Technical Report No. 6

SEED DISPERSAL METHODS IN HAWAIIAN METROSIDEROS

Carolyn Corn

Department of Botany
University of Hawaii
Honolulu, Hawaii

ISLAND ECOSYSTEMS IRP

U. S. International Biological Program

August 1972

ABSTRACT

Hawaiian *Metrosideros* seeds need 3 to 12 miles per hour wind velocity to become airborne, and can survive -30^{o}C temperatures for at least 6 hours. They also survive sea water soaking for 30 days followed by an additional 7 day desiccation period. These conditions substantiate a belief that *Metrosideros* species arrived in the islands by wind dispersal, and can also travel shorter distances by water currents.

INTRODUCTION

Long distance dispersal has been discussed by Guppy (1906) and Ridley (1930). Birds have been described as hypothetical and active agents in transporting seeds over long distances by such authors as Cruden (1966) and de Vlaming and Proctor (1968); wind as an active agent of long distance dispersal has been illustrated in insects by Yoshimoto and Gressitt (1961); and water dispersal and rafting have been reported by Powers (1911) and Zimmerman (1948).

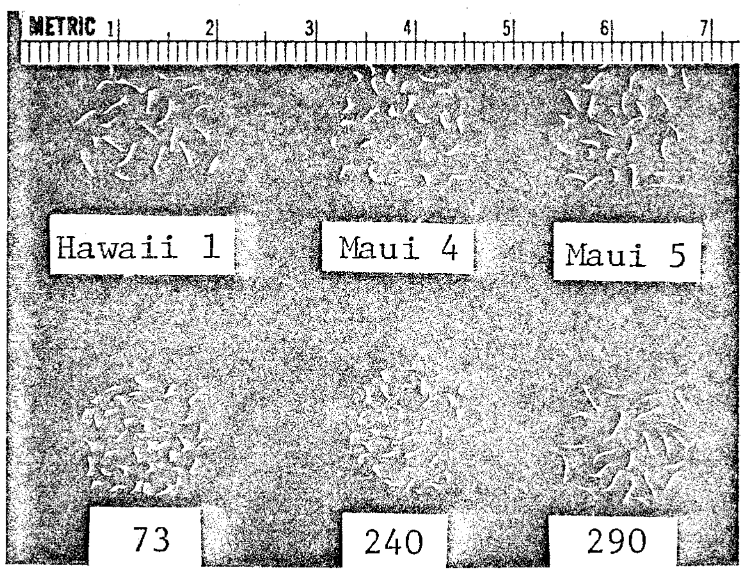
The Hawaiian flora and fauna are living proof that long distance dispersal is effective. Since the Hawaiian Islands are oceanic islands built in the last 20 million years by volcanism (Macdonald & Abbott, 1970) and isolated from other land masses by wind and water currents (Gressitt, 1961 and Visher, 1925) by distances of 2000 miles or more (except for Johnston Island, a small atoll some 600 miles to the southwest), plants and animals found on the islands must have ancestors that survived the long trip to the islands. The biota of these islands is considered to be most remarkable in terms of long-distance dispersal. Carlquist (1965, 1966, 1967, 1970), Fosberg (1963), and Zimmerman (1948) have indicated actual and hypothetical methods of dispersal for some of the native Hawaiian plants and animals. However, little experimental work has been done on seeds of native plants to see if they can survive transport by air, water, or bird.

Metrosideros seeds are numerous and small, but no data has been published on the wind velocities necessary to disperse the seeds, or if the seeds might be transported by water. A series of experiments were undertaken to indicate the potential dispersal mechanisms which could have been involved.

Hawaiian Metrosideros seed material is variable in size, shape, color, and weight. The small seeds may be straight, slightly curved, or curved as much as 90°, with the widest portion at the middle or curved part of the seed (figure 1). Upon cursory examination of the anatomical seed characteristics, the author believes that the Hawaiian seed material is similar to those described by Dawson (1970) from New Zealand Metrosideros. The embryo is surrounded by a seed coat of no more than a few cells in thickness, the outermost layer being lignified. Young mature seeds appear to be almost translucent, with seeds that have been stored becoming darker in color.

The genus is not only highly variable in seed characteristics, but also in vegetative and floral characters. This places the taxonomist in a difficult position. Rock (1917) described the genus as having 5 species - M. tremuloides, M. Waialealae, M. macropus, M. rugosa and M. collina. The first four species are found in small areas on the oldest main islands of Kauai and Oahu, with the fifth species, M. collina, subspecies polymorpha, occurring throughout all the main islands. He further divided this widespread subspecies into 15 varieties and forms. All of the seed material used in this paper are from trees that would be classified according to Rock (1917) as this subspecies. It occurs from sea level to almost 8300 feet elevation in areas with annual average rainfalls ranging from 30 to 450 inches. Where Metrosideros colonizes open lava fields, it occurs as a small tree or shrub; in wet fern forests it occurs as a tall tree 50 feet or more tall; and in bogs it occurs as a prostrate shrub blooming when only a few inches tall. It is the most common tree of the native forests.

Figure 1. Variation of Hawaiian <u>Metrosideros</u> seed from Hawaii, Maui, and Oahu.



