

Ecological Studies of the Cabbage Palm, *Sabal palmetto*.

III. Seed Germination and Seedling Establishment.

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Seed Germination

The majority of germination studies in palms have been on commercial species, especially the African oil palm, *Elaeis guineensis* Jacq. (Hussey, 1958; Rees, 1961, 1962, 1963). Germination studies on wild palms are few in the literature. Bannister (1970) studied germination in the sierra palm, *Prestoea montana* (Graham) Nicholson (as *Euterpe globosa*), in growth chambers and in a Puerto Rican rain forest. Read (1968) presented data for the Caribbean genus *Pseudophoenix* H. Wendland ex Sargent. Germination data for other wild palms have been reported in several popular journals; however, none were scientific studies.

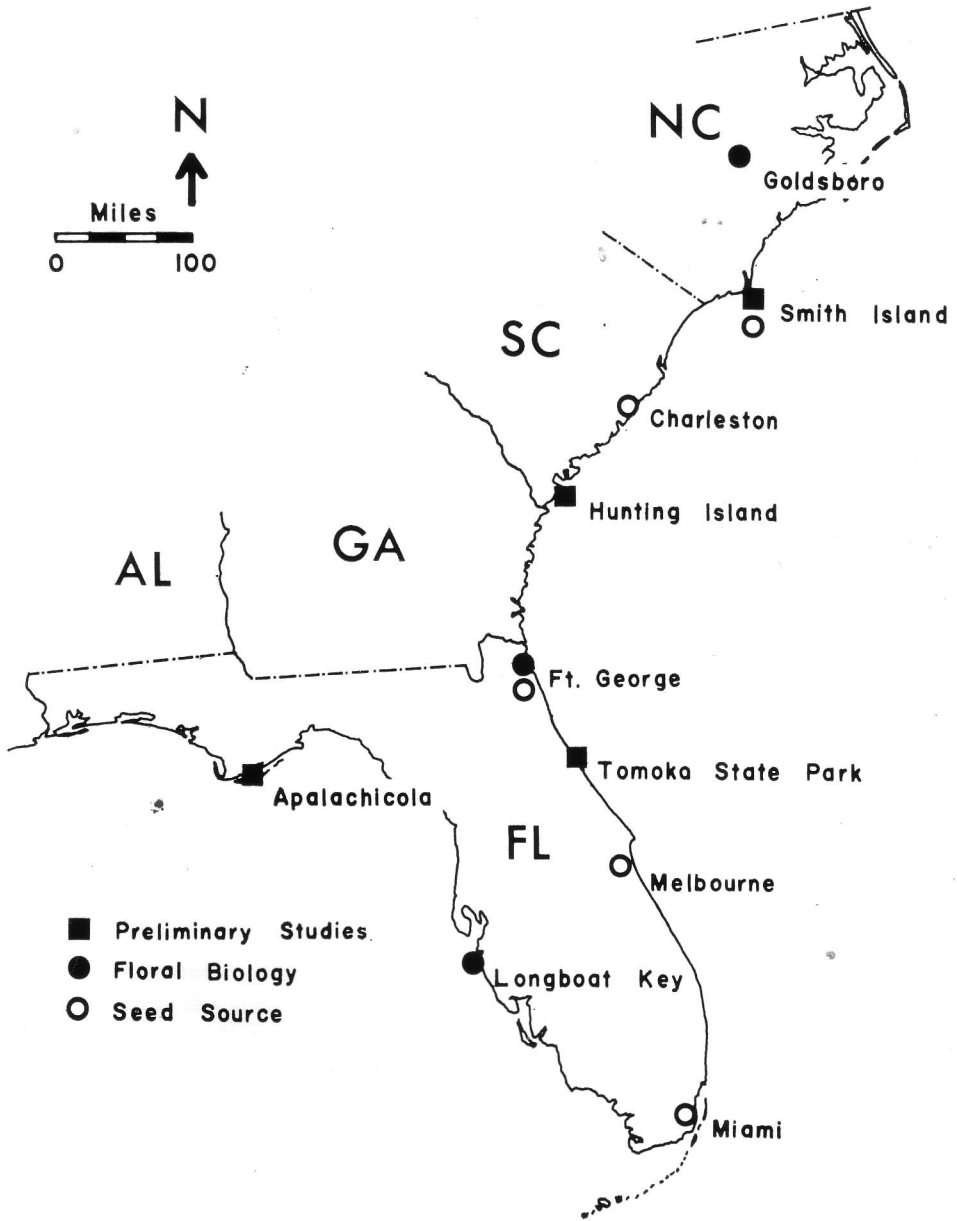
The inherent capabilities of seeds and their interaction with environmental factors determine the success or failure of the germination system. Both internal seed factors and external physical factors (Mayer and Poljakoff-Mayber, 1963) were investigated to determine the germination system in *Sabal palmetto*.

Materials and Methods

Seeds from five coastal populations (Brown, 1976a) were used to determine if germination response differed with latitude. Fresh, mature fruits were gathered in the fall and early winter of

1971–1972. Approximately 5,000 seeds from each site (Fig. 1) were collected and stored dry at room temperature (22° C). From these population samples, the required experimental samples were randomly selected. All experiments were carried out in the Southeastern Plant Environment Laboratory (N. C. State Phytotron) referred to below as the phytotron (Downs, Hellmers & Kramer, 1972).

Various experimental chambers in the phytotron were used for germination studies. Water-cooled Pfeiffer germinators were used for the temperature and salinity experiments. The illumination experiment was housed in an "Environmental Growth Chambers" walk-in controlled-environment room. Preliminary work suggested that 28 days was sufficient time to allow for germination under chamber conditions. Germination was considered successful upon emergence of the radicle from the seed. All germination tests were of a fixed model design with predetermined locations (populations), temperatures, salinity levels, and light conditions. Data were analyzed using the Statistical Analysis System (Barr and Goodnight, 1972). Details of the methodology and statistical analyses are recorded in Brown, 1973, and all statistical inferences are at the 95% confidence level.



