The Ecology of the Palms

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Webster's Third New International Dictionary defines ecology as "a branch of science concerned with the interrelationship of organisms and their environments especially as manifested by natural cycles and rhythms, community development and structure, interaction between different kinds of organisms, geographic distributions, and population alterations." In other words it deals with the pattern of relations between living things and their environments. In this regard we know so little concerning palms that it is difficult to know quite where to begin. That may seem like a contradiction, but in fact our knowledge of palm ecology consists almost entirely of widely diverse observations made over a considerable period of time, in conjunction with a rather limited understanding of many of the species involved. Nearly all we really have are broad generalizations. Palms in the New World, for example, are found naturally from about 36 degrees North Latitude (*Sabal minor*) in North Carolina to about 34 degrees South Latitude in Chile (*Jubaea*). In Europe *Chamaerops humilis* occurs near the 40th Parallel in Spain and Italy; *Rhopalostylis* occurs as far as 41 or 42 degrees South Latitude in New Zealand. This is not distribution, but rather an indication that a mild climate lacking severe winters occurs in these regions, and that a few noteworthy palm species can tolerate temperate climates at these extremes of latitude.

Palms occur naturally from sea level (*Nypa* in tidal estuaries and river deltas) to well over 3000 m. (9842 ft.) in the Andes of South America (*Ceroxylon*). It was once believed that the double coconut (*Lodoicea*) grew beneath the sea and only the huge fruits bobbed to the surface. Palms are also found growing in swamps and rivers of the Amazon basin, and under desert conditions, as the doum palms (*Hyphaene*) of Africa. Some species, such as those of *Washingtonia* or *Phoenix*, may appear to be highly tolerant of extremely xeric situations but the fact is that they are excellent indicators of ground water, for they do not occur unless there is a reliable source of water. *Copernicia* in Brazil, the source of carnauba wax, grows in areas normally inundated for many months of the year, only to be subjected alternately to drying and many months of almost no precipitation.

We most frequently think of palms as belonging to the dense jungles of the tropics but they may grow fully exposed to wind and sun like the coconut along the beach and the date palms of oases. Some appear to thrive only at the forest margins along rivers or road cuts. Certain species, such as *Calamus* in southeast Asia, though infrequent in the forest may become weedy and completely take over recently cleared land. The dominant understory palms of the same area are eliminated altogether when the forest is felled, exposing them to more intense illumination and a drier atmo-

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sphere. Rainforest as an optimum ecological formation varies considerably in regard to its palm content. Some genera and species may be prominent in the canopy or upper story vegetation while others occur only among the shrubs as undergrowth plants. Swamp forests are often erroneously thought to be associated with the jungle or rainforest, but they are quite often noted for the enormous numbers of individuals of a single species which may be dominant over hundreds or even thousands of square miles in South America. The species under these conditions appear to reflect the substrate and or the seasonality of the flooding.

Palm species may be found on all kinds of substrate; it may be sand or clay, deep humus or solid rock, and the soil may be acid or alkaline in reaction. As has already been stated, these are broad generalizations and all this quite likely could lead one to believe that palms are highly tolerant of widely diverse climatic and edaphic conditions. However, as true as this may be for the family as a whole, my experience leads me to the conclusion that most genera and species of palms are highly specific and narrow in their individual tolerances. For example the genera *Pseudophoenix*, *Coccothrinax*, *Thrinax*, and *Gaussia* are strictly calciphilous and occur only on eroded limestone or coralline sand. The species, especially of *Thrinax*, may be further restricted by limits of precipitation or concentrations of salts. Other genera may be restricted to acid rock, as is *Loxococcus* on the gneiss outcrops in Ceylon, and some species of *Syagrus* in South America. Still others are found only on acid humus deposits in dense forests where only the low availability of light may limit competition. In fact, when dealing with palms it is important to keep in mind that closely allied species may be isolated from one another simply by a change in soil, water, or light relations.

