

Swollen-Thorn Acacias of
Central America

Daniel H. Janzen



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ABSTRACT

Janzen, Daniel H. Swollen-Thorn Acacias of Central America. *Smithsonian Contributions to Botany*, number 13, 131 pages, 119 figures, 1974.—This nomenclatural, taxonomic, and ecological treatment of 11 Central American obligate ant-acacias (*Acacia allenii*, *A. chiapensis*, *A. collinsii*, *A. cookii*, *A. cornigera*, *A. gentlei*, *A. globulifera*, *A. hindsii*, *A. mayana*, *A. melanoceras*, and *A. sphaerocephala*) and one quasi-obligate ant-acacia (*Acacia ruddiae*) is based on extensive field study from 1963 to 1972 and on herbarium specimens where of use. The population boundaries of all species are mapped and described with respect to ecological parameters. Morphological variation, details of the interaction with the ants, and acacia reproductive biology are presented for most species.

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Swollen-Thorn Acacias of Central America

Daniel H. Janzen

Introduction

The swollen-thorn acacia group (*Acacia* species) is one of the two most diverse and widespread of the neotropical myrmecophytes. These acacias are the characteristic ant-plants in the drier lowlands ("tierra caliente") of Central America, just as the genus *Cecropia* (Moraceae) is the most conspicuous and diverse myrmecophyte of wetter habitats in Central and South America.

This monograph on the taxonomy and natural history of neotropical swollen-thorn acacias is offered at this time for several reasons. (1) The neotropical swollen-thorn acacias do not appear to constitute a tight phyletic unit, yet they share many adaptive ecological and morphological traits. They are thus outstanding examples of evolutionary convergence. The most noteworthy of the traits they have in common is that they are protected from herbivores by colonies of ants in the genus *Pseudomyrmex*, rather than by chemical traits as are most plants (Janzen, 1966a, 1967b; Rehr et al., 1973). (2) The ants can be readily removed, just as though one were able to easily remove the alkaloids and cyanogenic glycosides from the leaves of ordinary acacias such as *Acacia farnesiana*. This ease of experimentally disarming the plant means that the protective role of the obligate acacia-ants has been easy to study and provides an excellent system for understanding the coevolution of complex interactions between higher organisms. For further and more detailed comparative studies among the swollen-thorn acacias, a stable nomenclature is essential at this time. (3) Detailed data on populations of native wild Central American plants are noticeably absent from the literature. A better concept is needed of the population structures of a wide variety of tropical plants of different life forms and in different habitats in order to generate specific hypotheses that can lead to an understanding of complex tropical communities. (4) The lowland deciduous forests of Central America have nearly disappeared. The population structures of the species remaining in these habitats are already greatly altered. The swollen-thorn acacias are clearly in this category. I would like to summarize the ecological behavior of swollen-thorn acacias before their patterns are so far altered that we can no longer recognize the conditions that produced the genotypes we find in today's cattle pastures, roadsides, and abandoned fields. Most wild plants in high-yield agricultural areas must be studied under conditions not unlike studying elephants and deer in a zoo.

It is hoped that the incompleteness of the data and hypotheses offered here will encourage field biologists to look harder at why plants do what they do in natural habitats as well as in those badly altered by agriculture.

ACKNOWLEDGMENTS.—I am greatly indebted to Dr. Velva E. Rudd of the National Museum of Natural History for her very competent assistance and advice throughout this study. Her patience with the bumbings of an entomologist in the world of taxonomic botany immensely facilitated the unraveling of the nomenclatorial spaghetti surrounding the swollen-thorn acacias. Personnel in various

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herbaria have kindly allowed me to examine types and at times to borrow specimens.

A special acknowledgment is due Karen Janzen, who participated in the laborious task of recording field data and voucher specimens.

This study was supported by National Science Foundation Grant GB-5206, and is in part a by-product of NSF Grants GB-91, 1428, 7805, and 7819. Substantial portions of this study were completed while I was serving in Costa Rica as a faculty member for the Organization for Tropical Studies in Costa Rica (1965-1971). The paper is Contribution No. 1360 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

General Biology

The 12 species of swollen-thorn acacias in aggregate range from the Tropic of Cancer on both coasts of Mexico only as far south as northwestern Colombia. They are generally found at elevations below 1200 m (Figure 1). One Argentinian acacia, *Acacia caven* (Molina) Molina, has been suggested as a swollen-thorn acacia (Fiebrig, 1909; Chodat and Vischer, 1920); however, Wheeler (1942), Havrylenko (in litt.), and Willink (in litt.) have convinced me that the ants living in the thorns were only fortuitous invaders. My own unpublished observations of *A. caven* in Chile give no hint of myrmecophytism with this plant. Greenhouse *A. caven* (from Argentinian seeds) shows thorn and leaf development like that of normal acacias and therefore will not be discussed further. The African swollen-thorn acacias, or "whistle-thorn" acacias (e.g., *A. seyal*, *A. drepanolobium*, *A. formicarum*, *A. bussei*), appear to have a mutualistic interaction with ants of the pantropical myrmicine genus *Crematogaster* (Hocking, 1970; Monod and Schmitt, 1968; Bequaert, 1922). This is a clear case of mild convergence on the Central American system and is excluded from generalizations made in this paper. This restricted view should not, however, be taken to suggest that hypotheses based on the much better understood Central American system are irrelevant to the African system.

The pantropical and subtropical mimosoid legume genus *Acacia* contains at least 750 species, though the number may be reduced substantially if the synonymy found in this study is representative of the remainder of the genus. Plants of the genus

Acacia are primarily in areas with less than 3 meters of annual rainfall and with a well-developed dry season of 3-11 months duration. Throughout Africa and the neotropics, those species with foliar nectaries (probably all species) have a loose association with ants. Many genera of arboricolous ants (e.g., *Crematogaster*, *Pseudomyrmex*, *Camponotus*) visit these nectaries and in the process probably increase the intensity of their foraging activity on these plants compared with adjacent plants lacking nectaries. This, accompanied by similar benefits from parasitic Hymenoptera attracted to the nectaries, has probably been the selective force leading to the evolution of these nectaries (cf. Janzen, 1966a; Bequaert, 1922).

In a few cases, however, the ant and acacia interaction has evolved to a much higher level of complexity, that of obligatory mutualism (Janzen, 1966a). For background information, a brief résumé of the interaction in Central America is given in the following paragraphs. More details can be obtained from Janzen's (1967b) lengthy description of *Acacia cornigera* and *Pseudomyrmex ferruginea* in lowland eastern Mexico and in peripheral papers on ants and acacias (Janzen, 1967a, 1969a, 1969b, 1973; Beulig and Janzen, 1969).

A colony of obligate acacia-ants lives in the swollen, stipular thorns of one to several individual shrubs or small trees that have been given the subgeneric common name of "swollen-thorn acacia" (Janzen, 1967a). New World obligate acacia-ants are a behaviorally distinct group (at least 13 species: *P. belti*, *P. ferruginea*, *P. nigrocincta*, *P. venefica*, *P. satanica*, etc.—Janzen, ms) within the exclusively New World, and mostly tropical, genus *Pseudomyrmex* (150-200 species). Most species of *Pseudomyrmex* have small colonies in dead hollow stems above the ground in habitats ranging from brushy pastures to well-developed forest. The exceptions, besides obligate acacia-ants, are those with an obligate mutualistic interaction with the neotropical trees *Triplaris* (Polygonaceae) and *Tachigalia* (Leguminosae). I have never found any of the many species of obligate acacia-ants as a viable colony living elsewhere than in a swollen-thorn acacia. Those rare cases where swollen-thorn acacia populations are unoccupied by obligate acacia-ants are discussed in later parts of this paper.

New World swollen-thorn acacias differ morphologically and behaviorally from other acacias in

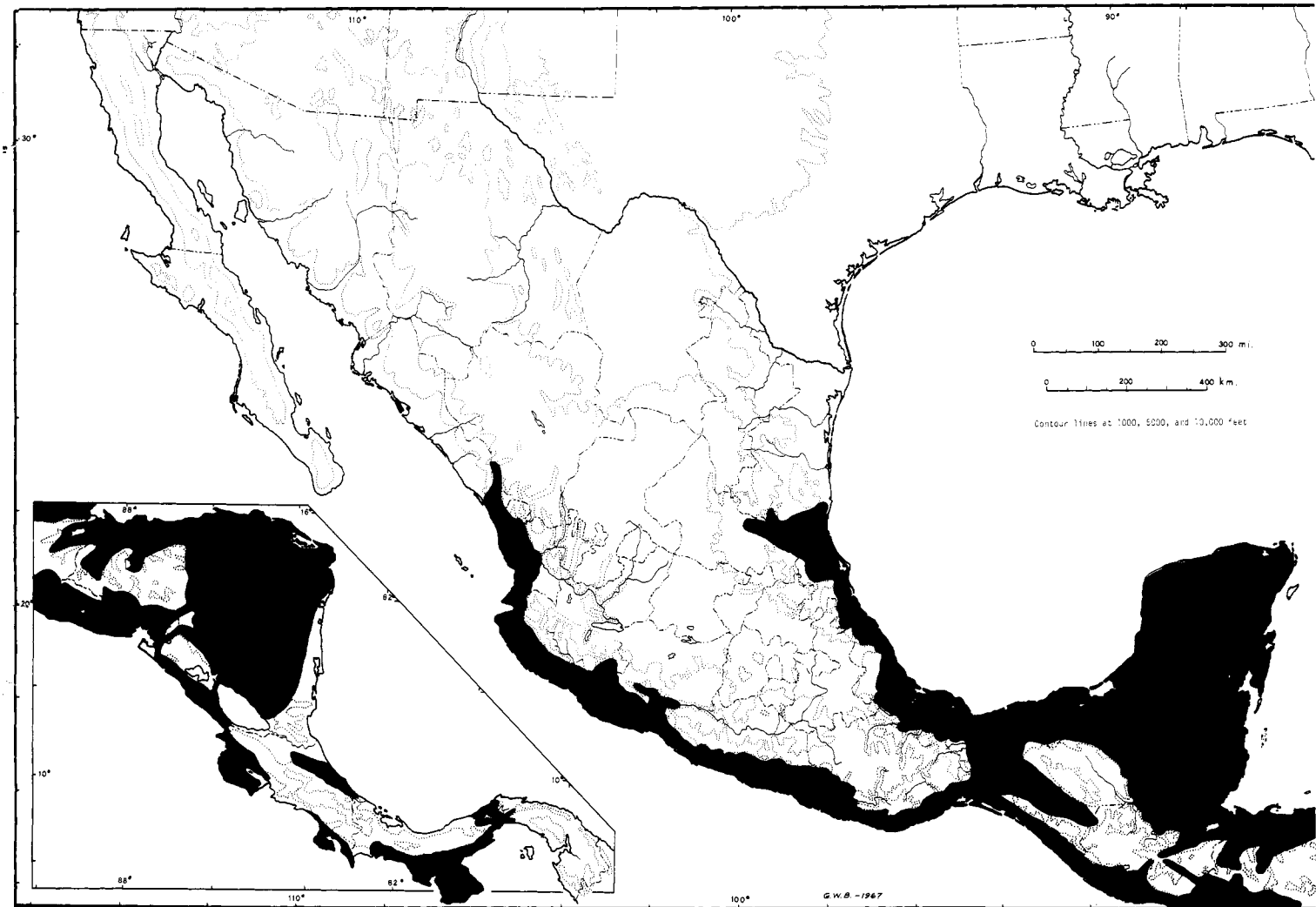


FIGURE 1.—General distribution of swollen-thorn acacias in Central America, based on herbarium records, field observations, and inferences from general vegetation. Contemporary distributions are usually continuous throughout the areas in black, owing to human destruction of the primary forest that previously isolated the swollen-thorn acacia subpopulations along river edges and in other kinds of disturbed vegetation.

that they have: (1) large and partly hollow stipular thorns that the ants clean out through an entrance hole cut in one thorn tip while the thorn is still green and relatively soft; (2) modified leaflet tips called Beltian bodies (see Rickson, 1968, 1969, 1971, for micromorphological details), which are har-

vested by the ants—these are the protein, lipid, and major carbohydrate sources of the ant larvae; (3) greatly enlarged foliar (petiolar) nectaries that are continually secreting the nectar that constitutes the primary carbohydrate and moisture source of the adult ants; (4) year round leaf production and

retention by most individuals, yielding a relatively continuous food source for the ants; and (5) lost most of the chemical and structural traits that protect other acacias from most herbivores (cf. Rehr et al., 1973). Swollen-thorn acacias differ ecologically from other acacias in that in natural habitats they cannot survive to reproductive maturity without the patrolling activities of a large colony of obligate acacia-ants. The ants remove herbivores (primary insects) and intrusive vegetation by biting and stinging the invading part of the plant (as do their relatives, *Pachysima*, living in *Barteria* trees in Africa—Janzen, 1972). By analogy, the ants substitute for the chemical and physical abilities of most acacias to deal with their predators and competitors. The one exception to the above generalizations, *A. ruddiae*, will be discussed in its own species account.

The species of obligate acacia-ants are not specific to a swollen-thorn acacia species, but rather to its life form. For example, *A. collinsii* has at least eight species of obligate acacia-ants living in it over its range from Mexico to Colombia, and all of these ants also live in other swollen-thorn acacias. In nature, one ant colony may be found occupying two adjacent individuals of two different swollen-thorn acacia species. The only species of swollen-thorn acacia that are occupied by only one species of ant are *A. melanoceras* (occupied by *Pseudomyrmex satanica*) and *A. allenii* (occupied by *Pseudomyrmex ferruginea*). They appear to be this way because the climate or resources will not support other ant species, rather than because the plants are unsuitable for other obligate acacia-ants. Both of these species of acacias will support other obligate acacia-ants in the greenhouse.

Swollen-thorn acacias grow in natural and man-made disturbed vegetation—both primary and secondary succession. *A. cornigera*, *A. hindsii*, and *A. collinsii* have very successfully invaded brushy pastures, roadsides, and fallow fields, and may constitute a major part of the standing biomass in some 1–5-year-old fallow regeneration. On the other hand, *A. allenii*, *A. melanoceras*, and *A. ruddiae* are apparently in danger of extinction because they do not maintain a breeding population except in very lightly disturbed, or undisturbed, primary rain forest.

In contrast to most other acacias, swollen-thorn acacias originally inhabited naturally disturbed

sites in forests—deciduous to evergreen—with 2–5 m annual rainfall. Other acacia species usually live in drier sites. The ability to compete with rapidly growing vegetation in wetter habitats is the direct result of the behavior of the occupant acacia-ants. In pruning vines out of the swollen-thorn acacia crown and in killing intruding branches from neighboring trees, they place the acacia in a highly insulated microhabitat (this is, incidentally, a form of allelopathy by the acacia—Janzen, 1969a). Second, since the growing points of the acacia are very heavily patrolled (protected) by ants, they lack the usual structural toughness associated with protection from herbivorous insects that is found in other acacia shoot tips. This tenderness is associated with a swollen-thorn acacia rate of vertical height increment high enough to make the acacia an effective competitor with other plants in wet sites. Ironically, this high growth rate would probably not be possible in drier sites, and in drier sites the acacia would not be able to support the ant colony owing to loss of leaves during the dry season. From the wettest to the driest sites the species are: *melanoceras*, *allenii*, *ruddiae*, *cookii*, *gentlei*, *chiapensis*, *globulifera*, *hindsii*, *mayana*, *sphaerocephala*, *cornigera*, and *collinsii*. This progression also ranges from those with the smallest geographic ranges to the largest, except for *A. mayana* and *A. sphaerocephala*, which have minute ranges.

It is noteworthy that some swollen-thorn acacias have the largest leaves of any acacia species. This may be useful in the cloudy weather which is more probable in the wetter sites than drier habitats; it is also “allowed” by the generally reduced problem of foliar water loss in wetter habitats. In the driest swollen-thorn acacia habitats, many of the larger leaves are dropped during the dry season, and then axillary clusters of very small leaves provide nectar and Beltian bodies for the ant colony. Very few swollen-thorns and their associated large leaves are produced during the dry season.

Even though they occupy wetter habitats than other acacias in general, swollen-thorn acacias disappear when annual rainfall exceeds about 4 m (e.g., the Puerto Viejo region of northeastern Costa Rica) and the dry season is less than two months' duration. The reason for this probably centers on the decreasing number of sunny hours per day as rainfall increases. When days are overcast in rain-forest areas, the amount of light reaching small

shrubs on the forest floor is very low, and it may be that the swollen-thorn acacia has been unable to convert its primitively heliophile physiology to that of total shade tolerance.

Their upper elevational limit is about 800 to 1200 m, depending on the moisture and temperature conditions at upper levels. The wetter and colder an elevational transect, the quicker the swollen-thorn acacias disappear from the vegetation with increasing altitude. Cold weather does not kill the ants on the acacias but restricts patrolling activities to the point where the acacia is either covered over by the rising vegetation, defoliated severely, or both. All species are found at sea level in at least some part of their range; their upper elevational limits vary widely, with *A. globulifera*, *A. sphaerocephala*, and *A. cornigera* attaining the greatest heights.

In contemporary communities (disturbed by man), swollen-thorn acacias reproduce very commonly by stump and root suckers and only rarely by seedlings. In naturally disturbed sites (where clearing of the vegetation is not periodically repeated), however, the rare seedlings are the usual means of population recruitment. Though a large seed crop is produced annually, most seeds are killed by bruchid beetles, against which the ants offer no defense (Janzen, 1967b, 1969c). There is a very high mortality rate of seedlings until the trees become occupied by an ant colony. Sucker shoots (often from lateral roots) are often near a large obligate acacia-ant colony, which simply incorporates the sucker into the colony's territory; this is especially noticeable with the obligate acacia-ant species that have multiple queens and thus unlimited colony size (e.g., *Pseudomyrmex venefica* in *A. hindsii* in western Mexico north of the Rio Balsas basin; Janzen, 1973). An unoccupied seedling must wait 9 months or longer for a founding queen ant to grow a young colony and by then the seedling is often well below the surrounding vegetation and therefore at a severe competitive disadvantage. Sucker shoots produce their first seed crop about 2 years earlier than do seedlings. Adults of either seedling or sucker shoot origin generally live 15–35 years.

Swollen-thorn acacias flower during the dry season, as do so many other deciduous forest woody plants (Janzen, 1967c), and are pollinated by relatively unspecific pollen-collecting bees. In the

greenhouse, swollen-thorn acacias never set fruit though they flower copiously. I infer from this that they are obligatory outcrossers. The bees are occasionally attacked by a worker ant, but these bees are persistent in getting at the flowers, and the ant's aggressiveness probably does little more than maximize cross-pollination by forcing bees to visit several trees. The small pods remain on the receptacle until the following dry season, growing large and maturing several months before the next crop of flowers. There may be mature pods on the tree with the flowers, but these are from the previous year except in the species in very wet sites, such as *A. allenii*, *A. ruddiae*, and *A. melanoceras*. The seeds are distributed by birds that either eat the pod entirely (only *A. cornigera* and *A. sphaerocephala*) or eat the cluster of seeds imbedded in a sweet moist pulp that is yellow or white pulp. Swollen-thorn acacias appear to be the only neotropical acacias with bird dispersed seeds (Janzen, 1969b). If it were not for bird dispersal, there would be virtually no survival of seeds because the bruchid beetles will kill virtually every seed that remains on the tree (Janzen, 1969c, 1971).

Swollen-thorn acacias have a representative flowering phenology. At any given site, nearly all mature plants bear open inflorescences for 4–8 weeks at about the same time each year. This flowering period may start anytime during the first 2 months of the dry season, depending on the species and the area. For a given species and area the timing is the same from year to year. A single species may show quite extreme variation from site to site in both the absolute dates of flowering and the dates relative to onset of wet and dry season. In general, however, at least 80 percent of the subpopulations of swollen-thorn acacias flower during the dry season.

In addition to the major peak of flowering shown by each species at each site, there are almost invariably some individual acacias that are out of phase with the remainder of their population. These are usually damaged, growing on locally peculiar drainage types (creek bottom or hill crest) or senescent. They are often helpful in taxonomically identifying the population, but are very misleading in understanding the morphology, ecology, and behavior of the population. Botanists have a tendency to collect these flowering or fruiting plants in preference to sterile individuals. This leads to erroneous records

of flowering times. These individuals often set little or no seed, which gives a false impression of seed-crop size. Those seeds that are produced are sometimes only mildly attacked by bruchids, giving the false impression that seed mortality is trivial for the population (see Janzen, 1968, for a discussion of this point among plants in general). These plants also may bear a reduced number of inflorescences per axil and inflorescence-bearing branch, and these branches are often sparser and smaller than on healthy acacias.

Swollen-thorn acacias have very thoroughly occupied most of the Central American habitat that looks as though it should support them; however, they have not yet spread into the semiarid areas of South America that are presently occupied by the species of plants that co-inhabit their Central American habitats. Their absence from the deciduous and semideciduous forests of Venezuela, Brazil, and Colombia is particularly striking. It seems reasonable to expect that these areas are not inimical to swollen-thorn acacias, but rather that they simply have not yet gotten there. *A. collinsii* in Colombia, however, must surely be a seed source for the remainder of the country. If swollen-thorn acacias were not such an economic pest in brushy Central American pastures, the obvious transplantation experiment would be well worthwhile.

Swollen-thorn acacias have not been generally successful at colonizing islands. They occur on offshore islands such as those in the Gulfo de Nicoya, Costa Rica, in the Gulfo de Fonseca, Honduras, and off the eastern coast of Yucatan, Mexico. The only far island they have reached is Isla Providencia, Colombia, in the Caribbean (about 125 miles off the coast of Nicaragua). *A. collinsii* is here occupied by one or two species of obligate acacia-ants. In colonizing islands, the acacia must already be there when the founding ant queen arrives; however, the acacia probably has little chance of surviving to reproduction unless occupied by an ant colony. It will take a high rate of simultaneous colonization by both ants and acacias for establishment. *A. cornigera*, introduced as an ornamental into Cuba (and Florida) without ants, has not escaped to form a noticeable population. While this may be in part due to a lack of pollinators, the absence of obligate acacia-ants may also contribute.

Since agricultural man came on the scene (at least since 1200–900 B.C.—Coe et al., 1967), the

population structure of most species of swollen-thorn acacia has probably been grossly altered. The majority of species have greatly increased their local density, absolute population sizes, and thoroughness of geographic coverage by invading fields, pastures, and roadsides which now connect the natural disturbance sites that occur along rivers, streams, and lakes. This means that the populations now observed are operating with a genotype evolved in slightly to grossly different habitats, and the local barriers to gene flow (climax forest on hills and ridges) have in great part been removed.

Present-day populations of swollen-thorn acacias show distinct clinal variation in traits such as leaflet size, thorn size and shape, life form, seed-pod morphology, and Beltian body traits. Rather than being solely the result of extreme sensitivity to small linear environmental changes, these may be the consequence of the recently established genetic continuity between previously isolated populations on different drainage systems.

Humans have probably not severely altered the gross geographic range of swollen-thorn acacias by their activities. They have, however, served as efficient long-range-dispersal agents. Fruits of *A. cornigera* are eaten by Central American Indians and, with modern bus transport being commonplace, seedlings are sometimes found near bus stops several hundred miles from a known acacia population. Further, cattle are often trucked long distances in Central America, and cattle eat the pods of *A. cornigera* and others. There are pockets of *A. cornigera* around cattle corrals scattered through the northern part of the Yucatan Peninsula; the natural vegetation at these sites is normally occupied by *A. collinsii* (though *A. cornigera* appears native to local wet sites in Yucatan).

General Comments on Swollen-Thorn Acacia Taxonomy

A close examination of the taxonomic status of swollen-thorn acacias is warranted by the fact that (1) as many as 25 percent of the swollen-thorn acacias in some herbaria are incorrectly determined, (2) there are at least 32 synonyms for the 10 previously described species, (3) swollen-thorn acacias have never been treated with monographic thoroughness (though there are short discussions in Safford, 1910, 1914, 1915, 1922; Rudd, 1964;

Schenck, 1913; Janzen, 1967b), and (4) their species-level taxonomy has become so confused that it is currently nearly impossible to generate a detailed discussion of the mutualistic interaction in a comparative and evolutionary framework.

Examination of the distributions of the type localities on the range maps of each species of swollen-thorn acacia leads one to suspect what is shown by examination of the types, namely that most synonyms are the result of the taxonomist possessing a herbarium sheet from two widely separated portions of a species population but having no information on the clinal changes across the connecting part of the population. Further taxonomic difficulties were generated by the greatly differing thorns that may be found on a single plant. There is no evidence that we are dealing with many sibling species but rather that there is extreme geographic variation of several conspicuous vegetative traits. Finally, the more conservative (reliable) vegetative traits of swollen-thorn acacias have not generally been used as taxonomic characters.

The early parts of this study emphasized the location and delimitation of populations of swollen-thorn acacias in Central America. Once these populations were understood geographically and morphologically, then the type specimens of swollen-thorn acacias were associated with them in the herbaria. Since virtually all the variation encountered in this study was clinal, and since the clines showed little or no concordance with the subpopulations of a given species (being contiguous almost without exception), there is no basis for the designation of infraspecific Latin names. Fortunately, the breaks between species are clearly delimited by many morphological, behavioral, and ecological traits in the numerous areas of sympatry.

The species discussed here are clearly morpho-species, but all circumstantial and ecological evidence indicates that they are independent evolutionary units that do not normally exchange genetic information. The various species grow side by side over much of their ranges with almost no obvious hybridization, though ant-acacias may introgress with nonant-acacias on occasion (e.g., *A. hindsii* × *A. pennatula* (Schlect. and Cham.) Benth. and *A. hindsii* × *A. cochliacantha* Humb. and Bonpl. in western Mexico). Those species that have no range overlap with other swollen-thorn acacias are presumed to be distinct species because of the

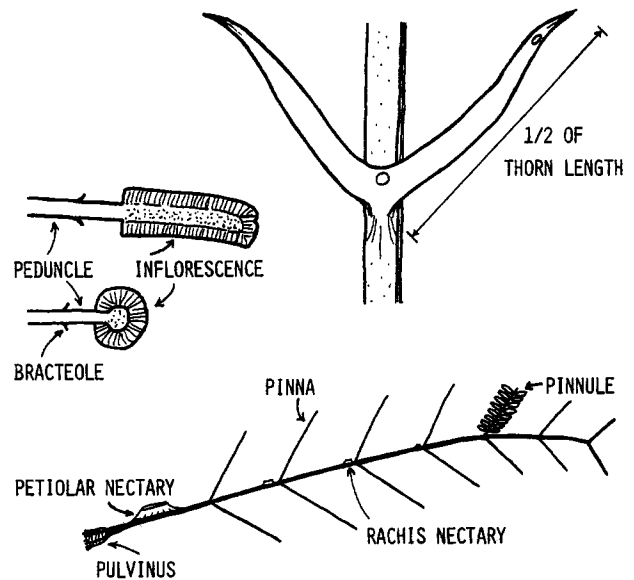


FIGURE 2.—Swollen-thorn acacia terminology.

many morphological and ecological differences between them and other acacia populations.

The total morphological variation within the populations of some of the widely distributed species (e.g., *A. cornigera*, *A. collinsii*, *A. hindsii*) is much greater than that within pairs of closely related species (e.g., *A. allenii* and *A. melanoceras*, *A. mayana* and *A. cornigera*). This, plus the impossibility of designating what might be called a "species-level" trait, prevents a uniform criterion for the designation of "species."

