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SURVIVAL STRATEGY OF PTELEA TRIFOLIATA DURING ESTABLISHMENT ON LAKE MICHIGAN SAND DUNES

By

Kenneth William McLeod

A DISSERTATION

Submitted to
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ABSTRACT

SURVIVAL STRATEGY OF PTELEA TRIFOLIATA DURING ESTABLISHMENT ON LAKE MICHIGAN SAND DUNES

By

Kenneth William McLeod

The microclimate, to which a seed or small seedling on the sand dunes of Lake Michigan is subjected, is characterized by high surface soil temperatures and low soil moisture during the summer. Low nitrogen availability is a permanent sand dune stress. This study attempted to determine the characteristics that enable some woody plants to successfully colonize sand dunes of Lake Michigan. Ptelea trifoliata, a large woody shrub, was chosen as a representative woody plant for study.

Ptelea fruits required stratification to relieve an embryo dormancy and reduce the effect of germination inhibitors found in samara and seed coat leachates. Germination and growth in the laboratory were stimulated by temperature and soil moisture conditions similar to early spring conditions. High temperatures (40°C), similar to summer temperatures, killed 90% of the imbibed seed. Seedling survival was dependent on root growth sufficient to furnish the seedling with water. The drought tolerance of very young seedlings was poor because of the

slow root elongation, but became greater as the root system developed. Growth in the laboratory was increased by moderate temperatures and nutrient addition.

The resistance to liquid water flow and the stomatal diffusive resistance of the Ptelea seedlings were mesophytic in character and, therefore, the high evaporative demand of the sand dune environment produced high transpiration rates. Because of high transpiration rates, seedling survival was found to depend upon the rapid growth of roots to a soil stratum containing an adequate supply of moisture. The shaded microhabitat was characterized by a relatively low evaporative demand and, consequently, greater soil moisture and seedling survival.

Even though Ptelea seedlings do not appear to be adapted to conserve water in the sand dune habitat with its high evaporative demand, they possess several other characteristics which allows the species to establish on sand dunes. These characteristics include the stimulation of germination and growth by a favorable spring environment, ability to withstand high soil temperatures and low soil nitrogen levels, and the ability to produce adventitious roots when sand accumulation occurs. These characteristics allow Ptelea trifoliata to establish on Lake Michigan sand dunes.

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INTRODUCTION

The sand dunes of Lake Michigan have been an important habitat in the advancement of ecological theory relating to plant community development. Cowles (1899, 1901) noted the horizontal gradient of plant communities from the unstable beach to the well developed rear dune and thus the entire successional sequence can be observed within a short distance. He attempted to use the static sand dune vegetation to illustrate the dynamic process of succession.

This led to more research on the seral changes of plants and animals on Lake Michigan sand dunes (Bruncken 1910, Chapman et al. 1926, Fuller 1918, Olson 1958, Van Denack 1961, Waterman 1917, 1922, Wohlrab, Tuveson and Olmstead 1963). The environmental gradients associated with the vegetational gradients were also noted (Fuller 1912a, 1912b, 1914, Park 1931, Strohecker 1937, 1938). The vegetation of marine sand dunes has also been studied extensively. The plant distribution on maritime dunes is strongly regulated by the salt spray or presence of salt in the soil (Oosting and Billings 1942). Lake Michigan sand dunes do not have this regulator as the lake is not saline.

A coastal sand dune system consists of beach, foredune, middune and rear dune areas. The beach is subject to wave action which washes debris ashore, including driftwood, dead animals and plants, and plant

propagules. The extent of beach area is dependent on the lake level and the wave action. The beach vegetation is called the strand community and is rooted vascular plants capable of withstanding the force of the waves and being submerged for indeterminate periods of time. This community is virtually absent on the Lake Michigan sand dunes because of fluctuating lake levels.

Behind the beach and beyond the influence of wave action is the foredune. The size and shape of the foredune is variable depending on whether it is formed around debris or vegetation. If the pioneering vegetation is arborescent, the foredune will be taller than if the vegetation is herbaceous. The foredune vegetation must survive sand accumulation and consequently it is composed of plants that can rapidly produce adventitious roots as the sand accumulates. The growth of some foredune plants is actually stimulated by sand burial.

The wind is deflected over the top of the foredune leaving an area behind the foredune free from the influence of wind. The middune exists in this area. It is a low flat area that is subject to little sand movement. When gaps in the foredune exist, the wind may scour out the sand, creating a depression which at higher lake levels will become a shallow pond. If the higher lake level should persist, a wet panne containing aquatic vegetation will develop. Since the sand movement is less in this area, the vegetation need not be adapted so strongly to sand blasting or burial. More mesophytic species are found in this area but

the species must still exist in sandy soil and are usually characterized by some form of xerophytic root system.

Further back from the beach, the wind deposits sand producing small dunes which are the beginning of the rear dune system. On the north and east shores of Lake Michigan, the rear dune, which attains heights of 128 m, is the relict of a former higher lake level. The small dunes on the windward side of this large rear dune are stable due to the presence of vegetation. Disturbance of the vegetation may result in sand movement, sometimes called a blowout. The vegetational composition on the rear dune is related to the extent to which the soil has been developed by early successional vegetation and is ultimately controlled by the slope and aspect of the individual site and the regional climax vegetation. Thus, in the Lake Michigan area, various types of deciduous forest are usually found on the undisturbed rear dunes.

The amount of ecological research carried out on the plants of the Great Lakes dune ecosystem is not as extensive as one might imagine. There are over 150 species of flowering plants associated with the dune habitat, but only a few have been studied; these include marram grass (Ammophilia breviligulata) by Laing (1958), bugseed (Corispermum hyssopifolium) by Van Asdall and Olmstead (1963), wormwood (Artemisia caudata) by Hicks (1938), and cottonwood (Populus deltoides) by Fuller (1912c). Waterman (1919) recognized the importance of the root system development of dune plants and observed its development in 16 species.

The factors governing the vegetational zonation have been studied by Olson (1958).

For a plant to establish itself on a sand dune, it must successfully cope with an unstable substrate, high summer temperatures, low surface soil moisture and low levels of soil nutrients. These environmental stresses are all consequences of the sand substrate. Pelton (1953) points to seed germination and seedling establishment as being the most critical time periods in the life cycle of a seed plant. In view of the aforementioned stresses, seedling establishment on a sand dune must be very difficult.

Consequently to determine the attributes of a woody plant that enables it to endure the stresses associated with sand dunes, a study of the germination and establishment of Ptelea trifoliata was undertaken. (All nomenclature according to Gleason and Cronquist (1963)). Ptelea is a shrub distributed primarily along waterways in moist forests of eastern North America. It is also found along the shoreline of Lake Michigan on the small fore and mid dunes. On these small dunes, the pioneering woody plants must establish on the infertile sand substrate but they rapidly increase the organic matter in the soil as they shade the soil surface and litter accumulates (Olson 1958), thus creating soil conditions more favorable for future woody plant establishment.

The environmental situations confronted by seedlings in streambank and sand dune habitats are very different. Ptelea was chosen for study because, although it is primarily a moist site plant, it is also

successful in the sand dune habitat. Also, its reproduction is entirely sexual, unlike other woody plants found on the open dunes, and thus it is dependent on the establishment of germinated seed. It was also hoped that Ptelea could be considered representative of woody plant establishment on sand dunes.

The primary objectives of the study were to describe the stresses to which establishing plants are exposed and to elucidate the survival strategy of Ptelea trifoliata during the critical establishment phase of its ecological life cycle. More specifically the objectives of the study were: (1) to describe a seed's microclimate on Lake Michigan sand dunes; (2) to determine the critical factors affecting Ptelea germination and seedling establishment on Lake Michigan sand dunes; and (3) to determine the transpiration and liquid and vaopr resistances to water flow of Ptelea seedlings.

DESCRIPTION OF PTELEA TRIFOLIATA

Ptelea trifoliata L. (Rutaceae) is a polygamo-dioecious shrub. Normally the shrub does not exceed five meters in height with the first branching of the trunk below a height of one meter. This gives a low spreading crown when open grown (Figure 1). Multiple stemmed individuals are not uncommon. The stem is reddish with abundant horizontal lenticles. On the Lake Michigan sand dunes near Saugatuck, Michigan, the trifoliate leaves of the Ptelea shrubs begin to appear in early May and are present until mid-October. White flowers are found in terminal cymes on the shrub by the beginning of June. Small fruits become apparent by the end of June. The fruit is a thin, flat, orbicular samara with a broad wing completely surrounding a two-celled body (Figure 2). The fruits ripen by mid-October and are variably persistent over the winter. At this time the fruit is approximately 23 mm in diameter and ranges from 0.026 to 0.067 g in weight (average of 0.046 g). Most fruits contain one seed but 10% contain two. The seed, as shown in Figure 3, are kidney shaped, 6.4 mm long, 2.3 mm in cross sectional diameter, and range in weight from 0.007 to 0.012 g (average of 0.0096 g). A black crispy outer layer and a thin brown membranous inner layer make up the seed coat. Inside the seed coat the embryo is completely embedded in endosperm tissue.

Figure 1. Typical open grown shrub of Ptelea trifoliata on the Lake Michigan sand dunes near Saugatuck, Michigan.

Figure 1.

Figure 2. Fruit clusters of Ptelea trifoliata.

Figure 2.

Figure 3. Seed of Ptelea trifoliata showing the two layered seed coat.

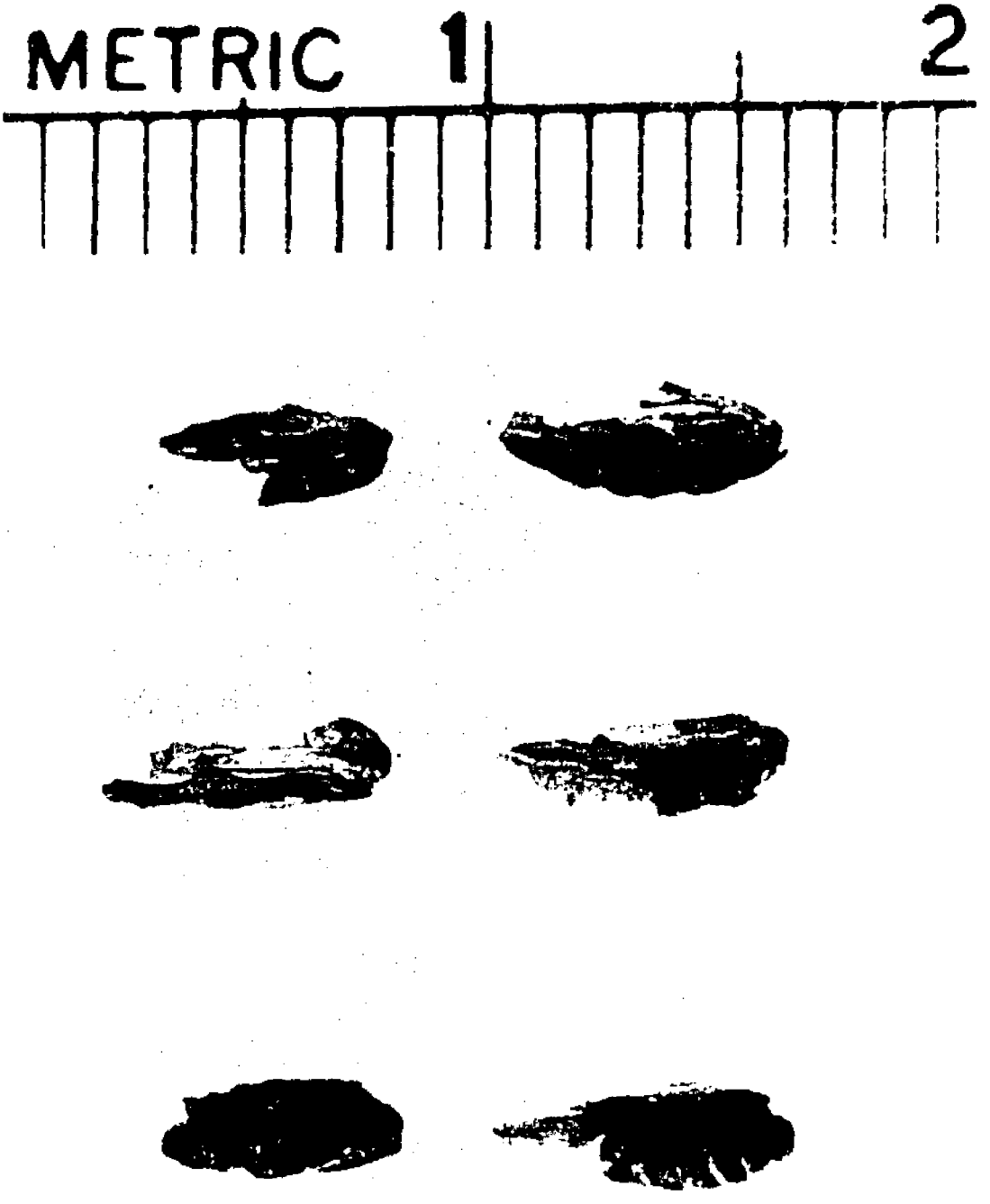

Figure 3.

Ptelea trifoliata, with common names hop tree, money tree, stinking ash, and wafer ash, is, according to Gleason and Cronquist (1963), found in moist or rich woods and thickets over most of eastern North America as far north as sourthern Ontario and south to Florida and northern Mexico. Gleason and Cronquist consider the sand dune plants as a separate variety.

