</td>
<td>0.7</td>
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<td>Eremophila willsii</td>
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Table 3 (Continued)
Species which could not be placed into sequence

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<th>C</th>
<th>B</th>
<th>A</th>
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<td>Mid slope</td>
<td>Lower slope</td>
<td>Swale</td>
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<td>Clayey sand</td>
<td>Hard soil</td>
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<th>A</th>
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<td>36-4</td>
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<td>13-1</td>
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Although the climatic factors of precipitation, temperature, and exposure to wind and solar radiation could vary enough along the transect to affect the distribution of species, the determination of the extent of their influence would require considerable effort. The only environmental factor of apparent importance with regard to variation in species distribution along the transect would be the soil: nutrients, salts, pH, texture, structure, and availability of moisture. No measurements of soil properties were taken, but data cited earlier from Crocker (1946) indicate that the first two are extremely low and the pH shows no extreme variation. Observations indicate, however, that the quadrat groups are related to soil texture and the factors of hardness and sand mobility.

Groups A and B have most species in common, though in varying amounts as measured by their frequencies (Table 3). The characteristic species of both groups is Aristida contorta. Group A is distinguished by the complete absence of Trachymene glaucifolia and by greater amounts of some of the species common to the two groups: Haloragis gossei, Isotropis wheeleri, Bassia convexula, Erodium cynorum, and Enneapogon polyphyllus. Species that could be considered characteristic of group B are Zygophyllum ammophilum, Triraphis mollis, Convolulus erubescens, and to a lesser extent, Blemmodia canescens and Ptilotus polystachyus. Because of their high frequency in other groups of the transect, the presence of such species as Calocepalus
knappii, Trachymene glaucifolia, Calotis hispidula, and Senecio gregorii are not useful in characterizing either of these two groups.

Group A is found in the lowest part of the swale where the soil, consisting of both red clayey sand and exposed subsurface alluvium, is extremely hard when dry. The eastern quadrats of the group are on higher ground, but this is also hard red clayey sand and the vegetation remains essentially the same. The quadrats of group B are on only slightly higher ground, but the soil is sandier and less compact and this is reflected in the change of species frequency values. The quadrats are less continuous in distribution because of mixing with quadrats from group C.

The further subdivision of the apparently heterogeneous group C of quadrats on Ptilotus polystachyus gave a slight indication of upper (non-P. polystachyus) and lower slope groupings for the west slope quadrats. Most of the east slope quadrats of group C were in the upper slope subgroup. On the slopes P. polystachyus grows mainly on the Triodia mounds. If quadrats are grouped into a "mound group" their distribution along the transect would be scattered because of the mosaic pattern of mounds on the slopes.

Fig. 4.—Distribution along both transects of the 150 mid-slope group C quadrats in the four groups defined by the similarity analysis (CENTCLAS). T1, transect 1; T2, transect 2.

A more detailed study of the situation was afforded by using the analytic programme that grouped quadrats on the basis of their similarity. Because of limitations in the size of problem that this programme could accept, only 150 quadrats from the main part (west slope) of group C were used. From this analysis the difference between the two main subgroups, upper slope (group C1) and lower slope (group C2), was much more apparent (Fig. 4) as were the species relationships (Table 4).

The species of relatively high frequency in group C1 are those commonly associated with the looser sand of the steep dune slopes (group D), although many are common to both subgroups: Abutilon octocarpum, Trachymene glaucifolia, Calandrinia balonensis, Tephrosia remotiflora, Sida cunninghamii, Cassia nemophila, Thryoptome maiussoni, and Triodia basedowii. The subdivision of group C1 into two groups, one with a high occurrence of Triodia basedowii (group C1A) and the other with Abutilon octocarpum (group C1B) reflects the passage of transect 1 through an almost pure stand of A. octocarpum. The contributions of other species to the differences between these two subgroups are minor. Unless the patchy growth of
### Table 4

**Species composition and percentage frequency in the quadrat groups defined by the similarity analysis (CENCLASS) of the 150 mid-slope group C quadrats.**

Species are arranged in order of their importance in contributing to the difference between group C1 and group C2 (GROUPER).

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<th>$C_1$</th>
<th>$C_{1B}$</th>
<th>$C_{1A}$</th>
<th>$C_2$</th>
<th>$C_{2B}$</th>
<th>$C_{2A}$</th>
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<td>Difference Value</td>
<td>Mid slope</td>
<td>Clayey sand</td>
<td>Triodia mound</td>
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<tr>
<td>Soil: Loose sand</td>
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<tr>
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<td></td>
<td>70 (38) (32)</td>
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<th>$C_{1A}$</th>
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<th>$C_{2B}$</th>
<th>$C_{2A}$</th>
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<td>Newcastelia spodtrotica</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0-766</td>
<td>1</td>
<td>—</td>
<td>3</td>
</tr>
<tr>
<td>Stenopetalum lineare</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0-766</td>
<td>1</td>
<td>—</td>
<td>3</td>
</tr>
<tr>
<td>Solanum ellipticum</td>
<td>1</td>
<td>2</td>
<td>—</td>
<td>0-632</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Eremophila macdonnellii</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>0-409</td>
<td>1</td>
<td>—</td>
<td>3</td>
</tr>
<tr>
<td>Blemodia canescens</td>
<td>1</td>
<td>2</td>
<td>—</td>
<td>0-248</td>
<td>3</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td>Acacia dictyophleba</td>
<td>4</td>
<td>6</td>
<td>—</td>
<td>0-162</td>
<td>6</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Creptaria dissitiflora</td>
<td>8</td>
<td>11</td>
<td>3</td>
<td>0-029</td>
<td>9</td>
<td>13</td>
<td>3</td>
</tr>
<tr>
<td>Myriocephalus stuartii</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>0-009</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Dicrasytis costelloi</td>
<td>1</td>
<td>2</td>
<td>—</td>
<td>0-005</td>
<td>1</td>
<td>3</td>
<td>—</td>
</tr>
<tr>
<td>Sida corrugata</td>
<td>1</td>
<td>2</td>
<td>—</td>
<td>0-005</td>
<td>1</td>
<td>3</td>
<td>—</td>
</tr>
</tbody>
</table>
A. octocarpum has environmental significance, these two groups of quadrats should be considered a single subgroup of group C, and will be considered so in this paper.

The situation is different, however, with regard to group C2. The species predominant in group C2A are those associated with the Triodia mounds: Calotis hispidula, Ptilotus polystachus, Senecio gregorii, Lepidium rotundum, Calandrinia polyandra, Bassia johnsonii, and the ubiquitous Calocephalus knappii. The other quadrats, group C2B, are those of the harder clayey sands of the intermound areas. Anguillaria dioica and Haloragis gossei are particularly characteristic here. The grasses, Aristida browniana and Eragrostis spp., are rarely on Triodia mounds, but have greater density near the mounds so were more likely to be included in overlapping mound quadrats. There are abundant seedlings of C. knappii on the intermound areas, but their growth is poor. Only on the Triodia mounds and in the swale does the species develop substantial cover.

The general picture, then, provided by the similarity analysis technique shows two mid-slope groups: the Triodia mound and the intermound; and an upper slope group on sandier soils. Although not all of the original group C quadrats could be used, the results were clear and could be applied to the situation in the field.

Lying on the still sandier soils of the steep east slope and steepest part of the west slope, group D has many species in common with the upper slope group C1 quadrats. However, it is characterized by a dense stand of Calandrinia polyandra and C. balonensis, both of which occur to a lesser extent in the Triodia mounds lower on the slopes. Mixed in with the Calandrinia is considerable Senecio gregorii and a lesser amount of Myriocephalus staurtii. During the peak flowering period these upper east slopes present a very colourful picture. From the data at hand it does not appear that there are major differences in the habitat distribution of the two Calandrinia species. Also characteristic of this group are Hibiscus kriechiauffianus, Dicrasytis costelloi, Eremophila willsii, and Sida cunninghamii. The sand, though very loose, is essentially stabilized in this area except for minor fluctuations in the active sand margin.

It is this active sand margin which, through its effect on the distribution of Calocephalus knappii, sharply defines group E. Certain species are wholly or mostly restricted to the active sand habitat: Zygochloa paradoxa, Ptilotus latifolius, Crotalaria cunninghamii, and Sida virgata. Zygochloa paradoxa is the characteristic species of this group. It grows in large tussocks up to 6 ft in diameter and 6 ft high. These tussocks are located mainly along the edges of the dune crest, building mounds as blown sand accumulates in the tussock. Though the grass may influence morphological changes in the dune crest, it is doubtful if it has an important role in the stabilizing of the active ridges since its cover is not continuous. Also, the presence of many degenerating Zygochloa mounds caused by erosion of sand indicates both its ineffectiveness in preventing this erosion and its apparent requirement for sand deposition for optimum growth. In these respects it is similar to Ammophila arenaria (L.) Link of the coastal sand dunes of Europe and North America. Other species which occur here grow in the protection of the larger ammophilous species or in relatively still hollows.

When the quadrats were again positioned along the transect in January, it was found that most of the vegetative cover was due to standing dead material of the previous winter's vegetation. Of the ephemeral species, only Calandrinia was still
alive and flowering, but the appearance of the plants was markedly changed. Though flowering profusely, the flowers were only a fraction of their winter size on very long upright stems. The leaves were also upright instead of on the ground, and had taken on a yellow-green appearance in contrast to the deep rich green colour of winter. Some plants were a reddish colour with limp leaves from which no water could be squeezed. The brightest aspect was provided by large green plants of Salsola kali growing right at the active sand margin, although this species (or its variety) was completely dried up on the lower slopes. No new species had appeared or additional cover developed in the intervening period during which only a few hundredths of an inch of rain had fallen.

(c) Permanent Plots

The Triodia mound permanent plot afforded a more detailed look at the vegetation of this habitat. These mounds form as tussocks of Triodia basedowii increase in diameter and the centres die out, thus creating the annular or ring tussock form. This phenomenon has been observed and described in detail by Burbidge (1945), but little appears to be known of the time period involved. As the open centre increases in size, it fills with sand blown off the dune crests. Eventually the tussock ring begins to die off, leaving only patches of grass around the end of the mound. The mound of the permanent plot is 20 in. high on the down slope side and joins the slope on the upper side. More rectangular than round in shape, its dimensions are c. 13 ft by 18 ft. It is fairly typical of the large, well-defined mounds in the area with only a fringe of marginal Triodia and supporting heavy growths of ephemeral species in favourable growing seasons (Fig. 5A).

Total vegetative cover for the 16 species recorded from the mound plot was 43.8%. Three species, fairly uniformly distributed throughout the plot, contributed most of the cover: Calocephalus knappii, 13.1%; Trachymene glaucifolia, 10.1%; and Calandrinia balonensis, 8.8%. Triodia basedowii, in seven isolated clumps along the margin, had a cover of 2.9%. While these species and the others listed in Table 5 are not restricted to the mounds, they flourish on these sites and the middle and upper slopes of the dunes present a mosaic of these mound communities. Some of the species, notably C. balonensis, Myriocephalus stuartii, Senecio gregorii, and Trachymene glaucifolia will grow together in very dense stands on the loose sand of the upper slopes. Others, C. knappii, Blennodia canescens, and Ptilotus polystachyus, for example, flourish in the stable, firmer clayey sands of the lower slopes and swale.

However, the apparently extremely favourable growing environment of the Triodia mounds favours the establishment of all these species, the floristic composition of any particular mound probably varying with seed supply. Reasons for the productivity of these mounds might be found in the relatively loose sand (good seed bed), the decaying roots of the Triodia plants (nutrients), and the ring of grass with a somewhat depressed centre (seed accumulation); and there is some evidence that the sand under the mounds is much more compact than under the bare areas surrounding the mound (retention of moisture in the accumulated sand of the mound).*

* An excavation made across one large mound showed a core of a very hard, dry sandy soil beginning at the old sand surface (8 in. below the mound surface) and extending down below the level of excavation (5 ft). The limits of this core corresponded with the edges of the mound. The transition to loose, moist sand was very sharp.
Fig. 5.—A. The *Triodia* mound permanent plot, viewed from the north-west. 
B. The inter-mound permanent plot, viewed from the north.
At the time the data were taken, August 1968, almost all the species were mature and flowering. Only *Salsola* and *Euphorbia* were in the seedling stage. The site was visited again in January 1969. Almost all the plants were still in position, but most species had shed seed and dried up. The *Salsola* seedlings had increased in size (the only change in cover from the August date) and were also drying up.

**Table 5**

PERCENTAGE COVER VALUES FOR THE SPECIES OF THE *TRIODIA* MOUND AND INTER-MOUND PERMANENT QUADRATS

<table>
<thead>
<tr>
<th>Species</th>
<th>Cover (%)</th>
<th>Triodia mound</th>
<th>Lower slope</th>
<th>Species</th>
<th>Cover (%)</th>
<th>Triodia mound</th>
<th>Lower slope</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Calandrinia balonensis</em></td>
<td>8·8</td>
<td>0·2</td>
<td></td>
<td><em>Pilulotus polysmashys</em></td>
<td>0·1</td>
<td>1·1</td>
<td></td>
</tr>
<tr>
<td><em>Calandrinia polyandra</em></td>
<td>1·4</td>
<td>—</td>
<td></td>
<td><em>Eragrostis spp.</em></td>
<td>—</td>
<td>4·2</td>
<td></td>
</tr>
<tr>
<td><em>Trachymene glaucifoila</em></td>
<td>10·1</td>
<td>0·6</td>
<td></td>
<td><em>Goodenia unilocula</em></td>
<td>—</td>
<td>1·4</td>
<td></td>
</tr>
<tr>
<td><em>Calostis hispida</em></td>
<td>4·0</td>
<td>0·5</td>
<td></td>
<td><em>Cassia pleurocarpa</em></td>
<td>—</td>
<td>3·0</td>
<td></td>
</tr>
<tr>
<td><em>Senecio gregorii</em></td>
<td>0·3</td>
<td>—</td>
<td></td>
<td><em>Halarogos gossel</em></td>
<td>—</td>
<td>0·5</td>
<td></td>
</tr>
<tr>
<td><em>Binnadia canescens</em></td>
<td>1·0</td>
<td>—</td>
<td></td>
<td><em>Anguillaria dioica</em></td>
<td>—</td>
<td>0·3</td>
<td></td>
</tr>
<tr>
<td><em>Triodia basedowii</em></td>
<td>2·9</td>
<td>1·7</td>
<td></td>
<td><em>Aristida contorta</em></td>
<td>—</td>
<td>0·4</td>
<td></td>
</tr>
<tr>
<td><em>Salsola kali</em></td>
<td>1·0</td>
<td>0·1</td>
<td></td>
<td><em>Crotalaria dissitiflora</em></td>
<td>—</td>
<td>0·8</td>
<td></td>
</tr>
<tr>
<td><em>Euphorbia spp.</em></td>
<td>0·1</td>
<td>0·8</td>
<td></td>
<td><em>Myriophyllum stuartii</em></td>
<td>—</td>
<td>0·1</td>
<td></td>
</tr>
<tr>
<td><em>Pilulotus latifolius</em></td>
<td>0·1</td>
<td>—</td>
<td></td>
<td><em>Isotropis wheeleri</em></td>
<td>—</td>
<td>0·2</td>
<td></td>
</tr>
<tr>
<td><em>Calopephalus knappii</em></td>
<td>13·1</td>
<td>3·1</td>
<td></td>
<td><em>Lepidium rotundum</em></td>
<td>—</td>
<td>0·4</td>
<td></td>
</tr>
<tr>
<td><em>Aristida browniana</em></td>
<td>0·5</td>
<td>3·5</td>
<td></td>
<td><em>Euphorbia eremophila</em></td>
<td>—</td>
<td>0·1</td>
<td></td>
</tr>
<tr>
<td><em>Abutilon ocotapum</em></td>
<td>0·2</td>
<td>1·3</td>
<td></td>
<td><em>Sida cunninghamii</em></td>
<td>—</td>
<td>0·1</td>
<td></td>
</tr>
<tr>
<td><em>Stenopetalum lineare</em></td>
<td>0·1</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eriachne aristidea</em></td>
<td>0·1</td>
<td>—</td>
<td></td>
<td>Total cover</td>
<td>43·8%</td>
<td>24·4%</td>
<td></td>
</tr>
</tbody>
</table>

The other plot is located lower down the slope in an area typical of the "between mound" habitat. The soil is a red clayey sand, very firm, frequently hard enough to make digging difficult (Fig. 5B). A total of 22 species were recorded with a total cover of 24·4% (Table 5). The bulk of the cover is provided by the grasses characteristic of this habitat: *Eragrostis spp.*, 4·2%, and *Aristida browniana*, 3·5%. *Calopephalus* (3·1%) is widespread in its distribution in the quadrat, but it occurs mostly as scattered seedlings on areas where a bit of loose sand has accumulated, apparently as a result of water movement or wind deposition. The density of scattered seedlings is a good indication of the depth or amount of sand accumulated. Two old *Triodia basedowii* mounds are included on the south end of the plot, and in the centre is a young *Triodia* plant, apparently in no way connected with the two mounds. Total *Triodia* cover is 1·7%. The large *Cassia pleurocarpa* recorded was about 3 ft tall.

At the January visit most plants had dried up. *Cassia*, *Crotalaria*, *Abutilon*, and *Sida*, all perennials, still had leaves. *Aristida* and *Eragrostis* had shed seed and were dry. The *Calopephalus* seedlings appeared to have matured as very small plants.

**(d) Tree Measurements**

The tree and shrub species are a distinctive feature of the research site vegetation yet they were poorly represented in the quadrat data. In Figure 6 are shown the
size class distributions of eight tree and shrub species of the area. Several of these, *Thryptomene maisonneuvi*, *Cassia nemophila*, *Hakea divaricata*, and *Acacia aneura*, show what could be called “normal” distribution curves. Because nothing is known of the growth rate of these species it is difficult to say whether this distribution is due to differences in environmental conditions affecting seedling establishment and/or seed production over time; or if the curves reflect growth variations within a single population established in a specific period of favourable environmental conditions.

![Graphs of size class distributions for eight shrub and tree species on the Simpson Desert research site.](image)

**Fig. 6.—** Size class distributions for eight shrub and tree species on the Simpson Desert research site. Numbers in parentheses after species names are mean heights in feet. Based on 50 measured individuals of each species, except *A. aneura* with 29 individuals.

Three of the species show two peaks in their size class curves: *Grevillea stenobotrya*, *Eucalyptus terminalis*, and *Acacia kempeana*. In these cases the explanation could include the presence of two populations, presumably established during different time periods. Differences in site conditions could cause the variation about the curve peaks, but because the individuals of each species grow within fairly restricted habitats this would not be likely to cause the double peaks. Other explanations are possible, but only long-term detailed studies would make possible the elucidation of the basic relationships.

The curve of one species, *Acacia murrayana*, could indicate a young, recently established population. This species is usually found in dense patches of a few larger trees and many smaller ones. During the course of field work in the area, the only seedlings observed of the measured species were those of *Thryptomene*. There were great numbers of these in the vicinity of the larger plants, all less than a foot high, many only an inch or two high.
At the very least these data indicate that the establishment and regeneration of the shrub and tree vegetation is not a continuous process. Successional relationships among the species are doubtful since none are found growing together (in the research area) and there is little in the curves to indicate expanding or degenerating populations. Such data could be a useful biological indicator of past microclimatic conditions if it were possible to correlate size with age.

Each of these tree and shrub species has a fairly definite distribution. *A. aneura* and *A. kempeana* are both in the swales, in separate patches, but usually with slight intermixing of individuals. *Eucalyptus terminalis* is distributed as widely spaced individuals or occasionally as closely spaced small groups on the lower slope, usually where it levels into the swale. *Hakea divaricata* is a lower and middle slope species, while *Cassia nemophila* is found on the middle and upper slopes. *T. maisonneuvi* seems restricted to the upper slopes right near the active sand margin, while both *Grevillea stenobotrya* and *A. murrayana* are found only on the active sand crests. Because of the method used in collecting the tree height data, it was not possible to make a direct correlation between tree distribution and the floristic quadrat groupings.

An interesting feature of *A. kempeana* is the area devoid of vegetation around 41 of the 50 individuals measured. To investigate further, crown diameter and the area of the non-vegetated ground was measured. The non-vegetated area extends out beyond the crown from 1 to 19 ft along the radius with an average of 8 ft. No causal factors for this suppression of ground vegetation could be found in the time available.

However, a similar effect was noted for various tree species of *Acacia*, *Eucalyptus*, and *Casuarina* in the Hunter Valley of New South Wales by Story (1967). After considerable field study, he concluded that the relatively bare circles around the trees were in some way related to the influence of the tree roots upon the grasses, but that no evidence of competition for soil water could be established.

In contrast to *A. kempeana*, an opposite effect was noted in the case of *Eucalyptus terminalis*. Each tree had a slight mound built up at its base extending roughly to the limits of the canopy. These mounds were covered with a thick growth of ephemerals very similar to the *Triodia* mounds. This same phenomenon was noted by Ebersohn and Lucas (1965) in south-western Queensland with quite a number of different tree species. Their investigations revealed that the increased vegetative growth was due to a higher phosphorus content in the soil under the trees. In the case of *Eucalyptus populnea*, for instance, there was 400 p.p.m. P₂O₅ directly under the canopy while 40 ft out there was only 26 p.p.m. P₂O₅.

With the other large tree species of the research site, *Acacia aneura*, no effect on the ground vegetation could be noted. Though it could be assumed that soil moisture and soil nutrient conditions might cause the effects noted with *A. kempeana* and *E. terminalis*, only detailed studies could decide this with any degree of certainty.

V. Conclusions

This study provides a detailed description of the vegetation of the Simpson Desert research site during a period of favourable growing conditions: relatively cool winter temperatures and high rainfall. At first appearance, the swale and lower slope shrub and tree species seem dense enough to have some influence on the vegetation
of these areas, but in reality they have very little general effect other than that already noted because of their wide spacing. During this season it is the ephemeral species that set the character of the vegetation. Zones of vegetation are obvious to the observer: the swale and lower slope outlined by the distinctive growth form and colour of *A. contorta*; the middle slopes by the dull green of *A. browniana*, *Eragrostis*, and *Triodia*, grading into the lighter and brighter colours of the upper slopes: *Abutilon*, *Hibiscus*, *Dierastylis*, *Newcastlia*, *Sida* spp., and *Calandrinia* spp.; and the crest zone.

The literature is replete with ideas and techniques for investigating the character of vegetation in terms of community structure. The use of hierarchical methods as developed and programmed by Williams and his colleagues is based on their ready availability and on personal interest. As far as is known, these programmes have not previously been used with desert vegetation of this type. It is felt that these computer analyses have provided useful information on the plant-environment relationships of the area through the definition of meaningful quadrat groupings. These groupings could be considered "plant communities" only in a general sense as is obvious from the species composition of the various groups. A better term might be "habitat types". The scattered distribution of the quadrats of some groups is due both to the transitional nature of the vegetation and to the fact that quadrat selection, in DIVINE, is based on the presence or absence of a single species. This, in turn, is affected both by the mechanics of the programme — which species is selected — and by the sampling method — size and number of quadrats. These topics are discussed in detail in the papers dealing with these techniques. However, it is felt that the number and size of quadrats was suited to the objectives of this study.

As a result of these analyses, seven quadrat groups or habitat types are recognized: swale hard clayey sand, lower slope clayey sand, mid-slope clayey sand, mid-slope *Triodia* mound, upper slope loose sand, steep slope loose sand, and crest mobile sand.

It appears that the present vegetation of the dunes is stable. The cycle is one of relatively short wet periods dominated by the ephemeral species alternating with long dry periods in which *Triodia* and *Zygochloa* become the main components of the vegetation. There is little to suggest that the vegetation is important in maintaining the stability of these sand dunes. During the driest periods of greatest potential sand mobility, plant cover is lowest. The present form of the dunes is a result of the dynamic interaction of the factors of wind, relief, and sand source and supply (Mabbutt 1968). Furthermore, there may be structural properties of the dunes themselves that would preserve their present form (J. A. Mabbutt, unpublished data) regardless of the degree of vegetative cover.

These unique natural characteristics plus the fact that most of the Simpson Desert has been essentially undisturbed by man make it a research area of great interest. This study is only a beginning effort and raises many questions of a fundamental nature with regard to desert plants and their environmental relationships.

**VI. ACKNOWLEDGMENTS**

This study was carried out while the author was a National Science Foundation Research Fellow with the CSIRO Rangelands Research Unit. Appreciation is expressed to Mr. R. A. Perry, Leader of the Unit, for providing the necessary facilities, equipment and computer time.
Special thanks are due to Mr. R. W. Millington for his help in organizing the field work, to Mr. J. R. Maconochie for his help in compiling the species list, and to Mr. R. Hodder for his willing help with the camp and field work.

Thanks are also given to Mr. and Mrs. Clark of Andado homestead whose assistance and hospitality were of great value in carrying out the work at the research site.

VII. References


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LIST OF PLANTS COLLECTED AT THE SIMPSON DESERT RESEARCH SITE, MARCH TO NOVEMBER 1968

Aizoaceae

Triandema pilosa F. Muell.

Amaranthaceae

Amaranthus grandiflorus (J. M. Black)
J. M. Black
Ptilotus latifolius R. Br.
Ptilotus obovatus (Gaudich) F. Muell.
Ptilotus polystachyus (Gaudich) F. Muell.

Boraginaceae

Heliotropium pleiopetalum F. Muell.
Omphalolappula concava (F. Muell.) Brand (1931)
Trichodesma zeylanicum (Burm. f.) R. Br.

Brunoniaceae

Brunonia australis Sm.

Caesalpiniaeeae

Cassia nemophila var. nemophila A. Cunn. ex Vogel
Cassia nemophila var. zygophylla (Benth.) Benth.
Cassia pleurocarpa F. Muell.

Chenopodiaceae

Bassia convexula R. H. Johnson
Bassia cornishiana F. Muell.
Bassia johnsonii E. Ising
Encyclaena tomenosa R. Br.
Salsola kali L.
Salsola kali L. var. strobilifera Benth.

Chloanthaceae

Dierastylis costellata Bailey
Newcastlia spodiotricha F. Muell.

Compositae

Anchusa pusillus Benth.
Brachycome ciliaris (Labill.) Less.
var. lanuginosa (Steetz) Benth.
Calceolaria knappii (F. Muell.) Ewart et White
Calotis erinacea Steetz
Calotis hispida F. Muell.
Calotis multicaulis (Turcz.) Druce (1917)
Helichrysum ambiguum Jurez.
Helichrysum cassianum Gaudich
Helichrysum davenportii F. Muell.
Helipterum chersleyae F. Muell.
Helipterum floribundum DC.
Helipterum moschatum (A. Cunn.) Benth.
Helipterum pterochaetum (F. Muell.) Benth.
Helipterum stipitatum F. Muell.
Helipterum tietkensii F. Muell.
Minuria leptophylla DC.
Myriocephalus stuartii (F. Muell. et Sond.) Benth.
Podolepis canescens A. Cunn. ex DC.
Rutidosis helichrysoides DC.
Senecio gregorii F. Muell.
Waitzia citrina (Benth.) Steetz

Convolvulaceae

Convolvulus erubescens Sims

Cruciferae

Blenndia canescens R. Br.
Blenndia pterosperma (Black) Black
Lepidium rotundum (Desv.) DC.
Stenopetalum lineare R. Br. ex DC.