Swollen-thorn acacias are readily determined to species in the field, either in vegetative or sexual phases. In fact, it is easier in the field than from herbarium specimens. Because of this, only occasional voucher specimens were collected in this study. Since swollen-thorn acacias are generally recognizable even from a fast-moving car, continuous distribution records along roads were often obtained in this study and are plotted on the distribution maps as continuous data rather than as "spot localities" as are usually taken from herbarium specimens. In most parts of Central America, the total absence of swollen-thorn acacias for more than 5 km along a road or watercourse means that they are absent for reasons other than persistent attempts by humans to remove them. Their absence within areas of secondary vegetation of a few hectares in extent may be due to nonhuman

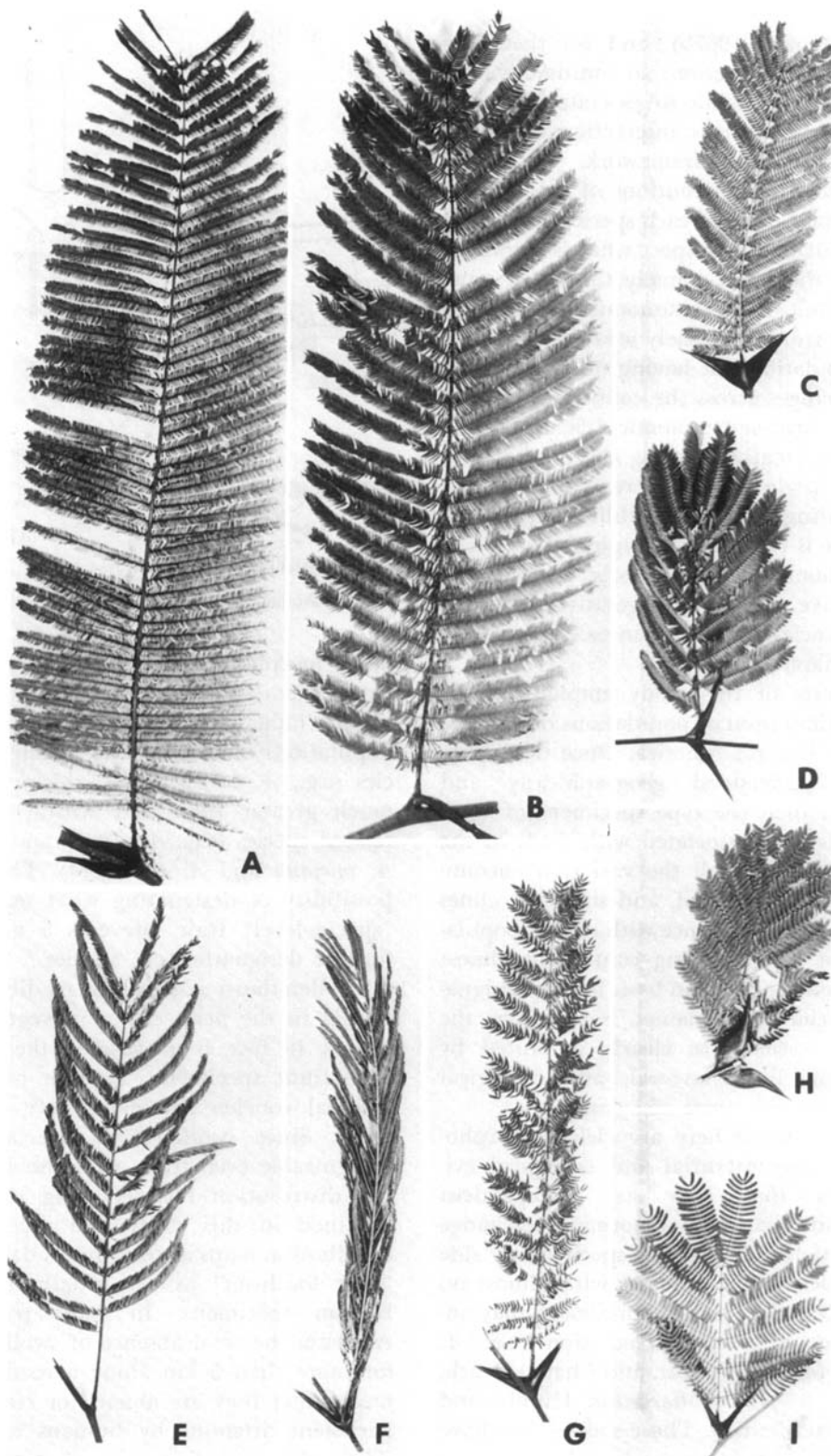


FIGURE 3.—Representative leaves subtended by type A swollen thorns: A, B, *Acacia cookii*; C, *A. hindsii*; D, *A. gentlei*; E, *A. ruddiae*; F, *A. globulifera*; G, *A. melanoceras*; H, *A. collinsii*; I, *A. cornigera*. (All photographs taken to same scale; the leaf of *A. cookii* in upper left-hand corner is 40 cm long.)



FIGURE 4.—Representative leaves subtended by type A swollen thorns: A, *Acacia allenii*; B, *A. mayana*; C, *A. chiapensis*; D, *A. sphaerocephala*; E, *A. chiapensis*. (Scale as in Figure 3.)

TABLE 1.—Meristic traits of two representative fully developed leaves subtended by type A thorns on lateral branches of occupied adult swollen-thorn acacias (mean for large samples are not presented since this would be a study in itself; these two leaf exemplars are judged to be representative by my own observations)

Species and thorn length (mm)	Total leaf length (mm)	Total number pinnae	Total number pinnules	Length longest pinna (mm)	\bar{X} length pinnae (mm)	\bar{X} length pinnules (mm)	\bar{X} width pinnules (mm)	Total pinnules on longest pinna	Number of nectaries on rachis	Number of nectaries on petiole
<i>allenii</i> (55+56)	383	34	1170	98	70.7	10.53	3.08	47	19	4
<i>allenii</i> (50+49)	401	38	1630	121	81.1	10.30	2.94	63	28	3
<i>hindsii</i> (41+42)	178	42	1924	47	36.3	4.46	1.58	56	21	0
<i>hindsii</i> (36+38)	150	42	1912	42	35.6	4.17	1.26	52	21	0
<i>cookii</i> (51+48)	404	96	12242	69	61.5	4.04	0.60	140	54	0
<i>cookii</i> (67+71)	367	58	7013	87	77.5	6.82	1.00	136	28	1
<i>mayana</i> (51+48)	225	20	1049	100	72.5	10.90	1.93	66	9	1
<i>collinsii</i> (46+48)	101	20	588	42	33.6	6.39	1.89	34	1	3
<i>collinsii</i> (42+43)	101	22	632	47	36.6	8.18	2.22	38	0	4
<i>gentlei</i> (48+48)	100	14	784	65	55.0	8.45	1.98	62	4	1
<i>gentlei</i> (38+39)	106	16	988	58	52.1	8.53	1.93	64	8	2
<i>globulifera</i> (43+44)	252	48	4007	62	49.2	5.51	1.00	89	8	4
<i>globulifera</i> (39+33)	228	52	4080	62	46.9	5.14	1.00	96	14	2
<i>cornigera</i> (45+47)	110	20	848	54	43.2	7.09	1.61	52	1	1
<i>cornigera</i> (43+42)	81	12	536	55	50.5	7.26	1.82	48	4	1
<i>ruddiae</i> (no thorn)	205	38	3200	67	61.4	5.77	1.18	88	20	2
<i>ruddiae</i> (no thorn)	258	74	8180	62	47.6	2.87	0.80	144	37	0
<i>chiapensis</i> (48+43)	288	74	7644	63	46.7	2.83	0.77	130	35	4
<i>chiapensis</i> (79+75)	190	42	2955	48	39.2	4.46	1.00	88	0	14
<i>sphaerocephala</i> (63+63)	155	26	952	54	36.7	6.34	1.90	46	0	1
<i>sphaerocephala</i> (54+52)	149	24	1072	53	46.1	6.23	1.76	52	0	1
<i>melanoceras</i> (36+34)	255	48	2134	49	38.9	4.90	1.12	54	25	18
<i>melanoceras</i> (32+45)	237	46	1592	35	28.8	5.46	1.10	42	24	21

factors, but more likely is due to repeated cutting immediately followed by burning. Relative changes in density are especially susceptible to human activity. It is therefore very difficult to determine what climates and/or habitats are "best" for swollen-thorn acacias. Cutting, burning, and grazing patterns up to at least 20 years previous may grossly influence both density and presence of swollen-thorn acacias. There are even cases of heavy insecticide use, where the ants, and apparently most other insects, have been killed and the unoccupied acacias are relatively healthy (e.g., *A. hindsii* in the Leon area of western Nicaragua, along cotton field edges).

Some of the herbarium specimens collected during this study have been deposited in the National Museum of Natural History of the Smithsonian Institution (US), Gray Herbarium (Harvard) (GH), New York Botanical Garden (NY), University of California at Berkeley (UC), Missouri Botanical Garden (Mo), Field Museum of Natural History (F),

University of Michigan (MICH), and University of Mexico (MEXA). The majority have been deposited as intact series at the Field Museum.

Despite their spectacular association with ants, swollen-thorn acacias have been poorly collected and generally receive little attention in regional floras. They are not famous for medicinal uses, which is not surprising since the ants are their "chemical" defense system. Collectors consistently avoid them (or more properly, avoid their ants). Those parts of the plants that are collected tend to be old foliage and branches, which are poorly patrolled by the ants and often unrepresentative of the foliage of the plant as a whole. The branches with well-developed swollen thorns, especially those with very large thorns on short laterals, are almost entirely missing from herbaria, presumably because they do not press easily and usually add a large number of ants to the plant press. This produces the illusion, when examining herbarium material, that the thorns of swollen-thorn acacias are gen-

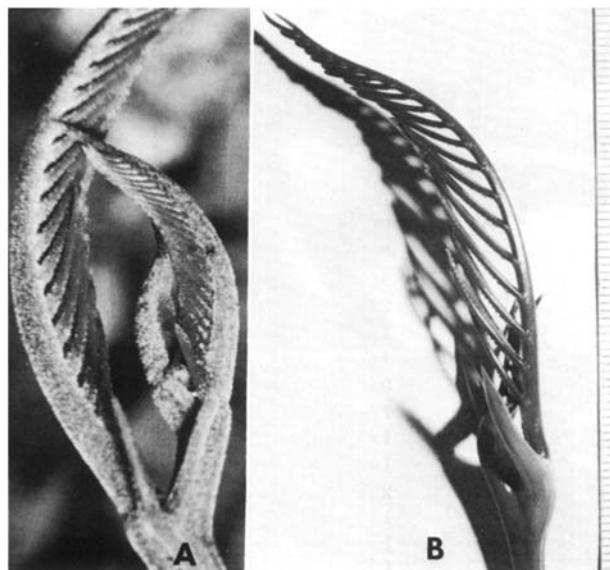


FIGURE 5.—Shoot tip from end of an elongating healthy branch: A, *Acacia cookii* from the Cardenas, Tabasco, Mexico, region; B, *A. allenii* from the Rincon, Osa Peninsula, Puntarenas Province, Costa Rica, region.

erally small, monomorphic, and without much geographic or intraplant variation.

Wheeler (1942) reviewed the generally undistinguished presence of swollen-thorn acacias in the literature prior to 1930. *Acacia cornigera* was the first to be described (Linnaeus, 1753) as *Mimosa cornigera*, but since it was based on a European greenhouse specimen, the ant interaction was not discussed at that time. The last species to be described in the current literature, *A. mayana* in 1937, is the rarest and most restricted of the swollen-thorn acacias. The two species described in the present paper (*A. allenii*, *A. ruddiae*) had been collected earlier, but the herbarium specimens were misidentified.

Herbarium specimens are often misleading in respect to the ant-acacia interaction. There is generally no way of knowing if the specimen is from a heavily occupied acacia, one that has recently lost its ant colony, or one that was never occupied. The presence of ant-entrance holes in the thorns are not reliable indicators of occupation because founding queens may have made them and because, once made, they last as long as the thorn (2 or more years). Occupied acacias (those with an ant colony large enough to patrol the tree) have fully devel-

oped lateral branches, short lateral branches with very large thorns, inflorescence-bearing branches, etc. Unoccupied ones have stunted branches with short internodes, smaller leaves, fewer inflorescences at times only partial damage and shading; directly, they are not a product of the ants.

From 60 to 95 percent of the mature swollen-thorn acacias of each species examined in this study were occupied by obligate acacia-ants. The exceptions are *A. ruddiae*, which is never occupied by obligate acacia-ants, and *A. sphaerocephala*. Where the latter species grows on the dunes south of Veracruz, Veracruz, Mexico, it is unoccupied within range of heavy wind and salt spray on leading dunes, but tenanted by *Crematogaster*. Those plants tenanted by other ants (they often use the hollow thorns for nest sites as they would use hollow branches on other trees) are unoccupied from the plant's viewpoint. The statements about vegetative characters in this paper are drawn from healthy and occupied acacias. Numerically, the majority of any swollen-thorn acacia population in repeatedly disturbed sites is made up of unoccupied seedlings and sucker shoots, but these are almost never noticed or collected because they are less than 50 cm tall and below the general weed canopy (mature acacias are usually emergent). These small plants are often much more difficult to identify to species than are the adults, owing to their convergence in leaf and thorn characteristics.

The swollen-thorn acacias did not escape from Britton and Rose's (1928) attempts to split the genus *Acacia* into more manageable subunits. The genera *Tauroceras* and *Myrmecodendron* were proposed but are not retained in the present study because they represent only one of the many ways the 12 species could be arbitrarily grouped, and thus add little to the understanding or ease of manipulation of the morphological affinities within the swollen-thorn acacias.

Perhaps of more importance in subgeneric taxonomy, the evolutionary affinities of the 12 species are not clear in most cases, and their speciation may have involved some very interesting complications. Despite their possession in common of many unique vegetative traits—Beltian bodies, swollen thorns, etc.—the swollen-thorn acacias appear to be a polyphyletic group within the genus *Acacia*. Pairs or triplets of species appear to be more similar in the majority of their traits to acacia species not

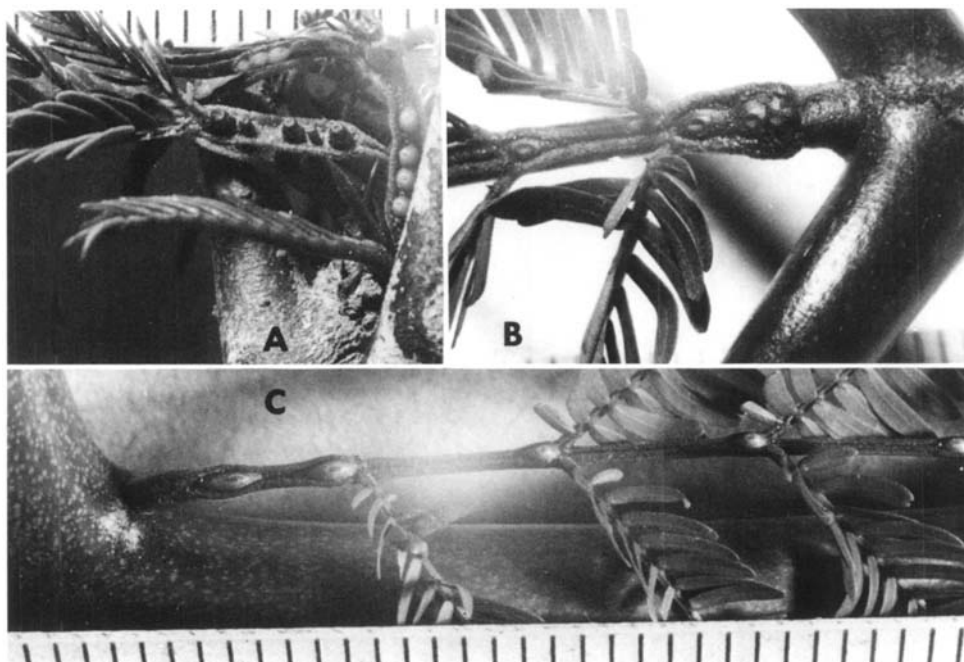


FIGURE 6.—Variation in nectary morphology on mature *A. globulifera* plants (and see Figure 7c): A, maximal number of petiolar nectaries, as occasionally found on old trees in tufts of leaves not subtended by swollen thorns (Honduras, site 26); B, maximal condensation of the petiolar nectary area, as characterizes leaves from type A thorns at high (cold) and dry areas (Honduras, site 28); C, maximal attenuation of the petiolar nectary area, as characterizes leaves from type A thorns on rapidly growing 2–4-year-old trees in riparian (wet) sites (Honduras, site 26).

Acacia collinsii sometimes has nectaries similar to Figure B, and *A. gentlei* sometimes has nectaries similar to Figure C (and see Figure 7).

involved in mutualism with ants than they are to other swollen-thorn acacias. Even the designation of subgenera based on these small groups seems to have little usefulness (e.g., *Tauroceras* would contain *A. cornigera*, *A. sphaerocephala*, and *A. mayana*).

The possibility of a polyphyletic origin for swollen-thorn acacias is especially noticeable if only the reproductive parts are compared. Three explanations are available. The first, and least likely in view of dissimilarity of sexual reproductive parts, is that a single swollen-thorn acacia evolved, and by classical speciation patterns split into the 12 modern populations (species) discussed in this paper. This carries the implausible implication that floral and fruit morphology are as evolutionarily unconservative as the vegetative parts of the plant, and that the similarity of the flowers and fruits of swollen-thorn acacias to those of nonant-acacias is simple convergence. The second possibility is that

each cluster of similar swollen-thorn acacias had an independently evolved, swollen-thorn acacia parental species. Here, the vegetative similarity between the clusters would be convergence selected for by the requirements of the mutualistic interaction. This also seems unlikely since it requires that a complex interaction must have arisen several times independently. The third hypothesis, and the one that I favor, is a combination of the two above by the mechanism of introgression. This would yield a reticulate phylogeny. Starting with one species of swollen-thorn acacia, new acacia species become part of the system by introgression of the set of ant-acacia traits into their genotype. The outcome is two species of swollen-thorn acacia, one of which (the donor) is probably not much changed while the other may change its ecology considerably since it now possesses a very different, and in some ways more effective, set of defenses against herbivores and competitors.

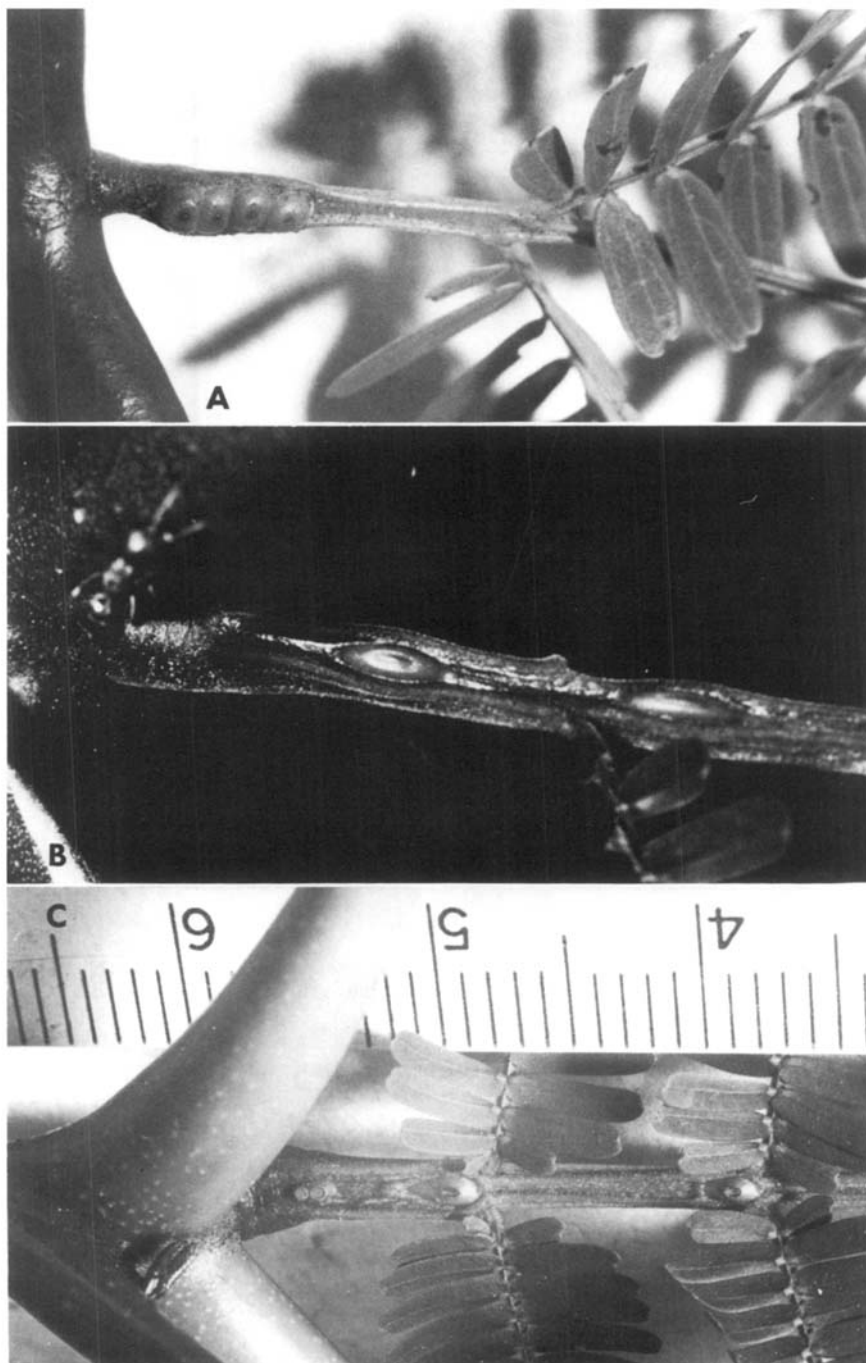


FIGURE 7.—A, Representative petiolar nectary on a leaf subtended by a type A thorn of *A. collinsii* from the moister end of the species' range; the number of nectaries may range from 1-4 and there never are rachis nectaries (Mexico, site 15). B, Representative petiolar and rachis nectary of *A. gentlei* on a leaf subtended by a type A thorn (Guatemala, site 21). C, Representative petiolar and rachis nectary of *A. globulifera* on a leaf subtended by a type A thorn (Guatemala, site 13).

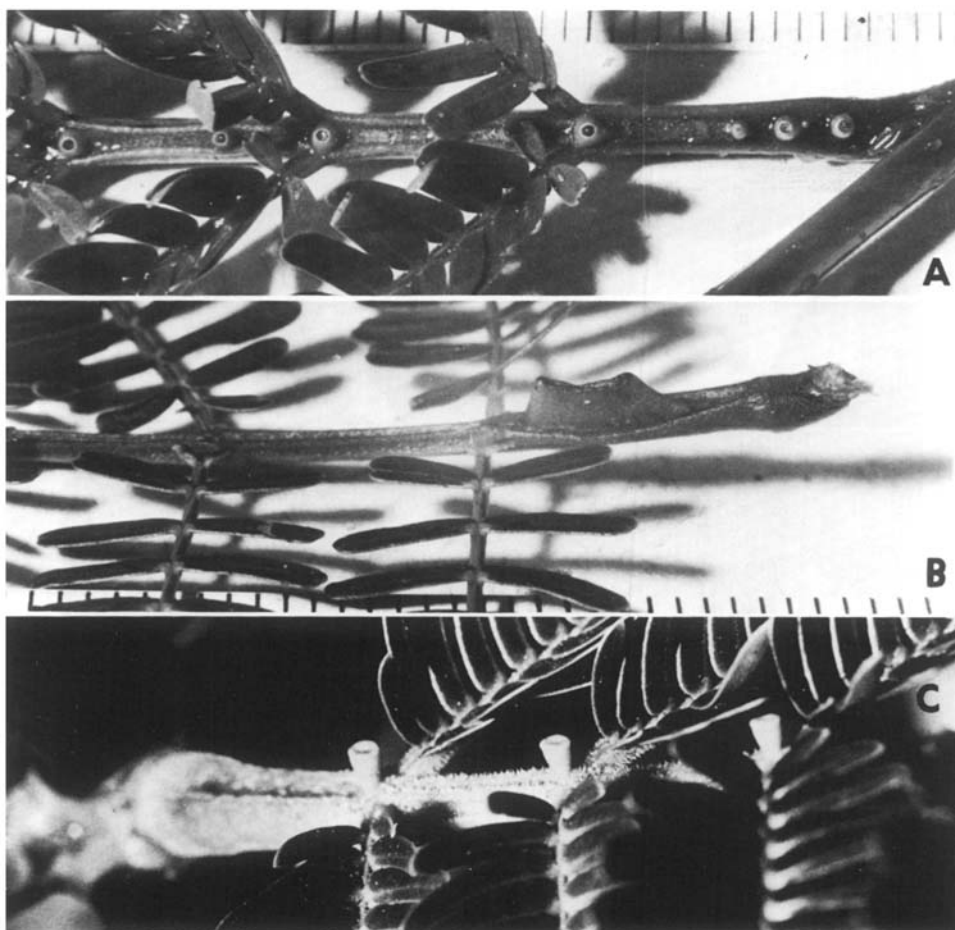


FIGURE 8.—A, Representative petiolar and rachis nectaries on leaf from type A thorn of *A. hindsii*; the number and size of rachis nectaries is variable (Mexico, site 17). B, Representative petiolar nectary of *A. cornigera*; on rare occasions there are two petiolar nectaries and a rachis nectary (Mexico, site 6). C, Representative petiolar and rachis nectaries on leaf from type A thorn of *A. ruddiae*; nectaries vary greatly in height (Guatemala, site 8).

This type of "speciation" (note that there is no net increase in the number of species of *Acacia*) will almost certainly result in a range extension for the ant-acacia interaction, and perhaps lead to contact with, and subsequent incorporation of, other nonant-acacia species. It appears to be occurring now between *A. hindsii* and *A. pennatula* (see later discussion of hybrids). This process, coupled with the usual kind of speciation, could easily lead to the present 12 species.

Materials, Methods, and Terminology

A bit of jargon has evolved in the discussion of swollen-thorn acacias and needs brief review here

(also see Janzen, 1967b). An "occupied" swollen-thorn acacia is one that has an ant colony large enough to patrol its surface with sufficient intensity such that the acacia will gain or remain in moderate to excellent health. An unoccupied acacia may therefore have founding queen ants in its thorns or have a large colony of an unprotective ant species tenanted its thorns. The "basal circle" is that circular patch of bare ground directly under a swollen-thorn acacia that results from the ants attacking seedlings and sucker shoots beneath the acacia. A "multiple-queen" ant colony is of one of the species that has egg-producing queens in many of the tree's thorns, in contrast to having only one

queen per colony. Multiple-queen ant colonies tend to be associated with swollen-thorn acacias that naturally occur as dense thickets, such as *A. hindsii* in western Mexico.

The stipular thorns of Neotropical swollen-thorn acacias are not galls in any sense of the word. Incidentally, despite the caution displayed by Hocking (1970), the enlarged thorns of African acacias are not galls either, as shown by their full development in North American greenhouses. "Type A" thorns are those more ordinary-appearing thorns to be found on long, lateral branches and on the central axis; "type B" thorns are the large and often convoluted thorns found on greatly shortened lateral branches. See Figure 2 for other morphological characteristics.

For precise localities, the lists under each species should be referred to, rather than to the distribution maps. Localities are listed under the state or province containing a reference town. The projected ranges on the distribution maps are just that; they are based on my intuition and the general ranges of other plants from the same habitats. They are probably overall correct in general, but cannot be expected to be accurate in detail. The key collection localities are given in the distribution figures as sites or as continuous distributions along roads (solid broad lines). Where my own distribution records overlap those obtained from herbarium specimens, to avoid redundancy I usually have not given the herbarium data. The site numbers are unique only within a species; for example, site 16 for *A. cornigera* is not the same locality as site 16 for *A. hindsii*. While some data are given as to the reproductive condition of the plants on the dates of observations or collection (fl = inflorescences, gp = immature fruits, mp = mature fruits), little reliance should be placed on these data in determining sexual timing owing to the collectors' habit of seeking out plants in flower and fruit but out of phase with the remainder of the population.

All scales shown in photographs are in millimeters unless the caption indicates otherwise.

In the terminology of this paper, "isotypes" are collections made from the same plant at the same time, while the "holotype" is only that herbarium sheet with the type on it. "NC" is used to signify a plant examined in the field but not collected. While Safford's descriptions sometimes were not in Latin, they were published before 1 January 1935 and are

still recognized as valid in accordance with Article 36 of the *International Code of Botanical Nomenclature* (1972).

General Morphological Traits

The leaves of swollen-thorn acacias differ from those of other Central American acacias primarily in being larger overall and having larger leaflets; in short, the leaves extend far past the tips of the swollen type A thorns and can be easily removed from the tree without contacting the thorns. On any given tree the leaves vary strongly in size as a function of season (smaller leaves being produced during the dry season) and part of the tree (smaller leaves being subtended by type B thorns). However, if only the leaves produced during the rainy season and subtended by fully developed type A thorns on lateral branches from healthy trees are considered (Figures 3 and 4, Table 1), there are diagnostic interspecific differences in leaf and leaflet size and shape. Not surprisingly, those species from the driest habitats have the smallest leaves (e.g., *A. collinsii*, *A. cornigera*, *A. hindsii*). There may be considerable variation within a species over its range on the parameter of leaf size. In Figure 3, a leaf from *A. cookii* at the northern and dry end of its range in the Cardenas, Tabasco, Mexico, area (Figure 3A) may be compared with a leaf from the wet end of the range in the Puerto Barrios, Guatemala region (Figure 3B). One species, *A. chiapensis*, shows strong variation at a given site as well, as earlier discussed for the Temascal, Oaxaca, Mexico, area (Janzen, 1967b); this variation (Figures 4C and 4E) is probably an expression of introgression of *Acacia macracantha* and *A. cornigera* genes into the *A. chiapensis* population in this area (and see Rehr et al., 1973).

The shoot tips on elongating branches of swollen-thorn acacias are unprotected physically (as well as chemically) when compared with other plants. The shoot tip of *A. allenii* in Figure 5B is representative of swollen-thorn acacias in being free of hairs or defensively sticky compounds and in having the newly expanding leaves quite separate and exposed. They are extremely brittle and easily broken, reminding one of the inner shoot of a celery plant. The shoot tips of *A. cookii* (Figure 5A) and *A. ruddiae* are more like those of nonant-acacias, with the new leaves clasped tightly around each other



FIGURE 9.—Ontogenetic development of nectaries of *A. collinsii*: A, characteristic seedling leaf produced at about the 20th node and often not subtended by swollen thorns; B, leaf subtended by type A thorn on juvenile but well occupied plant; C, leaf subtended by type A thorn on relatively short lateral branch in crown of mature acacia.

and covered with a dense pile of short stiff hairs. In the northern part of its range, *A. cookii* is sometimes unoccupied, and in this area the difference is more pronounced than in the Puerto Barrios, Guatemala, region where the shoot tips appear more like those of a regular swollen-thorn acacia.