METHODS AND RESULTS

Experiment #1. Seeds from various elevations and diverse tree varieties were gathered from the islands of Kauai, Oahu, Maui, and Hawaii. Those seed samples that exhibited the largest diversity in size, shape, and weight were used in this experiment to obtain seed measurements of maximum variability. Each seed sample was composed of 200 seeds from a single tree. These samples were weighed, and lengths and diameters measured before they were subjected to wind velocity experimentation. Seed weight was determined by weighing a 200 seed sample.

Wind velocity measurements were obtained by placing the seed sample on the lower cheesecloth of a seed sorter machine (figure 2), placing a glass tubing over it, starting the motor, increasing the wind velocity from 0 to 15 miles per hour, and recording when the first and last seeds of the sample were lifted into the upper part of the machine. The midpoint between the maximum and minimum wind velocity readings was obtained for each sample.

When the velocity of the wind upward was equal to the gravitational force pulling downward upon the seeds, the seeds remained suspended in mid-air. This flow rate was between 3.5 and 11.5 miles per hour, and at this wind velocity the seeds could be suspended indefinitely in air. This technique bypassed the necessity to compute theoretically the seed's surface area and mass to derive its floatability.

The 25 samples of seed show a range of seed size and weight. Individual seeds varied as much as .5 to 4.5 mm in length and .1 to .7 mm in width. However, the average length and width values computed for each 200 seed sample have less variation with the median of seed length between 1.0 and 3.0 mm and width between .1 and .5 mm. Table I gives these average values with standard

