ECOLOGICAL IMPLICATIONS OF GERMINATION STUDIES ON MICHIGAN AND NEW JERSEY SAND DUNE PLANTS

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William Thomas Gillis, Jr.

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ECOLOGICAL IMPLICATIONS OF GERMINATION STUDIES ON MICHIGAN AND NEW JERSEY SAND DUNE PLANTS

by

William Thomas Gillis, Jr.

AN ABSTRACT

Submitted to the College of Science and Arts
Michigan State University of Agriculture and
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APPROVED John E. Cantlon

William Gillis

ABSTRACT

A study was made of seed germination of sand dune plants of Michigan and New Jersey, and the findings related to the ecology of these species in terms of moisture, temperature, and salt concentration. Vegetation analysis was made by reconnaissance and by the line intercept transect method. Seeds were collected and dried; then standard germination tests were run on blotters in petri dishes to determine normal germination requirements. Some seeds were stored at 5° C. to permit an after-ripening chill, and then germinated at 20° C. Others were germinated at 40° C. for six hours daily. Others were soaked in sea water for twelves hours and then transferred to moist blotters. Some seedlings, normally germinated, were sprayed at intervals with sea water. Also, at three stages of germination seedlings were placed in a desiccator, and dried until wilting or necrosis was evident. After drying, the seedling was moistened with water to test for recovery.

Cold temperature treatments improved germination in ten out of twelve species tested. High temperatures decreased germination capacity: we can infer that burial or spring germination seem to be required for successful establishment. Seven out of twelve species had reduced germination capacity after treatment with sea water. Seeds of <u>Cakile</u> <u>edentula</u> from both New Jersey and Mich-

igan showed no difference in response to sea water soaking, but those of Ammophila breviligulata indicated racial differences with the New Jersey population salt-tolerant, and the Michigan population susceptible to salt damage. Calamovilfa longifolia, which does not grow in New Jersey, showed a marked increase in germination following soaking in sea water. Pinus rigida, which does not occur in Michigan, showed a salt-tolerance not exhibited by Pinus banksiana, its "ecological equivalent" in Michigan.

Eight out of twelve species showed salt spray damage, with Prunus pumila (from Michigan) being the most sensitive. Ammophila again showed the same racial difference in response to sea water spray. The pines responded accordingly. Neither Michigan nor New Jersey collections of Cakile seedlings exhibited salt spray damage, nor did Michigan collections of Lathyrus japonicus var. glaber.

Ammophila and Calamovilfa showed higher recovery in later stages of germination than in earlier. Gerardia pauperoula showed no recovery after the hypocotyl had emerged longer than 0.25 inch. Six out of twelve species recovered well from desiccation; of these, four were able to differentiate a new root.

Summary conclusion. The above findings indicate, at least in some areas, that germination characteristics appear to contribute to the ability to occur on particular sites in sand dune vegetation patterns.

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INTRODUCTION

According to Fuller (1914), sand dunes are habitats of atmospheric extremes. They are unique in that this habitat is dependent upon plants for its inception and for its continuance (Salisbury 1938). Many workers have discussed the ecological relations of plants already established on the dunes. Indeed, one of the pioneer papers in ecology was the classic in 1891 in which Warming discussed ecological relations of Danish dunes. Another pioneer account of the ecology of sand dunes was the work of Cowles (1899) on Lake Michigan dunes. These works have been guides in the development of ecological theory, Cowles' work being especially important in the United States. Little work, however, has been done of a concrete nature to explain how sand dune plants become established initially. The purpose of this paper is therefore to study some of the aspects regarding the ecology of seed germination, and to relate these factors to the dune environment in an effort to explain that age-old question of ecologists, "Why do organisms grow where they do?"

Dune associations are dependent largely upon vegetative reproduction for maintenance (Fuller 1914). Fuller went so far as to describe the dune community in terms of an "almost entire absence of seedlings." There is no question that such species as Ammophila breviligulata, which grows on Atlantic and Pacific coasts of the United States, as well as on the shores of the Great Lakes, is successful because it is able to keep up with depositing sand by its high cover and prolific vegetative reproduction. Yet, following disturbance, plants enter newly-disturbed areas, often some distance from established colonies. Ammophila or Cakile edentula*, for example, is one of the first plants to invade blowouts. Then too, old communities change by the influx of new individuals, indicating that establishment from seed does indeed occur. The existence of populations of annual plants likewise confirms the thesis that plants can reproduce from seed on sand dunes. A question remains: "Are there factors governing seed germination which operate to determine the niche these plants occupy on the dunes, or which permit the successful establishment of others?" I shall describe the dune communities of Lake Michigan and of the Atlantic Coast of New Jersey, and then consider them as environments for germination, examining the questions of moisture, cold, heat, and salt concentrations as factors impinging upon the seed.

The areas. In Michigan, various areas were examined and plant specimens and seeds collected from most of them. From north to south they are Sturgeon Bay, Sleeping Bear Dune, Manistee, Ludington, Grand Haven, Saugatuck, and Warren Dunes State Park. Of these, the dunes at Sleeping

*All binomials are corrected to agree with authorities given in Fernald (1950).

Bear were visited most frequently and provided the grestest portion of the collected seed. Most of the vegetation data came from either Sleeping Bear Dune or Saugatuck. Sleeping Bear Plateau is an area on the Manistee Moraine which forms the base upon which several perched dunes are found. The sand is largely lacustrine, not glacial, and was carried by the prevailing northwest winds. The sand was thrown on shore by the waves and then piled up by the wind. Because of the wind action, the western face of Sleeping Bear perched dune is not parallel to the lake, but faces the prevailing winds. It once stood forty-five meters above the level of the moraine, which is, in turn, about 150 meters above the lake (Gates 1950). Persons climbing to the top on a surveyors' trail initiated dislodgment of vegetation some thirty years ago. In 1915, some 200 acres of the top dropped into Lake Michigan and much sand continues to be blown eastward across the plateau (Waterman 1926). Although the plateau upon which Sleeping Bear is perched is a moraine rather than a beach, sand covers the ground surface and dunes are built up by wind action. Dune vegetation prevails. Transects were made here and near Saugatuck, Michigan. Those from Saugatuck are diagrammed in this paper because they can begin at the water's edge; those from Sleeping Bear must start 150 meters above the lake on the crest of the moraine.

In New Jersey, research was carried out at Island Beach, a sand bar nine miles long, the vegetation of which probably had its origin during the reign of Charlemagne (c. A.D. 800), and has remained relatively free from man's disturbance ever since (Terres 1952). It is located in Ocean County, two and one-half to four miles from the mainland. It has been owned by the Phipps Estate until a few years ago when procured by the State of New Jersey for eventual development as a state park for recreational and scientific purposes. At present, invasion by man is restricted to residents who owned leases before the advent of state ownership, a few fishermen, and research workers from Rutgers University who are encouraged to study the area. The bar is one-half to one mile in width with the Atlantic Ocean on the East and Barnegat Bay on the West. Vegetation progresses from the dunes proper to a thicket-forest close to the bay side on the widest portions of the bar.

The communities. As Cowles noted (1899), there is a striking similarity between the dunes of Denmark, as described by Warming (1891) and the Michigan dunes which he himself described, in spite of the marine environment of the Danish dunes. This similarity is understandably even more pronounced when the comparison is made with the dunes on the much nearer Atlantic Coast of the United States. Despite differences in substrate and parent material (calcareous in Michigan and siliceous in New Jersey), and in the fresh water vs. marine environments, the plant communities are fairly similar, especially in the physiognomy and in the number of species common to the two dune areas. An idea of the floristic similarity may be seen in Table I.

The principal dune-formers in Michigan are the perennials (Ammophila breviligulata, Prunus pumila, Populus deltoides, Calamovilfa longifolia, and Juniperus spp.) whose ability to spring up each year or whose woody habit enables the plants to keep pace with the depositing sand, and to continue to operate throughout the year in maintaining cover. They need not re-establish themselves each year to maintain their place on the dunes. Ammophila, for instance, is well adapted to this habitat, and does well under dune conditions. Its internodes elongate readily, keeping it above the depositing sand. Once deposition has stopped, frequently through the stabilizing action of the Ammophila plant itself, the plant ceases to flower (Olson 1951). Annuals and biennials also manage to invade more mobile sandy places, but they contribute little to dune formation. Examples of this type of establishment by annuals and biennials may be seen in Corispermum hyssopifolium, Arabis lyrata, Cakile edentula, and Artemisia caudata.