The extrafloral nectaries on the petiole and rachis of swollen-thorn acacia leaves are one of the most useful and reliable characters for species-level determinations. While extrafloral nectary morphology may vary strongly in detail from area to area for a few species (the most extreme case being *A. globulifera*, Figure 6), for the majority of species there is little geographic variation and at any given site the morphology is quite constant; it may be the only way to distinguish between

young plants of species that are easily separated as adults on the basis of thorn shape. Since the entire function of the extrafloral nectaries appears to be physiological—excreting sugar for the ant colony—they are not under strong pressure for adaptive external morphologies; much as with the thorns, I suspect that numerous different kinds of external morphology may be equally functional and that the interspecific variation is primarily due to interspecific differences in the adaptive peaks from which the different swollen-thorn acacia genotypes were derived. The extrafloral nectaries in Figures 7 and 8 and in Table 1 are representative of the gamut of interspecific variation. As a seedling grows, there is a progression of extrafloral nectary development (young sucker shoots from cut stumps tend to have

FIGURE 10.—A, Cross section of a 5-year-old main trunk of *A. hindsii* (Mexico, site 17). B, Conspicuous lenticels on 6-month-old branch of *A. ruddiae* (Costa Rica, site 5).

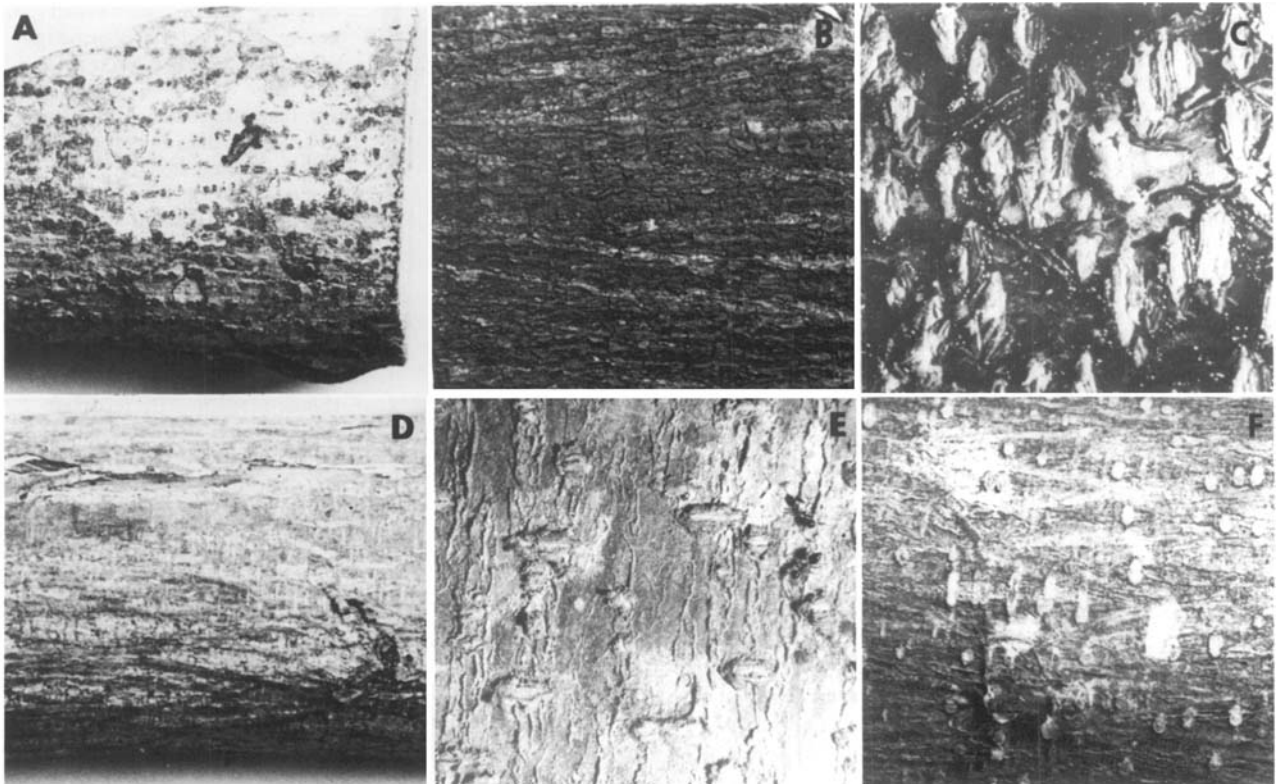
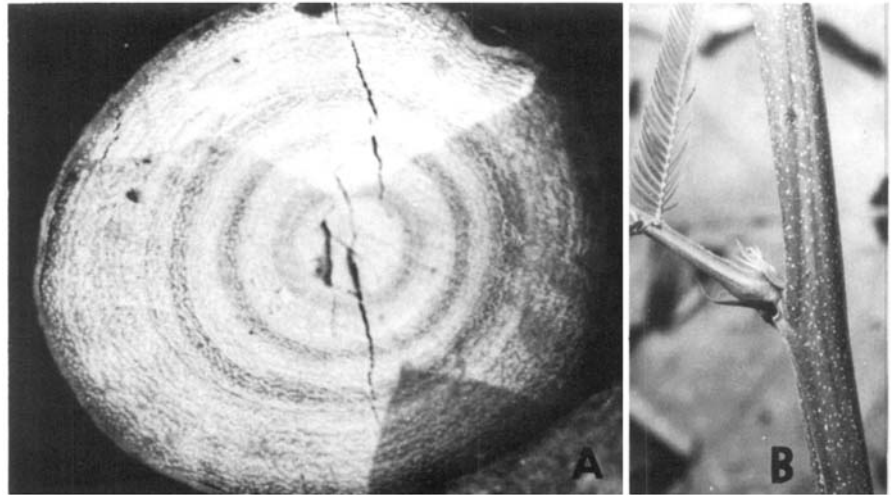


FIGURE 11.—Representative bark topography of 2-5-year-old main trunks of swollen-thorn acacias: A, *Acacia cornigera* (Mexico, site 26); B, *A. gentlei* (Guatemala, site 11); C, *A. chiapensis* (Mexico, site 9); D, *A. hindsii* (Mexico, site 15); E, *A. ruddiae* (Costa Rica, site 5); F, *A. allenii* (Costa Rica, site 5).

TABLE 2.—Swollen-thorn characteristics as based on fully developed thorns from occupied adult swollen-thorn acacias

Species	Thorn surface contour	External pubescence	Knobby projection on inner thorn wall at base	Thorn shape in cross section near base	General thorn configuration
<i>mayana</i>	smooth & slight ridges	none	present	elliptical with 2 sharp elongate projections	flat V that is bent downward slightly in larger thorns; never recurved around stem
<i>gentlei</i>	smooth	none	absent	round to slightly elliptical	flat V, slightly distorted and bent irregularly in the plane of the V; thorn may be closely appressed to stem longitudinally and partly bent around it
<i>globulifera</i>	smooth	none	absent	round	flat V, slightly to strongly curved downward; never recurved around stem
<i>melanoceras</i>	smoothed longitudinal ridges	none	present	round to elliptical	flat V, slightly curved downward in larger thorns
<i>cookii</i>	smooth	heavy	absent	round	heavily warped U, asymmetrical with one side or both twisted around the stem partly or fully; asymmetry highly regular in pattern
<i>ruddiae</i>	smooth & slight ridges sometimes	very light	absent	round to slight ellipse	flat V, tendency for one thorn half to be larger than the other; never recurved about stem
<i>chiapensis</i>	smooth	none	absent	round	flat V that may be bent slightly downward in very large type B thorns
<i>sphaerocephala</i>	smooth	none	absent	round	flat V; never recurved around the stem
<i>cornigera</i>	smooth	none	absent	round to slightly elliptical	flat V or U, bent upward or downward to various degrees; type B thorns often heavily recurved around stem, at right angles to it
<i>collinsii</i>	smooth	none	usually present	round to elliptical to very elongate and thin	flat V that may be very open and curve around the stem at various angles
<i>allenii</i>	smoothed longitudinal ridges	none	present	round to elliptical	flat V; never recurved around the stem
<i>hindsii</i>	smooth to faint smoothed longitudinal ridges	none	absent	elliptical to very elongate and thin	flat V; never recurved around the stem

foliar nectaries and other leaf traits essentially identical at the qualitative level to those of the adult crown). A characteristic progression is displayed in Figure 9; in general, with increasing age of the plant, the number of nectaries increases, their size increases, the distance between the first pair of pinnae and the thorn decreases, and nectar flow increases.

Swollen-thorn acacias are more "treelike" than other Central American acacias in that they tend to have more of the growth concentrated in the central axis (see figures in Janzen, 1967b). The wood is harder than that of most fast-growing tropical trees and generally displays obvious annual growth rings (Figure 10A); the slower wood production coincides with the dry season and, in areas with almost no dry season, the rings are much more difficult to see if they are present at all. The tree

bark (Figure 11; Table 5) is thin and often greenish; presumably considerable photosynthesis occurs just under the bark. There are well-developed lenticels on young branches (Figure 10B), and many of these persist on trunks 2-6 years old (e.g., Figures 11A, C, E, F).

The swollen thorns on adult acacias are very distinctive at the species (and sometimes local-population) level, but the differences are difficult to quantify and incorporate in a dichotomous key. Tables 2 and 3 attempt to organize some of these differences, but for a good feeling for the differences the reader must also compare the thorn photographs associated with each species account. Thorn color is perhaps one of the most useful diagnostic species-level traits at a given site, but varies strongly with location and the plant's history. Damage to green thorns may produce premature darkening of the

TABLE 3.— *Color of swollen thorns for seasoned and undamaged types A and B thorns from living branches on occupied adult swollen-thorn acacias*

<i>Species</i>	<i>Thorn color on adult plant over entire range</i>	<i>Usual color change from 50 cm to adult plant</i>	<i>Color at any one site among adult plants</i>	<i>Color among seedlings over entire range</i>	<i>Color clines where obvious</i>
<i>allenii</i>	very dark brown, nearly black; trace of red on green thorns	none	no variation observed	as adult	plants in full sun have slightly browner thorns than those in full shade
<i>cornigera</i>	dark brown, nearly black to ivory white; bicolor beige + ivory, brown + ivory	beige to dark brown; white to ivory	beige + brown; brown + very dark brown; ivory + brown	white to brown, usually beige	ivory in dry and hot lowlands to very dark brown in wet upper elevations; ivory in dry lowlands to brown in wet lowlands
<i>collinsii</i>	brown to ivory; darker thorns with reddish cast	beige to brown	beige + brown; beige + ivory	white to beige to brown	none obvious
<i>hindsii</i>	ivory to beige to black	beige to black; white to ivory; beige to brown	beige + black; ivory + beige; brown + black	ivory to beige, usually brown	lightest thorns in driest sites but black thorns there also; black thorns most common at low elevations, light at high elevations
<i>melanoceras</i>	very dark brown, nearly black; no trace of red on green thorns	none	no variation observed	as adult	none obvious
<i>gentlei</i>	red to brown to very dark brown	brown to reddish; light brown to dark brown	red + dark brown	reddish brown to brown	none obvious

TABLE 3.—Color of swollen thorns for seasoned and undamaged types A and B thorns from living branches on occupied adult swollen-thorn acacias—continued

Species	Thorn color on adult plant over entire range	Usual color change from 50 cm to adult plant	Color at any one site among adult plants	Color among seedlings over entire range	Color clines where obvious
<i>globulifera</i>	brown to olive to bicolor brown ivory and ivory+black	bicolor brown+ ivory; brown to white; white to black	brown to black to bicolor brown+ ivory	bicolor brown+ ivory; brown with white thorn tips	none obvious except that wet sites appear to have the darkest thorns
<i>chiapensis</i>	dark brown to very dark gray reddish cast to green thorns	none	no variation observed	dark brown to very dark gray	none obvious
<i>ruddiae</i>	dark brown to black; reddish cast to green thorns	none	no variation observed	dark brown to black	none obvious
<i>mayana</i>	very dark brown	none (seedling unknown)	no variation observed (only one plant known from each site)	as adult? (seedling unknown)	none obvious
<i>sphaerocephala</i>	dark brown to ivory; bicolor brown+ beige, black or very dark brown+ ivory; yellow	none	brown to ivory; bicolor dark brown+ ivory to yellow	usually cream to beige	darkest in wettest sites, most strongly bicolor inland and solid color near coast
<i>cookii</i>	dark brown to dark red	none	dark brown to dark red	as adult	none obvious

thorn wall. The death and drying (seasoning) of the thorn wall proceeds from tip to base, often resulting in temporarily bicolor or tricolor thorns; in some areas, however, all thorns are bicolor irrespective of age. The thorns of all species turn lighter with age and bleaching by the sun. There is likely to be some adaptive significance to thorn color in the context of optimizing the internal thorn microclimate for the ants. In addition to detailed swollen-thorn morphology, the placement of the thorns on the branches varies from species to species; when looking down the long axis of a branch, the thorns either radiate out in all directions or lie in two parallel planes, one on each side of the branch. This appears to be a by-product of leaf placement, rather than being adaptive in the context of the thorns themselves. In general, the species of dry regions tend to have small leaves—and thorns—radiating outward from all sides of branches that are often more vertical than horizontal (e.g., *A. collinsii*), while those of wetter areas often have the leaves in

a more or less horizontal plane from more horizontal branches. There are conspicuous differences among the species as to the proportion of leaves lacking swollen thorns (as in Figure 10B) but quantitative data are not available on this parameter. This parameter is also greatly confused by strong variation in swollen-thorn production as a function of tree age and health; in general, seedlings and senescent trees produce the fewest swollen thorns, and leaves produced during the dry season often lack swollen thorns. Though not discussed here, there is moderate interspecific and intraspecific variation in thickness of the thorn wall, thorn-wall hardness, longitudinal fiber orientation in the thorn wall, insulating quality of the thorn wall, point of attachment of the leaf to the thorn, ease of thorn removal, and rates of natural thorn shedding.

Healthy swollen-thorn acacias produce large numbers of bright yellow inflorescences during a short part of the dry season. They are either elongate cylindrical (Figure 12) or spherical (Figure 13) and

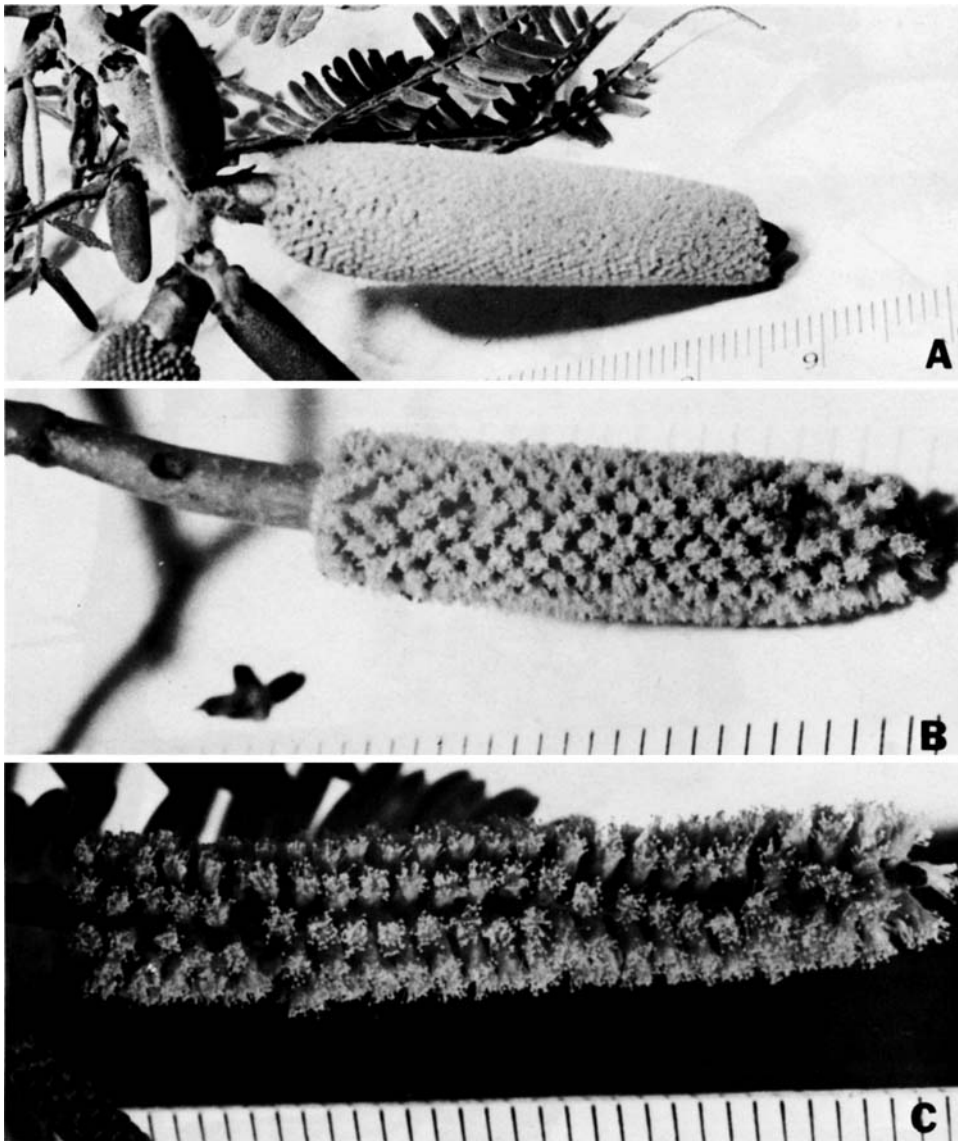


FIGURE 12.—Swollen-thorn acacias with elongate inflorescences: A, *Acacia cornigera* (Honduras, site 63); B, *A. collinsii* (Mexico, site 15); C, *A. hindsii* (Mexico, site 16).

composed of many individual florets (Table 4). Pollinators—pollen-gathering bees—generally move around over the surface, scraping off pollen with their legs; there is no evidence of nectar production. Those inflorescences that are pollinated are retained with their very small and immature pods through the following rainy season, but only a small fraction of the inflorescences are retained. Presumably the plant produces a great number of inflorescences to attract pollinators, and then sheds what it does not have sufficient energy to mature. *A.*

cornigera and *A. collinsii* have produced large quantities of flowers in greenhouses at the University of Kansas and the University of Chicago.

Swollen-thorn acacias differ from all other Central American acacias (and probably from the remainder of the genus) in having bird-dispersed seeds (Janzen, 1969c). The seeds are enclosed in a sweet white to yellow pulp or aril, and in all species except the *A. cornigera*, *A. sphaerocephala*, and *A. mayana* group the pod opens to expose the pulp when ripe (Figure 14; Table 5). Presumably this

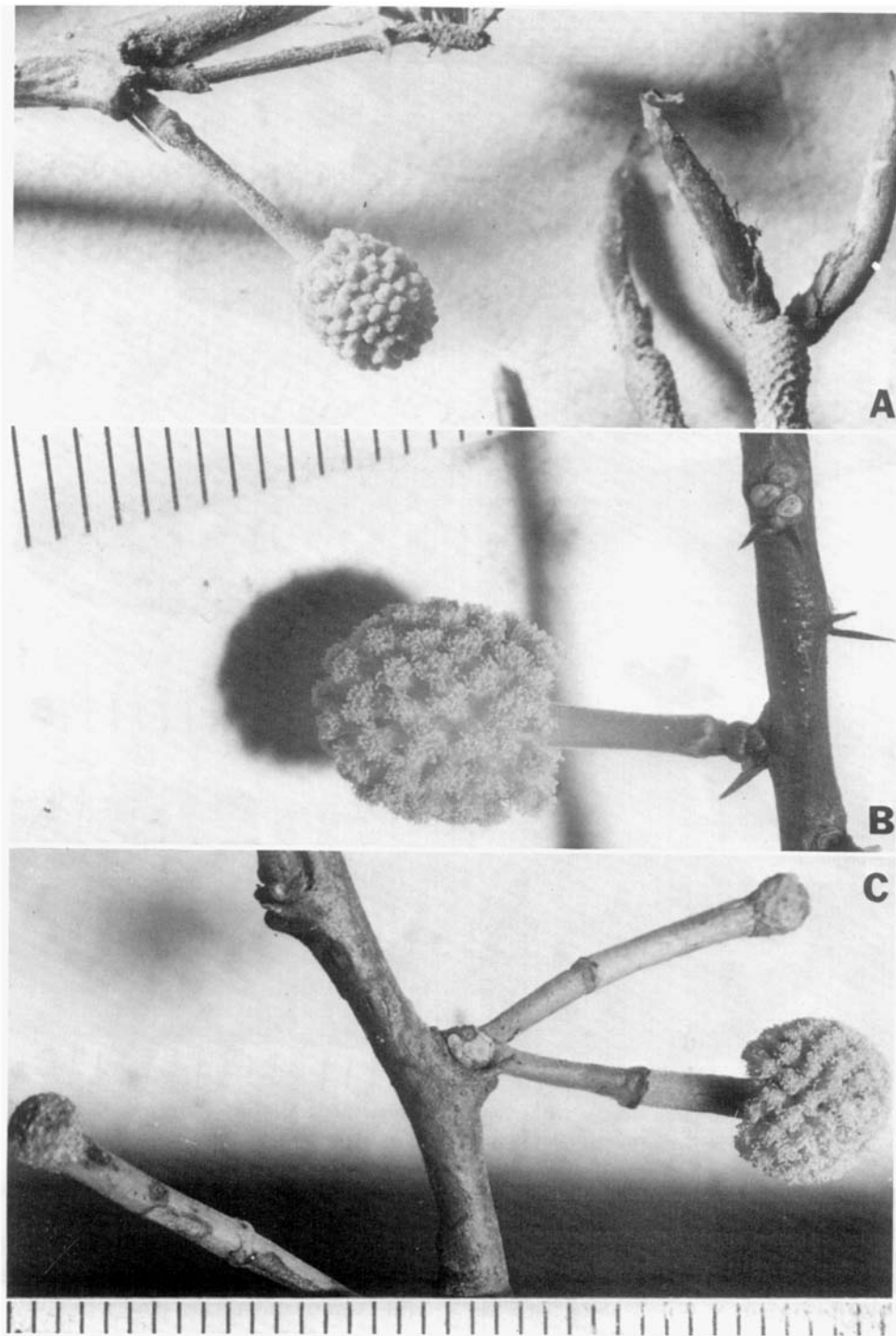


FIGURE 13.—Swollen-thorn acacias with spherical inflorescences: A, *Acacia globulifera*, florets unopened; two immature pods on receptacle on far right (Honduras, site 28); B, *A. melanoceras* (Canal Zone, site 6); C, *A. allenii* (Costa Rica, site 2).

TABLE 4.—Meristic parameters for inflorescences from occupied adult swollen-thorn acacias.

Species	General shape of inflorescence	Infl. max. diam. (mm)	Infl. max. length (mm)	Range infl. length (mm)	Peduncle length (mm)	Range peduncle length (mm)	Number florets this infl.	Distance from bracteole to infl. base (mm)	Range sexual branchlet length (cm)	Infl. per axil of sexual branchlet	Infl. bearing axils per sexual branchlet
<i>collinsii</i>	elongate	4	17	14-20	12	11-13	227	10	5-14	3-6	5-8
	cylinder	3.5	17.5	"	10	"	222	8	"	"	"
		4.5	26	22-26	16	14-18	301	12	2-3	2-3	5-6
<i>mayana</i>	terminally tapered cylinder	3.5	23	20-25	8	13-17	283	5.5	4-13	3-5	4-8
		5.0	30	25-34	3	1-4	1003	2	13	1-2	20
		4.5	46	40-50	10	5-12	1408	2	5-15	1	21
<i>gentlei</i>	elongate	4.0	23	20-24	14	8-12	533	8	2-14	1	4-15
	cylinder	3.8	21	"	8	"	534	5	"	"	"
		4.0	28	26-28	14	10-15	494	8	6-9	1	4-10
		4.0	29	"	15	"	519	10	"	"	"
<i>globulifera</i>	globular	5.5	5	4-5	6	6-12	69	6	1-9	2-5	4-11
		5.5	5	"	12	"	124	12	"	"	"
		?	?	?	12	10-12	?	12	8-22	2-5	10-20
<i>melanoceras</i>	globular	5	5	4-5	3	3-6	54	1	10-20	3-5	29-36
		5	5	"	6	"	117	1	"	"	"
<i>cookii</i>	globular	9	9	9-10	37	26-38	537	18	85-180	37-86	16-20
		6.5	6.5	6-7	8	8-18	105	4	10-23	25-46	5-18
<i>ruddiae</i>	globular	6	6	5.5-6.5	9	6-10	198	3	4-12	3-8	2-4
		6	6	"	9	"	182	3	"	"	"
<i>chiapensis</i>	globular	6.5	6.5	5.5-7.0	18	16-20	124	5	15-30	35-60	10-15
		6	6	"	20	"	120	3	"	"	"
<i>sphaerocephala</i>	nearly globular	7	11	10-14	12	8-12	340	10	2-18	3-4	2-12
	cylinder	7	10	"	12	"	319	10	"	"	"
<i>hindsii</i>	elongate	6	27	25-36	20	14-22	153	13	10-23	5-7	8-13
	cylinder	6	26	"	20	"	142	13	"	"	"
<i>cornigera</i>	slightly tapered	8	22	15-23	5	1-10	1112	4	5-20	1-4	4-13
	tylinder	9	28	"	6	"	992	5	"	"	"
<i>allenii</i>	globular	5	5	4-5	3	3-6	65	2	3-15	20-40	2-10
		5	5	"	7	"	91	3	"	"	"

difference reflects the ease with which birds can enter the crown and area beneath an occupied swollen-thorn acacia, as contrasted to mammals which are much more bothered by the ants. The pods of swollen-thorn acacias are very diagnostic at the species level except within the *A. cornigera* group. *A. collinsii* displays the most extreme geographic variation in pod morphology of all the species, ranging from very short and linear pods with thick walls in the drier parts of Panama to much longer, curved, and thin walls in Mexico and Guatemala. All swollen-thorn acacias have very hard seeds (except *A. allenii* and *A. melanoceras*) which pass through the intestinal tract unharmed and are scarified in the process. Swollen-thorn acacias are subject to heavy seed predation by bruchid beetles

(e.g., Janzen, 1969c) except for those species in very wet habitats—*A. melanoceras* and *A. allenii* and perhaps *A. ruddiae*. The general pattern is that the eggs are laid on the full sized and nearly mature pod, the larvae bore in through the pod wall and into a seed, and one larva matures inside each seed. Upon emerging from the pod, the new adult beetle will oviposit on pods that remain, resulting in destruction of that portion of the seed crop that has not been removed by dispersal agents (Janzen, 1969c.) Undamaged and scarified seeds yield almost 100 percent germination if taken from truly mature pods.