1. Location of field study sites and seed sources.

Seed size and energy

Although there was a difference in seed weight in samples from Miami and Smith Island, the difference was not

significant. Average weight of seed over the geographic range was 14 grams.

Bomb calorimetry revealed an average caloric value of 3.6 Kcal/gram of seed.

Table 1. Germination under constant thermoperiods (values are percent germination based on average of 100 seeds after 28 days at indicated temperatures)

Temperature	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
15.0° C	0.0	0.0	0.0	0.0	0.0
17.5	0.0	0.0	0.0	0.0	0.0
20.0	7.1	0.0	0.0	0.0	0.0
22.5	55.4	46.0	45.0	30.4	50.8
25.0	86.0	89.0	82.0	75.0	75.0
27.5	92.9	98.0	92.9	92.8	95.9
30.0	99.0	99.0	96.0	87.0	97.0
32.5	95.0	97.0	80.0	42.0	87.9
35.0	47.0	66.0	48.0	11.0	59.6
40.0	0.0	0.0	0.0	0.0	0.0

This is a low value compared to many other seeds (Leith, 1968) and reflects the absence of high energy carbohydrates, such as starch, in the seeds of *S. palmetto*.

Hydration

Hydration studies using distilled water and seeds from all sites revealed rapid linear water uptake for the first 24 hours. After 24 hours, uptake was curvilinear until equilibrium was reached. Uptake was directly proportional to temperature over the range of 15° C to 40° C. Average increase in fresh weight due to water uptake was 45–55%, depending on seed source. Water potential of dry-stored seed was determined to be approximately -965 atm. Details of these findings are reported in Brown, 1973.

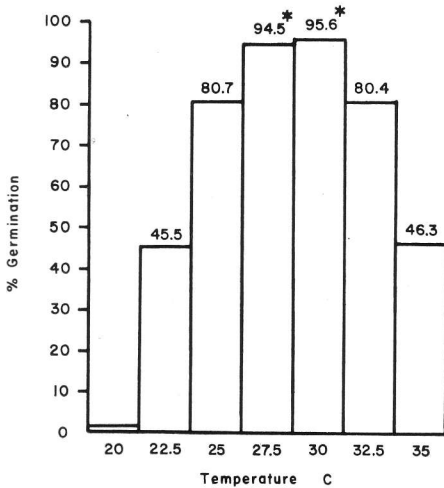
Constant Thermoperiods

Preliminary studies suggested that 30° C was optimal germination temperature for *Sabal palmetto*. Using this information and allowing 28 days incubation as a standard, further regimes were employed to determine germination response to constant temperatures.

Germination studies were conducted with 100 seeds from each population for each temperature. Thermoperiods used were: every 2.5 degrees between 15° and 35° C, and 40° C. Design was such that statistical tests for differences between population location (latitude) and temperature and interaction of temperature by location could be made. A daily record of germination was kept for 28 days.

No response was recorded at 15°, 17.5° and 40° C for the duration of the experiment (Table 1). Five of 10 dishes of Miami material responded at 20° C giving 7.1% total germination. As a result, only data from thermoperiods 20° through 35° C were analyzed statistically. Results from the Charleston population were so markedly different from all the others except for 25° and 27.5° C that the data were excluded from statistical analysis. This was a questionable population sample from the outset as only six trees were sampled, by proxy, at least one of which was a horticultural specimen of unknown origin.

Statistical analysis revealed significant temperature and location effects on percentage of germination; however, no



2. Effect of temperature on germination under constant thermoperiods (values are overall means, Charleston excluded; *indicates significant at 95% confidence).

latitudinal pattern emerged. In fact, there was no significant difference between means from Miami and Smith Island populations. Although 30° C was optimum temperature for all locations, it was not significantly different from 27.5° C but both of these temperatures resulted in significantly greater germination percentage than the other temperatures tested (Fig. 2). Read (1968) found a similar but narrower limit of response to temperature in several species of *Pseudophoenix*.

Alternating Thermoperiods

The alternating thermoperiods used were: 25°/15°, 30°/20°, 35°/25° and 40°/20° C with the higher temperature in effect for approximately 16 hours and the lower for eight hours. Daily germination was recorded for 28 days.

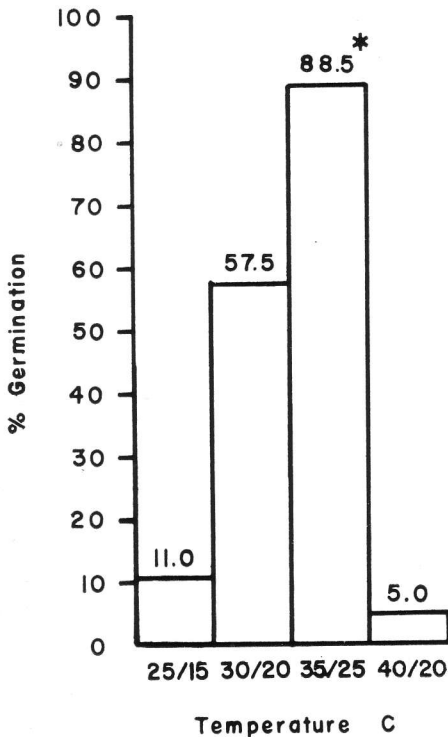
The response of the Charleston population was atypical as before and was excluded from analysis. Germination response was less uniform and lower than that under constant thermoperiods (Table 2). Analysis revealed significant temperature and location effects on percentage of germination. The 35°/25° C thermoperiod resulted in significantly greater percentage of germination than the other thermoperiods tested (Fig. 3). The location effect revealed a latitudinal difference: the two southern populations (Miami and Melbourne) had significantly greater germination than the mid-range (Ft. George) and northern (Smith Island) populations.