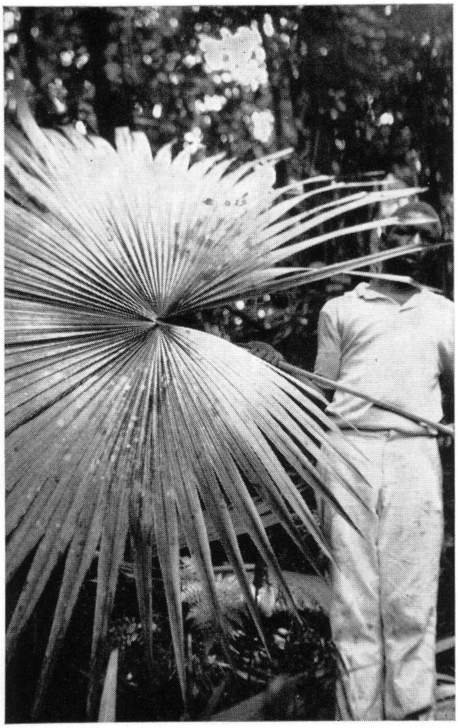
Some palms, as I shall show in *Thrinax*, are phenotypically highly plastic and, depending on the species, may be extremely specific in their edaphic requirements but highly tolerant of light or water extremes. It would of course be very difficult for an ecologist to study palm ecology were he unable to recognize whether or not distinct species were involved. Likewise it has been the bane of many past palm students that they could not adequately understand the plasticity of palms in relation to their immediate environment. Fragmentary herbarium specimens from widely separated regions give no clue as to possible disjunct edaphic conditions nor the gradual changes wrought by elevation or light factors when the substrate is the dominant factor in the distribution of a particular species. In Suriname we note from Wessels Boer's (1965) work that *Bactris campestris* is restricted to white sand savannas, where it is abundant, but is entirely lacking on red sand savannas and clay. On the other hand *Acrocomia lasiospatha* is found on the red sand and clay of the coastal plain but *not* on clay of the interior *nor* on white sand. Within a single genus it was noted that *Euterpe oleracea* was always found in poorly drained, often regularly inundated areas, while *Euterpe precatoria* was always on well-drained, never inundated places. The two species often grow very near one another but are separated by edaphic conditions.

Elevation is known to be a limiting factor in the occurrence of many species. But is it simply elevation, or the climatic conditions resulting from a combination of cooler temperatures and exposure to prevailing winds at a particular

1. *Thrinax excelsa* in the John Crow Mountains of Jamaica.

latitude? Many palm species appear to be unable to compete in a situation where the forest becomes too dense, and the incidence of damping-off disease possibly increases as a result of the sustained high relative humidity and cooler wet conditions. I have noted in my studies on seedling germination that soil temperature has a distinct effect on germination and rate of root growth. A soil temperature of 70°F or below could be a very limiting factor in the starting of plants at the cooler elevations, apart from the obvious effects of freezing at still higher elevations and latitudes. I have by no means exhausted the various situations under which palms may be found, but we know so little that the relationships between palm species and their environment escapes us unless intensive studies in the field are carried out under natural conditions.

There is one generalization that I would like to make which I believe bears testing. It is that over a broad area of uniform edaphic and climatic conditions the same species (plural) of palms will likely be seen. On the other hand a change in the substrate is likely to support distinct species, or even additional



2. A small leaf of *Thrinax excelsa* held by Winston Barret, George Proctor's young assistant, in the John Crow Mountains above Ecclesdown, Jamaica. The leaf is silvery-lepidote beneath.

genera. But a gradual change in atmospheric conditions when the edaphic conditions remain constant over a topographic or latitudinal gradient will probably present some so-called difficult or problem species. Furthermore, isolated populations of a genus, where climatic conditions differ significantly, will most likely result in quite different taxa. Examples of these situations occur in the genus *Thrinax* where intensive studies over a variety of environmental conditions demonstrate what appears to be a classic pattern.

Thrinax in Jamaica

Five species of *Thrinax* were reported in Jamaica at the time my studies (Read

3. *Thrinax radiata* at Morant Point, Jamaica, exposed to the full force of salt-laden breezes from the sea.