The genus Ptelea has been revised in the last 70 years. In 1906, Greene described 59 species of Ptelea in western and southwestern United States and Mexico. Bailey (1962) revised the genus to include only three species. Ptelea trifoliata was divided into five subspecies with 10 varieties.

The medicinal and economic importance of Ptelea, reviewed by Bailey (1960), has been known for a long time.

DESCRIPTION OF STUDY AREA

The study area is located on the Lake Michigan shore near Saugatuck, Allegan County, Michigan. Field observations and experiments were primarily conducted in a 0.30 ha stand of Ptelea trifoliata about 150 m east of the north end of the Oval Beach parking lot. The Ptelea stand is shown in Figure 4 and exists on low gently sloping dunes from one to four meters above lake level. Occasional solitary individuals exist outside the stand in the middune area. The Ptelea in the stand rarely exceed three meters in height and are usually clumped with few open grown plants. Associated vegetation in the stand is Juniperus communis, Pinus strobus, Quercus velutina, Rhus radicans, Saponaria officinalis, Smilacina stellata, and Vitis sp. Most field studies were conducted between 22 March 1973 and 11 November 1973 but some additional observations continued through September 1974.

The general habitat of the Saugatuck sand dune area is similar to the sand dune habitat previously described. The beach is much reduced due to recent high lake levels and is less than 10 m wide. The foredune area (approximately 20 m wide) is dominated by Ammophilia breviligulata with occasional woody plants such as Populus deltoides, Prunus pumila, Salix glaucophylloides, and S. syrticola. The middune

Figure 4. The study area on the Lake Michigan sand dunes near Saugatuck, Michigan, with the stand of Ptelea trifoliata in the foreground.

Figure 4.

is a large low flat area approximately 100 m wide. Ammophilia is gradually replaced by Andropogon scoparius and Calmovilfa longifolia along a gradient of increasing sand stability from the lake toward the rear dune. The woody foredune vegetation along with Cornus stolonifera, Hudsonia tomentosa, Juniperus communis, J. virginiana, and Vitis sp. continues to be sparcely found in the middune area. Associated herbs in this area are Arabis lyrata, Artemisia campestris, Asclepias syrica, Campanula rotundifolia, Cirsium Pitcheri, Euphorbia polygonifolia, Lithospermum caroliniense, and Monarda punctata. Wet pannes are also found in this area. They are dominated by species of Eleocharis, Cladium, Juncus and Carex and frequently bordered by Hypericum Kalmianum and Equisetum arvense. The rear dunes are found behind the middune and range in height from 2 to 75 m above lake level. On the small rear dunes the woody vegetation becomes more important. In addition to those woody plants previously listed, Pinus banksiana, P. strobus, Ptelea trifoliata, and Quercus velutina are present. The large rear dune supports a deciduous forest of variable composition. Forest species found here include Acer rubrum, A. saccharum, Fagus grandifolia, Fraxinus americana, Ostrya virginiana, Quercus alba, Q. rubra, Q. velutina, Sassafras albidium, Thuja occidentalis, Tilia americana, and Tsuga canadensis.

The United States Weather Bureau Climatological Data (1973a) supplies general climatic descriptions of many stations within Michigan. The closest station to the study area is South Haven Agricultural

Experiment Station (27.7 km SSW of the study area) and is located within several hundred meters of the lake shore and thus is probably very similar to the study area. The area has a cool climate with a mean annual temperature of 9.8°C (78 year average). The average temperature of the warmest and coolest months is 21.8°C (July) and -2.5°C (January) respectively. The annual precipitation is 95.81 cm with 58% occuring during the 172 day growing season. The precipitation is well distributed with only February receiving less than five centimeters. The total evaporation during the 1973 growing season from an evaporation pan was 88.75 cm. This was 93% of the annual precipitation and approximately 160% of the precipitation occurring during the growing season. Data for insolation and wind speed and direction are not available at this station, however these data are obtainable from the United States Weather Bureau Local Climatological Data for Grand Rapids, Michigan (1973c). This station is located 61.3 km ENE of the study area. During 1973, 46% of the possible annual sunshine was reported for this station with 62% of the year classified as cloudy. The percentage of cloudy days per month never fell below 33% during the year. The wind was from the southwest at an average speed of 0.849 m/sec.

METHODS AND MATERIALS

Soil Characteristics

To adequately describe the soil that exists in the sand dune habitat, numerous tests were conducted to determine its texture, nutrient content and water holding capacity.

Initially a pit was dug to the water table to observe the overall soil profile. The soil texture was determined by a series of graded-size screens through which the soil was sieved and by the hydrometer method (Bouyoucos 1951). The nutrient content of the sand was determined by use of a LaMotte soil testing kit. The field capacity of the sand was measured with a tension plate assembly (Hillel 1971) and also by wetting a large column of sand (37 cm diameter, 70 cm tall) and periodically removing samples until a constant soil moisture was reached. The permanent wilting point was determined with both sunflower (Helianthus annuus) and Ptelea, using the method of Briggs and Shantz (1912).

At approximately three week intervals during the growing season, soil moisture and temperature profiles were measured every four hours during a 24 hour sampling period. Soil moisture of field samples was determined by the gravimetric method on duplicate samples taken at 0, 5, 10, 25, 50, and 100 cm depths. The 0, 5, and 10 cm samples

were five centimeters long and centered at the listed depth. The other samples were 10 cm long and centered at the listed depth. This moisture was converted to soil moisture (volume basis) by multiplying it by the bulk density. Soil temperature was measured with a YSI telethermometer at the same depths. The depth to the water table was determined every three weeks by excavating to the free water surface. The capillary fringe was also determined by taking soil samples out of the pit wall at known heights above the free water surface and measuring the moisture content.

Seed Microclimate

Two microhabitats on the soil surface, shaded and full insolation, were described in detail. The sand movement in each microhabitat was determined by measuring changes in sand height on graduated stakes. A Weston light meter was used to measure the light intensity. Surface soil temperatures and soil moisture profiles to a depth of 75 cm were measured as previously described. Small (six centimeter diameter) aluminum cans were used as pans to determine the evaporative demand of the two microhabitats. The amount of rainfall penetrating the shrub canopy was measured with plastic rain gauges.

Seed Dormancy and Germination

Establishment of most plant populations must at some time be dependent on seed germination. Ptelea seed require stratification before

germination will occur (United States Department of Agriculture 1948). To determine what changes in the seed might be taking place during stratification, experiments using unstratified seed were conducted.

Fruits used for experiments were collected directly from shrubs on 13 September 1973, 13 October 1973 and 11 November 1973. The 13 September collection was layered in moist sand within muslin bags and placed in a 3°C cold room to stratify. The other two collections were stored dry in paper bags on the shelves of an air-conditioned laboratory until needed.

The dune sand utilized was collected at the study site, dried at 105°C in a forced air oven, and then passed through a #18 sieve.

In the following experiments, "laboratory conditions" refer to exposure to a combination of fluorescent and incandescent illumination of 510 ± 50 ft-c with a 16 hr photoperiod. Temperatures for day and night were 25.0 ± 1.7°C and 22.0 ± 0.6°C, respectively. Relative humidity was 25±5%. These conditions approximate those found in the shade at the study site during June.

Unless noted otherwise, fruits and seed were observed for two months to determine final germination percentage. Excised embryos were observed for only two weeks due to the rapid tissue softening. Distilled water was added when necessary and viability determined by the tetrazolium test (United States Department of Agriculture 1961) at the end of the test.

Unstratified Seed. The first of these experiments attempted to break the seed dormancy by chemical or physical treatments. Treatments used included leaching the fruits with water or chloroform for various time periods, soaking the seed in various concentrations of indole butyric acid, gibberellic acid, thiourea, or potassium nitrate, and applying wet heat (76.5°C) to the seed. The treated seed were placed on two sheets of damp Whatman #1 filter paper in a petri dish to observe germination under laboratory conditions. If whole fruits were treated, they were placed in petri dishes containing dune sand.

The control of dormancy has been attributed to various fruit parts depending on the species involved (Evenari 1949). To determine what parts of the Ptelea fruit might be controlling dormancy, the percent germination of various germinable units of the fruits was determined. The germinable units included the intact fruit, fruit with the samara tissue over the seed body punctured to allow rapid imbibition, seed excised from the fruit, excised seed with the seed coat removed, and excised embryos. In an additional treatment, the endosperm tissue surrounding the radicle was removed. After the germinable units were prepared, ten were placed on two layers of damp filter paper in each of five petri dishes per treatment and observed under laboratory conditions as described above.

To separate the possible causes of physical and chemical inhibition of germination, the embryos were excised and the remaining samara, seed coat, and endosperm tissues separated from each other.

Aqueous leachates of each tissue were prepared by soaking one gram tissue in ten milliliters of distilled water for two hours. Five milliliters of a leachate was used to dampen two layers of filter paper with ten embryos in each of five petri dishes for each treatment. Four concentrations of samara tissue leachate were used. The concentrations were one gram tissue in ten milliliters of distilled water, one gram in 50 ml, one gram in 100 ml, and one gram in 250 ml. These were observe as described above.

The samara tissue that surrounds the seed is very tough and resistant to tearing. This could possibly lead to a reduced rate of imbibition. Fruits in dune sand were imbibed for 1, 3, 5, 7, 9, 11, or 13 days. After imbibing for the desired length of time, the seed was removed from 20 fruits, weighed, oven dried, and reweighed to determine the moisture content of the seed. When the moisture content became constant they were assumed to be fully imbibed.

Viability was determined by the tetrazolium test after 55, 106, and 220 days to observe the effect of laboratory storage on the seed longevity.

Stratified Seed. At monthly intervals 15 stratified fruits were removed from the cold room and placed in a petri dish containing dune sand to allow germination under laboratory conditions. Additional fruits, yielding 25 seed, were also removed and the excised seed treated as above. This allowed determination of stratification duration required for germination and the influence of samara tissue on germination.

The previous experiment utilized an artificial continuous temperature stratification treatment. Obviously this is not what occurs in nature. Therefore stratification under cold room and natural conditions was compared. Fifty fruits were placed two centimeters below the dune sand surface in 9.5 cm drained styrofoam pots. These pots were buried in the Rose Lake Wildlife Research Area. An identically prepared set of pots was placed in the 3°C cold room and at monthly intervals one pot was removed from each treatment and returned to the laboratory for observation of germination.

Fruits are usually stratified outdoors by placing them between layers of sand or peat and protecting them from severe temperatures with insulating material such as straw. This careful treatment does not occur in nature. The fruit may be on the soil surface or possibly buried slightly. To examine whether seed stratify completely when on the surface, seed were stratified both on the surface and buried. A 55x37x10 cm wooden flat was divided into two sections. In one half 80 fruits were placed three centimeters below the dune sand surface and in the other half 80 fruits were placed at the surface with a slight sand cover to hold them in place. Wire screen (six wires per centimeter) was placed over each section to hold the fruits and sand surface in place. The top of the flats were covered by wire screen to prevent herbivory. Two flats were placed at the Rose Lake Wildlife Research Area on 1 November 1973. Two identically prepared flats were also placed in the 3°C cold room. One flat was removed from each location after 94

and 150 days of stratification and returned to the laboratory to observe germination. This procedure allowed determination of the effect of seed position on the effectiveness of stratification.

To examine any gross morphological changes that might occur during stratification, samara decomposition and seed and fruit dry weight were measured monthly. Fruits stratified in muslin bags in the 3°C cold room were used for this purpose. Also, fruits were naturally stratified in flat wire screen bags. Each bag had 25 fruits and was either left on the sand surface or buried three centimeters in the sand. The bags were contained in 55x37x10 cm wooden flats with wire screen over the top of the flats. Each flat was buried flush with the soil surface at the Rose Lake Wildlife Research Area. The fruits from a wire bag from the surface and one that had been buried along with fruits stratified in the cold room were examined monthly and dry weight determined for both the seed and fruit.

The tetrazolium test was used after 55, 106 and 220 days to determine the effect of stratification on seed viability.

To determine whether any germination inhibitors remained in the fully stratified fruit, the embryo were excised after 176 days of stratification. The fruit parts (samara, seed coat, and endosperm) were separated from each other. The leachates were prepared and the embryos treated with the leachates as in the earlier experiment.

The effects of several environmental variables which can modify the germination of fully stratified seed were examined by the following experiments.

The optimum temperature for seed germination was studied because this characteristic is species dependent (Kozlowski 1971). Fruits were stratified for 163 days in preparation for this experiment. Two centimeters of dune sand was placed in small culture dishes with 25 excised seed placed slightly below the sand surface. The dishes were covered by aluminum foil and placed in the appropriate temperature condition. The seven constant temperatures utilized ranged from 3 to 40°C. Four fluctuating temperature conditions were also used. The dishes were observed for seed germination daily for four weeks.

In the sand dune habitat temperature fluctuations are very large with inhibitory extremes. The response of Ptelea seed to these temperature extremes was studied. Excised seed, stratified for 195 days, were depressed slightly below the sand surface in 32 petri dishes. Twenty seed in each of eight dishes per treatment were used. Treatments included two fruit conditions, fully imbibed or dry, and two temperature treatments, laboratory conditions or a heat treatment. The heat treatment was four hours of 40°C, seventeen hours of 25°C, and three hours of transition to or from the 40°C. Two dishes per treatment were removed weekly for four weeks. One dish per treatment was observed for germination and the viability of the seed in the other dish was determined by the tetrazolium test. In addition to yielding information on the immediate effect of the treatments on germination, the effect of the treatments on seed viability and hence survival was also determined.