In an attempt to correlate the findings of the alternating thermoperiods experiment with natural conditions, field studies were conducted at Ft. George on July 14, 1972. Soil temperature conditions where seeds were actively germinating were determined. In an area under forest shade, seeds were germinating within the top 2.5 cm. of soil. Minimum temperature at this depth was 24° C and at

Table 2. Germination under alternating thermoperiods (values are percent germination based on average of 100 seeds after 28 days at indicated temperatures)

Temperature	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
25°/15° C	19.0	14.0	4.0	2.0	7.0
30/20	71.0	70.6	35.0	20.0	54.0
35/25*	100.0	96.0	80.0	34.0	78.7
40/20*	12.0	4.0	4.0	4.0	0.0

* Average of 50 seeds.



3. Effect of temperature on germination under alternating thermoperiods (values are overall means, Charleston excluded; *indicates significant at 95% confidence level).

the surface, 25° C. Maximum temperature at 2.5 cm. depth was 27° C and at the surface, 28° C.

On a sunny plot exposed to sun from approximately 1000 to 1600 EDT, seeds were not germinating within the top 2.5 cm. of soil. At this location temperature within the top 2.5 cm. of soil fluctuated widely and rapidly with passage of clouds over the area. Maximum reading at 2.5 cm. depth was 38° C, while maximum at the surface was 46° C. Some seeds were buried deeper than usual at this site due to a winter storm which covered the area with beach sand. Seeds at 7.5 cm. depth, where maximum temperature was 31° C, were germinating. These temperatures

and germination observations are in reasonable correspondence with those in the experimental germination studies. Even though maximum response occurred at a constant 30° C, germination in *S. palmetto* may occur slowly over long periods under normal diurnal temperature cycles in nature similar to that found in *Elaeis guineensis* by Hussey (1958).

Illumination

This experiment was conducted to determine if germination response is influenced by light or by darkness. For each population a set of 50 seeds was placed in a black cloth bag on a tray and another set of 50 left exposed, lying adjacent. The chamber used had a standard alternating thermoperiod of 30°/26° C and long-day photoperiod (9 hour day, 3 hour light break mid-way through the dark period). Daily germination was recorded for 28 days.

Charleston response was again atypical and excluded from analysis. Light was inhibitory at all locations but remained so for less time at the two southernmost locations where number of days to first germination in light was noticeably lower than at Ft. George or Smith Island (Table 3). Average germination for all populations was five times greater in dark than in light and began in 9.5 days compared to 24.5 days in the light. The inhibitory mechanism appears to break down in the presence of favorable moisture and temperature conditions with the passage of time.

Field observations revealed that seeds exposed to the sun do not germinate, while those in darkness buried by sand or organic debris do, when temperature and moisture are favorable.

Further carefully controlled experiments to determine the interrelationship of light quality and quantity, tempera-

Table 3. Germination under light and dark conditions (values are percent germination based on average of 50 seeds after 28 days; numbers in parentheses are average number of days to first germination)

Condition	Location					
	Miami	Melbourne	Ft. George	Charleston	Smith Island	Average (excluding Charleston)
Light	30.0 (22.2)	20.0 (20.8)	2.0 (27.6)	0.0 ^s (-)	6.0 (27.4)	14.5% (24.5)
Dark	82.0 (7.8)	72.0 (7.8)	72.0 (10.0)	38.0 (15.4)	76.0 (12.4)	75.5%* (9.5)*

* Indicates significant difference.

ture and moisture are needed to discern the adaptive significance, if any, of this mechanism.

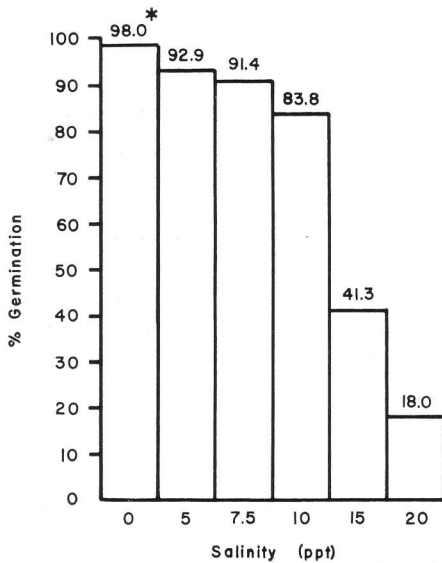
Salinity

A series of tests was conducted to determine the germination response of seeds exposed to salinity levels up to near sea strength (30 ppt). Dishes of 50 seeds were initially moistened with 0 (demineralized water), 5, 7.5, 10, 15, 20, and 30 parts per thousand NaCl solutions and placed in the 30° C chamber. No further solution was added. Daily germination was recorded for 28 days. Condition of seedlings, in regard to root and shoot development, was noted at termination.

Charleston response was again atypical and therefore excluded from analysis. Germination decreased with increasing salinity and there was no response at 30 ppt (Table 4). The responses at 5 ppt and 7.5 ppt were not significantly different from each other but both were significantly lower than the control (0 ppt). The greatest effect came between 10 and 15 ppt NaCl where average germination dropped from 83.8% to 41.3% and root development of some seedlings was noticeably abnormal (Fig. 4). At 20 ppt NaCl, abnormal root growth (stubby, non-branching primary roots) was recorded on all germinated seedlings in all populations. Higher maximum germination at 20 ppt NaCl was attained by both

Table 4. Germination under various substrate salinities (values are percent germination based on average of 50 seeds after 28 days at constant 30° C)

Salinity (ppt)	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
0.0	98.0	100.0	96.0	84.0	98.0
5.0	91.8	96.0	96.0	46.4	88.0
7.5	94.0	96.0	89.8	46.0	85.8
10.0	75.6	84.0	88.0	34.0	87.6
15.0	55.3	41.1	24.7	10.0	44.0
20.0	22.0	28.0	14.0	0.0	8.0
30.0	0.0	0.0	0.0	0.0	0.0



4. Effect of salinity on germination at constant 30° C (values are overall means, Charleston excluded; *indicates significant at 95% confidence level).