1974) were begun. There are really only three good species native to that island, and one other species, under numerous names, is widely distributed elsewhere. The problem, as it has turned out, was of two sorts: first, a lack of a proper understanding of the type species; and second, a total lack of understanding of phenotypic variability within and between populations.

Soon after work was begun on the genus in Jamaica it became clear that plants which were known as *Thrinax rex* were instead to be called *T. excelsa* (Figs. 1, 2) and that the plants which were called *T. excelsa* in Jamaica (and in the nursery trade) should be called *T. radiata*[1]. Likewise, the plants known as *T. parviflora* in Florida and elsewhere should also be *T. radiata.* The plants under the name *T. parviflora* in Jamaica were correctly named, but their variants were not well understood. Two names

[1] By reason of a further complication of typification, the name *Thrinax multiflora* has more recently been applied by the author to what should properly be called *T. radiata* as a result of recent anatomical findings, and even the name *T. floridana* must be relegated to synonymy.

now reduced to synonymy of *T. parviflora* are *T. tessellata* and *T. harrisiana.* Both the latter names were based on inadequate specimens and a poor understanding of phenotypic variability and ecotypic variation.

Thrinax species are strict calciphiles, occurring on coralline sand and weathered limestone outcrops from sea level to over 3000 ft. (914 m.) elevation. They are distributed from areas of strong seasonal drought with an average rainfall of 39–44 in. (100–112 cm.) per year [and no more than six months with less than 3⅛ in. (8 cm.) per month] to regions having more than 300 in. (762 cm.) of rain per year. *Thrinax excelsa* and *T. parviflora* are restricted entirely to exceedingly well-drained sites far from the influence of salt spray. The former occurs in Lower Montane Rain Forest, the latter in Evergreen Woodland or Dry Evergreen Thicket.[2]

Thrinax radiata, the most widely distributed species of the genus, occurs naturally in the littoral throughout the northern Caribbean and nearby shores of the Gulf Stream, north and west from Hispaniola. It is a palm species which in nature is confined to saline conditions of the littoral, but only where there is adequate rainfall (Fig. 3). In 1958 G. F. Asprey and A. R. Loveless described an addition to their list of "Littoral Dry Evergreen" formations in Jamaica. The formation, which they called "Littoral Palm thicket," occurs on a raised, flat, soilless, coralline limestone shelf, 10 to 25 ft. (3.05 to 7.62 m.) above sea level, exposed to the full force of the strong salt-laden Northeast Trade Winds at Galina Point, Jamaica. This species forms a characteristic feature of littoral hedge, becoming increasingly plentiful on the inland side, ". . . where it would appear to take the place of Littoral Evergreen bushland, but no explanation as to why this occurs can be offered." The authors further pointed out that "The raised limestone beach is dominated by *Thrinax parviflora* [sic][3] to the exclusion of other plants. The trees grow out of fissures in the bare soilless rock and vary in height from 7.5–12 m. (25–40 ft.). They are spaced, on the average, about 1.2 m. (4 ft.) apart and form a closed canopy. The palm reproduces actively since seedlings abound and the plant is evidently in a most favourable environment."

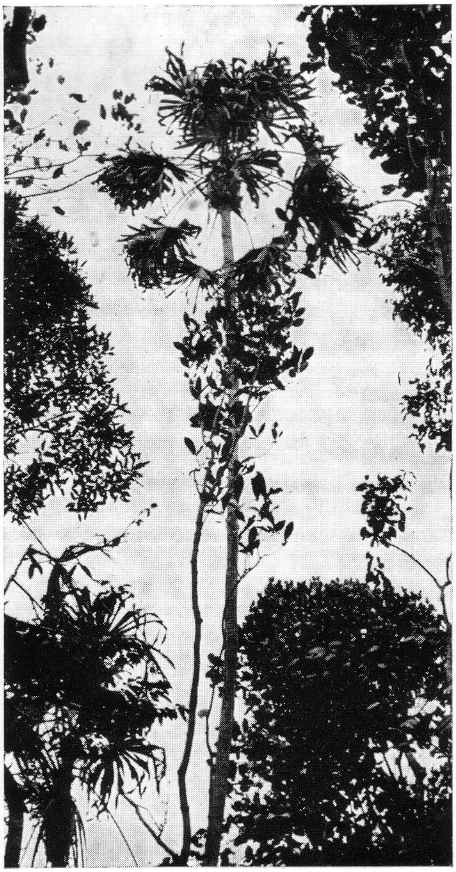
Meteorological data, based on records for Richmond Llandovery Sugar Estate some distance to the west of Galina Point, indicated 55 to 70 in. (139.7–177.8 cm.) of rain per year, which when compared with evaporation figures over the same period of seventy years, presents a condition where there are only five months in an average year when precipitation exceeds evaporation. It must be realized however that the use of such figures in a region of abrupt climatic changes within very short distances, depending on exposure and topography, is indeed tenuous. According to the most recent rainfall figures, Galina Point, at the western edge of one of the wettest regions of the island, has between 60 and 80 in. (152.4–203.2 cm.) of rain per year. These observations are brought out because, even as Asprey and Loveless observed, ". . . the only major anomaly in the data is brought about by the megaphyllous