With considerable experience in studying the populations in the field, all species of swollen-thorn acacias can be correctly identified from specimens

TABLE 5.—*Reproductive and other traits of swollen-thorn acacias recorded from occupied adult trees*

<i>Species</i>	<i>Estimated age at first seed reproduction (yrs)</i>	<i>Pod valve color when mature</i>	<i>Pod dehiscion behavior</i>	<i>Aril color</i>	<i>Color of mature seed</i>	<i>Maximum height of adult (m)</i>	<i>Maximum basal diameter (cm)</i>	<i>Life form of adult</i>	<i>Bark color and texture</i>
<i>mayana</i>	4-6	maroon	indehiscent	yellow	dark brown	4-5	10	single trunk tree	smooth gray-green
<i>gentlei</i>	6	black	dehiscent along both margins but centrally together	pale yellow	olive green	14	12-25	single trunk tree	rough rust red
<i>globulifera</i>	5	black	dehiscent along one margin and strongly curled	yellow	olive green	8	12	single trunk tree	olive drab to reddish
<i>melanoceras</i>	8	greenish black	dehiscent along one margin	white	black	12	15	single or multiple trunk tree	green to light brown
<i>cookii</i>	8	black	?	?	?	20	30	single trunk tree	dark brown
<i>ruddiae</i>	10+	greenish black	?	?	?	18	50	single trunk tree	smooth gray-green with longitudinal whitish cracks
<i>chiapensis</i>	6-7	dark brown	dehiscent along both margins	white	greenish beige	5	20	single trunk tree	rough rust red
<i>sphaerocephala</i>	4	maroon yellow red	indehiscent	yellow	black	1-4	15	single trunk tree to multiple trunk shrub	smooth gray-green
<i>hindsii</i>	6	brown with waxy bloom	dehiscent along one margin	yellow	dark brown	18	35	single trunk tree to multiple trunk tree	smooth gray-green
<i>cornigera</i>	4	maroon yellow red		yellow	black	6-18	20	single trunk tree	smooth gray-green to rough brown
<i>allenii</i>	7	greenish black	dehiscent along both margins	white	black	25	25	single trunk tree	green to light brown,
<i>collinsii</i>	4	dark brown	dehiscent along both margins	yellow	olive drab to black	6	15	single trunk tree	rough silvery gray to brown

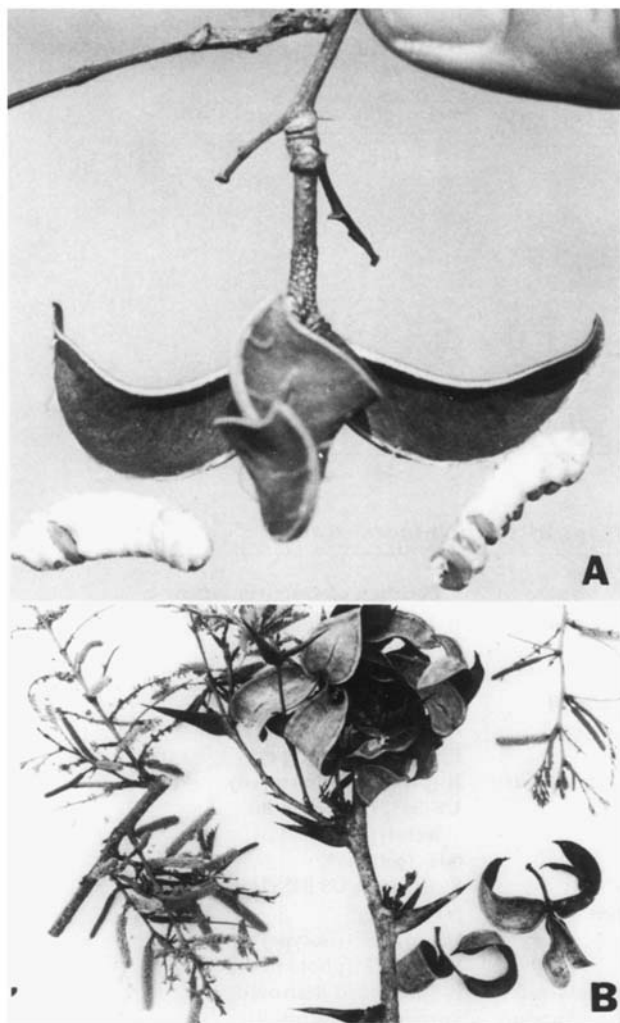


FIGURE 14.—A, Newly dehiscent fruits of *A. collinsii*, with the yellow pulp enclosing the seeds and hanging down beneath the valves on thin fibers; birds pick these off in flight (Costa Rica, site 71). B, Opened pod valves of *A. hindsii*; the pulp and seeds have been removed by birds (Mexico, site 17).

from adult trees even if the localities are unknown. Individual variation owing to local ecological factors, however, can make this process confusing, and knowledge of the collection site often aids tremendously in quick and accurate identification; the field work in this study was extensive and intensive enough so that the reader should be extremely suspicious if his identification leads him to decide that he has located a population of a given species far from the ranges listed under the individual

species accounts. Table 6 presents the degrees of sympatry and gives some feeling for the amount of caution required to identify the species on collection locality only; *A. melanoceras* and *A. allenii* are the only species that are never sympatric with other swollen-thorn acacias.

While hybrids of swollen-thorn acacias with other acacias (*A. globulifera*, *A. hindsii*, *A. collinsii*, and *A. chiapensis* are the offenders in this case) may be difficult to place to species, swollen-thorn acacias apparently hybridize only very rarely (though understandably they might be difficult to notice); I have seen only one, and that was a single plant of *A. cornigera* × *A. sphaerocephala* on the dunes south of the city of Veracruz, Mexico.

Taxonomic Information

While working with a population of swollen-thorn acacias, one should have no difficulty in identifying them with key A. Key B is provided for use in conjunction with key A, when flowers and fruit are not available. On occasion there may be some difficulty in identifying old and very incomplete herbarium material with these keys, but that is not likely to be a significant problem inasmuch as the value of species-level determinations for such material is highly questionable anyway. When a population of swollen-thorn acacias is encountered during the rainy season, sexual material may be difficult to locate. If one searches for damaged trees, however, often an occasional inflorescence-bearing branch may be located. Since the immature infructescences are retained on the tree through the rainy season, careful search for these usually succeeds in locating sexual material. It is worth noting that the inflorescence receptacle generally retains its shape while bearing immature or mature fruits (e.g., Figure 112), allowing easy use of the first couplet of key A even when fresh inflorescences are not available. The physical locations of the type specimens of swollen-thorn acacias are given in Table 7, but these are generally of little use in identification.

Vernacular names are of little use in correct identification of swollen-thorn acacias, inasmuch as they tend to be lumped under "cornizuelo" or some similar word at a given site (Table 8), in contrast to the other acacias which generally carry names such as "guisache."

TABLE 6.—*Sympatry of swollen-thorn acacias* (+ indicates that they may be found growing within 200 m of each other in some part of the range and that the populations overlap)

Species	cor.	sph.	may.	glo.	coo.	hin.	col.	mel.	all.	rud.	gen.	chi.
<i>cornigera</i>	+											
<i>sphaerocephala</i>	+	+										
<i>mayana</i>	+	○	+									
<i>globulifera</i>	+	○	○	+								
<i>cookii</i>	+	○	○	○	+							
<i>hindsii</i>	+	○	○	+	○	+						
<i>collinsii</i>	+	○	○	+	○	+	+					
<i>melanoceras</i>	○	○	○	○	○	○		+				
<i>allenii</i>	○	○	○	○	○	○	○	○	+			
<i>ruddiae</i>	○	○	○	○	+	○	○	○	○	+		
<i>gentlei</i>	+	○	○	○	+	+	○	○	○	+	+	
<i>chiapensis</i>	+	○	○	+	+	○	○	○	○	○	+	+

TABLE 7.—*Location of type specimens of swollen-thorn acacias*

Name	Type location and sheet number	Synonyms	Location of synonym types		
<i>collinsii</i>	US 692159* NY (cotype)*	<i>yucatanensis</i>	B (presumed destroyed) GH ("type collection")* US 571618 ("type coll.")*		
		<i>nelsonii</i>	US 399366 (type)* F 417619 (paratype)* F 417618 (paratype)*		
		<i>costaricensis</i>	B (presumed destroyed) US 943274 (potential lectotype)* GH (cotype)* K (same as US 943274)†		
		<i>penonomensis</i>	NY (type)* US 677927 (isotype)* US 764673 (photo of type)*		
		<i>panamensis</i>	B (presumed destroyed)		
		<i>veracruzensis</i>	(presumed destroyed) US 764683 (frag. and photo)* US 764684 (frag.)*		
		<i>dolichocephala</i>	F 189552 (type)* US 692164 (isotype)* NY (isotype)*		
		<i>mayana</i>	US 1688106 (isotype)* GH (isotype)* MICH (type)* NY (isotype)*		
		<i>cornigera</i>	BM (no number) US 2396019 (frag. and photo)*	<i>spadicigera</i>	US 764687 (frag. and photo)*
				<i>cubensis</i>	GH (type)* US 764633 (frag. and photo)* MO 16066, 46866 (type)*
<i>nicoyensis</i>	B (presumed destroyed) US 577752 ("type coll.")* GH ("type collection")* K (cotype)† NY (isotype)*				
<i>hernandezii</i>	US 692170 (type)*				
<i>sphaerocephala</i>	(presumed destroyed) US 764680 (frag. and photo)*				

TABLE 7.—Location of type specimens of swollen-thorn acacias—continued

Name	Type location and sheet number	Synonyms	Location of synonym types
			GH (isotype)* NY (isotype)*
		<i>furcella</i>	US 692166 (type)*
		<i>interjecta</i>	unknown
		<i>rossiana</i>	MO (no number)* US (photo)*
		<i>campecheana</i>	B (presumed destroyed)
		<i>turgida</i>	(photo only, in Wheeler, 1942)
<i>hindsii</i>	K (no number)†	<i>bursaria</i>	B (presumed destroyed) GH (cotype)* K (cotype)†
		<i>tepicana</i>	US 637234 (type)*
		<i>sinaloensis</i>	US 636818 (type)* NY (isotype)*
<i>cookii</i>	US 574387 (type)* US 764658 (paratype)*	<i>bucerophora</i>	US 764696 (frag. & photo)* F 659304 ("type")* GH ("type")*
<i>globulifera</i>	F 58707 (type)* F 36458 (isotype?)* US 1267507 (isotype?)* GH (isotype?)* NY (isotype)*	<i>donnelliana</i>	US 943282 (type)*
<i>chiapensis</i>	US 692157 (type)* F 464247 (photo)*		
<i>gentlei</i>	F 1000801 (type)*		
<i>melanoceras</i>	locality unknown	<i>multiglandulosa</i>	B (presumed destroyed) US (photo, no. 1281)*
<i>allenii</i>	US (type)*		
<i>ruddii</i>	US (type)*		
Name	Type location and sheet numbers	Hybrids	
<i>gladiata</i>	US 764660 (frag. & photo)* MO 46838 (type)* US 764659 (frag. & photo)* US 716563 ("paratype")*	<i>A. hindsii</i> × <i>A. cochliacantha</i> Humb. and Bonpl. ex Willd.	
<i>hirtipes</i>	US 694036 (type)*	<i>A. hindsii</i> × <i>A. pennatula</i> Benth.	
<i>standleyi</i>	US 637251 (type)*	<i>A. hindsii</i> × <i>A. pennatula</i> or <i>A. macracantha</i>	
<i>oaxacanum</i>	US 1208317 (type)*	<i>A. hindsii</i> × <i>A. pennatula</i>	

* Examined in this study; numbers refer to herbarium sheet numbers.

† Information provided by Sir George Taylor (in litt.).

TABLE 8.—Vernacular names of swollen-thorn acacias in Central America as provided by local informants (currently these names are applied with considerable imprecision)

Acacia species	Vernacular	Geographic region
<i>mayana</i>	cruzetillo	Campeche, Yucatan, Mexico
<i>globulifera</i>	cachetoro ishcanal	Coban, Alta Vera Paz, Guatemala
<i>cornigera</i>	cornizuelo blanco cachetoro ishcanal cornizuelo cornizuelo	Yucatan, Mexico Coban, Alta Vera Paz, Guatemala lowland eastern and southern Mexico, generally throughout Central America

TABLE 8.—*Vernacular names of swollen-thorn acacias in Central America as provided by local informants* (currently these names are applied with considerable imprecision)—continued

<i>Acacia species</i>	<i>Vernacular</i>	<i>Geographic region</i>
	cuernitos	Veracruz, Oaxaca, Mexico
	ishcanal blanco	El Salvador
	cuernos de toro	San Luis Potosi, Veracruz, Chiapas, Tabasco, Mexico
<i>hindsii</i>	ishcanal	Pacific lowlands of Guatemala
	ixcanal	
	carnizuelo	Central Honduras
	torito	Salina Cruz, Oaxaca, Mexico
	cornezuelo	Michoacan, Guerrero, Mexico
	garaterrera	Sinaloa, Nayarit, Mexico
	jarretadera	
<i>gentlei</i>	cockspur	British Honduras
	red cockspur	
<i>collinsii</i>	cockspur	Isla Providencia, Colombia
	crowsfoot	British Honduras
	cachitos	Pacific coast of Panama
	subin	Yucatan Peninsula, Mexico
	cornezuelo	Chiapas, Yucatan, Mexico, Colombia
<i>melanoceras</i>	cuernitos	Porto Bello, Panama
	cachitos	Panama
<i>sphaerocephala</i>	cornezuelo	Veracruz, Mexico
<i>cookii</i>	guascanal	Guatemala
	cockspur	Guatemala

A. Key to Mature Central American Swollen-Thorn Acacias, Based on All Traits

1. Inflorescence distinctly globular 2
 - Inflorescence very elongate or at least distinctly longer than broad 3
2. Leaves from type A thorns (on lateral branches) over 30 cm long 4
 - Leaves from type A thorns (on lateral branches) less than 25 cm long 5
3. Pinnules less than 1 mm wide 6
 - Pinnules 2 or more mm wide 7
4. Petiole deeply grooved, young thorns pubescent, nectaries barely raised above surface of petiole and elongate, occupied by obligate acacia-ants 1. *A. cookii*
 - Petiole slightly grooved, young thorns glabrous, nectaries strongly outstanding conical, not occupied by obligate acacia-ants 2. *A. ruddiae*
5. Petiole with many nectaries (8-30) 3. *A. melanoceras*
 - Petiole with few nectaries (0-6) 4. *A. allenii*
6. Petiole with many nectaries (6-25) closely packed and often not in a straight line, wood very soft 5. *A. chiapensis*
 - Petiole with few and widely spaced nectaries (1-5) in a straight line 6. *A. globulifera*
7. Inflorescence peduncle very thick, at least half as wide as inflorescence, nectaries trough shaped 8
 - Inflorescence peduncle very thin, less than one-fourth as wide as the inflorescence, nectaries round 9
8. Inflorescence 3-4 times as long as broad; secondary venation clearly visible on leaflets 9
 - Inflorescence one and one-half times as long as broad, approaching a globular form; secondary venation on leaflets not visible 7. *A. sphaerocephala*
9. Swollen-thorns round in cross section 8. *A. cornigera*
 - Swollen-thorns triangular in cross section 9. *A. mayana*
10. Inflorescence approaching globular form, but nearly twice as long as wide
 - Hybrid of *A. hindsii* with other *Acacia* species
 - Inflorescence very elongate, 3-8 times as long as broad 11

11. Seed pods less than 8 cm long, valves curling heavily upon opening 12
 Seed pods more than 12 cm long, curling only slightly upon opening 10. *A. gentlei*
 12. Petiolar nectaries dome shaped in lateral view with 1 mm or greater diameter, usually
 3-4 very close together in widened part of petiole and none on rachis 11. *A. collinsii*
 Petiolar nectaries cylindrical in lateral view with less than 1 mm diameter, usually 1 or
 more on the petiole and one at junction of each pinna with rachis 12. *A. hindsii*

B. Key to Mature Central American Swollen-Thorn Acacias, Based on Vegetative Traits

1. Petiolar nectary trough shaped, much longer than broad (Figure 8B) 2
 Petiolar nectaries circular (domes, cups, conical) 4
 2. Type A thorns triangular in cross section 9. *A. mayana*
 Type A thorns circular or elliptical in cross section 3
 3. Secondary venation on leaflets clearly visible 8. *A. cornigera*
 Secondary venation on leaflets not visible 7. *A. sphaerocephala*
 4. Type A thorns very heavily flattened, nectaries scattered on petiole and rachis, and small
 enough so as not to cause heavy swelling of petiole or rachis (Figure 8A) 12. *A. hindsii*
 Type A thorns circular or elliptical in cross section, nectaries various 5
 5. Nectaries restricted to petiole and broad dome shaped (Figures 7A, 9) 11. *A. collinsii*
 Nectaries other than above 6
 6. From type A thorns on lateral branches, leaves 30 cm or more long 7
 From type A thorns on lateral branches, leaves less than 25 cm long 10
 7. Pinnules less than 1 mm wide 8
 Pinnules more than 2 mm wide 9
 8. Petiole deeply grooved, young thorns pubescent (and sometimes old thorns), nectaries
 elongate and low (Figures 18A, 18B), obligate acacia-ant entrance holes in thorns near
 apex 1. *A. cookii*
 Petiole only slightly grooved, young thorns glabrous, nectaries conical and well raised
 above petiole and rachis (Figure 8c), never with obligate acacia-ant entrance holes in
 thorns near apex 2. *A. ruddiae*
 9. Petiole with many nectaries (8-30) (from Panama and Canal Zone) 3. *A. melanoceras*
 Petiole with few nectaries (0-6) (from Costa Rica) 4. *A. allenii*
 10. Petiole with many nectaries (6-25) closely packed and often not in a straight line
 5. *A. chiapensis*
 Petiole with 1 to few nectaries; if more than one, then linearly arranged 11
 11. Extrafloral nectaries as in Figures 6 and 7c, almost always more than one on the petiole
 6. *A. globulifera*
 Extrafloral nectaries as in Figure 7b, almost never more than one on the petiole, bark and
 thorns deep red or mahogany in color, type A thorns very slender (as little as 3 mm di-
 ameter at base) 10. *A. gentlei*

1. *Acacia cookii* Safford

Acacia cookii Safford, 1910:677.

Acacia bucerophora B. L. Robinson, 1913:502.

Mymecodendron cookii (Safford) Britton and Rose, 1928:93.

Acacia cookii is easily distinguished from all other swollen-thorn acacias by its tomentose, long and thin thorns that bend back around the stem and are often bilaterally asymmetrical (Figures 15, 16). *A. collinsii* type A thorns may also wrap around the branch that bears them, but they are very short and thick. Only the type B thorns of *A. cornigera* wrap around the branch that bears them. *A. ruddiae* thorns may be tomentose when green, but they are glabrous upon maturing.

The type specimens for both *A. cookii* and *A. bucerophora* are representative of specimens from the southern part of the population (Figure 17). The branch designated as the type of *A. cookii* (from site 1) lacks swollen thorns and was probably taken from the end of a long and old reproductive branch such as that in Figure 15b. Since the inflorescences on the type are still in bud, the peduncles are much shorter than they are when in flower (e.g., Figures 15b, 16b). The leaves of the type specimen are not from the inflorescence-bearing branch; they are of the form normally subtended by large type A thorns (cf. ends of branch in Figure 18) and were probably broken from the branches in

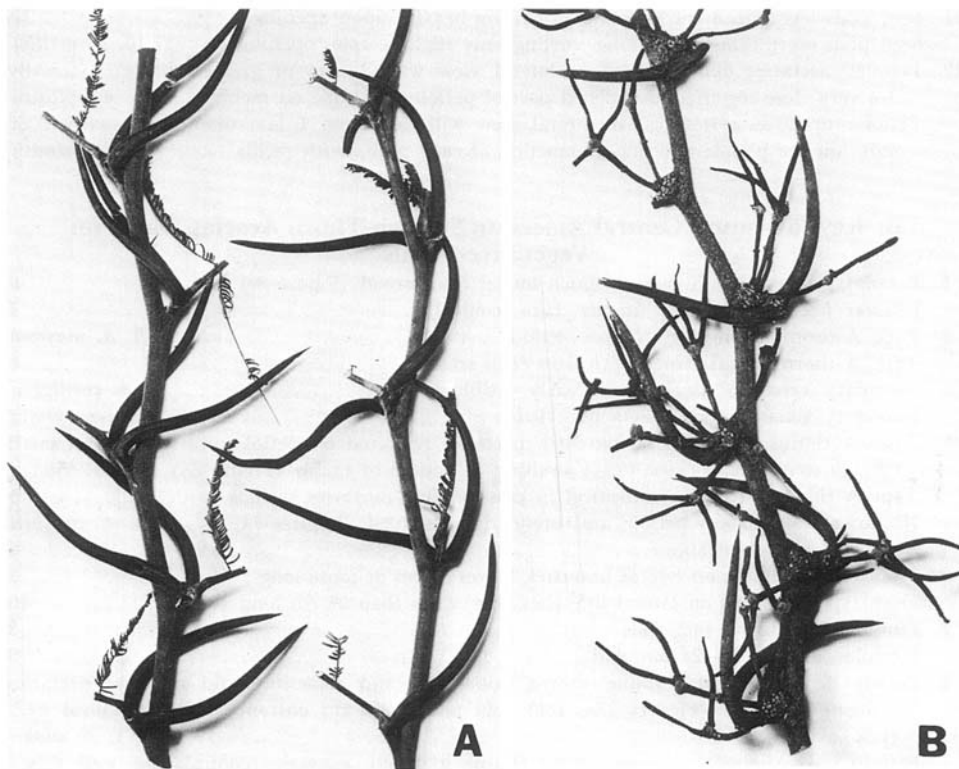


FIGURE 15.—Lateral branches from mature *A. cookii* (Guatemala, site 4): A, sterile branch with fully developed thorns characteristic of the southern part of the acacia's range; B, reproductive branch with axillary inflorescences characteristic of the southern part of the acacia's range.

order to avoid pressing the ant-filled thorns. The type specimen of *A. bucerophora* (site 3) differs in no significant way from that of *A. cookii*. The single thorn of the specimen is old and rotted and therefore not the dark brown that is characteristic of most thorns on a tree of *A. cookii*. The single small seed pod is immature and shrunken, giving the illusion of being thin, while in fact *A. cookii* pods are over 1 cm wide and very long (Figure 19).

The northern and southern parts of the *A. cookii* population differ on a number of morphological traits; however, these differences appear to be the result of comparing the two ends of a cline, since the intermediate elevation wet-forest habitat of *A. cookii* is continuous from the northern to southern part of the range. This hypothesis can only be verified by collections from the area between the broken distribution in Figure 17. Some of the more outstanding changes in *A. cookii* in progressing from the northern to the southern part of the range are: (1) shortening of the type A thorns (cf. Figures 15A

vs. 16A); (2) shortening of the sexual branchlets (cf. Figures 15B vs. 16B); (3) increased number of inflorescences per inflorescence-bearing axil; (4) increased number of Beltian bodies per mature leaf; and (5) increased percentage of the acacia plants being occupied.

KEY COLLECTION LOCALITIES

1. Type of *A. cookii*: Finca Trece Aguas near Secanquim, Depto. Alta Verapaz, Guatemala (300 m). III-8-1907, G.P. Goll, no. 102 (US 692154), fl.
2. Paratype of *A. cookii*: Secanquim, Alta Verapaz, Guatemala (300 m). VI-4-1905, O.F. Cook, no. 4.
3. Type of *A. bucerophora*: about Toledo, 4 mi from the coast and 5 mi from Punta Gorda, Belize Prov., British Honduras (sea level). III-29-1907, M.E. Peck, no. 632.
4. 2.8 mi W Puerto Matias de Galvez (on road to Escobas), Depto. Izabal, Guatemala (10 m). VIII-10-1967, DHJ, no. 1524, gp.
5. 9.8 mi W Cardenas on Mexico 180, Tabasco, Mexico (10 m). VI-17-1966, DHJ, no. 515.
6. From Km 56 sign post, 9.8 mi N turn off Tapilula to 10.8

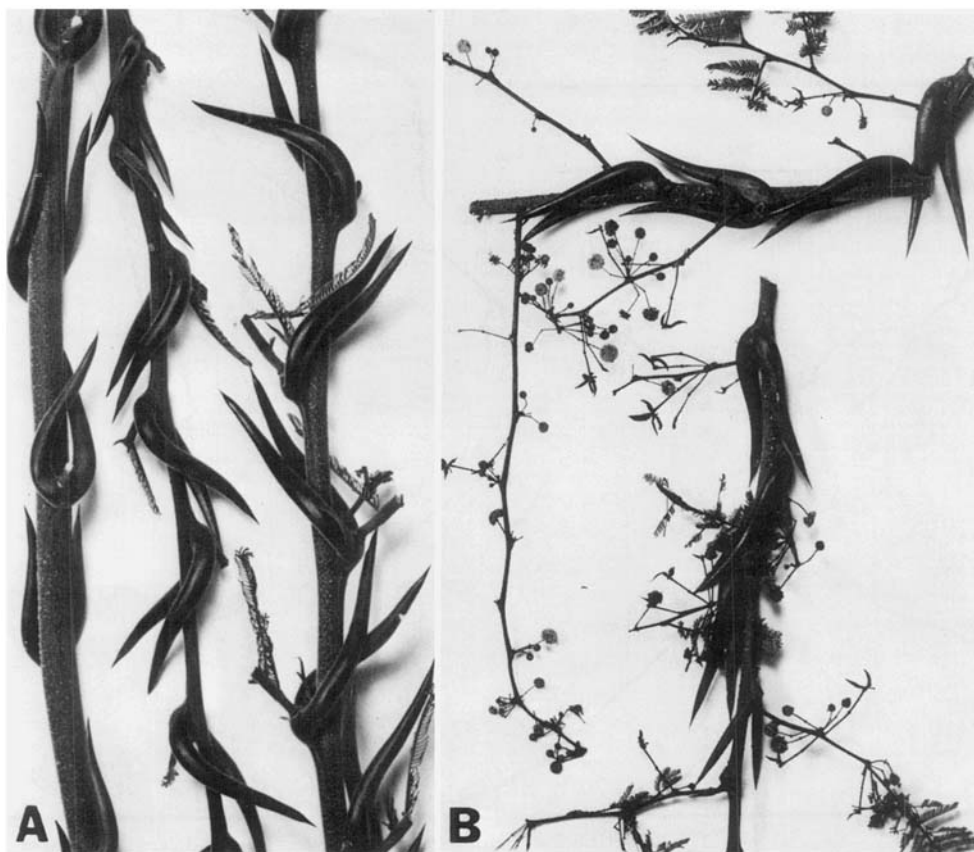


FIGURE 16.—Lateral branches from mature *A. cookii*: A, sterile branch with fully developed thorns characteristic of the northern part of the acacia's range (Mexico, site 7); B, reproductive branch with long sexual branchlets characteristic of the northern part of the acacia's range (Mexico, site 6).

mi S Pichucalco on Villa Hermosa-Tuxtla Gutierrez highway, Chiapas, Mexico (240 to 380 m). VII-10-1966, *DHJ*, nos. 530, 537, fl.

7. N side of Chontalpa, 26 mi S Cardenas, Tabasco, Mexico (80 m). VI-17-1966, *DHJ*, nos. 548, 550.
8. Along river, Lancetilla Valley, near Tela, Atlantida, Honduras (5 m). XII-19-1927 to III-27-1928, *P.C. Standley*, no. 54627.
9. Rd. from Secanquim to Sepacuite, Depto. Alta Verapaz, Guatemala. IV-1-1902, *O.F. Cook* and *R.F. Griggs*, no. 374 (US 408103).
10. Sierra del Mico, between Los Amates and Lake Izabal, Depto. Izabal, Guatemala (650 m). II-27-1908, *W.A. Kellerman*, no. 7169 (US 2442365, US 2442347), fl.
11. Between Virginia and Lago Izabal, Montana del Mico, Depto. Izabal, Guatemala (50-100 m). IV-4-1940, *J.A. Steyermark*, no. 38758 (F 1056559).
12. British Honduras. 1944 (F 1403119).
13. Big Rock, British Honduras (65 m). XII-16-1932, *W.A. Schipp*, no. 1072 (F 713932).
14. Maskall, British Honduras? I-1934, *P.H. Gentle*, no. 1121 (F 739552).

NATURAL HISTORY

Acacia cookii is a narrowly distributed species that has its highest densities at intermediate elevation sites (200 to 400 m) with very mild dry seasons (e.g., sites 1,2,6). At site 6, this habitat was slightly higher than that of *A. cornigera* and *A. chiapensis*, where all three occur along the east-facing foothills of the Sierras in western Tabasco, Mexico. Occasional adults of *A. cookii* were found at lower and drier sites (sites 5,7) in the northern part of the range, but their sympatry with *A. cornigera* and *A. chiapensis* may have been the result of seed dispersal by road-building machinery. In the southern part of the range, isolated plants (e.g., site 4) generally grow in naturally disturbed sites along rivers in very wet forests. They are sympatric with *A. gentlei* at these sites (as at other Guatemalan sites such as sites 10 and 11), and there is no evidence

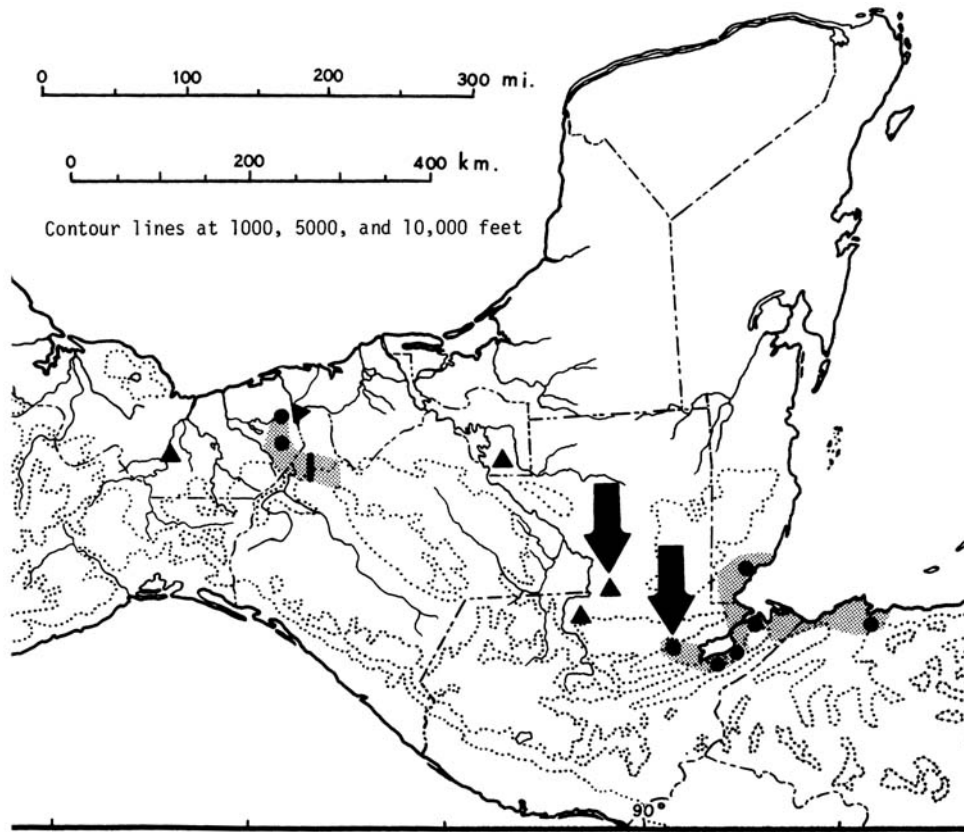


FIGURE 17.—General postulated distribution (stippled area; type localities indicated by arrows).
 ● collection site of *A. cookii* ▲ collection site of *A. mayana*

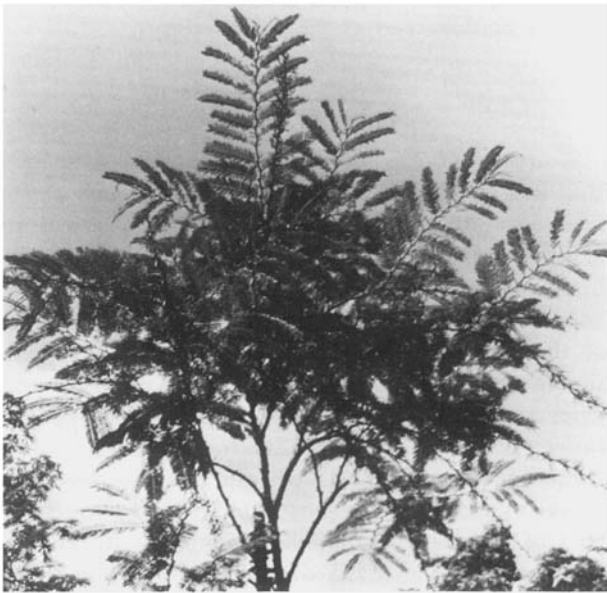


FIGURE 18.—Crown of mature 5-m-tall *A. cookii* growing along creek in rain forest (Guatemala, site 4).

that they are unnatural populations. *A. cookii* disappears when the wet forest is cut in areas like site 4; this local extinction is probably due to the same causes as cited for *A. allenii* and *A. melanoceras*. In the northern part of the range, where the dry season is more severe, *A. cookii* appears to be able to persist in the face of repeated wilting and occasional burning. It was very common as a roadside and pasture tree shrub at site 6.