Miami and Melbourne populations, but abnormal subsequent seedling growth negated the importance of this.

The effect of salt on the viability of seeds becomes complex with increasing time and higher salinities. However, the results of this study and the study of viability after extended periods in sea-strength salt solutions reported in a previous article (Brown, 1976b) indicate that, initially, NaCl solutions up to 35

ppt are not toxic but inhibitory. Initial inhibition may be due to a water potential and imbibition problem but with the passage of time at substrate salinities of 15 ppt and above toxic effects begin to occur and carry over into seedling growth if germination occurs.

Mention has been made of the abundant local presence of this species around the edges of salt marshes. It is in these habitats that salt stress in regard to germination would occur. Analysis of top soil from such an area at Tomoka State Park, Florida revealed an average salinity of 5.13 ppt during the summer germinating season. The experimental results suggest that *S. palmetto* is well adapted to handle such salinity levels from the standpoint of seed imbibition and germination.

High Temperature Reaction

After exposure of seeds to the 40° C constant thermoperiod, in which germination did not occur, two groups of seeds were placed into 30° C chambers. One group of 50 seeds each from all five populations had received 28 days at 40° C, the other 56 days. Average germination after placement in 30° C for the five populations was 99.2% and 97.6%, respectively, and average time to first germination was 3.32 and 1.96 days, respectively (Table 5). Also, there was

Table 5. Germination at 30° C after 40° C treatment (values are percent germination based on average of 50 seeds after 28 days; numbers in parentheses are number of days to first germination)

Days at 40° C	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
28	100.0 (3.2)	100.0 (3.0)	98.0 (3.4)	97.8 (3.2)	100.0 (3.8)
56	98.0 (1.8)	98.0 (2.0)	100.0 (2.2)	98.0 (1.8)	94.0 (2.0)

little or no "tailing off" as maximum germination response in all cases was reached in 13 days or less. Some process is occurring at 40° C which, for at least 56 days, enables seed to emerge very quickly, at very high percentages, when placed at optimum temperature (30° C). The atypical and erratic germination results previously noted for the Charleston population were overridden by this high temperature treatment. Rees (1960) states that high temperatures (38–40° C) are required by *Elaeis guineensis* for early stages of the germination process. This is believed to be an adaptation to the hot dry season which follows fruit maturation. However, the occurrence of a high temperature reaction in *S. palmetto* has no apparent ecological significance in that it is not a prerequisite for germination.

Germination System Summary

The moisture and temperature requirements for germination of *S. palmetto* are satisfactorily met throughout the natural range by the coincidence of the rains and high soil temperatures of summer. Results of the various temperature experiments suggest that in the soil a minimum temperature at or above 20° C must be met before germination processes are initiated. Up to a point, reactions in the germination pathway can proceed at higher, sublethal temperatures, but for completion of steps resulting in radicle emergence, a maximum temperature somewhere between 35° and 40° C must not be exceeded.

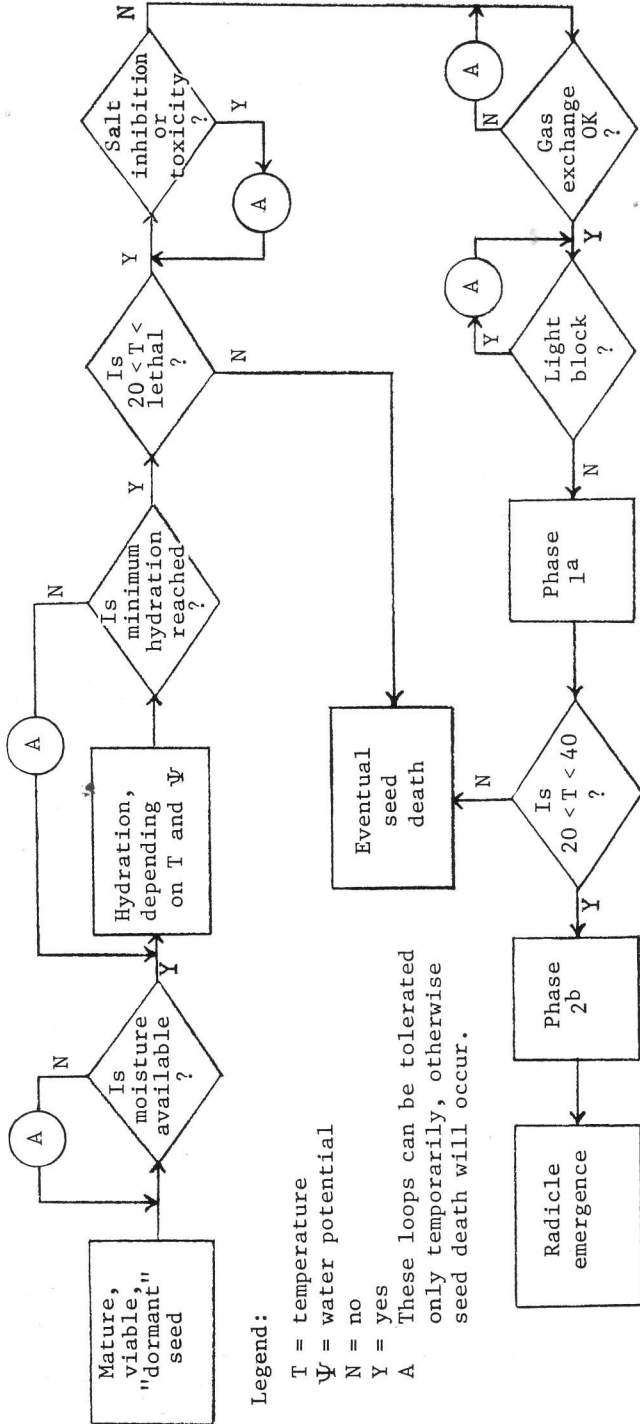
Substrate salinity levels normally encountered in the terrestrial estuarine environment have been adapted to and present no problem for germination.