Next the effect of light on seed germination was studied. Twenty-five excised seed, stratified for 223 days were placed in each of two petri dishes filled with dune sand. Both were left under laboratory conditions, one dish was enclosed in aluminum foil to create dark conditions. Germination was observed for four weeks.

Additionally, excised seed, stratified for 188 days, were placed 0, 1, 2, and 4 cm below the dune sand surface in drained 10.5 cm plastic pots. Two pots, each containing ten seed, were used per treatment depth. Germination was observed for four weeks.

In dune conditions the seed must germinate in a very porous, low water retaining medium. The frequency of rainfall is, therefore, very important because only small quantities of water can be retained between rainfalls. Eighteen excised seed, stratified for 129 days, were placed slightly under the sand surface in each of 6 drained 10.5 cm plastic pots. Treatments were watering to saturation every one, two, or three days. Two pots per treatment were used and germination was observed for four weeks.

Fruit Loss

The removal of the fruits from the site was observed and documented. Forty-two fruits were stapled through the samara tissue onto each of 8-21.6x27.9 cm pieces of cardboard. The fruits could not be shaken from the cardboard but could easily be torn off. Four cards were placed on the sand surface and four buried one centimeter deep at the study site on 10 November 1973. They were observed on 6 December 1973 and 18 May 1974 for fruit removal.

The Seedling

Seedling Growth and Survival. A very precarious phase of the life cycle follows seed germination. During this time the radicle must develop into an extensive root system capable of supplying the young plant with adequate nutrients and water. Also leaves must be produced capable of manufacturing enough photosynthate to maintain the root and shoot systems. Adverse environmental conditions during this time can easily lead to seedling death. First year Ptelea seedlings were observed during the 1973 growing season to determine survival and growth. To do this, two 1x20 m transects were established in the study area. The transects were perpendicular to each other and formed a cross within the Ptelea stand. The transcets were examined closely for seedlings, which were then marked with a six millimeter diameter red dowel rod and mapped. Approximately every two weeks, the seedlings were examined for growth and survival. An attempt was made to identify the cause of seedling mortality. If the seedling was in place but totally dehydrated, the mortality cause was listed as dehydration. If the seedling had existed in a location that had recently received obvious vehicular traffic from all-terrain vehicles, the mortality was listed as being due to traffic. A miscellaneous category was used for any other seedling mortalities.

Also, seedlings outside the transects were excavated, washed of sand and the growth parameters of shoot height, root depth, number of leaves, and total weight measured. Small trees (less than ten years

old) were also excavated. In addition to the above growth parameters, crown width, root spread, and root, stem, and leaf dry weights were determined for each tree.

Adverse environmental factors that can lead to seedling mortality or reduced growth include temperature, soil moisture, and sand movement. Each of these factors was investigated.

Glass-sided boxes were utilized to determine the effects of soil temperature and watering frequency on seedling growth. The box design is shown in Figure 5. Utilization of this box allowed observation of the roots during the treatment. The experimental design was factorial with 3 levels of soil temperature (13.0 ± 1.7, 24.0 ± 2.8, or 32.0 ± 1.1°C) and 3 frequencies of watering (every 1, 2, or 3 days). The soil was saturated at each watering. The 24°C treatment utilized laboratory conditions with 680 ± 160 ft-c, while the 13°C and 32°C treatments were conducted in growth chambers with light intensities of 650 ± 70 ft-c and 710 ± 160 ft-c, respectively. The seed were stratified for 168 days and then germinated on filter paper under laboratory conditions. After the radicle had begun to emerge, they were transplanted into the growth boxes (3 seed per box). As germination was not uniformly timed, the seed were held until a complete set of temperature treatments could be filled and the other temperature treatments set up as the seed became available. The glass side was covered with aluminum foil to prevent root illumination and the boxes inclined with the glass side down to force the roots against the glass. The plants were

Figure 5. Design of glass-sided boxes for root observation

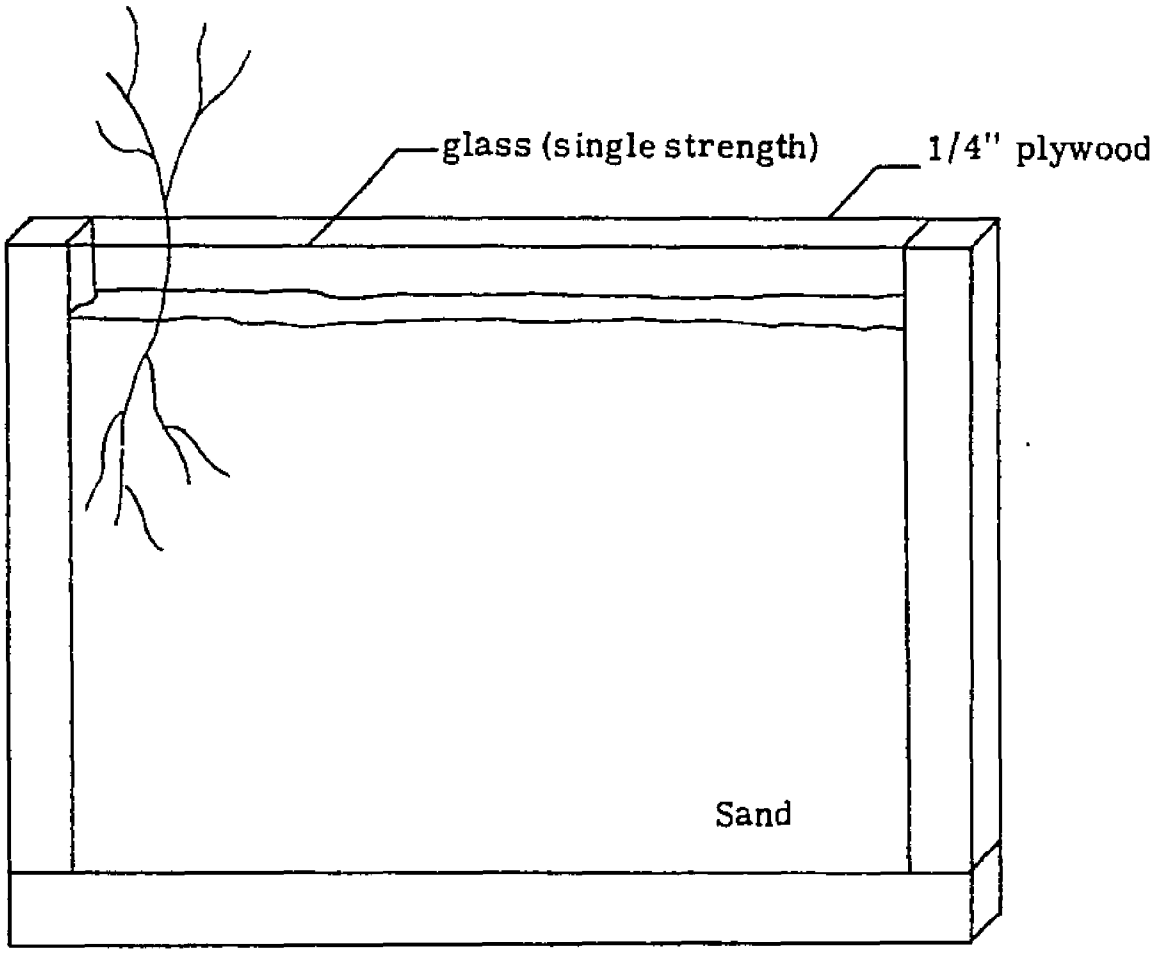

Figure 5.

observed every two days and shoot height, root depth and spread, and number of leaves recorded. The root system was traced onto acetate sheets for a permanent record. The plants were allowed to grow for 32 days at which time some roots were reaching the bottom of the growth boxes. Dry weights of the leaves, roots and stems were measured at the end of the experiment.

To examine seedling drought tolerance, morphologically similar seedlings of Ptelea and tomato (Lycopersicon esculentum var. Homestead) were subjected to drought simultaneously. Tomato was chosen because of its similarity in size to Ptelea in the cotyledonary leaf stage. The seed were germinated in 10.5 cm drained plastic pots and allowed to grow under laboratory conditions until the cotyledonary leaf stage was reached. At this time the separate pots of Ptelea and tomato were watered to saturation and thinned to give equal number of seedlings per pot. Water was then withheld and the time to wilting noted. After all seedlings in a pot had wilted, they were washed from the sand and the root characteristics were noted.

To quantify the effect of nutrient addition on seedling growth, nutrient solutions of known composition were applied to the seedlings. The six solutions were prepared according to Machlis and Torrey (1956) and included complete nutrients, complete minus nitrogen, complete minus potassium, complete minus phosphorus, complete minus nitrogen, potassium and phosphorus, and distilled water. Seed stratified for 172 days were germinated on filter paper under laboratory conditions. As

the radicle began to emerge the seedlings were transplanted to individual 10.5 cm drained clay pots and allowed to grow under laboratory conditions. For the first week the seedlings were watered only with distilled water. After this time the sand was saturated twice weekly with the appropriate nutrient solution in addition to being watered with distilled water when needed. Eight to eleven plants per treatment were grown for 5 weeks. At this time the plants were washed of sand and the length of the stem and root, number of leaves, and dry weights of the leaves, stem and roots recorded.

Sand movement can be a very important force as illustrated by the tree cemetaries present in many dune areas. To investigate the effect of sand movement on seedling growth, sand was removed or added to three week old Ptelea seedlings. Sand was added to cover the cotyledonary leaves and up to the node of the first true leaf. The addition was possible with the use of collars on 10.5 cm clay pots. In another treatment, the sand was removed by a low pressure water force until approximately 1/3 of the root system was above the sand level. These plants along with a control group were watered to soil saturation with distilled water every three days. At the end of five weeks the plants were washed of sand and the growth parameters, as in the nutrition experiment, recorded.

Seedling Transpiration and Resistances to Water Flow. Water conservation is an important requirement of all terrestrial plants. Conservation of water must be balanced, however, with the need to exchange gasses necessary for metabolism.

Transpiration of well watered plants was measured by the phytometer method (Kramer 1969) at the study site on 12 and 13 September 1973. Seedlings and one year old plants that had been transplanted from the field and allowed to establish themselves in 10.5 cm plastic pots were used. Simultaneously, evaporation from a free water surface and a wet sand surface were measured as before. To compare microhabitats, measurements were taken both in full insolation and in the shade of a large Ptelea.

During drought conditions, the transpiration rate of plants is extremely important. Transpiration of seedlings transplanted from the field and potted in dune sand in 10.5 cm plastic pots was measured by the phytometer method. The transpiration rate was measured for a gradient of conditions from well watered through wilting, as the plants utilized their water supply under laboratory conditions.

The whole plant liquid flow resistance was calculated from the equation by van den Honert (1948): $T = (\Psi_l - \Psi_s)/R$, where T is the transpirational flux at steady state (cm^3(water) · cm^{-2}(leaf area) · sec^{-1}), Ψ_l and Ψ_s are the water potential (bars) of the leaf and soil respectively, and R is the resistance (bar · sec · cm^{-1}). Twelve week old laboratory grown seedlings were placed under test conditions (Day 35.5±1.1°C, R.H. 40±2%, 316±36 ft-c for 15 hours; Night 21.0± 0.5°C, R.H. 85±5%). Transpiration was measured by the phytometer method until steady state conditions were attained. From the second leaf down, a leaf disc was then cut and placed in a peltier-cooled dew

point hygrometer chamber for leaf water potential determination (Campbell, Campbell, and Barlow 1973). The soil water potential was considered to be zero as the plants were well watered. Because the leaves are hypostomatous, the leaf area for transpiration is equal to the actual leaf outline. Resistance was then calculated.

Leaf diffusive resistance to water vapor flow was measured with a diffusion porometer (Kanemasu, Thurtell, and Tanner 1969). Seedlings and one year old plants, transplanted from the field, were used under the conditions outlined above. Diffusive resistance was measured both for the upper and lower epidermis and under both day and night conditions.

RESULTS

Soil Characteristics

Soil Texture. The dune soil is greater than 98% sand. Coarse sand at a depth of 50 cm is overlain by a medium sand. Textural classification is according to the United States Department of Agriculture (USDA Handbook 1951). The uppermost soil layer is slightly darkened by organic matter. The bulk densities of the surface and 25 cm depth are similar (1.54 and 1.55 g/cm^3, respectively), but significantly different (5% level) from the 50 cm depth (1.45 g/cm^3).

Soil Nutrients. The amounts of phosphorus and potassium in the sand are adequate for plant growth, 12.5 ppm and less than 50 ppm, respectively. But the amounts of ammonia-nitrogen (very low) and nitrate-nitrogen ($<$ 5 ppm) are low, as is common on Lake Michigan sand dunes (Olson 1958).

Soil Water Parameters. The field capacity as determined by the frequent sampling of a wetted soil column is low, 3.8% by volume, and this value was substantiated to within 0.14% by the tension plate method. The permanent wilting point as determined using sunflower and Ptelea seedlings is 1.16 and 1.71% respectively. The difference between the field capacity and permanent wilting point is defined as the storage capacity which in this case is very low (approximately two percent).

The seasonal change in the soil moisture is shown in Figure 6. The soil moisture of the surface and 25 cm depth is shown as it is within this zone that the roots of the first year seedling would occupy. The maximum and minimum daily soil moisture values occurred at night and during the daytime respectively. This was because of vaporization of the soil water as the soil heated during the day and condensation of the water vapor on the sand particles as the sand rapidly cooled at night. Thus there was a detectable diurnal change in soil moisture. The water table fluctuated primarily in response to precipitation, but never fell below a depth of 1.75 m. The presence of a suspended water table was very common and frequently obscured the extent of the capillary fringe, which was quite small due to the large pore size and low water holding capacity of sand.