The hard seeds of *A. cookii* are attacked by unidentified bruchids to the same degree as those of swollen-thorn acacias of drier areas. The seeds are dispersed by birds; the pods dehisce incompletely and the dark seeds are buried in a white, sweet pulp. The seed crops are not unusually large, but the large number of inflorescences per axil is matched only by the axils of *A. chiapensis* (Figure 20A). In the southern part of the range, where the inflorescence-bearing branch is reduced to a bump in the thorn axil (Figure 15B), an average number of inflorescences per axil may be as high as 64 for a

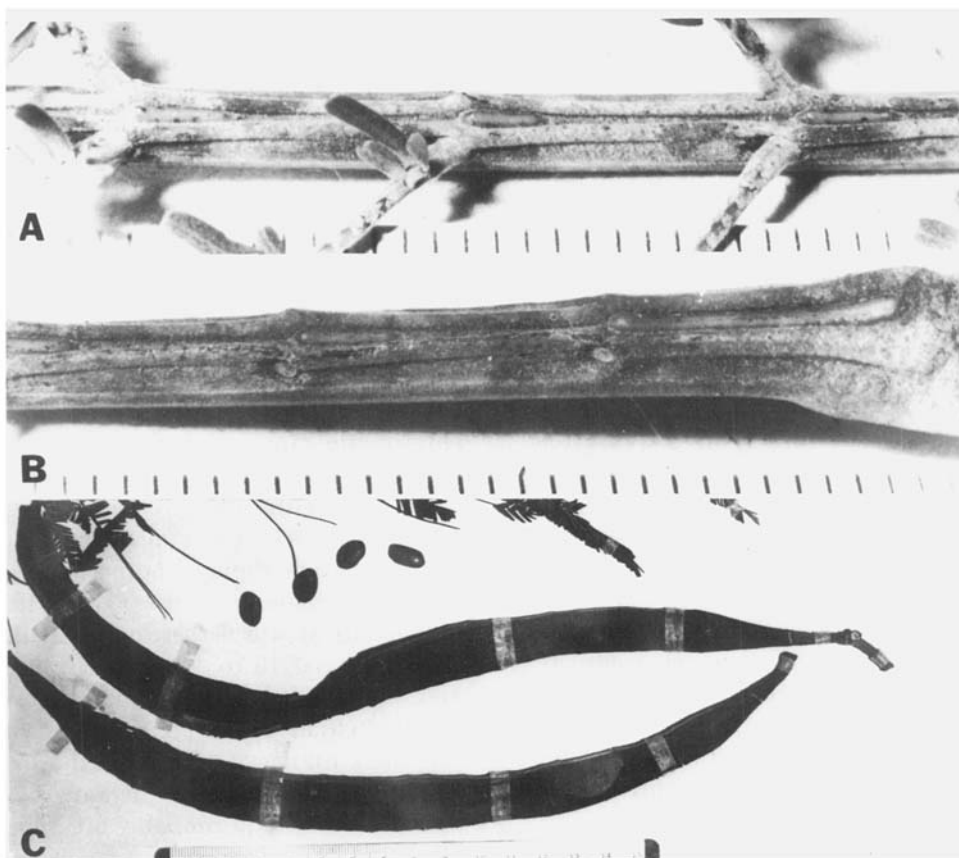


FIGURE 19.—*Acacia cookii* (Guatemala): A, rachis nectaries on leaf subtended by type A thorn (site 4); B, petiolar nectaries of leaf; C, mature seed pods (site 1, US 692155).

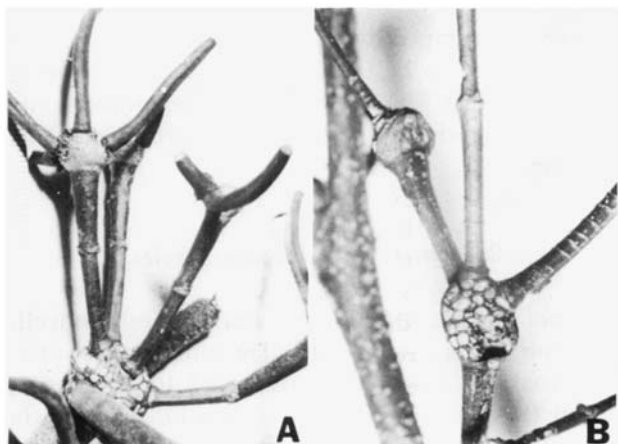


FIGURE 20.—Axillary inflorescences: A, immature pods of *A. chiapensis* (Mexico, site 9); B, bud scars (with two infructescence peduncles projecting to 12:00 and 2:00 o'clock) of *A. cookii* (Guatemala, site 4).

large sample (Figures 20B, 22). In the northern part of the range, where the sexual branchlets are long, a sample of 10 axils on a representative branch had a mean of 32 inflorescences per axil (16, 29, 29, 29, 31, 31, 35, 37, 38, 42).

The pattern of development of *A. cookii* from seedling to adult is unknown, but I have no reason to suspect it differs in any substantial way from that of other wet-forest, swollen-thorn acacias such as *A. allenii*. At site 4, the mature trees had a relatively dense crown (Figure 18) perched on top of a single and straight thin trunk. Based on growth rings, in wet forest the trees die of senescence when about 15 to 25 years old. In slightly drier sites (definitely site 6 and probably sites 1 and 2) the old trees may attain the largest size of any swollen-thorn acacia, except perhaps *A. hindsii* in western Mexico and *A. ruddiae* in the Costa Rican mountains. Growing

in old landslide scars at site 6, there were trees of *A. cookii* up to 30 m tall, up to 20 m across the crown, and with a DBH as much as 40 to 50 cm. The ant colonies were not examined in these trees, but I suspect that they were either a multiple-queen species or they restricted their patrolling to the newer foliage. While the crowns of these acacias were very large, the actual amount of green foliage was small compared to what it would be in another species of legume of equal size during the rainy season.

It is possible that the herbivore pressure is somewhat reduced at this site and/or that *A. cookii* in this area has better chemical defenses than do most swollen-thorn acacias. I suspect this because roadside clumps of poorly occupied *A. cookii* at site 6 had foliage with very little herbivore damage. I favor this hypothesis because the *A. cookii* growing at site 5 was in a lowland roadside pasture where unoccupied *A. cornigera* was being heavily defoliated by insects that normally feed on other species of plants. This *A. cookii* was, however, completely unoccupied and almost in perfect condition. At least 5 years old, the plant was 4 m tall and had a crown similar in foliage density to the one in Figure 18. About one out of every four shoot tips had been

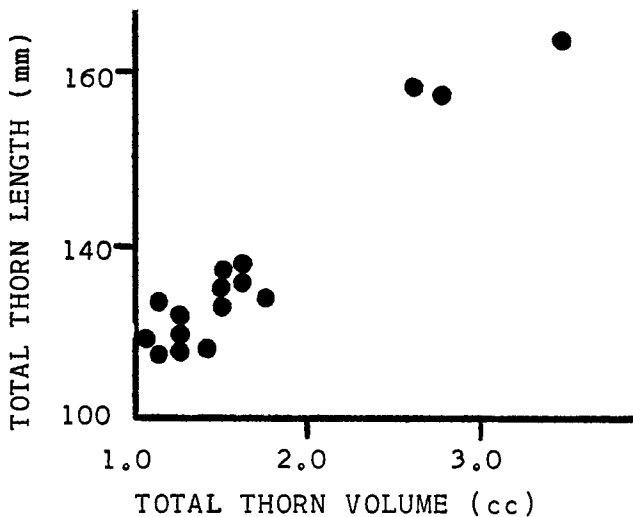


FIGURE 21.—Distribution of 131.3 cc of thorn volume among 19 very large type B thorns from one adult *A. cookii* (Guatemala, site 4). While the largest to be found, these thorns had a maximum diameter in cross section of 5–7 mm.

eaten off by insects, which is about the frequency usually observed during the rainy season on non-ant-acacias and occupied swollen-thorn acacias.

These comments should not be construed to indicate that *A. cookii* does not have a mutualistic association with its ants. At site 6 there was ample defoliation of unoccupied sucker shoots, in contrast to occupied ones. This indicates that the results of removing the ants would have had an effect on *A. cookii* much like that with *A. allenii*, but not as dramatic as with *A. cornigera* or *A. collinsii*.

It is possible that *A. cookii* is still in the process of coevolving a tighter mutualism with its occupant ants—*Pseudomyrmex ferruginea* in the northern part of the range, and *P. ferruginea* plus an unidentified species in the southern part. Its petiolar nectaries (Figure 19B) are morphologically poorly developed—their sugar production rate may be high, however—though the nectaries on the rachis may compensate for this (Figure 19A). On some individuals at site 6 there were Beltian bodies on only the basal 10 to 30 pinnules, and even at the sites where the healthiest ant colonies occur (e.g., site 4), Beltian bodies are produced on only about half the pinnules. The swollen thorns on *A. cookii* in the northern part of the range are very thin-walled—birds could probably break into them with ease—and they harden very soon after attaining full size, which allows the ant only a short time to cut an entrance hole. The very narrow thorns have a volume (Figure 21) representative of that of other swollen-thorn acacias because of their extreme length; however, these narrow thorns probably make very cramped living quarters for the ants. The largest thorns to be found (Figure 21) had a mean volume of only 1.64 cc, which is representative only of *A. chiapensis*, *A. globulifera*, *A. gentlei*, and *A. ruddiae*.

2. *Acacia ruddiae*, new species

Arbol usque ad 20 m alta; ramuli novelli puberuli, glabrescentes; stipulae spinescentes interdum magnae, teretisculae, usque ad 10 cm longae, 9 mm latae; folia circiter 15–40 cm longa; nectaria sessilia cupulata ad juncturas pinnarum omnium et 0–2 in petiolis; pinnae (12–) 25–40-jugae, 4–5 cm longae; pinnulae 65–75-jugae, lineariae, 2–4 mm longae, 0.5–1.2 mm latae, acutae vel obtusae,

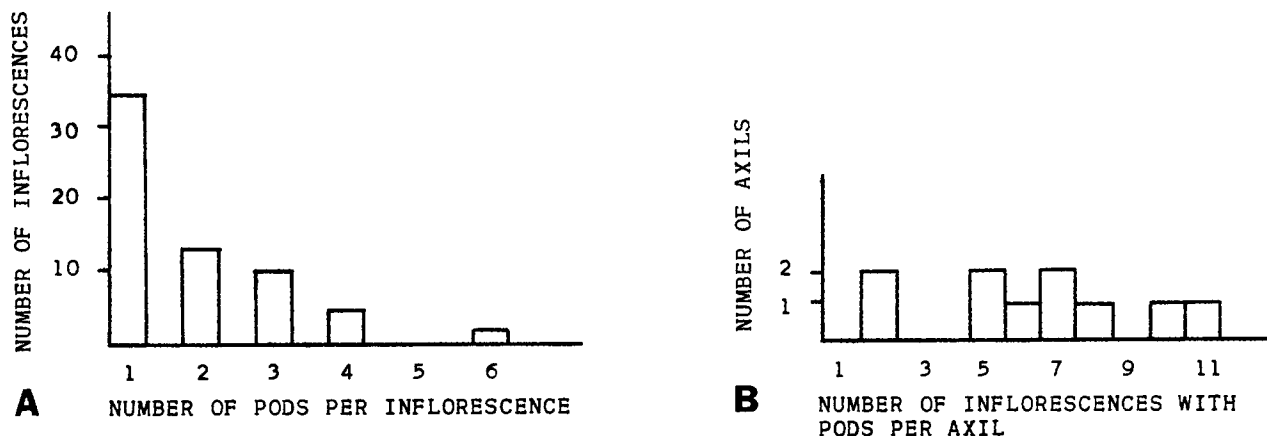


FIGURE 22.—*Acacia cookii* (Guatemala, site 4): A, distribution of 113 seed pods among 63 infructescences; B, distribution of the 63 infructescences among their 10 axils. There were 642 inflorescences produced by these 10 axils.

puberulae; flores aurei in capitulo globoso; involu-cellum annulare in medio pedunculo; legumina (immatura) atrobrunnea, puberula, granulata glabrescentes, oblonga, 5 cm longa, 7 mm lata, complanata, obtusa, stipite 5 mm longo; legumina matura probabiliter usque ad 6–8 cm longa.

TYPE.—*D. H. Janzen* 828, Costa Rica, Limon Province, ferry landing, Moin River, Moin, 13 February 1965 (holotype US 2639554; isotypes CAS, F, GH, MEXU, MICH, MO, NY, UC).

Type tree 20 m tall with 35 cm diameter trunk 1 m above ground; gray-green bipinnate leaves mostly 15 to 40 cm long with 50 to 80 pinnae per leaf, pinnae 40 to 50 mm long with 130 to 150 pinnules per pinnae, pinnules 2.5 to 3.0 mm long and 0.75 to 1.0 mm wide (up to 9,000 pinnules per leaf); occasional swollen-thorns on less than 10 percent of the nodes and very frequently only one side of the thorn swollen, thorns not occupied by obligate acacia-ants but by a miscellany of other ant species; no food bodies (Beltian bodies) on pinnules; single nectary at junction of each pinna with rachis, 0 to 2 nectaries on petiole, nectaries cylindrical up to 1 mm tall; yellow inflorescences spherical and up to 6 mm diameter, peduncle up to 10 mm long and 0.50 to 0.75 mm thick; immature fruits flat and slightly curved, probably 6 to 8 cm long at maturity.

Acacia ruddiae is distinctive by never being occupied by obligate acacia-ants, lacking swollen thorns on most branches except the bases of some lateral branches, having better than 5,000 very small leaflets

per leaf, growing in rain forest, becoming a very large tree, and by its range (Figure 23). It also differs from other Central American members of the genus *Acacia* by the same traits; it is undoubtedly distinguishable from the remainder of the genus by fine details of flower, fruit, and leaf structure, but it is impossible to know these differences at the present state of *Acacia* taxonomy.

The tree from which the type specimens (13 sheets) were collected was at least 30 years old, and perhaps much older, and was still standing in 1967. It was about 80 m south (west side of the road) of the south beach of the ferry landing on the Moin River and 200 m from the ocean beach, at Moin, Costa Rica (site 1). The branches were cut from high in the tree and were representative of the 1–2-year-old branches in the canopy. Although the specimens were collected during the dry season, the area was still subjected to frequent rains and the tree was only partly deciduous. It was at the end of its flowering season, and the full sized but immature green pods were from the same flower crop, rather than from the previous year's flowers as is usual with acacias of drier habitats. As is usual with the canopy branches from *A. ruddiae* this size, there are few swollen thorns on the branches. The tree from which the type specimens were collected was exceptional in two respects: First, most of the *A. ruddiae* population in this area has long since been destroyed by housing development. Second, the tree grew in a relatively open site and thus had strong

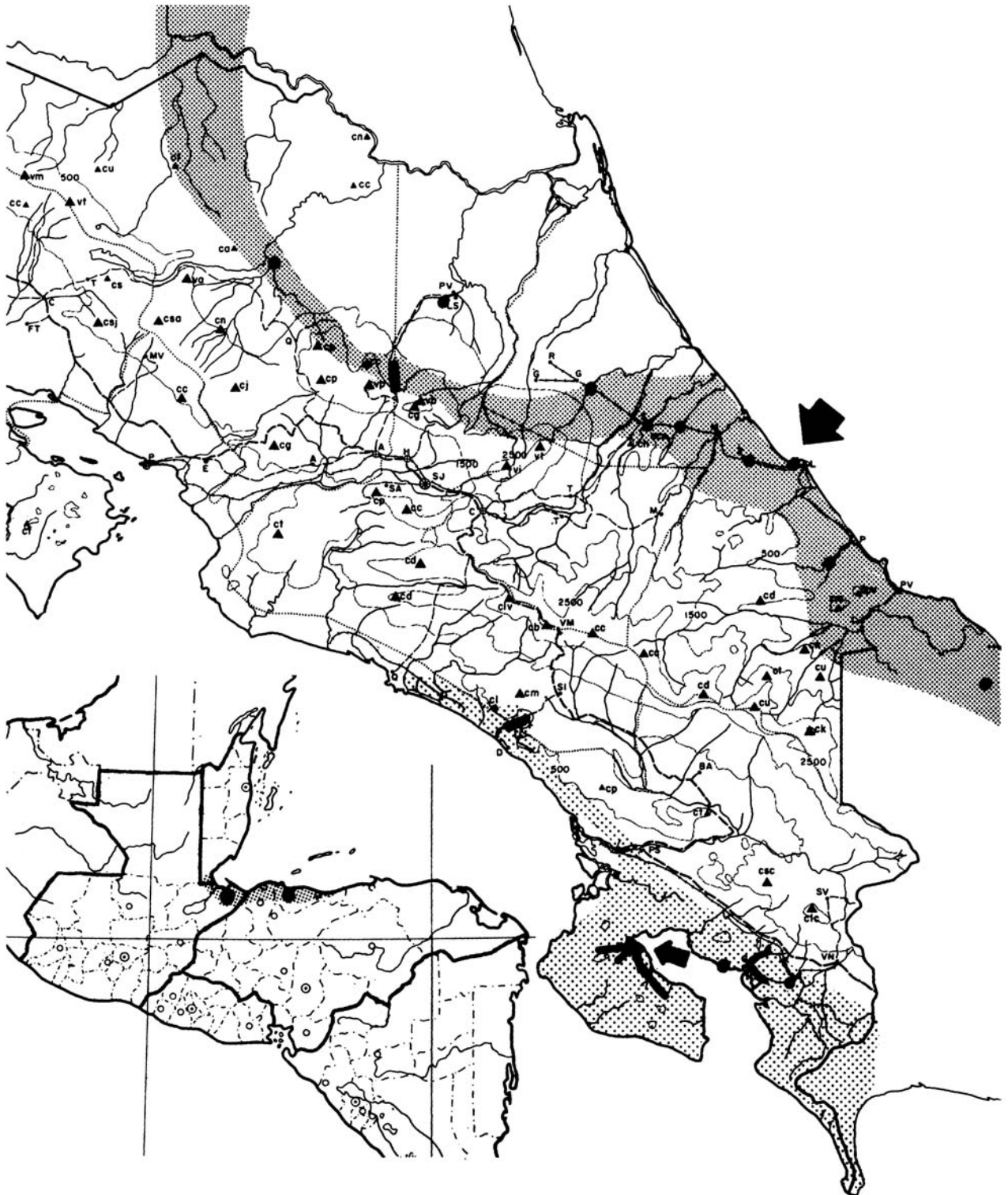


FIGURE 23.—General postulated distribution (heavily stippled area) and specific collection sites of *A. ruddiae* (all on the Caribbean side of Central America). General postulated distribution (lightly stippled area) and specific collection sites of *A. allenii* (all on the Pacific side of Central America).

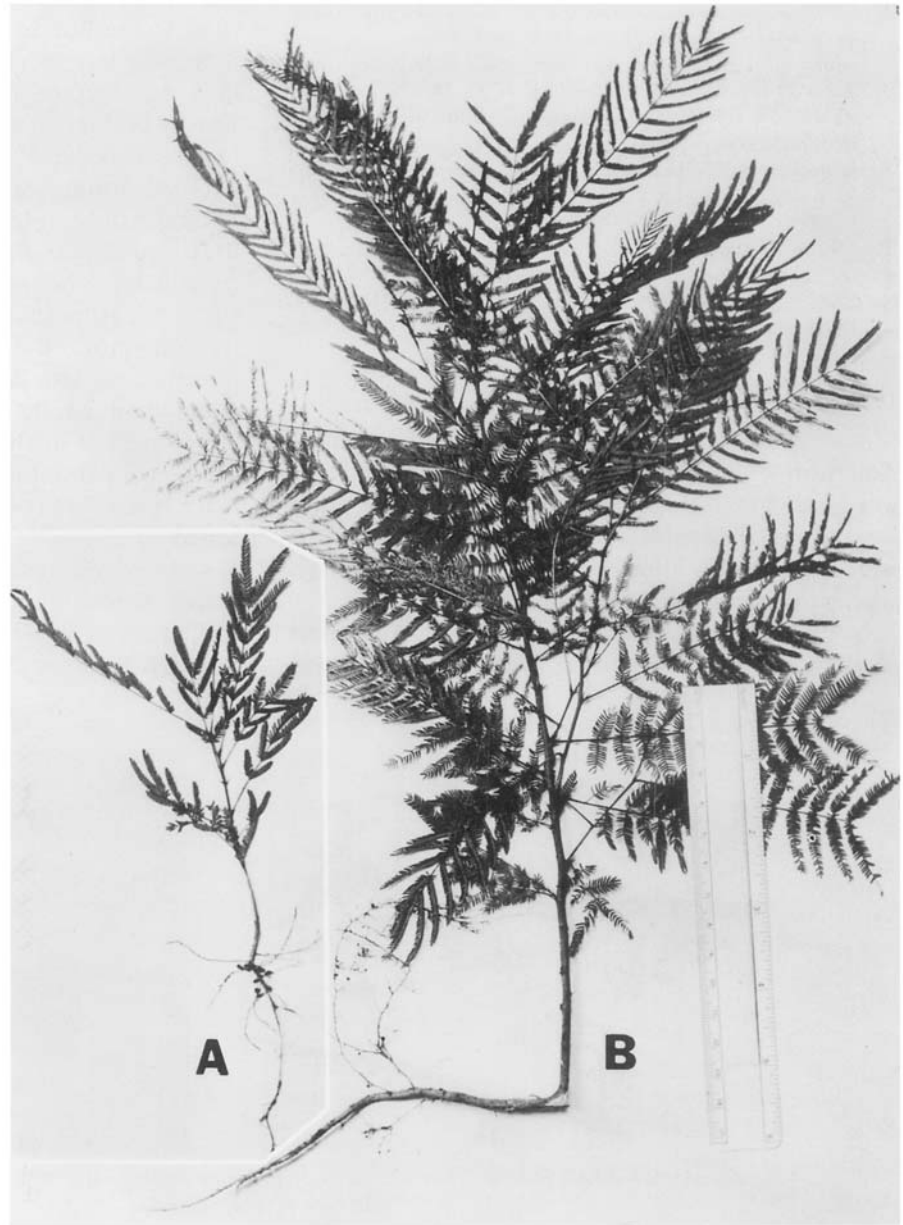
development of lateral branches; most *A. ruddiae* are involved in intense intertree competition and thus are tall and slender.

This acacia is named in honor of Dr. Velva E. Rudd whose unfailing assistance and encouragement has greatly aided in bringing this study to completion, and whose taxonomic work with Leguminosae will always be a tremendous assistance to field biologists.

Acacia ruddiae is included with the swollen-thorn

acacias, despite the fact that it is not occupied by obligate acacia-ants, because it appears to represent an intermediate step in one of several possible evolutionary pathways to the evolution of swollen-thorn acacias. Its ecology is therefore of special significance in this study. *A. ruddiae* is the only Central American acacia, aside from hybrids of swollen-thorn acacias with nonant-acacias, that appears to represent an intermediate step in the evolution of a New World swollen-thorn acacias.

FIGURE 24.—*Acacia ruddiae*: A, very young seedling; note nodules on roots (Costa Rica, site 5); B, young sapling (Costa Rica, site 5).



KEY COLLECTION LOCALITIES

1. TYPE.—Ferry landing, Moin River, Moin, Limon Prov., Costa Rica. II-13-1965, *DHJ*, no. 828, fl. gp.
2. Pandora, Limon Prov., Costa Rica. VIII-26-1963, *C.D. Michner*, nc.
3. 16 mi N Vara Blanca on road from Heredia to Puerto Viejo (Sarapiquí Dist.), Heredia Prov., Costa Rica (320 m). V-1-1965, *DHJ*, no. 819, fl.
4. 1 km W La Virgin, Sarapiquí Dist., Heredia Prov., Costa Rica (80 m). IX-5-1971, *DHJ*, nc.
5. 1 km W La Lola (on Limon-Siquirres railroad), Limon Prov., Costa Rica. VIII-19-1963, *DHJ*, nos. 1868, 1872, 1873, 1874, 1875, 1876, 1877, 1878, 1881.
6. 11 mi N Florencia, San Carlo Dist., Alajuela Prov., Costa Rica. VII-14-1963, *DHJ*, no. 1883, 1885, 1866.
7. Along Changuinola River, Changuinola Valley, Bocas del Toro Prov., Panama. II-29-1924, *V. C. Dunlap*, no. 462 (F 709739, US 1405662) (listed incorrectly as "*A. cookii*" in Woodson and Schery), fl.
8. Lancetilla valley near Tela, Depto. Atlantida, Honduras. VI-6-1927 to III-20-1928, *P. C. Standley*, no. 54627 (US 1408382).
9. 1.9 mi W Puerto Matias de Galvez (on road to Escobas), Izabal, Guatemala. VIII-10-1967, *DHJ*, no. 1582.
10. 27.4 mi S Puerto Barrios, Izabal, Guatemala. VIII-8-1967, *DHJ*, nc.

NATURAL HISTORY

Acacia ruddiae is one of the most peculiar Central American members of the genus. It lives in very wet forest habitats, which is distinctly unlike other acacias, yet does not have the obligate acacia-ants which generally allow survival of swollen-thorn acacias in wet habitats (Janzen, 1966a).

In Costa Rica, where the only large populations of *A. ruddiae* have been encountered, the natural

habitat of this tree is in primary succession along lowland rivers through rain forest (sites 4, 5), swamp edges (site 5), and in large, old landslide scars on the sides of very steep gorges (site 3). These areas receive 4 to 5 m of rain a year and have a poorly developed dry season of 1 to 2 months with occasional rains. Some of the sites occupied by *A. melanoceras* and *A. allenii* receive as much rainfall, but have a more noticeable dry season. Judging from the paucity of collections, *A. ruddiae* apparently also exists as a very rare tree in the rain forest that extends in a narrow strip up along the Caribbean coast to the Puerto Barrios area of Guatemala (sites 8 and 9), but there is no reason to believe that it does not become locally common in these forests just as it does in Costa Rica.

Acacia ruddiae is by no means generally distributed throughout the rain forest of the Costa Rican Caribbean lowlands. At site 4 it was common in 1- to 30-year-old primary succession on gravel river banks and grew to a 25-m-tall tree with 30 cm DBH; it had not, however, extended its population out into the surrounding old cacao groves and pastures. At site 5 there was a large population along about a mile of old river bank, and occasional large saplings in the immediately adjacent parts of a banana plantation and on swamp edges in primary forest. Many of the swamp trees were old and scattered widely, in contrast with the many adjacent and even-aged *A. ruddiae* along the river. Extensive search throughout many other swamps and disturbed forest habitats within ten miles located no other *A. ruddiae*. At site 3, *A. ruddiae* occurs only

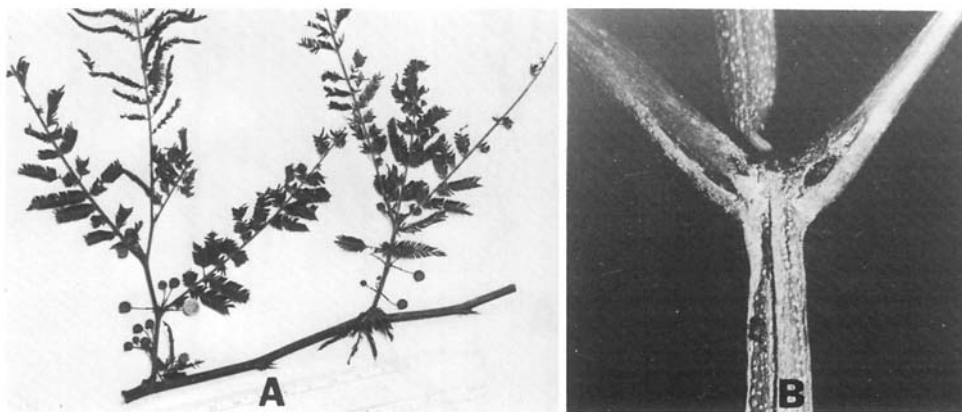


FIGURE 25.—*Acacia ruddiae* (Costa Rica): A, representative flowering branch (site 1); B, naturally split type A thorn (site 6).