The plant has evolved an incompletely understood mechanism whereby exposure to sunlight prevents or retards radicle emergence. This inhibition is readily

overcome when the seed is covered by sand or organic debris. This may be adaptively significant in preventing radicle emergence into an unfavorably dry microenvironment or it may be that the undeveloped embryo has a light-sensitive period necessary for certain early developmental steps before emergence.

Data analysis indicated no strong latitudinal differences in germination in this species except in response to alternating thermoperiods, where southern populations had significantly higher germination percentage. The response to salinity, illumination, and constant temperature by all populations indicate that these factors, individually, are rather constant in effect and occurrence over the latitudinal range of the species. The lower response to alternating thermoperiods observed with increasing latitude suggests a selection pressure against germination at temperatures departing from the maximum response range of 27.5° to 30° C. This is a logical occurrence as it would restrict germination to the warmer spring and summer months and tend to prevent germination in fall or winter when low temperatures unfavorable to seedling establishment are most likely to occur.

When conditions are satisfactory, the germination pathway culminates in radicle emergence. The radicle and shoot apex are pushed down into the soil by the downward extension of the cotyledonary stalk. The cotyledon remains in the seed and acts as a haustorium, expanding with absorption of the endosperm. The embryonic seedling is thus planted in the soil remotely from the seed in a manner common to several palm genera (Tomlinson, 1960a). This phenomenon has been evoked as an adaptation by palms to a normally dry habitat (Rees, 1960). The microhabitat of the germinating *S. palmetto* seed is certainly subject to periodic rapid drying



^aInitial biochemical activity (production of enzymes, breakdown and resynthesis of stored materials).
^bCell division and elongation.

5. Generalized flow diagram of possible sequence of germination events.

in summer months. The cotyledonary stalk may provide an adaptive mechanism to place the embryonic plant quickly below dry surface sands into layers where moisture is adequate for further development.

Figure 5 depicts possible events leading to germination and allows a concise consideration of the coordination of functions in the seed in response to environment (Amein, 1966).

Seedling Establishment

Seedling establishment is the stage of a plant life cycle which begins with the emerging seedling and continues until the seedling reaches the autotrophic state. Stebbins (1971) suggests that this stage is the weakest link in the life cycle of plant species in their colonization of new territory. *Sabal palmetto*, which outside of peninsular Florida is found in warmer habitats along the Gulf and Atlantic coasts, has been thought to be limited in its range by cold winter temperatures (Small, 1923). Observations of reproducing introductions at some distances north and west of the natural range have led me to question the validity of this explanation.

Investigations were thus made to determine the general environmental requirements of successful establishment of seedlings with particular regard to temperature. Field observations were made throughout both the natural and horticultural range. Controlled laboratory experiments were conducted on Miami and Smith Island seedlings in the phytotron walk-in environment rooms.

Morphology and Development

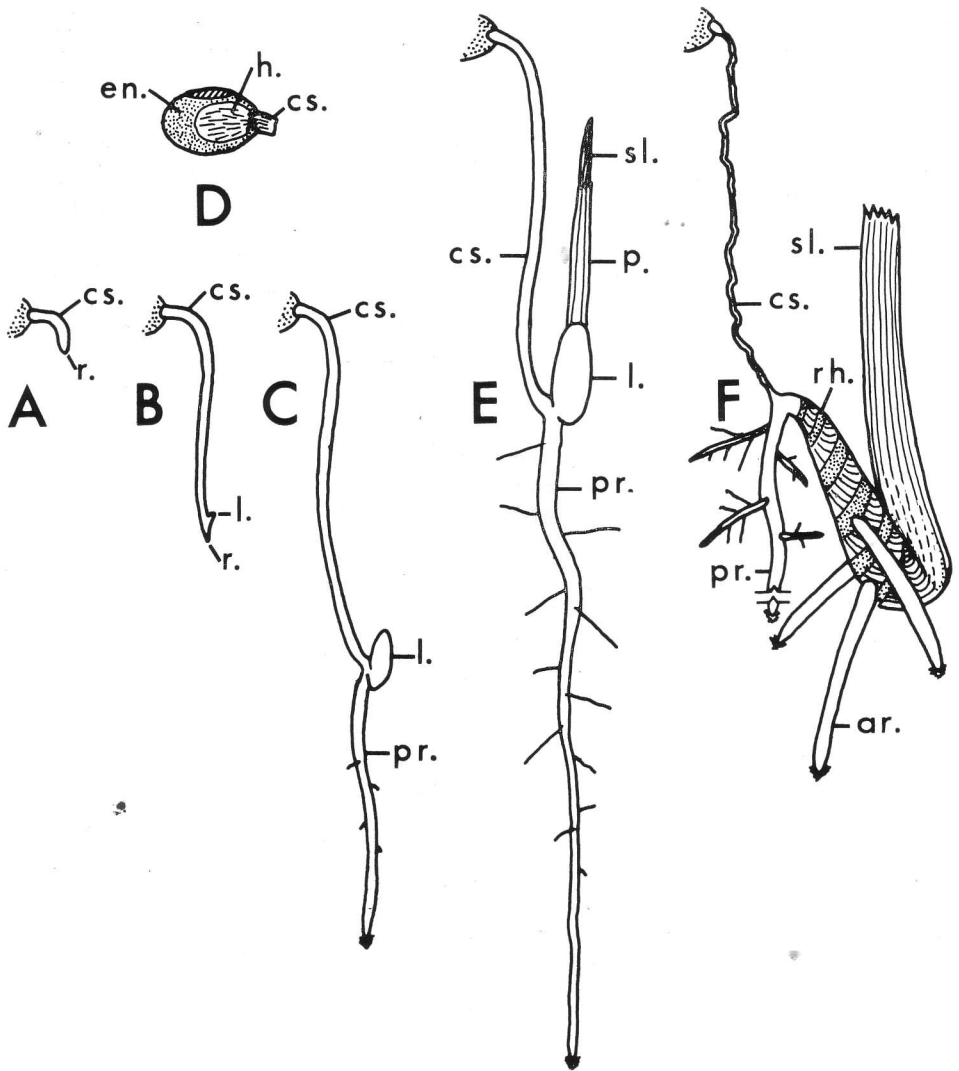
General considerations of early seedling development in palms are discussed by Tomlinson (1960b). In *S. palmetto*, after radicle emergence, further development occurs primarily as elongation of

the cotyledonary stalk, with its distally attached radicle and epicotyl, and growth of the haustorium (cotyledon) within the seed (Fig. 6).