In Michigan these principal dune formers occur in three primary "associations" (Cowles 1899): the Ammophila ** association (with its associate, Calamovilfa), the Prunus

**Cowles' use of the term does not in all cases agree with the European phytosociologists' concept of the term.

Table I - Most common plant species from sand dunes exclusive of the dune forest in Michigan and in New Jersey, after Cowles (1899) and Harshberger (1900). Binomials have been changed to agree with Fernald (1950).

	Michigan	New Jersey
Abies balsamea	X	
Acer saccharum	X	
A. rubra		X
Achillea millefolium	X	X
Amelanchier spp.	X	X
Ammophila breviligulata	X	X
Andropogon scoparius	X	X
Anemone cylindrica	X	
Arabis lyrata	X	
Arctostaphylos uva-ursi	X	X
Artemisia caudata	X	
A. stellariana		X
Asclepias syriaca	X	
Aster laevis	X	
Cakile edentula	X	X
Calamovilfa longifolia	X	
Campanula rotundifolia	X	
Carex kobomugi		X
Celtis occidentalis	X	
Cirsium pitcheri	X	
Celastrus scandens	X	X
Corispermum hyssopifolium	X	
Cornus stolonifera	X	
Dirca palustris	X	
Elymus canadensis	X	
Euphorbia corollata	X	
E. polygonifolia	X	X
Gerardia paupercula	X	X
Hamamelis virginiana	X	
Hudsonia ericoides		X
H. tomentosa	X	
Ilex opaca		X
Juncus balticus var. littoralis	X	
J. effusus	X	X
Juniperus communis	X	
J. communis var. depressa	X	
J. horizontalis	X	
J. virginiana	X	X
Lathyrus japonicus var. glaber	X	X
Lithospermum croceum	X	
Myrica pennsylvanica		X
Oenothera spp.	X	
Opuntia humifusa	X	X

	Michigan	New Jersey
Parthenocissus quinquefolia		X
Pinus banksiana	X	
P. echinata		X
P. resinosa	X	
P. rigida		X
P. strobus	X	
P. virginiana		X
Poa compressa	X	
Polygonum amphibium var. stipulaceum	X	
Populus deltoides	X	
P. balsamifera	X	X
Prenanthes alba	X	
Prunus maritima		X
P. pumila	X	
P. serotina	X	X
P. virginiana	X	X
Ptelea trifoliata	X	
Rosa blanda	X	
R. engelmanii	X	
R. virginiana		X
Rhus copallina	X	X
R. radicans	X	X
R. typhina	X	X
Salix glaucophylloides var. glaucophylla	X	
S. interior	X	
S. syrticola	X	
Salsola kali	X	X
Sassafras albidum	X	X
Shepherdia canadensis	X	
Smilacina stellata	X	X
Smilax hispida	X	
S. rotundifolia		X
Solidago nemoralis	X	X
S. sempervirens		X
Solidago spp.	X	
Tanacetum huronense	X	
Thuja occidentalis	X	
Tsuga canadensis	X	
Vaccinium angustifolium	X	X
V. corymbosum		X
V. myrtilloides	X	
V. vacillans	X	
Vitis aestivalis	X	
Xanthium pennsylvanicum	X	
Zigadenus glaucus	X	

pumila association, and the Populus deltoides association The Ammophila association is the one nearest the water or, on any depositing slope. The latter is evident at Sleeping Bear Dune where the Ammophila association appears fully three-quarters of a mile from the water, but on a rapidly moving sand slope. Cakile edentula is present in this association also. The Prunus association appears on the dunes once they have been stabilized by Ammophila and Calamovilfa, but it may occur as a pioneer on occasional sand-swept areas. It must consequently be able to establish itself from seed on even the unstable sites. The Populus deltoides association frequently appears in relic clumps, but it starts new associations under exceptionally favorable conditions (Fuller 1912). This association may be composed of Salix syrticola, S. interior, S. glaucophylloides var. glaucophylla, Cornus stolonifera as well as Populus; the latter may be replaced by Populus balsamifera in the north (Waterman 1917).

There are, in addition to the dune-forming associations, other associations in the sand community. Secondary openings may be invaded by Juniperus virginiana, J. communis, or J. communis var. depressa. The more northerly dunes have Arctostaphylos uva-ursi and Juniperus horizontalis in these openings to a greater extent than those farther south (Olson 1951). In the low pannes behind the foredunes, Hudsonia tomentosa is a frequent contributor to cover.

On the New Jersey dunes, the principal dune-formers occur in "associations" (sensu Cowles) similar to those in Michigan. These are an *Ammophila* association, with a highly local variable in *Carex kobomugi* at Island Beach (Small 1954), a *Rhus radicans* association, and another shrub-liana association. *Calamovilfa* is entirely absent from the *Ammophila* association in New Jersey, but *Cakile* is present. The *Rhus* association is composed chiefly of *Rhus radicans*, *Smilacina stellata*, and *Myrica pennsylvanica*. The shrub-liana association may contain *Prunus maritima*, *Vaccinium corymbosum*, *Ilex opaca*, *Juniperus virginiana*, *Smilax rotundifolia*, and *Parthenocissus quinquefolia*. *Hudsonia tomentosa* occurs here as in Michigan dunes on the pannes, but *H. ericoides* is also present. The "lows" immediately behind the foredunes are occupied largely by the *Rhus* association. The strands are remarkably similar from New Jersey southward, except that *Lathyrus* drops out in southern New Jersey (Fernald 1950), and *Ammophila* drops out in North Carolina to be replaced by *Uniola paniculata* (Oosting 1954).

Dunes as environments. Cowles (1899) suggested six tenets as requirements for dune stabilization by plants, the first of which was the rapid germination as found in a plant like *Corispermum*. He observes that annuals, biennials, and perennials all can reproduce by seed on the dunes, and he suggests that in the bottom of blowouts, where the water table is closer to the surface, they are more likely to succeed. He cites Populus, Salix, and Juncus as genera which especially fit this category. These three have seeds which are viable for only a few days after dispersal. If proper moisture is not immediately available to the seeds, they will die.

Perusal of the literature reveals several references to the germination of seeds on dunes. Cowles (1899) cites Ammophila as one of the first plants to obtain a foothold. He adds that on the more or less protected sites behind the foredune, seeds of Corispermum germinate readily. This vigor is likewise true for Zigadenus glaucus (McCoy 1918) and Artemisia caudata (Hicks 1938).

Environmental factors surrounding germination of seeds of sand dune plants have also been cited in reference to water, temperature, and sea salt concentration. Few species need moisture as critically as Populus and Salix, as mentioned above. The pannes, behind the foredunes, where the wind has swept out the sand to the depth of the level of the lake waters, are excellent places to supply the moisture necessary (Fuller 1914).

Conservation of soil moisture takes on some interesting facets on dunes. Salisbury (1952) points out that older dunes tend to have a higher moisture-holding capacity in the surface inch, following rain, than elsewhere in the dune.

Within eighteen hours, however, this moisture has evaporated from the top, so the surface has become one of the driest layers of the dune. Waterman (1917) has recorded data for Michigan which agrees with Salisbury's work. Salisbury further points out that internal dew formation tends to bring water to the surface at night, reaching a maximum in concentration at three feet, but nonetheless showing an increase over the daylight values all the way to the surface. At the three-inch depth, this figure rose to 0.6%, a gain of 0.4% over the day value. He cites the wilting percentage here at 0.5%. We note that the night value brings the soil moisture above the wilting percentage. The other phenomenon of interest in conservation of soil moisture is a dry mulch which the wind forms at the surface, preventing germination except after spring and summer rains. Following a rain, however, this mulch retards evaporation from lower soil layers (McCoy 1918). Even a short distance under the surface, the sand is cool and moist. The conserving action of the dry mulch together with the small demand upon water by the sparse vegetation makes this vegetation adaptable to the soil moisture found in dunes.

However important may be the soil moisture, Cowles (1899) believes that paucity of plant life on exposed sites is due not solely to reduced soil water. Intense heat on the dune surfaces might well be a determining factor in the germination process. Dune surfaces, because of their sand makeup, heat up rapidly and reach intensely high temperatures due to the low specific heat of the sand (Chapman, Wall, Garlough, and Schmidt 1931). However, the large size of the sand particles and the dryness of the surface grains yield characteristics of a poor heat conductor. Surface heat, therefore, is not conducted downward. It is conceivable that seeds which cannot tolerate high summer temperatures may require burial for survival, or they might germinate early in the summer before temperatures become excessive. Salisbury (1934) found in studies in England that surface temperatures of sand dunes often reach 40° C. at midday in summer. As Geiger (1950) has pointed out, it is also significant that, as the temperature increases arithmetically, the time necessary to kill seedlings decreases geometrically.

