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to twenty-four seeds. When mature, the fruit fragments into indehiscent single-seeded segments, leaving behind the rim that outlines the pod margin. Pods are mature by September but continue to ripen through January in the lowlands. In evergreen forest areas, *M. pigra* remains seasonal in flower and fruit production, but some flowers and fruits can be found throughout the year.

In Guanacaste many of the seeds germinate when they are first wetted, but if 100% germination is desired, a small notch must be filed in the seed coat before moistening. In the wetter areas, the seeds seem to germinate with less delay, and large pod fragments may be found on the ground with many seedlings growing from the segments (in wet areas the pods do not fracture so neatly).

The foliage of *M. pigra* is made up of fine leaflets with many sharp, recurved spines on the undersides of the petioles, petiolets, and stems. *M. pigra* foliage has been rejected by odor by captive collared peccaries, white-tailed deer, and a tapir. Cattle and horses not browse it even when the pasture is extremely dry and food very scarce, but the leaflets are fed on by several species of chrysomelid beetles. It is becoming a serious weed, as an introduced plant, in tropical Australia.

In the moist northwestern corner of Guanacaste, north of La Cruz, the seeds of *M. pigra* are heavily preyed on by the larvae of *Acanthoscelides zebrata*. The adult bruchid lays its eggs among the hairs on the pods, and the larvae bore through the pod wall and into the seeds when full sized but not yet hard. There is one bruchid larva per seed, and it eats all of the seed content. South of La Cruz, throughout Guanacaste and Puntarenas provinces, *M. pigra* seeds are preyed on by the larvae of *Acanthoscelides pigrae* (Janzen 1980). In the area of San Miguel to Puerto Viejo, Heredia Province, the seeds are eaten by the smaller *Acanthoscelides pigricola* (Kingsolver 1980). In Costa Rica these bruchid beetles prey on no other species of seed. Immature seeds are occasionally killed by sucking Hemiptera (Pentatomidae) that puncture the green fruits.

Each *Mimosa pigra* bush seems to have a subset of the local population of adult *Acanthoscelides pigrae* or whichever species of bruchid beetle is associated with it. At dawn, just after the inflorescences have opened, the adult beetles can be found climbing about over the inflorescences, presumably eating pollen and nectar. If captured, they are replaced by another group of beetles the next morning. If this is repeated for several mornings, the number abruptly declines on the third or fourth morning; the small number that appear each subsequent morning probably represent the daily immigration input to the bush (Janzen 1975).

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Monstera tenuis (Chirravaca, Mano de Tigre, Monstera)

T. Ray

The genus *Monstera* (fig. 7.81) includes about twenty-two species and is about the same size as the genus *Syngonium*. Like *Syngonium*, *Monstera* is restricted to the Neotropics and has its center of diversity in Central America. However, there is a much greater diversity of growth habits within the genus *Monstera* than within *Syngonium*.

I will begin by using the species *Monstera tenuis* (formerly *M. gigantea*) to illustrate some points. *M. tenuis* produces large infructescences, about 30 cm long, containing about one thousand fruits each. In the cacao groves at La Selva, where *M. tenuis* has attained a very high population density, the fruit is poorly dispersed. The seeds tend to fall in great density directly below the parent plant. The seeds, about 1 cm long, have no dormancy and germinate to produce a long, slender sprout, about 1 mm in diameter, with tiny bractlike leaves at the nodes, which are spaced at 6 cm intervals. These sprouts are green but have very little photosynthetic surface and so are almost entirely dependent on seed reserves. This contrasts with the *Syngonium* habit of establishing a rosette of leaves first.

The *M. tenuis* seedling is capable of reaching a length of 1 or 2 m on seed reserves. The seedlings do not produce leaves until they reach a tree; thus the seedling will die if it does not encounter a tree while on seed reserves. This not only means that a seedling must fall within 1 or 2 m of a tree if it is to survive, but also that it must grow directly toward the tree lest it waste its reserves in aimless wanderings. It is not surprising that these seeds are strongly skototropic (Strong and Ray 1975). This is strikingly displayed when the seeds fall in dense clusters around the base of a tree. The green seedlings stand out against the brown leaf litter and all point toward the tree, looking like short spokes of a wheel with the tree at the hub.