Morphology of the emerging seedling is an important factor in establishment (Harper, Lovell, & Moore, 1970), especially as it relates to the ability to penetrate the soil. In *S. palmetto*, the elongating radicle-cotyledonary stalk structure, 1-2 mm. diameter and tubular, is well designed for this. The cotyledonary stalk, which exhibits negative geotropism, penetrates the soil and normally expands to about 4 cm. in length. Depth of placement of the radicle-epicotyl axis will depend upon the initial depth of seed deposition.

From this approximate depth of 4 cm., the primary root penetrates farther into the soil and becomes branched. Visible shoot growth begins with the development of the ligule which is ruptured by the expanding sheath and seedling leaves. The first seedling leaf emerges through the sheath and remains plicately folded while penetrating the soil to the surface. Once above the surface the seedling leaf expands and unfolds reaching a final length usually less than 15 cm. and width less than 1.5 cm. From this point on the seedling is autotrophic and essentially established. While the linear seedling leaves are expanding, stem growth is established obliquely downward resulting in formation of a rhizome (Tomlinson, 1960b).

Downward growth of the rhizome continues for an undetermined time, probably many years, until an upright position is assumed and the rhizome gradually emerges to form the trunk. A variable number of simple seedling leaves are produced for at least two years in the laboratory and probably much longer in nature. No fewer than 10 of these leaves are produced before



6. Morphology of early seedling development. A-C, successive stages in development to about $3\frac{1}{2}$ weeks, all $\times 2$; D, longitudinal section through seed at stage C showing haustorium, $\times 2\frac{1}{2}$; E, six-week-old seedling, $\times 2$; F, one-year-old seedling showing downward rhizome development, $\times 2$. (ar, adventitious root; cs, cotyledonary stalk; en, endosperm; h, haustorium; l, ligule; p, plumule; pr, primary root; r, radicle; rh, rhizome; sl, seedling.)

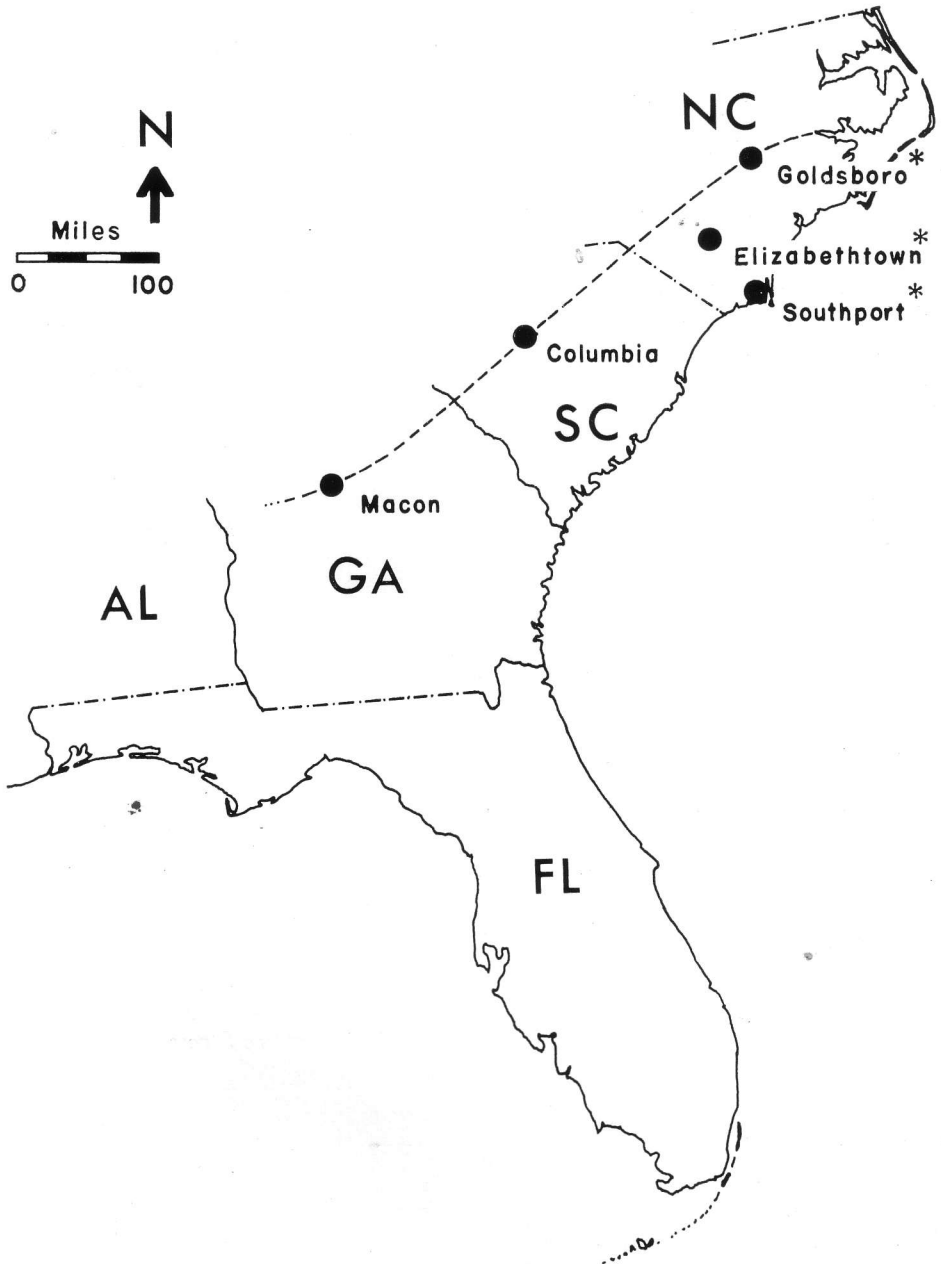
the first dissection into a few segments occurs.