In 1931, Chapman et al. found that temperatures on dunes in Minnesota were similar to those of Salisbury's in England (36-46° C. in afternoon in July) at 45° N. Lat. Maguire (1955) has recorded temperatures which might approach 61° C. in March and up to 90° C. at the end of July on a cloudless day! In any event, the surface of the sand can be seen to be extremely warm in mid-summer. Seeds that are buffeted on the sand surface must be able to withstand these temperatures to survive.

Little reference in the literature has been made to salt concentrations as influencing the establishment of vegetation on marine dunes. Zohary and Fahn (1952) suggested that the salt content of the soil nearest the tidal mark on the beach is responsible for keeping certain plants off, and permitting others on the beach. No data substantiated this statement. Salisbury (1952) indicates that Agropyron junceum can grow normally in a 1.5% salt solution and can tolerate considerable periods of inundation by sea water, but Ammophila arenaria cannot, and he cites papers in which "osmotic suction" of roots of dune plants is reported as being 130-290 lb/sq. in. in England and up to 630 lb/sq. in. in dune plants of Algeria and of California.

The amount of salt in marine coastal soils has been the study of several investigators. Davis (1942) concluded that soil solutions might contain up to three per cent salt, whereas sea water has 3.5% soluble salts. And soluble salts in the sand of the windward side of the foredune approach a maximum of 1.81 mg/100 g. of soil. Gooding (1947), in his studies on the Barbados Islands, records the following salt concentrations in the sand at fifteen-centimeter depths:

50 meters from the ocean - 0.0128%
100 meters from the ocean - 0.0082%
150 meters from the ocean - 0.0064%

This is accounted for by salt spray and from rare inundation by unusual storms.

The Problem. In connection with a consideration of the questions of moisture, temperature, and salt concentration, certain ideas arise concerning the impact of these factors on seed germination.

Cold. Is a pre-chilling, as an after-ripening treatment necessary for germination? If so, seeds will do well anywhere they will be exposed to freezing winter temperatures. Spring thaws can break their dormancy. These plants might not do well where a series of temperatures of less than five degrees did not prevail for more than three weeks, but such conditions are not found in either Michigan or New Jersey. The pre-chill requirement may have evolved as a factor prohibiting fall germination when seedlings might be killed by the onset of winter.

High temperatures. Will high temperatures such as the recorded forty degrees reduce germination capacity? If so, then the seed in question must depend upon burial, or it must germinate early in the spring in order to be successful. Once germination is initiated, will heat kill the seed?

Salt water. Does sea water impede germination, or is the critical concentration to impede germination obtained via salt spray after initial germination? Seeds affected in this way cannot establish themselves on the middle beach in New Jersey where inundation during winter storms is frequent. If small quantities of salt impede germination, these plants would find difficulty in becoming established almost anywhere in the New Jersey sand community, except in areas highly protected from salt spray.

Desiccation. Is there any ability on the part of seedlings of sand dune species to withstand drying out? If so, can these plants, once desiccated, recover from desiccation equally well? The desiccation resistance of a species may play a role in vegetation zonation.

MATERIALS AND METHODS

Vegetation studies. Analyses of selected areas of the vegetation of Michigan dunes and of New Jersey dunes were made by reconnaissance and by line intercept studies. The latter studies were made along three parallel transects laid out fifty meters apart near Saugatuck, Michigan and a similar group of three on Island Beach, N.J. These transects extended from the water's edge at high tide in New Jersey (or the arbitrary farthest lakeward advance of higher vegetation - the "ordinary high water mark" of the Michigan Department of Conservation), to the dune forest. The linear distance occupied by each species along the line is recorded (Buell and Cantlon 1950). Voucher specimens of species dealt with are deposited in the Beal-Darlington Herbarium at Michigan State University.

Germination studies. Seeds used in the experiments had been collected from study areas, air-dried during the 1956 season, and stored in sealed jars. Germination trials were carried out in petri dishes on moist blotting paper. Records were kept of percentage germination and of the length of time required for germination.

For germination trials, fifty or one hundred, depending on seed size or on quantity of seed available, seeds were placed on two thicknesses of moist blotting paper in the petri dishes and then placed in germinators at 20° C. constant temperature. Three replicates of those experiments which produced positive data were carried out.

A quantity of seed from each collected species was placed in a refrigerator at 5° C. on moist blotting paper in petri dishes to permit after-ripening if necessary. Pre-chilling was continued for four weeks (minimum) before attempting germination.

For high temperature experiments, the previously pre-chilled seeds were started as described above at 20° C., but were shifted daily to forty degrees for six hours and then returned to twenty degrees for eighteen hours.

I employed three types of experiments with sea water, obtained from the Marine Biological Laboratory at Woods Hole, Massachusetts. (a) Seeds were placed in sea water for twelve hours and then were permitted to germinate on distilled-water-moistened blotters. (b) The seeds began treatment directly on blotters moistened with sea water. (c) Seedlings germinated in distilled water were sprayed with a blast of sea water from a medicinal atomizer from a distance of one foot. Although pressure on the atomizer varied, a "standard blast" was devised by a sharp, short squeeze on the bulb. I shot such blasts at eight pieces of blotting paper which were then dried to constant weight and the weight determined. The amount of residues remaining approximated 0.003 grams per square centimeter. In spraying the seedlings, I shot up to ten such blasts on the seedlings and noted damage two hours after each shot, up to ten blasts. Spraying was discontinued when more than 75% of the seedlings had shown detrimental effects.

Desiccation work was as follows: seeds germinated normally in petri dishes until the seedlings reached the following stages of development: (a) hypocotyl protruding less than 0.25 inch, (b) hypocotyl protruding greater than 0.25 inch, and (c) both hypocotyl and epicotyl emerging. Seedlings at these stages were placed in a calcium chloride desiccator. When the emergent organs of all seedlings in a given dish showed signs of wilting or of necrosis, the seeds were removed from the desiccator, and water was added to the blotters for the recovery test. Length of time to bring about wilting, and recovery percentages following wilting were recorded.

Some seeds seemed to need a scarification treatment. These seeds were experimentally subjected to scarification with concentrated sulphuric acid for varying lengths of time. For most of them, one-half hour soakings in H_2SO_4 seemed adequate to permit near-complete germination. These seeds were then washed for fifteen minutes in distilled water to remove excess acid, prior to placing them in petri dishes for germination tests. Controls were also soaked for a like period of time in distilled water and then started in petri dishes simultaneously.

RESULTS

Vegetation. The results of transects at Saugatuck, Michigan are shown in Fig. 1. Figs. 2 and 3 show the dune crest, a low area behind the foredune, and the transition to the dune forest. The beach from the water's edge to the foredune may have *Cakile edentula*, *Ammophila breviligulata*, and *Calamovilfa longifolia*. Some *Prunus pumila* and *Populus deltoides* may even be present. On the foredune, the beach grasses (*Ammophila* and *Calamovilfa*) are important, but even trees and shrubs like *Populus*, *Prunus*, and *Salix syrticola* or *Salix glaucophylloides var. glaucophylla* may be present. *Vitis aestivalis*, *Cornus stolonifera*, *Equisetum hyemale*, *Salix syrticola*, and *Juniperus spp.*, plus both beach grasses dominate the lee side of the dune. The low area behind the

Fig. 1 - Transects at Saugatuck, Michigan, summer 1956. The beginning of the transect on the left was determined by the beginning of higher vegetation. The symbols representing *Ammophila* also include *Calamovilfa*, and those which represent *Hudsonia* also include *Andropogon scoparius*.