[2] According to a classification by J. S. Beard, 1944, 1955.

[3] Asprey and Loveless (1958) failed to distinguish between *T. parviflora*, a conspicuous element in their studies on the Dry Evergreen Thicket at Portland Ridge on the south coast of Jamaica (Loveless and Asprey, 1957), and the very different *T. radiata* at their Galina Point study area.

palm *Thrinax parviflora* [*sic*]." Had they recognized that the palm in question was distinct from the palm in their Portland Ridge studies a very important fact would have been realized and quite different conclusions might have been reached. They would have recognized that *Thrinax radiata,* which only occurs in areas of regular deposition of salt accompanied by regular high rainfall, is a true halophyte and that *T. parviflora,* of their Portland Ridge studies, is not. As Asprey and Loveless themselves noted, ". . . the presence of *Philodendron* sp. among the fringing woodland plants indicates a moist habitat, . . ." from which they concluded, ". . . the relationship of Palm thicket to rainfall distribution might repay further investigation." They further observed that, "In view of the fact that the rainfall along the stretch of coastline in which Fort Point and Galena Point are situated is more than twice as much as at Port Henderson, [Near Portland Ridge on the south coast]. . ., it might at first sight seem surprising that Evergreen bushland is found at both centres." This is not at all surprising for they did not in fact find bushland at Galina Point, it was displaced by Palm thicket, and the bushland described at Fort Point (36 miles west of Galina Point) is in a much drier area than suggested by the Richmond Llandovery rainfall records. One can only agree with Asprey and Loveless, ". . . that the vegetation reflects the climate far more accurately than any meteorological data."

The plants which were described as a distinct species under the name *T. tessellata* are in fact typical (as to the type specimen) *Thrinax parviflora* (Fig. 4). Apart from that, the basis for distinguishing them from the lowland forms was the occurrence of a "tessellate" pattern of the epicarp of the mature fruit,



4. *Thrinax parviflora* at Holly Mount Hill on Mt. Diablo, Jamaica. Note the curly form of the leaf. This is the phase that was once called *T. tessellata.*

hence the epithet. This condition is a common but by no means constant condition of the fruits on plants growing in the cool moist environment of the mountains, ridges and cockpits throughout Jamaica. The atmospheric conditions there foster a fungus infestation which alters the epidermis of the fruit during maturation. The situation does not occur in drier situations at lower elevations or on dry ridges. In the same environment where fungal damage is common on the fruit, the branches of the inflorescence undergo another equally dramatic