Figure 2. Seed Sorting Machine

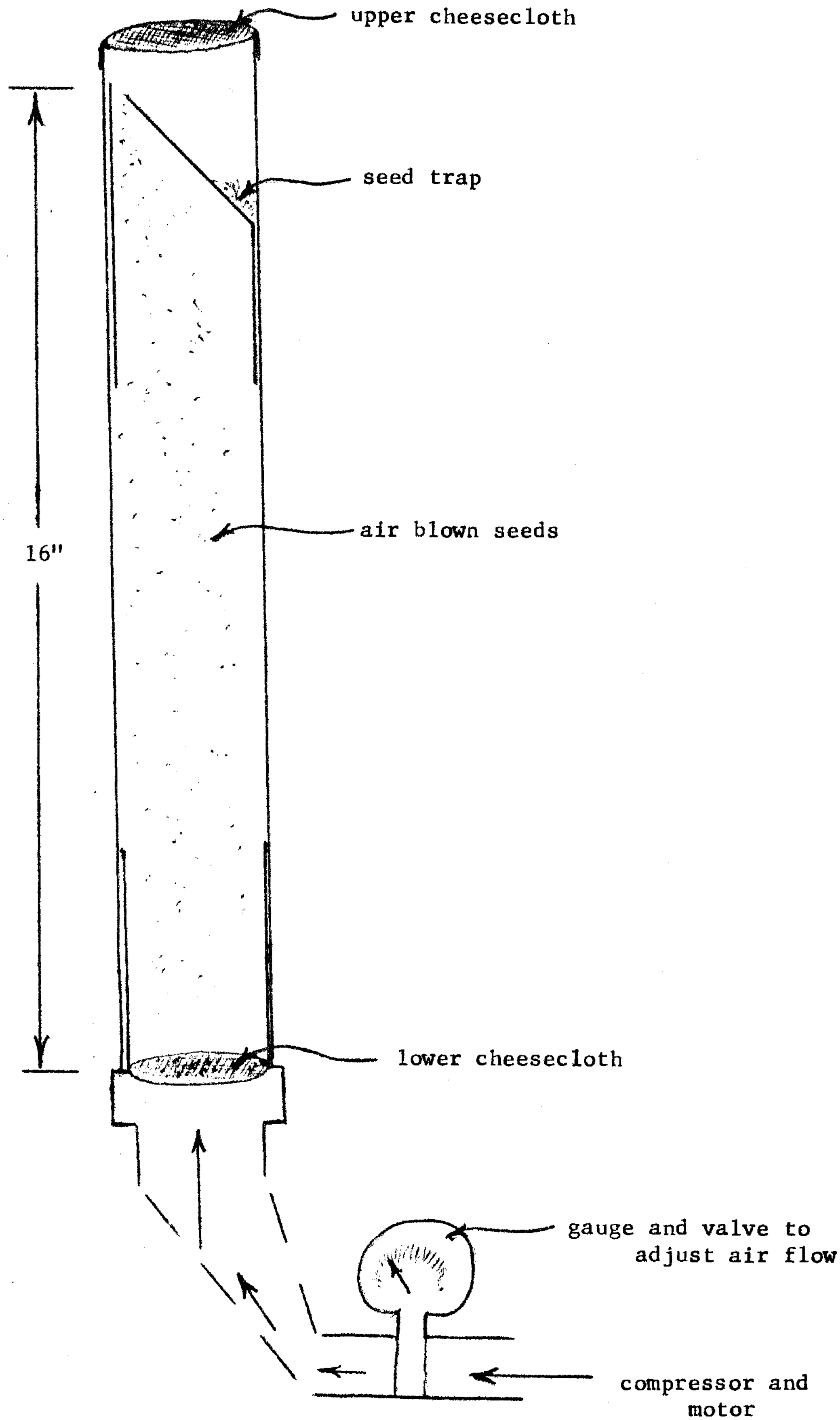


TABLE I

Sample No.	Locality	Elevation (ft)	Seed length (mm)	Seed width (mm)	Seed weight (mg)	Wind velocity to suspend seeds (mi/hr) Minimum	Maximum	Median
H-1	Hawaii: Volcano House	4100	2.71±.54	.23±.05	.0530	3.5	9.5	6.5
H-2	Hawaii: Puu Huluhulu	3200	2.60±.51	.25±.06	.0705	4.5	11.5	8.0
H-3	Hawaii: Waldron Ridge	3800	2.21±.64	.24±.05	.0500	3.5	9.5	6.5
H-4	Hawaii: Halemaumau	3700	2.16±.42	.22±.04	.0400	3.5	9.5	6.5
M-4	Maui: Waikomoi Lower Pipeline Trail	3000	1.84±.32	.39±.09	.0895	3.5	11.5	7.5
M-5	Maui: Fleming Mt. House West Maui	2980	2.26±.47	.32±.07	.0535	3.5	10.5	7.0
K-289	Kauai: Kokee	3300	1.90±.44	.23±.08	.0715	5.5	11.0	8.5
73	Oahu: Kipapa Trail	2500	1.64±.42	.19±.06	.0320	4.5	10.5	7.5
78	Oahu: Kipapa Trail	2500	1.74±.37	.22±.07	.0430	3.5	10.5	7.0
211	Oahu: Palikea	2500	1.72±.31	.24±.05	.0450	4.5	9.5	7.0
214	Oahu: Palikea	2600	1.66±.35	.36±.09	.1367	3.5	11.5	7.5
215	Oahu: Palikea	2700	1.65±.39	.36±.10	.0850	6.5	11.5	9.0
216	Oahu: Palikea	2800	2.06±.56	.43±.09	.1340	3.5	11.5	7.5
224	Oahu: Palikea	2600	1.49±.41	.25±.07	.0555	5.5	10.0	8.0
225	Oahu: Palikea	2800	1.91±.45	.34±.10	.0735	5.5	10.5	8.0
239	Oahu: Palikea	2600	1.70±.34	.23±.06	.0500	3.5	10.0	7.5
240	Oahu: Palikea	2600	1.72±.32	.30±.06	.0610	4.5	10.5	7.5
263	Oahu: Laie Trail	1000	1.88±.57	.39±.08	.1090	3.5	11.5	7.5
268	Oahu: Laie Trail	1125	2.12±.36	.26±.06	.0525	5.5	10.5	8.0
273	Oahu: Laie Trail	1350	1.49±.23	.36±.07	.0640	5.5	10.5	8.0
275	Oahu: Laie Trail	1350	1.84±.36	.41±.07	.0785	5.5	10.0	8.0
279	Oahu: Laie Trail	1400	1.58±.47	.30±.07	.0505	5.5	10.0	8.0
280	Oahu: Laie Trail	--	2.62±.52	.20±.07	.0500	5.5	10.5	8.0
287	Oahu: Palikea	2600	2.17±.47	.36±.09	.1315	5.5	11.5	8.5
290	Oahu: University of Hawaii	250	2.77±.57	.22±.06	.0625	5.5	10.0	8.0

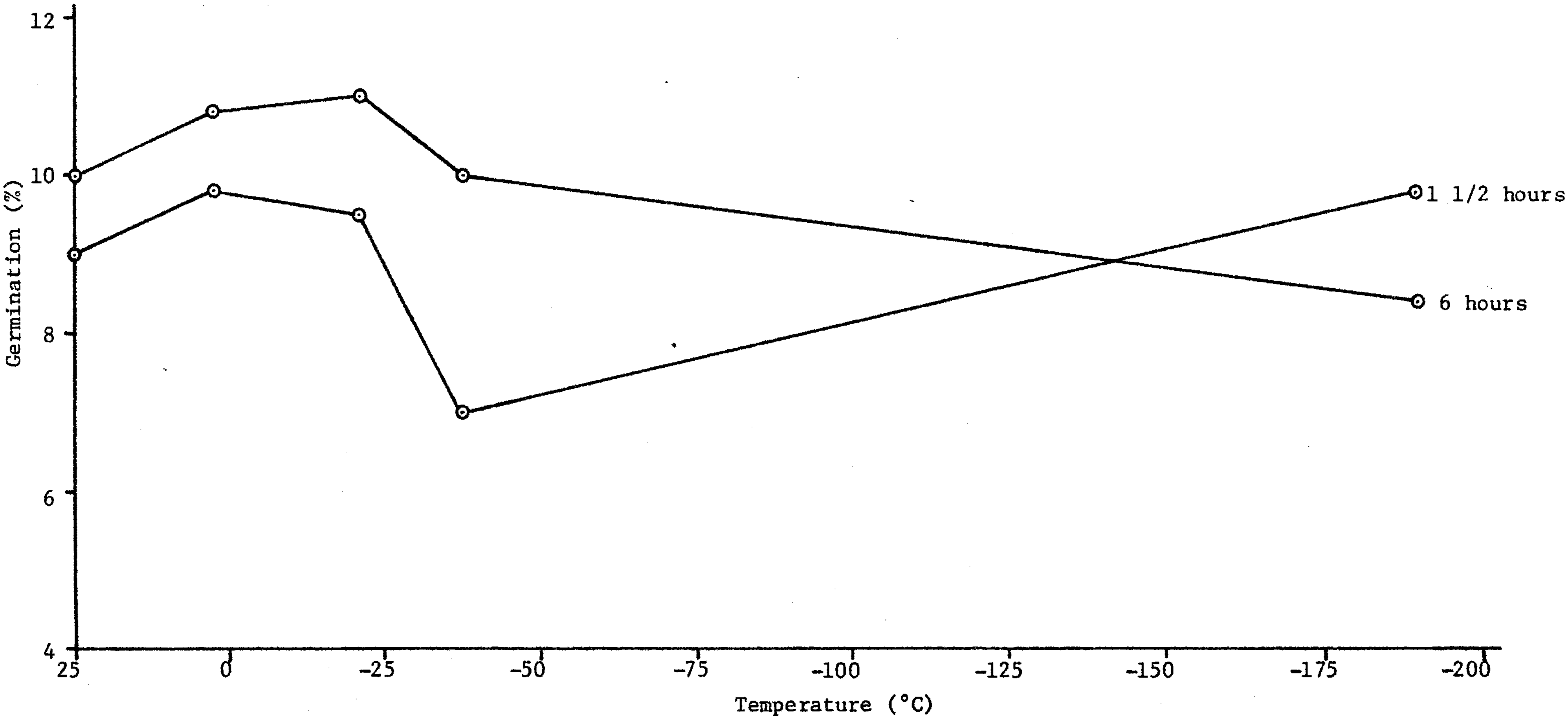
deviations. The average individual seed weights of the 25 samples ranged from 0.040 to 0.137 mg. with the mean weight of all samples as 0.07 mg.