Fig. 1 - Transects at Saugatuck, Michigan. Summer 1956

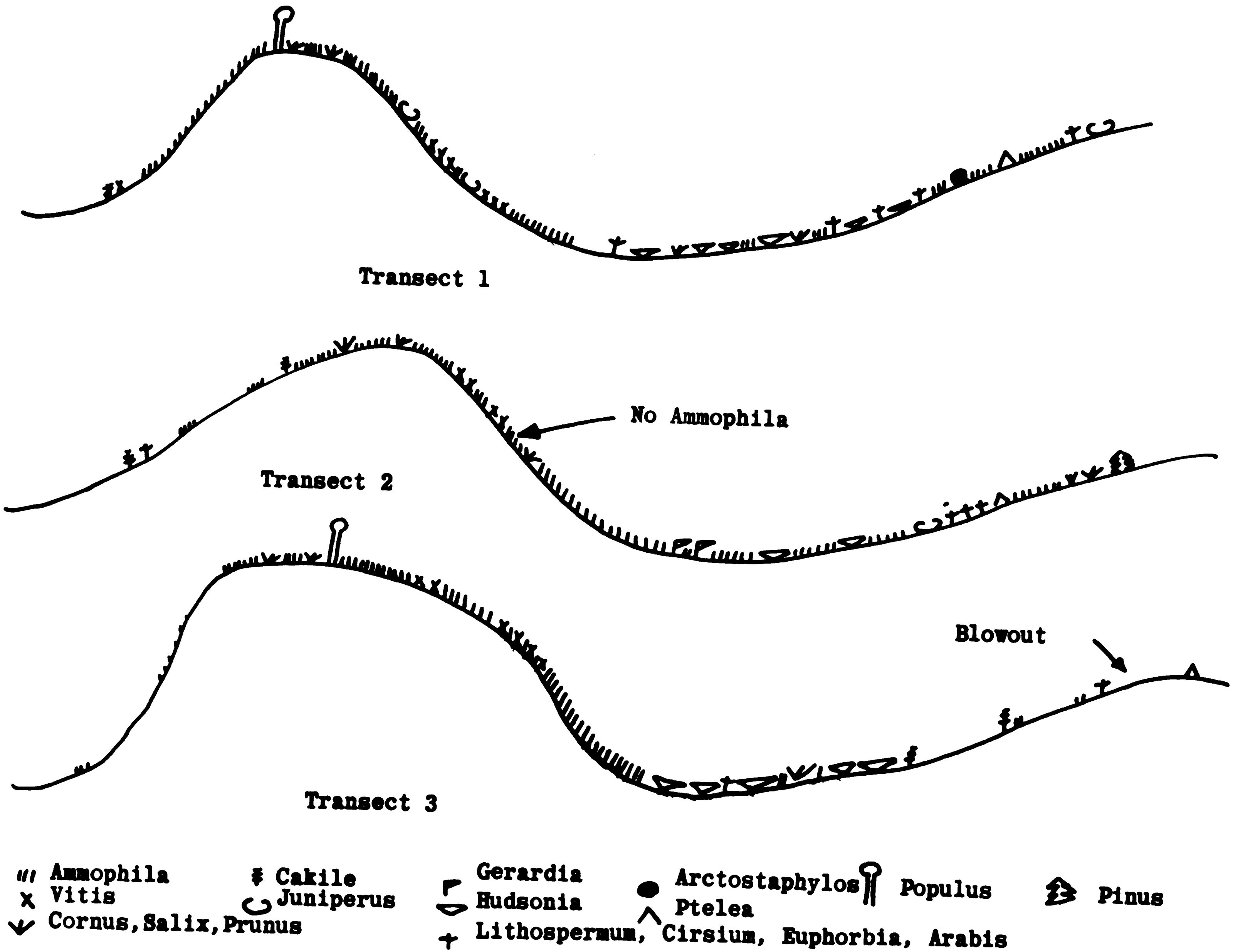


Fig. 2 - Michigan beaches.
Left - Strand as seen from the crest of the foredune at Saugatuck, Michigan, fall, 1955.

Right - Low area behind foredune, looking toward the dune forest at Sturgeon Bay, Michigan, summer, 1956.

Fig. 3 - Low area behind perched foredune, Sleeping Bear Dune, north of Empire, Michigan, Summer, 1956. Note prominent blowout on crest of dune, showing remnant of dune forest (Thujas) in the background. Note also the cottonwoods (Populus deltoides) in the foreground.

dune may have Artemisia caudata, Andropogon scoparius, Cakile edentula, Ammophila, Calamovilfa, Melilotus alba, Lithospermum croceum, with Gerardia paupercula and Eleocharis sp., Potentilla anserina in wet spots. The drier sites on the "low" yields Arabis lyrata or A. drummondii, Lithospermum, Cirsium pitcheri, Hudsonia tomentosa, Corispermum hyssopifolium, Arctostaphylos uva-ursi, and Asclepias syriaca. Beyond the "low" there is then a transition to the dune forest on the back dune with such species as Ptelea trifoliata, Dirca palustris, Ammophila, Tsuga canadensis, and Taxus sp.

The transects studied in New Jersey began at the edge of the ocean at high tide and extended to the road running behind the small back dune. The results are diagrammed in Fig. 4. Fig. 5 and 6 show sites at various points across the sand bar at Island Beach, N.J. Different species of the same genus occupy similar niches in Michigan and in New Jersey. Similarities of the dune environment are great enough to permit such floristic similarities.

As in Michigan, the lower beach is devoid of vegetation. The upper beach may have isolated individuals of Cakile or Ammophila. The foredune is stabilized largely by Ammophila, but occasionally Euphorbia polygonifolia, Cakile, or Artemisia stellariana appear. In occasional instances, Lathyrus japonicus var. glaber is present but it did not

Fig. 4 - Transects made at Island Beach, N.J., summer 1956. The distance from the base of the foredune on the left to the water is forty meters. The symbol "shrub" stands for Prunus maritima, Ilex opaca, Vaccinium corymbosum, or occasional Myrica pennsylvanicum. The term "liana" stands for Smilax rotundifolia or Parthenocissus quinquefolia.

Fig. 4 - Transects at Island Beach, N.J. summer 1956. Ocean forty meters to left of foredune.

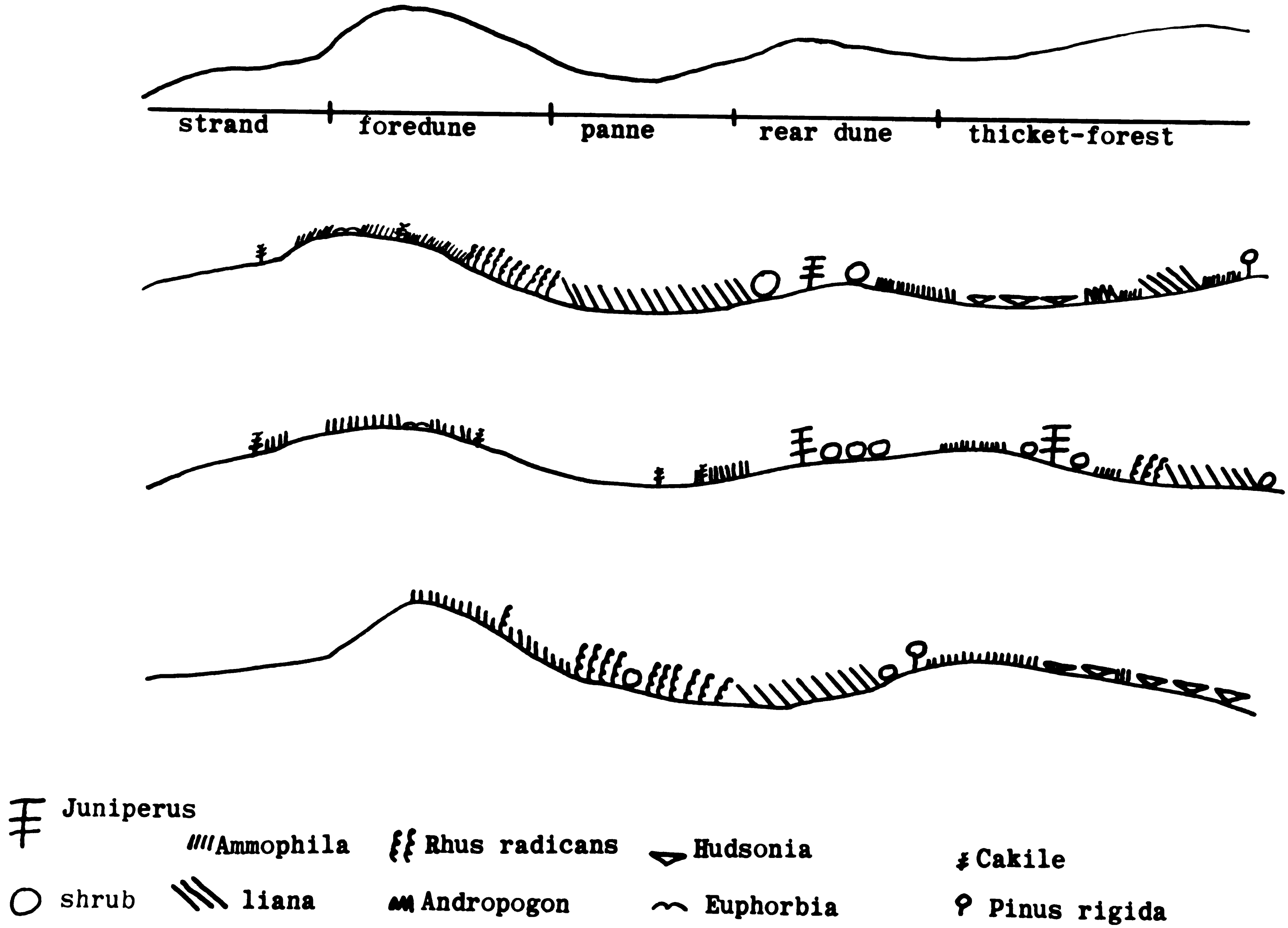
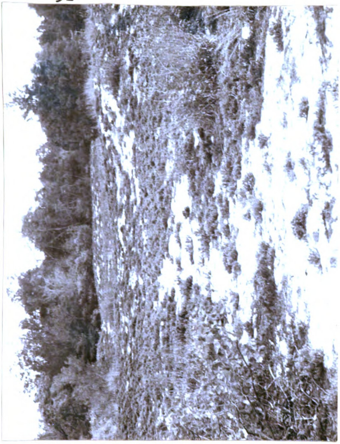