Soil Temperature. Although the average annual temperature in the experimental area was quite mild (9.8°C), the maximum soil temperatures were extreme (51°C, Figure 7). The diurnal fluctuation was also very large. The surface soil temperatures are shown in Figure 7, as this is the area of greatest temperature fluctuation. The diurnal temperature profile for the soil, to a 100 cm depth, and the air, to a 50 cm height, is shown in Figure 8 for a clear summer day.

Seed Microclimate

Detectable sand movement occurred only at the most open site (free of vegetation). At this site a 1.5 cm accumulation occurred during the growing season. The solar intensity at midday was reduced

Figure 6. Percent soil moisture by volume during the 1973 growing season. The bars represent the diurnal range of soil moisture during the 24 hour sampling period.

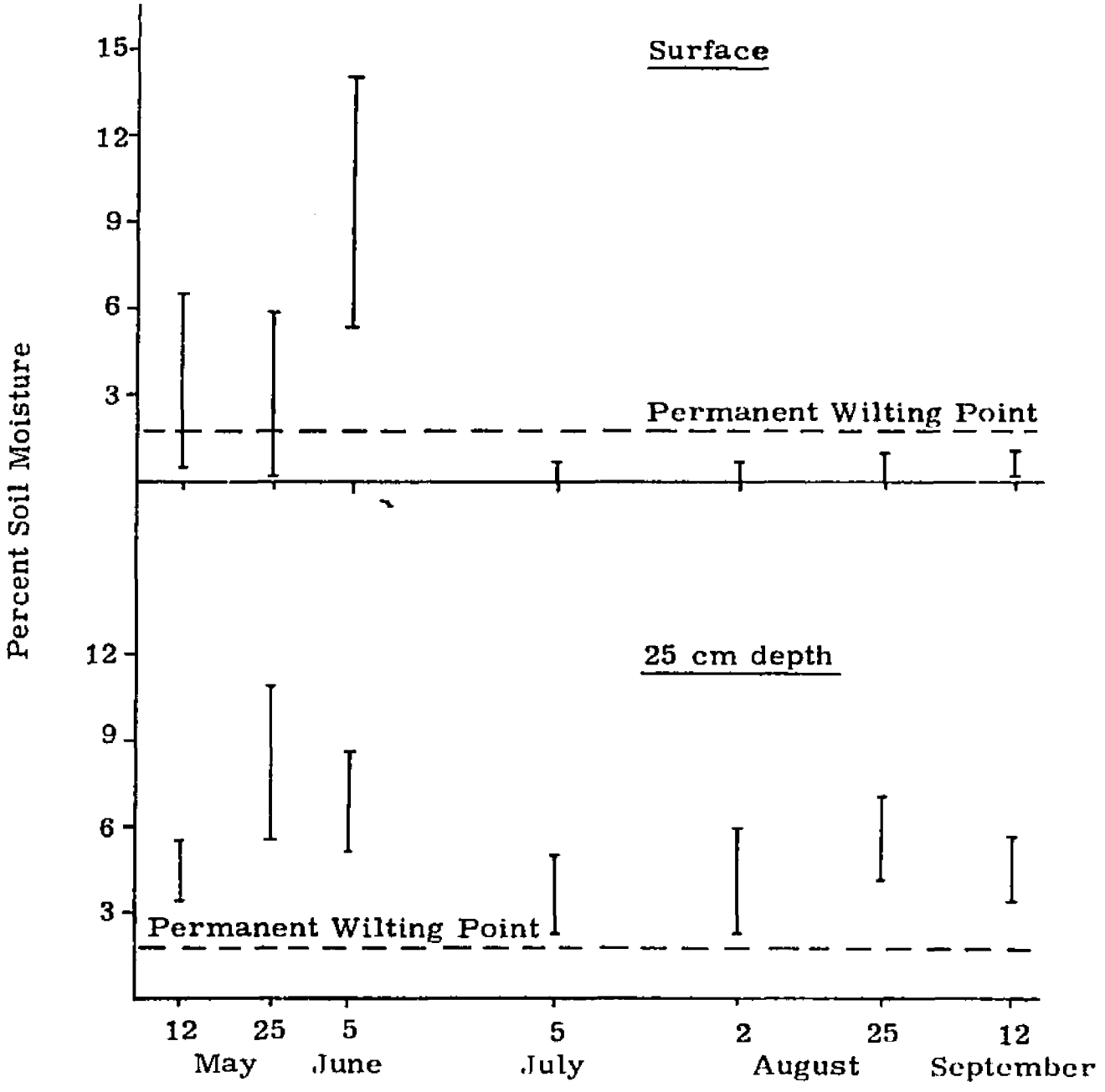
Surface
15
12
9
6
3
Permanent Wilting Point
Percent Soil Moisture
25 cm depth
12
9
6
3
Permanent Wilting Point
12
25
5
5
2
25
12
May
June
July
August
September

Figure 6.

Figure 7. Surface soil temperatures during the 1973 growing season at Saugatuck, Michigan. The bars represent the diurnal range of soil temperature during the 24 hour sampling period with the mean shown within the bar.

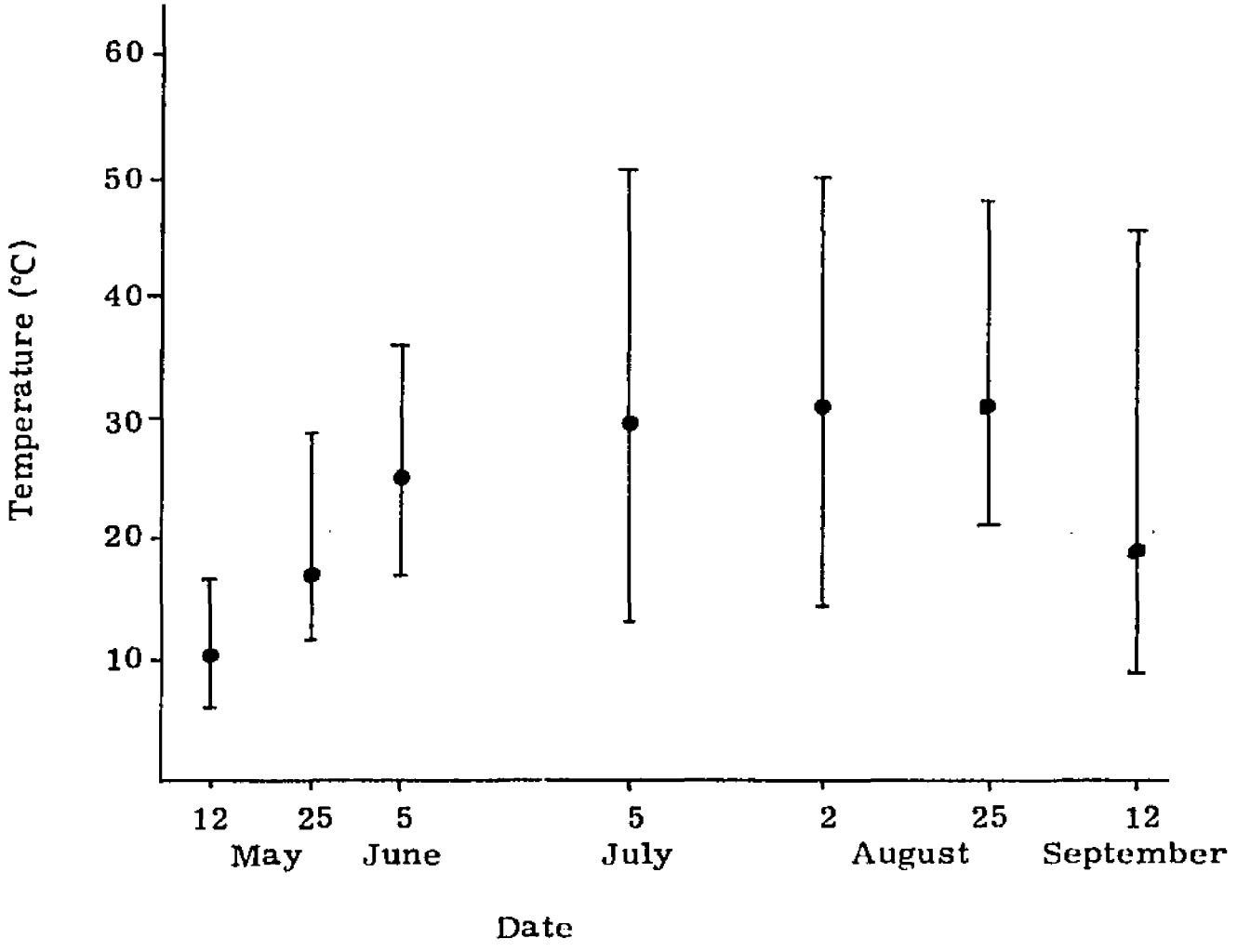
60
50
40
30
20
10
Temperature (°C)
12
May
25
5
June
5
July
2
August
25
12
September
Date

Figure 7.

Figure 8. Temperature profile in and above the soil on 5 July 1973

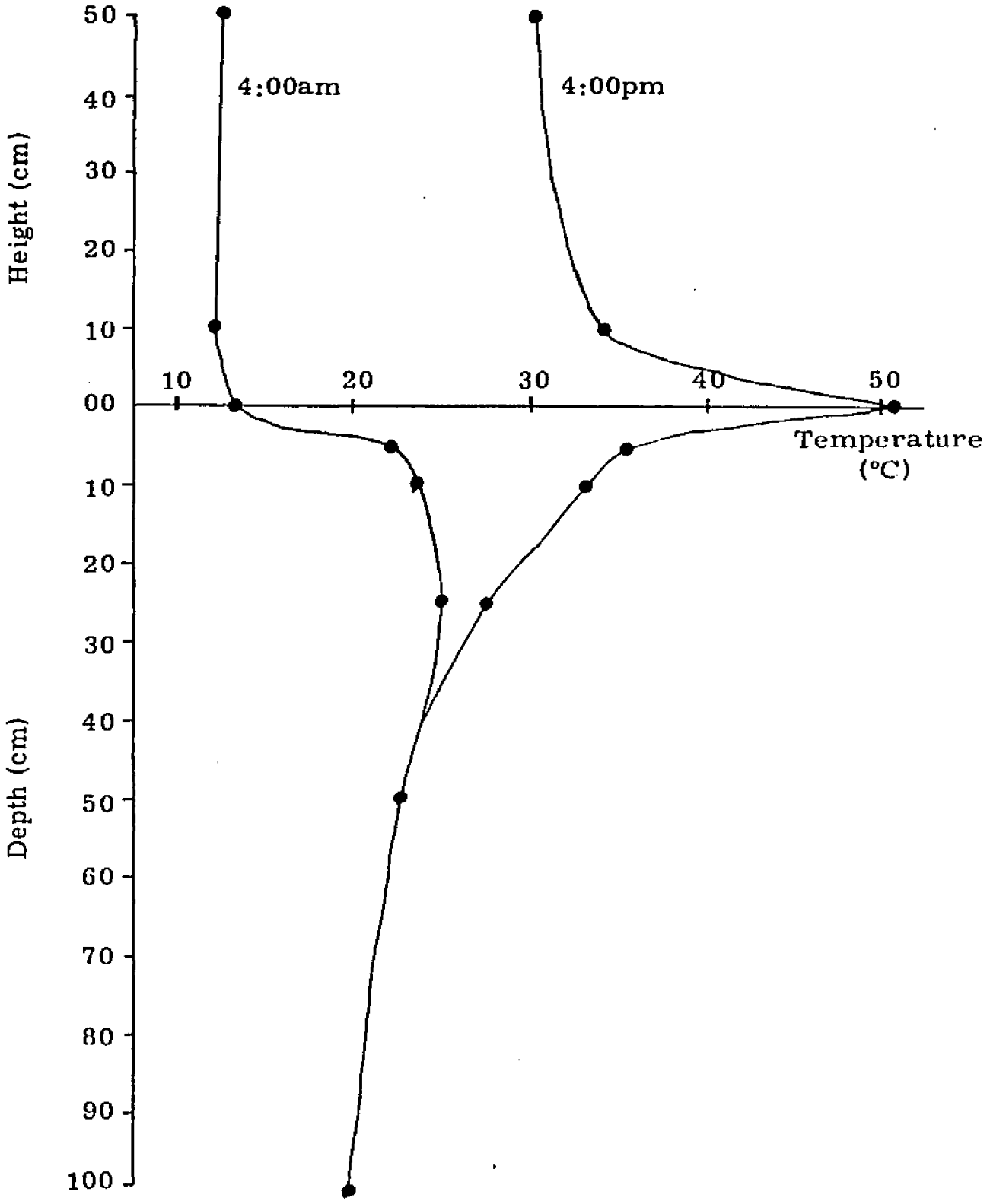
4:00am
4:00pm
Height (cm)
Depth (cm)
Temperature (°C)
50
40
30
20
10
00
10
20
30
40
50
60
70
80
90
100

Figure 8.

by an average of 85% under the canopy of a mature Ptelea, but because of the lack of a continuous canopy, the morning, late afternoon and early evening reductions were 64, 74, and 70% respectively. Because of the reduced solar input, the surface sand temperature rarely exceeded 35°C and was usually less than 30°C. The evaporative demand of the exposed and sheltered microhabitats was very different with the evaporation in the full sun being 1.7 times that in the shade. Because of canopy interception, the shaded area received only 59% of the possible rainfall. These differences in microclimate gave rise to different soil moisture profiles. The surface soil moisture in the open area was rapidly lost because of the high evaporative demand. Drying occurred from the surface down. In the shaded areas the evaporative demand at the soil surface was lower and the plant roots utilized the water from the lower soil depths. Thus the soil moisture in the shaded areas was depleted more uniformly with depth. Typical soil moisture profiles for open and shaded areas are shown in Figure 9.