Experiment #2. This experiment was initiated to demonstrate whether the seeds could withstand the freezing temperatures of the upper atmosphere. A seed sample from a tree at Halemaumau on the island of Hawaii was chosen since it had good viability (8 to 12%). The seeds were separated into samples of approximately 200 each and placed at 25°C (room temperature), 2°C (refrigerator), -22°C (freezer), -33°C (freezer), and -192°C (liquid nitrogen). At the end of 1-1/2 hours, one-half of each sample was removed, and at 6 hours the rest were removed, allowed to thaw at room temperature, placed on moist paper in petri dishes and watered.

Figure 3 presents the results of the experiment. The seeds can survive these freezing temperatures without damage to the embryo. The -30°C temperature is comparable to temperatures found in the jet stream and upper air masses.

Experiment #3. This experiment demonstrated the seed's ability to be dispersed in fresh and salt water. Six seed samples from Oahu (4 samples from 600 feet and 2 samples from 2600 feet) were used to determine tolerances to salt water. Twelve 800 ml. plastic containers were used, in which 6 containers had 400 ml. each of fresh water and 6 containers had 400 ml. each of salt water. Salt water of 32 °/oo salinity was collected from the reef outside Kewalo Basin, Oahu. Approximately 1000 seeds were placed in each container and the containers were covered and agitated several times a week. Between 50 and 100 seeds were removed after 2, 8, 22, and 30 days from the salt water, placed in petri dishes, washed, and watered with fresh water.

Figure 3. Germination of Seeds after Subjection to Low Temperatures



Those seeds placed in fresh water germinated in 4 to 6 days, with seeds and seedlings remaining on the surface or below the surface of the water. In contrast, those seeds placed in salt water did not germinate. However, when the seeds in salt water were removed and given fresh water, they germinated as well as their controls.

Approximately one half of the seeds placed in salt water remained suspended on the surface of the salt water, in spite of agitation. (Surface tension may be an important factor in their ability to float, although trapped air inside the seed may also contribute to their ability to remain buoyant.) Both the seeds that float and those that sank germinated in petri dishes with fresh water after 30 days, although a higher percentage of germination was recorded in the floating seeds. The seeds can germinate after being in salt water for at least 30 days (Fig. 4).

Figure 5 records the amount of seedling survival after the seeds left in the salt water for varying lengths of time were germinated in fresh water. These figures were obtained one month after seed germination. The two samples from 2600 feet elevation have no seedling survival while the seeds from 600 feet elevation are still healthy. There may be two explanations for these differences. There may be an actual difference in the ability of the two sets of seed to produce viable seedlings after a month of sea water emersion. However, the two samples from 2600 feet elevation were from low germinating seed samples and are too small a sample on which to extrapolate to actual field populations. Further seed from other trees at 2600 feet elevation should be tested in the same manner to see if there is actually a trend toward loss (or absence) of dispersibility of upland populations after prolonged seed soakings in sea water. Further