Field Studies

Seedlings grow very little in nature during their first year due to a middle to late summer germination sequence over

most of the range. Above-ground growth by late fall normally consists of one fully expanded seedling leaf. The rate of production of seedling leaves in subsequent years is unknown.

The number of plants in the mature (reproducing) stage was noticeably small



7. Horticultural range of *S. palmetto* (location of observed reproduction outside the natural range indicated by*).

in the interior of maritime forests. Survival among seedlings to the three- to four-leaf stage was relatively high but greatly decreased beyond this stage. In contrast is the obviously high rate of survival of plants in all age categories along some water courses and edges of salt marshes.

The initial number of germinating seedlings in these two areas can be expected to be quite different due to seed predation (Brown, 1976b). This would explain the low initial number of seedlings in the maritime forest but it does not explain the loss of young established seedlings in the same habitat. Some factors, as yet unknown, are at work to cause this decrease in survival. Whatever the cause, it is not the lack of ability to establish seedlings which results in low density of *S. palmetto* in the maritime forest habitat.

Attempts were made to correlate the natural range of successful establishment with climatic factors, especially temperature. There was some correspondence with the mean annual number of days with minimum temperature of 0° C and below. Correspondence with the 30-day isogram existed along the South and North Carolina coast lines but did not hold south of South Carolina. A closer correspondence occurred with the mean length of freeze-free period. The 270-day isogram was close to the distribution line in all of Florida, Georgia, and South Carolina. Discrepancy occurred along the northern South Carolina coast and the North Carolina coast where the plant was found farther north. No correlation with annual or monthly rainfall or semiannual evaporation rate was detected.

Investigations into the horticultural range of the plant revealed that climatic factors do not appear to be limiting the species to its natural range (Fig. 7).

Observations in North Carolina revealed reproduction far to the north and inland of the species' northernmost natural extension. In Elizabethtown, Southport on the mainland opposite Smith Island, and Goldsboro, large old trees have given rise to numerous seedlings and juvenile plants in urban sites. It is noteworthy that many several-year-old plants are thriving in a hedge row without benefit of protection from structures at the Goldsboro site (Fig. 8). A single plant had been brought from Smith Island in 1910. All of these locations have climates colder than adjacent coastal areas as documented in U. S. Weather Bureau records.

The successful reproductive activities of plants at these locations suggests strongly that minimum winter temperatures are not limiting *S. palmetto* to its current natural range. This fact, along with the occurrence of established seedlings in widely divergent moisture, soil, and light conditions in the natural range, suggests that physical factors are minimally involved in seedling attrition. Thus, further biotic attrition, beyond seed predation, appears probable. Only long-term studies on survival of seedlings in the field will provide information on the causes and timing of seedling attrition.

Low Temperature Stress

A series of experiments was designed to determine the duration of certain cold temperature regimes required to terminate life processes in *S. palmetto* seedlings. Three thermoperiods were selected: 9°/-6°, 9°/0°, and 9°/6° (day/night temperatures, degrees C) with 9-hr. light periods. A control and initial growth chamber was established with 30°/22° C thermoperiod and long days (9 hr. plus 3-hr. light break during dark period). This chamber was set up to



8. *Sabal palmetto* reproduction outside the natural range at Goldsboro, N. C. A, plant brought in from Smith Island in 1910. B, progeny of plant shown in A.

approximate average temperature and light conditions throughout the natural range during the summer growth period. In addition, an intermediate chamber was maintained with 22°/14° C thermoperiod and short days (9 hrs. light). This chamber was used to acclimate plants moving in and out of the cold treatments. Seedlings were subjected to the treatment thermoperiods for various times: 9°/-6° up to 6 weeks, 9°/0° up to 10 weeks, and 9°/6° up to 12 weeks. The maximum, 12 weeks for 9°/6° thermoperiod, was selected to exceed the number of weeks of vulnerability to that average temperature range in North Carolina coastal plain winters.

The complete experiment was conducted with both Smith Island and Miami seedlings in an attempt to detect any difference in cold tolerance with latitude. Seedlings from earlier germination experiments were planted in even particle-sized quartz sand and grown off in the 30°/22° control chamber until they were approximately equal in development to seedlings in nature going into their first winter; *i.e.*, at least one fully expanded seedling leaf. All plants received standard Phytotron nutrient solution once a day and were flushed with demineralized water once a week. Details of methodology, scheduling, and statistical analysis are described in Brown (1973).

The results revealed no significant difference (95% confidence level) in response between Miami and Smith Island seedlings at the temperatures employed. After one week of exposure all plants from both populations in the 9°/-6° thermoperiod were dead. Although

a few individual Smith Island plants died after various exposure times at both 9°/0° and 9°/6° thermoperiods, all plants from both populations receiving maximum exposures to both thermoperiods survived. Visible signs of stress, manifested as leaf tip burn, occurred in both populations and for all durations of the treatment thermoperiods; however, Miami plants at 9°/6° thermoperiod showed the least damage of any group. The expected death at longer exposure times at the 9°/0° thermoperiod failed to materialize. The 9°/0° thermoperiod represents a temperature range rare in Miami for one day, much less one to 10 weeks. This would seem to indicate that, since no apparent selection for cold resistance has developed in the Smith Island population, low temperatures experienced in nature are not a limiting factor in establishment of seedlings of the species in its current range.