Seed Dormancy and Germination

Unstratified Seed. Attempts to chemically overcome the stratification requirement proved generally unsuccessful. Frankland (1961) has successfully used gibberellic acid, thiourea, and potassium nitrate to overcome the necessity for stratification in other woody plants, but their effectiveness on Ptelea was slight. The effects of the chemicals was felt to be real as no germination was obtained with several hundred Ptelea seed used in other treatments.

Figure 9. Percent soil moisture by volume in two microhabitats on 26 August 1973.

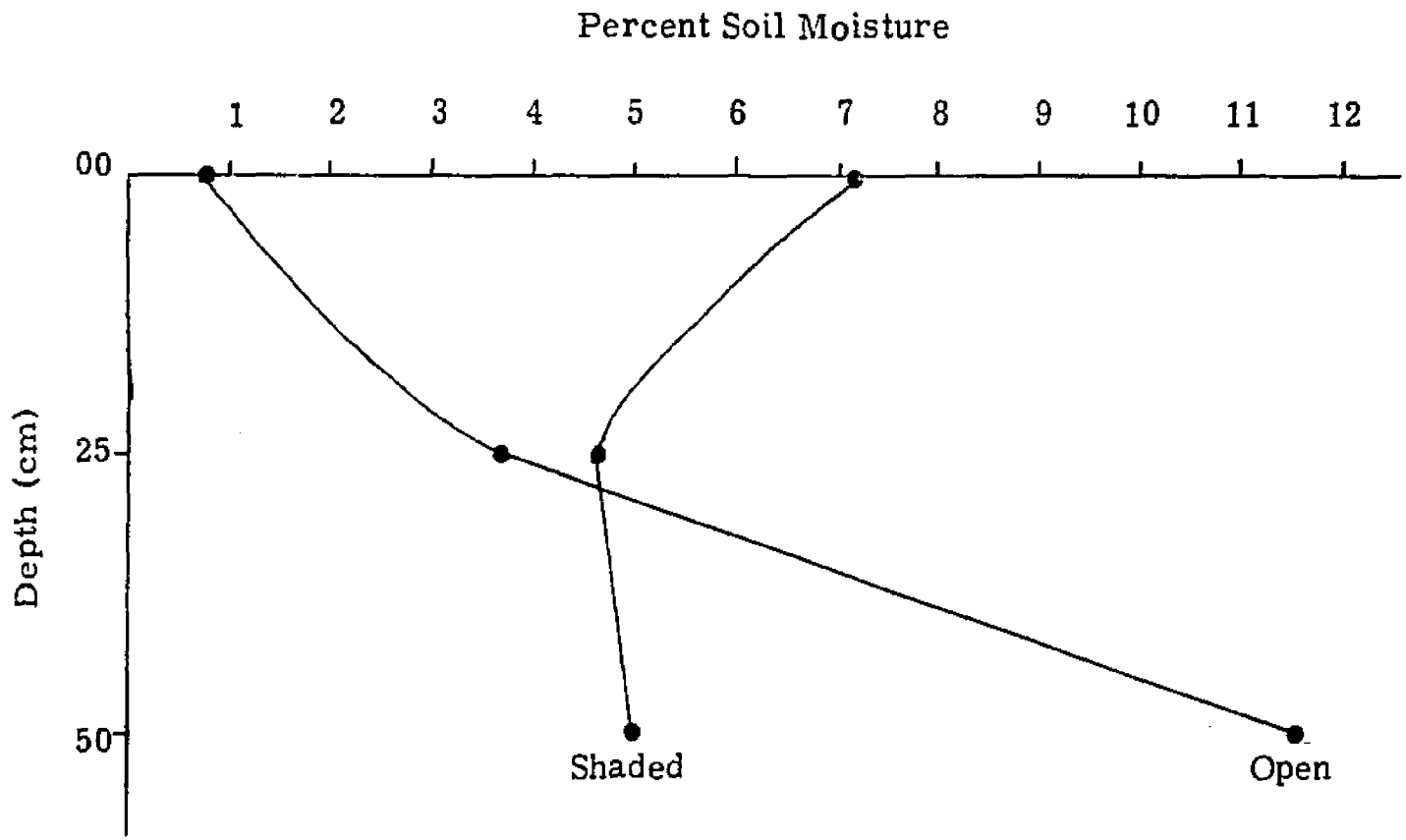
Percent Soil Moisture
1
2
3
4
5
6
7
8
9
10
11
12
00
25
50
Depth (cm)
Shaded
Open

Figure 9.

The results from attempts to germinate various germinable units is shown in Table 1. No germination was observed for whole fruits, punctured fruits or whole seed. If the seed coat was removed, 17% germination occurred. Thus some inhibition of germination is due to the seed coat or its products. By excising the embryos from the endosperm, germination was 39.5%. When only the endosperm tissue that covered the radicle was removed, 25% germination occurred. This suggests that the control by the endosperm tissue is simply physical resistance to radicle elongation. Germination of completely formed embryos was only 39.5% when removed from the influence of all the other fruit parts and if unstratified excised embryos were allowed to grow, the exhibited the characteristics of a physiological dwarf (sluggish growth and very short internodes) and therefore have a true embryo dormancy also.

The inhibition by the seed coat could be either chemical or physical (Koller 1956). Physical inhibition would be a mechanical resistance to gas or water exchange. The germination inhibition produced by fruit part leachates is shown in Table 2. The seed coat leachate inhibited germination by 84.5%. The effect of the samara leachate was extremely variable (10.3 to 103.3%) while the endosperm leachate had a smaller effect (23.0%). The variability in the germination inhibition of the samara leachate may be due to the fact that the fruits were collected from many shrubs, which may have had quite different levels of these inhibitors.

Table 1. Germination[1] of various germinable units from unstratified Ptelea fruit

Unit tested	Percent Germination[2]
Fruit	00.0 ± 0.0
Punctured fruit	00.0 ± 0.0
Whole seed	00.0 ± 0.0
Seed minus seed coat	17.0 ± 1.0
Seed minus seed coat with tip removed	25.0 ± 9.0
Excised embryo	39.5 ± 8.5

[1]Average of two replicates, each using 50 units per treatment.
[2]Mean ± one standard error

Table 2. Effects of aqueous leachates of fruit parts on the germination[1] of excised embryos

Leachate	Percent Germination[2]
Samara	33.00 ± 27.00
Seed coat	9.00 ± 1.00
Endosperm	44.75 ± 1.25
Control	58.10 ± 10.10

[1] Average of two replicates, each using 50 embryos per treatment.
[2] Mean ± one standard error.

The most concentrated samara leachate, identical to the concentration used in the previous test, allowed no germination. As the concentration decreased, the germination increased (Table 3).

The samara tissue also modified germination by prolonging full imbibition until the seventh day of exposure of the fruits to wet sand. The seed viability while stored on the laboratory shelf remained above 90% even after 220 days of storage.

Stratified Seed. The length and temperature of stratification are extremely variable for different plants (United States Department of Agriculture 1948). Germination of seed exposed to different lengths of stratification is shown in Table 4. Seed germination in intact fruits was rare (maximum 5.6%), but increased to 68% when the seed were excised. Maximum germination, 68%, occurred after 181 days of stratification. Cold room stratification was effective only if the seed were subsequently excised, indicating that the samara tissue was still inhibiting germination.

During cold room stratification the samara tissue showed very little degradation, whereas under natural conditions degradation was considerable. The effect on germination of the two stratification conditions is shown in Table 5. Germination did occur in this test under cold room stratification conditions even though the seed were left in the samara tissue. The difference in germination between natural and cold room conditions was slight except for the 160 day stratification period. At this time spring warming had begun and the seed under natural stratification conditions were germinating in the stratification container.

Table 3. Effect of different concentrations of samara leachates on the germination of excised embryos[1]

Relative Concentration	Percent Germination
1.00[2]	00.0
0.20	7.7
0.10	7.7
0.04	15.4
0.00 (Control)	100.0

[1]Fifty embryos per treatment.
[2]One gram samara tissue soaked in ten milliliters distilled water for two hours.

Table 4. Effect of cold room stratification on the germination of Ptelea trifoliata

Duration of stratification[1] (days)	Percent Germination	
	Excised seed[2]	Fruits[3]
96	7.6	4.0
124	3.6	0.0
150	36.0	0.0
181	68.0	0.0
211	48.0	5.6
242	16.0	0.0

[1]Stratification began on 2 October 1973.
[2]Twenty-five seed per treatment.
[3]Fifteen fruits per treatment.

Table 5. Effect of two types of cold stratification on the germination[1] of Ptelea trifoliata

Duration of stratification (days)[2]	Percent Germination	
	3°C Cold room	Natural
00	0.0	0.0
46	0.0	3.9
75	1.8	0.0
100	1.7	8.1
130	17.5	17.2
160	11.4	36.3[3]

[1]Fifty fruits per treatment.
[2]Stratification begun on 26 November 1973.
[3]Germination occurred in field before pots were returned to laboratory.

The results of artificially and naturally stratifying the fruits at and under the sand surface were difficult to interpret because of low germination under all the treatments. The highest germination percentage occurred with fruit buried for 150 days in the cold room, but this was only 8.5%. Essentially no germination occurred under the other treatments. From this test, the effect of the stratification treatments on the samara degradation was very apparent. After 94 days, 50.6% of the buried and 31.6% of the surface fruits under natural stratification had at least half of the samara tissue decomposed. At this time, the samara degradation of the naturally stratified fruits was over three times that occurring under cold room conditions. After 150 days, 64.8 and 71.4% of the samaras were decomposed under the artificial and natural treatments, respectively.

The attempt to determine gross weight changes of the fruit and seed during stratification was unsuccessful. The variability of the individuals proved to be too great and obscured the treatment effect, although the dry weights tended to decrease.

The viability of the seed remained high through the stratification process, never falling below 95%.

The effects of fruit and seed coat leachates on unstratified excised embryos have been discussed. The leachate effect on stratified excised embryos is shown in Table 6. The fruit leachate had no effect on the embryo germination. The inhibitory effect of the seed coat leachate was still present but reduced to 76.9%.

Table 6. Effect of aqueous leachates on the germination of stratified[1] excised embryos[2]

Leachate	Percent Germination
Control	100.0
Endosperm	69.2
Seed Coat	23.1
Fruit	92.3

[1]Stratified for 176 days.
[2]Twenty-five embryos per treatment.

Table 7 shows the germination response of Ptelea to different temperature regimes. A 17°C constant temperature gave the optimum germination (60%) of the constant temperature conditions. A fluctuating temperature regime with a 19.8°C average gave optimum germination of the entire test (72%). It is very common for fluctuating temperatures to promote germination (Kozlowski 1971). This has usually been attributed to the various metabolic germination processes which require different temperatures. At temperatures below optimum, germination was delayed with 90% of the seed still viable yet ungerminated at the end of the test. Higher than optimum temperatures enhanced the rate of seed germination but viability of the seed remaining at the end of the test decreased as the treatment temperature increased.

The attempt to germinate Ptelea seed under constant 35 or 40°C temperature regimes proved unsuccessful. Also the percentage of viable seed was very low at the conclusion of the test. Since it was common to record surface soil temperatures in excess of 40°C for several hours per day on the dunes, the seed must be able to survive these temperatures. Survival, as expressed by viability (Table 8), was high if the seed were not imbibed. If the seed were imbibed, the viability decreased greatly in the heat treatment and only slightly when subjected to more moderate temperatures. Thus imbibed seed were killed by the heat treatment created in the laboratory experiment which was similar to temperatures found on the dunes. The high temperatures would dry the seed and possibly this would allow the seed to remain viable rather than be killed by the high temperature.

Table 7. Effect of temperature on the germination[1] of *Ptelea* seed[2] stratified for 163 days

Temperature (°C)	Percent Germination
2	0.0
13	32.0
17	60.0
24	12.0
30	8.0
35	0.0
40	0.0
19.8[3]	72.0
22.4[4]	60.0
23.5[5]	24.0
24.0[6]	16.0

[1]Germination percent after four weeks.
[2]Twenty-five seed per treatment.
[3]Average of 9 hours of 16°C and 15 hours of 22°C.
[4]Average of 10 hours of 20°C and 14 hours of 24°C.
[5]Average of 12 hours of 21°C and 12 hours of 26°C.
[6]Average of 12 hours of 21°C and 12 hours of 27°C.

Table 8. Effect of a 40°C heat treatment for four hours per day on the viability and germination of stratified[1] *Ptelea* seed[2]

Treatment length (weeks)	Dry Seed		Imbibed Seed	
	Temperature Treatment			
	Laboratory	Heat	Laboratory	Heat
1 % Viability	100	100	100	85
% Germination	20	10	45	40
2 % Viability	90	90	85	40
% Germination	30	25		10
3 % Viability	90	90	90	55
% Germination	30	15		5
4 % Viability	95	85	90	45
% Germination	10	15		0

[1]Stratified for 195 days.
[2]Forty seed per treatment.

Imbibed seed under moderate temperatures gave maximum germination (45%). The other treatments gave reduced germination because of either the heat treatment or the drying of the seed following stratification (Table 8).