Cucurbitaceae

Melothria maderaspata (L.) Cogn.

Euphorbiaceae

Euphorbia drummondii Boiss.
Euphorbia eremophila A. Cunn. ex Hook.
Euphorbia wheeleri Baill.

Geraniaceae

Erodium cygnorum Nees subsp. glandulosum Carolin

Goodeniaceae

Calagynne berardiana (Gaudich) F. Muell.
Goodenia cycloptera R. Br.
Goodenia unilobata J. M. Black
Leschenaultia divericata F. Muell.
Scaevola aemula R. Br.
Scaevola depauperata R. Br.
Scaevola parvifolia F. Muell. ex Benth.
Velleia glabrata Carolin

Gramineae

Aristida browniana Henr.
Aristida contorta F. Muell.
Danthonia bipartita F. Muell.
Digitaria brownii (R. et S.) Hughes
Enneapogon cylindricus N. T. Burbidge
Appendix I (Continued)

Enneapogon polyphyllus (Domin)
N. T. Burbidge
Eragrostis dielsii Pilger
Eragrostis eriopoda Benth.
Eragrostis laniflora Benth.
Eriachne aristidea F. Muell.
Neurachne muelleri Hack.
Plagiostemum refractum (F. Muell.) Benth.
Triodia basedowii Pritzel
Triraphis mollis R. Br.
Zygochloa paradoxa (R. Br.) S. T. Blake

Haloragaceae
Haloragis gossei F. Muell.

Lilaceae
Anguillaria dioica R. Br.
Corynotheca lateriflora (R. Br.) Benth.
Thysanotus R. Br.

Malvaceae
Amblyanth otocarpum F. Muell.
Hibiscus krichauflianus F. Muell.
Sida platycalyx F. Muell. ex Benth.
Sida corrigata Lindl. sens. lat.
Sida cunninghamii White
Sida macrophylla F. Muell. ex Benth.
Sida virgata Hook.

Mimosaceae
Acacia aneura F. Muell. ex Benth.
Acacia dictyophleba F. Muell.
Acacia kempeana F. Muell.
Acacia ligulata A. Cunn. ex Benth.
Acacia linophylla W. V. Fitzg.
Acacia murrayana F. Muell. ex Benth.
Acacia ramulosa W. V. Fitzg.
Acacia tetragonophylla F. Muell.

Myoporaceae
Eremophila latrobei F. Muell.
Eremophila longifolia (R. Br.) F. Muell.
Eremophila macdonnellii F. Muell.
Eremophila obovata L. S. Smith
Eremophila wilksii F. Muell.

Myrtaceae
Eucalyptus terminalis F. Muell.
Thryptomene maisonneuvii F. Muell.

Papilionaceae
Crotalaria cunninghamii R. Br.
Crotalaria dissitiflora Benth.
Isotropis wheeleri F. Muell.
Psoralea affin. eriantha Benth.
Pychosema trifoliolatum F. Muell.
Swainsona microphylla A. Gray
subsp. affinis A. Lee
Tephrosia remotiflora F. Muell. ex Benth.
Tephrosia affin. purpurea Pers.

Phytolaccaceae
Gyrostemon ramulosus Desf.

Portulaceae
Calandrinia balonensis Lindl.
Calandrinia disperma J. M. Black
Calandrinia polyandra Benth.
Portulaca intraterrana J. M. Black

Proteaceae
Grevillea stenobotrya F. Muell.
Hakea divaricata L. Johnson

Rubiaceae
Oldenlandia (Plum.) L.
Pomax umbellata (Sol. ex Gaertn.) Miq.

Sapindaceae
Dodonea attenuata A. Cunn.

Solanaceae
Nicotiana ingulba J. M. Black
Solanum ellipticum R. Br.
Solanum esuriae Lindl.

Umbelliferae
Trachymene glaucifolia (F. Muell.) Benth.

Zygophyllaceae
Tribulus macrocarpus F. Muell.
Zygophyllum annuophilum F. Muell.
THE ECOLOGY OF EUROPEAN BEACHGRASS
(AMMOPHILA ARENARIA (L.) LINK)

A REVIEW OF THE LITERATURE

Oregon Department of Fish and Wildlife
Nongame Wildlife Program
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Alfred M. Wiedemann, PhD
The Evergreen State College

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THE ECOLOGY OF EUROPEAN BEACHGRASS (AMMOPHILA ARENARIA (L.) LINK)   
A REVIEW OF THE LITERATURE   
Alfred M. Wiedemann, PhD

ABSTRACT

A review of the historical importance, taxonomy, and ecology of European beachgrass (Ammophila arenaria (L.) Link) is made including recent research in adaptive growth and physiology. Disease, predation, and tolerance of disturbance is noted. The threat of the species, as an introduced exotic, to native landscapes and organisms is discussed. Two programs of organized eradication efforts are reviewed. It is concluded that control or eradication of the species is difficult, and the most effective methods to date involve the use of chemical herbicides.

INTRODUCTION

European beachgrass (Ammophila arenaria (L.) Link) is native to Europe, ranging between Lat. 63°N and Lat. 30°N along the sandy coasts of the Atlantic Ocean, the North Sea, the Baltic, the Mediterranean, and the Black Sea. Highly adapted to the drifting sand conditions of coastal dunes, it has been valued for centuries as a dune stabilizer. As populations increased in Europe, land, including coastal dune areas, became more valuable. Moving sand dunes were not compatible with agricultural lands, roads, and towns.

The first recorded use of plants to stabilize sand dunes was in 1307 on 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 (Gerhardt 1900, Olsson-Seffer 1909). European beachgrass became so important to the protection of coastal areas that, in the time of William III (1689-1702), an act of Parliament was passed to preserve the grass along the Scottish coast. Penalties were provided for its destruction. The possession of stalks within 8 miles (13 km) of the coast was a penal offense! This was a drastic measure since the dune grasses were the basis of an extensive industry producing ropes, mats, roof thatch, and coarse paper from the roots, stems, and leaves, respectively (Lamson-Scribner 1894).
In their exploration, discovery, and settlement of lands in the "New World," Europeans carried this attitude with them. Coastal areas were attractive for settlement, and with settlement came problems of blowing sand and eroding beaches. On Cape Cod, Massachusetts, there was once a law requiring the townspeople to "turn-out" to plant beachgrass (Ammophila breviligulata, a closely related, native American species) in April. Penalties were provided for neglecting this duty. In Provincetown, a "beachgrass committee" was directed to plant the grass on private property showing bare sand (Lamson-Scribner 1894, Ross 1897). By 1869, blowing sand was a problem for rapidly growing San Francisco, and by 1898, a total of 200 ha had been planted to European beachgrass (Lamb 1898). Interestingly enough, the seeds for this planting were imported from Australia, where the species had been earlier introduced by the English colonists. It was also introduced to New Zealand and the Falkland Islands about the same time.

European beachgrass spread rapidly up and down the west coast of the United States. Much of this spread can be attributed to planting projects by various government agencies to protect waterways, roads and railroads, water supplies, forests, recreation areas, and private property. In 1935, about 1,214 ha near the Columbia River were planted to stabilizing grasses, mostly European beachgrass (Schwendiman 1977). Through the 1950's, extensive areas were planted in the Florence area (Green 1965). As a result of this activity, and the natural ability of the species to spread rapidly, Ammophila is today found along the entire coast of western North America, from the Queen Charlotte Islands to southern California (Brecken and Barbour 1974).

The result of the establishment and spread of this species has been a drastic alteration in the character of the dune systems along the coast. European beachgrass grows most vigorously where there is wind-blown sand, primarily the area just above the high tide line. Here it has produced a high, wide, continuous ridge of sand, the foredune. This change has been remarkable in the rate at which it occurred and in the visible results. Lamb (1898) reports that, at the end of the 19th century, there was no "littoral dune," just sand from the beach to the tree line. Cooper (1958) notes the lack of a prominent foredune prior to 1940. Wiedemann (1966, pp. 160, 163,
(179) provides striking photographic comparisons, showing the rapid establishment of European beachgrass.

While the value of the species in terms of the human economy can hardly be questioned, the cost in terms of the natural environment has been great. The present Ammophila-dominated foredune has replaced the original low, rounded, open mounds formed by the native "sand-loving" species (Wiedemann 1984, pp. 74-75). While these native species are not threatened with extinction, the beauty of form and color they gave to the dune landscape is no longer seen. Animals may be affected as well. Slobodchikoff and Doyen (1977), working on the coastal dunes of central California, report that European beachgrass reduced the number and diversity of sand-dwelling arthropods, mainly through alteration of the optimum habitat. Most recently, the Oregon Department of Fish and Wildlife has raised the possibility that Ammophila has altered the nesting habitat for the snowy plover (Charadrius alexandrinus), and is considering the control or eradication of European beachgrass at least over limited areas (personal communications, Charlie Bruce, Oregon Department of Fish and Wildlife, Corvallis, Oregon).

The notion of control or eradication of such a highly-esteemed species is a novel one, yet there is increasing concern about the effects of its introduction on native species and landscapes. Heyligers (1984) discusses this for southeastern Australia. Johnson (1982) notes that the New Zealand National Parks Act of 1980 specifies that introduced plant species, including Ammophila arenaria, be exterminated in the national parks. In California, The Nature Conservancy has decided to attempt eradication of Ammophila in the Lanphere-Christensen Dunes Preserve (personal communication, S. VanHook, Lanphere-Christensen Dunes Preserve, Arcata, California, 1983).

The purpose of this paper is to review the literature on European beachgrass with a view toward learning what might be done to aid in the control or eradication of the species in certain situations. To this end a literature search, using the BIOSIS Previews database (contains citations from Biological Abstracts, Biological Abstracts/RRM, and BioResearch Index) was conducted. The key words used were "Ammophila arenaria," "European beachgrass," and "marram grass." The search covered the period 1969 to 1985.
Of the many references produced, those dealing with the species in a
synecological context, those in which mention of the species was incidental to
the main work being reported, and those published in journals difficult to
obtain and/or read (chiefly Eastern European) are not considered in this
paper. A significant work is that of Huiskes (1979a) in which is summarized
(as part of the "Biological Flora of the British Isles" series) what is known
about the species as it occurs in Europe. The most recent literature in that
work is dated 1977. Description, taxonomy, and ecology as recorded in that
and other works prior to 1977 will be summarized or added to in this paper as
seems appropriate.

DESCRIPTION

Detailed descriptions of the species are found in Huiskes (1979a),
Hitchcock (1950), Hitchcock et al. (1969), and Munz and Keck (1959). It is an
erect perennial with flowering stems up to 1 m tall. The stems are tufted
from tough, scaly rhizomes that spread horizontally and vertically. The leaf
blades are tough, fibrous, and inrolled to a sharp point (except when just
emerging or under moist conditions). They are 2-4 mm wide when flattened,
without auricles, and 15-10 mm broad. The outer surface is smooth and
grayish-green without distinct ribs; the inner surface is whitish and closely
ribbed. The spikelets are 1-flowered, 10-15 mm long, the lemma of the single
flower 1-3 mm shorter. The species is distinguished from the very similar
American beachgrass (Ammophila breviligulata), introduced on west coast dunes,
by the thicker, shorter (1-3 mm) ligule of the latter; and from American
dunegrass (Elymus mollis), by the flat, wide, more bluish-green blades and
spike inflorescence (paired multiflowered spikelets) of the latter. The
plants are most robust and vigorous, with deepest color, in habitats where
annual sand burial, up to 1 m, occurs annually. In the absence of sand burial
the plants become less robust. Along the Oregon coast, new leaves appear at
the beginning of April and flowers appear toward the middle of May. Few
plants flower in the absence of sand burial.

TAXONOMY

The species has a complex name history (Hitchcock et al. 1969). Linnaeus
applied the name Arundo arenaria in 1753. In 1809, Host described the genus
Ammophila, but gave this plant the species name arundinacea. Finally, in 1827, Link described the species as Ammophila arenaria, retaining the Linnaean species name and assigning it to the genus of Host. Other names are found in the older literature: Calamagrostis arenaria Roth (1788), Psamma arenaria R. & S. (1817), Phalaris maritima Nutt. (1818), Phalaris ammophila Link (1821), and Arundo littoralis Beauv. ex Steud. (1840). Two varieties are recognized in Europe: var. genuina is found in northern and central Europe as far south as Portugal, and var. arundinacea is found from central Portugal southward. They are distinguished on the basis of rather small differences in leaf, panicle, and glume characteristics (Huiskes 1979a). The native American Ammophila breviligulata Fernald, found on the Atlantic Coast and the shores of the Great Lakes, is considered by Europeans to be a subspecies of Ammophila arenaria (Ammophila arenaria ssp. breviligulata (Fernald) Maire et Weiller).

The chromosome count is 2n=28. In Europe there is a hybrid, Ammophila arenaria x Calamagrostis epigejos (L.) Roth, the latter species found in damp woods on heavy soils (Rihan and Gray 1985). It has morphological and growth characteristics midway between the two species. It is a sterile hexaploid, 2n=42, with 28 chromosomes from Ammophila and 14 from Calamagrostis. It is known by several names: xAmmophila baltica (Flugge)Brand; xAmmocalamagrostis baltica (Schrad.)P. Fourn.; and Ammophila baltica (Flugge)Link. The hybrid seems useful in stabilization work because it provides faster total cover than Ammophila arenaria.

The vernacular, or common, name varies similarly. In North America it is called European beachgrass. In the United Kingdom, and most other places in the world where it has been introduced, it is called marram. Also spelled murrum and marrem, the word is thought to be derived from the Gaelic muram or the Danish marhalm, both meaning "sea straw" (Lamson-Scribner 1894). It has also been known as sea matweed and gourbet (Kellogg 1915), and psamma and sea sandreed (Hitchcock 1950).
ECOLOGY

Habitat

The optimal habitat for European beachgrass is open, well-drained, wind-blown sandy soils with adequate moisture, either as soil reserve or in the form of evenly distributed rainfall, lying between approximately 35° and 55° latitude in either hemisphere. Its absolute latitudinal limits are about 30° and 63°, but growth is poor at these extremes. It grows, but does not flower, in the Faroe Islands at 62°N (Huiskes 1979a). It occurs as far south as the Mediterranean coast of Egypt, 30°N (Ayyad 1973). It is absent from the southern California flora at 33°N (Barbour et al. 1976). It is introduced and established in New Zealand, and southeastern and southwestern Australia. I have seen it in the Perth region (32°S) but did not observe flowering. In one report from South Africa (Lubke 1983) it was not reported in a coastal vegetation survey near Port Alfred, eastern Cape (33°S). There are no reports from South America. The closely related American species, A. breviligulata, reaches its southern limit on the American east coast in North Carolina, 35°N, where it is considered short lived and susceptible to disease and insect predation (Woodhouse et al. 1977).

The species grows well on soils of wide-ranging chemical and nutrient status. Huiskes (1979a) reports soil pH ranging from 4.6 to 9.1. In New Zealand, soil pH ranges from 5.3 to 8.0 (Smith et al. 1985). It thrives on highly calcareous soils, with CaCO₃ ranging from 5% to 58% (Huiskes 1979a, Page et al. 1985). Nutrient status of soils where European beachgrass is the dominant species is invariably low, with total nitrogen typically less than 0.05% dry weight and organic matter 1% or less. On the Oregon coast, pH varies from 5.8 to 7.4 on the foredune with organic matter less than 0.5% (Wiedemann 1966). It is not salt tolerant; more than 1% salt in the soil can inhibit growth (Huiskes 1979).

On areas where sand accretion is consistently heavy (windward sides of foredunes and mounds) European beachgrass is the only species present providing total ground cover. On the lee sides of foredunes and mounds, the grass does not grow as vigorously and other species begin to enter the
community. In older, more stabilized areas, European beachgrass continues to diminish in importance as typical meadow species of the area form the ground cover (Wiedemann 1984).

**Growth**

The seeds of European beachgrass germinate readily, both in open places on the mobile sand of foredunes, and in the damp soils of deflation plains. Huiskes (1977) reports, however, that establishment rarely takes place from seed. On mobile sands, the seedlings die from either erosion or total burial, and on the wet areas, poor drainage makes survival difficult. On the Oregon coast, seedlings probably account for the great number of widely scattered hummocks found in the lower dune areas, which are damp in winter but dry out sufficiently in summer to permit sand to blow, or are adjacent to areas of open, blowing sand. Once sand accumulates around a well-established seedling, new roots are formed in the dry sand layer.

A certain amount of dispersal and establishment can also probably be accounted for by the spread of rhizome fragments. Each winter along the Northwest coast, storms generate large waves that erode the foredune and wash away masses of vegetation. It is not know, however, how long the rhizomes can withstand immersion in salt water and remain alive.

Once established, the plant develops a strong and vigorous rhizome system, both horizontal and vertical. Under conditions of intensive sand burial, the vertical system is most active. Many new shoots develop from the nodes of these rhizomes, creating the tufted growth form of the species. New shoots also originate from horizontal rhizomes, but not at great distances from the parent plant, perhaps 1.5 m at most. The growth pattern has been well-documented (Gemmell et al. 1953, Greig-Smith 1961, Greig-Smith et al. 1947).

In a study comparing the growth of European beachgrass with the native American dunegrass (*Elymus mollis*) Pavlik (1983c) found that the former allocates a greater proportion (83-90%) of its organic carbon production to above ground leaf tissue, while the latter allocates more (61-70%) to the
stability of enzymes which could be affected by rising leaf temperatures after stomatal closure. Moisture stress itself inhibits protein synthesis, but stabilizing enzymes could allow for a more rapid resumption of synthesis when full metabolic rates resume. This in turn would allow for a more rapid resumption of growth.

The accumulated evidence seems to indicate a species superbly adapted for the condition of this coast: strong onshore winds blowing through the entire year, moderate temperature regime, abundant rainfall, and an abundant sand supply. Unlike American dunegrass, however, European beachgrass is virtually an obligate psammophyte. When sand accretion around the plant decreases, vigor declines. With no accretion, which occurs on older dunes in advanced stages of stabilization, flowering and continued rhizome development cease, and the plant enters a period of maintenance growth, new leaves being produced only to replace leaves that have died.

This situation is referred to in the literature as "the Ammophila problem" and much study has been devoted to it. Marshall (1965) reviewed explanations for this phenomenon (increase in organic matter, lack of nutrients in the absence of blown sand, age effect, poor aeration of roots and rhizomes, secreted toxic substances, competition from other plants, increasing soil acidity), and then went on to develop his own explanation.

"Decline in vigor of Ammophila arenaria in the absence of sand accretion probably results from the lowered replacement of old roots by new adventitious roots due to competition, perhaps initially for water and consequently for nutrients, by the roots of other species in the surface and layers where the site of adventitious root production is located."

Huiskes opposes the notion that fresh root formation is inhibited, but in effect agrees that the decline in density of European beachgrass in stabilized dune areas is caused by the monopolization of nutrients by more shallowly rooted species (Huiskes 1980), and that the greater the number of associated species, the lower the carrying capacity for European beachgrass (Huiskes and Harper 1979).
Both Wallen (1980) and Gray (1985) discuss "aging" or "developmental maturity" as possible reasons for the decline of European beachgrass, the former noting that with time the plant redistributes assimilates, from building new material to maintaining a big biomass. Whether the aging is physiological or ecological is uncertain. Eldred and Maun (1982), working with American beachgrass (A. breviligulata) note the same decline in vigor as sand accretion slows and other species become established. They also note, however, that new sand deposition, or fertilization, can rejuvenate "old" plants (a phenomenon noted by Huiskes (1980) for A. arenaria as well).

I have noted this rejuvenation response along the Oregon coast. It is easily seen in areas where Ammophila was planted and left with no follow-up shrub and tree plantings. A foredune-like ridge develops on the windward sides of the plantings. Initial vigorous growth of the grass throughout the planting stops sand movement. The plants in from the edges of the planting soon lose vigor and cover decreases. With extreme loss of cover, or death, bare spaces are opened, allowing sand to drift against adjacent plants which resume vigorous growth. This results eventually in the development of many mounds or hummocks over the planted area, these mounds eventually reaching 3-4 m in height. An example of this can be found at the seaward edge of the plantings south of the Siuslaw River in Oregon.

The debate about the "Ammophila problem" continues. A question of equal interest concerns the ability of the species to produce enormous biomass on an apparently sterile substrate. Certainly the extensive root system plays a role in this. Main roots can often be traced (under conditions of mound erosion) for several meters from a large plant. Newly deposited sand is quickly exploited by new roots developing on vigorous rhizomes. Much of the nutrient cycling system of the dunes nearest the beach has been attributed to the sea (van der Valk 1974). Work by LeClerc and Robin (1983) suggests that Ammophila may have special adaptations for nitrate reduction and storage. Critical nitrates may also be supplied by non-symbiotic nitrogen-fixing bacteria (Ahmad and Neckelmann 1978). Abdel-Wahab (1975) and Abdel-Wahab and Wareing (1980) have collected bacilli from the root zone of Ammophila, and claim to have established the role of these bacilli in the nitrate economy of Ammophila. Vesicular-arbuscular mycorrhizas have been isolated from dunes in
Scotland (Nicolson and Johnston 1979) and Italy (Giovannetti and Nicolson 1983). In both cases, roots of *Ammophila* were found infected with endophytic mycelium. Nicolson and Johnston conclude that these mycorrhizas play a critical role in the growth of plants such as *Ammophila* which grow in harsh environments.

**Disease, Predation, and Disturbance**

European beachgrass seems little affected by plant parasites and disease. In his study of the species in the British Isles, Huiskes (1979a) lists a number of basidiomycetes, ascomycetes, and deuteromycetes found on senescing or dead plant parts. These are apparently part of the "normal" fungal flora since none was mentioned as causing problems for the plant. No diseases were reported.

The related American beachgrass (*A. breviligulata*), however, appears to be subject to a severe fungal disease, *Marasmius* blight (Lucas et al. 1971). It was first seen along the Outer Banks of North Carolina as a drying-out of the grass in circular areas of varying sizes up to 15 ft (5 m) in diameter. Mycelium and basidiocarps of a species of *Marasmius* were found on dead and dying plants. Attempts to replant the grass in the diseased areas have been unsuccessful.

A number of insect feeders are listed for European beachgrass by Huiskes (1979a) but none feed exclusively on the species. The larvae of one species, *Meromyza pratorum* (Diptera, Chloropidae) feeds exclusively on *Ammophila* in western Europe, but also feeds on other grasses in other parts of Europe (Huiskes 1979b). The larvae feed on developing leaves, killing up to 40% of the shoots. Shoot density of *Ammophila* does not seem to be affected by this level of predation.

On the Atlantic Coast of North America, a scale insect, *Eriococcus carolinae*, feeds on and kills American beachgrass (*A. breviligulata*) from North Carolina north to New Jersey (Campbell and Fuzy 1972). The extent of damage ranged from slight to severe, most damage occurring to the grass
growing on the lee side of the foredune and in settle areas. The insect seems to be host-specific.

Few mammals graze on European beachgrass. In Europe, rabbits are the most common feeders on young leaves, but take very little. Sheep and cattle will graze on it, but only as a last resort (Huiskes 1979a). There are numerous rabbits and other mammals in the dunes along the Oregon coast, especially in the shrub-dominated deflation plain inland from the foredune, but grazing on European beachgrass has never been observed. In the mid-1960's, I observed extensive harvesting of mature European beachgrass seed heads by California ground squirrels (Citellus beecheyi), especially in the Sandlake area near Tillamook. The Ammophila mounds were also used for their burrows. In recent years, very few of these animals have been seen. Other animals probably use Ammophila-dominated areas for the cover they provide. Pitts and Barbour (1979), working at Point Reyes National Seashore, California, noted that deer mice (Peromyscus maniculatus) preferred stands of European beachgrass for nesting habitat.

Ammophila has little resistance to trampling and disturbance caused by human and vehicular traffic. As recreational pressure has increased in western Europe and eastern North America, many studies have been initiated to determine the effect of human traffic on the grass. Studies in Europe (Boorman and Fuller 1977 and Hylgaard and Liddle 1981 for example) have found Ammophila easily destroyed by trampling. Since preservation of the foredune is of prime concern, various management plans are proposed to concentrate movement along established trails. The same concerns are addressed for the dunes of the national seashores of the east coast of the United States (Godfrey and Godfrey 1974). On critical beach areas, human traffic is banned to prevent destruction of the beachgrass.

On the west coast of the United States, vehicular traffic (ORV or "off-road vehicle") is a major destructive factor (Wiedemann 1984). The dune area at Sandlake, near Tillamook, Oregon, is a good example. Here vehicles have destroyed European beachgrass over a large area. Surviving mounds increase in height as sand from bare areas is blown onto them. The mounds are continuously eroded, however, as vehicles drive around them and onto the lower
slopes. Many gaps have been opened in the foredune. Not only European beachgrass is affected, of course. Other dune plant communities are also destroyed, including what remains of the pre-Ammophila communities. The long-term effects of this disturbance are not known. With cessation of vehicular traffic, European beachgrass would probably recover as long as plants were still present.

Control

There is no reference in the literature concerning the control or eradication of European beachgrass although, as noted previously, there are concerns from areas where the grass has been introduced. Two programs of organized eradication efforts are known.

At the Lanphere-Christensen Dunes Preserve, Arcata, California, work has been ongoing since 1983. Initial experiments with burning, herbicides, and salting were not successful, and major emphasis was placed on digging utilizing volunteers and crews from the California Conservation Corps. This is difficult, time-consuming work, and while the species has been controlled, eradication using this method does not seem possible. New experiments are underway with herbicides, and salting trials are planned (personal communication, A. Pickart, Lanphere-Christensen Dune Preserve, Arcata, California, 1987). The herbicide used is glyphosate (trade name Round-Up) and has been applied with varying success. On the basis of initial trials, it seems to be most effective when applied in the flowering stage. Applications at other stages of growth have proven ineffective.