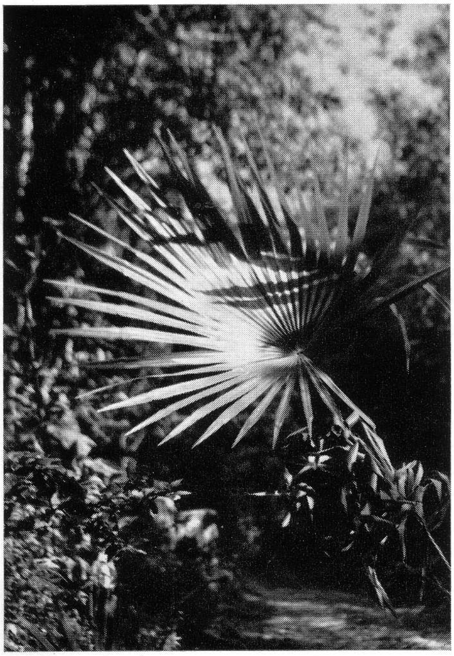
5. *Thrinax parviflora* growing along the cliffs overhanging Ramgoat Cave in the Cockpit Country of Jamaica. Note the broad, flat aspect of the leaf blade but with a tendency to have the segments twisted.

alteration of the epidermal tissue. Extensive grazing by a particular caterpillar, resulting in alternating trenches in a checkerboard fashion, is so common at the uppermost peaks as to often completely obscure the normal nature of the epidermis. At lower elevations, and on dry ridges, caterpillar grazing of epidermal tissue is quite rare. Both of these situations are direct effects of the ecology. The cool, moist environment of the higher ridges and peaks fosters attack on and considerable depredation of the palm's fruiting capabilities by both plant and animal predators. Elsewhere the climatic conditions are not conducive to such severe predation on reproductive structures because the predators do not find the drier climate suitable.

Another effect of the ecological system on *Thrinax* results in an extreme phenotypic variability which has all too often, in numerous genera, resulted in the superfluous naming of "new" species. One of these, *Thrinax harrisiana* (now also a synonym of *T. parviflora*), was described as new on the basis of its extremely short floral pedicels. This character, also used in support of *T. tessellata* in conjunction with a number of other quantitative characters, was the subject of intensive analysis in Jamaica.

Thrinax parviflora, an endemic palm in Jamaica, is a highly variable and polymorphic species (Figs. 4–7) and occurs over an equally variable and complex system of environments, from near sea level to about 3000 ft. (914 m.) elevation. Considerable effort has been expended in attempting to correlate variability of phenotype with the environment. However, lacking experimental evidence (e.g., transplant experiments etc.) of any genetic bases for the variation, it is difficult to do more than describe the range of variation in the various environmental zones. The extent of variability can be and has been measured by field studies on plants in forty-two localities throughout the entire range of distribution of the species.[4]

If a line were drawn on a map of Jamaica from Portland Ridge, in the south, to the northern slopes of Mt. Diablo (Fig. 8) it would pass through regions of low to high elevations from sea level to about 3000 ft. (914 m.), and from hot, dry, nearly xerophytic conditions to cool, moist, mesophytic