Ptelea seed failed to germinate in the dark while germination in the light was 16%. This was a low germination percentage but not abnormal considering the stratification length. When the seed were planted at four different depths the germination was equal, 15%, although two-thirds of the seed that germinated at the four centimeter depth never emerged from the ground. It appears that the lack of germination recorded in the earlier test was probably because of accumulation of gasses in the closed container because germination occurred in other more open yet still dark containers.

The watering frequencies used had little effect on Ptelea seed germination. When saturated every two or three days, the germination was 22.2%. When the seed were watered daily, the germination was 16.7%. The reduction in germination was probably due to interference with gas exchange.

Fruit Loss

After the winter had passed, 97.6% of the fruits placed on the sand surface had been removed by various agents, while only 9.5% of the buried fruits were missing. Therefore removal of fruits was greatly reduced by slight burial.

The Seedling

Seedling Growth and Survival. Seed germination in the study area was confined to a short period in early May. Survival of the seedlings found in the transects is shown in Figure 10. The density of first year seedlings was 1.9/m^2, but only 10.5% of these seedlings survived the first growing season. Dehydration was responsible for 63.2% of the mortality, while 22.1% died due to vehicular traffic and 14.7% died due to miscellaneous causes. This high mortality rate was responsible for the low density (0.2/m^2) of one year old seedlings found in the same area. One year old seedlings had a 50% survival rate with all of the mortality due to dehydration. The period of greatest mortality was between 6 June and 26 June 1973. During this period a ten day drought with only a trace of rain on the tenth day occurred. This drought was very likely the cause of the mortality as the seedlings were less than four weeks old. The root development was probably not great enough to allow utilization of the soil water in the deeper soil layers.

Survival of the field seedlings was dependent upon the seedling microhabitat. The open habitat was very unfavorable (Figure 11). The primary causes of mortality in the open habitat were dehydration (40.0%) and vehicular traffic (37.1%). The shaded habitat allowed 24.5% of the seedlings to survive the growing season. Once again, the primary cause of mortality was dehydration (91.9%). In the transects more seedlings (density 1.23/m^2) were found in the shaded habitat than in the open habitat (density 0.88/m^2) during the 1973 growing season.

Figure 10. Survivorship curve for Ptelea seedlings during the 1973 growing season based on seedling age

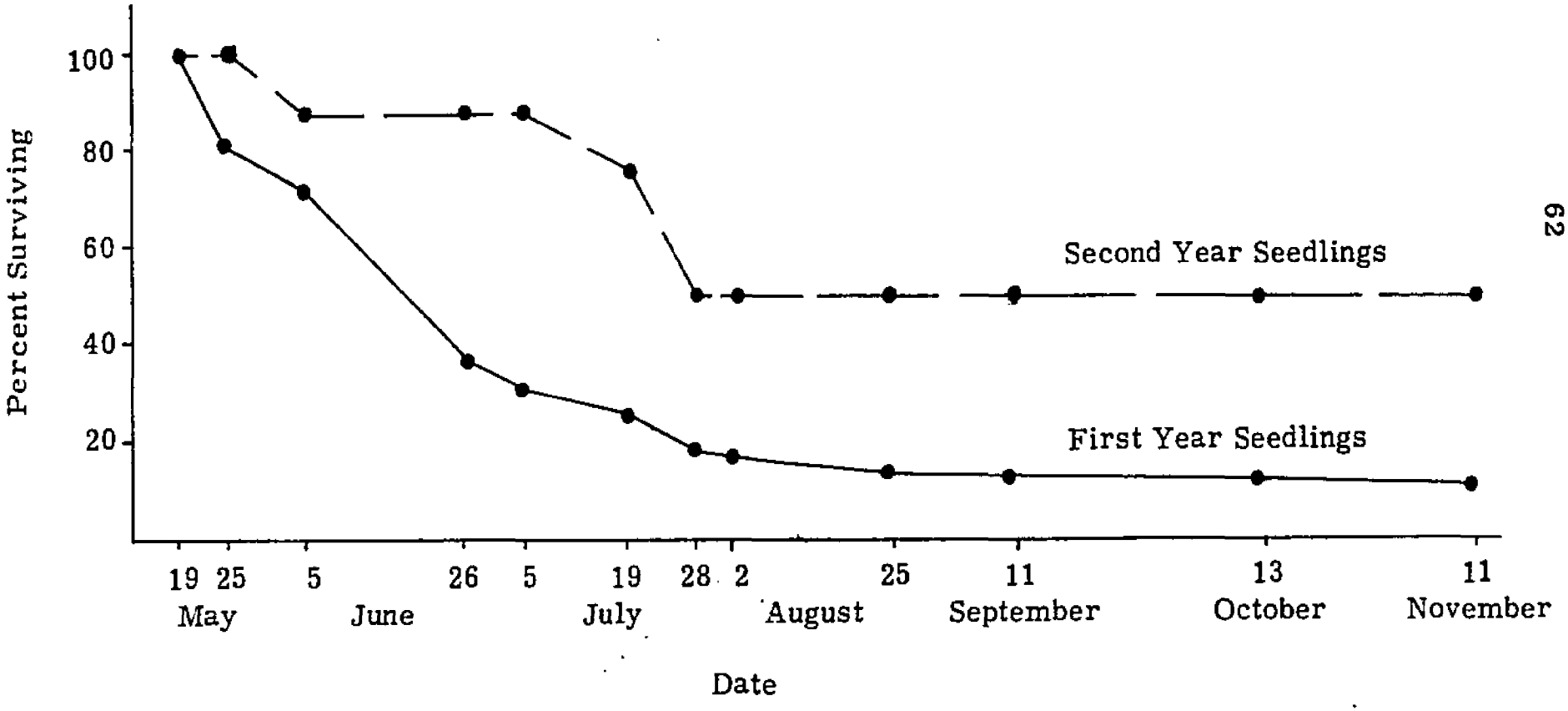
Percent Surviving
100
80
60
40
20
Second Year Seedlings
First Year Seedlings
19 25 5 26 5 19 28 2 25 11 13 11
May June July August September October November
Date

Figure 10.

Figure 11. Survivorship curve of Ptelea seedlings during the 1973 growing season based on microhabitat

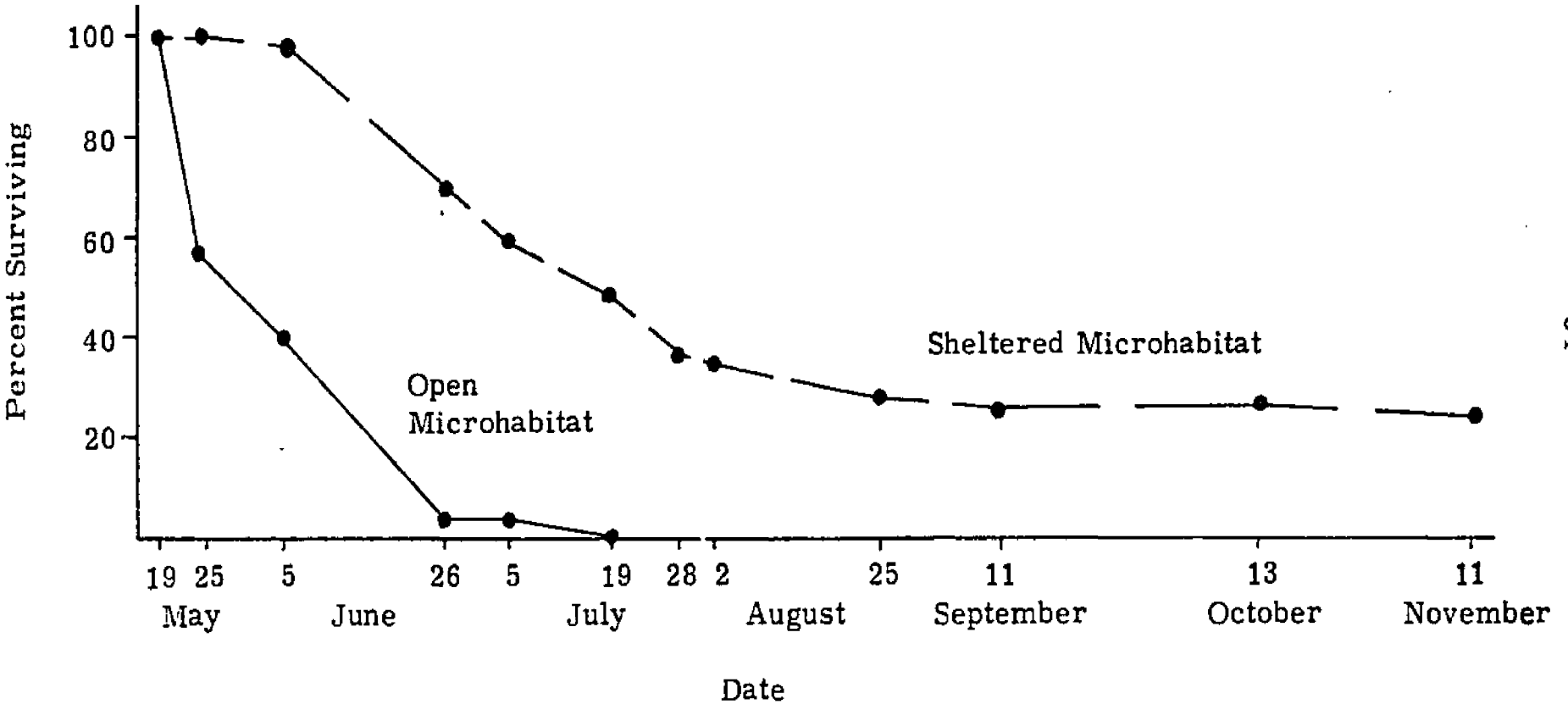
Percent Surviving
100
80
60
40
20
Sheltered Microhabitat
Open
Microhabitat
19 25 5 26 5 19 28 2 25 11 13 11
May June July August September October November
Date

Figure 11.

The germination process of Ptelea proceeds relatively slowly. Once the seed was planted, it was 5 to 20 days before the hypocotyl hook emerged from the soil surface. For the next week the cotyledonary leaves were the only photosynthetic organs until the first true leaf was formed. This leaf was frequently simple while all subsequently produced leaves were trifoliate. The periodic excavation of seedlings through the summer allowed observation of their growth during the first growing season (Figure 12). The age was most strongly correlated with total weight ($r = .92$). An average of three leaves were retained by the seedling during the summer, regardless of age. The larger plants, from one to ten years old, were extremely variable in their growth parameters. One observation that might explain this variability was that the remnants of former shoot systems were frequently found at the root crown. These former shoot systems could have been destroyed through herbivory or mechanical breakage.

The development of an adequate root system is the prime necessity of a newly germinated seedling. The root growth was observed in the soil temperature-watering frequency experiment. Most rapid growth was found at 24°C and a watering frequency of two days. The 13°C temperature did not create any adverse soil moisture conditions and the effect of watering frequency was small. A short, thick, infrequently branched root system was produced. In the 32°C treatment, as the watering frequency decreased, rapid root elongation occurred producing a thin, sparsely branched root system. Thus the

Figure 12. Growth of seedlings at study site during the 1973 growing season. Mean $\pm$ one standard error shown on figure.

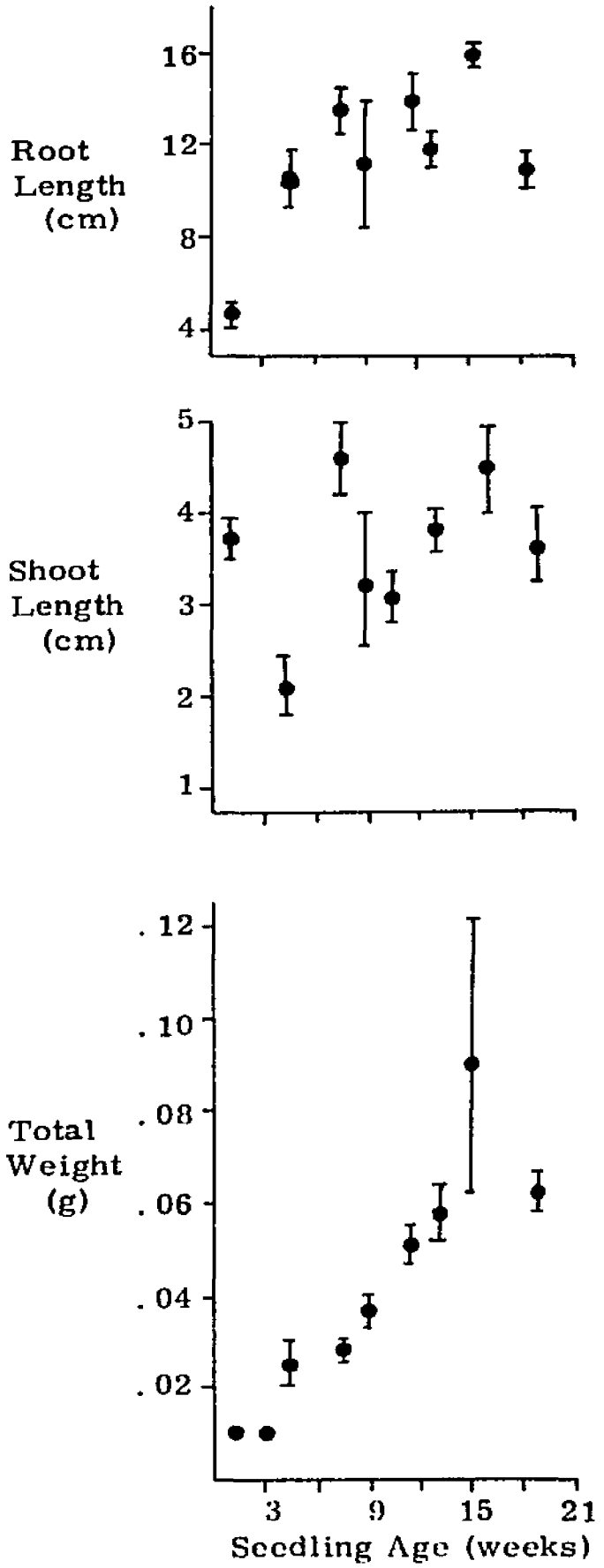
Root Length (cm)
16
12
8
4
Shoot Length (cm)
5
4
3
2
1
Total Weight (g)
. 12
. 10
. 08
. 06
. 04
. 02
3
9
15
21
Seedling Age (weeks)

Figure 12.

roots grew deeper in response to increasing soil aridity at this temperature. At 24°C, the rooting depth was greatest when watered every two days and less at the other two frequencies. The root system had more secondary root development and occupied a greater soil volume. The experimental effect on the roots is shown in Figure 13 and Table 9. Similar growth responses to the treatments were found in regard to shoot, stem, leaf and total weights and root/shoot weight ratio. The only parameters not affected were number of leaves, root spread and shoot height.