Extensive eradication efforts are underway at Fiordland National Park in New Zealand (personal communication, P.N. Johnson, DSIR, Dunedin, New Zealand, 1987). Ammophila is considered a serious threat to native plant communities, and is given priority (along with gorse and broom) in the exotic plant eradication/control program. The use of herbicides characterizes the main control effort. Two chemicals, Valpa L and Round-Up, are very effective in killing Ammophila. Also used are Tordon 2G Prills and Tordon 520 DS. Limited digging is also employed.
CONCLUSION

A picture emerges of a species that is almost perfectly adapted to a very precise set of habitat conditions. Within that habitat it has no competitors and essentially no predators or diseases. It can spread quickly by seed, through rhizome growth, and by the dissemination of rhizome fragments. Environmental conditions along the northwest coast of North America are almost perfect for its establishment and spread: moderate temperatures, sufficient rainfall, an abundant sand supply, and strong, consistent, on-shore winds. In some respects this is a better habitat for the species than many places in its native Europe (particularly wind and sand supply).

Control or eradication in a situation where it has become as firmly established as it has along the Northwest coasts is likely to be very difficult. Unless done over a large area to remove seed and rhizome resources, cleared areas will regenerate quickly. Mechanical removal is probably effective only in limited areas with small patches, and then would have to be monitored for several years to remove regrowth. Application of salt will probably prove ineffective. Although sensitive to salt in the soil water, high rainfalls leach salt out quickly. It is not known how long rhizomes can tolerate salt. Biological control is probably not possible. The only documented case of fungal disease (Marasmus) is known from the American species A. breviligulata. The genus causes disease in many other species of grasses. Introduction, even experimentally, for the purpose of control should be approached with caution. The use of herbicides seems at present to promise the most success, but even that seems limited. Continued work at the Lanphere-Christensen Dunes Preserve, this year (1987) using a truck-mounted pressurized sprayer to cover the foredune, will yield more information.

At any rate, it appears European beachgrass is permanently established along the Northwest coast. It is still widely used for stabilization purposes, by both public agencies (Carroll 1987) and private individuals and organizations, and will continue to be used in any situation where drifting sand interferes with human activity. The efforts of an organization like the Lanphere-Christensen Dunes Preserve should be supported because one day the preserve will provide the only view of what the dunes looked like prior to the introduction of European beachgrass.
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THE COASTAL PARABOLA DUNE SYSTEM AT
SAND LAKE, TILLAMOOK COUNTY,
OREGON, U.S.A.

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ABSTRACT
The parabola dune system at Sand Lake, Tillamook County, Oregon (45°18'N,
124°58'W) consists of a complex of stabilized and active dunes covering an area of
about 6.3 km². The boundary of the system is formed by the largest and oldest of the
parabola dunes. Its forested ridges extend 4500 m northeasterly from the shore and
are 1700 m apart at their windward ends. The stabilized ridges of more recent dunes
lie within these large ridges. A sequence of massive (25 m high) active parabola
dunes is presently moving along the axis of the system, driven by strong southwesterly
winter storm winds at the rate of about 5 m per year. Thermoluminescence dating
indicates that sand in the oldest dune was deposited 1600 yrs BP on a surface of
weathered sand dated at 11200 yrs BP. The forest on the dunes is composed of Pseudo
dotula menziesii, Pinus contorta, and Picea sitchensis. In recent years, the establishment
of the exotic grass, Ammophila arenaria, and increasingly heavy recreational use (off-
road vehicle traffic) have considerably altered the dune landscape.

INTRODUCTION

Sand dunes occur along 45% of the Oregon coast from the California border
north to the Columbia River (42° to 46°N). In his description of these dunes
and study of their dynamics, Cooper (1958) classified them into 30 geographic
localities. Each locality is characterized by a number of different dune forms.
A characteristic pattern of dune forms that recurs in the dune landscape is a
dune system. Each dune system is named according to its predominant dune form (Wiedemann 1984; Olson and van der Maarel 1989).

Four dune systems are recognized along the Oregon coast: parabola dune,
transverse dune, parallel ridge, and bay dune. The characteristics of the Oregon
coast which influence the type of dune system that will develop in a locality are
land form and wind regime. Broad, low coastal plains are interrupted by sea
cliffs, headlands, promontories, bays, and estuaries. The annual wind regime varies markedly between summer and winter. In summer, offshore winds from the N-NW predominate. These winds have the greatest average velocity. In winter, low velocity offshore winds predominate, but offshore storm winds from the south to southwest of very high velocity occur frequently. These winter storm winds, frequently of gale force, are the prime movers of sand. Both the massive winter transverse dunes (oblique dunes), and the largest of the parabola dunes, are products of their work.

DESCRIPTION

Parabola dunes are the dominant feature of 9 of the 27 dune systems along the Oregon coast. Most are found in association with bays or estuaries, and most are formed by the action of the winter storm winds along a southwest to northeast axis. One of the largest and most impressive of the parabola dune systems, covering approximately 6.3 km², is located about 20 km southwest of the north coastal town of Tillamook (45°18'N, 124°58'W - Figures 1 and 2). It lies just south of Cape Lookout, a 200 m high basalt ridge that extends 3 km out into the ocean. At the south end of the system is Sand Lake, a large (5.5 km²) tidal flat of channels, sand and mud flats, salt marsh, and the outlets of a few small streams.

The Sand Lake dune system was described briefly by Cooper (1958) from aerial photographs of the area. The following description is based on 25 years of field work and observation. The system consists basically of a series of nested parabola dunes, extending about 5 km from the shore to the mountain front of Cape Lookout along an axis oriented approximately N30°E from the almost due north trend of the coastline (Fig. 3). It rests on a substratum of hard, reddish sand which appears at the shore just north of the Sand Lake outlet and rises gradually northward to about 30 m at the outer (seaward) margin of the complex, continuing to meet the mountain front of Cape Lookout. This substratum appears to tilt down inland, away from the beach, and is exposed on the eroding sand surface at the south end of the system, and at the edge of Sand Lake.

Dune Form and Movement

The outermost (primary) parabola dune is the largest; it is mostly intact except for erosion at the seaward ends and overtopping and erosion at the terminal end (Fig. 4). The existing lateral ridges are about 27 m high over substratum (as measured from features at or near substratum level), and 1.7 km
FIGURE 1 Sand Lake parabola dune system.
apart at the existing widest point. The seaward end of the outer ridge (nearest the shore) lies on the 30 m high substratum sea cliff and that of the inner ridge lies just above sea level (7m). The outer ridge is about 2.7 km long; the inner 4.5 km long (including the eroded and overtopped segments of the upper end). At the seaward end of the outer ridge is a small (4 ha) shallow lake, the inner shore formed by the steep slope of the ridge. It lies about 100 m in from the sea cliff, at an elevation of 26m. It is fed by a small stream running along the base of the ridge, and drains downward through the substratum, emerging as seeps along
the base of the seacliff. Near the seaward end of the inner ridge the forest cover has been destroyed and only a remnant remains at the very end, where the ridge is 31 m high (M1 in Figure 4). The deforested part of the ridge is lower because of erosion.

Remnants of a smaller (secondary) parabola dune are found within the ridges of the larger. Both the seaward ends and the apex have been eroded and overtopped, and it appears it did not extend as far to the northeast as the primary dune. This dune has a hairpin shape, with lateral ridges almost parallel to each other, and about 600 m apart. The trend of this dune, N17°E, is more northerly than the primary dune. From inspection of aerial photographs, these secondary ridges seem to be as high as the primary ridges. The outer slopes of the lateral ridges of both the primary and secondary parabola dunes are very steep, right at the slipface angle of 33°. The forested terrain between the primary and secondary dunes is irregular, with swales, small ridges, and blowouts.

The current phase of active dune movement extends the entire length of the system, consisting of four parabola dunes moving along the central axis. Dune I (Fig. 4) is the most recent to begin moving, while Dune IV has overtopped the apex of the primary parabola. Dunes II and III are moving through a relatively narrow trough in the forest cover, while Dune I is moving on a wider front. At the terminal end (northeast) there is an active slipface on all three sides, though the ridge is highest at the northwest corner. Most of this large, almost square, open area (the terminal sand plain) is blowout terrain with a few transverse ridges of 1 to 2 m height formed by the winter winds. The advancing apex of Dune II, constricted by the narrow corridor through the forest, is very high, about 25 m (Fig. 5). Dune I is a little lower, and Dune III is the lowest. The lateral ridges of all three dunes are invading forest as they move through the corridor.

The large deflation surface windward of Dune I has developing vegetation. In the winter, water stands along the lowest side of the deflation surface, at the base of the outer lateral ridge. A large (1 ha) pool of water, up to 1 m deep, also collects each winter at the base of the slipface of Dune I. It usually dissipates by early summer. A tall (16 m) forested mound 200 m seaward of the end of the forested inner primary ridge described above is probably a remnant of the Dune I inner lateral ridge (M2). At the south end of the system is a sandspit of about 1 km length ending at the mouth of Sand Lake.
FIGURE 4 Map of the Sand Lake parabola dune system. Labeled features discussed in the text. Base map adapted from Cooper (1958).
The movement of these large active parabola dunes under the driving force of the southwesterly winds of winter is relatively rapid. Measurement of the rate of advance of Dune I carried out over a 4 yr period from April, 1964, to April, 1968, indicates an average movement of 5.4 m/yr. In addition, a marker stake placed at the center of the windward base of the dune in August, 1964, was recovered in August, 1988, 85 m from the windward base, indicating a rate of 4.3 m/yr. The higher rate for the 1964-68 period reflects a very large advance in the last year of the study.
Sediment and Soils

The composition of the sands of the Sand Lake dune system is 90% quartz and feldspar with heavier, darker minerals occurring in small amounts (less than 1%), and miscellaneous particles of mixed or indeterminate composition making up the remainder (Twenhofel 1946). Particle size is medium to fine (50% 0.5 to 0.25 mm, 49% 0.25 to 0.125 mm, and 1% 0.125 to 0.0625 mm). The color is generally a light gray.

Soil profile development in these sands begins with a weak light yellow mottling in the sand just beneath the surface. With further weathering the mottling becomes stronger and the sand becomes yellow-brown in color. The sand just beneath the surface begins to turn a dark gray with continued loss of iron. As the dark gray layer deepens, the sand beneath it turns brown and the yellow-brown layer extends deeper into the profile.

The dune soils were studied in five locations (Fig. 4). Profiles were described for all five locations, samples for thermoluminescence dating (TL) were taken at three, and a sample for radiocarbon dating at one. The TL determinations estimating time of sand deposition were carried out at the Radiocarbon Dating Laboratory, University of Helsinki. Mejdahl (1988) discusses the method.

Location S1. Top of the outer primary ridge, near the terminal, eroded end. Dense, well-developed forest about 100 yrs old. Profile: 0-40 cm, weakly mottled light gray; light gray below. No TL date.

Location S2. Top of the outer primary ridge, 600 m south of S1. Dense, well-developed coniferous forest, 150-200 yrs old. Profile: 0-5 cm, dark gray; 5-25 cm, brown; 25-66 cm, strongly mottled yellow-brown; weakly mottled light gray below. No TL date.

Location S3. Inner primary dune ridge along Galloway Road. Because of an excavation at the base of the dune it was possible to study the profile and take the TL sample about 3 m in from the base of the dune. The TL sample was taken 1.5 m from the surface and 1 m into the face of the cut. Dense, well-developed coniferous forest about 150 yrs old. Profile: 0-18 cm, dark gray; 18-69 cm, brown; 69-145 cm, strongly mottled yellow-brown; weakly mottled light gray below. TL date: 1600 ± 200 yrs.

Location S4. Two buried profiles, one beneath the other, in an eroding mound on an active sand area beyond the forested ends of the outer primary and secondary ridges with no clear connection to either ridge. The profiles
slope 28° toward the shore. TL samples were taken 1 m below the top of the upper profile and 0.5 m below the top of the lower profile, each 1 m into the face of the mound. Profile: 0-30 cm, dark gray; 30-97 cm, brown; 97-158 cm, strongly mottled yellow-brown; 158-166 cm, dark gray with embedded small pieces of burned wood (lower buried profile); strongly mottled yellow-brown below. TL dates: upper profile, 1200 ± 150 yrs; lower profile, 1600 ± 200 yrs.

Location S5. Exposed substratum on the beach in the vicinity of S4. Exposed section is 1 m high above the upper beach and rises northward. Recent sand about 15 cm thick on the surface. TL sample taken 0.5 m below the surface and 1 m into the face. Sample of burned wood embedded in the surface taken for radiocarbon date. Profile: 0-15 cm, dark gray argillic with a loamy sand texture; 10-25 cm, yellow-brown argillic with a slightly higher clay content. Weakly mottled yellow below. TL date: 11200 ± 1500 yrs. Radiocarbon date: 4820 ± 120 yrs.

VEGETATION

The climate of the Oregon coast is characterized by wet mild winters and relatively dry cool summers. The climatic data recorded at Newport, Oregon, a coastal city 64 km south of Sand Lake, is typical of the entire Oregon coast. The average annual temperature is 10.8°C, varying from a high of 14.2°C in August to a low of 6.4°C in January. The average annual precipitation is 1679 mm, with 21 mm occurring in July and 274 mm in December. Of the annual precipitation, 6.2% falls during the summer months, June to August.

Under these climatic conditions, vegetation becomes established quickly and develops rapidly, especially on low, stable areas close to the water table (Fig. 6; Appendix I). At Sand Lake, the active sand of the massive parabola dunes moving up the axis of the system is bare of vegetation. The remnants of the primary and secondary parabola ridges and the low areas between them are heavily forested. The terminal sand plain at the northeast end of the system and the flanks of the active parabola dunes are being colonized by species tolerant of sand burial. The large deflation surface windward of Dune I has a well-developed meadow and a developing coniferous forest.

The present beach foredune, sandspit, and active lateral ridges of Dune I are dominated by a community consisting almost entirely of the introduced *Ammophila arenaria*. The only other abundant associate is *Lathyrus japonicus*, found mostly along the beach foredune. On the sandspit and other blowing sand areas, *Ammophila* forms large mounds or hummocks which tend to erode away
after reaching a certain maximum size (as much as 4 m tall). Where there is a high density of such hummocks, sand activity is reduced and species less tolerant of sand burial become established, eventually stabilizing the mounded area.

The primary native foredune species is *Elymus (Leymus) mollis*, which forms low, rounded mounds. Associated with it, on foredunes and on active sand such as the lateral ridges of the parabola dunes, are *Abronia latifolia*, *Ambrosia*
chamissonis, and Tanacetum douglasii. Only bare remnants of this community exist at Sand Lake today, and little is found elsewhere along the coast, having been almost completely replaced by Ammophila arenaria. (The best existing examples can be seen at the Lanphere-Christensen Dunes Preserve, Arcata, California, the result of years of restoration work.)

The most widespread active sand pioneer community is composed of a number of species that tolerate sand burial, and which eventually develop into a closed cover that permits the establishment of species intolerant of sand movement. The principle species of this community are Poa macrantha, Lathyrus littoralis, Carex macrocephala, Glehnia leiocarpa, and Convolvulus soldanella. At Sand Lake, this community is found primarily on the active parts of the terminal sand plain at the northeast end of the system.

As sand begins to stabilize, species of the meadow community become established: Lupinus littoralis, Fragaria chiloensis, Festuca rubra, Polygonum paronychia, Achillea millefolium, and a wide assortment of introduced meadow species such as Hypochaeris radicata and Aira praecox. A successional shrub stage occurs with the establishment of Gaultheria shallon and Vaccinium ovatum. This stage can develop quickly into an impenetrable shrub thicket up to 2 m tall. Generally, Pinus contorta becomes established at about the same time as the shrub species, and it eventually becomes the dominant species. As the trees mature, Rhododendron macrophyllum becomes dominant in the understory. With age, the Pinus forests open up (the canopy thins and trees fall) and Tsuga heterophylla and Pseudotsuga menziesii become dominant, the latter being more common on the upper slopes and ridges, the former on the mid and lower dune slopes. The shrub understory in these older forests is an impenetrable stand of predominantly Rhododendron macrophyllum and Vaccinium ovatum, although Arctostaphylos columbiana occurs in significant amounts on the ridgetops. Large areas of the outer primary and secondary ridges are covered by these older forests.

In somewhat sheltered places there are large areas of bare sand that are relatively inactive. This occurs along the western side of the terminal sand plain and on the outer lateral ridge of Dune III. In this situation, a sand plain community dominated by Festuca rubra and Solidago spathulata develops. In the most sheltered areas, the moss, Rhacomitrium canescens, gradually covers the surface, and is followed by Arctostaphylos uva-ursi, with eventual progression to Pinus contorta forest (Fig. 7).
In the swales between sand ridges, and on the deflation plains, water commonly stands on the surface for 3 or more months of the year (winter months). Marsh species such as *Juncus falcatus* and *Trifolium wormskjoldii* initiate vegetation development. Common associates include *Juncus nevadensis*, *Aster subspicatus*, *Epilobium watsonii*, and *Sisyrinchium californicum*. A shrub stage develops rapidly with *Salix hookeriana*, *Myrica californica*, and *Gaultheria shallon* the primary species. Seedlings of *Pinus contorta*, *Picea sitchensis*, and *Alnus rubra* establish quickly. The proportions of these tree species in the developing forest vary widely. Almost pure stands of *Picea* can occur. Where *Pinus* dominates,
Picea usually eventually appears, beginning to rapidly outgrow the Pinus at about 5 m in height. Alnus is never a major component in these forests. Development is toward a Picea forest with the eventual establishment of Tsuga heterophylla and Thuja plicata. Old forests of this type occur in only a few swales along the seaward side of the system at Sand Lake.

HUMAN DISTURBANCE AND MANAGEMENT HISTORY

Settlement and Use 1886-1967

The first settlers in the area claimed land in 1886 under the Homestead Act. These claims were located along the shore north of the outer primary ridge. The lake there bears the name of one of these families. In the next 35 years most of the land bordering the dune system, as well as some dune land, was claimed. In 1910 and 1913 land was acquired along the shore bluff to establish seaside resorts: "Sand Lake-by-the-Sea" and "Bright Waters." These properties were platted in the 1940s, but eventually reverted to county ownership for non-payment of taxes.

The property north of Chamberlain Lake was purchased by the Boy Scouts of America in 1925. In the early days the only access was by trail and a primitive plank road. The trail was widened by the military to supply lookouts during World War II. In 1950 a power line was put in across the dunes and a logging road was constructed in 1954. The camp is still in use.

The present ownership of the dune lands is a mixture of public and private holdings. The United States Forest Service owns 436 ha which is administered as part of the Hebo Ranger District of the Siuslaw National Forest. Much of this land came to the Forest Service from the public domain at the time the Forest Service was organized in 1907. The rest was acquired through transfer from other public agencies, such as Tillamook County, and by donation or purchase from private owners. Tillamook County owns 127 ha. The Oregon Division of State Lands manages the beach and estuary below mean high tide (2.4 m), and Oregon State Parks and Recreation has jurisdiction from the "beach zone line" (4.9 m) to mean high tide. The remainder of the land is in private ownership.

The earliest descriptions of the Sand Lake dune area are notes in the records of the County Surveyor (1882-1890). At the south end, where Galloway Road crosses the dunes to the beach, were "rolling hills with fir and hemlock," but to the north, along the inner primary and secondary ridges there was "timber deadened by fire," "scattered fir timber," and "sand glades." The forest on the
outer ridges was described as "big timber." The meander line along the beach had adjoining "high banks and sand hills," and "high bluff banks covered with dead timber."

Local, long-time residents of the area provide additional information about past conditions and change (interviews by the author, 1964-65). Fires were common prior to settlement and continued to be so afterward as settlers burned the sand hills to keep the brush down. The last fire on the dunes was in the mid-1930s. Most of these fires were on the inner secondary and primary ridges and the lower ground between them. The varied patches of forest with different sized trees and different densities reflects this burning history.

In the surveyor's records, a note states that there was timber in the area between the end of the inner primary ridge and the beach (today crossed by the Galloway Road beach access). A son of one of the settlers affirmed this, and said that only a narrow "blow sand strip" existed. He and another informant also said that an earlier settler had cut a road through the timber to the beach, and had also burned the timber in the area. This occurred around 1900. In 1963 a forest of snags protruded from active sand for some 1000 m north of the present day forest remnants (M1,M2). The same fire also destroyed timber on the primary inner ridge, and sand became active there. The present broad front of Dune I is probably a result of this burn, the inner lateral ridge of the dune having advanced eastward and northeastward into the burned forest.

Photographs taken in the early 1920's show the sandspit bare of vegetation. (Fig. 8) A local resident said it was flat, and had only a few Abronia mounds toward the shore. The Dune I deflation plain was wet sand, "quicksand," and bare of plants. The first vertical aerial photographs of this area, taken in 1939, show these characteristics clearly; however, there seems to be an increased density of mounds toward the end of the sandspit. This could have been the beginning of the Ammophila "invasion."

Ammophila arenaria was first planted in the late 1930's, by the Civilian Conservation Corps, on the active part of the inner primary ridge between the forest remnant (M1) and the main forest of the ridge. In the early 1950's, a wide band of Ammophila was planted across the top end of Dune III by the Boy Scouts, who also set out thousands of plants along the beach front of Camp Meriwether. Also about this time, a "beachgrass (Ammophila) nursery" of about 10 ha was established on the sandspit just south of the Galloway Road beach access. It is clearly defined in a 1953 aerial photograph that also shows the increasing number of Ammophila hummocks and the developing foredune.
FIGURE 8 Comparative photographs showing the establishment of Ammophila arenaria at Sand Lake. View is west across the Dune I deflation plain. Top: about 1925. Bottom: January, 1965. Dark areas on the deflation plain are wet sand.

The Forest Service made a small planting in front of the advancing apex of Dune II in 1966 to protect a planned road across the active sand to the outer ridges. The road, intended as access to a proposed new campground, was not constructed, nor was the campground. Most recently, Ammophila was planted by Tillamook County to stabilize sand on both sides of the new road constructed over Cape Lookout and crossing the terminal sand plain near its upper end.

By 1965 the Ammophila foredune was a ridge 4-8 m high over substratum. Ammophila hummocks covered the sandspit and were developing on the active
FIGURE 9 The Ammophila nursery on the sandspit at Sand Lake in 1964. View to southwest. Note foredune-like ridges at right. Trees are Pinus contorta. Galloway Road beach access across the bottom.
lateral ridges of Dunes I and II and on the higher parts of the Dune I deflation plain (Fig. 8). A foredune type ridge 8 m high had developed on the south and west sides of the beachgrass nursery (Fig. 9). The planting by the Boy Scouts on Dune III had also raised into a broad, rounded ridge about 8 m above the original level of planting. Only a few scattered plants had become established on active blowouts of the terminal sand plain. None had become established on the sheltered west side of this sand plain.

The native mound builders—Abronia, Ambrosia, Elymus—were present but infrequently encountered. The pioneer Poa-Lathyrus community covered large areas of the higher active sand blowouts, slopes, and ridges along the shore, and on the terminal sand plain. The Dune I deflation plain had a well-developed meadow in which plants of the shrub and tree stages were appearing. Scattered Pinus contorta were up to 1 m tall. It was at this point that another element of change became a significant factor.

Recreational Impacts

Until the late 1960’s, recreational use of the area had been light. The Galloway Road beach access extension was built in the early 1950’s. In 1957 the Forest Service established a small picnic area with a well and hand pump on the southeast corner of the sand spit. "Dune buggies" were a novelty; even on weekends in mid-summer only a few would be seen. For the Independence Day weekend of 1967, 12 families were reported visiting the picnic site. However, in the following three years, visitor use increased dramatically. The Forest Service estimated 8000 "visitor days" (one visitor for 12 hrs) for 1968, 15000 for 1969, and 26000 for 1970. Much of this increase was due to increasing Off Road Vehicle (ORV) activity, including the opening of a "drag strip" on Tillamook County land on the sand spit behind the foredune.

To cope with the increasing activity, both vehicle traffic and numbers of people, the Forest Service imposed restrictions in 1971. These restrictions included the designation of certain areas as off-limits to vehicle traffic, requiring the use of mufflers and spark arrestors on the ORVs, and requiring a special use permit for events attracting large numbers of people. It is of interest to note that copies of the notice of restrictions were sent to 40 organized off-road vehicle clubs, most of them in western Oregon.

The Forest Service also constructed a 25 unit campground in 1973 on the site of the beach grass nursery. Another 76 units were added in 1975. Each unit of the campground has large parking areas to accommodate ORVs and their
trailers. The campground has its own water system, sewer treatment plant, trailer dump station, and seven comfort stations.

By the end of the 1970's, with the advent of more sophisticated and mass-produced all-terrain vehicles and their increasing popularity, severe problems had developed in managing the area. It was estimated that in 1979 as many as 6500 people were present on weekends, with ORVs numbered in the thousands. Area residents complained of noise, traffic, and vandalism; fatal accidents occurred on the dunes; and sanitation and litter problems required urgent action.

Implementation of Management Plan

It soon became obvious that some kind of organized, long-range management plan needed to be developed. To this end the Sand Lake Management Team was formed in 1979 with the Forest Service as the lead agency. After a year of planning, which involved extensive public input, the Sand Lake Management Plan (USDA Forest Service 1980) was put into effect on 31 March 1980. The principle provisions of the plan include:

1. An advance registration/permit system that would limit use to a predetermined capacity of 1700 "street legal, licensed vehicles" on three-day holiday weekends—Memorial Day at the end of May, Independence Day at the beginning of July (in some years this is not a three-day weekend holiday), and Labor Day at the beginning of September.

2. Additional overnight camping to be provided and the development of a staging area off the Cape Lookout Road. Access roads other than Galloway Road would be blocked.

3. Year round closure of Sand Lake, the portion of the beach and sandspit south of Galloway Road (beach access), and the terminal sand plain north of the Cape Lookout Road.

4. Cooperative law enforcement by Forest Service, county, and state police with 24-hr patrol coverage during the holiday weekends.

The number of permits issued was at or near maximum for the first two years (1980 and 1981) after the management plan was adopted, with a gradual drop
### Table 1. Number of permits issued (P) and number of permitted vehicles entered (E) at Sand Lake for the three holiday weekends, 1980-1989. (* – not a three day weekend)

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In number from 1982 to 1989 (Table 1). The number of permitted vehicles entering on the holiday weekends was at first about 75% of the permits issued. In the following years vehicle entry remained more or less constant. These numbers may seem low, but considering that each street licensed vehicle can tow one or more off-road vehicles, the total number on the sand dunes can be quite high. Some elaborate trailers can carry as many as six of the small three or four wheel machines. The present access permit fee is $5.00.

Additional camping was provided by the development of two large parking lots, one between the two forest remnants (M1, M2) and the other just to west of the west remnant. Camping in these areas means the parking of trailers and motor homes. Camping is also permitted on the dunes. The most heavily utilized areas are the Dune I deflation plain and the western sheltered part of the sand plain south of the Cape Lookout road. Litter is a major problem in these areas. Once each year a number of off-road vehicle clubs cooperate to stage a clean-up. In 1990 this took place in April. The present daily fee for the developed campground is $7 for the first vehicle and $3 for each additional vehicle. The fee for the parking lot, whether parking or camping, is $4.
The closures have been generally effective, with most of the violations taking place on the terminal sand plain north of the Cape Lookout Road, and even these have been minimal in their impact. The staging area was not developed because the anticipated need did not materialize, and the drag strip on county land has been inactive for several years. One of the access roads (near the S1 soil study location) has been closed.