Fig. 5 - Left - Strand at Island Beach, N.J. with ocean to the left and foredune to the right. The strand here is forty meters wide. Spring, 1957.

Right - _Ammophila breviligulata_ on strand in front of foredune with ocean in background. Spring, 1957.

Fig. 6 - Left - View of shrub-liana low area behind the foredune (background). Prominent species in foreground are *Myrica pennsylvanica* and *Rhus radicans*. Island Beach, N.J., spring, 1957.

Right - *Hudsonia* bald at Island Beach, N.J. looking toward the thicket-forest, spring. 1957.



appear in any transect. On the lee side of the foredune, Ammophila gives way to a tangle of Rhus radicans and some Smilax rotundifolia or Parthenocissus quinquefolia. In some instances, this area is unstable in the form of a blowout. The first invaders are Cakile (see Fig. 7) or Ammophila. In some lower, wetter spots, there is a vast tangle of such shrubs as Prunus maritima, Myrica pennsylvanica, and Ilex opaca together with the Smilax and Parthenocissus. On the back dune, Juniperus virginiana is found: it has a characteristic "espalier" shape described by Boyce (1954) with older leaves killed back and only tufts of young leaves remaining (Fig. 8). Prunus and Myrica are abundant here, and still Smilax winds around the woody plants. The next "low" area is frequently a Hudsonia-lichen bald, but occasionally clumps of Andropogon scoparius or Opuntia humifusa enter. Ammophila appears throughout the transect, but is least abundant or even absent on stabilized dune crests behind the main foredune. As one approaches the thicket-forest, the vegetation becomes more varied with perhaps Ilex, Prunus, Pinus rigida, or Rhus and its "associates" present. Wet, boggy spots lie scattered along the bar where Typha, Phragmites, Sphagnum, and other species of wet sites are found.

Germination data. The results of germination tests may be seen in Tables II, III, and Iv. Some of the more striking results are shown graphically in Fig. 9, 10, and

Fig. 7 - *Cakile edentula* seedlings at the base of the parent plant in blowout at Island Beach, N.J., spring, 1957.

Fig. 8 - Low-shrubby site at Island Beach, N.J. showing espalier salt spray-wind form of *Juniperus virginiana*, spring, 1957.

TABLE II. Germination Percentages on Untreated and Pre-Chilled Seeds. (20° C.)
One hundred seeds were used for each trial except where indicated by *.
Figures indicate percentages for each trial with average in parentheses.

	Untreated	Pre-Chill	Nitrate plus Pre-Chill
Ammophila breviligulata (Mich.)	6, 3, 10 (6)	90, 78, 84 (84)	91, 90, 83 (88)
Ammophila breviligulata (N.J.)	15, 22, 24 (20)	89, 90, 87 (89)	89, 90, 93 (91)
Calamovilfa longifolia	12, 14, 10 (12)	46, 40, 43 (43)	89, 92, 93 (91)
Cakile edentula (Mich.)	16, 16, 18 (16)	16, 14, 18 (16)	14, 18, 18 (17)
Cakile edentula (N.J.)	24, 20, 27 (24)	22, 16, 16 (18)	24, 16, 16 (19)
Arabis lyrata	88, 88, 86 (88)	--	--
Pinus banksiana	33, 35, 30 (33)	45, 62, 49 (52)	40, 50, 54 (48)
Pinus rigida	54, 49, 58 (54)	64, 86, 87 (79)	84, 86, 84 (84)
* Corispermum hyssopifolium	6, 16, 12 (11)	60, 66, 68 (64)	--
Gerardia paupercula	0, 0, 0 (0)	100, 98, 99 (99)	--
* Prunus pumila	0, 0, 0 (0)	92, 80, 86 (86)	--
* Lathyrus japonicus var. glaber (scarified)	99, 99, 100 (99)	--	--

* Fifty seeds used.

TABLE III - **Treatment of seeds with sea water.** Soaking was for twelve hours and then the seeds were removed and placed in petri dishes on blotters moistened with distilled water.
Spray treatment records number of application s of sea water spray and the percentage wilted at the end of the last application. Carried out at 20° .

	Soaked in sea water	Control (ave. % germination)	Spray treatment # trials	Spray treatment % wilted
Ammophila breviligulata (Mich.)	8, 9, 9 (9)	[illegible]	8	88
Ammophila breviligulata (N.J.)	84, 80, 89 (84)	[illegible]	10	0
Calamovilfa longifolia	75, 79, 80 (77)	[illegible]	10	40
Cakile edentula (Mich.)	14, 19, 22 (18)	[illegible]	10	0
Cakile edentula (N.J.)	14, 23, 26 (21)	13	10	0
Arabis lyrata	0, 0, 0 (0)	86	2	75
Pinus banksiana	0, 0, 0 (0)	52	5	90
Pinus rigida	70, 75, 66 (70)	79	8	94
* Corispermum hyssopifolium	18, 20, 20 (19)	[illegible]	3	96
Gerardia paupercula	86, 89, 92 (89)	99	3	70
* Prunus pumila	0, 0, 0 (0)	85	1	87
* Lathyrus japonicus var. glaber	98, 99, 99 (99)	99	10	0