In the drought tolerance test, tomato seedlings lived an average of 7.1 days before wilting occurred while Ptelea seedlings lived for only 4.5 days. Seedling excavation showed that differences in root growth probably accounted for the difference in drought tolerance. Tomato roots averaged 10.4 cm in length while Ptelea roots averaged only 3.1 cm.

The seedlings responded strongly to nutrient addition. The responses as measured by leaf, stem, root and total seedling dry weights are shown in Table 10. Addition of complete nutrient solution gave significantly greater growth than did addition of distilled water only. When single nutrients were deleted, the seedlings grew least when nitrogen was not present. The deletion of nitrogen, potassium, and phosphorus produced less growth than in any single nutrient deletion treatment but greater than in the distilled water treatment. Similar treatment effects were also measured in the number of leaves and shoot weight

Figure 13. Representative root systems showing the effect of temperature on the root habitat. Roots are shown at actual scale.

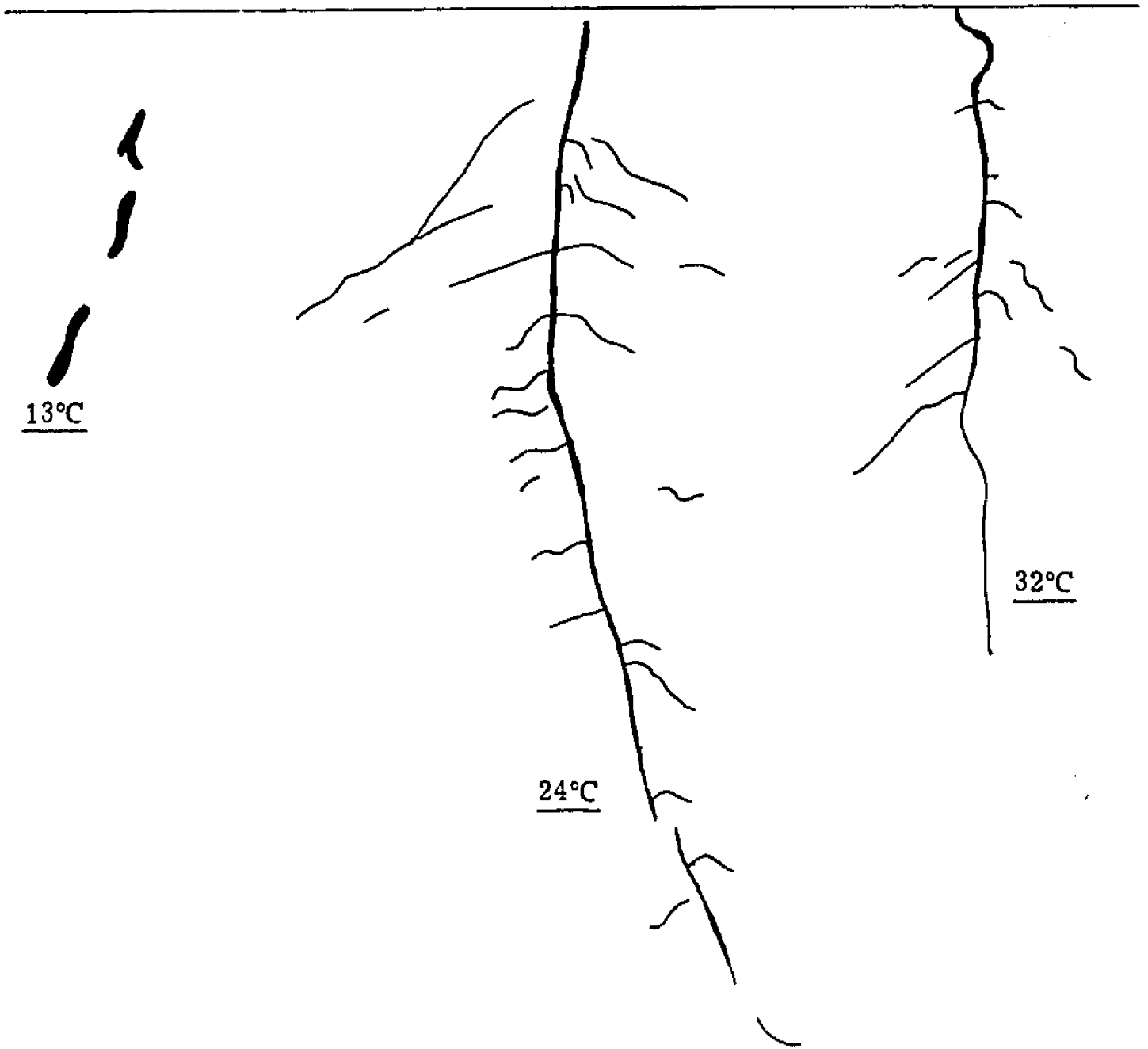

Figure 13.

Table 9. Effect of temperature and watering frequency on the root development of Ptelea seedlings[1]

Temperature	Growth parameter	Watering frequency		
		Daily	Every 2 days	Every 3 days
13°C	Depth(cm)	5.3a	7.0a	6.5a
	Weight(mg)	2.4a	3.0ab	2.8ab
24°C	Depth(cm)	12.6b	17.3c	12.2b
	Weight(mg)	11.9d	15.0e	12.7d
32°C	Depth(cm)	7.3a	10.2b	12.6b
	Weight(mg)	5.7bc	5.8bc	6.8c

[1]Significance determined using Tukey's test. Values sharing the same letter within the same growth parameter are not significantly different at 5% level. Average of nine plants per treatment.

Table 10. Average dry weight(mg)[1] of Ptelea seedlings grown in different nutrient solutions

Plant part	Nutrient solutions					
	Complete	-N	-P	-K	-NPK	Distilled Water
Stem	15.3	9.7	12.3	9.7	9.1	8.9
	b	a	ab	a	a	a
Leaf	71.4	35.5	40.3	46.8	23.8	24.3
	b	a	a	ab	a	a
Root	40.2	26.5	26.7	32.2	21.9	19.2
	b	a	a	ab	a	a
Total	126.9	71.7	79.3	88.9	54.9	52.5
	b	a	a	ab	a	a

[1]Significance determined using Tukey's test. Values sharing the same letter within the same plant part are not significantly different at 5% level. Average of eight to eleven plants per treatment.

while the shoot and root length and root/shoot weight ratio showed no treatment effect.

The only significant difference, using Tukey's test, between the partially buried and undercut seedlings was the number of leaves retained by the seedlings. The buried seedlings retained an average of 3.57 leaves while the undercut seedlings held only 2.57 leaves. No significant differences in treatment effects were found in the other growth parameters. It was noted, however, that 28.5% of the partially buried seedlings had produced adventitious roots at the cotyledonary node.

Seedling Transpiration and Resistances to Water Flow. Transpiration rates under field conditions are shown in Table 11. The evaporative demand was less in the shaded area, this was evidenced by the transpiration rates in the two habitats. Evaporation rates from wet soil and leaf surfaces were approximately 90 and 80% of that from a free water surface, respectively. The potential evaporation is not the actual evaporation of water from the soil in situ since the actual evapotranspiration declines as the soil moisture declines (Slayter 1956). Transpiration rates during drought conditions are shown in Table 12. Transpiration rate of well watered plants was 22.7 g(water) · dm^{-2}(leaf) · 24 $hours^{-1}$. Transpiration decreased during the drought but daily values were erratic. Transpiration at wilting was still 16.5% of that occurring in a well watered plant.

Table 11. Daytime water loss under field conditions on two different days

Habitat	Type of loss	9-12	9-13
20% of full sun	Evaporation[1]	3.14	2.45
	Transpiration[2]	1.96	2.66
	Evaporation[3]	4.39	2.43
Full sun	Evaporation[1]	4.92	4.10
	Transpiration[2]	4.19	3.67
	Evaporation[3]	5.52	4.13

[1](g water lost · dm^{-2} (soil) · hr^{-1}). Average of 4 replicates.
[2](g water lost · dm^{-2}(leaf) · hr^{-1}). Average of 4 replicates.
[3]From evaporation pan (g water lost · dm^{-2} (water surface) · hr^{-1}). Average of 4 replicates.

Table 12. Transpiration of Ptelea seedlings[1] under laboratory conditions during decreasing soil moisture

Days before wilting	Transpiration (g water lost · dm^{-2} (leaf) · 24 $hours^{-1}$)
19	22.70
16	12.31
15	15.47
14	17.61
13	17.04
12	11.33
11	14.75
10	7.36
9	8.76
8	9.44
7	7.38
6	5.64
5	7.14
4	4.63
3	6.74
2	6.34
1	7.25
0	3.76

[1]Average of three replicates.

Internal liquid flow resistance for six replicates ranged from 1.17×10^6 to 5.98×10^6 and averaged 3.75×10^6 bar · sec · cm^{-1}, while the leaf water potentials ranged between -9.3 to -12.3 bars. Steady state transpiration during these measurements of Ptelea seedlings averaged 1.39 g (water) · dm^{-2} (leaf) · hr^{-1}. The vapor diffusive resistances are shown in Table 13. The resistances of one year old plants were 1.5 times greater than first year seedlings.

Table 13. Diffusive resistance of two ages of Ptelea trifoliata seedlings[1]

	Stomatal condition	Age	Resistance ($sec \cdot cm^{-1}$)
Lower epidermis[2]	Open stomates	Seedling	11.40
		One year old	17.47
	Closed stomates	Seedling	40.28
		One year old	79.01
Upper epidermis[2]	No stomates	Seedling	293.48

[1]Average of four replicates.
[2]Boundary layer resistance = 0.56 $sec \cdot cm^{-1}$.

DISCUSSION

The discussion that follows is divided into three sections. In the first section, the climatic conditions to which the dune plants are subjected on the shore of Lake Michigan are reviewed. The second and third sections utilize laboratory experiments and field studies to describe the ecological life cycle and the physiological ecology, respectively, of Ptelea trifoliata as they help to explain the success of this shrub in an environment where few other shrub species are found.

It is recognized that laboratory experiments are not an absolute indicator of how a plant will react in nature, but such experiments do provide an indication of the plant reaction. Therefore the laboratory experiments and field studies have been combined to give a more complete description of Ptelea trifoliata.

Dune Climate

Although the summer climate associated with the shore of Lake Michigan can be described as moderate, the microclimate of the sand surface on which seed and seedlings exist is more severe, as exhibited by the low plant density, diversity, and apparent productivity. The severity in microclimate can be inhibitory or lethal to young plants.

When water is absent, the temperature buffering capacity of the soil is reduced; during the summer the temperature of the surface sand at midday may be as much as 63% greater than the temperature of the air and commonly exceeds 50°C. Water stress occurs frequently, largely because the sand substrate is very poor in its ability to hold moisture. During most of the 1973 growing season, there was less than half of the possible storage capacity in the top ten centimeters of sand. The quantity of available soil water increases with depth until at 25 cm, water is permanently available for plant usage. The rapid evaporation of water from the surface sand helps to prevent evaporation of subsurface moisture. The nightly recharge of soil moisture and formation of dew because of condensation may be important in allowing plants to regain the turgor lost during the daylight hours.

Harper, Williams, and Sagar (1965) related differences in success of seed germination and seedling establishment to very slight microclimatological differences. Microclimatological variation is pronounced in the sand dune habitat. For example, shaded habitats, in contrast to open habitats, are characterized by less sand movement, lower solar intensity, less fluctuation of soil temperature, smaller quantities of precipitation, and lower evaporative demand. The lower maximum soil temperature and lower evaporative demand in shaded habitats create soil moisture conditions which are relatively more favorable for seedling establishment.