Basic law enforcement has been provided by the county which keeps a full-time deputy in the area. This is supplemented on holiday weekends by extra county deputies and Forest Service personnel. (The Oregon State Patrol is responsible for policing the beaches.) Law enforcement remains a problem area. The cost for personnel and equipment is high and the work force is spread thin. A recent report on the situation (Anderson 1989) points out that often there is only one officer for 3,000 to 5,000 people. In addition, the problem is compounded, according to one officer, by "...Honda ATVs that go 70 mph..." and, "...drinking, family beefs, people not using common sense." The county is seeking additional revenue from Sand Lake user fees to help pay its costs.

As would be expected, this intensive vehicular traffic has had an effect on the dune vegetation. Probably most significant is the almost complete destruction of the Arctostaphylos/Rhacomitrium community, especially where it was best developed and most abundant on the relatively sheltered area along the west side of the terminal sand plain. Both high density camping and heavy traffic broke up the delicate Rhacomitrium carpet, and today only traces are left under the larger trees. The pioneer Poa-Lathyrus and Festuca-Solidago communities have also been destroyed on the active sand ridges and slopes next to the shore and on the sand plain area south of the Cape Lookout Road. North of the road, where ORV traffic is prohibited, these communities are in good shape.

Another dramatic effect of this traffic has been the extensive destruction of the Ammophila cover. On the deflation plain and lower slopes of the Dune I, II, and III lateral ridges Ammophila has practically disappeared. On the higher slopes of these ridges the formerly dense cover of Ammophila has been broken up into numberless small patches. Vehicle traffic and wind erode the sand around these patches and they turn into eroding mounds. It is highly unlikely that Ammophila would be completely eliminated, and it would return quickly should the disturbance cease. The entire sandspit south of the Galloway Road beach access is either covered with Ammophila or in various stages of succession to meadow. The former beachgrass nursery still has Ammophila, but there is a rapidly growing Pinus forest with trees to 8 m tall.
CONCLUDING THOUGHTS

This brief account does not, and can not, deal with the many interesting questions that occur in describing this dune area. Both the size of the system, in area and amount of sand, and the arrangement of the sequential parabola dune episodes are unique along the Pacific Northwest coast. What influence does the coastal topography, especially Cape Lookout, have on the formation of the system? What is the role of the wind regime, especially that of the northwest winds? Why are the trends of the primary and secondary dunes so different? What is a possible time sequence for the various episodes? What can be learned about soil formation? What will be the effect of current events?

Of the last question one can speculate that over the millennia of dune cycles none of these contemporary events and activities is likely to have much effect on the dunes as a functioning system. Ammophila will return when the ORVs depart (the Rhacomitrium will return also, but it will take longer). Trees will replace the Ammophila. Sand will accumulate on the sandspit. The forest will burn, and another parabola dune episode will begin. As the sand shifts, future generations will find the artifacts of our time and culture: mufflers, beer cans, and perhaps even a black plastic pen or two lost by the wandering inquirer.

ACKNOWLEDGEMENTS

I would like to express my thanks to the District Ranger and his staff of the Hebo Ranger Station, Siuslaw National Forest, for their helpfulness in answering my questions and giving me access to the Sand Lake files. Special appreciation is expressed for the information provided me by long-time residents of the Sand Lake area, especially Mrs. Otis Edwards, Mr. Ezra Galloway, Mr. Sam Nelson, and Mr. G. H. Oberleufer. Discussions and a site visit with Dr. Jim Stroh, my geologist colleague at The Evergreen State College, were stimulating and informative, and his contribution is acknowledged. Special thanks are due Dr. Olavi Heikkilä, University of Oulu, and Dr. Högne Jungner, Radiocarbon Dating Laboratory, University of Helsinki, for the thermoluminescence and radiocarbon dates. Photograph credits: Figures 2 and 5, Art Hare, Seattle, Washington; Figure 3, U.S. Coast and Geodetic Survey; Figures 7, 8, and 9 by the author.

REFERENCES


County Surveyor. 1882-1890. Records of the County Surveyor. Tillamook County, Tillamook, Oregon.


Appendix I  Standard and common names of plant species named in the text. All names after Hitchcock and Cronquist (1973) except *Rhacodendron*.

<table>
<thead>
<tr>
<th>Standard Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Abronia latifolia</em> Eschsch.</td>
<td>Yellow Sand-verbena</td>
</tr>
<tr>
<td><em>Achillea millefolium</em> L.</td>
<td>Yarrow</td>
</tr>
<tr>
<td><em>Aira caryophyllea</em> L.</td>
<td>Silver Hairgrass</td>
</tr>
<tr>
<td><em>Alnus rubra</em> Bong.</td>
<td>Red Alder</td>
</tr>
<tr>
<td><em>Ambrosia chamissonis</em> (Less.)Greene</td>
<td>Silver Bursage</td>
</tr>
<tr>
<td><em>Ammophila arenaria</em> (L.)Link</td>
<td>European Beachgrass</td>
</tr>
<tr>
<td><em>Arctostaphylos columbiana</em> Piper</td>
<td>Bristly Manzanita</td>
</tr>
<tr>
<td><em>Arctostaphylos uva-ursi</em> (L.)Spreng</td>
<td>Kinnikinnik</td>
</tr>
<tr>
<td><em>Aster subspicatus</em> Nees.</td>
<td>Douglas Aster</td>
</tr>
<tr>
<td><em>Carex macrocephala</em> Willd.</td>
<td>Large-headed Sedge</td>
</tr>
<tr>
<td><em>Convolveis soldanella</em> L.</td>
<td>Beach Morning Glory</td>
</tr>
<tr>
<td><em>Elymus</em> (<em>Levus</em>) <em>mollis</em> Trin.</td>
<td>American Dunegrass</td>
</tr>
<tr>
<td><em>Epilobium watsonii</em> Barbey</td>
<td>Watson's Willowherb</td>
</tr>
<tr>
<td><em>Festuca rubra</em> L.</td>
<td>Red Fescue</td>
</tr>
<tr>
<td><em>Fragaria chiloensis</em> (L.)Duchesne</td>
<td>Coast Strawberry</td>
</tr>
<tr>
<td><em>Gaultheria shalonn</em> Pursh</td>
<td>Salal</td>
</tr>
<tr>
<td><em>Gleghia leiocarpa</em> Mathias</td>
<td>American Glehnia</td>
</tr>
<tr>
<td><em>Hypocharis radicata</em> L.</td>
<td>Hairy Cats-eye</td>
</tr>
<tr>
<td><em>Juncus faicatus</em> E.Meyer</td>
<td>Sickle-leaved Rush</td>
</tr>
<tr>
<td><em>Juncus nevadensis</em> Wats.</td>
<td>Sierra Rush</td>
</tr>
<tr>
<td><em>Lathurus japonicus</em> Willd.</td>
<td>Maritime Pea</td>
</tr>
<tr>
<td><em>Lathurus littoralis</em> (Nutt.)Endl.</td>
<td>Beach Pea</td>
</tr>
<tr>
<td><em>Lupinus littoralis</em> Doug.</td>
<td>Seashore Lupine</td>
</tr>
<tr>
<td><em>Myrica californica</em> Cham.</td>
<td>Pacific Wax-myrtle</td>
</tr>
<tr>
<td><em>Picea sitchensis</em> (Bong.)Carr.</td>
<td>Sitka Spruce</td>
</tr>
<tr>
<td><em>Pinus contorta</em> Doug.</td>
<td>Lodgepole Pine</td>
</tr>
<tr>
<td><em>Poa macrantha</em> Vasey</td>
<td>Seashore Bluegrass</td>
</tr>
<tr>
<td><em>Polygonum paronchica</em> C.S.</td>
<td>Black Knotweed</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em> (Mirbel) Franco</td>
<td>Douglas fir</td>
</tr>
<tr>
<td><em>Rhacodendron canescens</em> (Hedw.)Brid.</td>
<td>Western Rhododendron</td>
</tr>
<tr>
<td><em>Rhododendron macrophyllum</em> G.Don</td>
<td>Hooker Willow</td>
</tr>
<tr>
<td><em>Salix hookeriana</em> Barratt</td>
<td>Golden-eye Grass</td>
</tr>
<tr>
<td><em>Sisyrinchium californicum</em> (Ker.-Gawl.) Dryand.</td>
<td>Dune Goldenrod</td>
</tr>
<tr>
<td><em>Solidago spathulata</em> DC.</td>
<td>Springbank Clover</td>
</tr>
<tr>
<td><em>Trifolium wormskjoldii</em> Lehm.</td>
<td>Western Hemlock</td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em> (Raf.)Sarg.</td>
<td>Evergreen Huckleberry</td>
</tr>
<tr>
<td><em>Vaccinium ovatum</em> Pursh</td>
<td></td>
</tr>
</tbody>
</table>


ECOSYSTEMS OF THE WORLD 2B

DRY COASTAL ECOSYSTEMS
AFRICA, AMERICA, ASIA AND OCEANIA

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Chapter 23

DRY COASTAL ECOSYSTEMS OF NORTHWESTERN NORTH AMERICA

A.M. WIEDEMANN

GENERAL DESCRIPTION

The dry coastal ecosystems of northwestern North America extend from the Queen Charlotte Islands (54°N) in the Canadian province of British Columbia 1800 km south to Cape Mendocino (40°N) in the American state of California (Fig. 23.1). Mountain ranges adjoin the coastline for its entire length. These mountains, varying widely in origin and structural materials, have given rise to a variety of striking topographic features.

A comprehensive description of the dune systems of the Pacific Northwest coast of the USA can be found in work by Wiedemann (1984). Information on plants and plant communities is available in work by Wiedemann (1966) and Wiedemann et al. (1969). Proctor et al. (1980) gave a detailed review of all aspects of the ecology of the Pacific Northwest coast of the United States.

The northernmost part of this coast, in British Columbia, is bordered by the Coast Mountains, a range with peaks exceeding 3000 m in elevation. It is described as a massive batholith, 1600 km long, composed of metamorphic rock and granitic intrusions. Glaciation and subsidence have produced a coast of steep slopes dropping directly into the sea. It is indented with deep ravines, narrow intricate valleys and long fiords cut back into the uplands, some for over 100 km. To the west is a submerged mountain range represented by a chain of islands. Of these, Vancouver Island is the largest, 480 km long and 320 km wide, with peaks rising to over 2000 m. Farther north the Queen Charlotte Islands stretch for more than 300 km. Coastal plains are few and narrow, but on the larger islands a few are large enough to permit the development of sand dune systems.

The rugged Olympic Mountains form the coast in the northern half of the state of Washington. These mountains are in the form of two volcanic belts which encircle a large interior area containing sedimentary rocks. The outer belt was formed in the Eocene, while the inner was deposited late in the Mesozoic. These mountains rise to 3500 m and meet the sea in spectacular, erosion-resistant sea cliffs which have not permitted the formation of the broad beaches and terraces necessary for the development of sand dunes.

The Washington and Oregon Coast Ranges extend from southern Washington south to the Klamath Mountains in southern Oregon. They are characterized by Tertiary and Pleistocene sedimentary deposits and igneous intrusions. The sedimentary formations had their origin in the Early Eocene when a eugeosyncline occupied the area from the Klamath Mountains (42°N) north to Vancouver Island and east to the present-day Cascade Mountains (about 150 km inland).

The initial deposits were volcanic in origin, but by Middle Eocene uplift activity to the south and subsequent erosion contributed arkosic sands and 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 the Late Eocene tuffaceous silts and clays began to be deposited by the streams and rivers flowing from the surrounding highlands. The deposition continued and increased considerably during the Oligocene and into the Miocene when arkosic sands and silts were also laid down in great amounts.

During the Middle Miocene, vigorous volcan
activity formed many of the basaltic intrusions and headlands which remain today as erosional remnants. Toward the end of the Miocene uplift began which was to form the Coast Range. This uplift reached its maximum height during the Pliocene, when peneplanation began. The erosion of the thick sedimentary beds was rapid, resulting in today’s low, rounded mountains reaching at most 500 m elevation. Erosion on the seaward side resulted in the formation of plains and terraces of varying width on which extensive sand dune systems occur. Where basalts are part of the mountain structure, promontories, headlands, and sea cliffs are common. Associated with these areas are numerous sea stacks and small, steep-sided islands which are erosional remnants isolated from the mainland.

The Klamath Mountains are old and geologically complex. Their history begins in the Palaeozoic with the deposition of volcanic and sedimentary rocks. Metamorphosis and folding were followed by additional deposition in the
Triassic. Extensive metamorphism followed. During the Jurassic more sediments were deposited and these were subsequently intruded by ultramafic and granitic volcanic rock. In the Early Cretaceous additional deposition of sediments took place, followed by folding and deformation in the Middle Cretaceous. Extensive penepalation occurred in the Miocene and Pliocene resulting in the present-day topography. Because of the erosion-resistant rock the development of terraces suitable for the development of sand dunes has been somewhat limited, and extensive terraces are found only in a few places.

Sea-level changes, the result of both land (tectonic) and water (eustatic) rise and fall, have played a significant role in the history of the northwestern North American coast. During the Late Pliocene and Early Pleistocene there occurred a period of extreme submergence, indicated by wave-cut terraces found as high as 450 m above present sea level. Subsequent uplift lowered the shoreline to about 90 m below present sea level, and it was during the period of low sea level during glaciations that the rivers and streams cut their trenches across the continental shelf. Resubmergence then took place again. Attempts to correlate eustatic activity with the many terraces found at many elevations along the coast are complicated by the instability of the coastal ranges.

The climate of this coastal region is marine, and although it appears to be remarkably uniform throughout, there are shifts that are reflected in the vegetation. Breckon and Barbour (1974), using the unmodified Köppen system, show a shift in climate at 46°N. To the north it is a Cfb climate – mesothermal with no dry season, while southward it is Csb – mediterranean with a summer dry period. As is shown in Table 23.1, temperatures decline slightly northward, while precipitation declines somewhat more markedly southward. Clouds and fog are present throughout the year, with cloudy skies occurring on half the days of the year. Fog becomes increasingly common southward, especially during the summer, occurring on nearly half the days of June through September.

The annual wind regime has a predictable seasonal cycle. In summer (June to August) onshore winds from the sector N–NW greatly predominate. These winds have a high average velocity. In winter (December to February) offshore winds of low velocity are most frequent. Onshore winds from the sector S–SW are relatively infrequent during this period, but they have the greatest velocities of the seasonal cycle. Spring (March to May) and autumn (September to November) wind conditions are transitional.

**PHYSIOGRAPHY OF THE SAND DUNES**

Sand dune systems have developed wherever shoreline features were conducive to the accumulation of large amounts of sand: broad beaches, terraces, coastal plains, and shallow bays. Along the northern half of the coast, the only dune systems of any size are on the Queen Charlotte Islands. By contrast, dune systems are found along 400 km of the 950 km of coast in Washington, Oregon, and northern California.

The origin of these dune systems can be traced to the eustatic activity associated with the cycles of glaciation during and since the Pleistocene. Each cyclic resubmergence resulted in sand dune activity in places where the shore topography permitted. Earlier dune systems were usually obliterated by later activity although in some places the earlier dunes extended farther inland and still remain, distinguishable by their reddish color and iron concretions.

The last major lowering of the shoreline – to about 140 m below present sea level – coincided with the maximum of the last, or Wisconsin, glaciation (about 20,000 years ago). Subsequent resubmergence slowed about 6000 years ago, at which time the present dunes reached their farthest inland advance and greatest volume (except for those systems on accreting shorelines near the major rivers). Cooper (1958, 1967) postulated that most areas had become completely stabilized by this time. Rejuvenation then occurred, apparently along the entire coast at approximately the same time. Based on studies of sand movement, this probably took place about 3000 years ago.

**Substrate**

The immediate sources of the sediments that form the dune systems are the many rivers draining the coastal mountains (the two major rivers, the Fraser and the Columbia, drain large areas of
TABLE 23.1
Average precipitation and temperature data for three locations on the northwestern coast of North America

<table>
<thead>
<tr>
<th>Location</th>
<th>Precipitation (mm)</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>January</td>
<td>July</td>
</tr>
<tr>
<td>Massett, British Columbia (54°02'N)</td>
<td>154</td>
<td>68</td>
</tr>
<tr>
<td>North Head, Washington (46°18'N)</td>
<td>220</td>
<td>24</td>
</tr>
<tr>
<td>Eureka, California (40°47'N)</td>
<td>155</td>
<td>2</td>
</tr>
</tbody>
</table>

interior mountains as well), and shore formations exposed to wave attack and erosion. The sediments are medium to fine sands, 99% of the particles in most samples falling in the size range of 0.5 to 0.12 mm. Their composition is primarily (70–90%) quartz and feldspar with heavier, darker minerals in minute amounts. No shell materials are present. The color of the sand varies slightly from place to place, ranging from light yellowish-brown to a darker brownish-gray. In southern Oregon and northern California high concentrations of coarse, dark sediments result in black beaches and dunes in some areas.

On the active dune sands there is no accumulation of organic matter and nutrient status is very low. Reaction ranges from slightly alkaline on the beach (pH 7.4) to neutral just above the extreme high-tide line (pH 7.0) and becoming moderately acidic with increasing distance from the shore (pH 6.0). A true soil can be seen developing under old-growth coniferous vegetation. In general the soil profile is characterized by a thin, very dark gray surface horizon of up to 12 cm depth, grading into a dark yellowish-brown layer of up to 50 cm depth with reddish-brown and yellow stains along root channels, and finally grading into the light yellowish-brown of the original dune sands. These soils are acid in reaction (pH 5.1 to 6.0), have excessive drainage, and are low in nutrients and humus.

On the lower areas imperfectly drained soils develop which have a thin surface layer of dark gray to almost black organic matter under which is grayish sand. There may be stains of yellowish-brown, and iron-cemented nodules deeper in the gray sand. These soils are very acid (pH 4.5 to 5.0) and poor in nutrients and humus. With long continued standing water and plant growth, extremely acid peat soils will develop with partially decomposed organic material reaching a depth of 1.5 m.

Dune forms

The coastal sand dune landscape is a complex mosaic of many dune forms. These forms are the basic morphological units making up the coastal dune systems of the various dune localities along the coast of this region.

Foredune

The foredune is a ridge of sand parallel to the beach just above the limit of ordinary wave action. Along this coast the foredune has attained heights of 10 m and a base width of over 100 m. Its seaward side is steep, while the lee side slopes gently from the crest. Along most of the coast this type of foredune has developed relatively recently with the introduction of Ammophila arenaria around the beginning of this century. Prior to the introduction of this species, the foredune was generally a series of closely spaced mounds formed by native plant species. Remnants of this kind of foredune can still be found on a few dune areas in northern California (Fig. 23.2).

Transverse dune

The northwest winds of summer are responsible for the development of transverse dunes with crests at right angles to the resultant wind direction (N10°W). These dunes, which move in the direction of the resultant wind, occur in regular patterns on broad, open areas. The crests are sinuous and vary greatly in length; some can be traced for more
than 1000 m. Intercrest distance averages 34 m. In profile the windward slopes are long and gentle, ranging from 3 to 12°, while the lee slope is a slipface at about 33°. The height from the base varies from 1 to 6 m. During the winter the strong southwesterly winds erode the transverse dunes severely. Rejuvenation of the dunes seems to occur on the foundation remaining from the previous year.

**Oblique dune**

On very extensive open areas with an abundant sand supply, massive oblique dunes develop that have crests oriented at right angles to the southwesterly winds of winter (Fig. 23.3). They occur as a series of more or less parallel ridges with an average intercrest distance of 300 m. The length of the crests is usually less than 1000 m, but can reach 2000 m. The average height above the inter-dune base is 25 m with extremes to 60 m. These dunes move an average of 3.8 m yr⁻¹ in the general direction of the resultant southwesterly winds. However, because of sand transport by the northerly winds of summer and the inhibition of transport by winter rains, the resultant sand transport is at an angle of 71°, or oblique, to the dune trend (Hunter et al., 1983).

**Retention ridge**

Sand deposited on the windward side of a vegetation barrier forms a retention ridge with a long, gentle windward slope and a steep lee slope (slipface). The ridge moves forward (downwind) slowly, and if it becomes massive enough, it will advance over and destroy the vegetation barrier. Generally it is a long continuous ridge moving under the influence of both summer and winter winds. Plants can colonize the steep lee slopes of
still active ridges if the rate of deposition is relatively slow. The effectiveness of the process can be seen in the well-developed forests on the steep lee slopes of some of the older, stabilized ridges.

Parabola dune
A parabola dune is basically a U-shaped or parabolic retention ridge (Fig. 23.4). Its origin is dependent upon an abundant sand supply, well-developed vegetation, and a strong unidirectional effective wind. It is highest and most massive at the apex which may be as much as 35 m above the base and in profile shows a gradual slope to windward and a steep slipface on the lee side. Parabola dunes may range in size from as much as 4 km in length with 1.5 km between the ends of the marginal ridges to much smaller dunes less than 100 m long. Vegetation develops on the marginal ridges and the entire dune becomes stabilized. Under certain conditions the apex can be blown out, leaving marginal ridges as two more or less parallel sand ridges. New parabola dunes may form later. If they are large they will override and destroy the earlier stabilized dune, or, if smaller, may advance between the marginal ridges of the earlier dune.

Deflation plain
Where the wind erodes the sand surface down to the water table a wet sand surface, or deflation
plain, results which is very resistant to further erosion. This commonly occurs where there has been a total interruption of the sand supply such as on the lee side of the extensive foredunes. Here, a deflation plain has come into existence that has increased in width steadily over the past 40 years and in some places is now up to 2 km wide. Deflation plains are also found at the base of the windward slopes of parabola dunes. Because of the stability of the deflation surface and the abundant moisture, vegetation develops rapidly.

**Blow-out**

Sand erosion where vegetation has been disturbed results in a blow-out. It can take the form of a long, narrow trough with a moving pile of sand at its head (a possible incipient parabola dune), or a saucer-shaped bowl with sand piled along the rim. The size varies considerably, from a few square meters to several hectares in area. As troughs or bowls enlarge they may join to form a sand plain. Revegetation commonly occurs, especially if sheltering vegetation develops around the blow-out area.

**Sand hummock**

Mounds of sand formed around plant species that can tolerate extensive sand burial can reach 5 m in height. These sand hummocks are cyclic dune forms either being formed, or, having reached some maximum size, being eroded away. In some cases hummocks can become stabilized. This happens when they are sheltered from strong winds (because of the development of vegetation or other dune forms to windward), or if stabilizing vegetation develops quickly enough to prevent erosion.

**Sand plain**

A broad expanse of sand, relatively level to gently sloping, is a sand plain. The surface may
be irregular but there are no pronounced changes in relief. It is relatively dry and sand movement is minimal (usually because of sheltering vegetation). Sand plains can develop to windward of retention ridges and parabola-dune complexes or result from extensive blowout activity. Vegetation develops on these areas, but establishment is much slower than that which occurs on deflation plains.

Swale

Low-lying areas between sand ridges are swales. They are wet, with standing water common in winter, and frequently all year long. Swales are common in localities where a prograding shoreline has resulted in a series of relatively closely spaced sand ridges. Successive ridges produced by the marginal ridges of adjacent parabola dunes may also have swales between them. The depressions between successive oblique dunes, if wet, are also a type of swale.

Remnant forest mound

Remnant forest mounds have their origin in the degradation of previously stabilized dune forms. They vary in size from 200 to 500 m in diameter and up to 50 m high. Old-growth forest covers the top while younger vegetation develops on the eroding (and in some cases, accreting) sides. The forest on the top of one of these mounds was calculated to be at least 500 years old.

Dune lake

Bodies of water are found both on the dunes and along the inner margin of the dunes at the base of retention ridge slipfaces. These latter are called marginal lakes, and they originate either through the damming of small streams by the dune sands moving inland, or by dune groundwater flowing out of the dunes into the depression between the sand mass and the mountain front. These lakes can range in size up to 1100 ha with depths to 15 m. Dune ponds and small dune lakes form on the deflation surfaces and in the swales between dune ridges, and usually are the result of the dune surface intersecting the groundwater table. The largest reach 100 ha in area and are relatively permanent. Many smaller ponds are ephemeral, drying up toward the beginning of the summer season and appearing again the following winter. They can range in size from a fraction of a hectare to about 5 ha in area.

Dune systems

A dune system is characterized by a set of dune forms recurring in a pattern over the dune landscape and by the nature of the coastal landform they occupy. Certain dune forms tend to be typical of a given system, but they are not restricted to that system.

Parallel ridge system

This system is best developed on the prograding shoreline north and south of the Columbia River. Sunset Beach Road, just north of Seaside, Oregon, provides an excellent cross-sectional view of this system. Its characteristic dune form is the stabilized foredune. These foredune ridges are arranged in a parallel series that extends over 2 km inland in some places. Development of the system began when the sea reached its maximum elevation after the last glaciation, about 6000 years ago.

Parallel ridge systems are also found where a series of retention ridges have become stabilized. They usually represent the culmination (through stabilization) of a long period of sand activity in which the sand of a number of dune forms eventually becomes incorporated into a single retention ridge. Rejuvenation can result in the development of another retention ridge, parallel to the first, which also can become stabilized.

Parabola dune system

Parabola dunes are the dominant dune form in these systems. They are the result of unidirectional effective winds, both northwesterly and southerly. Many are associated with rivers and bays. Where successive parabola dunes have been formed, stabilized remnants of earlier dunes are usually present. An excellent example of such a system is found at Sand Lake, on the south side of Cape Lookout on the Oregon coast (Fig. 23.5). Where many small parabolas constitute the system (as on the north coast of California at Arcata) the adjacent marginal ridges may merge and erode away. A form of a retention ridge would then result.
Fig. 23.5. Map of the parabola dune system at Sand Lake, Oregon (just south of Cape Lookout). Four active parabola dunes (I-IV) are moving within and over the stabilized dune ridges of two older parabola dunes. The lack of Ammophila arenaria north of the campground is due to severe disturbance by off-road vehicles. The vegetation beyond the limits of the dune system is mostly coastal forest (Tsuga-Picea).
Transverse ridge system

Extensive areas of transverse dunes and massive oblique dunes are the most common forms in these systems. They are found primarily along the south-central Oregon coast where conditions are favorable to the accumulation of large amounts of sand. Good examples can be seen north and south of Reedsport, Oregon (Fig. 23.6). Marginal lakes are also characteristic of this system because of the wide front over which the sand has moved inland. Most of the remnant forest mounds are also found in these systems. Figure 23.7 gives a cross-section through a typical transverse ridge system with oblique dunes.