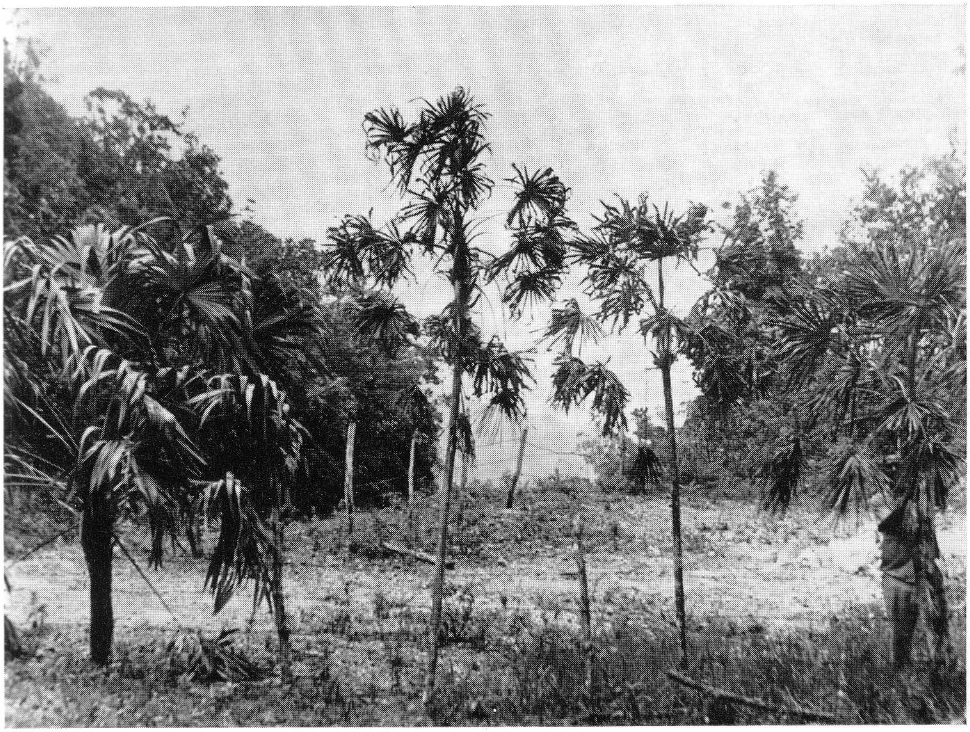


6. Juvenile (left) and adult (right) forms of leaves of *Thrinax parviflora* at the highest elevations near Holly Mount Hill on Mt. Diablo, Jamaica.

woodlands and high pinnacles frequently bathed with mist. The rainfall varies from less than 50 in. (126 cm.) per year at Portland Ridge to more than 70 in. (178 cm.) per year on the heights of Mt. Diablo. Along the line, changes in temperature and moisture availability are mostly gradual up to the middle elevations on Mt. Diablo where, as a result of the combined effect of exposure, elevation, and the very steep escarpment, the changes are more abrupt. At the elevation where cloud formation most frequently occurs, noticeable differences in the climate and flora are evident over a very short distance. *Thrinax parviflora* grows on nearly every natural outcrop of limestone along the transect.

During the course of the study, numerous collections were made on nearly

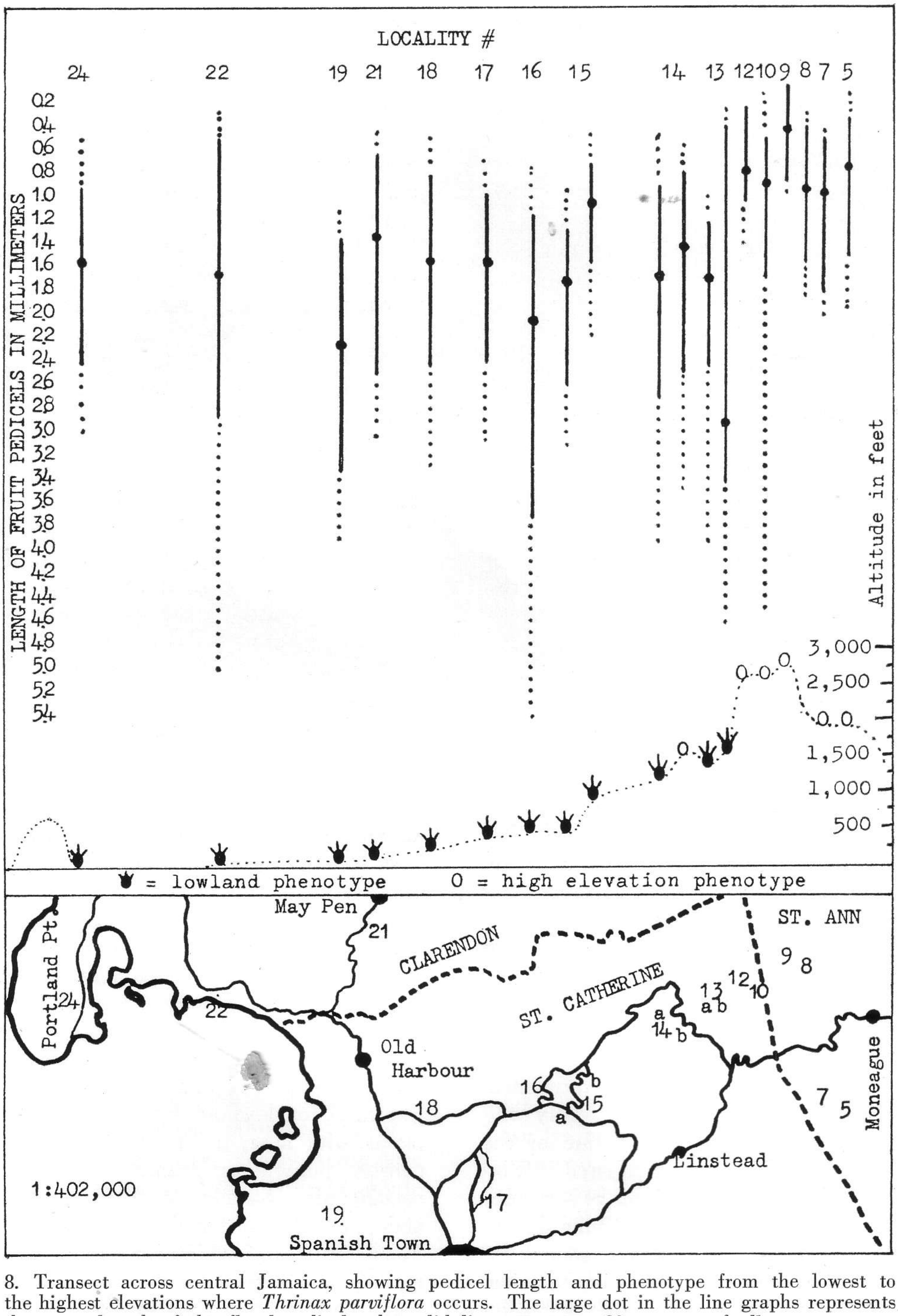
[4] A similar problem with *Metrosideros* and altitudinal variation in Hawaii has recently been published by Corn and Hiesey (1973). The research approach was different but the problems and conclusions are perhaps similar.