Upon reaching a tree, the seedling begins to produce small round leaves (2 cm in diameter) that are pressed flat against the tree trunk and cover the stem. Along with leaf production comes a shortening of the internodes and the

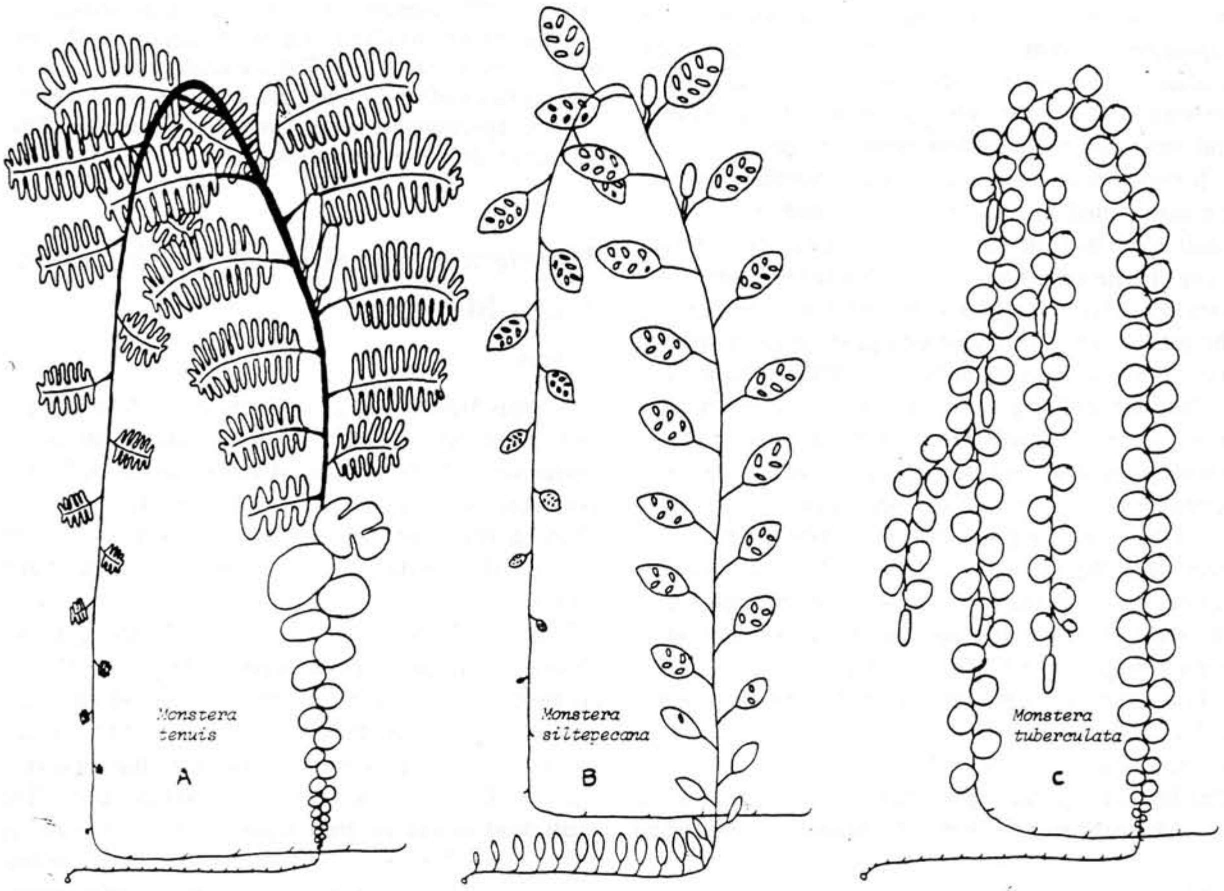

FIGURE 7.81. *Monstera* spp. (drawing, T. Ray).

beginning of stem thickening. Successive leaves will be of increasing size as the stem climbs the tree. As in *Syngonium*, the climbing stem retains the ability to switch to the leafless form and return to the ground if it reaches the top of a tree. When the successive leaves attain a diameter of about 25–30 cm, a dramatic change in leaf form occurs. The leaves develop deep clefts and become pinnatifid, having the appearance of fern fronds (fig. 7.81*a*). Unlike the round leaves, these are held away from the trunk of the tree on their petioles. The size of successive leaves continues to increase after the change in form, until the leaves reach a length of as much as 125 cm. At this size the petiole will be 60 cm long and the stem will be 8 cm in diameter.

As in *Syngonium*, flowering is terminal, but the branch is continued by an axillary shoot, and the stem flowers and fruits repeatedly as it climbs. Also, should the stem reach the top of the tree, even the most mature stem is capable of returning to the ground, with a change in stem form involving internode elongation and reduction of stem diameter and leaf size. In such cases the mature leaf form is retained in successively smaller leaves, even when the leaf size has been reduced well below that size at which the change to mature leaf form occurred. By the time the hanging stem reaches the ground, the leaves will have been reduced to bracts, and the internodes will be long and slender. This resembles the leafless seedling, but on a larger scale: the internodes are longer (20 cm) and thicker (9 mm). These stems are analagous to type A_h of *Syngonium*.