Barrier dune system

These dune systems are defined by their location on sand spits, barrier dunes, or peninsulas formed across the mouths of bays. They can range in width from several hundred meters to several kilometers, and in length from three to over ten kilometers. There is no typical set of dune forms.

Fig. 23.6. Transverse dune system, vertical aerial photograph. South is at the top. Ground features from left to right: US Highway 101, forested inner dune margin with blow-outs, retention ridge, oblique dune zone, forested remnants, transverse ridge zone, deflation plain, foredune, and beach. The path of the northwest summer winds lies diagonally across the photograph from lower right to upper left. Area is just south of Florence, Oregon. Distance from the beach to the highway is about 3 km. (U.S. Geodetic Survey photograph. October, 1955.)
The foredune, sand plain, deflation plain, blowout, and swale are the most common forms seen. Netarts Bay, just north of Cape Lookout on the Oregon coast, has an excellent example of a barrier dune system on a bay spit. On larger peninsulas, such as the Samoa Peninsula on Humboldt Bay near Arcata, California, parabola dunes and transverse dunes can occur.

**FLORA, VEGETATION AND FAUNA OF THE SAND DUNES**

**Flora**

The vascular plant flora of the coastal dunes appears to be remarkably uniform from the Queen Charlotte Islands to Cape Mendocino. However there is a subtle shift in the flora due to the climatic shift at 46° N noted above. This shift is not reflected in the flora until 43°30' N, near Coos Bay, Oregon. While not abrupt, it does mark the southern limit of the Subarctic Beach Flora and the northern limit of the Dry Mediterranean Beach Flora (Barbour et al., 1975; see Chapter 24). This boundary also corresponds closely to the northern boundary of the California Floristic Province (Howell, 1957) and the boundary at 44°N given by Hitchcock and Cronquist (1973) for the northward extension of the Klamath Flora.

The significance of this boundary can be seen in the presence or absence of species. The dune species *Phacelia argentea* and *Artemisia pyrocerephala* do not occur north of Coos Bay while *Carex macrocephala* occurs only north of this point. Some species occur throughout the region but are more abundant in one part or the other. *Picea sitchensis*, for example, is much more common in the forests of the north while *Baccharis pilularis* is a major component of the shrub communities in the south.

A number of species are endemic to this coastal region. Breckon and Barbour (1974) and Barbour et al. (1975) list 10 species and subspecies as "maritime endemics" (restricted to maritime habitats), and one species as "inland-maritime endemic" (occurs both in maritime and inland habitats, but endemic to western North America) (Table 23.2). Most of these endemic species range

**TABLE 23.2**

Latitudinal ranges for the endemic flowering plant species of the sand dunes of the northwestern coast of North America. (From Barbour et al., 1975 and Breckon and Barbour, 1974; see also Chapter 24.)

<table>
<thead>
<tr>
<th>Species</th>
<th>Limits, Northern Latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>North</td>
</tr>
<tr>
<td><strong>Maritime endemic</strong></td>
<td></td>
</tr>
<tr>
<td><em>Glehnia littoralis</em></td>
<td></td>
</tr>
<tr>
<td>ssp. leiodocarpa</td>
<td>60°</td>
</tr>
<tr>
<td><em>Ambrosia chamissonis</em></td>
<td>54°</td>
</tr>
<tr>
<td><em>Abronia latifolia</em></td>
<td>54°</td>
</tr>
<tr>
<td><em>Lathyrus littoralis</em></td>
<td>54°</td>
</tr>
<tr>
<td><em>Poa douglasii</em></td>
<td>54°</td>
</tr>
<tr>
<td><em>Agrostis pallens</em></td>
<td>54°</td>
</tr>
<tr>
<td><em>Tanacetum douglasii</em></td>
<td>49°</td>
</tr>
<tr>
<td><em>Polygonum parvuchia</em></td>
<td>48°30'</td>
</tr>
<tr>
<td><em>Ambrosia chamissonis</em></td>
<td>47°30'</td>
</tr>
<tr>
<td>ssp. canadensis</td>
<td></td>
</tr>
<tr>
<td><em>Camissonia cheiranthifolia</em></td>
<td>43°30'</td>
</tr>
<tr>
<td><strong>Inland-maritime endemic</strong></td>
<td></td>
</tr>
<tr>
<td><em>Agoseris apargioides</em></td>
<td>42°</td>
</tr>
</tbody>
</table>
the full length of the northwest coast with their southern limits just south of Cape Mendocino where another climatic shift, from mediterranean to semi-arid, takes place between 37° and 36°30'N latitude. All of the species are found in unstable sand habitats, either in the hummock/foresetdune zone or blowout/shifting sand areas inland from the foredune.

The entire coastal region is included in the *Picea sitchensis* zone of Franklin and Dyrness (1973) in which *Picea sitchensis* and *Tsuga heterophylla* are the dominant forest climax species. Because of the variability and instability of the sand dune environment, this climax forest is rarely present. Instead, a mosaic of plant communities is seen, reflecting both a wide range of habitats and a successional sequence toward the zonal climax.

Of the nearly 200 commonly occurring vascular plant species (see Munz and Keck, 1959) found on the sand dunes, only the pioneer species tolerant of sand burial are unique to dune habitats. Once stabilization has occurred, species generally common in the area become established, including those of the zonal climax. Bryophytes and lichens do occur, but in general are not significant components of the plant communities.

**Plant communities**

The native pioneer foredune vegetation is composed of the *Elymus (Leymus) mollis–Abronia latifolia* community (1). These species, along with others such as *Ambrosia chamissonis, Calystegia soldanella,* and *Tanacetum douglasii* form the low hummock complexes (foresetedunes) that used to be widespread along the coastal dunes just above the high-tide line. This community occurs in its pure form only in a few places today, and nowhere is it extensive.

The upper beach and active sand habitat has been largely taken over by the *Ammophila arenaria* community (2). There are very few associated species in the places where the sand is most active (the windward side and the crest of the foredune). In the north *Lathyrus japonicus* is most common and in southern Oregon and northern California *Lupinus arboresus* is distinctive in the community. Occasionally the native hummock species will occur in this community.

On areas back from the foredune zone and on sand plains where sand is a little less active, a group of species pioneers that rapidly covers the ground surface rather than forms hummocks. This *Poa douglasii–Lathyrus littoralis* community (3) has distinctive associates: *Carex macrocephala, Erigeron glaucus, Erigonum latifolium, Glenha leiocarpa, Poa confinis,* and others. Plant cover may range from very open to completely closed. *Ammophila arenaria* can become established in this community in its early stages when sand is more active, or the community can become established in stands of *Ammophila* that have begun to deteriorate because of the lack of blowing sand. Both because of the spread of *Ammophila,* and because of increased off-road vehicle activity, this community does not occur extensively anywhere.

Where sand is shifted by the wind only slightly, such as on sheltered sand plains, old blowouts, or other disturbed areas, the *Festuca rubra–Solidago spathulata* community (4) develops. This community is found primarily in the north of the region, while in the south, the *Artemisia pycnocephala–Solidago spathulata* community² is more common in similar habitats. Other species found in this community include *Lupinus littoralis, Polygonum paronychia,* and *Fragaria chiloensis.* The species of this community will also be found in deteriorating *Ammophila arenaria* stands.

The damp, stable sand surfaces of the deflation plains provide an ideal habitat for the rapid development of plant communities. In places where there is ample moisture, but no standing water during any part of the year, the *Festuca rubra–Lupinus littoralis* community (6) develops. This is the typical “meadow” of the sand dunes, and is the community that is probably richest in numbers of species, almost all of which are also common to adjacent non-dune meadows.

Where water stands on the surface for one to three months during the winter, the *Juncus falcatus–Trifolium wormskjoldii* community (7) is found. This community is also high in numbers of species. Where water stands four to six months of the year, the *Carex obtusa–Potentilla pacifica* community (8) occurs.

¹The number in parentheses is the community number for purposes of reference to the successional diagram in Fig. 23.8. Species of the same stratum are separated by a dash (–); those of different strata by a slash (/).

²Not shown on Fig. 23.8.
In many of these communities individual shrub and tree seedlings will be present quite early. Several types of shrub community can develop. The *Gaultheria shallon*–*Vaccinium ovatum* community (11) will occur on drier sites (sand plains, slopes and ridges) mainly in the north of the region, while in northern California the *Baccharis pilularis*/*Scrophularia californica* community\(^1\) is found on the drier sites with *Lupinus arboresus* as a frequent associate. On quiet sand plains and inactive blow-outs, the unusual *Arctostaphylos uva-ursi*/*Racomitrium canescens* community (13) can be found. Because such areas are favored by off-road vehicle enthusiasts, the occurrence of this community is becoming very limited. In the wetter areas, where water stands to some extent during the year (deflation plains and swales), the *Salix hookeriana*–*Myrica californica* community (14) is most common. In all four of these communities seedlings of *Pinus contorta* are almost always found, while many of the wetter sites will also have *Picea sitchensis* seedlings.

The most common forest community is the *Pinus contorta*/*Rhododendron macrophyllum* community (15) developing mostly on the higher, well-drained sites. When mature, at about 100 years, these forests have open canopies, and it is not unusual to find *Pseudotsuga menziesii* both as young and canopy trees. In northern California *Rhododendron macrophyllum* is absent in these forests, but *Garrya elliptica*, infrequent in the north, is common. The *Pinus contorta*/*Arctostaphylos columbiana* community (16) is frequently encountered on sandridge tops and other dry sites where the forest canopy is open. *Cladonia rangiferina* is commonly present.

On the deflation plains, a *Picea sitchensis*–*Pinus contorta*/*Salix hookeriana*/*Eurhynchium oreganum* community (17) develops. The relative amounts of *Picea* and *Pinus* present in any stand will vary considerably, depending on such factors as seed supply and exposure to wind and salt spray. Usually the *Pinus* stand is initially dense and provides shelter to the *Picea* seedlings which are not tolerant of salt spray. In these situations, *Picea* becomes evident when it reaches about 4 m in height, and generally begins growing more rapidly than *Pinus*.

Where water stands a good part of the year, a *Pinus contorta*/*Carex obnupta* community (18) is commonly found. *Sphagnum* spp. can occasionally be found in these places. Also in wet habitats, but where acid bog conditions have developed, a *Thuja plicata*/*Ledum glandulosum* community (19) can occur. *Sphagnum* is frequently present, and, in a very few places, *Darlingtonia californica* has become established.

Given sufficient time, a climax-type forest can develop. Only small areas exist on the present-day dunes. On the higher, drier sites, the *Pseudotsuga menziesii*/*Rhododendron macrophyllum* community (20) eventually develops from the initial *Pinus contorta* forest. *Tsuga heterophylla* is a frequent associate. In northern California *Abies grandis* occurs with the *Pseudotsuga* on the dunes. On the moister areas the zonal or climatic climax can develop: the *Tsuga heterophylla*–*Picea sitchensis*/*Gaultheria shallon*/*Blechnum spicant* community (21). Very little of this type forest is found on the dunes.

The successional relationships that can be traced among these communities are illustrated in Fig. 23.8. Some of these relationships may be easy to see in the field, while others are a bit more difficult because the "dividing line" between communities may be indistinct or because the communities occur in patchwork-like mosaics. The *Ammophila arenaria* and the *Elymus (Leymus)* mollis–*Abronia latifolia* communities are a sort of "pioneer climax" because of the instability of the habitat. Vegetation becomes established; hummocks form and then erode away to re-form elsewhere. Occasionally permanent stabilization takes place because erosion is reduced by the development of surrounding vegetation.

In general there are no successional relationships among the five herbaceous communities that develop on sites with varying degrees of sand activity and levels of soil moisture. However, both the *Festuca rubra*–*Solidago spathulata* community and the *Poa douglasii*–*Lathyrus litoralis* community could be succeeded by the *Festuca rubra*–*Lupinus litoralis* community if moisture conditions are favorable.

The shrub communities invariably follow on from one of the herbaceous communities. Close to the shore shrub vegetation may persist indefinitely because wind and salt spray inhibit the growth of trees. Trees may be present, but they never grow taller than the predominant shrubs. The forest communities usually succeed the shrub communi-
Fig. 23.8. General successional relationships of sand-dune plant communities on the coastal dunes of northwestern North America. Plant communities found only on dunes in northern California are not included. The number in parentheses before each plant community refers to the number of that community in the text where the standard Latin name of the community is given. The solid line shows the most common and obvious successional pathways. The dashed line shows the less-common or possible pathways.
ties, but it is not unusual for the tree species to become established in the herbaceous vegetation. When this happens thickets of either *Pinus contorta* or *Picea sitchensis* can develop that grow into older forests having a minimum of understory vegetation.

**Fauna**

The coastal dune areas provide a wide variety of habitats for vertebrate animals. In general the animals found in these habitats are the same as those found farther inland in similar habitats. The dune habitats may be generalized as beach, open sand, meadow and grassland, shrubland, forest, and wetlands (marshes, lakes, and ponds).

On the beach species of *Calidris* (sandpipers), *Charadrius* (plovers), and *Larus* (gulls) are the most common vertebrates. *Charadrius alexandrinus* nests on restricted areas along the upper beach, usually at the base of the foredune. The nesting habitat of this species has been much disturbed in recent years by off-road vehicle activity.

The commonest mammals encountered in the grassy meadows are *Citellus beecheyi* (California ground squirrel) and *Sylvilagus bachmani* (brush rabbit). Characteristic birds include *Charadrius vociferus*, *Turdus migratorius*, and small seedeaters such as *Passerculus sandwichensis* and *Carduelis tristis*. *Circus cyaneus* is a commonly seen bird of prey flying over these areas.

The shrub habitat provides cover for the larger *Odocoileus hemionus* (black-tail deer) as well as *Sylvilagus*. Common birds include *Melospiza melodia*, *Psaltriparus minimus* and *Zonotrichia leucophrys*. In the forests are found *Ursus americanus* (black bear), *Eutamias townsendi* (Townsend chipmunk), and *Tamiasciurus douglasii* (chickaree). In addition there are a number of small mammals of the genera *Peromyscus* and *Sorex* that are generally abundant but not conspicuous. There are many passerine birds, the most characteristic perhaps being *Chamaea fasciata*, wren tit (*Cyanocittta stelleri*), *Parus rufescens*, *Regulus calendula* and *R. sarrapa*.

Inhabitants of the marshes, lakes, and ponds vary according to the amount of open water, but will almost always include *Anas platyrhynchos*, *Ardea herodias* and *Castor canadensis*.

The invertebrate fauna of the dunes is poorly known. The bee fauna (superfamily Apoidea) of the coastal dunes at Humboldt Bay in northern California has been studied by Gordon (1983). His work covers floral visitation, species distributions, nesting locations, flight seasons, and abundance estimates for 43 species in 6 families. Table 23.3 provides a survey of habitat types and their plant community types with additional characteristic animals.

**SEA CLIFFS, HEADLANDS, ISLANDS, AND SEA STACKS**

Almost the entire northern part of this coast, from northern Washington to the north of British Columbia, is characterized by steep slopes and vertical cliffs that drop directly into the sea. To the south, in addition to sea cliffs, there are headlands, promontories, islands, and sea stacks.

Typical of the headlands is Cascade Head (45°5′N) on the central Oregon coast. It has vertical sea cliffs rising more than 150 m above the sea and a shore front of more than 8 km. The basalt mass that forms it covers an area of about 18 km² and its highest point lies at 238 m above sea level.

A little farther north, Cape Lookout (45°20′N) is a narrow basalt promontory jutting out to sea for a distance of 2.8 km. Its south side is a vertical cliff 250 m high.

The offshore islands and sea stacks range in size from about 15 ha to bits of rock a fraction of a hectare in area. Many exceed 30 m in height; others are constantly flooded by surf. They take the form of flat-topped or tilted islands, caves, arches, and vertical pinnacles. Along the Oregon coast there are 56 named islands and island groups, totaling about 210 ha in area. Along the Washington coast there are some 870 islands and rocks with a total area of about 61 ha. Typical of these offshore islands is a group of three relatively large and three smaller islands known as Three Arch Rocks, lying about 1 km offshore near Oceanside, Oregon, just north of Cape Lookout.

The primary habitat variables for plants are soils and topography. On the broad headlands and

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1 Bird names follow that shown in the 34th supplement of the American Ornithologist's Union check-list of North American birds.
### TABLE 23.3

Characteristic animals of the dune habitats along the northwestern coast of North America

<table>
<thead>
<tr>
<th>Habitat and associated plant communities</th>
<th>Habitat conditions</th>
<th>Characteristic animals of the dune habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open, active sand</td>
<td>Foredune and hummock</td>
<td><em>Bembix americana conata</em></td>
</tr>
<tr>
<td><em>Elymus mollis</em>—<em>Abronia latifolia</em></td>
<td>Foredune and hummock</td>
<td><em>Emphoropsis miserabilis</em></td>
</tr>
<tr>
<td><em>Ammodilia arenaria</em></td>
<td>Active sand</td>
<td><em>Polyphylla decemlineata</em></td>
</tr>
<tr>
<td><em>Poa douglasii</em>—<em>Lathyrus litoralis</em></td>
<td>Open, inactive sand</td>
<td><em>Megachile wheeleri</em></td>
</tr>
<tr>
<td>Meadow and grassland</td>
<td>Inactive sand, northern California</td>
<td><em>Passerculus sandwichensis</em></td>
</tr>
<tr>
<td><em>Festuca rubra</em>—<em>Solidago spathulata</em></td>
<td>Dry meadows</td>
<td><em>Sturnella neglecta</em></td>
</tr>
<tr>
<td><em>Artemisia pycnocephala</em>—<em>Solidago spathulata</em></td>
<td>Wet meadows</td>
<td><em>Thamnophis sirtalis</em></td>
</tr>
<tr>
<td><em>Festuca rubra</em>—<em>Lupinus litoralis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Juncus falcatus</em>—<em>Trifolium wormskjoldii</em></td>
<td>Standing water</td>
<td><em>Cistothorus palustris</em></td>
</tr>
<tr>
<td>Marsh</td>
<td></td>
<td><em>Taricha granulosa</em></td>
</tr>
<tr>
<td><em>Carex obnupta</em>—<em>Potentilla pacifica</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gaultheria shallon</em>—<em>Vaccinium ovatum</em></td>
<td>Mesic sites, north of California</td>
<td><em>Turdus migratorius</em></td>
</tr>
<tr>
<td><em>Baccharis pilularis</em>—<em>Scrophularia californica</em></td>
<td>Dry sites, northern California</td>
<td><em>Zonotrichia leucophrys</em></td>
</tr>
<tr>
<td><em>Arctostaphylos uva-ursi</em>—<em>Racomitrium canescens</em></td>
<td>Dry, inactive sand sites</td>
<td><em>Psaltriparus minimus</em></td>
</tr>
<tr>
<td><em>Salix hookeriana</em>—<em>Myrica californica</em></td>
<td>Wet sites, some standing water</td>
<td><em>Peromyscus maniculatus</em></td>
</tr>
<tr>
<td>Forest</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus contorta</em>—<em>Rhododendron macrophyllum</em></td>
<td>Mesic dune slopes and plains</td>
<td><em>Sylvilagus bachmani</em></td>
</tr>
<tr>
<td><em>Pinus contorta</em>—<em>Arctostaphylos columbiana</em></td>
<td>Dry dune ridge tops</td>
<td><em>Odocoileus hemionus</em></td>
</tr>
<tr>
<td><em>Picea sitchensis</em>—<em>Pinus contorta</em>—<em>Salix hookeriana</em>—<em>Eurychnium oreganum</em></td>
<td>Wet swales and deflation plains</td>
<td><em>Junco hyemalis</em></td>
</tr>
<tr>
<td><em>Pinus contorta</em>—<em>Carex obnupta</em>—<em>Pseudotsuga menziesii</em>—<em>Rhododendron macrophyllum</em></td>
<td>Standing water</td>
<td><em>Troglodytes troglodytes</em></td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em>—<em>Picea sitchensis</em>—<em>Gaultheria shallon</em>—<em>Blechnum spicant</em></td>
<td>Dry upper dune slopes</td>
<td><em>Dryocopus pileatus</em></td>
</tr>
<tr>
<td></td>
<td>Moist deflation plains — the zonal climax community</td>
<td><em>Cyanocitta stelleri</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Scapanus orarius</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Hyla regilla</em></td>
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</tr>
</tbody>
</table>

Tops of sea cliffs the soils can be deep, relatively rich, and fine-textured. They are typically acid (pH 5.0–5.5), high in organic matter (15–20%) and total nitrogen (0.5%), and low in base saturation (10%). On cliffs and promontories the soils are generally very shallow. Bare rock is the substrate of all but the largest of the sea stacks and islands.

The zonal climax plant community, *Tsuga*—*Picea*—*Gaultheria*—*Blechnum*, is found wherever slope and soils permit (and where it has not been removed by fire or logging). Cascade Head supports a fine old-growth stand of this community. Some individual specimens of *Picea sitchensis* exceed 2 m in diameter. On seaward-facing, wind-swept slopes of the northern and central Oregon coast a type of "headland meadow" is encountered. Good examples are found on Cascade Head. A number of plant communities are present. The most important being the *Artemisia suksdorfii*—*Solidago canadensis* herbaceous community and the *Rubus parviflorus*/*Polystichum munitum* shrub community.

In southern Oregon and northern California, shoreline vegetation dominated by herb and shrub communities is much more common. Typical species on exposed seaward slopes include *Eriogonum latifolium*, *Scirpus setaceus*, and *Zigadenus fremontii*. Shrub communities are dominated by
Ceanothus integerrimus, Garrya elliptica, Rhododendron occidentale, Alnus sinuata, and Arctostaphylos columbiana.

The vegetation of the islands and sea stacks is composed mostly of low-growing herbs and shrubs. Species of Poaceae and Cyperaceae predominate on many. Dwarfed conifers may be present. Some of the larger islands have sufficient soil to support small stands of the coastal Tsuga–Picea forest.

The animals of the meadow, shrub, and forest habitats would be generally the same as those shown for similar habitats on the sand dunes. A variety of marine mammals utilize the small islands and sea-cliff caves. The most abundant is Eumetopias jubatus (northern sea lion). Zalophus californianus (California sea lion) and Phoca vitulina (harbor seal) are also present. Colonial seabirds are abundant and during the breeding season the cliffs, sea stacks, and islands may be literally covered with nesting birds. The commonest include the gulls Larus glaucescens and L. occidentalis, the cormorants Phalacrocorax penicillatus, P. auritus, and P. pelagicus. Uria aalge (common murre), and Cepphus columba (pigeon guillemot). Where soils of some depth are present, burrow nesters are common. These include Fratercula cirrhata (tufted puffin), Cerorhinca monocerata (rhinoceros auklet), Oceanodroma leucorhoa (Leach’s petrel), and O. furcata (fork-tailed petrel).

EXPLOITATION AND CONSERVATION

Like sand dunes everywhere, those of the Pacific northwest coast have been altered through human activity. Numerous small towns are located on dune lands, especially those near rivers and bays. Resort development has increased significantly in the past 30 years. Agricultural use, once quite extensive, is now minimal although the effects are quite noticeable. The headlands and promontories are generally too rugged and inaccessible for development. The cutting of timber is the primary activity on these areas.

Much of the coast is in public ownership. While disturbance and certain kinds of exploitation are not entirely eliminated, there are varying degrees of protection and management in many cases, and these lands are mostly accessible to the public.

Federal, state/provincial, and local governments are involved in this ownership. Many of the islands and sea stacks are part of the United States Fish and Wildlife Service’s wildlife refuge system. Much of Cascade Head and the sand dunes from Florence to Coos Bay, Oregon, are part of the United States National Forest system.

Naikoon Park on Graham Island of the Queen Charlotte Islands; Leadbetter Point in Washington; Netarts Spit, Cape Lookout, Bullard’s Beach, and Humbug Mountain in Oregon; and the Point St. George dunes in California are all parts of state/provincial park systems. To these examples of public ownership may be added those of private conservation organizations such as the Nature Conservancy which has preserves on Cascade Head and on the dunes near Arcata, California.

Two major forms of disturbance, both relatively recent phenomena, threaten plant and animal communities on the sand dunes. The widespread establishment of Ammophila arenaria, both because of intentional stabilization plantings and through natural spread, has caused significant changes in the active sand vegetation. Native hummock- and foredune-forming species have been replaced almost entirely by Ammophila. While not “endangered”, such species as Abronia latifolia, A. umbellata, Calystegia soldanella, Carex macrocephala, Elymus mollis, Glehnia leiocarpa, Lathyrus litoralis and Phacelia argentea are not nearly as common as they once were, and in some areas are difficult to find. Recent attempts to control or eradicate Ammophila have not been successful.

The increased use over the past 20 years of the sand dunes for off-road vehicle recreation has also resulted in severe disturbance to the active sand habitat. The intensity of this use can be seen at places like the Sand Lake dune system where, on a three-day summer holiday, upwards of 5000 vehicles may be present on the 4 km² of open sand and meadow. Such intensive disturbance can result in the almost total destruction of the foredune, hummock, and sand-plain vegetation. While such disturbance is of little consequence to Ammophila, its effect on the native plant communities is catastrophic. Of possibly even greater consequence is the destruction of habitat for invertebrates such as bees and wasps which utilize open-sand and hummock areas for both nesting and foraging.
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Distribution and Effects of *Ammophila breviligulata* Fern. (American beachgrass) on the Foredunes of the Washington Coast

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ABSTRACT


Since the turn of the century, the foredunes on the west coast of North America have become dominated by *Ammophila arenaria* due to extensive sand stabilization plantings. *Ammophila breviligulata* was planted less extensively than *A. arenaria*. However, *A. breviligulata* has come to singularly dominate the foredunes of Washington in the southern half of the state and its range extends north along the entire coast. By comparing the distribution of current *A. breviligulata* and *A. arenaria* communities with historic shorelines, it was found that this invasion occurred in the last 50 years and the locus of the invasion was determined. A comparison of foredunes dominated by *A. breviligulata* with existing *A. arenaria* foredunes shows that this colonization has had minimal impact on the species diversity of the dunes, but it has resulted in a lowering of the mean height of the foredune crests.

ADDITIONAL INDEX WORDS: *Ammophila arenaria*, dune morphology, introduced species, coastal plant communities.

INTRODUCTION

*Ammophila breviligulata* Fern. (American beachgrass) is native to the East Coast and Great Lakes Region of North America (Baldwin and Maun, 1983; Gleason and Cronquist, 1963; Olson, 1958a,b; Hitchcock, 1950; Cowles, 1899), and it has been intensively studied within this native range (Maun and Baye, 1989). It is a pioneer species adapted to dynamic coastal dune systems where it is, typically, the major dune building plant species present (Disraeli, 1984; Dunlop and Crown, 1985). It rapidly becomes senescent when dune areas stabilize and is then rapidly replaced by other species (Disraeli, 1984; Van der Valk, 1975; Eldred and Maun, 1982).