Figure 4. Seed Germination after Soaking in Sea Water

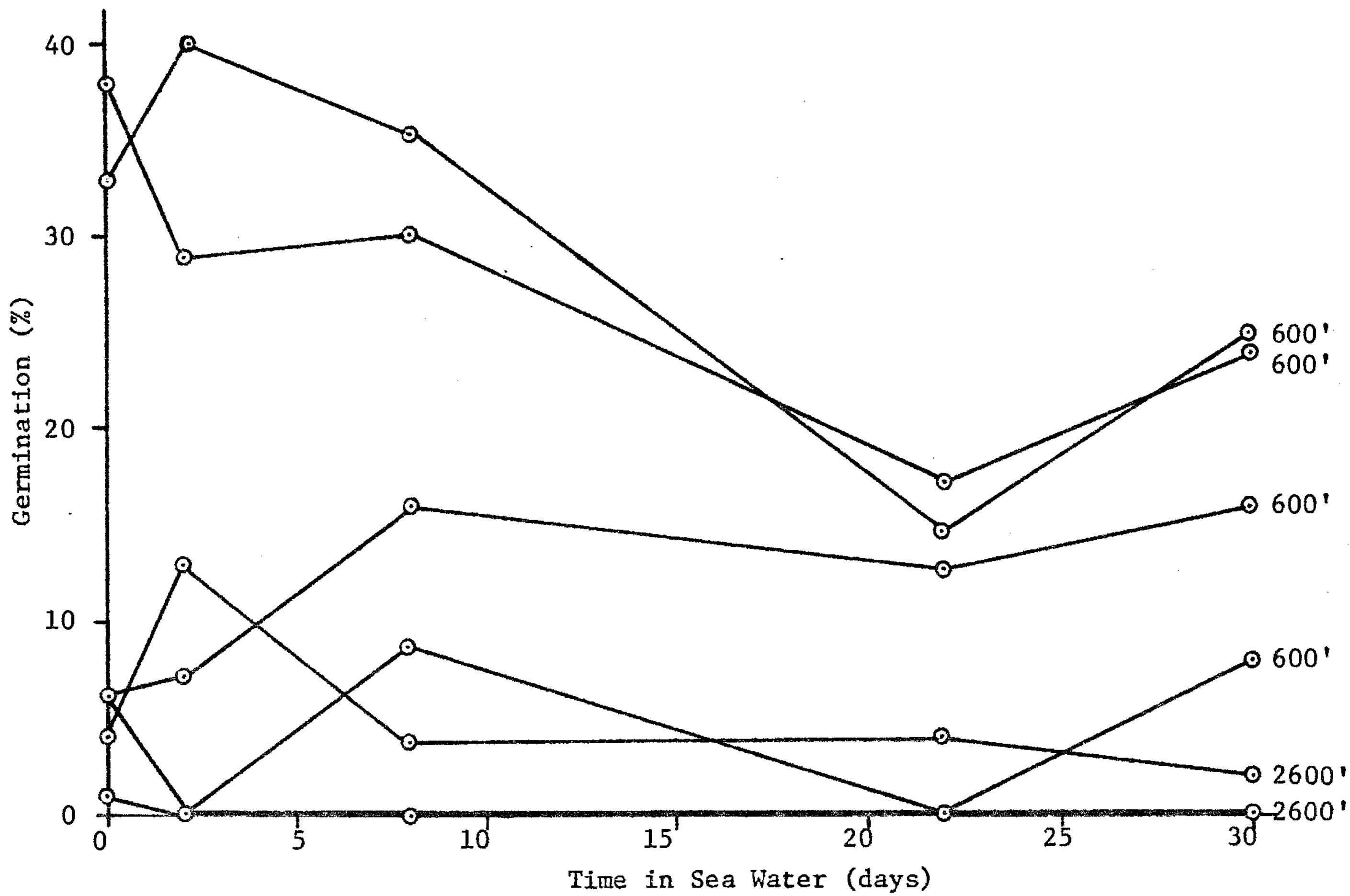
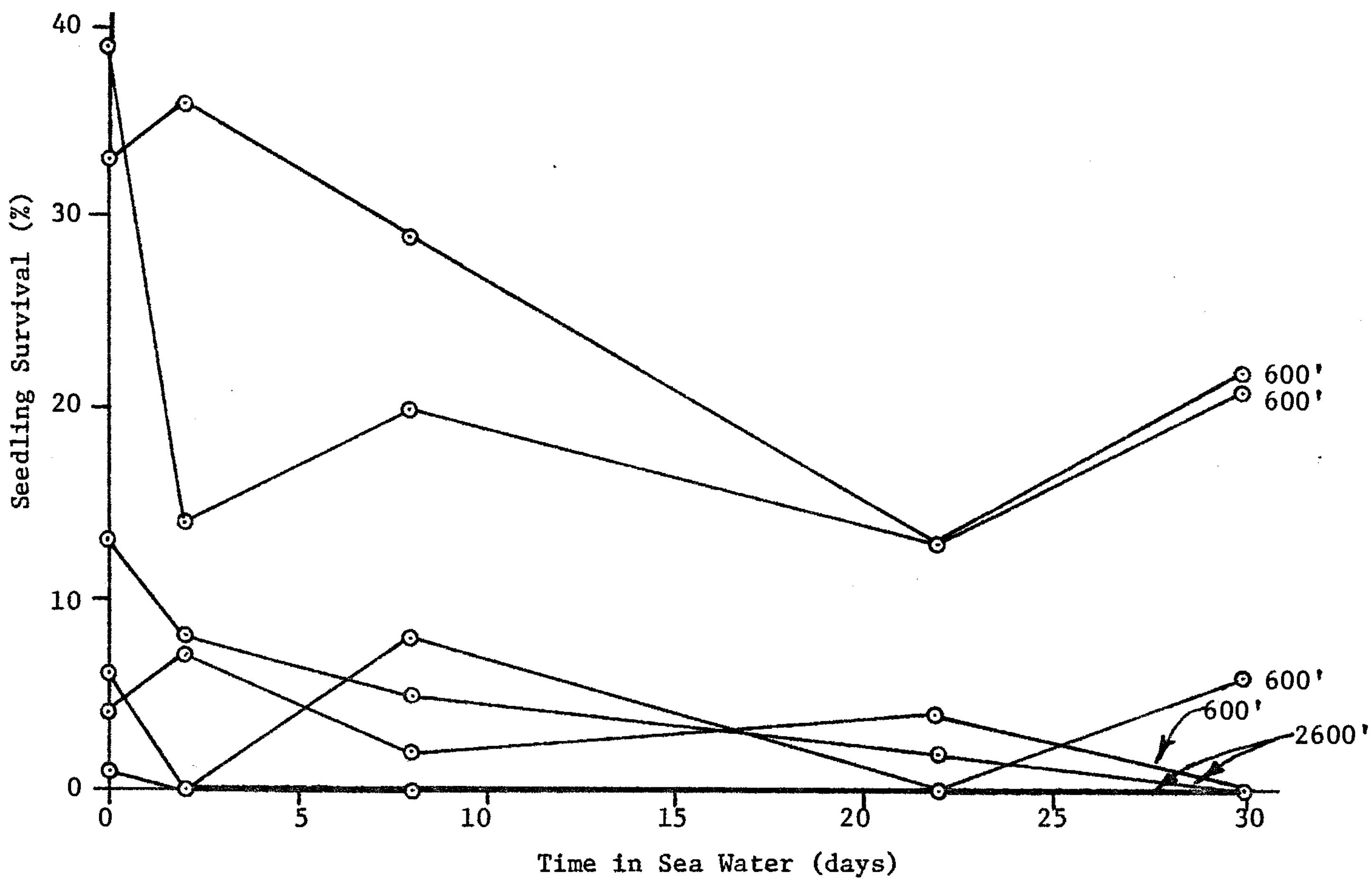