The dramatic change in leaf form, from round appressed leaves to pinnatifid leaves, has atracted considerable attention. The common folklore that has arisen states that the leaves change form in response to higher light levels that the stem encounters when it climbs a tree. A simple observation should cast doubt on this hypothesis. A tree standing in an open field receives rather uniformly high insolation on the lower portion of the trunk. Yet, when *M. tenuis* grows on such a trunk, it does not switch to the mature leaf form at the base of the tree. We still see the same progression of gradually increasing leaf sizes, and the switch in form still occurs when the leaves are about 25–30 cm in diameter (Oberbauer et al. 1980). At the higher light levels, however, the increase in leaf size will occur more rapidly, so that the change in leaf form will occur lower on the trunk.

These observations can be more clearly understood if we make a distinction between changes of form induced by a change in environmental conditions and changes of form resulting from the unfolding of a developmental process. Under the strict definitions that I will use in this paper, the term heterophylly will refer only to those changes of form that are induced by some change in environmental conditions, and heteroblasty will refer to those changes that will occur even in a perfectly uniform environment. The latter are generally developmental changes that occur as the plant matures. The changes of form that occur in a climbing stem are heteroblastic changes. The stem need not encounter higher light levels as it climbs. Light may affect the rate at which the changes occur, but it does not affect their nature.

Thus we may consider *M. tenuis* to be composed of three heteroblastic series: the leafless seedling, the climbing stem, and the descending stem and ground runner. Switching between these three forms is stimulated by gaining or losing contact with a tree trunk. Thus the change in form from the leafless seedling to the leafy climber may be considered heterophyllic change, since it is induced by a change in the environment—contact with a tree. This change in form will not occur in a uniform environment.

A heteroblastic series is essentially an ontogenetic pathway. In some cases the end form is reached quite rapidly, after which the form no longer changes. When the *M. tenuis* seed germinates, for example, there is a short series of segments with increasing internode length, after which there is no further change. In other cases there will be a cycling of forms. Form A of *Syngonium* for example, alternates between forms T_1 and T_2. To sum up, changes in form need not be interpreted as a response to changes in environmental conditions. They may be ontogenetic changes that will occur even in a uniform environment, though the rate of change may be affected by environmental factors.

The most significant differences between the growth habit of *M. tenuis* and that of *Syngonium* is that the *M. tenuis* seedling does not make leaves until it reaches a tree. However, there are species of *Monstera* that make leaves before reaching a tree. But, unlike *Syngonium*, the leaves are more or less evenly spaced along the stem (fig. 7.81*b*) rather than clumped into rosettes alternating with "leafless" stems.

There are additional species of *Monstera* that exhibit yet another variation in growth habit. In some species the pendant stems do not go through the reduction in leaf size and internode diameter characteristic of *Syngonium*, but continue to produce leaves, and even fruit, while descending to the ground. In *M. tuberculata* (fig. 7.81*c*) flowering occurs only in pendant stems. The various growth habits found in *Monstera* have been described by Michael Madison (1977) in his revision of the genus. The work includes an excellent key to the species, as well as photographs of each species.

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Mora megistosperma (Alcornoque, Mora)

D. H. Janzen

This large, cesalpinaceous legume tree (= *Mora oleifera*) grows immediately behind the mangroves on the Golfo Dulce and in postmangrove habitats on the sides of the Osa Peninsula facing the Pacific Ocean. It has been studied only in Corcovado National Park, but other species of *Mora* have been studied in northern South America (Rankin 1978). It may also be found as a riverbank tree (fig. 7.82*a*) in estuarine areas free of mangroves (e.g., Boca Sirena, southern Corcovado National Park). The largest adults have a dbh of 2–4 m, but these plants almost always have the tops snapped off 5–10 m above the ground and are hollow (they stump sprout heavily from the stump top). More normal-appearing trees occur in nearly pure stands, and large reproductives may attain a height of 30–45 m and be 1–2 m in diameter just above the buttresses. The bole is straight and cylindrical but covered with knobs from which small adventitious shoots are persistently produced even in heavy shade.

The leaves normally have four large opposite leaflets. In late November they all turn yellow and drop, leaving the trees synchronously leafless for 1–2 weeks. The new leaves are very bright green when first produced.

The 8–12 cm long "catkin" of tiny, white flowers is produced in May. A large flower crop would be five hundred inflorescences (one hundred to three hundred flowers per inflorescence). Only a small fraction of these are open on the tree on any given day. They are presumably pollinated by moths at night or by miscellaneous small insects during the day. As many as fifteen tiny fruits may be set per inflorescence, but most are quickly shed. By August each tree has a small crop of enormous brown fruits. A large tree with a fully insolated crown (isolated on a riverbank) may bear up to five hundred, but in intact