*Ammophila arenaria* (L.) Link (European beachgrass or marram grass) is a native of Europe similar to *A. breviligulata* in its adaptations to the coastal dune ecosystems. *A. arenaria* has been widely planted on the west coast of North America for dune stabilization since the early 1900's. It has become naturalized along nearly the entire coastline (Barbour and Major, 1988; Hitchcock et al., 1969; Hitchcock, 1950) and is a dominant feature in the coastal ecosystem, replacing many of the native communities in the foredune habitat (Pavlik, 1983).

Because of the overwhelming success of the *A. arenaria* plantings, there has been little use of *A. breviligulata* for dune stabilization on the west coast. Accordingly, very little information on the status of *A. breviligulata* on the west coast of North America is available. A review of this literature and the collection history leads to the conclusion that *A. breviligulata* exists on the west coast only as persistent remnant populations (Maun and Baye, 1989; Barbour et al., 1975; Barbour et al., 1976).

The only sizable planting of *A. breviligulata* that has been recorded was a part of the Warrenton Dunes Stabilization project on the Clatsop Peninsula in Oregon near the mouth of the Columbia River. The Soil Conservation Service undertook this project in 1935; and up to that time, it was one of the largest dune stabilization projects in the western United States. A nursery was established at Warrenton, Oregon, and 1,214 ha were progressively stabilized with a variety of species including *A. breviligulata* (Schwendiman, 1977). *A. breviligulata* from this nursery was also

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planted at the south end of the Long Beach Peninsula at Ilwaco (Figures 1, 2).

At present, the densest populations of *A. breviligulata* are located between the mouth of the Columbia River and Westport, 75 km to the north. In this area, *A. breviligulata* is almost singularly dominant on the foredune, the first dune landward of the beach. The dominance of *A. breviligulata* decreases beyond these boundaries to the north and south. This distribution pattern indicates that the Clatsop and Ilwaco plantings were the likely source of the naturalized populations of *A. breviligulata* now found on the Washington and Oregon coastal dunes.

The primary dispersal mechanism of *A. breviligulata* is through waterborne rhizome fragments (Maun, 1984), and the dominant current on the southern Washington coast is the northward longshore current (Phipps, 1990). If the source of the *A. breviligulata* invasion was the Clatsop and Ilwaco plantings, the longshore current would have rapidly spread rhizome fragments along the accreting shoreline of the Long Beach Peninsula allowing *A. breviligulata* to colonize the beach and replace *A. arenaria* as the dominant dune forming species.

If this scenario were the case, it should be possible to locate the transition from one *Ammophila* species to the other. Since both species have extremely low vegetative and sexual reproductive rates in stabilized dune areas (Olson, 1958a), it is unlikely that there would have been significant invasion by either population in the highly stable backdune areas. Willis (1963) found that even fertilization could not stimulate senescent *Ammophila* populations to the point of expansion.

If there is no invasion in the backdune areas and the transition zone is stable, then the border between the two communities actually represents the location of the historic shoreline or foredune crest when *A. breviligulata* replaced *A. arenaria* as the foredune’s dominant grass.

The timing of the introduction of *A. breviligulata* was determined by comparing the *A. breviligulata*/*A. arenaria* transition zone to the location of historic foredunes as determined from a chronological sequence of aerial photos. The southern portion of the Washington coast is characterized by a broad band of sand beach and dunes as far north as the Copalis River (47° 08' 00" N Lat). These dunes are examples of the parallel dune system described by Wiedemann (1984) as typical of prograding shorelines in this area. North of this point the rocky headlands are close to the beach and prevent any major dune formation (Figures 1 and 2).

The objectives of this research were threefold: to determine the source, location, and time period of the major introductions of the exotic species *A. breviligulata*; to establish the current range and habit of *A. breviligulata* on the Washington Coast; and to determine if the *A. breviligulata* and *A. arenaria* foredunes differ significantly in structure or plant species diversity.

**METHODS**

**Study Sites**

The quantitative fieldwork for the determination of the source and timing of the introduction of *A. breviligulata* and the characterization of the current *Ammophila* dunes took place on the foredunes of the Washington Coast from North Head near the state’s southern border at the mouth of the Columbia River (46° 17' 30" N Lat) north to Westport (46° 52' 30" N Lat). In addition, the distribution of *A. breviligulata* was surveyed along the western and northern coastlines of Washington as far east as Port Angeles and the north half...
of the coast of Oregon as far south as Sand Lake (Figures 1 and 2).

The Introduction of *A. breviligulata*

The localization of the *A. breviligulata/A. arenaria* transition zone on the Long Beach Peninsula at 17 transects was mapped onto a 1:12,000 scale aerial photograph series taken on 31 July 1988, one month prior to the time the measurements were taken. Initially, 21 transect locations were chosen at one mile intervals beginning at the Seaview beach access and running north to Leadbetter Point. However, four locations were eliminated due to human disturbances in the backdune area.

The historic foredune position was determined using a series of historic aerial photos (1949, 1964, 1970, 1974, and 1982). The location of the foredune for each of these years was determined at each transect and mapped onto the 1988 photo series. It was then possible to measure the distance to the east or west that each historic dune lay from the *A. breviligulata/A. arenaria* transition zone (Figure 3).

**Field Sampling**

The quantitative fieldwork on dune shape and vegetative characteristics was completed between July and October of 1988. A second series of 34 transects, 19 on the Long Beach Peninsula and 15 between Cape Shoalwater at the north edge of the mouth of Willapa Bay and Westport, were selected randomly. In addition, several transects were established on the specific dunes where *A. arenaria* was dominant. None of these transects coincided with those used for the historic shoreline study.

The foredune profile was mapped by measuring the height at 5 m intervals (survey stations) along a 50–75 m transect (depending on foredune width) running perpendicular to the foredune. This profile was used to calculate the slope, length, and height of the west face of the foredune. The transect started at the lower limit of the vegetation. This point was given an arbitrary elevation of zero m. The dune crest height was measured independently, if it did not coincide with one of the survey stations. In addition, the following data were collected at these survey stations within a 20 by 50 cm rectangular quadrat placed perpendicular to the transect line and centered on each survey stake: (a) the total number shoots of each species of *Ammophila* in the quadrat; (b) the width of the second lowest live leaf at a point 2 cm distal from the ligule on the culm nearest the southeast corner of the quadrat; (c) the number of *Ammophila* inflorescences in the quadrat; and (d) the % cover (using the 1–10 Domin Cover Class scale) within the quadrat of all plant species, vegetative litter, and bare ground.

*A. breviligulata* and *A. arenaria* generally occurred in discrete stands, and were readily distinguishable in the field on the basis of ligule length, inflorescence morphology, phenology, and foliar characteristics (Seabloom, 1991). Specimens of both species from a number of representative locations in Washington and Oregon were deposited in the University of Washington Herbarium, Seattle, Washington.

Because the transect profiles varied widely, each transect was divided into four habitat zones to facilitate comparative analysis (Figure 4). This zonal approach permits the comparison of the distinct environments present on each foredune by correcting for the specific profile of each foredune. The beach (Zone I) extends from the seaward line of vegetation east to the seaward toe of the dune; the windward slope (Zone II) extends from this
Figure 3. Location of the transition between the *Ammophila breviligulata* and *Ammophila arenaria* communities in relation to the locations of six historic foredunes on the Long Beach Peninsula.
Beach | Windward Slope | Leeward Slope | Backdune

I | II | III | IV

West

Figure 4. Four Zones of the coastal foredune.

point to just past the crest of the foredune; The leeward slope (Zone III) extends from the limit of high sand accretion just past the foredune crest to the landward toe of the dune; and the backdune (Zone IV) includes all of the area east this point.

The vegetative and dune profile data were compared between dune zones using an ANOVA followed by a Fisher's Test for Least Significant Differences to locate the sources of the detected variance. An ANOVA was also used to compare *A. breviligulata* and *A. arenaria* populations. The Simpson and Shannon indices were used to compare species diversity between dune zones and *Ammophila* communities (Brower and Zar, 1977).

RESULTS

The Introduction of *A. breviligulata*

In 0.76 of the transects, the transition between *A. breviligulata* and *A. arenaria* dominated stands occurred between the location of the 1964 and the 1974 or the 1970 and 1974 shorelines. In all but one transect, the transition zone was bounded by the 1941 and the 1974 shorelines. This one variation occurred because there was no information available prior to 1964 at that location (Figure 3).

Current Range and Habit of *A. breviligulata*

Within its current range on the west coast, *A. breviligulata* occupies two distinct habitats. First, it is the dominant vegetation on the foredunes in the quantitative study area which ranges from North Head at the southern end of the Long Beach Peninsula to Westport, where it is present in nearly monospecific stands in Zones II, III, and IV (Figures 1 and 5). On the dune systems north of Westport both species of *Ammophila* alternate as the dominant foredune species. The only sizable unmixed *A. arenaria* foredune community located in Washington was at Twin Harbors State Park south of Westport where five acres was planted in 1981 as part of a cooperative project between the Soil Conservation Service and the Washington Parks and Recreation Commission. This population now covers about 3 km of coastline.

The second niche *A. breviligulata* occupies is the area between the shoreward toe of the foredune and the lower limit of vegetation (Zone I). In this area, it creates hummocks, usually less than 2 m in diameter, along with a number of native hummock forming species, including *Ambrosia chamissonis* (silver bursage), *Cakile edentula* (American searocket), and *Abronia latifolia* (yellow sand-verbena).

In this more marginal habitat, *A. breviligulata* can be found along the entire Washington coast as far north as Shi Shi Beach and south to Sand Lake in Oregon, although its frequency decreases markedly at the northern and southern limits of this range. *A. breviligulata* can also be found scattered on sand bars and spits in Willapa Bay and Grays Harbor, although this habitat is dominated by the native *Elymus mollis* (American dune-grass) (Figure 1).
Neither species of Ammophila was located along the northern edge of the Olympic Peninsula, but *A. breviligulata* is present at Port Townsend and both *A. breviligulata* and *A. arenaria* are present in the San Juan Archipelago (Figure 1).

Field observations of the *A. breviligulata* population on the Long Beach Peninsula distinguished three distinct geographic units on the basis of dune shape and vegetative characteristics. The South Unit extends from North Head to Long Beach and is characterized by a low foredune with minimally developed beach plant communities characterized by *Cakile edentula*. The Central Unit extends from Long Beach, north to Ocean Park and has a low *A. breviligulata* foredune somewhat similar to the southern Unit; however, Zone I in this Unit has a well developed vegetative community dominated by *Ambrosia chamissonis* with *Cakile edentula* and *Abronia latifolia* as associated species. The North Unit extends from Ocean Park north to Leadbetter Point and has a steep foredune of *A. breviligulata* with little or no beach vegetation (Figure 2).

An ANOVA comparison of these three geographic units showed that their foredunes differed significantly in height of the crest, length of the windward face, and slope of the windward face. In all three parameters, the only equivalency was between the height of the dunes in the South and Central Units (Figure 6). The species diversity of the plant communities in these three Units was not found to be significantly different (Figure 7).

The percent cover of live *A. breviligulata* plants and vegetative litter increases markedly from the beach to the dune, but remains constant on the entire foredune (Figure 8A-F). Stem density reaches its maximum on the seaward slope of the dune in Zone II (Figure 8B) and flowering occurs almost entirely in Zone I (Figure 8C). Leaf width also appears to be an indicator of the vigor of the individual plants since it diminishes steadily with increasing distance from the beach. The width remains equivalent in Zones I and II but drops consecutively in Zone III and again in Zone IV (Figure 8D). The presence of bare ground in the transects drops as the cover value of *A. breviligulata* increases and the individual vigor of the plants is declining (Figure 8E).

This decrease in the vigor of the Ammophila stands was paralleled by an increase in species...
diversity in the stable backdune areas as compared to the high depositional environment of Zones I and II (Figure 9).

Comparison of *A. breviligulata* and *A. arenaria* Foredunes

A comparison of the foredune communities dominated by *A. breviligulata* versus those dominated by *A. arenaria* showed equivalent species diversity indices in all the Zones except Zone II (Figure 10). In this Zone, *A. arenaria* foredune communities have a slightly higher species diversity than the *A. breviligulata* dominated foredunes. Both the Simpson and the Shannon indices show this difference at the same confidence level.

The overall stem density between the *Ammophila* species was compared over the entire set of samples. All of the samples with density values of zero were excluded from this comparison. This was done in order to compare mean stem density within a stand rather than the importance of the species in the study area as a whole. The stem density was significantly (*P = 0.012*) greater for *A. arenaria* (203 stems/m²) than for *A. breviligulata* (79 stems/m²).

Comparing the means of the three dune shape parameters for the entire population of foredunes showed that the population of *A. arenaria* dunes, which had a mean elevation of 4.52 m, were significantly taller than the *A. breviligulata* dune which had an overall mean of 2.82 m. However, while the *A. breviligulata* dunes were only 67% as long as the *A. arenaria* dunes, the ANOVA failed to detect a difference between the two populations (*P = 0.147*). The slope of the windward face of the dunes associated with both species of *Ammophila* was nearly identical and there was no difference detected in the ANOVA (Table 1).

**DISCUSSION AND CONCLUSIONS**

The current locus of *A. breviligulata* on the west coast supports the conclusion that the colonization source was the Clatsop and Ilwaco plantings which began in 1935. This conclusion is in accord with the timing of the colonization of the Long Beach Peninsula foredunes as determined by examining the distribution of *A. breviligulata* and *A. arenaria* in relation to the location of historic shorelines. These findings indicate that *A. breviligulata* replaced *A. arenaria* as the primary foredune colonizing species between 1941 and 1974, and it is most likely that the majority of the colonization occurred in the ten year period from 1964 to 1974 (Figure 3).

The maximum stem density in Washington populations (Figure 8B) occurs in a similar successional stage and within the range of values given for stands along Lake Michigan, which range from 110 to 150 stems/m² and the cover values of 50 to 59% (KRAJNYK and MAUN, 1981; OLSON, 1958a). However, flowering occurs almost entirely in Zone I in Washington (Figure 8C) while on Lake Erie flowering reaches its peak in the adolescent growth phase when stem density is the highest (KRAJNYK and MAUN, 1981). This is equivalent to Zone II where the flowering rates were low for the Washington populations (Figure 8C).

While the overall % cover of *A. breviligulata* shows a marked increase from the beach to the dune, the cover values remain relatively constant on the foredune proper in Zones II, III, and IV (Figure 8A). However, the vigor of the individual
plants diminishes as indicated by decreasing leaf width and depressed vegetative and sexual reproduction (Figure 8B,C,D). *A. breviligulata* maintains a constant high cover value as the dune matures by replacing stands comprised of highly vigorous and reproductive individuals with scattered senescent plants interspersed in dense mats of litter (Figure 8E and F).

This is typical of East Coast populations where stands in areas with heavy deposition have high individual vigor with patchy distribution, and those populations in stable or erosional areas have a more even distribution of less vigorous plants (Disraeli, 1984).

Thus, the overall ecology of *A. breviligulata* on the west coast in its range as an exotic resembles that within its native range, with its vigor highly dependent on sand deposition and with this dependence manifesting itself in a series of successional changes reflecting a gradual decline in the reproductive vigor of the stand and its constituent individual plants. This decline allows other species to invade the senescing *Ammophila* community, increasing the species diversity (Figure 9). This successional pattern of the west coast populations of *A. breviligulata* is analogous to the growth phases described in the Great Lakes Region (Eldred and Maun, 1982; Krajnyk and
and in North Carolina (Van der Valk, 1975) with the exception of the location of the highest rates of sexual reproduction.

It is likely that the replacement of A. arenaria by A. breviligulata in the role of foredune colonizer had little effect on the overall species diversity. The only significant difference between the A. breviligulata population and the A. arenaria population was in Zone II where both the diversity indices showed that A. arenaria had a slightly higher diversity. It is likely that this is a result of the prevalence of the A. arenaria/Lathyrus japonicus (maritime pea) association in this zone. L. japonicus is one of the few plant species which can maintain a moderately high cover value in Ammophila dominated dunes, and it is not as common in the A. breviligulata dominated dunes as it is in those dominated by A. arenaria.

Although there was little difference in species diversity between the foredunes of the two Ammophila species, the shape of the foredune associated with each species was significantly different. The difference total crest height was the only measure of dune shape which this study was able to detect. However, the mean lengths of the windward face of the two populations appear to be quite different, and it is likely that the failure to discern a difference in the length of the windward face represents a Type I error due to the limited availability of A. arenaria foredunes in the study site (n = 6) (Table 1).

The greater height of the A. arenaria dunes is probably attributable to two factors. First, it has a higher sand trapping potential created by a higher stem density than A. breviligulata; and, secondly, its leaves are more persistent in the winter due to their more erect growth and tighter inrolling. The highest levels of sand movement occur as a result of high winter winds (Wiedemann, 1984), and the more persistent leaves of A. arenaria allows them to continue entrapping sand during this period when potential deposition is...
Table 1. Comparison of the means of three dune characters of Ammophila breviligulata and Ammophila arenaria foredunes.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Ammophila breviligulata</th>
<th>Ammophila arenaria</th>
<th>Significant at α = 0.01</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crest height</td>
<td>2.817 m</td>
<td>4.516 m</td>
<td>Yes</td>
</tr>
<tr>
<td>Distance to crest</td>
<td>15.637 m</td>
<td>23.330 m</td>
<td>No</td>
</tr>
<tr>
<td>Slope (height:length)</td>
<td>0.261</td>
<td>0.259</td>
<td>No</td>
</tr>
</tbody>
</table>

the highest. A. breviligulata's leaves tend to die back and become flattereded into mats early in the winter where they are quickly buried by sand deposition.

MANAGEMENT IMPLICATIONS

The conservation of native plant communities is not affected differentially by either species to a degree which would warrant in management strategies. Both species of Ammophila depress species diversity to a very high degree and are a serious threat to the existence of diverse native plant communities. However, the species' effects on dune shape do have management implications.

The difference in the shapes of the Ammophila dunes affects structural and aesthetic characters of the foredune. The lower A. breviligulata dune may be more susceptible to breaching during storm or flood events. If this is true, then the introduction of A. breviligulata may have placed the coastal communities of southern Washington at a higher risk to flood or erosion damage. Conversely, local residents may appreciate more visual access to the beach when their houses are located behind an A. breviligulata dune. This may result in a lowered incidence of illegal dune grading which immediately increases the risk of a damaging flood event, and causes a funnelling of wind which can cause weathering on neighboring structures. It may be that an unbreached A. breviligulata dune may provide a better balance between protecting coastal communities and allowing visual access to the beach than a tall dune which is regularly breached by illegal grading.

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The *Ammophila* problem on the Northwest Coast of North America

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Abstract

In the 125 years since its introduction *Ammophila arenaria* (L.) Link has spread along the entire west coast of North America. This has resulted in the development of a high, wide foredune dominated exclusively by *Ammophila*. On the central Oregon coast there is no evidence of a foredune existing prior to the introduction of this species. Because this large foredune blocks virtually all inland movement of beach sand, it is thought that the spectacular winter transverse dunes of the central Oregon coast will rapidly deteriorate and stabilise, resulting in the loss of their scenic and recreational values. There is much evidence that the dune landscape of this coast has gone through several major cycles of stabilisation and rejuvenation since sea level reached maximum elevation after the last glaciation. Since there are several native plant species capable of building a well-developed foredune, the absence of a foredune might be explained by this local coastline history. At present the highly invasive and aggressive *Ammophila* has out-competed the native species and has drastically reduced their habitat. The biology of *Ammophila* is reviewed and the efforts to control or eradicate the species are discussed. It is suggested, for management purposes, that *Ammophila* will not significantly alter the natural stabilisation-rejuvenation cycles. On the other hand, native foredune plant communities will become increasingly uncommon, and efforts should be made to preserve examples of these diverse and highly specialised communities.

Keywords: *Ammophila*; Dunes; Control; North America; Vegetation

1. Introduction

Extensive sand dunes occur along the Pacific Northwest coast of North America from Cape Mendocino (L.40°N) north to Vancouver Island (L.49°N), a distance of about 1000 km (Fig. 1). These dune areas range in size from a few square kilometres at the mouths of rivers to sand sheets extending continuously up to 60 km along the coast and reaching 4 km inland. There is active sand on almost all of these areas, with natural vegetative stabilisation taking place in all of its seral forms (Wiedemann, 1984; Wiedemann, 1993).

The maritime climate of this region is mild and remarkably uniform. The mean annual temperature varies from 10.0°C in the north to 11.2°C in the south. Average summer temperatures are no higher than 15.1°C; average winter temperatures are no lower than 5.6°C. Mean annual precipitation, all as rainfall, ranges from 91 cm (south) to 148 cm (north) with 80% occurring in the winter months. Cloudy skies and fog occur on more than half the days of the year. The wind regime is predominantly onshore. In summer (May to September) it is continuous and...
strong from the northwest; in winter (November to March) winds occur as very strong, low pressure storms from the south and southwest (Cooper, 1958).

The dune vegetation consists mostly of seral meadow, shrub, and forest plant communities, the species composition determined by sand stability and the availability of moisture (Wiedemann, 1966; Wiedemann, 1984; Kumler, 1969). The stable Climax communities are found in only a few locations of long-term sand stability.

Sand supply, wind regime and vegetation have resulted in the formation of many characteristic dune forms (Wiedemann, 1984). The very large parabola dune systems (Wiedemann, 1990) and the massive winter transverse dunes (Hunter et al., 1983) are unique features of these coastal dunes. The parabola dunes occur at the mouths of rivers and in places where unidirectional winds predominate. They range up to 4 km in length with 1.5 km between the marginal ridges. Extensive, well-developed parabola dune systems occur at Sand Lake, Oregon, and at Arcata, California.

The winter transverse dunes are formed by winter storm winds (Fig. 2). These dunes can reach 60 m in height (base to crest), are up to 2000 m long, and are spaced about 300 m apart in the area of their occurrence between Florence and Coos Bay, Oregon. These dunes are included in the Oregon Dunes National Recreation Area (administered and managed by the U.S. Forest Service) and are highly valued for their scenic qualities and opportunities for recreation (hiking and 'dune buggy' driving).

![Diagram of the Northwest Coast of North America](image)

Fig. 1. Northwest Coast of North America. Localities mentioned in the text: winter transverse dunes between Florence and Coos Bay; Tenmile Creek just north of Coos Bay; Sand Lake just south of Cape Lookout; the Clatsop Plains on the south side of the mouth of the Columbia River; and Humboldt Bay at Arcata. Blackened areas indicate major sand dune systems.
2. The *Ammophila* problem

Over the past several years, managers of publicly owned lands (such as the Oregon Dunes National Recreation Area) have become concerned with the spread and increasing dominance of exotic plant species. One of these is *Ammophila arenaria* (L.) Link, a European species introduced to the west coast of North America in 1868 and for the next 100 years planted widely for stabilisation purposes (Fig. 3a). It is felt to have such a significant negative impact on natural physical and biotic dune processes, that large areas of scenic moving dunes are in danger of stabilisation and that native plant communities are threatened with extinction. The purpose of this paper is to examine these concerns and to discuss them in the light of the natural physical processes of dune stabilisation and rejuvenation and the ecology of *Ammophila arenaria*. The paper concludes with an evaluation of current management practices and plans related to these concerns.

The foredune, the ridge of sand along the upper beach above the mean high tide line, is of particular interest to this discussion. It is formed by the accumulation of sand in vegetation that is tolerant of sand burial. This vegetation is dominated at present almost exclusively by *Ammophila*. Cooper (1958) asserts that there was either no foredune, or only a weakly developed one, on the Oregon coast prior to the introduction of this species. Aerial photographs taken in the 1930s show little or no vegetation at the high tide line along the central Oregon coast (Wiedemann, 1966). This apparent absence of a well-developed foredune prior to the spread of *Ammophila* is somewhat mysterious since there are a number of native plant species capable of producing such a beach ridge. While there is considerable evidence that these species have played a very important role in foredune formation in the past (Rankin, 1983), only scattered remnants of a 'native plant foredune' can be found along the coast today (Fig. 3b). It must be concluded that the present strong, high (up to 10 m) foredune has been formed primarily by *Ammophila*. As a result this species has largely replaced the native foredune building plant communities.

Two concerns have arisen as a result of the successful naturalisation and spread of *Ammophila arenaria*. The first is reflected in management plan-
Fig. 3. Foredune ridges. (a) Formed by *Ammophila arenaria*. (b) Formed by native plant species.
ning documents and press reports which imply that
the imminent loss of the large winter transverse dune
landscape is the direct consequence of the establish-
ment of this species. In its draft environmental im-
pact statement, the Siuslaw National Forest (1993, p.
IV–15) declares, ‘The general process of sand scour
and deflation plain formation can only be reversed
by destroying the foredune. If [the present rate of
encroachment] continues, the open sand that exists
today will be essentially vegetated and stabilised
within 50 years.’ In a newspaper article, Smith (1993)
publicises this dramatic prediction, ‘Encroachment
by the beachgrass (Ammophila arenaria)... also
means extensive loss of recreation areas.’

This conclusion is based on the assumption that
the active coastal sand dunes, especially the massive
winter transverse dunes, owe their origin and mainte-
nance to a continuous supply of sand from the beach.
The reasoning behind this conclusion is that the
establishment of Ammophila and the subsequent
development of the foredune ridge have interrupted this
sand supply. As a result, the sand surface on the lee
side of the foredune is eroded to the water table,
forming a ‘deflation plain’ on which vegetation
quickly becomes established. This erosion/stabiliza-
tion process continues until the dunes, in effect, ‘die
of sand starvation’, their scenic and recreation values
lost forever.

The second concern grows out of the loss of
native plant communities. These foredune producing
communities (Leymus mollis-Abronia latifolia and
Poa macrantha-Lathyrus littoralis communities of
Wiedemann, 1984) have been literally crowded out
of their habitats by the aggressive Ammophila. It
would appear that these communities are in danger
of extinction (although the species of which they are
composed are probably not in such danger).

In response to these concerns, attention has been
directed to the possibility of controlling or eradicat-
ing Ammophila. In the first case above it is hoped
this would remove the foredune and permit sand to
move inland, maintaining the large winter transverse
dunes. In the second, competition from an aggressive
exotic species would be removed and active sand
habitat restored for the native species. As will be
shown, control of eradication may be feasible over

Fig. 4. Buried soil profiles on the remnant dune mass on top of Cape Kiwanda, immediately south of the Sand Lake dune system in Oregon.
The area in the foreground is a boat launching site. The numerous vehicles are associated with this activity.
small areas for specific purposes such as habitat restoration, but it is impractical as a means of slowing or reversing natural cyclic processes.