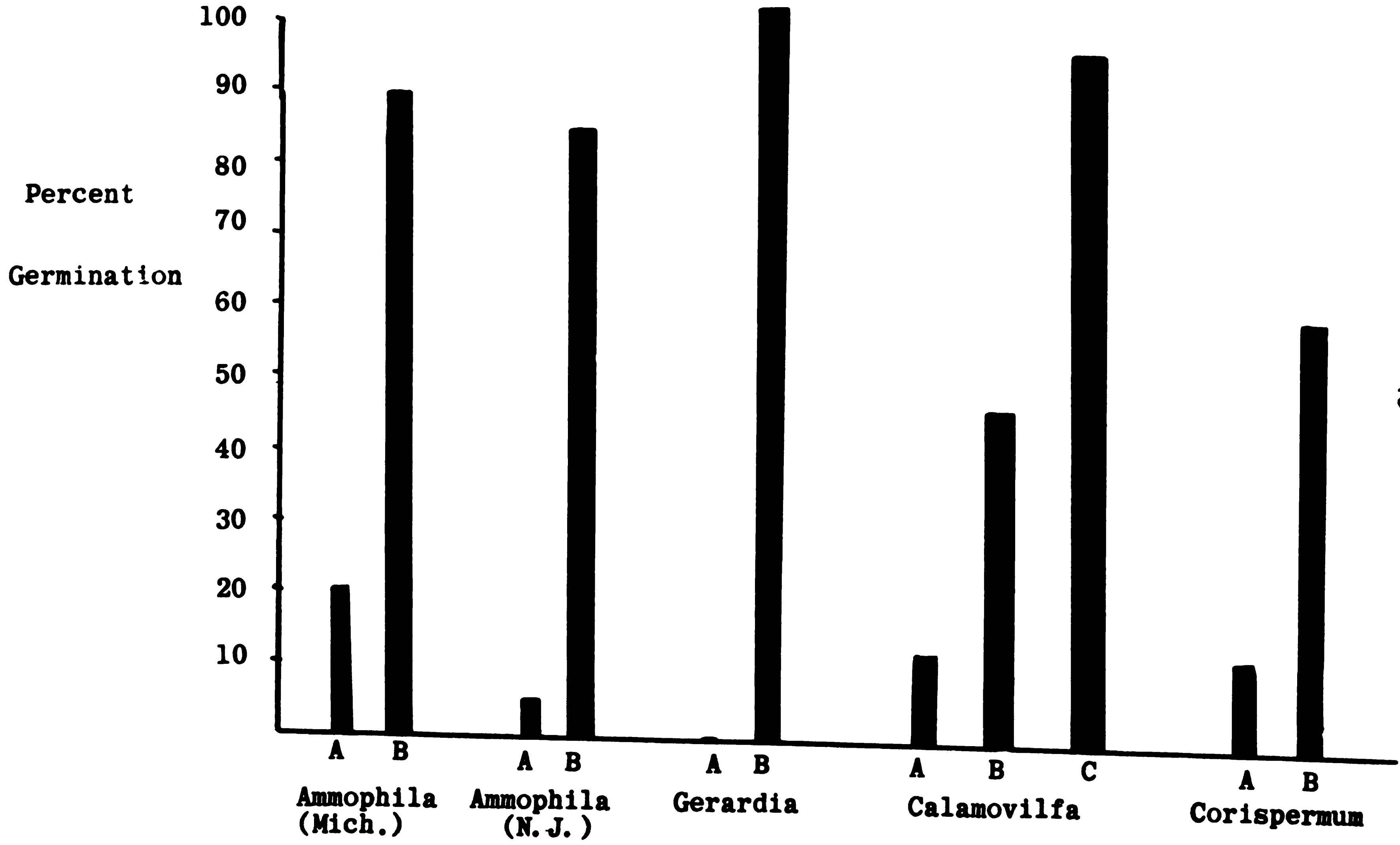
*Fifty seeds; all others one hundred

TABLE IV. Germination under high temperatures (40° C.), and desiccation.
A-Hypocotyl emerged 0.25 inch or less, expressed in days to show wilting or necrosis
B-Hypocotyl emerged more than 0.25 inch, expressed in days to show wilting or necrosis
C-Hypocotyl and epicotyl both emerged, expressed in days to show wilting or necrosis
Per cent recovery is for a five-day period.

	High Temperatures	A	% Recovery	B	% Recovery	C	% Recovery
Ammophila breviligulata (Mich.)	65, 68, 73 (69)	2	22	3	35	4	78
Ammophila breviligulata (N.J.)	74, 74, 75 (74)	2	16	3	52	4	52
Calamovilfa longifolia	80, 74, 92 (82)	6	16	7	14	7	53
Cakile edentula (Mich.)	8, 8, 8 (8)	1	0	1	0	½	0
Cakile edentula (N.J.)	8, 10, 7 (8)	1	0	1	0	½	0
Arabis lyrata	18, 14, 21 (18)	2	72	3	70	3	70
Pinus banksiana	0, 0, 0 (0)	½	96	½	95	½	5
Pinus rigida	8, 9, 10 (9)	1½	93	1½	95	1½	77
* Corispermum hyssopifolium	32, 33, 35 (33)	1	81	2	72	3½	8
Gerardia paupercula	16, 18, 18 (18)	2	78	1½	0	3	0
* Prunus pumila	24, 28, 32 (28)	4	8	4	0	4	0
* Lathyrus japonicus var. glaber (scarified)	18, 16, 24 (20)	6	89	8	80	8	81

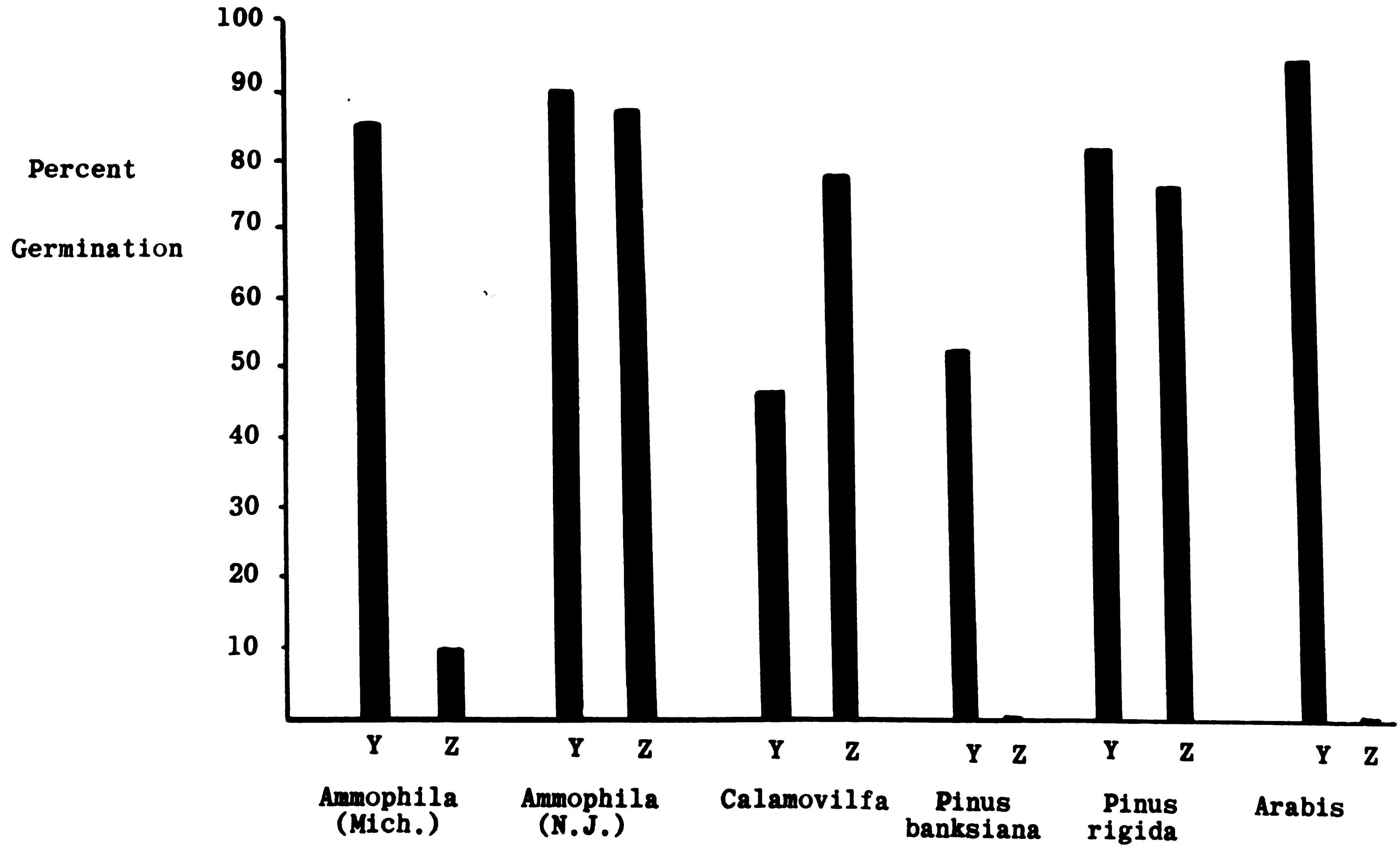
*Fifty seeds used; others used one hundred per test.

Fig. 9 - Importance of pre-chill on certain sand dune plant species. All are germinated with distilled water except Treatment C with *Calamovilfa*.



A - no pre-chill B - pre-chill C - pre-chill with NO_3 added

Fig. 10 - Effect of Sea water on germination of certain sand dune plant species.



Y - Pre-chill, germinated in distilled water

Z - Pre-chill, 12-hour soaking in sea water, germinated in distilled water

Fig. 11 - Calamovilfa longifolia seeds germinating in petri dish.

A- Soaked for 12 hours in sea water before germinated.

B- Soaked for 12 hours in distilled water before germinated.