Figure 5. Survival One Month after Germination of Seedlings Soaked in Sea Water



sampling may demonstrate that seeds from higher elevations may survive and germinate after soaking in sea water for 1 month.

What can be seen in figure 5 is a decrease of seedling survival with time in sea water. Most of the 6 seed samples in figures 4 and 5 showed less germination and viability after 30 days of sea water exposure. If the number of seedlings surviving (figure 5) is divided by the number of seeds that germinated (figure 4), an index for seedling survival can be obtained as follows:

$$\text{seedling survival index} = \frac{\text{Number of seedlings surviving after 30 days}}{\text{Number of seeds that germinate}}$$

If these data are plotted on graph paper with time along the x-axis and the seedling survival index as the y-axis, a curve is obtained. If these same data are presented on a semi-logarithmic scale as in figure 6, the points are more linear. It may be possible that several factors may be influencing their survival rate.

If one projects the maximum line drawn in figure 6, the point where it crosses the x-axis is approximately 130 days, which is less than half the survival time of these same seeds in air when they are stored in containers at 25°C and 60 percent humidity. This would indicate that (although the test was terminated after 30 days), their rate of decreased seedling viability indicates they could not withstand prolonged sea water emersion for more than a few months in duration. This would exclude sea water dispersal over long distances, but would be plausible for short distances; for example, between islands of the same island chain.

Experiment #4. This experiment was planned to see if the seeds that remained in salt water for a month could be desiccated for a period of time and still germinate. The seed sample with the highest seed germination (15 to 40%) from experiment #3 was used in this experiment. About 400 seeds

Figure 6. Semi-logrithmic plot of the seedling survival ratio after seeds were soaked for 0, 2, 8, 22, and 30 days in sea water.