3. Dune stabilisation and rejuvenation cycles

The stabilisation of moving sand by plants and the development of a forest cover is a natural process on this coast with its mild temperatures and abundant precipitation. While at present almost all of the dune areas along the Pacific Northwest coast are active, it is obvious that stabilisation has occurred many times in the past, with large areas of the dunes covered with mature forest. Standing and fallen dead trees, some of large size, protrude from active sand or are uncovered by moving dunes. Even more impressive are the buried soil profiles, some deep and well-developed, that are exposed as older dunes are eroded by the wind (Fig. 4). Currently, stabilisation by vegetation is taking place in all seral stages, but assuming this to result from the introduction and spread of a single exotic plant species is to overlook the abundant evidence of a natural and continuous process.

That there are recurring cycles of stabilisation and rejuvenation is obvious, but the time involved in these cycles is more difficult to determine. The use of thermoluminescence and C\textsuperscript{14} dating techniques on the central Oregon coastal dunes indicates that certain dune features associated with cyclic events recur repeatedly and are relatively recent in origin. The present day dune sands rest on a bed of very compact reddish sand with a well-developed soil profile. Two thermoluminescence dates gave deposition times of 11,200 years ago (Sand Lake) and 18,300 years ago (Tennmile Creek), both times when the sea level was much lower than present. A piece of charred wood embedded in the surface of the Sand Lake profile gave a C\textsuperscript{14} date of 4820 years ago, indicating well-established vegetation at about the time the sea reached present levels (Wiedemann, 1990; Heikkinen, 1993).

As sea level rose, sand accumulated and moved inland, forming the basis of the present dune system. At Sand Lake there developed a series of massive parabola dunes, the largest over 4000 m long. One or more cycles of rejuvenation may have been involved in the formation of this dune, which is largely intact today. Two thermoluminescence dates, determined from samples taken 1700 m apart on the marginal arms of this dune under a well-developed soil profile, gave a deposition time of 1600 years ago for both samples. A sample from a younger profile, overlying the older, gave a deposition time of 1200 years ago. A series of active parabola dunes is presently moving up the axis of the system. Based on studies of their rate of movement, the four presently active dunes had their origins about 900, 670, 440, and 250 years ago (Wiedemann, 1990).

Farther south, at Tennmile Creek, a deposition time (thermoluminescence) of 1060 years ago was determined for a sand sample taken in an eroded soil profile near the eroded base of one of the large forested remnant dunes. Tree trunks and stumps exposed by eroding sands throughout this area gave C\textsuperscript{14} dates of 90, 170, 180, 390 and 570 years ago (Heikkinen, 1993). Based on his study of the forested remnant dunes and old-growth forest presently growing on undisturbed dune slopes in this area, Cooper (1958) estimated that this area was fully stabilised and forested some 300 to 500 years ago.

In a detailed study of the large, parallel ridge system on the prograding Clatsop Plains at the mouth of the Columbia River, Rankin (1983) determined ‘time lines’, placed at 2500, 1500, 800, and 400 years ago, which separated major phases of dune formation. These time lines represent the most recent time period in which the beach zone was located during either a lull in progradation, a time of coastline erosion, or a period of accretion. He relates these periods to changes in relative sea level and concludes, based on a study of dune form and size, that most accretion took place during periods of minor drops in sea level, and least when sea level was high.

Pacific Watershed Associates (1991) propose that coseismic uplift or subsidence of a dune field and adjacent sea floor can provide the mechanism for triggering dune instability and widespread sand movement. They provide evidence from the Humboldt Bay parabola dune complex in northern California of a rapid tectonic subsidence in the area of several meters, about 300 years ago, which resulted in the destruction of the foredune and adjacent vegetation. Gradual seismic rebound exposed sand de-
posits which were then blown inland to create the present dune system. Based on C\textsuperscript{14} data, similar events probably occurred 1100 and 1600 years ago in this area.

Komar and Shih (1993), studying cliff erosion along the Oregon coast, have hypothesised the occurrence of a major subduction earthquake 300 years ago that resulted in a significant drop of the shoreline, causing the erosion of cliffs and other shore features. In the period since that time, tectonic uplift has exceeded eustatic sea level rise on the southern Oregon coast and in the north at the mouth of the Columbia River, while eustatic sea level rise is exceeding tectonic uplift along the north central Oregon coast. They also report that major earthquakes were estimated to have occurred at least six times in the past 4000 years along the Washington and Oregon coast, with intervals ranging from 300 to 1000 years.

It has also been suggested that atmospheric phenomena may be involved in these dune cycles. Ranwell (1972) speculates that exceptionally stormy weather and astronomical events that affect tidal maxima might play a role. He notes that these tidal maxima occur in 1700 year cycles, the last occurring in 1443, 560 years ago. A previous maximum could have taken place 2260 years ago. Komar and Shih (1993) discuss the effect of the 1982–83 El Niño on coastal erosion and sand transport. They report that during this time stronger waves from the southwest enhanced northward sand transport.

Cooper (1967) believes these coastal dunes were completely stabilised when sea level reached its maximum post-glacial level, and that there was a long period of relative stability. He places the beginning of the current cycles of rejuvenation at about 2700 years ago. This seems to be supported by deep well drilling data from the central Oregon coast (Wiedemann, 1984) that indicates a much higher rate of sand deposition after 2340 years ago. It is possible that a major event around that time not only brought about rejuvenation, but also increased the amount of sand brought onto the beaches.

When plotted on a time scale, these various events and the interpretations of them discussed above, seem to cluster in a way that suggests four major periods of sand dune activity (Fig. 5). These clusters are centred at 400, 1050, 1650, and 2400 years ago. They represent events associated with the renewal of sand movement and subsequent stabilisation. Some of the events were probably associated with minor, local activity, which could account for some of the spread in the pattern. For the 3000 years over which dates are available, however, there is a strong suggestion of major cyclic activity affecting the entire region.

In his discussion of coastal foredune zonation, Doing (1985) notes that zonal communities, particularly those closest to the water, are vulnerable to the local history of coastlines. Rising sea levels, and the attendant retreating coast may affect the development of such communities. The apparent absence of a pre-Ammophila foredune along much of the Oregon coast might well be the result of the local history.

**Pacific Northwest Coastal Dunes**

**Stabilization and Rejuvenation Events**


![Diagram](image)

Fig. 5. Timeline of events related to cycles of stabilization and rejuvenation. Encircling dashed lines suggest clusters of events related to major periods of activity. See text for discussion of these events.
of this coast. Native plant foredunes appear to begin as low, more or less separate hummocks which over time coalesce to form a continuous ridge (Fig. 3b). The parallel ridges of the Clatsop Plains, a progressive series of foredunes, were formed very effectively in this way on a prograding shoreline. However, because of the open nature of its beginning stages, this ridge may take a longer time to develop than that formed by the more aggressive Ammophila. The work of Rankin (1983) provides indirect evidence of this. As noted previously, the central Oregon coast is an erosional coast, with a relative rise in sea level. Severe winter storms in recent times have significantly eroded the Ammophila foredune, and it is quite likely that a lower, weaker ridge could easily have been swept away by storm waves. This probably occurred frequently enough in pre-Ammophila times to prevent the establishment of an effective foredune barrier.

All of the available evidence indicates that the development of vegetation and the eventual stabilisation of active sand is a natural event along this coastline. The small areas of existing old-growth forest, with large trees up to 1 m in diameter, on 33° slopes, attest to this process. Rejuvenation and stabilisation are cyclic, but stability is maintained for long periods of time long enough for significant soil profiles to develop. In a historical context, Ammophila arenaria may, at most, somewhat shorten the time involved in the initial events, but it is not uniquely responsible for the stabilisation process.

4. Ecological impacts and control of Ammophila arenaria

Since its introduction 125 years ago, Ammophila arenaria has had a much more profound impact on dune biota than on physical processes. Thousands of hectares of west coast sand dunes were stabilised in this century, the majority located in Oregon (Reckendorf et al., 1987). One of the largest was the Soil Conservation Service’s 1215 ha planting of Ammophila at the mouth of the Columbia River in 1935–1949 (Reckendorf et al., 1987). From 1949 to 1964 the U.S. Forest Service and the Bureau of Land Management planted Ammophila on about 300 ha between the Suislaw and Silcoos Rivers just south of Florence, Oregon (Green, 1965). Such large-scale plantings are no longer being implemented, but Ammophila continues to be used as a stabiliser in some smaller coastal development projects, including occasional uses sanctioned by the California Coastal Commission (California Coastal Commission, 1989). Ammophila breviligulata Fern., a conger native to eastern and central North America and similar in biology and ecology (Maun and Baye, 1989), was also introduced to the west coast for use in stabilisation planting. In the one small area of the Washington coast where it dominates its growth and effect is very similar to that of A. arenaria (Seabloom and Wiedemann, 1994).

Many of the original stabilisation projects were initiated in response to human activities that had either created a sand erosion problem or created the need for stabilisation of naturally mobile dunes. It has not been determined to what extent these plantings were made directly into the more open foredune cover, thereby displacing native foredune vegetation. However, in addition to this direct displacement of native vegetation, undocumented displacement losses have occurred as the result of its subsequent naturalisation and spread. The spread of Ammophila into adjacent dunes can occur very rapidly. At one site in Humboldt County, California, the area occupied by Ammophila was shown to increase 574% in 50 years, from 54 to 197 ha, despite removal of more than 30 ha during this time period to make way for industrial development (Buell, 1992).

Ammophila is well suited as a biological invader. Efficient dispersal is a crucial life history feature of invasive species (Bazazz, 1986). Baye (1990) demonstrated that Ammophila has the potential to survive marine transport during dormancy over a period of at least eight tidal cycles, and concluded that exposure to cold seawater was not a limiting factor to long-distance dispersal and colonisation.

In determining the likelihood of invasion, the characteristics of a target community have been recognised to be as important as those of the biological invader (Lodge, 1993). Coastal dunes possess many of the traits believed to enhance invasibility. Foredunes, in particular, are characterised by constant disturbance, an important factor in susceptibility to invasion (Orians, 1986; Rejmanek, 1989). The vegetation on naturally colonised dunes is charac-
terised by low cover, a trait also associated with invisibility (Baker, 1985).

The biology of *Ammophila* is well documented in the literature (Wiedemann, 1987; Miller, 1988). *Ammophila* produces viable seeds that germinate readily (Bencie, 1990). It has been reported in the European literature that seeds germinate only in dune slack areas where sand is moist (Huiskes, 1977), but Bencie (1990) found *Ammophila* seedlings emerging in both foredune and inland (slack) areas. The seedlings were actually more prevalent in foredune areas, possibly due to enhanced flower production on the foredunes. Although survivorship from seedlings has not been examined, the existence of many isolated hummocks on the margins of inland dune swales demonstrates that seedlings do give rise to new individuals in these areas (Wiedemann, 1987).

In its native range, *Ammophila*’s primary mode of expansion is vegetative (Huiskes, 1979), a common means of spread on this continent as well. Once established, *Ammophila* develops a vigorous rhizome system, both horizontal and vertical. Active sand burial stimulates the production of new shoots from vertical and to a lesser degree horizontal rhizomes (Gemmell et al., 1953; Greig-Smith, 1961). In the absence of moving sand *Ammophila* declines in vigour, a phenomenon that has been attributed to a number of causes including physiological ‘ageing’ expressed as reduced root production (Wallen, 1980; Gray, 1985), and competition (Huiskes, 1980). More recently, van der Putten et al. (1988) have argued that *Ammophila* roots growing in stable sand dunes are infected by harmful micro-organisms that reduce the formation of new tillers. Fresh sand accumulation prevents the build up of these pathogens.

The purported reasons for *Ammophila*’s competitive superiority are also numerous, and include morphological as well as physiological advantages. Pavlik (1983a); Pavlik (1983b); Pavlik (1983c); Pavlik (1984); Pavlik (1985) found that in *Ammophila*, allocation among organs is directed preferentially to blades, and allocation among functions favours photosynthesis. Consequently, *Ammophila* has a higher nitrogen use efficiency than the native dune grass *Leymus mollis*, resulting in enhanced long term carbon gain. The buds of *Ammophila* tend to be localised near the parent ramet on vertical rhizomes, and therefore contribute preferentially to the vertical, rather than the horizontal, rhizome system. This results in an intensive arrangement of biomass and accounts for *Ammophila*’s phalanx-type spread.

These characteristics of the species result in the rapid and massive accumulation of sand in the foredune zone. In areas where native species create lower and more open foredunes in the early stages of development (as noted above) the effect on foredune morphology is dramatic. Heyligers (1985) noted this same dramatic effect of introduced species in the coastal dunes of southeast Australia. In addition to altering foredune morphology (at least in the early stages of foredune development), the dense, highly competitive growth of *Ammophila* drastically reduces native plant habitat.

The displacement of native vegetation by *Ammophila* has so far been demonstrated only indirectly. Barbour et al. (1976) documented a negative correlation between *Ammophila* and species diversity on 34 beaches along the Pacific Coast. Boyd (1992) further detected a differential response among several foredune species. Of five native species examined, three were negatively associated with *Ammophila* while two were not influenced. A 5-year study directly examining the effect of *Ammophila* on native species in situ is currently being conducted by The Nature Conservancy and Humboldt State University.

The rapidity of *Ammophila*’s spread combined with its apparent ability to displace native vegetation has spawned concern among ecologists, resulting in attempts to control the species as well as to restore dunes to a pre-*Ammophila* condition. The first systematic study of *Ammophila* control methods was conducted by Van Hook (1983); Van Hook (1985) at a site owned by The Nature Conservancy on Humboldt Bay. Based on the observed effect of digging, mowing, burning and the application of herbicides and rock salt, Van Hook recommended a regime of repeated digging of the above-ground portions of the plant in order to deplete underground stored nutrients.

Following these recommendations, a pilot restoration project was conducted by Humboldt State University and The Nature Conservancy at the Humboldt Bay site, using a refinement of Van Hook’s method. Isolated stands of *Ammophila*, ranging in
Fig. 6. Removal of Ammophila and restoration of native plant communities. (a) Experimental plot before treatment (digging of Ammophila). (b) Experimental plot one year after treatment ended. All native species are volunteers.
size from 50–120 m², were dug to remove both aerial portions and rhizomes to a depth of approximately 30 cm (Pickart et al., 1990). The stands were first dug in February, as the plants emerged from dormancy, and then re-treated on a regular basis through two growing seasons. Complete eradication was achieved in 2 years, with accompanying increase in native cover from a mean of 2.7% before treatment to 38% one year after treatment ended (Fig. 6a,b). No native plants were intentionally introduced, but relicual native species present in the plot at the beginning of treatment were retained, and these plants increased dramatically in cover when released from competition with Ammophila (Pickart et al., 1990).

Despite the exorbitant cost of manual removal of Ammophila, The Nature Conservancy has initiated a multi-year restoration effort to remove 4 ha of Ammophila and restore the site to the natural foredune community. Two ha of beachgrass (spread out in a patchwork fashion among the total of 4 ha) were treated in 1992. The amount of labour required for the second year of treatment was substantially greater than in the pilot project, reflecting less careful and consistent application of the treatment in a large scale project employing numerous workers. At the end of the second season (September, 1993) resprouts were sparse. Whether or not a third season of digging is required remains to be seen, but native plants have recovered rapidly in areas of removal. The cost of this restoration in 1994, $20,000 per ha, would prohibit its implementation on a massive scale. Although this site is probably more expensive than most due to its inaccessibility, the cost does not include revegetation, which may be necessary if a large, continuous area were to be denuded.

Alternative, less costly means of eradication, are still being explored. The California Department of Parks and Recreation, with the University of California at Davis, is continuing to seek a chemical means of control, focusing on the herbicide Roundup® (glyphosate). Unpublished data in the Plant Ecology Section of the University indicates that success has been limited with the exception of the soil fumigant Vapam® (metam-sodium), use of which would pose significant problems. Biologists at Bureau of Land Management in Coos Bay, Oregon, in collaboration with Siuslaw National Forest and Oregon State University at Corvallis are beginning experiments with seawater immersion (Dunham, 1993). Ammophila will be subjected to regular seawater drenchings during late spring or early summer in an attempt to determine whether the treatment affects the capacity of Ammophila to regenerate from buried buds.

5. Management considerations

In the documents related to the development of a management plan for the Oregon Dunes National Recreation Area, much emphasis is placed upon the role of Ammophila arenaria and its effect on the dune landscape. This emphasis was a response to public pressure calling for the protection and preservation of the dune landscape (as it is seen today) and native plants through the eradication of Ammophila.

It is assumed in these documents that the present foredune cuts off the sand supply to winter transverse dunes, which, as a result, will gradually disappear. To date no studies show that beach sand is necessary for the maintenance of these dunes. In 1982 a 450 m section of a foredune on the National Recreation Area was levelled with earth moving equipment, the sand pushed into the surf. Unpublished data in the Department of Geoscience, Oregon State University, indicate that very little sand has moved inland off the beach since that time. Even if sand budget studies were to show that beach sand was important to the maintenance of these dunes, the cost of removing the foredune (and with it, Ammophila arenaria), and preventing its re-establishment, would be enormous and prohibitive. In addition, as has been shown, it would be interfering with a natural cyclic process, one that would be very difficult to prevent.

The large winter transverse dunes will eventually be stabilised, but probably not in their present form. Their direction of movement, north-easterly on a north-south trending coast, is taking them gradually inland at about 3.8 m year⁻¹ (Hunter et al., 1983). Their landward ends gradually merge with a massive north-south retention ridge that itself advances very slowly eastward into established forest. Eventually these transverse dunes will be entirely incorporated into the large retention ridge, with a wide, flat, plain sloping gently seaward (west). Sand movement will slow and vegetation will move eastward across the
plain (from the present deflation plain) and up the gentle windward slope. Vegetation will also become established on the steep lee slope.

At the current rate and direction of sand movement this will take considerable time, at least as measured from the human perspective. A not unreasonable estimate might be 1000 years, a time that has little significance in the spans of human political interest and activity. For this reason, removal of *Ammophila* for aesthetic reasons, or for the purported objective of restoring natural dune cycles, should take a back seat to those efforts designed to restore threatened dune plant communities.

However, until more economical methods become available, the large scale reversal of *Ammophila*'s ecological impact on the northwest coastal dune systems is not feasible. Therefore, the prioritisation of any restoration efforts that are undertaken is extremely important. Funds expended towards this effort should be directed to projects having the greatest ecological return. These efforts should be further prioritised to give preference to projects that have a likelihood of long term viability because they are large in size or are adjacent to existing, relatively undisturbed dune communities, and those that will receive long term management and maintenance. Priority should also be given to controlling incipient, 'satellite' establishments of *Ammophila* that threaten existing natural communities (Moody and Mack, 1988).

Given the intense competition for existing resource management funds, it is imperative that these funds be expended in such a way that preservation of biological diversity is accomplished. If possible, efforts should also be leveraged with matching funds or as demonstration projects. These principles are well illustrated at The Nature Conservancy’s Humboldt Bay restoration site. Here, 4 ha of *Ammophila*-degraded foredune are being restored by manual removal of the grass. This area is a recent incursion of *Ammophila* into a 180 ha complex of pristine dune communities. Restoration by The Nature Conservancy has acted as a catalyst for additional restoration projects on surrounding properties owned by partner agencies including the Bureau of Land Management. If efforts continue, the result will be 7 km of largely *Ammophila*-free foredune, the largest such stretch in the Pacific Northwest.

References

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Coastal Foredune Development, Oregon, USA

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ABSTRACT


Early observation and records from this century indicate that a foredune was absent along the central Oregon coast in an area where topography, sand supply, and wind regime highly favored the formation of a foredune. Well-developed foredunes formed by native dune species are present both north and south of this area. With the introduction and spread of Ammophila arenaria (L.) Link, a substantial foredune (175 m wide at the base, with a crest height of 7.8 m) developed in less than 20 years. The grass also invaded existing foredunes and crowded out native dune species in much of their range. The growth characteristics of native and introduced dune species, climatic events, and coastal geologic stability all seem to be involved in these events. A topographic profile and vegetation transect was made across the foredune in 1965 at Carter Lake, just south of Florence, Oregon. The same transect was resurveyed in 1995. Changes in dune profile and in the composition of vegetation suggest that the foredune has attained a mature size and form and that permanent stabilization with native species is taking place. The habitat and growth of the native dune-forming species will remain much reduced, but they are not threatened with extinction.

ADDITIONAL INDEX WORDS: Ammophila arenaria, deflation plain, driftwood, Elymus mollis, native dune-forming species.

INTRODUCTION

Extensive dune systems occur along the Pacific Northwest coast of North America from Cape Mendocino (40°N) north to the Queen Charlotte Islands (54°N), a distance of over 1600 km (Figure 1). These systems include the parabolic dunes associated primarily with the outlets of rivers, large parallel ridge systems on prograding shorelines, and the transverse dune fields of the central Oregon coastal plains (Wiedemann, 1984; 1993). Early observers of the central Oregon coast dunes remarked on the singular absence of a well-developed foredune (upper beach ridge) in an area where all of the necessary elements were present for the formation of such a ridge (Cooper, 1958). These elements include strong near-round, on-shore winds, a plentiful sand supply, a flat coastal plain extending inland as much as 4 km along a shoreline over 60 km long, and the presence of many native dune-building plant species. The earliest aerial photographs (1939) show only a low rounded sand ridge formed around scattered clumps of vegetation and a broad line of driftwood consisting of large logs and uprooted trees.

Ammophila arenaria (L.) Link (European Beach Grass, Marram Grass), a dune building species native to Europe, was first planted in 1888 at San Francisco to stabilize the large active dunes in that area. The species spread rapidly, both naturally and through its increasing use as a sand stabilizer. By the early 1950's aerial photographs show a definite foredune ridge composed of many large, closely spaced hummocks, in most places not yet consolidated into a continuous ridge. The beginnings of a narrow, unvegetated deflation plain at the lee edge of the ridge is evident.

Figure 1. Map of the Pacific Northwest coastal dune areas (in black). The central Oregon coastal dunes lie between Florence and Coos Bay. The Carter Lake site is just south of Florence.

98024 received and accepted in revision 3 March 1998.
Errata

-the caption for Fig.2 belongs to Fig.3
-the caption for Fig.3 belongs to Fig.2
-p.47, second column, line 8: 7.3 should read 8.3
-p.48, second column, line 8: The sentence beginning with, "This driftwood..." should read: "This driftwood was the result of the extensive logging of the coastal forest in the last half of the 19th century and first half of the 20th."

By 1963 a high, wide foredune had been formed by Ammophila along the entire length of the central Oregon coast shoreline (Figure 2). A unique feature of this foredune was the presence of a "driftwood zone" along the lower part of the lower lee slope, 150 m from the beach. The adjoining deflation plain was considerably wider and had been colonized by many species of plants, including tree and shrub seedlings. Ammophila had also spread into existing foredunes along most of the northwest coast, crowding out the native dune forming species.

Up to that time no one had studied either the vegetation of the deflation plains or the development of the foredune. How large the foredune would get and what forms it would take were unknown. Equally unknown was the possible fate of the native dune-forming species whose habitat was being rapidly taken over by the introduced Ammophila. And finally, why the absence of a well-developed foredune ridge in this area? In 1965 a long-term study was initiated to seek answers to these and other questions. The purpose of this paper is to report on that part of the study dealing with the development of the foredune and its vegetation over a 30 year period.

**METHODS**

In May, 1965, a topographic and vegetation transect was established at Carter Lake on what is today the Oregon Dunes National Recreation Area. The study site is 15 km south of Florence, Oregon (43°51'30"N; 124°9'W). The transect begins at the inner edge of the vegetated deflation plain and ends at the seaward base of the foredune (approximate mean high tide level), a distance of 600 m. The two ends were marked to facilitate future study. Topographic data were taken using conventional leveling traverse techniques and equipment. Vegetation data (% cover for each species) were taken from 1 m² quadrats located at regular intervals along the transect.

In May, 1995, the transect was resurveyed. Topographic profile and vegetation data were taken as in 1965. In addition a 75 m by 75 m plot on the lower lee slope of the foredune, bordering the edge of the deflation plain, was sampled for developing shrub and tree vegetation along 4 evenly spaced transects. The number of contacts, irrespective of cover, was recorded for each species.

**RESULTS**

The topographic data is presented on a profile graph for the two years, 1965 and 1995. Vegetation cover data for selected species is presented as a series of histograms under the foredune profile (Figure 3). Table 1 lists the principal plant species occurring along the foredune section of the transect, and Table 2 shows the shrubs and trees encountered in the 75 × 75 m plot and the number of contacts for each. Only
SUMMARY

Optimum plot size and shape for safflower yield trials was calculated using data from a safflower uniformity trial planted at Farmington, Utah, in 1960. The area used was harvested as 1782 one row by five-foot basic plots, of which 1188 plots were used in this study. This latter was due to a high yield differential between one-third of the field, and the other two-thirds of the field caused by an uneven moisture retention of the soil.

Optimum plot size was calculated in three ways. Using comparable variances, it was found to be 8 times the basic unit. Taking into account soil heterogeneity and relative costs, two basic units was found to be optimum. By specifying certain levels of information desired, a convenient plot size of 8 times the basic unit was calculated.

It was found that plot shape had little effect on variances, so a width of two rows was indicated, so that the plots might be most efficiently handled.

All factors considered, an optimum plot size and shape for safflower yield trials was found to be 8 times the basic unit, or 3.33 feet wide by 20 feet long.
the data from the foredune section of the transect are presented and discussed in this paper.

The results of the 1965 survey are described in Wiedemann (1966). The foredune covered a distance of 175 m along the transect, from its seaward base at about mean high tide level (as determined by the general line of vegetation at the base of the foredune) to the start of the deflation plain (change in vegetation and the beginning of the marsh zone). Its maximum height was 7.5 m above a line running from the seaward base of the foredune to the start of the deflation plain, this high point located about 75 m from the seaward base. In the driftwood zone there were many large logs, most completely exposed. They ranged in size up to 6.5 m long and 0.75 m in diameter.

The vegetation of the foredune consisted almost exclusively of *Ammophila arenaria*. Its cover was greatest from half-way up the windward slope to the crest. It was absent from the lower windward slope and decreased in cover down the leeward slope. A few other species were present, most notably *Frageria chiloensis* and *Lupinus littoralis*. There were no shrub or tree species present on any part of the lee slope. The remainder of the transect crossed deflation plain herbaceous meadow, where a few scattered low shrubs and tree seedlings were present.

In 1995 the width of the foredune along the transect was essentially the same. The crest height had increased to 7.3 m and had shifted seaward, 53 m from the seaward base of the foredune. The result of this shift was to create a steeper windward slope. The lower lee slope had decreased in height along most of its distance. The areas under each of the profiles are about the same, indicating no appreciable difference in total sand accumulation. The logs of the driftwood zone were still visible, but in various stages of advanced decomposition.

The cover of *Ammophila arenaria* in 1995 was about the same on the upper lee slope and crest, and increased some-
Table 1. Principal coastal foredune species, Oregon, USA. (Names after Hitchcock and Cronquist, 1973). * Introducted species.