A

11. Fig. 9 shows the differences in germination with and without a pre-chill treatment. Arabis lyrata does not need any such pre-chill, but Gerardia will not germinate at all without such treatment, and will germinate almost completely with such treatment. Ammophila, Calamovilfa, and Corispermum respond favorably to such a treatment, with the degree of germination stepped up by the cold treatment.

As shown in Fig. 10, most species from the Michigan sites are adversely affected by the soaking in sea water, but the New Jersey species show little effect. It is especially interesting to note the racial adaptation of the New Jersey population of Ammophila to salt tolerance. (See Fig. 12) The epicotyls of its seedlings in the New Jersey population averaged 14 mm. long after five days, whereas those of the Michigan population were only 3.3 mm. for those that germinated. Calamovilfa is the only plant whose germination is enhanced by soaking in sea water (see Fig. 11). No species germinated directly in sea water (note Table III). A small number of Pinus rigida seeds from the Adirondack Mountains of New York State (purchased from the Pearce Seed Co., New York City) produced in one test 72% germination after soaking in sea water for twelve hours.

Those seeds for which poor germination results were obtained are listed, together with germination results, in Table V. Perhaps further study involving application

Fig. 12 - Germinating <u>Ammophila</u> <u>breviligulata</u> seeds.
A - Seeds from the Michigan population
B - Seeds from the New Jersey population

Both sets of seeds were soaked for 12 hours in sea water and then placed on blotting paper moistened with distilled water.

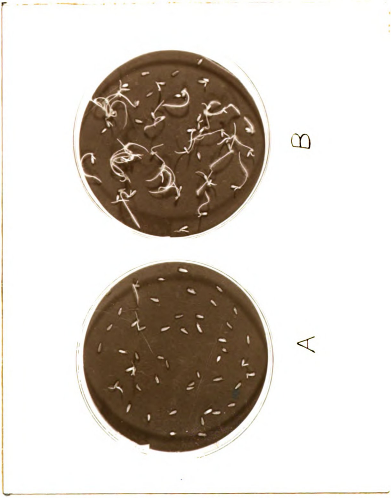

B
A

TABLE V. Species with Poor Germination (After-ripened ones indicated by *)
One hundred seeds per test.

	Collected	Test Length	% in water 20° C.	% in water 20-30° C.	% in NO_3 20° C.	% scarified ½ hour
Asclepias syriaca	Michigan	3 weeks	6	-	2	-
Campanula rotundifolia	Michigan	4 weeks	10	-	10	0
* Camranula rotundifolia	Michigan	3 weeks	3	-	-	-
Carex kobomugi	New Jersey	3 weeks	0	0	0	0
* Carex kobomugi	New Jersey	3 weeks	0	0	0	0
Celastrus scandens	Michigan	3 weeks	2	4	14	0
Euphorbia corollata	Michigan	4 weeks	4	6	2	0
* Euphorbia corollata	Michigan	3 weeks	5	9	5	0
E. polygonifolia	New Jersey	4 weeks	0	0	0	0
* E. polygonifolia	New Jersey	3 weeks	0	0	0	0
Juniperus horizontalis	Michigan	4 weeks	0	0	0	0
* J. horizontalis	Michigan	3 weeks	0	0	0	0
Prunus maritima	New Jersey	4 weeks	0	0	0	-
Rhus radicans (1955 crop)	New Jersey	4 weeks	2	0	0	6
* Rhus radicans (1955 crop)	New Jersey	4 weeks	6	-	-	0
Rhus radicans (1956 crop)	New Jersey	4 weeks	6	0	16	6
* Rhus radicans (1956 crop)	New Jersey	4 weeks	8	0	0	-
Rhus radicans	Michigan	4 weeks	0	0	0	0
* Rhus radicans	Michigan	4 weeks	0	0	0	0
Smilax rotundifolia	New Jersey	4 weeks	0	0	0	0
* S. rotundifolia	New Jersey	4 weeks	0	0	0	0
Smilacina stellata	New Jersey	4 weeks	0	0	0	0
* Smilacina stellata	New Jersey	4 weeks	0	0	0	0

of combinations of various tests will produce fruitful results with these species too.

DISCUSSION

Germination as a factor in zonation. To say that seed germination factors control the presence or absence of a species in a habitat would be a gross overstatement, but to infer that factors which tend to control or limit the ability of a seed to germinate under certain conditions also tend to limit the ability of that species to establish itself under the given conditions merits consideration. Let us consider in this field the influence on seed germination of temperature, desiccation, and sea salts, noting particularly responses to those conditions encountered in the study areas.

Temperature. Except for two species discussed below, all those tested responded to an after-ripening re-chill treatment with a more rapid and a higher total germination. Ammophila disappears south of North Carolina and a pre-chill was needed for significant germination. It is possible that one of the factors which govern the limits of the range of Ammophila may be the presence of the low temperature period prior to germination. When 5° C. temperatures occur for weeks only occasionally, establishment of the species would not be enhanced. One might infer that lower germination percentages and slower germination without cold treatment may reduce the frequency of appearance of Ammophila on southern dunes, but applying tests similar to those mentioned above to southern races will be necessary before adequate evaluation may be made.

High temperatures of 40° C. for part of each day had significant effects upon seed germination. Ammophila germinates, but the seedlings show signs of necrosis after several days at high temperatures, but Calamovilfa does well under the same circumstances. This might mean that Ammophila needs to be buried whereas Calamovilfa does not. It also may indicate that Ammophila needs to germinate in the spring, as it does, before temperatures grow to be excessively high. Both Pinus banksiana and P. rigida are apparently uninjured by a short exposure to high temperatures; in fact, more rapid germination is brought about by the high temperatures. Several day-old seedlings, on the other hand, exposed to these temperatures were killed. Most of the other species tested showed adverse effects due to high temperatures.

Lathyrus is not greatly affected by high temperatures, especially if of short duration. Its large seed is frequently seen carried along by the wind on the dune surface, where it will be exposed to the rigors of high temperature. That Lathyrus did not show poorer germination capacity due to high temperatures is therefore significant.

Lathyrus, unlike other seeds mentioned here, needed a scarification treatment before successful germination. Although acid was used in the laboratory, enzymatic action of bacteria and fungi probably account for scarification of seed coat in nature. Scarification of the seed coat may serve the same function as a pre-chill in other seeds, i.e. preventing germination until the winter is past.

Desiccation. The tolerance of a seedling to drying is important to its successful establishment. Bormann (1953), when studying drought-resistance of Pinus taeda compared to Liquidambar styraciflua, observed greater drought-resistance in younger seedlings. Pinus banksiana wilted faster than P. rigida, but recovery in both was good. The roots of P. banksiana arched up over the blotting paper, but the roots of P. rigida burrowed into the blotting paper. This latter tendency to penetrate the substrate better may be indicative of the greater ability of P. rigida to withstand drying out. Bormann's studies (1953) noted a similar phenomenon in the nature of the taproot of Liquidambar. Pinus banksiana is usually found on Michigan dunes in the mesic sites covered with protection from evaporation by Arctostaphylos and Juniperus horizontalis or other species affording good cover.

Effects of desiccation have been worked out in seedlings of Pisum sativum by Nemmer and Luyet (1954). They have shown that drying of pea seedlings had more detrimental effects as the seedling matured. Younger seedlings (6-9 mm. long) could withstand drying to 30% water content, but older ones (10-25 mm. long) died when reduced to 40-60% water content. Recovery, by addition of water, was more successful for the younger seedlings than for the older ones. In fact, younger seedlings could be re-dried several times without permanent damage. Most of the seeds I worked with wilted in ½-2 days in the desiccator, but Lathyrus and Calamovilfa existed in this state for six days before wilting occurred. The Lathyrus seed has a smaller surface-to-volume ratio than most of the other seeds; it probably takes longer to deplete its stored supplied of water than the other seeds do. Prunus pumila has a seed larger than that of Lathyrus, yet the length of time to produce wilting symptoms in Prunus is much reduced, although it is still longer than for most of the other species tested. Recovery percentages indicate, however, that Lathyrus is capable of returning to vigorous growth, but Prunus has virtually no drought resistance. Although Prunus may take four days to wilt initially, possibly because of the water which may be trapped between the endocarp and the seed coat, it is unable to recover from wilting. Its ability to pioneer some sand-swept areas may be due in part to the moisture which is trapped in the fruit.