Fruit Production, Germination and Seedling Establishment of Ptelea trifoliata

On the sand dunes, Ptelea begins to flower in early June and by the end of June small fruits are visible. The mature fruits begin to fall by mid-October and most of the fruits are shed by January. The 1971 fruit production was 338,000/ha (P. G. Murphy pers. comm.). The fruits require stratification and cannot germinate during the year in which they are produced. The dormancy is enforced by inhibitors found in aqueous leachates of the seed coat and samara tissue. The chemical composition of these leachates is unknown but Ptelea leaves are known to contain alkaloids and coumarins (Bailey, Mooken, and Bailey 1971, Dreyer 1969, Herlin, Bailey, and Bailey 1966, Mooken, Bailey, and Bailey 1969, Szendrei et al. 1973). Coumarins are strong germination inhibitors, while the effects of alkaloids are more variable, depending on concentration (Evenari 1949). Whether these compounds can be translocated from the leaves to the fruits is unknown (although alkaloids are translocated to the fruits of tomato (Salisbury and Ross 1969)). Dreyer (1969) found small quantities of a furoquinoline alkaloid in Ptelea aptera fruits. Thus coumarins and alkaloids found in Ptelea trifoliata fruits may possibly be translocated to the fruits where they could inhibit germination. Whether the general coumarin or alkaloid groups are actually found in Ptelea trifoliata fruits could be determined by thin layer chromatography, but exact determination of the compounds present would be much more difficult. These inhibitors

may play a role similar to the germination inhibitors found by Went (1955) in desert seed. Germination of the desert seed only occurred after the inhibitors had been leached from the seed by critical rates of precipitation. Regardless of the effect of inhibitors, Ptelea seed must be stratified to remove a true embryo dormancy, which is the primary factor controlling dormancy.

Ptelea fruits buried under natural conditions required 160 days of stratification to initiate germination. Under this treatment, the duration of stratification required was shortest and the samara tissue had largely decomposed.

Ptelea germination at both the study site and Rose Lake Wildlife Research Area occurred in early May. The maximum germination of stratified Ptelea seed in the laboratory occurred at temperatures (19.8°C) corresponding to the field temperatures of May or early June. Seed maintained at lower temperatures (13°C) were slow to germinate and the total percent germination was reduced by 40%. Thus stratified seed are delayed in germinating by low temperatures. Germination was not reduced by the two day drought created in the laboratory. Longer droughts, while not lethal to seed, prevents them from germinating the first season subsequent to stratification.

Surface sand temperatures of 40°C or greater frequently occur during the summer. In a laboratory experiment it was shown that dry seed can withstand these temperatures but fully imbibed seed are killed.

The growth rate of Ptelea seedlings at the study area was greatest in the spring. This corresponds to the optimum temperature (24°C) for growth as found in the laboratory. Seedling growth in the laboratory was reduced by 66% at cooler temperatures. During the first growing season, the total root elongation was greater than the total shoot elongation. By the end of the first growing season, roots penetrated to the 15-20 cm depth where water is available most of the time.

Seedling growth was increased 141% by addition of a complete nutrient solution in a laboratory experiment.

Sand instability (partial burial or undercutting) did not adversely affect the growth of Ptelea seedlings in the laboratory. The seedlings did respond to partial burial by producing adventitious roots.

Although more than 300,000 fruits/ha (approximately 375,000 seed) are produced annually, in 1973 only 19,000/ha successfully established seedlings. The survival of these seedlings to the second year was very low (10.5%), but the survival of second year seedlings is greater (50%). Rates of mortality decline with age but nevertheless only 12.5 plants/ha (0.004% of original seed production) reach the age of twenty years (P. G. Murphy pers. comm.).

The primary cause of seedling mortality is dehydration. Observations of excavated seedlings that were dehydrated revealed no disease symptoms or reduction of the root system. Thus, dehydration probably results from the low amounts of available soil water in the top ten

centimeters of sand during the summer. This is the area from which the seedling roots must obtain water because of their slow root elongation.

Whereas no Ptelea seedlings survived in open habitats, 24.5% survived in shaded habitats. This difference is thought to reflect the relatively more favorable water relations in the shaded habitat where 1.9 times more soil moisture is available in the top 25 cm of sand and the evaporative demand is 58.9% less.

Response of Ptelea trifoliata to the Environmental Stresses on Sand Dunes

The major environmental stresses of plants inhabiting sand dunes will be characterized and the manner in which Ptelea copes with the stress will be described. The stresses to be characterized are high light intensity, high soil temperature, high evaporative demand, drought, low soil nitrogen, and sand instability.

On a clear summer day the light intensity on the sand dunes ranges from 7,000 to 10,000 ft-c, while the light intensity under a Ptelea shrub is 5 to 40% of full sunlight. Ptelea seedlings have a light saturation point of 3500 ft-c and are considered heliophytes. Seedlings of other woody vegetation found on the open dunes grow best in full sunlight and are also heliophytes. According to the United States Department of Agriculture (1965) seedlings of the mesic trees found on the forested rear dune grow best in shaded habitats and are sciophytes. While not fully understood, sciophytes can be characterized by their

low metabolic rates (Grime 1966). He also noted that the growth rates and yields of sciophytes are lower than for heliophytes. The reduced growth rate could make the seedlings more susceptible to the other stresses of the sand dunes. Thus one property of Ptelea that could allow its survival on the open dunes is its ability to utilize light intensities up to 3500 ft-c while the sciophytic seedlings of the woody species in the adjacent forest habitat cannot fully utilize this light intensity.

Another stress of the sand dunes which might be inhibitory to seedling establishment is the high soil surface temperatures during the summer which frequently remain above 45°C for four hours per day and reach a maximum of 51°C. In many species of woody plants, especially conifers (Bates 1924, Hartley 1918, Levitt 1972, Toumey and Neethling 1924) soil temperatures greater than 45°C cause seedling mortality by destroying the conductive and cambial tissues, thus girdling the stem (Daubenmire 1959). The dead Ptelea seedlings at the study site, however, did not appear to be damaged by the high temperatures, as their stems were not shrunken or collapsed at the base.

The most serious stress for a young woody seedling on the sand dunes is drought. Even though annual precipitation exceeds 88.75 cm, drought-like conditions occur frequently on the dunes because of the low water retention of sand. The weather records for the period 1969 to 1973 indicate that droughts (rainless periods) of six days or longer occurred an average of five times per growing season (May to October). Because an average of only 1.6 of these droughts occurred during May

and June, while the precipitation was 10.16 cm, soil moisture was available when the seedlings were young and most susceptible to drought.

In combination with drought conditions, the high surface soil temperatures of the sand dune habitat create high daily evaporative demands (up to 38.6 $g \cdot dm^{-2} \cdot 24\ hrs^{-1}$) during the growing season. In comparison it is interesting to note that the mean daily evaporative demand during the 1973 growing season for Tucson, Arizona, was only 48.2 $g \cdot dm^{-2} \cdot 24\ hrs^{-1}$, although maximum rate was 81.8 $g \cdot dm^{-2} \cdot 24\ hrs^{-1}$ (United States Weather Bureau 1973b). Thus the high evaporative demand increases the moisture stress during a drought.

Although the evaporative demand is primarily responsible for the transpiration rate, the rate can be modified by the flow resistances which are species specific. Comparison of the resistances of different species is difficult because of the scarcity of appropriate data in the literature. Ptelea seedlings have a mesic (i.e. relatively low) stomatal resistance when compared to the oak and maple seedlings observed by Wuenscher and Kozlowski (1971). Thus, the leaves are mesic in regard to adaptation to prevent water loss. However, these resistances are approximately four times greater than those reported for corn and soybean (Boyer 1970). The liquid flow resistances of soybean, bean and sunflower (1971) and sunflower (1974) have been reported by Boyer. Ptelea, under well watered conditions, has an average resistance of 3.6 $bar \cdot sec \cdot cm^{-1}$ compared to bean (0.4 $bar \cdot sec \cdot cm^{-1}$),

sunflower (0.6 bar · sec · cm^{-1}) and soybean (1.5 bar · sec · cm^{-1}). The importance of the liquid flow resistance calculated from the transpiration rate of well watered plants is difficult to assess because the resistance varies with the transpiration rate (Boyer 1974). The resistance of the plant at very low transpiration rates can be 30 times greater than the value for a well watered plant (Boyer 1974). Nevertheless, a relatively low resistance under well watered conditions will cause plants to utilize more water during the day than plants with a high resistance and should enable the plants to regain turgor faster at night. A longer period at night spent at maximum turgor should increase leaf expansion (Boyer 1968).

Because of the mesic resistances of Ptelea seedlings and the high evaporative demand of the sand dune environment, the transpiration rate of Ptelea is higher than that reported for other woody seedlings under field conditions (Kramer 1969) and very similar to the maximum rates of two desert shrubs reported by Moore, White, and Caldwell (1972). Thus the water loss from Ptelea seedlings is very high.

Because of slow root elongation and high transpiration rates of Ptelea seedlings, the drought tolerance in the laboratory of two week old seedlings is poorer than similarly aged tomato seedlings, which have low drought resistance (Levitt, Sullivan, and Krull 1960). A nine day drought, when the Ptelea seedlings were only four weeks old caused 36.1% of the total mortality at the study site during the 1973 growing season. At 12 weeks of age, the drought tolerance of Ptelea

seedlings, as measured by the leaf water potential while the plants were subjected to specific soil moisture tensions, was similar to that reported by Seidel (1972) for black and white oak. Thus favorable soil moisture conditions must exist during the early establishment period of Ptelea seedlings because young seedlings are very sensitive to drought but the sensitivity decreases as the root system develops.

Although high transpiration rates coupled with high evaporative demand may result in desiccation under some conditions, such as low soil moisture, Kramer (1969) indicated that high transpiration rates can beneficially cool the plant because of the heat transfer during evaporation. Poljakoff-Mayber and Gale (1972) found that a transpiration reduction of 40% increased the leaf temperature by 2.0-2.5°C under desert conditions. Leaf temperatures above 44°C can kill leaf cells (Levitt 1972). Thus the high transpiration rate could possibly allow Ptelea seedlings to tolerate the high temperatures.

Olson (1958) noted that the pioneer plants on open sand "must be admirably adapted to reusing what limited nitrogen supply they have." This is because the nitrogen content of the dune sand is less than five part per million. Mitchell and Chandler (1939) found that red oak, white oak, red maple, sugar maple, beech, white ash, and basswood, species that are found on the better developed soils adjacent to the open dunes, require at least 25 ppm N to survive. The roots of Ptelea seedlings, however, grow sufficiently during the first growing season to allow seedling survival. Although it responds favorably to fertilization

in the laboratory, low nitrogen does not completely inhibit Ptelea growth whereas it has been indicated that the growth of woody species inhabiting the forest would be inadequate to survive at the nitrogen levels found in dune sand.

A characteristic that allows the woody plants to inhabit the unstable Lake Michigan sand dunes is easily visible as these plants can produce adventitious roots, while the woody plants of the forested rear dune rarely do (United States Department of Agriculture 1965). Kurz (1939) found that seven dune plants in Florida, including scrub live-oak and magnolia, tolerated sand accumulation by rapid shoot elongation and production of adventitious roots. The production of adventitious roots is an adaptation which allows adequate gas exchange between the roots and the atmosphere when poor aeration conditions exist (Hosner and Boyce 1962). In the laboratory Ptelea seedlings produced adventitious roots at the cotyledonary node and showed no reduction in growth when partially buried. In addition numerous mature Ptelea shrubs at the study site showed no apparent deleterious effects even though the root crown had been exposed by sand removal. Thus Ptelea is not harmed by the sand instability.

Although Ptelea seedlings possess no single characteristic that explains their ability to survive in the rigorous dune habitat, they do possess many characteristics that contribute to their success. Ptelea seedlings survived soil temperatures that has been indicated to be lethal to conifer seedlings. The nitrogen content of dune sand has been

shown to be insufficient to allow survival of many of the forest species inhabiting the rear dune, although Ptelea seedlings grew sufficiently under these poor nitrogen conditions to reach a permanent water supply during the first growing season. Ptelea seedlings can rapidly produce adventitious roots, while many mesic forest species only do so very slowly. Ptelea seedlings can utilize light intensities between 1000 and 3500 ft-c which the mesic forest seedlings cannot utilize. This leads to higher metabolic rates and increased growth. Ptelea germination and growth are stimulated by the temperatures and soil moisture conditions existing in early spring, which is common for plants requiring stratification. But the survival of the seedlings is not enhanced by any adaptation to conserve water because the plant resistances to water flow are mesic and consequently high transpiration rates occur in the sand dune habitat.

SUMMARY

1. The high summer temperature and evaporative demand of the sand dune habitat coupled with the low water retention and low nitrogen content of the sand creates a severe environment.

2. The germination of Ptelea trifoliata seed is delayed until spring by a stratification requirement. This dormancy is imposed by chemical inhibitors and a true embryo dormancy.

3. By spring the dormancy has been removed and early spring temperatures promote the most rapid and greatest percent germination. The most favorable soil moisture conditions also exist at this time. If germination does not occur at this time, the seed do not germinate in the warm and dry summer environment.

4. The young seedlings are frequently subjected to drought-like conditions and their survival is dependent on root growth adequate to supply the seedlings with water.

5. Growth is maximum at moderate temperatures but seedlings can survive the high surface soil temperatures during the summer.

6. Seedling growth on the infertile sand is reduced but sufficient for survival. Higher soil nutrient levels increase growth.

7. Ptelea seedling growth and survival were not inhibited by partial sand burial or removal.

8. Ptelea seedlings are not adapted for reduction of water loss. The liquid flow and diffusive resistances are similar to that for mesic plants previously reported. Because of the mesic resistances to water flow of Ptelea seedlings, the transpiration rate is high when under the high evaporative demand of the sand dune environment.

9. Seedling survival is greater in the shaded habitats than in the open habitats. It was felt this was because of the more favorable soil moisture conditions existing in the shaded habitats.

10. Finally, we may conclude that the survival strategy of Ptelea trifoliata included several characteristics which contribute to its ability to cope with environmental stresses. No individual characteristic is sufficient to explain its success in the rigorous dune habitat.

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