<table>
<thead>
<tr>
<th>Tolerant of sand burial, dune and hummock forming, pioneer species:</th>
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<tbody>
<tr>
<td>Ammophila arenaria (L.) Link</td>
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<tr>
<td>Elymus mollis Trin.</td>
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<tr>
<td>Abronia latifolia Eacche</td>
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<tr>
<td>Ambrosia chamissonis (Less.) Green</td>
</tr>
<tr>
<td>Tanacetum douglasii DC</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tolerant of sand burial, sand stabilizing, pioneering species:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carex macrocephala Wild.</td>
</tr>
<tr>
<td>Convolvulus soldanella L.</td>
</tr>
<tr>
<td>Fragaria chiloensis (L.) Duchesne</td>
</tr>
<tr>
<td>Glehnia leioarpa Mathias</td>
</tr>
<tr>
<td>Lathyrus japonicus Wild.</td>
</tr>
<tr>
<td>Lathyrus litoralis (Nutt.) Endl.</td>
</tr>
<tr>
<td>Lupinus litoralis Dougl.</td>
</tr>
<tr>
<td>Pos macrantha Vasey</td>
</tr>
<tr>
<td>Polygonum parvifolia C.S.</td>
</tr>
</tbody>
</table>

Not tolerant of sand burial, herbaceous meadow species:

| Achillea mearisii Bong. | Yarrow |
| Aria praecox L.* | Little Hairgrass |
| Aster subspicatus Nees. | Douglas Aster |
| Anaphalis margaritacea (L.) B. & H. | Pearly Everlastings |
| Cerastium arvense L.* | Field Chickweed |
| Festuca rubra L. | Red Fescue |
| Hypehorax radicata L.* | Hairy Cats-ear |
| Montia spathulata (Dougl.) Howell | Common Montia |
| Rumex acetosella L.* | Red Sorrel |

Not tolerant of sand burial, shrub and tree species:

| Arcostaphylos uva-ursi (L.) Spreng | Kinnikinnick |
| Cytisus scoparius (L.) Link* | Scot’s Broom |
| Gaultheria shallon Pursh | Salal |
| Myrica californica Cham. | Pacific Wax Myrtle |
| Vaccinium oxym Pursh | Evergreen Huckleberry |
| Picea sitchensis (Bong. Carr. | Sitka Spruce |
| Pinus contorta Dougl. | Lodgepole Pine |

Table 2. Frequency of foredune lee slope shrub and tree species, based on line contact in four evenly spaced transects in a 75 x 75m plot.

<table>
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<tr>
<th>Species</th>
<th>No. contacts</th>
<th>Frequency (%)</th>
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<tr>
<td>Vaccinium oxym</td>
<td>229</td>
<td>41</td>
</tr>
<tr>
<td>Cytisus scoparius</td>
<td>210</td>
<td>37</td>
</tr>
<tr>
<td>Gaultheria shallon*</td>
<td>68</td>
<td>12</td>
</tr>
<tr>
<td>Myrica californica</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td>Pinus contorta</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
<td>Arctostaphylos uva-ursi</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Baccharis pilularis**</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Picea sitchensis</td>
<td>3</td>
<td>&lt;1</td>
</tr>
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* Forms very large mat colonies, up to 25 m²
** Baccharis pilularis DC. Chaparral Broom

what on the lee slope. Part of the extension of its cover to the lower windward slope reflects the occurrence of "embryo dunes", small temporary dunes that form at the foot of the foredune between occurrences of severe winter storms with their strong erosive wave action. Several new plant species were present, most notably Elymus mollis and Lathyrus japonicus on the crest. Rumex acetosella from the crest and down the lee slope, and the shrub species Gaultheria shallon and Cytisus scoparius on the lower lee slope. Fragaria chiloensis, Aria praecox, and Aster subspicatus all increased in cover, while Lupinus litoralis, prominent in 1965, had decreased in cover by 1995.

The shrub and tree plot provides additional information on the extent to which these life forms had become established in the 30 years since the first survey. Most abundant were the shrubs Vaccinium oxym and Cytisus scoparius with 229 and 210 contacts respectively. The shrub, Gaultheria shallon had fewer contacts (68), but had formed large mat-like colonies at each contact point. Pinus contorta had 11 contacts, and Picea sitchensis, had 3.

**DISCUSSION**

The foredune seen today along the central Oregon coast appears to have developed since the early 1940's. There is no record of its initial formative stages. The scattered vegetation hummocks seen in the 1939 aerial photographs were most probably native dune colonizers capable of producing large mounds, such as Abronia latifolia and Tanacetum douglasii both common along the shore in pre-Ammophila times. The development of a low ridge at this time was mostly the result of sand accumulating in great piles of driftwood lining the upper beach. This driftwood was the result of the extensive logging of the coastal forest in the last half of the 18th century and first half of the 19th. As far as can be determined, no stabilization plantings were made specifically to establish a foredune. However, the grass was extensively planted along this part of the coast in the 1920's and again in the 1950's and early 1960's, mostly along the inner edge of the active dune margin, to prevent sand from blowing into rivers and onto railroads and highways.

It must be assumed that, for the most part, the spread of Ammophila along the immediate shoreline was natural, either through seedling establishment or by rhizomes transported by ocean currents and wave action (it has been demonstrated that the rhizomes will tolerate periods of sea water immersion even though the plant itself is intolerant of salt). Once established in a zone of blowing sand, the plant responds quickly to burial and grows rapidly, generating vertical tillers in great profusion (as well as horizontal spreading rhizomes). Much has been written about this species and its extraordinary adaptation to sand burial (HUISKES, 1979; PAVLIK, 1983).

The foredune developed in depth on a base of piled driftwood as a broad belt of individual hummocks formed on widely separated individuals or groups of individuals. (In many places today hummocks like these, up to 3 m in height and 5 m in diameter can be seen in active sand areas in the process of colonization by Ammophila.) Spaces between the hummocks eventually colonized until a consolidated ridge developed. This ridge was almost symmetrical in 1965, with a gradual windward slope to a peak located at about half the width of the ridge. As the grass spread down the windward slope, the slope became steeper, the crest higher, and the ridge asymmetric. With the increasing steepness of the windward slope, more sand collected in Ammophila plants established at the foot of the slope, giving rise to the small, temporal "embryo dunes".

The Ammophila hummocks on the lee slope were smaller and lower. Winds descending the slope eroded the surface be-
between them, depositing some sand onto the adjoining deflation plain and some onto adjoining grass plants, stimulating growth and increasing cover and surface stability. Native and exotic weedy herbaceous species common in the adjoining deflation plain quickly became established. Most of these species reflect the basic stability of the sand surface on the lee slope. The two new species appearing on the windward slope and crest have special significance. As less sand is deposited on the high crest of the foredune, the vigor of Ammophila declines (Hope-Simpson and Jeffries, 1966) and open spaces occur. Erosion takes place, the sand moving downwind or into adjoining grass plants. One result is the creation of an uneven ridge line, the other the creation of open spaces where native dune plants can be come established. Elymus mollis, the native dune-building grass, has become established along the entire windward slope and on the crest. Another native dune species, Lathyrus japonicus has also become established in the same habitat. Ammophila has a strong competitive advantage over Elymus under certain conditions of massive sand transport by the wind, but its loss of vigor under conditions approaching stability put it at a disadvantage.

On the lee slope the transition from herbaceous vegetation to shrub and tree thicket is presently well under way. The four most abundant shrub species are all represented in the adjoining deflation plain vegetation, which had developed into a dense, impenetrable thicket during the 30 year period. Vaccinium and Gaultheria are two of the most common shrubs in the forests of the Pacific Northwest. Myrica californica is most common in moist soils, but is often found on higher dune slopes. Cytisus scoparius is a common weedy shrub present along the edges of the deflation plain. It was a common constituent of early stabilization plantings. Both Baccharis pilularis and Arctostaphylos uva-ursi are dry site species of open areas, the latter often forming large mat colonies. Tree seedlings are just appearing. Pinus contorta is the pioneer tree species on both low and high sites in the dunes, while Picea sitchensis is common on the more moist sites. In its seedling stage it is intolerant of the salt spray off the ocean, but when it reaches about 5 m in height, it will begin to appear above the surrounding pines and eventually become the dominant species.

CONCLUSIONS

The many native dune species have formed large foredunes in the past. These foredunes are found both north and south
of the area discussed here (although they are mostly dominated by *Ammophila* at present). These foredunes begin as low mounds around individual plants. These mounds, however, develop slowly and much more time is required to arrive at consolidation and ridge formation (Figure 4). On stable or accreting coasts this slow development time was apparently not a problem. On the central Oregon coast, an eroding coast (KOMAR and SHIH, 1983), the great winter storm waves would wash any developing foredune into the sea. The piles of driftwood and the arrival of *Ammophila arenaria* changed this situation dramatically.

Building on a foundation of logs extending 150 m inland, the grass built a massive foredune in something less than twenty years. Despite its size, storm waves have, at times, eroded as much as 5 to 10 m of the front of the dune into the sea, creating a sea wall several meters high (Figure 5). By 1995 the foredune seems to have reached a mature size and shape. Shrub and tree vegetation will continue to develop into a typical dune thicket right to the crest. *Ammophila* will disappear under the cover of the dune thicket (as will *Cytisus scoparius*), but will continue to thrive on the unstable windward slope and base. Open spaces on the crest (as well as in scattered blowouts caused by disturbance to the established vegetation) will insure the survival of the native dune species. They will never, however, occur in the abundance of the pre-*Ammophila* days.

**ACKNOWLEDGEMENTS**

I wish to thank Robert Obermire for his help in the establishing the original transect in 1965. I would also like to acknowledge the cooperation and help of the staff of the headquarters of the Oregon Dunes National Recreation Area, Reedsport, Oregon, in the resurvey of the transect in May, 1995. Finally, my appreciation to the students of the 1995 Plant Ecology Program of the Evergreen State College whose enthusiasm and labor in helping cut the line through the deflation plain thicket and collect the data made this resurvey easier and enjoyable.

**LITERATURE CITED**


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ESTIMATION OF OPTIMUM PLOT SIZE AND SHAPE
FOR USE IN SAFFLOWER YIELD TRIALS
by
Alfred Max Wiedemann

A thesis submitted in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Agronomy

Approved:

Thesis Director

Major Professor

Head of Department

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah
1962
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Furthermore, I would like to express my thanks to Dr. L. N. Leininger for his guidance and help in the writing of this thesis; and to Dr. D. R. McAllister for his assistance in planning my work, both as an undergraduate and as a graduate student.
INTRODUCTION

One of the big problems encountered in experimental yield trials of field crops is the variation that occurs in yield estimates regardless of how the trial is handled with respect to variety or treatment. This so-called "natural" variation is the result of such factors as heredity, human error, and environment.

The factor of environment is particularly important, especially as it pertains to the heterogeneous nature of the soil of a given field. Almost any experimental site will vary in fertility from one area to the next, thereby causing a considerable variation in yield from one plot to the next even though elaborate attempts are made to remove all variation.

Variance in yield will fluctuate according to the size and shape of the plots, generally decreasing with increasing plot size. However, not all plot sizes and shapes are equally efficient from the standpoint of cost of operation, so an effort must be made to determine the minimum variance along with the minimum cost.

Each field crop must have this optimum plot size and shape determined for it. Since very little work has been done on safflower in this respect, it will be the purpose of this study: (1) to determine the safflower plot size
and shape which will give the least variation possible and still produce the information desired in an experiment where all of the plots are alike with respect to variety and treatment; and (2) to correlate cost figures with plot size and shape to obtain information regarding the most economical plot size and shape consistent with the minimum levels of natural variation desired.

To achieve these purposes three different methods will be used. Two have been quite extensively used in the past by other investigators working on this type of problem with other crops, while the other method has been only recently proposed.
THE ECOLOGY OF PACIFIC NORTHWEST COASTAL SAND DUNES: A COMMUNITY PROFILE

by

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National Coastal Ecosystems Team
Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, D.C. 20240
PREFACE

It was just twenty years ago, in the summer of 1963, that I began my study of the Pacific Northwest coastal sand dunes. At that time ecological awareness was just beginning to creep into the national social consciousness. In the years that followed, wetlands and shorelines became the focus of widespread interest and concern. Coastal sand dunes shared in this focus from a number of perspectives. The sand dunes became increasingly valuable as real estate and as playfields for motorized recreation. They were also seen as great natural laboratories where biological and geological processes could be observed in accelerated action.

To be able to deal with these conflicting interests in something as complex as a natural ecosystem, responsible public agencies need as much information as possible. This is one of the main purposes of the community profile series of which this publication is a part. In putting together this profile, I have drawn on my many years experience with the sand dunes of the Pacific Northwest. I have also tried to locate as much of the great amount of published and unpublished material on the dunes as possible.

I have organized what I know and what I have learned from other sources into six chapters. The first gives general background information and an overview of the area under consideration: the Pacific coast from Cape Flattery, Washington, to Cape Mendocino, California. In the second I have summarized the environmental setting, emphasizing those factors involved in shaping the dune landscape. The third chapter is an attempt at a classification system for dune forms, a subject of great interest to those studying inland dunes, but not yet applied to coastal dunes. The history of the dune processes of this area and the possible future course of events is the subject of the fourth chapter. In the fifth chapter I have put down my present notions about the plant communities of the dunes. The result of an ongoing, subjective classification process based on much looking and thinking, it is not likely that the list of communities contained herein will remain stable. This does not detract from their present usefulness, however, since the shifts in view and thought are likely to be subtle and slow. This chapter also summarizes the wildlife habitats of the dunes and briefly characterizes each one. The last part of the sixth chapter on human impact emphasizes management problems—the major concerns in looking at the dunes from the viewpoint of both the biologist and the manager.

The appendices include a complete list of the dune areas (localities) in the coastal region defined above, as well as lists of characteristic plants and animals. For these latter lists I have tried to
avoid making a list for the sake of listing. I have included only those plants and animals that have actually been observed in the plant communities and habitats of the dunes. For those who would like to take a detailed look at the dunes, I have included in the appendix detailed descriptions of two very different dune systems that I know very well. Visiting them would be a rewarding experience.

Credits for maps, diagrams, photographs, and tables that are not my own are given in parenthesis at the end of the figure and table captions. For each photograph I have included locality information and the date it was taken.

This description of the Pacific Northwest coastal dunes is by no means complete. In looking at something as complex as a sand dune ecosystem, every bit of data fitted into the total known picture shifts the perspective and the interpretation. It is my hope that this community profile will start or add to that experience for anyone interested in the coastal sand dunes.

A.M. Wiedemann
30 September 1983

Comments on or requests for this publication should be addressed to:

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(504) 255-6511; FTS 685-6511
CONTRIBUTIONS TO THE PLANT ECOLOGY
OF THE OREGON COASTAL SAND DUNES

by

ALFRED MAX WIEDEMANN

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1966
APPROVED:

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Professor of Botany
In Charge of Major

[Signature]
Chairman of Department of Botany and Plant Pathology

[Signature]
Dean of Graduate School

Date thesis is presented April 27, 1966

Typed by Opal Grossnicklaus
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Special appreciation is expressed to the author's major professor, Dr. W. W. Chilcote, who has given advice and encouragement in the course of this study; and who, more importantly, as a personal friend, has helped the author shape a philosophy of life that is consistent with his calling as an ecologist.

Acknowledgement is made of Special Use Permit No. 2710 issued by the Siuslaw National Forest, U.S. Forest Service, to allow the establishment of permanent transects and quadrats on dune lands within the national forest boundaries. Thanks are expressed for the help and cooperation of forest service personnel in the Supervisor's Office, Corvallis, Oregon; at the Hebo Ranger Station, Hebo, Oregon; and at the Smith River Ranger Station, Gardiner, Oregon.

Special thanks go to Mr. Wilber Ternyik, Florence, Oregon, for much local information on the dunes and for the use of his Dodge Power Wagon during the period spent studying the large deflation plain west of Cleawox Lake; and to Don Brackett of the Soil Conservation Service, Florence, Oregon, for time spent discussing the
sand dunes with the author and for the use of certain aerial photographs.

Also, sincere appreciation is expressed to LaRea Johnston for help in the identification of the plant species; to H. H. Millsap for help with the diagrams and photographs; to Robert Obermire for help with the Carter Lake Transect; to Diantha Green States for help with the aerial photography and to Joyce Wiedemann for the drawing of the folding quadrat.
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Alfred Max Wiedemann for the Ph. D. in Botany (Name) (Degree) (Major) (Plant Ecology)

Date thesis is presented April 27, 1966

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

Abstract approved (Major professor)

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 obtupta* 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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An Introduction to the
Natural History of
The Evergreen State College Campus
Olympia, Washington
AN INTRODUCTION TO THE
NATURAL HISTORY OF
THE EVERGREEN STATE COLLEGE CAMPUS
OLYMPIA, WASHINGTON, USA

First Edition

Compiled by
Dr. Alfred M. Wiedemann
Member of the Faculty

The Evergreen State College
Olympia, Washington

1987
INTRODUCTION

This collection of papers has been brought together in this volume to provide an introduction to the natural history of the Evergreen campus. Most of the papers were written by students who had studied their organisms of interest in considerable depth, and used this opportunity to bring together their knowledge and skills. There are some limitations to their use. The moss and lichen keys, for instance, include only the most common species encountered on campus; probably two or three times as many occur here. There have been some changes and additions to the landscape plantings on campus that are not reflected in the ornamental plant guide, but these are relatively minor. The slug and snail key is complete, but has not been tested extensively. None of this should affect the usefulness of the papers as introductory works; resources for advanced work are available. An illustrated key to the campus "summer flora" is in preparation. It is hoped that eventually information on campus birds, mammals, reptiles, and marine shore organisms will be available. Comments on these papers are requested and needed to improve their quality and usefulness. Errors, inconsistencies, and ambiguities often remain in spite of the close scrutiny of the authors. Of the authors of these papers, Pene Speaks lives in Olympia and works on environmental projects when the opportunity arises. Susan Campbell also lives in Olympia, and is enrolled in Evergreen's graduate program in environmental studies. Daphne Smith lives in Eugene, Oregon, where she completed her doctorate in lichenology last year. Timothy Pierce is working on his doctorate in malacology at Michigan State University. Finally, this volume is dedicated to the memory of Christine Schwennesen whose untimely death in 1982 left an empty place in the lives of many who knew and respected her.

A.M. Wiedemann
1 December 1987

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Plant Associations of the Oregon Dunes National Recreation Area

Red fescue association and shore pine/bearberry association.
PLANT ASSOCIATIONS
OF THE
OREGON DUNES NATIONAL RECREATION AREA
SIUSLAW NATIONAL FOREST, OREGON

Minimal differences in movement of sand can influence vegetation: at right, the seashore bluegrass association on slightly shifting sand at the foot of a dune slip face; at left, the red fescue association on relatively stable sand, slowly being buried by the slip face.

by

John A. Christy, James S. Kagan,
and
Alfred M. Wiedemann

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Photographs by John Christy

Cover photos: Shore pine/bearberry association and red fescue association.

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SUMMARY

This book is a guide to the plant associations of the Oregon Dunes National Recreation Area. It includes general descriptions of the physical and biological setting of the Recreation Area: its climate, geology, landscape, soils, wildlife, and ecological processes. Analysis of quantitative field data identified 52 plant associations occurring in the Recreation Area, and others surely escaped our detection. Vegetation is classified according to the National Vegetation Classification System (Federal Geographic Data Committee 1996; Anderson et al. 1998; Grossman et al. 1998). Ordination of stand data, and delineation of successional pathways indicate that the vegetation is arranged along gradients of moisture, stand structure, soil development, and successional age. Keys identifying each association are followed by descriptions of each association. Descriptions of each association include acronym, ecoclass code (Hall 1998), environment, vegetation and ecology, succession, distribution and history, management issues, and previous studies. Appendices summarize vegetation data, and list vascular plants known or reported from the Recreation Area.

PREVIOUS WORK

The Oregon Dunes National Recreation Area is well known for its towering dunes, reputedly the largest of their kind in the world, and a seemingly endless expanse of shifting sand. People come from all over the world to see, study, and play in this spectacular landscape. Some people have even tried to farm it.

Many scientists have worked in the Recreation Area, creating a wealth of information which helped in the compilation of this guide. Munger (1910, 1967) conducted the first survey of forest types on the Recreation Area, two years after it was acquired by the Forest Service. House (1914a, 1914b, 1918), Peck (1919) and Cooper (1936) were the first to describe vegetation in and near the Recreation Area. Egler (1934), while assisting Cooper in the field, gathered data and wrote the first account of vegetation ecology in the Recreation Area. Cooper's (1958) monograph on the structural features, history and ecology of the dunes remains the definitive reference for any work on the Recreation Area. Kumler (1963, 1969) was the first to describe the forest associations of the Recreation Area in any detail. Wiedemann (1966, 1984, 1993), Wiedemann et al. (1969), and Wiedemann and Pickart (1996) produced a series of comprehensive overviews of dune ecology in the Recreation Area and elsewhere along the Pacific coast. Leuthner (1969) studied the lichen flora of dunes in the Florence area, including two sites in the Recreation Area at Cleawox Lake and Carter Lake. Pinto et al. (1972) provided descriptions, including useful site-specific information, in a planning document for the newly-created Recreation Area. Lund (1973) wrote a brief description of dune landforms, based on the earlier work of Cooper (1958). Newman (1974, 1983) studied dynamics of deflation plains between Carter Lake and Tahkenitch Creek. Wilde (1982), while working in the Sutton Creek dune sheet just north of the Recreation Area, documented changes caused by the advent of European beachgrass -- processes also occurring within the boundaries of the Recreation Area. Quaye (1982) described several Sitka spruce associations from headlands north of the Recreation Area. Hemstrom and Logan (1986) focused most of their work on forests farther inland, but provided descriptions for some of the forest associations on the Recreation Area. Pilz et al. (1996) and Hosford et al. (1997) are investigating the productivity of commercially-valuable matsutake mushrooms in different habitats on the Recreation Area, and monitoring the response of matsutake to different harvest regimes. McCune et al. (1997) reported several rare lichens from the Recreation Area, collected at Eel Creek and Carter Lake.
Plants of the
Oregon Coastal Dunes

Alfred Wiegmann
Dennis T. Smith
Plants of the
Oregon Coastal Dunes

Alfred M. Wiedemann
La Rea J. Dennis
Frank H. Smith

Oregon State University Press
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Introduction

This book was originally published in 1969 and has, for nearly 30 years, served as a guide to the natural history of the Oregon coastal dunes and to the plants found on them. In this edition we have updated the scientific names of the plant species to correspond with those in current use in local floras.

During these past thirty years changes have occurred in the dune landscape. The deflation plains, developing on the lee side of the foredune and between the lateral ridges of the large parabola dunes, were vegetated mostly by meadow species, with a few tree and shrub seedlings. Today impassable thickets of trees, coast pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) and shrubs western wax myrtle (*Myrica californica*), coast willow (*Salix hookeriana*) and evergreen huckleberry (*Vaccinium ovatum*) have grown up, requiring trails to be cut for access to the beach.

On the foredune and other areas of active, blowing sand, the continued spread of European beach-grass (*Ammophila arenaria*) has resulted in the suppression of the native dune-building and sand-stabilizing species. While not generally threatened with extinction, many of these species, such as the yellow abronia (*Abronia latifolia*), gray beach pea (*Lathyrus littoralis*), beach morning-glory (*Calystegia soldanella*), American dune-grass (*Elymus mollis*) and large-headed sedge (*Carex macrocephala*) are no longer seen in the abundance of thirty years ago. One endangered species, pink sandverbena (*Abronia umbellata* ssp. *breviflora*) which was once abundant along the coast from British Columbia to northern California is now restricted to a few sites from the central Oregon coast south. Since 1991 efforts have been underway by the Plant Conservation Biology Program of the Oregon Department of Agriculture to reintroduce this species to create new populations. Reintroduction has been most successful in sites where European Beach-grass has been brought under control.

Control of European beach-grass has been undertaken, with some success, in certain areas to improve the habitat for an endangered bird, the snowy plover (*Charadrius alexandrinus* ssp. * Introduced
nivosus). In addition, biological control agents (primarily seed weevils and the Gorse Spider mite) have been introduced by the Oregon Department of Agriculture in cooperation with other agencies and private land owners to help control the spread of gorse (*Ulex europaeus*) and Scotch broom (*Cytisus scoparius*).

The main purpose of this book is to help visitors to the sand dunes, regardless of their background, to become a little more familiar with the landscape they see, and with the forces of nature operating within that landscape. A great deal of satisfaction can be obtained through knowing something of the story behind the things one sees in nature: the effect of climate, why plants grow where they do, the names of the plants, etc.

The sand dunes of the Oregon coast offer some of the most spectacular seashore landscapes to be found anywhere in the country. Readily accessible by highway, they have become a source of interest to increasing numbers of travelers to the Northwest. Oregon's excellent State Park system and the establishment of the Oregon Dunes National Recreation Area (ODNRA) also draw large numbers of visitors to the dunes areas.

The first chapter of this book deals with the sand dune area as a whole—its geologic history, climate, dune forms and formation of dunes, and some general observations on the vegetation. Much of this information was put together from many sources, and numbers in parentheses throughout the text refer to a bibliography which lists the major sources of information.

The next four chapters discuss the plants and plant communities of the sand dunes. The information is based largely on the dune areas from Tillamook Head to Coos Bay. Many plants of the Clatsop area dune ridges are included, but this area has many additional species that have been introduced by the activities of man. Likewise, the coast below Coos Bay has a slightly different climate from that of the rest of the Oregon coast, and consequently there are many additional plant species present.

The plants included in this book are only those that might be considered common on the dunes. It does not include at least as many more that are less common. It does not include roadside plants of the "non-dune" coastal forest, except when these occur on the dunes.
Common names are used in the discussion with the scientific name given in parentheses the first time it is used in a chapter. Whenever possible, it is desirable to learn the scientific names of plants, since common names can be a source of much confusion.

The taxonomic key of Chapter 6 includes ninety of the plants one is most likely to see on the sand dunes. Instructions for its use precede the actual key. In addition to the plants in the key, forty other species are described in the description section. Identifying characteristics are based on flowers and leaves, which would make it most useful during the spring and summer months. However, the key, together with the photographs and descriptions of the plants in Chapter 7, should make it possible to identify many of these species throughout the year. Mosses and lichens are not included in the key. A glossary is included that gives definitions of commonly used botanical terms.

A number of individuals assisted in the preparation of this work; namely, Kenton L. Chambers, William W. Chilcote, Ronald J. Tyril, the late Weldon K. Johnston, Richard R. Halse and Thomas N. Kaye. We wish to thank them for their valuable assistance.

The photographs were taken by the late Frank H. Smith, with the exception of Ceanothus thyrsiflorus (blue blossom), which was kindly furnished to us by Mr. and Mrs. Orin Hess of Wedderburn, Oregon.