7. Morphological (phenotypic) variability of *Thrinax parviflora* on the Blue Mountain trail of Mt. Diablo, Jamaica. The plants were cut and removed to one place for the photograph.

every accessible area along an irregular line from south to north, and on Mt. Diablo, in an attempt to obtain adequate material over a range of variable ecology. The transect runs through two of three intensive study areas which were previously the focal point of the major study of the species for a monograph. Samples of inflorescences and leaves were taken from every available plant at each area. In addition, pedicel measurements were taken from every collection locality along the route of the transect and these are compared in Figure 8. It is obvious, as can be seen also in Figure 8, that from the results shown, the length of the pedicels cannot be used for separating taxa in Jamaica. Although the plants at high elevation have a predominance of short pedicels, those of lower elevations exhibit an abundance of pedicels in the same length ranges, and there is considerable overlap at the 90% level.

There are only two apparently reliable characters which can be used to characterize the high and low elevation phenotypes along the transect. These are the hastula and the degree of puberulence on the primary branches of the inflorescence. The designation in Figure 8 for lowland forms represents plants with long, pointed hastulas and densely puberulous primary branches, accompanied usually by large leaves and relatively short and stout caudices. The designation for high elevation forms represents plants with short, acute or blunt hastulas and glabrous to lightly puberulent primary branches.



8. Transect across central Jamaica, showing pedicel length and phenotype from the lowest to the highest elevations where *Thrinax parviflora* occurs. The large dot in the line graphs represents the mean length of the floral pedicels, the solid line represents 90 percent of all measurements and the broken line indicates 5 percent of the total taken off each end of the range.

Along the southern face of Mt. Diablo an exceedingly steep escarpment rises nearly 2000 ft. (609 m.) above the valley. Along most of the escarpment, which faces south, climatic conditions up to about 1650 ft. (502.92 m.) elevation are very similar to those at lower elevations. Full exposure to the sun, particularly in the winter months, perfect drainage, and average rainfall permit a Dry Evergreen thicket type vegetation in which the palms are almost indistinguishable from plants growing near sea level on Portland Ridge. At approximately 2000 ft. (609 m.) elevation the vegetation changes to open woodland in protected valleys and gorges, and tall slender plants of the typical high elevation palm dominate the exposed ridges and rocky pinnacles. There does not appear to be a transition zone for the palms along the trail because suitable rocky outcrop was not encountered between 1650 and 2500 ft. (502.92 and 762 m.) elevation. It is important to note here that the point between 1700 and 2000 ft. (518.16 and 609 m.) elevation is the altitude at which clouds generally form and obscure the peaks and ridges, commonly throughout the year but more frequently in the late summer and winter months. The clouds and mists which are common above 2000 ft. (609 m.) elevation on Mt. Diablo result partly from and contribute to the higher moisture availability and cooler temperatures which are reflected in a different flora.