FIGURE 26.—Representative branches of *A. ruddiae*: A, without swollen thorns from the crown of a large adult (Guatemala, site 9); B, from main trunk of large tree (Costa Rica, site 5).

in a small portion of the total landslide area in this strongly dissected topography. It has not spread along the road into other disturbed habitats from this site. While detailed weather data are not available for site 3, it may be slightly drier—hence better insulated—than other disturbed sites slightly above or below it in elevation. This is indicated by the high success of grasses in early stages of succession here, in contrast with dicot regeneration at casually cleared sites a few miles farther up or down the road.

Seedlings growing in deep shade resemble those of *A. melanoceras* and *A. allenii* in that the leaves are arranged in a whorl so that in vertical view, they do not overlap. When growing on bare gravel bars, the seedlings are more bushy and asymmetrical in appearance (Figure 24B). The nodules on the rootlets of *A. ruddiae* seedlings are more noticeable than on any other swollen-thorn acacia (Figure 24A).

The seedlings differ from those of all other swollen-thorn acacias in lacking swollen thorns. The first swollen thorns do not appear until the plant is 1 to 3 m tall and has several hundred leaves. The nectaries (Figure 8c), however, are produced as soon as on any swollen-thorn acacia. The first ones appear on the rachis just below the point where the pinnae join the rachis, and petiolar nectaries begin to appear on the 25th to about the 50th leaf. There are no Beltian bodies on *A. ruddiae*, and thus the only contact that the seedlings may have with ants is when occasional worker ants visit the nectaries and forage on the leaf surfaces. In this sense the young *A. ruddiae* are no different from nonant-acacias, except that the nectaries are larger than on nonant-acacias and may therefore produce more nectar.

On saplings, the first swollen thorns are scattered along the main trunk and lateral branches. They are very thin-walled, hollow, easily crushed, and

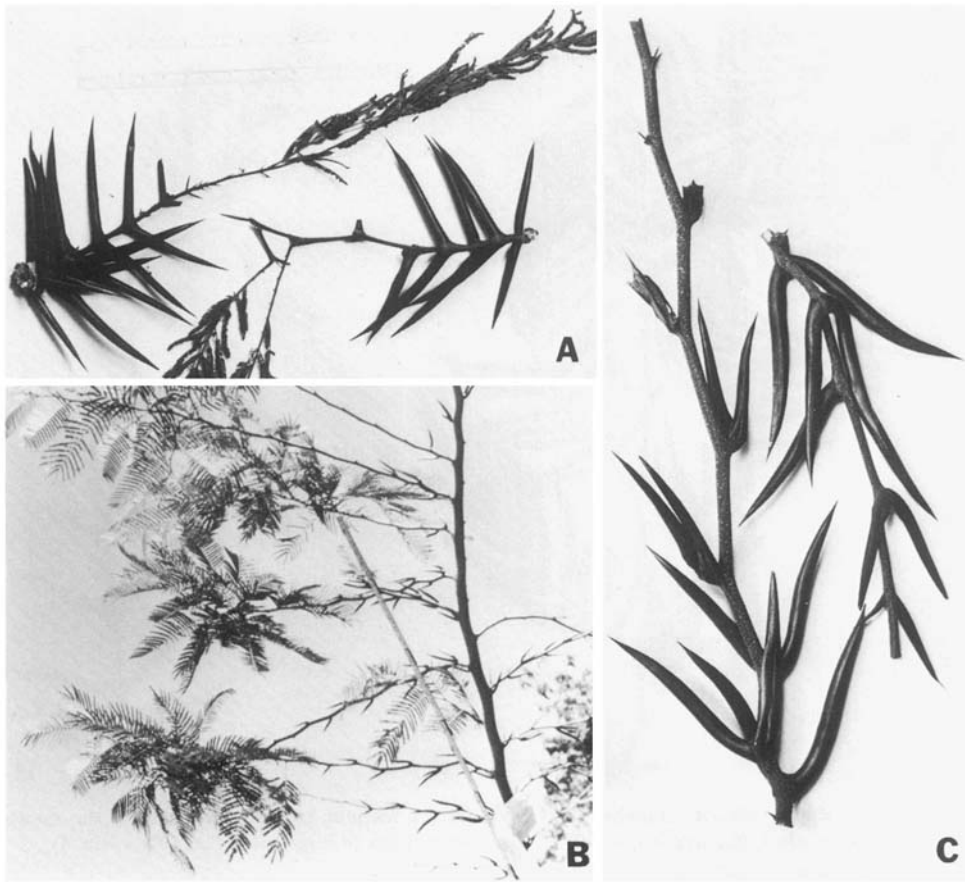


FIGURE 27.—*Acacia ruddiae* (Guatemala, site 9): A, type B thorns on short lateral branches from main trunk; B, representative crown section of 4-m-tall sapling; C, well developed type A thorns from the crown in Figure B.

occasionally only half of the stipule is enlarged. They often split at the base upon drying (Figure 25B), and ants, especially *Crematogaster*, often use this as an entrance hole. As the tree grows larger, some of the lateral branches have no thorns at all (Figure 26A), some branches have large swollen thorns at the base and tufts of leaves at the ends (Figures 27A, 27B), and some branches are very short and bear thorns best classified as type B (Figures 27A, C). The *A. ruddiae* in the Puerto Barrios area (sites 8 and 9) had most of its swollen thorns on branches such as those in Figures 26B and 27, while in Costa Rica the branches were usually very short with many thorns (as in Figure 27A) or very long with just a few scattered thorns (Figure 28A). The lower trunk of a large, old *A. ruddiae* is covered

with short branches with many thorns, making the tree very difficult to climb.

The crowns of *A. ruddiae* are more diffuse than any other swollen-thorn acacia and therefore look more like most mimosaceous legumes than do swollen-thorn acacias. Looking up through a crown (e.g., Figure 28B), one can often see large amounts of sky; only the most densely leafed branches (e.g., Figure 51A) look like typical swollen-thorn acacia branches. This is the case despite the fact that the crowns of *A. ruddiae* are usually fully insolated; while the young seedlings appear to grow fairly well in heavy shade, the mature trees almost always have canopy level or emergent crowns, suggesting that *A. ruddiae* probably cannot mature in heavy or broken shade.



FIGURE 28.—*Acacia ruddiae* (Costa Rica, site 6): A, lateral branches in crown of adult; B, looking up through crown of young adult.

The trees of *A. ruddiae* do not bear flowers until they are in the 8 to 15 m height and 15 to 30 cm DBH class. Small clusters of yellow and bee-pollinated inflorescences (Figure 25A) are scattered through the crown and not concentrated on main sexual branches as is common for swollen-thorn acacias. The seed pods appear to mature during the 2 to 4 months immediately following flowering, as with *A. melanoceras* and *A. allenii*, rather than waiting until the following dry season as with dryland, swollen-thorn acacias.

Adults of *A. ruddiae* show no more obvious insect damage than do other acacias not occupied by obligate acacia-ants. Since some have no ants living on them at all—though some worker ants forage in the foliage for nectar and probably insects—this immunity is likely due to the usual kinds of chemical defenses encountered in ordinary acacias. Shoot tips of *A. ruddiae* are slow growing in comparison with more usual swollen-thorn acacias. Associated with this they are very tough, compact, bitter in taste, and covered with dense hair (Figure 5A). They strongly resemble those of *A. macracantha* and *A. farnesiana*.

By virtue of the very well developed foliar nectaries and enlarged thorns, *A. ruddiae* has far more ants foraging on its leaf surfaces than ordinary nonant-acacias. None of these ants are obligate acacia-ants, but rather those species—*Pseudomyrmex*, *Crematogaster*, *Camponotus*—that live throughout the general forest canopy and that forage for dead, moribund, or live insects on foliage in general. While queens of obligate acacia-ants may occasionally be dispersed into habitats with *A. ruddiae* (definitely the case at sites 9 and 10 in Guatemala), I have never seen one of the characteristic type of entrance holes made by these queens in about 2,500 swollen-thorns examined carefully on 16 individual trees of *A. ruddiae*.

To examine the use made of *A. ruddiae* thorns by ants, a representative 3 m tall, fully insulated sapling growing in river-edge vegetation at site 4 was completely dissected. The acacia had 798 leaves on 51 branches; far less than 20 percent of the large leaves produced by the acacia were subtended by swollen thorns. Of the 371 thorns, 302 were, or had been, tenanted by some insect (on a "typical" swollen-thorn acacia, all thorns would have been).

Nineteen percent of the thorns had split naturally at the base, and all of these thorns had been entered by insects. Of all the thorns that had been entered by insects, by any means, 20 percent had parts of ant colonies in them or queens attempting to start a colony. Of the remaining thorns that had been entered, 95 percent contained microlepidopterous larvae, weevil larvae, and Orthoptera eggs. When these insects emerge, the acacia thorns are very likely to be occupied by ants. Spiders and other insects tenanted the remaining 5 percent of the thorns lacking ants. The ants represented at least 7 species in 5 genera—*Solenopsis*, *Crematogaster*, *Camponotus*, *Pseudomyrmex*, *Paracryptocerus*. While a detailed census is not available, cursory examination of *A. ruddiae* thorns in large old trees shows almost every thorn to have a part of an ant colony in it. It is extremely likely that the continual foraging of these ant species on the foliage occasionally results in less herbivore damage to the tree than if the ants were not present.

If a mutant strain of *A. ruddiae* provided any type of solid food to the ants, the probability is very high that it would quickly lead to the evolution of a strongly mutualistic interaction. It is impossible to know if *A. ruddiae* represents the gradual degeneration of a once intense mutualism or is on its way to more mutualistic interaction. The latter is more likely, since the former would require a strong relaxation of selection pressure by herbivores, such as might occur if a swollen-thorn acacia were to immigrate to a small oceanic island. The evolution of a type of Beltian body may be starting to occur with *A. ruddiae*; some of the plants at site 4 have clear tips on the pinnules, extending into the leaf about 0.25 to 0.5 mm. If the ants were to start to chew on this for moisture or nutrients during the time of year when insect prey is scarcest, and therefore maintain larger colony sizes than on plants lacking this modified pinnule tip, the evolution of a food body might occur. This is likely to be the way that typical Beltian bodies first appeared on acacias. Plants with a larger year-round population of ants would probably be less damaged by the periodic small outbreaks of host-specific insects that probably occur on many tropical trees, and certainly occur with nonant-acacias. Interestingly, the species of ant that began this behavior would be likely to concentrate more of its foraging on the acacia and less off, and be likely to

tenant an increasingly greater proportion of the thorns on the acacia. This could occur either through faster colony growth than could occur with ant species totally dependent on insect prey for growth, or through the ants moving into thorns left untenanted during periodic population lows in the other species of ants. Once the entire ant colony becomes concentrated in the acacia, it has a vested interest in the health of the acacia and coevolution of the interaction should occur at an ever increasing rate (Janzen, 1966a). As will be discussed further in respect to hybrids, this acacia appears to be a plant that would have greatly increased fitness by the gaining of the genetic information necessary for the production of Beltian bodies. This could well happen through introgression with a wet-forest acacia such as *A. melanoceras* at the southern end of the range of *A. ruddiae*, or *A. gentlei* or *A. cookii*, and the northern end of the range of *A. ruddiae*.

3. *Acacia melanoceras* Buerling

Acacia melanoceras Buerling, 1854:362.

Acacia multiglandulosa Schenck, 1913:362.

Myrmecodendron melanoceras (Buerling) Britton and Rose, 1928:93.

Acacia melanoceras is easily recognized since it is the only swollen-thorn acacia in the wet lowlands of central Panama and the Canal Zone (Figure 29). Where its distribution is tangent with that of *A. collinsii*, about halfway through the Canal Zone, *A. melanoceras* is easily distinguished from that dry-forest species since *A. melanoceras* has a very large number of nectaries on the leaf petiole, longitudinally ridged swollen thorns, spherical inflorescences, and huge leaves.

I have been unable to locate the type specimen of *A. melanoceras* and it is likely destroyed; however, the type specimen of *A. multiglandulosa* (at Berlin, now destroyed, but represented by Field Museum photo 1281 ex Berlin) is from the same locality as that of *A. melanoceras* (site 1) and is probably described from the same specimen or a duplicate specimen of the same collection. The description of the type of both *A. melanoceras* and *A. multiglandulosa* agrees completely with the characteristics of the swollen-thorn acacia population whose distribution is plotted in Figure 29. The type specimen of *A. multiglandulosa* is a representa-

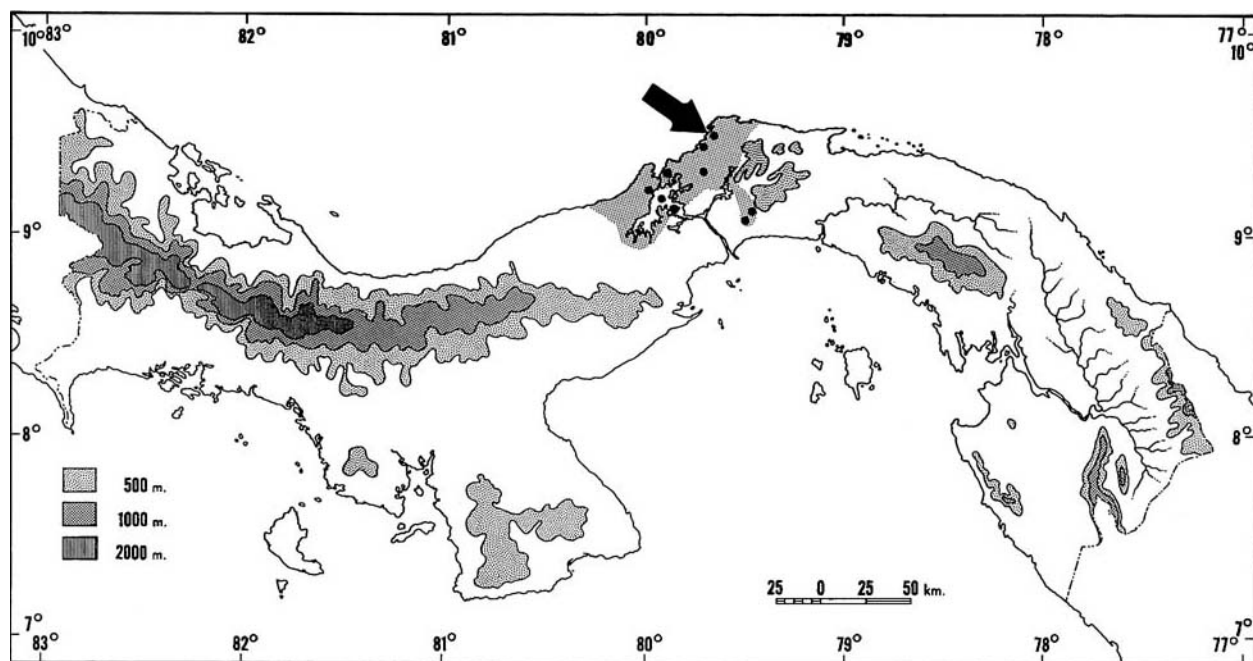


FIGURE 29.—General postulated distribution (stippled area) and specific collections sites of *A. melanoceras* in Panama.

tive distal end of a fertile branch from an adult acacia. Very long (20 cm) inflorescence-bearing branchlets such as the one on the type of *A. multiglandulosa* are commonly seen on old trees growing along river edges that have their crowns partly shaded by taller trees. The absence of swollen thorns on a branch bearing sexual branchlets, as is the case with the type specimen, is commonplace in old crowns of *A. melanoceras*. In 1915, Safford redescribed *A. melanoceras*, but under the name of *A. multiglandulosa*.

KEY COLLECTION LOCALITIES

1. Types of *A. melanoceras* and *A. multiglandulosa*: Portobello (Porto Bello), Colon, Panama (sea level). 1824, *J.G. Billberg*, no. 289.
2. Head of Gatun Valley, Canal Zone, Panama. 1914, *H. Pittier*, no. 6745 (US 716562, US 716560, US 716561; Safford 1915, Wheeler 1942).
3. Headwaters Rio Agua Salud, Canal Zone, Panama. *Wheeler*, III-6-1923 (Wheeler, 1942).
4. Marajal, near Colon, Canal Zone, Panama. *Wheeler*, VII-26-1924 (Wheeler, 1942).
5. Cerro Jefe, several mi N Cerro Azul, Panama, Panama. *R.D. Dressler*, VIII-28-1967 (pers. comm. plus thorn sample).
6. 400 m upriver (east bank) from the bridge at Rio Piedras, Colon. Panama. VII-3-1967, *DHJ*, nos. 1641, 1912, 1913, 1915, 1916, gp, mp.
7. Southwest corner of Zorro Island (in Gatun Lake), 5 km NW Nueva Providencia, Canal Zone, Panama. VII-7-1967, *DHJ*, no. 1894, gp.
8. 10 m post on Al. Ar. Trail, Barro Colorado Island, Gatun Lake, Canal Zone, Panama. *DHJ*, VII-7-1967, nc (I am indebted to R.D. Dressler for showing me this plant).
9. 7 km SW Gatun Locks on road to Escobal, Canal Zone, Panama. *DHJ*, VII-10-1967, nc (I am indebted to M. Nauman for showing me these plants).
10. France Field, Canal Zone, Panama (sea level). VIII-1924, *D. Fairchild* (US 1405611).
11. Between France Field and Catival, Colon Prov., Panama. I-9-1924, *P.C. Standley*, no. 30378 (US 1219256).
12. Near Frijoles, Rio Agua Salud, Canal Zone, Panama. III-6-1923, *C.V. Piper*, no. 5853 (US 1167694, US 1166375).
13. Margarita Swamp, Canal Zone, Panama. VI-28-1923, *O.F. Cook* and *R.D. Martin*, no. 14 (US 1491829).
14. Peña Blanca Bay, Barro Colorado Island, Canal Zone, Panama. VII-3-1934, *Shattuck*, no. 1087 (US 2366760).
15. Hills N of Frijoles, Canal Zone, Panama (50 m). XII-19-1923, *P.C. Standley*, no. 27582, (US 1217650).
16. Margarita Swamp near France Field, Canal Zone, Panama (sea level). II-1925, *J.B. Shropshire* (US 1208884, US 1208883, US 1208885), mp.
17. Barro Colorado Island, Canal Zone, Panama. VIII-1927, *L.A. Kenoyer*, no. 373 (US 1319142).

NATURAL HISTORY

Acacia melanoceras is one of the seven species of swollen-thorn acacias with small geographic ranges (*A. allenii*, *A. mayana*, *A. ruddiae*, *A. sphaerocephala*, *A. cookii*, *A. gentlei*, the others), and like these species is restricted to comparatively wet and undisturbed forests. In 1928 Standley reported *A. melanoceras* as common in the forests on the Atlantic slopes of the Canal Zone; in comparison with the more widely distributed dry-land species, it is nevertheless very rare. For example, in contemporary forested habitats there appear to be at least 100 adult plants of *A. collinsii* on the dry Pacific side of Panama for every one adult *A. melanoceras* on the Atlantic side. It is of course impossible to know to what degree this difference is due to *A. collinsii* becoming much more common with the development of brushy cattle pastures and wasteland. One thing may be said with certainty, however, and that is that *A. melanoceras* disappears from any habitat subjected to disturbances that are any more catastrophic than infrequent logging.

Since the Atlantic side of Panama, aside from banana farming, is infrequently logged, it is likely that the contemporary distribution of *A. melanoceras* is not much different from that of pre-Colombian times.

Every reproductively mature *A. melanoceras* found in this study (sites 6 to 9) was in second-growth woody vegetation that had grown better than 15 years without further disturbance. All sites were either areas that had been clear-cut long before for logging or farming (e.g., Barro Colorado Island) or had been swept clean by a flooding river. Seedlings (Figure 30A) were found only in the full shade of canopies 10 to 15 m tall, and on wet to moderately well-drained soil. *A. melanoceras* generally becomes reproductively mature under, or in, jagged breaks in the general canopy; they are almost never fully insolated. Senescent canopies are often directly under a small hole in the general canopy (Figure 31). Neither mature plants nor seedlings are common at any site. Two adults per acre is a high density for *A. melanoceras*. Adults and young plants almost always occur as single

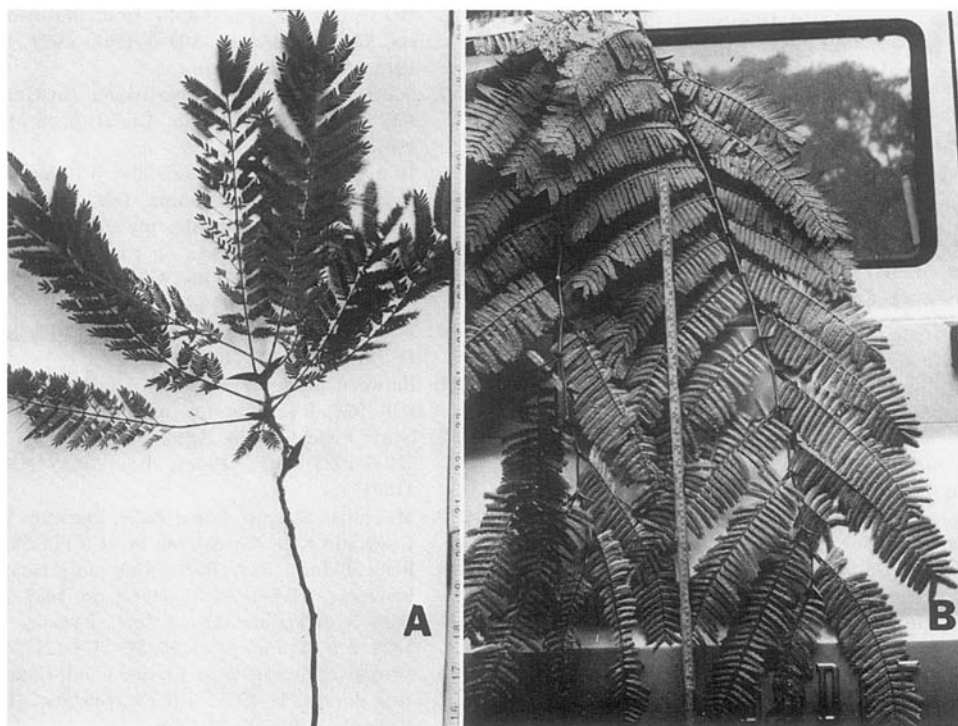


FIGURE 30.—*Acacia melanoceras*: A, seedling from deep forest shade (scale in inches; Panama, site 6); B, normal lateral branch from 6-m-tall plant (Canal Zone, site 9).



FIGURE 31.—*Acacia melanoceras* (Panama, site 6): A, looking up through crown of 15-m-tall mature tree that is still reproducing, but only poorly; B, looking up through senescent crown of 12-m-tall tree that has lost its ant colony.

shoots. The only clump of shoots encountered in this study was at site 6 on the edge of an island at Gatun Lake. A single tree—based on tree rings, at least 27 years old—had produced a large number of root suckers and seedlings covering an area about 20 by 30 m. The cluster was on the north side of a hill and situated such that the taller forest trees shaded it, yet the opening caused by the lake led to day-long indirect insolation. Wheeler (1942) illustrates a small clump at site 4; the plant has the appearance of a cluster of stump and root sprouts from a large adult that was cut when the swamp was cleared of forest.

Acacia melanoceras appears to be completely absent in repeatedly disturbed pasture, field edges, roadsides, cleared swamps, etc., in the central and northern part of the Canal Zone and adjacent areas in Panama; however, it is still present in adjacent relatively undisturbed forest, or forest that has been allowed to regenerate for a long time. Extinction of *A. melanoceras* following human disturbance is probably based on the following factors:

(1) *A. melanoceras* does not set seed until at least 8 to 10 years old; I have found heavy seed production only on very healthy old trees that are in partial shade of a tall broken forest canopy. Such a long time in reaching reproductive maturity is likely due to the shady microhabitat occupied by this acacia. (2) When adults or subadults are exposed to direct insolation by clearing the forest, they become very shrubby, stunted, and die after 1 to 3 years. They produce no seed during this time. Failure to grow in full sunlight appears to have two causes: First, the leaves are probably genetically programmed to operate most efficiently at low-light density and air temperature, and the opposite microclimate is probably damaging. Second, large numbers of phytophagous insects in young secondary succession probably find the acacia to be very edible. Shoot tips are repeatedly eaten off the vertically elongating shoots, resulting in a bush life form which is probably very inefficient. It is not obvious, however, why the occupant *Pseudomyrmex satanica*, which is so effective at protecting *A. melanoceras*

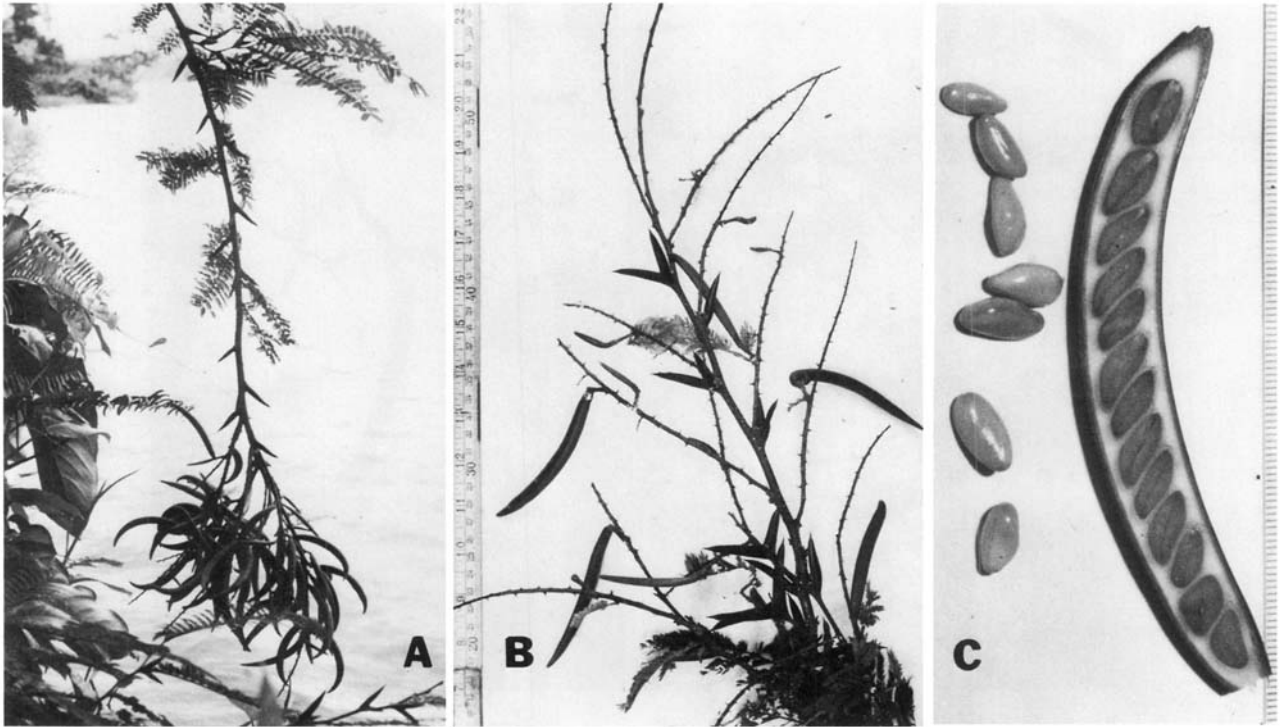


FIGURE 32.—*Acacia melanoceras*: A, reproductive branch with extraordinarily heavy pod set (Canal Zone, site 7); B, reproductive branchlets with representative pod set (Panama, site 6); C, longitudinal section through immature but full-sized pod (Canal Zone, site 7).

in the forest, is apparently so ineffective in more open sites. It may be that their protective abilities per insect attacking are the same in both habitats, but that the plant is less able to repair the more frequent damage in the open. (3) *A. melanoceras* does not sprout readily from cut stumps. The stumps of many young and mature *A. melanoceras* die without sucker-shoot regeneration, in strong contrast to the behavior of other swollen-thorn acacias. It may be that heavily shaded plants have insufficient energy reserves stored in their roots for reproduction by sucker shoots. (4) The seed of *A. melanoceras* (Figure 32c) has a soft seed coat and apparently needs to germinate immediately. Even if a seed is dispersed into early stages of succession, it would probably die of desiccation if it arrived during the dry season of one of the dry "spells" during the wet season. (5) Being soft-seeded, *A. melanoceras* cannot be dispersed by the same species of birds that disperse the hard seeds of species living in drier habitats (e.g., *A. cornigera*, *A. hindsii*, *A. collinsii*); these birds (e.g., jays, derby fly-catch-

ers) pass the hard seeds through their gizzard unharmed, while a seed of *A. melanoceras* would surely be digested. Any dispersal of these soft seeds must be via birds that regurgitate seeds (e.g., trogons, cotingas). These birds characteristically live in older stages of succession and primary forest and are unlikely to disperse *A. melanoceras* seeds out into large tracts of young second growth. (6) Since the seedlings of *A. melanoceras* are normally found only in heavily shaded forest understory, it would not be surprising to find that the queens of *P. satanica* do not search in dry or fully insolated sites. The young acacia would then be competing with many fast-growing plants with a very high density of herbivorous insects. It is possible that the searching queens of *P. ferruginea*, coming from *A. collinsii* growing in young second growth, could occupy young *A. melanoceras*. *A. collinsii*, however, has not yet invaded much of the disturbed land left when forest suitable to *A. melanoceras* was cleared. This general interaction could perhaps be observed if half of an island such as Barro Colorado

Island were clear-cut and turned into brushy pasture.