The recovery data in general are subject to some error in that two different criteria were used to indicate recovery: either initiation of growth of a new root, or return of turgor. Ammophila, Calamovilfa, and Lathyrus grew new roots; the remaining seedlings simply regained turgor. All those which may produce a new root showed greater recovery percentages than almost all other species. The percentages of recovery for the above-mentioned forms appear to increase with ages, but grasses typically develop seminal roots; not so with Pisum (Nemmer & Luyet 1954) but it should be pointed out that necrosis of the root tip is the criterion for recognizing desiccation in the earliest stages, while simple wilting served in the more advanced stages. Thus the degree of desiccation damage was greater in the younger stages, notwithstanding the findings of Nemmer and Luyet from anatomical studies that necrosis is a superficial phenomenon. Temporary recovery may appear as it does in the return of moisture simply as in reviving wilted cut flowers, but true recovery from drought lies in the ability of certain seedlings to regenerate a new root. The ability to grow new roots is of advantage to Ammophila, Calamovilfa, and Lathyrus, since they grow in sites of motile sand where drying becomes a problem, due to the dry, blowing sand.

For those seedlings which do not regenerate a new root as a mechanism of recovery from drought, recovery is fairly good for the most part in early seedling stages, but drops off as the seedling matures. These data are in agreement with those of Nemmer and Luyet for Pisum. Inasmuch as necrosis from drought is superficial, then wilting used as indicative of response may simply mean that the outer tissues have wilted. Recovery, then, is a measure of the ability of the inner core of root meristem to resume activity. Gerardia, however, recovers from drought in its earliest stages only. Beyond this point, it has virtually no drought resistance. Gerardia is characteristically a species of the wet, low sites behind the foredunes. It is possible that in drier sites, the probability of drying out after hypocotyl emergence becomes prohibitive. By the same token, Arabis has the drought resistance which Gerardia lacks, since it can apparently recover fairly well from desiccation even at advanced stages of seedling development. Cakile, although a species of the drier, unstable sites, has no resistance to drought in the seedling stage, but young plants with four or more leaves kept in the laboratory without addition of moisture remain succulent for several days. As shown in Fig. 8, many Cakile seeds may germinate together, as in the site immediately around last season's parent plant. Depth of burial or rapid root penetration exhibited by Cakile may figure in its successful establishment.

Corispermum is found on very dry sites in the low area between the fore- and back- dunes, but it seems to be quite susceptible to drying-out damage. It does, however, produce a very rapidly growing root which can penetrate into the soil readily. Despite its susceptibility to drought, Corispermum is able to tap moist sand below the surface by means of a fast-growing root.

Calamovilfa bears mentioning in regard to its response to desiccation. Its seedlings remained vigorous for the longest exposure to drying, outside of Lathyrus. It is characteristically found on sites of moving sand where the seeds may easily be covered and uncovered. From Fig. 1, one sees that Calamovilfa is found on the lee- or depositing slope.

Salt as a factor in geographical separation. Results of salt treatments are interesting. All species except Prunus, Arabis, and Pinus banksiana germinated to a greater or lesser extent following soaking in sea water for twelve hours. These three species are those which are found in Michigan and not in New Jersey, and therefore do not normally become exposed to salt spray in their environment.

Calamovilfa actually germinates better after a soaking in sea water than without such a treatment. This fact is at first anomalous, since this species is not found on ocean dunes. It should be noted, however, that it also germinates better when treated with a 0.2% KNO_3 solution (see Figs. 10 and 11), so its adaptation to more successful germination after immersion in sea water may be tied in more closely with a factor of mineral nutrition from sea salts, rather than a response to sea salt alone.

Germination of Ammophila from New Jersey after soaking in sea water was about as good as normal germination. The percentage germination as well as the length of the seedling were much better than these same characteristics of Michigan populations of Ammophila (See Fig. 10 and 12). Sea spray also brought about a differential response between New Jersey and Michigan populations in that the Michigan populations, although somewhat resistant to salt damage wilted after eight treatments. It is apparent that Ammophila possesses in New Jersey a race which is not so greatly affected by salt as is its counterpart in the Michigan populations, or the inland populations have simply lost a salt tolerance.

Tests on other seeds soaked in sea water produced noteworthy results. Pinus rigida, which is found only on New Jersey dunes, not in Michigan, is tolerant of soaking in sea water, but, as previously mentioned, Pinus banksiana, which grows in Michigan and not in New Jersey, is not. Gerardia and Lathyrus, which grow in both areas but were collected only from Michigan, are not affected much by soaking in sea water. These plants have not developed population differences in reaction to sea water, as have populations of Ammophila.

Salt spray damage to young seedlings has effects which are quite different for different species. Tests made by spraying seedlings reveal that only one sea water blast is sufficient to wilt Prunus pumila. It is interesting that this species does not appear in New Jersey, where salt spray is definitely an important environmental factor. Salt spray has been known to produce aberrations in growth forms, the espalier form of some vegetation as an example. Cakile from either state is unaffected by even ten such blasts with sea water. Michigan Ammophila shows a slightly greater susceptibility to salt spray damage than does its New Jersey counterpart, with about as many plants wilting after three treatments as after 8 treatments for the marine form. The other inland species tested showed very slight tolerance to salt spray.

Coupin (1898) found that Cakile growing in 4% NaCl died, that growing in 3% fared moderately well, and that growing in a 2.8% solution thrived. He noted the relation of successful growth in salt concentrations approaching that of sea water (3.5%). Garden peas and vetch were killed in concentrations of NaCl of only 1%. He writes (translated from the French): "We shall conclude therefore that maritime plants are adapted almost exactly to the proportion of sodium chloride contained in the sea...." Perhaps this idea may be carried further to include salt spray tolerance also.

Species with poor germination or with poor seed drop.

Various seeds responded poorly to seed tests. Neither nitrate, nor alternating pemperatures, nor pre-chill, nor scarification produced substantial germination. These species are noted in Table V. Other species like Artemisia stellariana or Lathyrus in New Jersey did not set seed well during the season studied. On the other hand, seeds of Artemisia caudata undoubtedly set seed during my absence from Michigan, since seedlings of it were found this spring.

Carex kobomugi was treated in a variety of ways, inasmuch as no one has heretofore germinated any of its seeds (Small 1954). Treatment with triphenyl-tetrazolium chloride as an indicator of viability (Cottrell 1947) suggested that the embryos were not living. All other seeds for which good germination was not obtained were subjected to the whole series of treatments. It is possible that a combination of treatments will prove successful in future experimentation.

CONCLUSIONS

1. Cold temperatures for a period of time are necessary for successful germination of most species that were tested from either New Jersey or Michigan. Ten out of twelve species exhibited improved germination.

2. In view of high surface temperatures reported for dune soils, burial or early spring germination seem to be required for successful establishment.

3. Of twelve species whose seeds were soaked in sea water, seven had reduced germinative capacity. Seeds of *Cakile edentula* collected in both areas showed no difference in germination response to soaking in sea water, while those of *Ammophila breviligulata* indicated racial differences. The Michigan population showed a marked reduction in germination following a soaking in sea water. Experiments with *Lathyrus*, which occurs in both areas, suggests that all species do not exhibit salt resistant races: the Michigan population shows no reduction in germination following a soaking in sea water. *Calamovilfa*, which does not occur on New Jersey dunes, shows a marked increase in germination following a soaking in sea water. *Pinus rigida* which does not occur in Michigan shows a salt-tolerance not exhibited by *P. banksiana*, its "ecological equivalent" in Michigan.

4. Of twelve species subjected to salt spray, eight showed damage, *Prunus pumila* being the most sensitive. *Ammophila* again exhibited a racial difference in resistance to sea water, the Michigan collection showing greatest damage. Again the pines showed a differential reaction to salt, *P. rigida* showing a salt tolerance lacking in its Michigan counterpart, *P. banksiana*. Neither Michigan nor New Jersey collections of *Cakile* seedlings exhibited salt spray damage, nor did Michigan collections of *Lathyrus*.

5. Seeds at different stages of germination showed different degrees of recovery following desiccation. *Ammophila* and *Calamovilfa* showed a higher recovery in later stages of germination. *Gerardia*, on the other hand, showed no recovery when desiccation took place after the hypocotyl had emerged more than 0.25 inch. Six out of twelve species tested showed an ability to recover following desiccation. Of these six, four, including *Calamovilfa*, *Lathyrus*, and two populations of *Ammophila*, were able to differentiate a new root.

Summary conclusion. The above findings indicate, at least in some areas, that germination characteristics appear to contribute to the ability to occur on particular sites on the sand dune vegetation patterns.

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