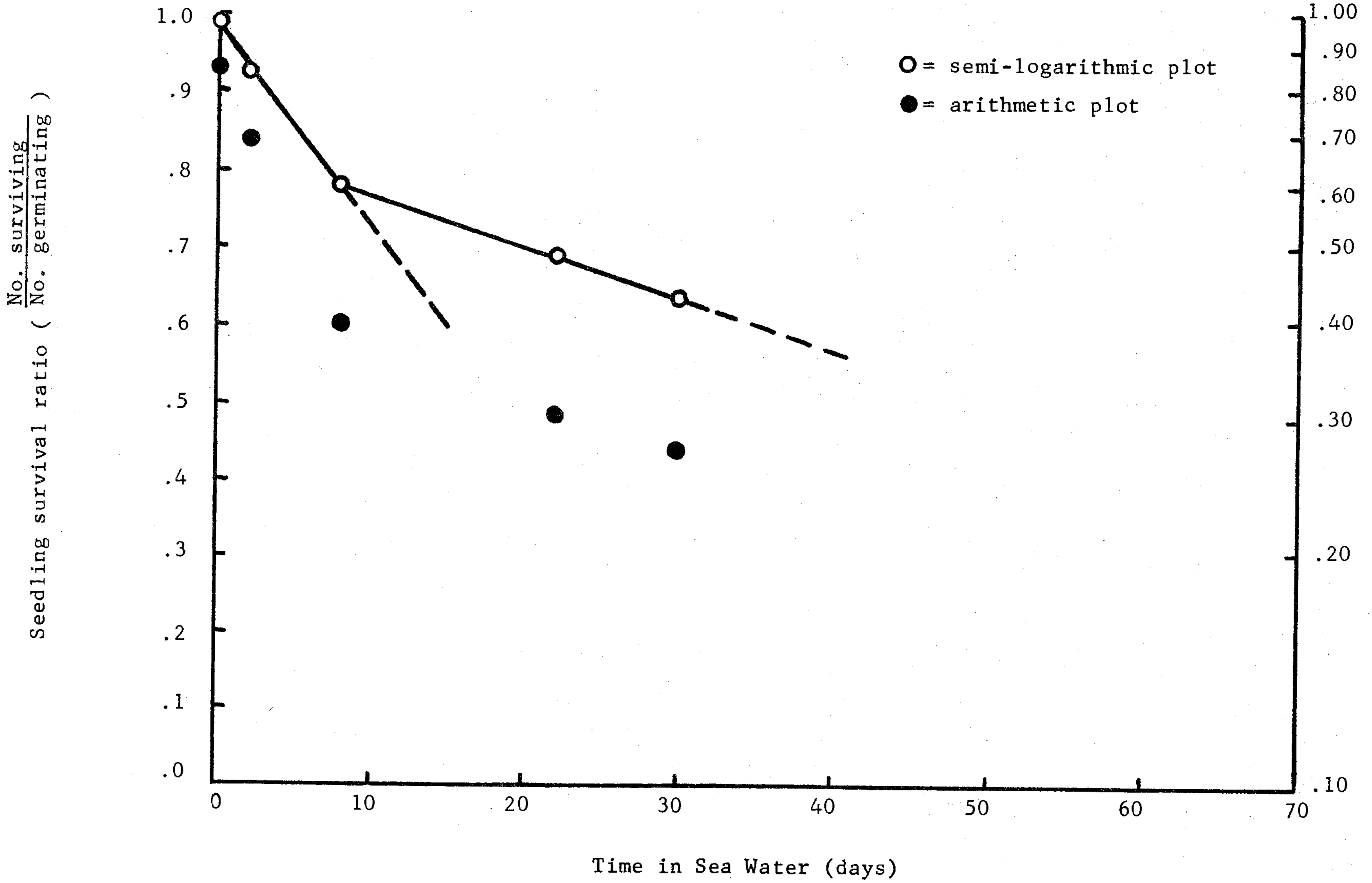
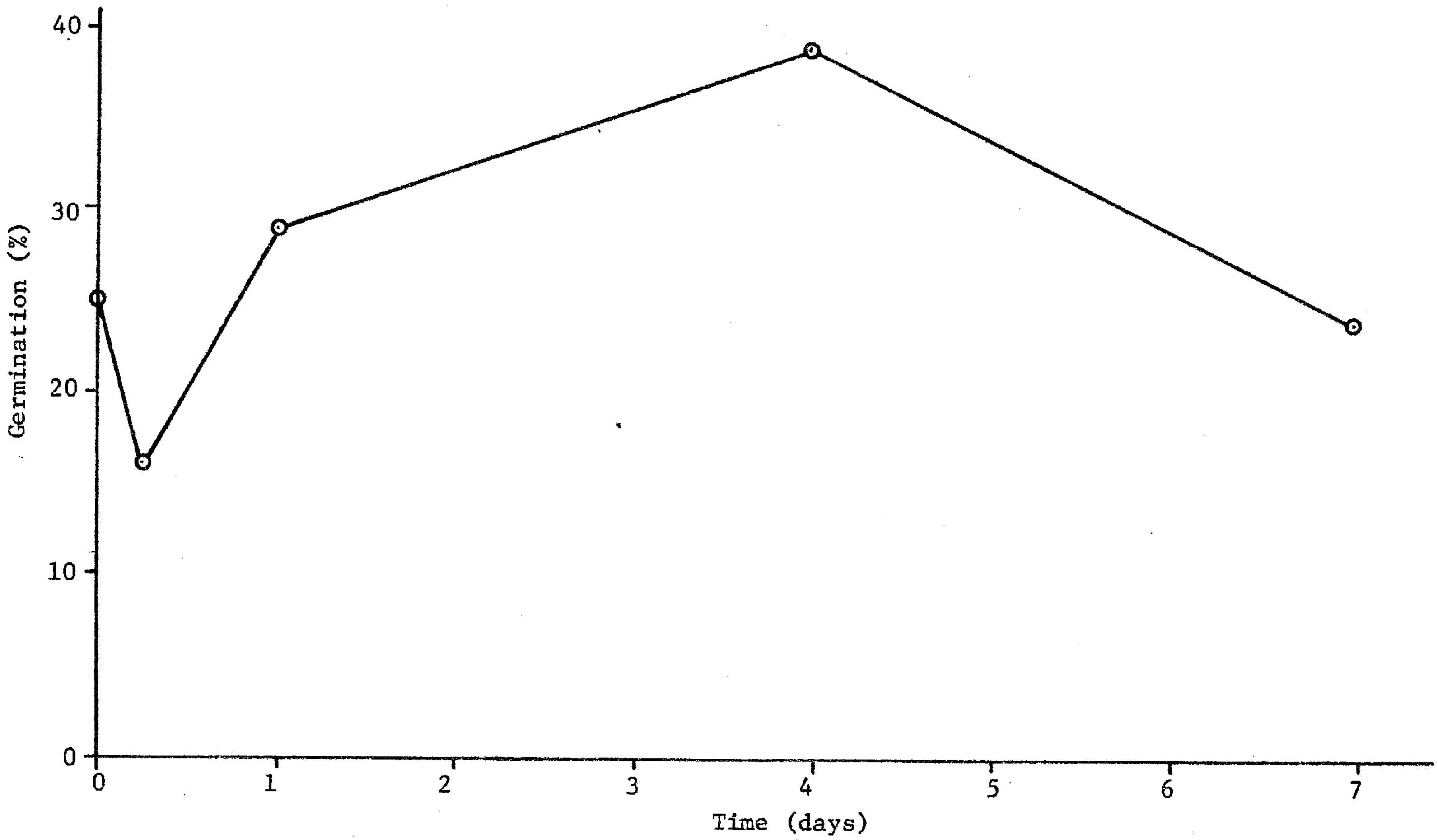