Acacia melanoceras, *A. allenii*, and *A. ruddiae* live in the wettest sites occupied by the genus in Central America. The dry season in its habitats is indistinct and the sites generally receive 3.5 to 5.5 m of rainfall. At sites 6 and 7, the roots of *A. melanoceras* were under water or in mud almost all year. The cluster of fruits in Figure 32A hung down to within a few inches of Gatun Lake. The bark of *A. melanoceras* is almost always damp from rain and those parts of the acacia not patrolled by ants often become covered with lichens and other epiphytes.

That *A. melanoceras* lives in wet forest that lacks other acacia, and for the most part other mimosoid legumes, may explain in part why quite healthy but unoccupied adults are occasionally encountered in the forest. Judging from the holes in the thorns, these acacias were at one time occupied by large ant colonies, which died for unknown reasons. In contrast to the subsequent death of the tree that would have occurred were this a dry-land acacia, the abandoned acacias appear to live a number of years, bear successive seed crops, and are at times tenanted by a variety of other ants that normally live in hollow twigs in the general canopy. These unoccupied acacias suffer herbivore damage, but it is not very severe (in contrast to individuals even with a strong ant colony in insolated sites a few hundred meters away). I suspect that in leaving

behind the younger stages of succession and the large number of insects it harbors, especially those that normally feed on mimosoid legumes, *A. melanoceras* has moved into a habitat of reduced herbivore pressure. Such a strategy is likely to be effective until over evolutionary time other mimosoid legumes make the same move for the same reason.

While *A. melanoceras* appears to be pollinated by small bees—Halictidae, Megachilidae, *Ceratina* in the Apidae—pollination is either very ineffectual or the plant has little reserves for maturing fruits. The seed crops on almost every tree examined have been very small, ranging from 2 to 30 pods; the long flowering branchlets (Figure 32B) set only 1 or 2 pods per branchlet and often none at all. The 13-seed pod in Figure 32c is representative of the number of seeds per pod; *A. melanoceras* does not show the strong variation in number of seeds per pod found in the acacias of drier sites. The large pod crop on the acacia at site 7 provides several lines of evidence to suggest that the usual small seed crop is due to lack of energy reserves rather than poor pollination: (1) This tree was growing in an exceptionally good site, as is evidenced by the large number of healthy sucker shoots, had an immense ant colony, and large amounts of lush foliage (as in Figure 30B and contrasted with Figure 31A). There were no other adult swollen-thorn acacias within at least 200 m of this plant (down the island) and at least 500 m

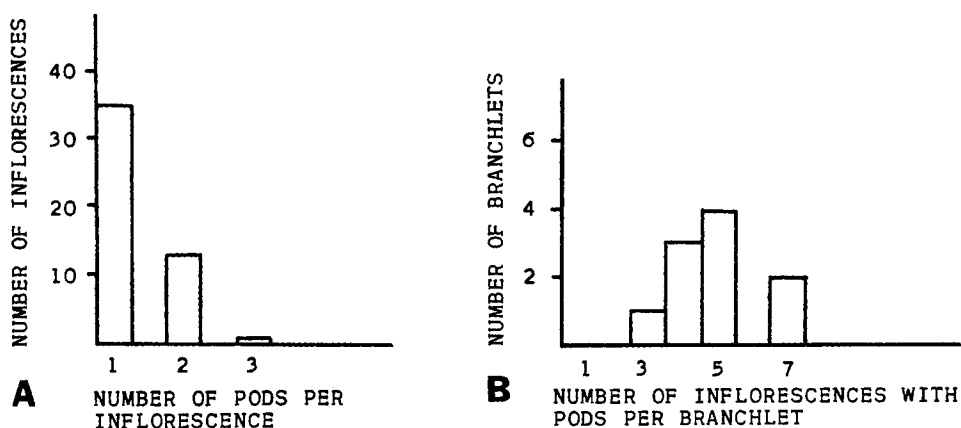


FIGURE 33.—*Acacia melanoceras* (Canal Zone, site 7): A, distribution of 64 mature pods among the 49 infructescences on 10 sexual branchlets from one tree with an extraordinary seed crop; B, distribution of the 49 infructescences in Figure A among the 10 sexual branchlets.

across the lake. This plant set at least 900 pods in large clumps such as that in Figure 32A. The implication is that the tree is self pollinated, or else the clump of shoots originated from two seeds. (2) The total number of inflorescences produced by each sexual branchlet appeared to be no different from that of other acacias examined that had produced only 0 or 1 pod per sexual branchlet. The number of sexual branchlets per major tree branch was likewise no different in any obvious way; however, the number of inflorescences that produced pods, per branchlet, was much higher (Figure 33B) than is usually observed with *A. melanoceras*. Two sexual branchlets had 7 pods each on them, and none had only one. (3) There were even more than one pod set per inflorescence in many cases (Figure 33A). That the pods were distributed among the

inflorescences in this manner, rather than being uniformly distributed (i.e., retain more inflorescences, each with one fruit), suggests the possibility that the plant chooses out-crossed female florets as those to mature. This tree had an average of 31 inflorescence-bearing axils per sexual branchlet (=10). Its total crop of about 18,540 inflorescences produced about 960 pods on 735 inflorescences for a total seed crop of about 10,560 seeds. There are about 10 female florets on each inflorescence, meaning that only 0.6 percent of the tree's ovules matured.

Associated with the small seed crop observed on most adult *A. melanoceras*, it is particularly noteworthy that this species is free from predation by the bruchid beetles that take such a high toll of hard-seeded acacias. This means that virtually every

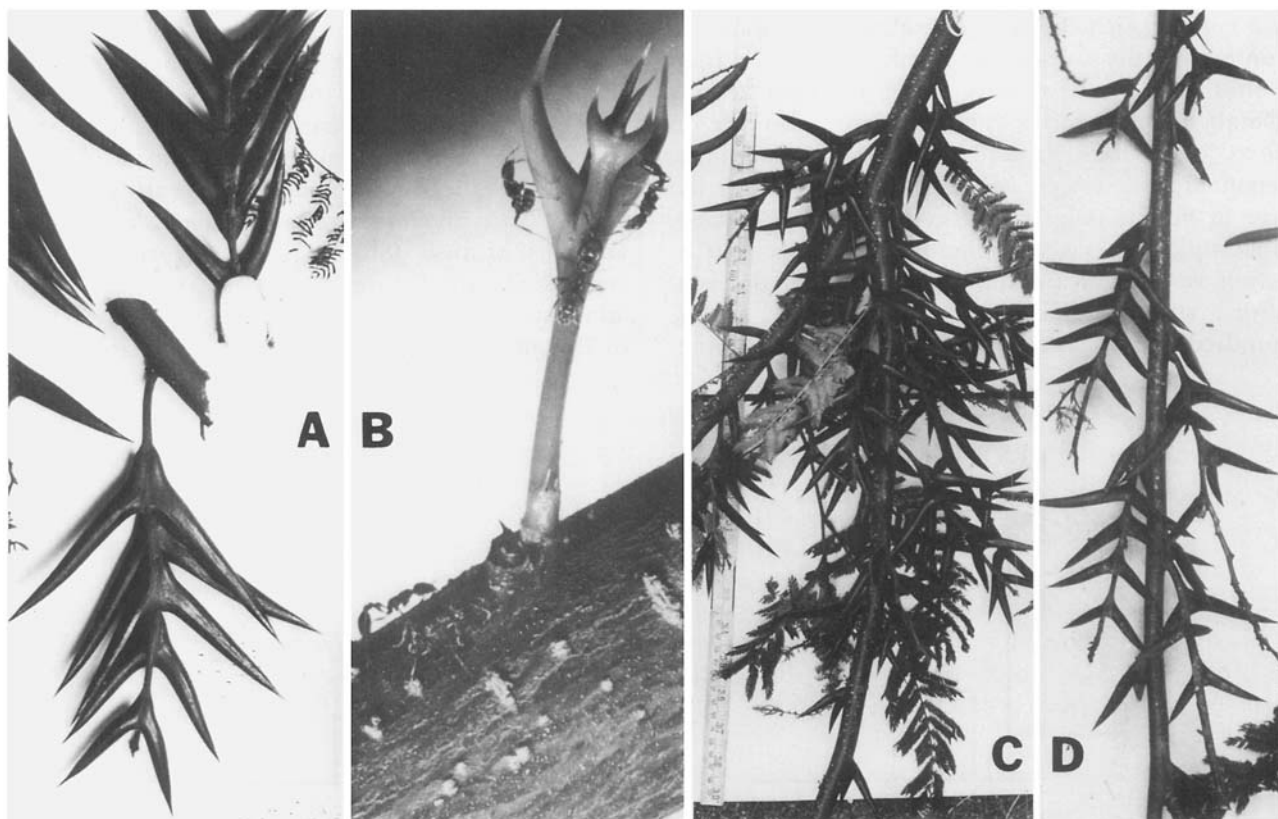


FIGURE 34.—*Acacia melanoceras* (A–C, Canal Zone, site 7): A, type B thorns on short lateral branches from the main trunk of a mature tree; B, immature type B thorns on newly developing short lateral branch from same trunk; ants are *Pseudomyrmex satanica*; C, maximally developed cluster of type B thorns on lateral branch of same tree; D, type B thorns on lateral branch from crown of very old *A. melanoceras* (Panama, site 6).

seed dispersed by the plant is viable, in contrast to the case with hard-seeded, swollen-thorn acacias where most seeds are killed by bruchids before the seeds are dispersed. In short, the average number of viable seeds produced per adult *A. melanoceras* is likely to be as great as for acacias of drier sites that initially produce many more seeds.

A seedling of *A. melanoceras* (Figure 30A) can probably germinate and grow slowly to adulthood almost anywhere in the forest, in strong contrast to the seedlings of hard-seeded, swollen-thorn acacias, which must land in a fairly young stage of succession to survive. This means that a certain large fraction of the viable seeds produced by dry-land acacias will not make it to the stage where they have any chance at all of surviving. Therefore, the apparently smaller seed crop of *A. melanoceras* may in fact not mean that any fewer saplings develop per adult than is the case with dry-land, swollen-thorn acacias.

Throughout its range, I found *A. melanoceras* to be occupied only by *Pseudomyrmex satanica* (Figure 34B). (The "*Pseudomyrmex satan*" cited by Standley in 1928 is a misspelling.) Wheeler (1942) likewise had no records of other obligate acacia-ants in *A. melanoceras*. Since *P. satanica* is restricted to *A. melanoceras*, the ant will probably go extinct as the remaining forest in Panama is converted to agricultural land. *P. satanica* is probably a "wet forest derivative" of the widespread *P. ferruginea*, which occupied *A. collinsii* in the drier parts of Panama, among other places. As will be discussed later, the part of the *P. ferruginea* population occupying *A. allenii* on the Osa Peninsula and the Golfito region in Costa Rica probably represents an intermediate form of the same type of speciation event. *P. satanica* is easily distinguished from *P. ferruginea* in Panama by the former's black color, habit of holding the gaster curled under the body (Figure 34B), and having multiple-queen colonies. Unoccupied adults of *A. melanoceras* are tenanted by the usual miscellaneous array of ants found in unoccupied swollen-thorn acacias: *Crematogaster*, *Azteca*, *Camponotus*, *Paracryptocerus*, and *Pseudomyrmex*. Since, as mentioned previously, unoccupied *A. melanoceras* seems to survive fairly well in well-developed forest, these colonies may attain unusually large size for ants tenanting swollen-thorn acacias. At times an *Azteca* or *Crematogaster* colony will take over all the thorns on the tree, but the

ants' foraging on the acacia foliage is not thorough enough to prevent frequent damage by herbivores. *P. satanica* founding queens establish themselves in the thorns of *A. melanoceras* seedlings at the stage shown in Figure 30A. Until the ant colony has grown large enough to patrol the young shoot, growth is not rapid enough for the plant to have more than 3 to 6 intact thorns less than two years old) at any one time. Not only is the number of founding queens in the system small as compared with dry-land, swollen-thorn acacias, but one very rarely finds searching queens on the outside of the acacia. This indicates that few queens are produced by adult colonies or that the queens have a difficult time locating the widely spaced seedlings. Both possibilities are probably true.

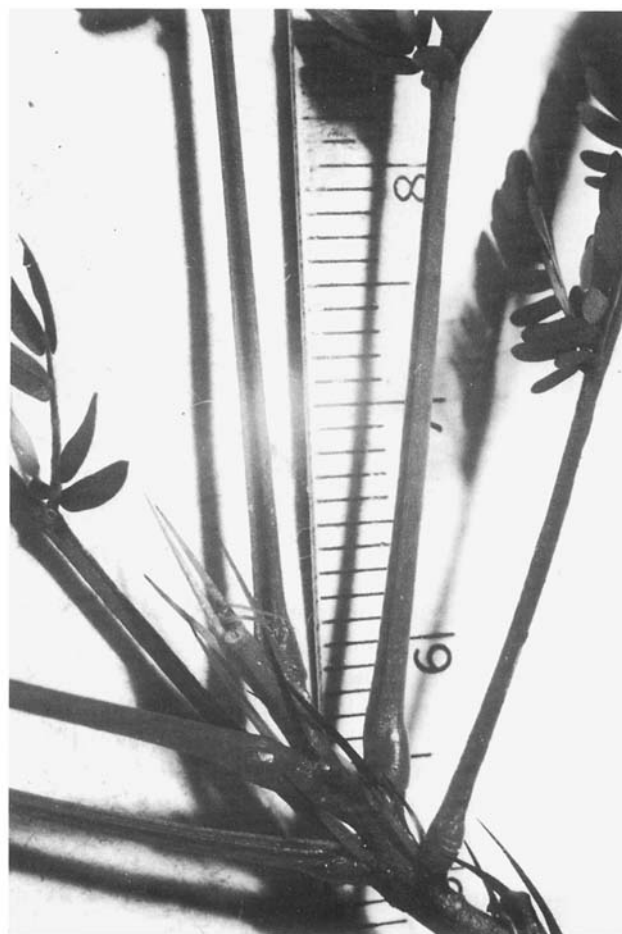


FIGURE 35.—Dormant shoot tip and "crown" of *A. melanoceras* seedling above point where latest swollen-thorns were produced (Panama, site 6).



FIGURE 36.—*Acacia melanoceras* (Panama, site 6): A, petiolar nectaries characteristic of seedling leaves near swollen thorns; B, maximal development of petiolar nectaries in crown of old plant; C, minimal petiolar nectary development of large leaves subtended by type A thorns on lateral branches of 5-m-tall subadult.

Leaf production on the seedling acacia differs from that of dry-land acacias. The seedling produces 1–4 leaves subtended by swollen thorns followed by a cluster of leaves without swollen thorns (Figure 35). By the time that swollen thorns have rotted off (about 1.5 years later), the leaves have been shed and the process is repeated if an ant colony has not become established. How long the seedling can continue this process is unknown, but I have found seedlings that have gone through this process at least five times. The seedling in Figure 30A had done it at least four times, yet was only 53 cm tall.

On the very young seedlings there may be no nectaries on the leaves (Figure 35) except those

TABLE 9.—Distribution of leaflets among the 9 leaves on a 40-cm-tall seedling of *A. melanoceras* at the time of production of its first swollen thorn (a total of 52 leaves had been produced by the seedling, and the thorn was on the 50th node)

Leaf number	Rachis length (mm)	Petiolo length (mm)	Number of pinnae	Number of pinnules
1	83	44	16	428
2	108	22	22	604
3	104	37	18	492
4	117	30	24	660
5	112	27	27	492
6	113	24	28	774
7	116	28	24	654
8	108	30	22	598
9	109	32	21	572

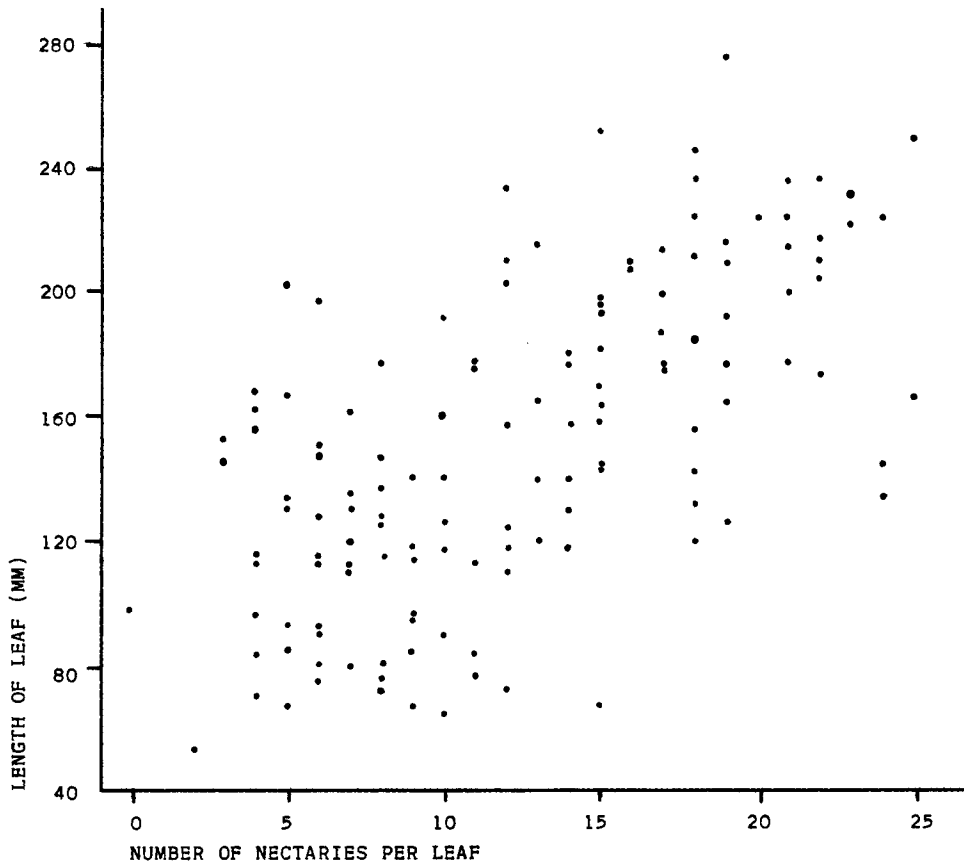


FIGURE 37.—Distribution of 1256 petiolar nectaries among 24 leaves of *A. melanoceras* from sterile lateral branches in an adult crown (Panama, site 6).

subtended by, or close to, swollen thorns (Figure 36A). As the plant matures, the number of petiolar nectaries increases through the progression shown in Figures 9A, B, C. The distribution of petiolar nectaries among the leaves (Figure 30B) in a mature acacia's crown (Figure 37) displays all the frequencies that can be observed by watching seedlings develop, but the majority of leaves have between 5 and 20 nectaries. The leaves of *A. melanoceras* (Figure 30B) are at least three times the size of those found on dry-land acacias. The number of nectaries is higher on adults of *A. melanoceras* than on any other swollen-thorn acacia. On some *A. melanoceras* there are even nectaries on the pinnae. Owing to the shaded nature of its habitat, however, nectar production may be very low.

Beltian body production by *A. melanoceras* is never fully developed, again probably from the relatively high cost to the plant of Beltian bodies

in a habitat with low solar energy input and (perhaps) somewhat reduced herbivore loads. The first leaves on a seedling, as is usual with swollen-thorn acacias, have no Beltian bodies. By the time the leaves are developed to the level described in Table 9, there are 1 to 3 Beltian bodies per new leaf; a dry-land acacia would have been producing 10 to 20 per leaf by the time it had produced this many (52) leaves, even when growing in the shade. Even the very large and healthy acacia at site 6 was producing Beltian bodies on only about half its pinnules.

On adult *A. melanoceras*, type B thorns appear on a small stubby branchlet (Figure 34B) which quickly elongates to 5 to 10 cm (Figure 34A). On large and healthy occupied acacias, such as the one at site 6, there may be many of these short shoots in relatively tight clusters (Figure 34C). On acacias in poorer condition, they are usually scattered along

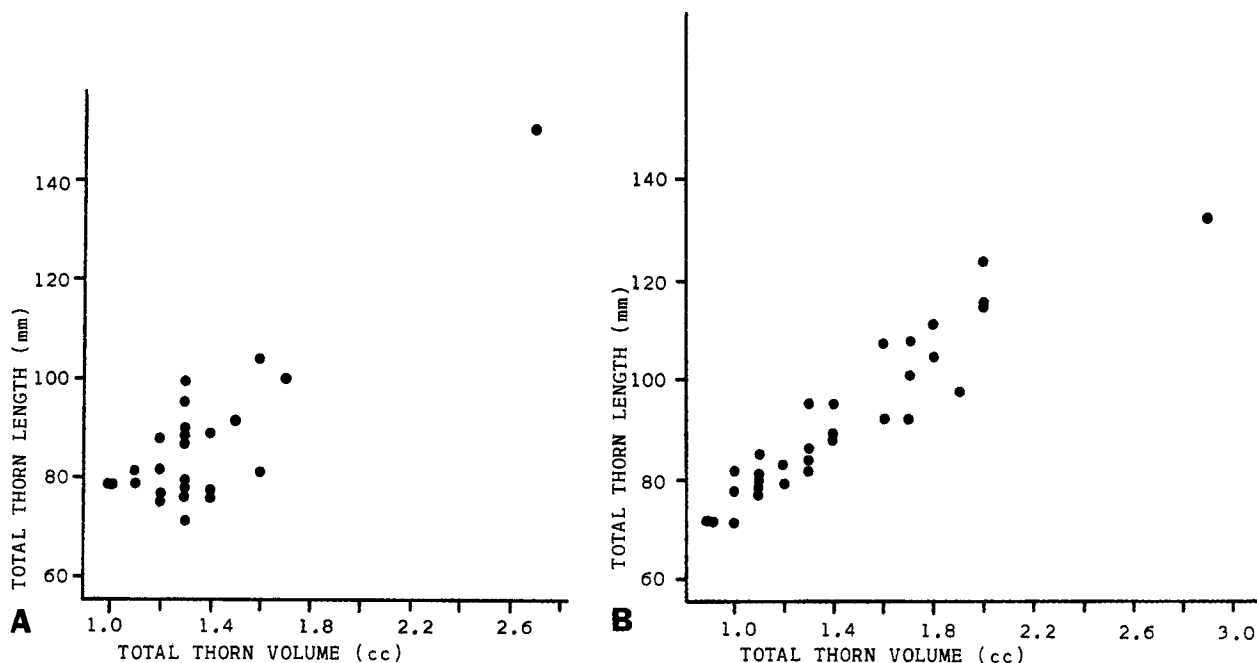


FIGURE 38.—Mature *A. melanoceras* (Canal Zone): A, distribution of total thorn volume among the 25 largest type B thorns (site 9); B, distribution of thorn volume among the 31 largest type B thorns (site 7).

the branches (Figure 34d). The volumes of *A. melanoceras* type B thorns (Figure 38) are not spectacular and are rarely more than twice that of type A thorns. The similarity of the two different sets of thorns in Figure 38 is probably representative of variation in type B thorns throughout the range of *A. melanoceras*.

Several aspects of the biology of *A. melanoceras* reflect its occupation by a multiple-queen species of ant: (1) As noted, there is not a great difference in size or toughness between type A and type B thorns. While *P. satanica* colonies do not have the great number of queens characteristic of *P. venefica* and the undescribed multiple-queen *Pseudomyrmex* in *Acacia hindsii* in western Mexico (Janzen, 1973), they do have 5 to 20 or more per colony and this means that the loss of a queen-thorn to a bird or other predator is not fatal to the colony. This means that the primary selective pressure for very large and strong type B thorns has been removed. (2) When there is the rare opportunity for an *A. melanoceras* to reproduce vigorously with root suckers, as at site 6, the multiple-queen colony can expand indefinitely to provide patrolling for the increased surface area of foliage. Therefore, while

A. melanoceras normally occurs as single plants that could easily be patrolled by a single-queen colony, when the situation arises, the plant can greatly increase in size (and presumably seed production). The acacia is effectively polymorphic for growth form. (3) The new searching queens may on occasion be absorbed by the colony that produced them rather than go off in search of seedlings. This may result in a lower survival of seedlings than would be the case with a single-queen ant species situation. On the other hand, the presence of several queens in a young seedling are all contributing workers to the development of the young plant. (4) When the opportunity occurs for the growth of a cluster of *A. melanoceras* shoots occupied by one multiple-queen colony, the shoots are free of competition from immediately adjacent vegetation. As is usually the case with large multiple-queen colonies, *P. satanica* is especially effective at killing foliage that contacts its acacia. Incidentally, as the name suggests, *P. satanica* is very aggressive toward a wide variety of foreign objects. These ants are perhaps the most difficult of the obligate acacia-ant species to work with, primarily because they run inside

one's clothing rather than just on top as is the case with the other species. As mentioned before, this means that a large cluster of *A. melanoceras* occupied by a large colony of *P. satanica* tends to be in extremely good condition.

4. *Acacia allenii*, new species

Arbol usque ad 25 m alta; ramuli novelli minute velutini, glabrescentes; stipulae spinescentes interdum magnae, teretiusculae, porcatae, usque ad 4 cm longae, 1 cm latae; folia 20–40 cm longa; nectaria sessilia cupulata ad juncturas pinnarum omnium et 1–10 in petiolis; pinnae (5–) 10–20-jugae, 7–10 cm longae; pinnulae (10–) 20–30-jugae, oblongae, lineare, vel ellipticae, (3–) 5–10 mm longae, 1–4 mm latae, obtusae, glabrae; flores aurei in capitulo globoso; involucellum annulare in medio pedunculo vel inferiore, interdum basi; legumina (immatura) atrobrunnea, puberula, granulata, glabrescentes, lineares, 8 cm longa, 8 mm lata, complanata, acuta sessiles vel subsessiles.

TYPE.—*D. H. Janzen* 1769, Costa Rica, Puntarenas Province, Osa Peninsula, bank of tributary of Río Agua Buena, 3.5 mi SW of Rincón, 9 March 1967 (holotype US 2639555; isotypes F, GH, MEXU, MICH, MO, NY, UC). PARATYPES.—Costa Rica: Puntarenas: Forested hills near Golfito, Golfo Dulce, *P. H. Allen* 5997 (US). 3.4 mi E of Golfito, *Janzen* 1658 (F, MICH, MO, NY, UC, US). 6 mi S of Rincón on the "Road to the Pacific," *Janzen* 2000 (F, GH, MEXU, MICH, MO, NY, UC, US).

Type tree 8 m tall with widely spaced branches and very dark green bipinnately compound leaves 20 to 40 cm long. Pinnules 8 to 11 mm long, 2 to 3.5 mm wide and up to 60 per pinna. Pinnae 7 to 10 cm long and up to 40 per leaf. 2 to 10 widely spaced petiolar nectaries and 1 to 2 nectaries on rachis at bases of pinnae. Swollen stipular thorns dark brown and up to 4 cm long and 1 cm wide at base, external thorn walls with low and rounded longitudinal ridges. New leaves with orange-yellow food body on tip of each pinnule. Internode length 5 to 10 cm on lateral branches. Sterile specimen. Fruits and flowers described below from other specimens. *Janzen* field collection number 1769. Types deposited in U. S. National Herbarium, Smithsonian Institution.

This plant is named in honor of Paul H. Allen, who collected the first specimen (site 1) and did so

much to aid plant biologists working in Central American wet forests. In his book (*Allen, 1962*) *A. allenii* is identified as *A. melanoceras*, a mistake easily made if one is working from herbarium specimens of either species. His specimen from site 1 bears immature inflorescences but was not chosen as the type because its leaves were badly damaged and very small. This type of foliage is typical of flower-bearing branches but not sterile branches. Sexual material is of almost no use for identification or reference since plants bearing fruits or flowers are extremely rare in time and space. For these reasons, a sterile plant was chosen for the type (site 6). Specimens of mature pods are not available from any *A. allenii*, and the only good collection of flowers (site 5, no. 2000) is from a nearly leafless tree. The tree from which the type specimen was taken was growing approximately in the center of the geographic range of *A. allenii* (Figure 23), and along a creek bank in lightly disturbed "rain forest," which seems to be the normal habitat for *A. allenii*. Its foliage is very representative of sterile and mature plants of the species; the plant was 4 m tall and originated as a sucker shoot from a 22 cm diameter downed trunk that was at least 25 years old. I estimate that the shoot would have flowered for the first time within the next 3 to 4 years. It was occupied by a large colony of *Pseudomyrmex ferruginea*.