The greatest extremes in phenotypic expression are coincidentally found on the south-facing escarpment of Mt. Diablo above an area known as Charlton. At an elevation between 1500 and 1650 ft. (457.2 and 502.92 m.) elevation (locality #13) there are several palms which exhibit among themselves the largest trunk and leaf dimensions and although two of the plants in the group had pedicel lengths averaging within the normal range of means for lowland forms, the third plant exhibited exceptionally long pedicels which caused the mean for the group to be among the longest pedicel lengths of any population on the island.

Near the upper limit of the escarpment, overlooking the group of exceptional plants just mentioned, typical high elevation plants occur between 2000 and 2650 ft. (609 and 807.72 m.) elevation in the cloud zone. The very tall, slender-stemmed palms with very small, tightly folded and curled leaf blades grow among somewhat dwarfed thicket wherein occur numerous epiphytes, ferns and herbaceous plants.

The breeding system of *Thrinax parviflora* is very complex and is not completely understood. However, over a two-year period, it has been observed that plants of high elevations and in the cockpit country bloom only during the winter months. The lowland form has been observed to bloom only during the warmer summer months. Although *Thrinax* flowers are essentially wind-pollinated, the difference in blooming season would effectively isolate the two forms if the control is genetic in origin. What we do not know is whether or not the high elevation form would retain its winter-blooming habit if grown in the lowlands.

Another pertinent problem is the means of seed dispersal. Doves are said to feed on the "tatch-peas." The doves are extremely plentiful when the palms are in fruit but are uncommon near palms at other times. It is extremely likely that seeds of plants at the higher elevations are deposited on the drier lower cliffs and slopes through the medium of dove dispersal. Whether such seeds will germinate and compete with the lowland form is unknown. Preconditioning of the seeds or genetic differences may, in fact, prevent random occurrences of a biotype[5] outside its special niche, broad as that may be.

The accumulated data suggest that there are indeed two distinct climatic zones (one above, the other below the elevation of regular cloud formation) which support two different biotypes of *Thrinax parviflora.* Were it not for the extreme phenotypic plasticity of each, it might be possible to map their patterns of distribution. However, herbarium specimens are wholly inadequate for this task, and in two years it was only possible to study adequately about 50 or so local populations. When flying in and out of Jamaica, every peak, ridge, and rocky slope appears from the air to support great numbers of *Thrinax parviflora.* One character, the hastula, retains its distinctiveness and when used in conjunction with puberulence militates very strongly for distinct biotypes. In order to stabilize the nomenclature and typify the species, it has been necessary to delimit two subspecies which will be described elsewhere.

[5] Biotype: a collection of individuals which are genotypically all essentially the same. Experimental proof of biotypes in *Thrinax parviflora* is not feasible, but evidence suggests the distinct possibility of biotypes.

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Biennial Meeting Reminder

Don't forget to plan for the Biennial Meeting at Fairchild Tropical Garden, Miami, June 22, 23, and 24, 1974.

June 22: Welcoming-Reception hosted by the South Florida members at Corbin Educational Building, 6–8 p.m.

June 23: registration 10 a.m. to 1:30 p.m. (lunch served at Corbin Building, $1.50); Biennial Meeting at 1:30 p.m.; banquet 7 p.m.

June 24: tour of Jennings Estate 8:30–9:15 a.m.; lunch for out-of-town members at home of Paul Drummond followed by tour of Nat DeLeon's garden nearby and John Turner's atrium garden; supper 6:30–7 p.m. (about $1.75) at home of Teddie and Ted Buhler followed by slides.

June 25: tours to Nassau or Key West or in Miami.

June 26: depart for home or on tour to Colombia.