Figure 7. Seed Germination after 30 Days in Sea Water followed by Desiccation Periods Shown Below



that had been soaking in salt water for 30 days were removed and placed in 4 open petri dishes. The dishes with about 100 seeds apiece were allowed to dry at room temperature and humidity for 6 hours, 1, 4, and 7 days before water was added. These survived all drying periods tested at room humidity and 25°C temperature (figure 7).

Bird transportation of the seeds to the Hawaiian Islands seems highly unlikely. The fruit is a dry brownish capsule with dry seeds that are unattractive to birds. Field observations by the author fail to find any birds that visit the seed capsules. Efforts to feed two tame barred doves, *Geopelia striata striata*, that normally eat grass seeds of a similar size resulted in failure. If the seeds are soaked no sticky substance is produced, and microscopic examination of the seed coat reveals no spikes, barbs, or projections on the seed coat that might adhere to bird feathers. Birds could have carried the seeds caked in mud on their feet.

DISCUSSION AND CONCLUSIONS

Wind dispersal, as shown in experiment #1, is probably the chief seed dispersal mechanism of this genus, especially since the plant grows at many elevations on many Pacific Islands within the trade wind belt. These trade winds average 5 to 15 miles per hour and have a drying effect upon the vegetation. The seed capsules on *Metrosideros* plants, although mature, will not split open until there is a dry spell. Once the capsules split, they remain open (Corn, unpublished observations). Some of the stronger trade winds undoubtedly carry these seeds far from the parent plant, especially where the plants are on the windward side of an uphill slope. However, there is an inversion layer above which the trades do not blow (at approximately 8000 feet elevation, and this is the upper level that *Metrosideros* is found in the Hawaiian Islands). This inversion above Hawaii and other high Pacific Islands is disrupted by some of the strong winter storms and there is air exchange into the upper atmosphere. These same seeds if caught in an updraft could enter the upper atmosphere and might come into contact with the jet stream and get carried great distances within a few hours, before being caught in a wind eddy and drifting back toward earth. Experiment #2 indicates that these seeds can withstand the upper atmospheric temperatures.

However, once these seeds drop back down to earth what are their chances of landing in a suitable habitat? When one considers the amount of available land in the Pacific verses the open ocean, one could say small, very small. However, if we go back to experiment #3 we find that the seeds also survive at least for short periods in fresh and salt water. This means that the seeds might still survive even though they do not settle on a small high island. This gives the seeds another method of arrival to a new habitat to establish themselves. They can wash down fresh water streams for several days, or float around or inbetween the islands for at least a month. If and when they arrive at a new location it would be onto an unsuitable wave-washed surface upon which Metrosideros does not grow.

However, experiment #4 indicates that these seeds can survive desiccation after floating in salt water, which could give these seeds a chance of survival by allowing the sea breezes to blow the seeds inland to a more suitable habitat. Although this may sound far fetched, figure 7 illustrates that this could have happened on Oahu, where seeds from a plant collected at 600 feet elevation have survived 30 days in sea water followed by 7 days of desiccation to produce viable seedlings one month old. (If the few viable seeds from 2600 feet elevation in the Waianae Range that were unable to survive this same treatment in figure 6 can be substantiated by a larger sample size, there may be at least two seed types on one island that show two methods of arrival (or admittedly some higher elevation plants may have lost this ability to withstand salt water).

These results have some far reaching implications. Metrosideros seeds could have arrived in the Hawaiian Islands by several methods at several times. Also, within the Hawaiian Islands there may have been multiple introductions between the islands, resulting in the restocking of isolated genepools giving new gene combinations to the established population.

The author gives a higher priority to air dispersal than to sea dispersal over long distances, because (1) the seeds remain viable for only 9 months when stored at room temperatures; (2) data in figure 5 indicates that these same seeds give reduced seedling survival and viability after a month or more in sea water; (3) oceanic drift is a slower method of dispersal (especially where long distances are involved) giving more time for destructive forces to take over, for example a fish trying to eat a floating object, marine microbes attacking the seed coat and/or embryo, or the seed's surface being affected by hatching larvae, such as barnicles.

ACKNOWLEDGEMENTS

A special thanks to Dr. Ronald C. Taylor, Geosciences Department, for his invaluable ideas and help on methods of obtaining meteorological data; to Dr. Joel Fox, Mechanical Engineering, who helped solve some of the thermodynamic problems that arise with wind tunnel measurements; to Mr. Bernard Shinbara, Federal & State Weed Analyst, who permitted me to modify a seed sorting machine for these studies. Also thanks to Dr. Charles Lamoureux for advice on literature.

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