Growth Under Favorable Conditions

The 10 control plants used in the low temperature stress experiment were further utilized in studies grown under favorable temperature conditions. The goal of these investigations was to ascertain whether or not ecotypic differences occur between Miami and Smith Island populations.

Biomass and photosynthetic rate were determined. Shoot and root weights were taken and shoot/root ratios were calculated. Photosynthetic rate was determined for the seven best plants from each location in an open system using a cylindrical leaf chamber and differential gas analyzer. Details of methodol-

9. Growth of Miami and Smith Island seedlings under favorable conditions. A, eight-month-old groups. B, eight-month-old individuals. C, two-year-old individuals. Miami material on right in all instances. →

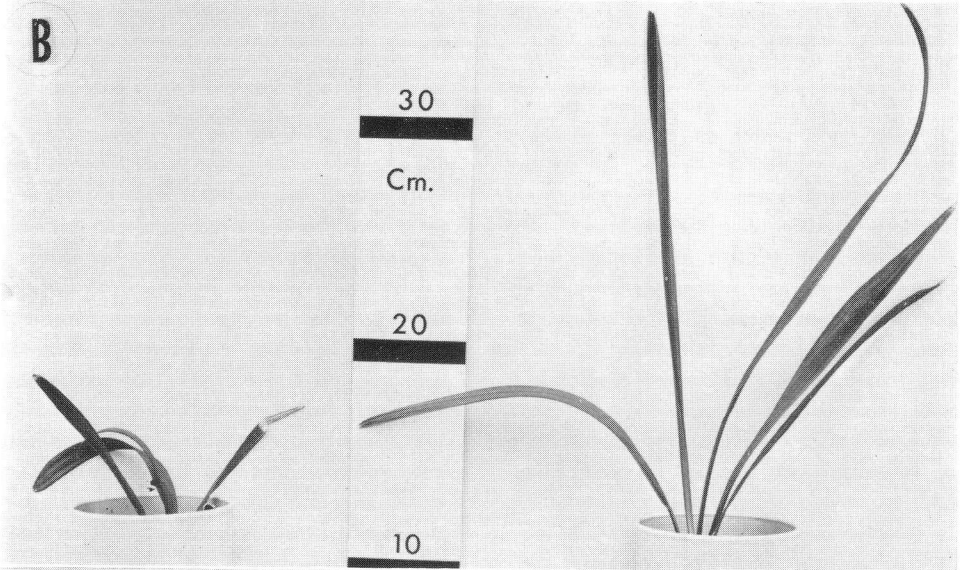
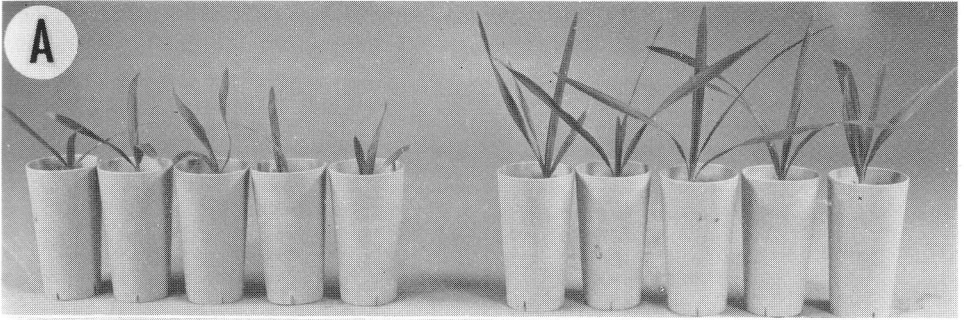


Table 6. Average biomass and photosynthetic rate determinations (biomass calculations based on 10 plants, each location; photosynthetic rate based on best seven plants, each location)

Statistic	Location	
	Miami	Smith Island
Shoot weight (g)	1.11	0.43
Root weight (g)	0.42	0.22
Total biomass (g)	1.53*	0.65
Shoot/root ratio	2.66	2.03
Photosynthetic rate (g carbon/cm ² /sec)	8.14×10^{-9} *	3.20×10^{-9}

* Indicates significant difference.

ogy are documented in Brown (1973). Biomass and photosynthetic rate means were statistically analyzed and inferences made at the 95% confidence level.

Approximately the same average number of leaves were produced by both populations over the 18-week study period (Miami, 4.1; Smith Island, 3.7), but growth rates and size of plants were noticeably different. The Miami plants were larger and had an expansion rate of 0.4 mm per day for the emerging leaf, twice that of Smith Island seedlings. In addition, foliar morphology was different. Miami seedlings had long, narrow leaves, while Smith Island seedlings had much shorter, broader leaves (Fig. 9).

Analysis revealed a close correlation between biomass and photosynthetic rate at each location. A significant difference in both biomass and photosynthetic rate occurred between locations (Table 6). Miami seedlings had a photosynthetic rate 2.54 times that of Smith Island seedlings. The efficiency of this unit-area photosynthetic advantage was evident in Miami total biomass which was 2.35 times greater. The greater shoot/root ratio of Miami seedlings indicates that a greater percentage of the total energy available is directed toward shoot growth than in Smith Island seedlings.

These differences occurred under identical growth chamber conditions indicating genetically fixed differences characteristic of ecotypes. Within the coastal zone, at least, *S. palmetto* exhibits physiological (photosynthetic) ecotypes responding to some unknown factor or factors varying between the extremes of the range. However, since edaphic and climatic factors are divergent between the two populations and rates were calculated under one set of conditions, no conclusions on the importance of the apparent ecotypic differences were made.

Seedling Establishment Summary

Based on its particular geographic range, *S. palmetto* appears well adapted for establishment in a wide range of habitats. Low survival rates in the interior of maritime forest habitats are not due to seedling establishment problems but to undetermined environmental factors at a later stage.

No evidence of low temperature restrictions on range extension were found. On the contrary, reproduction from horticultural plantings reveals that the species is quite capable of establishing seedlings farther north and west of its current natural range. This suggests

that some other stage of the life cycle is limiting the spread of the species.

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