Acacia allenii is very similar (and presumably very closely related) to *A. melanoceras*. I feel justified in distinguishing it as a separate species on the following grounds:

1. The population of *A. allenii* appears separated from that of *A. melanoceras* by at least 100 miles (and probably more) and by the Continental Divide. Despite careful searching, neither plant has been found in the wet and relatively undisturbed forests along the Pacific side of the mountains running through the western half of Panama. It seems that by the time one moves high enough in the mountains to find sufficient rainfall for *A. allenii* or *A. melanoceras*, it is too cold for the species. *A. collinsii* occupies the drier areas between the ranges of *A. allenii* and of *A. melanoceras*. In view of the long geographic distance between *A. allenii* and *A. melanoceras*, genetic exchange by either pollen or seed flow seems extremely improbable. This is not meant to imply, however, that there would not be extensive exchange of genetic

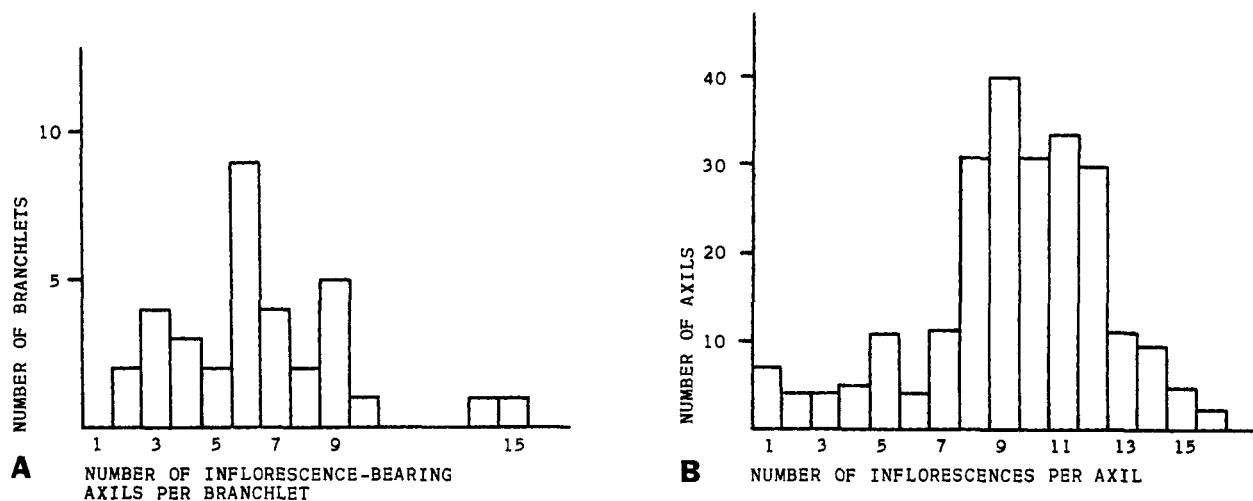


FIGURE 39.—*Acacia allenii* (Costa Rica, site 5): A, distribution of 242 inflorescence-bearing axils among 37 sexual branchlets from the crown of a 22-m-tall tree; B, distribution of 2255 inflorescences among the 242 axils in Figure A.

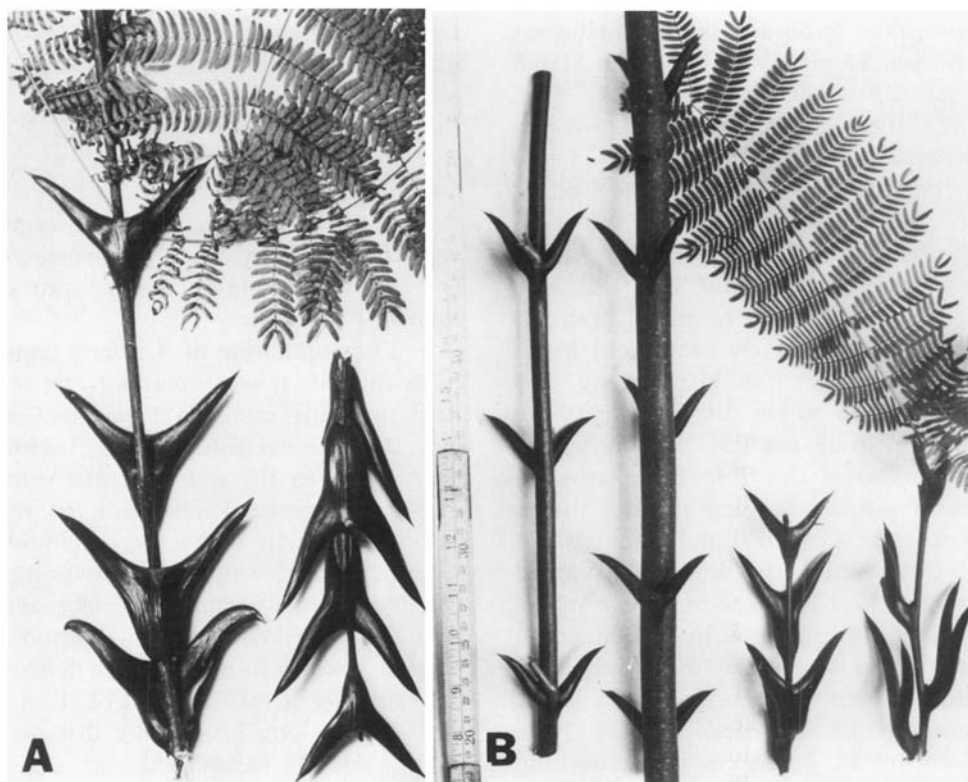


FIGURE 40.—*Acacia allenii* (Costa Rica): A, left, type B thorns on the base of a lateral branch with terminal type A thorns; right, type B thorns on a short lateral branch from the main trunk (site 2); B, left, type A thorns on lateral branches and main trunk of 3-m sapling; right, type B thorns on short lateral branches of the same tree (site 5).

material were this gap to be bridged in some manner. This seems unlikely, since both species become even more rare than they already are as their habitat comes under agricultural influence.

2. The foliage of *A. allenii* is more similar to that of *A. melanoceras* than it is to any other acacia. However, leaves from mature *A. allenii* are easily distinguished from those of *A. melanoceras*, since a leaf of *A. allenii* usually has only 1 to 5 petiolar nectaries and has pinnules with about twice the surface area of those of *A. melanoceras*. These two differences, along with the floral traits described below, are consistent throughout the population of *A. allenii*.

3. Inflorescences of *A. melanoceras* are borne on long (up to 45 cm) sexual branchlets that tend to be bunched near the ends of sterile branches; inflorescences of *A. allenii* are borne on short (3 to 15 cm) sexual branchlets scattered along major branches and therefore throughout the crown. The number of axils with inflorescences on a sexual branchlet (Figure 39, 42A) is about half that of *A. melanoceras*. While each sexual branch of *A. melanoceras* has 1 to 5 inflorescences per axil, each inflorescence-bearing axil on *A. allenii* has up to 15 or 16 with a mean at about 9 for large samples.

4. The type B swollen thorns of *A. melanoceras* are normally found on short branches, while those of *A. allenii* are much more likely to be strung along the lower parts of a branch that bears large leaves and type A thorns on its distal portion (Figure 40A). *A. allenii* thorns regularly have an inward projection that partly occludes the basal part of the thorn cavity. This is almost always absent from the thorns of *A. melanoceras*.

5. The differences between *A. allenii* and *A. melanoceras* are of the same magnitude that can be encountered over the ranges of one widely spread species such as *A. collinsii*, *A. cornigera*, or *A. hindsii*. However, these widespread species appear to have continuous ranges and almost always the variation is clinal in nature. *A. allenii* and *A. melanoceras* each appear to be going its own way evolutionarily, and I have no reason to suspect that their similarity will persist through time. If for no other reason, they are likely to diverge since *A. melanoceras* is occupied exclusively by a multiple-queen ant colony while *A. allenii* is occupied by a single-queen species. There is always the possibility that *P. ferruginea* will evolve multiple-queen

behavior and thereby evolutionarily "catch up" with *P. satanica* in *A. melanoceras*. In the meantime, however, *A. melanoceras* will likely have further diverged from *A. allenii*.

6. When describing the ecology of these two populations, lumping them under one Latin name destroys resolution. To call them mutual "subspecies" is to infer a common evolutionary origin, when in fact *A. melanoceras* may be a wet-forest derivative of the Panamanian portion of the *A. collinsii* population, while *A. allenii* may be a wet-forest derivative of the Costa Rican portion of the *A. collinsii* population. Even if one is in fact the result of a long-distance, overland-seed dispersal from the other's population (the most likely origin), we still have no way of knowing which is the "parent" species and which the "subspecies."

KEY COLLECTION LOCALITIES

All specimens are from Puntarenas Province, Costa Rica.

1. Forested hills near Golfito. III-3-1951, *P. H. Allen*, no. 5997 (USNH 2085794). *Allen* (1952) reports *A. allenii* as occasional in pastures around Golfito.
2. 2.5 mi E (inland) of Dominical. *DHJ*, VI-25-1967, no. 1669, mp.
3. 3.4 mi E Golfito. *DHJ*, VI-28-1967, no. 1658, fl.
4. 11.0 mi E Golfito. *DHJ*, VI-28-1967, II-28-1965, nc.
5. Within 8 miles of Rincón along road to the Pacific and along highland road, Osa Peninsula. *DHJ*, III-1-3-1965, no. 791, 803, 811, 812, 813; III-10-1968, no. 2000, fl.
6. TYPE.—bank of tributary of Rio Agua Buena, 3.5 mi SW Rincón, Osa Peninsula. *DHJ*, III-9-1967, no 1769.

NATURAL HISTORY

Like *A. melanoceras*, *A. allenii* has a very narrow geographic range (Figure 23) which probably reflects rather narrow tolerances of moisture and temperature. Its uppermost elevation record (160 m at site 2) is probably representative for the entire range, and, incidentally, is probably about the same as that for *A. melanoceras* on the Atlantic side of Panama. *A. allenii* is occasionally found in somewhat drier sites than *A. melanoceras* (such as landslide succession, roadsides), but otherwise it appears to have the same ecological difficulty with invading disturbed habitats as detailed for *A. melanoceras*.

Acacia allenii provides a somewhat better test than *A. melanoceras* of the prediction that both species are likely to become extinct with the intro-

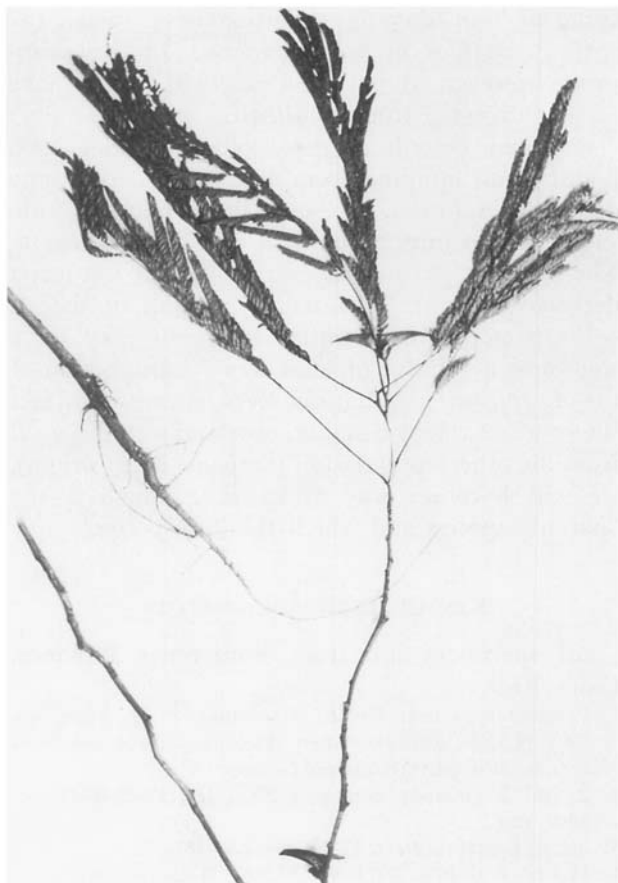


FIGURE 41.—Seedling of *A. allenii*; note single swollen thorn in crown and old rotted thorn near bottom of photo (Costa Rica, site 5).

duction of European-type agriculture to a particular site. Allen (1952), based on experience around Golfito in the 1940s, when much primary forest was being cleared, reported that *A. allenii* was an occasional plant in brushy pastures. Today (1965–1970) it is totally absent from the pastures in the Golfito region but may still be encountered on the forest edge where fields are being pushed back into the forest, especially along the road between Golfito and the Pan-American highway. When the forest is cleared, the stumps of *A. allenii* produce small shrubby bushes. Like those of *A. melanoceras* under the same circumstances, these pasture shrubs may live for 1 to 4 years and attain a height of 2 to 3 m—in the forest they live as long as 25 years and attain a height of 22 m. Since the ant colonies in these shrubs are quite ineffective at clearing the

vegetation from around the acacia, pasture fires normally kill the acacia and its ant colony. In late stages of woody succession such as on landslides or undisturbed regeneration following logging, light ground fires kill neither the acacia nor ant colony (Janzen, 1967a).

In the general area of Rincón on the Osa Peninsula, healthy seedlings of *A. allenii* in the 0.5 to 2 m size class occur at a density of at least 1 per hectare in old natural secondary succession (such as along creeks and rivers) ranging from 20 to 40 years of age. These young plants are often occupied by colonies of *P. ferruginea* with 25 to 300 workers. A high percentage of these seedlings appear to attain reproductive maturity since the same habitats have densities of adults as high as one per 5 hectares. When an area is cleared by logging and then allowed to return to forest, the density may be much higher, indicating that in uniform woody succession, seedling survival is higher than in the fragmented successional stages along rain-forest waterways and landslides. For example, the lower part of the hillside immediately north of the airstrip near Rincón was almost clear-cut in the late 1940s and then allowed to regenerate undisturbed. The density of adult or subadult *A. allenii* in this site is about 3 per hectare. Along logging roads, *A. allenii* adults or subadults may attain a density as high as 4 per linear mile of road.

The seedlings (e.g., Figure 41) of *A. allenii* are morphologically and physiologically very similar to those of *A. melanoceras*. For purposes of later comparison with dry-land, swollen-thorn acacia seedlings, I offer the following description of a 90 cm tall *A. allenii* seedling (site 5). The plant was growing in deep shade in undisturbed forest on level ground and had a tap root 22 cm long and 8 mm in diameter at ground level. As do other swollen-thorn acacias, the rootlets had nodules on them. The taproot went straight down and had 8 lateral roots of 1 to 2 mm diameter. The stem had narrowed to 5 mm diameter at 10 cm above the ground. Based on leaf scars, between 93 and 110 leaves had been produced, 8 of which were on the plant. Between 10 and 14 swollen thorns had been produced, 2 of which were still intact and contained founding queens of *P. ferruginea*. The swollen thorns had the longitudinal shallow grooves characteristic of adult plants of both *A. allenii* and *A. melanoceras*. Their volumes were 0.8 and 0.9 cc.

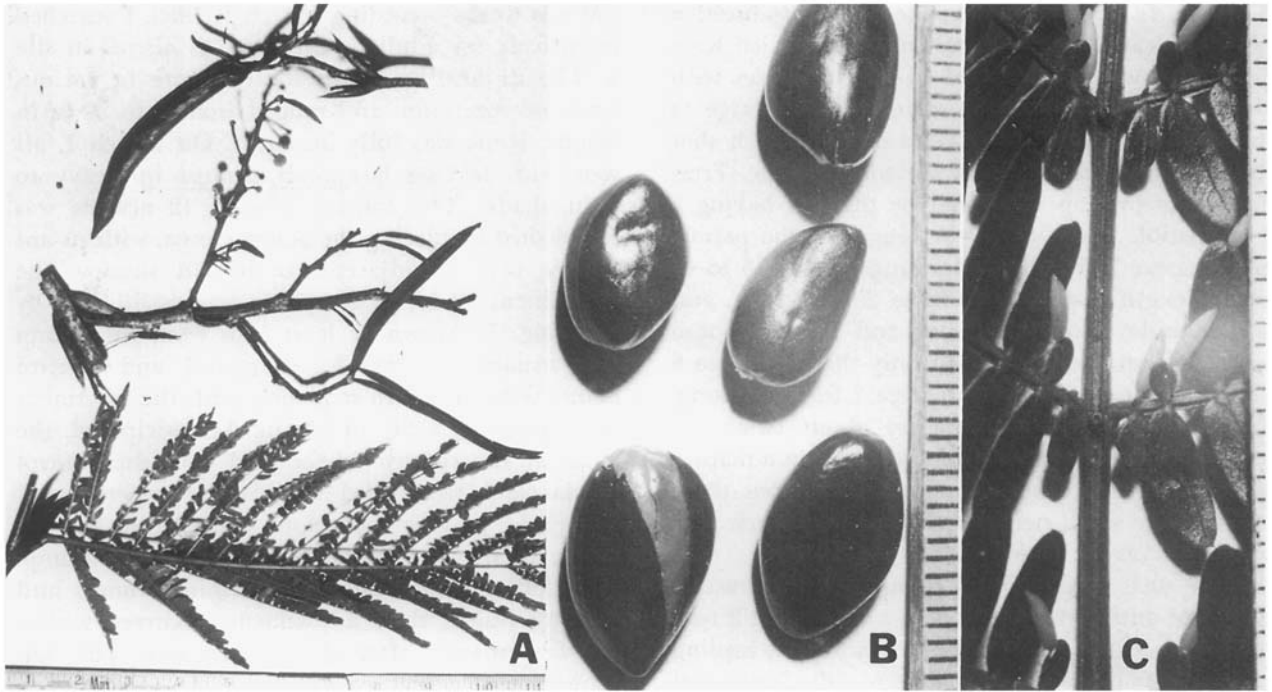


FIGURE 42.—*Acacia allenii* (Costa Rica): A, sexual branchlet (site 2); B, mature seeds; seed in lower left had split its thin seed coat and was starting to germinate before it left the pod (site 2); C, rachis nectaries on leaf subtended by a type A thorn (site 5).

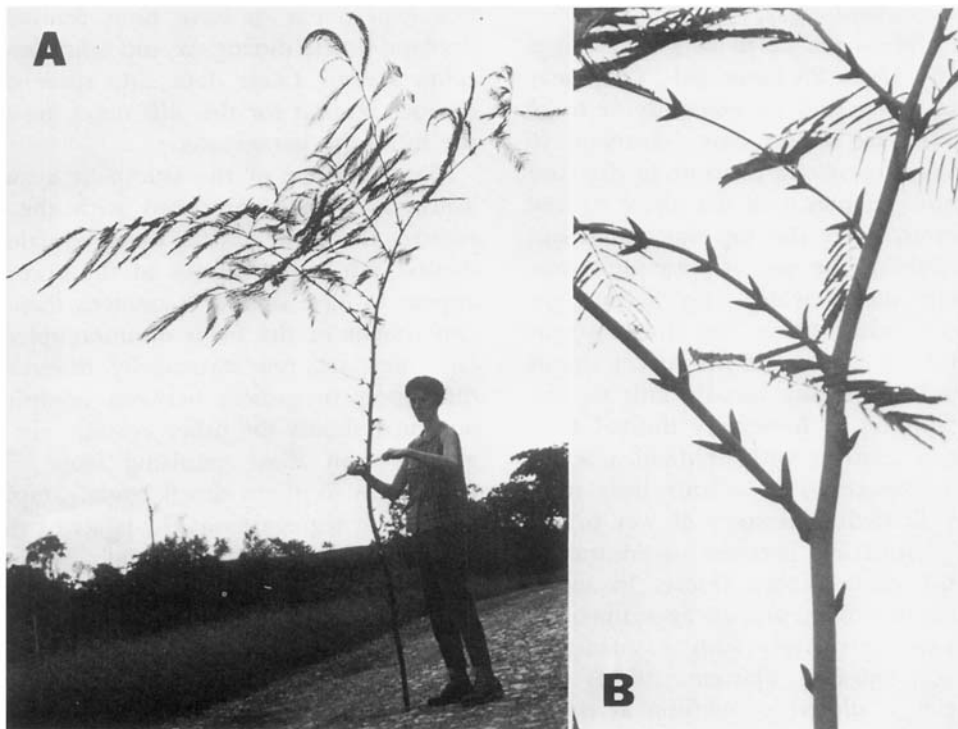


FIGURE 43.—*Acacia allenii* (Costa Rica, site 4): A, sapling that was growing in full shade; B, type A thorns in crown center of the sapling.

As with *A. melanoceras*, the seedling produced a whorl of leaves without swollen thorns which were either followed or preceded by several leaves with swollen thorns. The leaves were nearly as large as those of an adult, and radiated outward such that they did not overlap on a horizontal plane. Freedom from overlap was aided by the leaf having a 3 cm petiole about twice the length of the petiole on a mature leaf. The leaves ranged from 15 to 18 cm in length, had pinnae 22 to 29 mm long, and had pinnules 6 to 7 mm long and 1.5 to 2.0 mm wide. Beltian bodies were on only the basal 3 to 6 pinnules of each pinna, and were 2 to 4 mm long. These large Beltian bodies are about twice the length and 4 times the volume of those on a mature plant. There were no petiolar nectaries, but there was a single small nectary at the base of each pair of pinnae (as in Figure 42c).

Once such a seedling is occupied by an active colony of ants, it will grow into a sapling in 2 to 3 years such as the one in Figure 43A. As the sapling grows, it maintains a single-stem life form and produces virtually no root sucker shoots. In very young second growth, the plant becomes very bushy owing to insects eating off the growing shoot tips (again as with *A. melanoceras*).

Seed-bearing adults have 12 to 20 growth rings and are probably 15 to 23 years old. They may attain a DBH of 35 cm and are generally 12 to 25 m tall. The adults are almost never emergent to the general canopy (in strong contrast to dry-land species). Senescent canopies look like those figured for *A. melanoceras*. After the top has rotted out and the trunk fallen, the root crown sometimes produces a single sucker which may become occupied and grow to adult status. The same happens if a healthy adult is cut, but if the sucker shoots are then removed, the stump usually fails to produce more. It appears to have very limited food reserves (again, in contrast with dry-land acacias).

As does *A. melanoceras*, *A. allenii* lives in a habitat (heavily shaded understory of wet forest) of less intense defoliation pressure as contrasted with the dry-land, swollen-thorn acacias. In an attempt to quantify this difference, an experiment of the type conducted extensively with *A. cornigera* in lowland eastern Mexico (Janzen, 1967b) was performed on the *A. allenii* population at site 5 (cf. similar experiment for *A. collinsii* for direct comparative data for a dry-land species). During

the two weeks preceding March 1, 1968, I searched intensively for adult or subadult *A. allenii* in site 5. The 21 healthy plants located were in various kinds of vegetation and ranged from 5 to 20 m in height. None was fully insolated. On March 1, all were cut, leaving 60-cm-tall stumps in heavy to light shade. The control plot of 12 acacias was established by placing the acacia crown, with its ant colony, over or adjacent to the cut stump. The experimental plot of 9 acacias was established by dragging the crown at least 5 m from the stump and usually farther. Experimental and control plants were mixed in sequence, with the treatment determined by a flip of a coin. As anticipated, the ants—or the colony—abandoned 6 of the control acacias and reoccupied one of the experimental stumps by moving the colony 6.5 m from the old crown to the new sucker shoots from the stump. This left a final tally of 7 occupied stumps and 14 unoccupied; these adjustments occurred within the first month after the stumps were cut. On September 17, 1968, six and a half months later, a variety of parameters were recorded (Table 10). The effect of an ant colony on sucker regeneration is obvious, but it is not nearly as dramatic as were this experiment to have been conducted with a dry-land acacia during six and a half months of the rainy season. These data, and some of the more obvious reasons for this difference are discussed in the following paragraphs.

The diameter of the stump of a swollen-thorn acacia is weakly correlated with the amount of reserves the plant has for the production of sucker shoots. While the stumps of the occupied acacias appear to have smaller diameters, thus biasing the experiment in the favor of unoccupied shoots, in fact they are not statistically different. Further, differences in growth between occupied and unoccupied shoots for other reasons are usually far greater than those resulting from difference in stump size. Without much larger samples, it is impossible to segregate out the effect of stump size.

The tallest sucker shoot may originate at any point on the side of the 60 cm stump. For this reason, small samples tend to have a very high variance in the total height of the plant in the early stages of sucker regeneration. That the occupied and unoccupied acacias have significantly different total heights only at the 0.025 (t-test) level is a reflection of this high variance. In this

TABLE 10.—General condition of occupied and unoccupied *A. allenii* after 6.5 months of sucker shoot growth from cut stumps (see text for details), Costa Rica, site 5

Measurements	Occupied (n=7)	Unoccupied (n=14)
Stump diameter (mm)		
average	40	56
s.d.	17	28
median	44	52
range	18-67	11-115
Maximum height of shoots (cm)		
average	157	81
s.d.	73	50
median	172	85
range	41-245	0-182
Length of longest shoot (cm)		
average	112	34
s.d.	105	29
median	117	37
range	18-202	0-83
Number of suckers per stump		
average	6.6	10.6
s.d.	1.8	6.5
median	6	13
range	4-9	0-18
Number of intact shoot tips per stump		
average	5.0	1.8
s.d.	2.0	1.6
median	5	1
range	3-7	0-6
Number of damaged shoot tips per stump		
average	1.9	12.0
s.d.	1.6	9.1
median	2	11
range	0-5	0-29
Number of swollen thorns per shoot		
average	22	20
s.d.	22	23
median	15	5
range	0-57	0-69
Number of leaves per stump		
average	48	32
s.d.	20	26
median	44	27
range	16-74	0-73
Total live weight of leaves per stump (gm)	76	10

respect, the results are not outstandingly different from those expected in a drier habitat, except that in the dry land experiment this high variance would have disappeared within about 3 months of sucker regeneration.

Much less so than with dry-land acacias, *A. allenii* suckers are not "racing" to maintain a spot in the general canopy. They are already far below it and a difference of a few centimeters in height, between occupied and unoccupied, is not so important as it is with an acacia whose survival to reproductive maturity depends on remaining isolated. With *A. allenii*, success in height increment is measured in the size of eventual seed crops, rather than in living or dying during a short period.

Of course it is the length of the "leading" sucker shoot that usually determines the height of the regenerating acacia, though sometimes the longest sucker originated low on the stump and this is in fact shorter than the tallest sucker. The significant difference at the 0.005 level (t-test) between the length of occupied and unoccupied suckers is the result of feeding damage by insects. If no shoot tips are damaged on the growing sucker, one or two quickly become the primary suckers and vertical elongation of the others nearly ceases. There is an occasional loss of a shoot tip on an occupied acacia (usually the moth larva, *Coxina hadenoides*, which appears to be host-specific on swollen-thorn acacias, cf. Janzen, 1967b). If the main sucker shoot is generally undamaged, however, a new vertically elongating branch is produced from a leaf axil high upon the main sucker shoot when the shoot tip is eaten and the "single trunk" life form is not lost. If there is repeated loss of sucker shoot tips to insects, however, as is the case of unoccupied shoots, many short suckers are produced, none of which grow very tall.

In striking contrast to sucker height, length of shoot, and condition of the shoot tips, the number of swollen thorns and leaves are not significantly different between the occupied and unoccupied acacias. However, the total live weight of leaves on the occupied acacias was 8 times as great as on the unoccupied acacias.

All of the above data suggest that the following system is operating. On an unoccupied acacia, the insects that will feed on it encounter it at wide intervals. In between times, the plant has the

chance to grow new sucker shoots to replace those eaten off. The long time between attacks by herbivores almost certainly reflects a low density of these insects. This in turn is probably brought about by the low productivity of the understory community and the absence of other mimosaceous legumes. This is in strong contrast to dry-land sites, where the insects arrive so frequently that most new shoots are eaten off before they have grown more than a centimeter. Phytophagous insects, however, find the *A. allenii* shoots often enough so that no one shoot ever becomes large enough to assume physiological dominance over the others. The result is a stump crowned with a scrawny clump of as many as 30 short shoots. Not only do suitable herbivores more rarely encounter the acacia, but when they do, they appear to feed primarily on the newest leaves and shoot tips. The old leaves are gradually nibbled at, but are rarely eaten in entirety. This results in the very great difference in leaf weight between the occupied and unoccupied

acacias. A swollen thorn is edible only when very young, and thus if herbivores find the plant only occasionally, swollen thorns may accumulate almost as fast as damaged leaves.

Judging from natural experiments of the types described above, unoccupied *A. allenii* eventually die. During the six and a half months of this experiment, however, only two (14 percent) of the unoccupied stumps died. In a dry-land experiment, the percentage would have been between 30 and 60 percent during one rainy season. Lowered herbivore pressure is partly responsible, but the obvious shade tolerance of *A. allenii* is another factor. Suckers of dry-land, swollen-thorn acacias in shade, such as the *A. allenii* stumps received, would have ceased growth almost entirely within about 3 months. In the dry areas, a major effect of the herbivores was to make the acacia lose the race for a spot in the sun. Such an interaction does not occur here. Incidentally, *P. ferruginea* has not lost its propensity to kill vegetation contacting the canopy

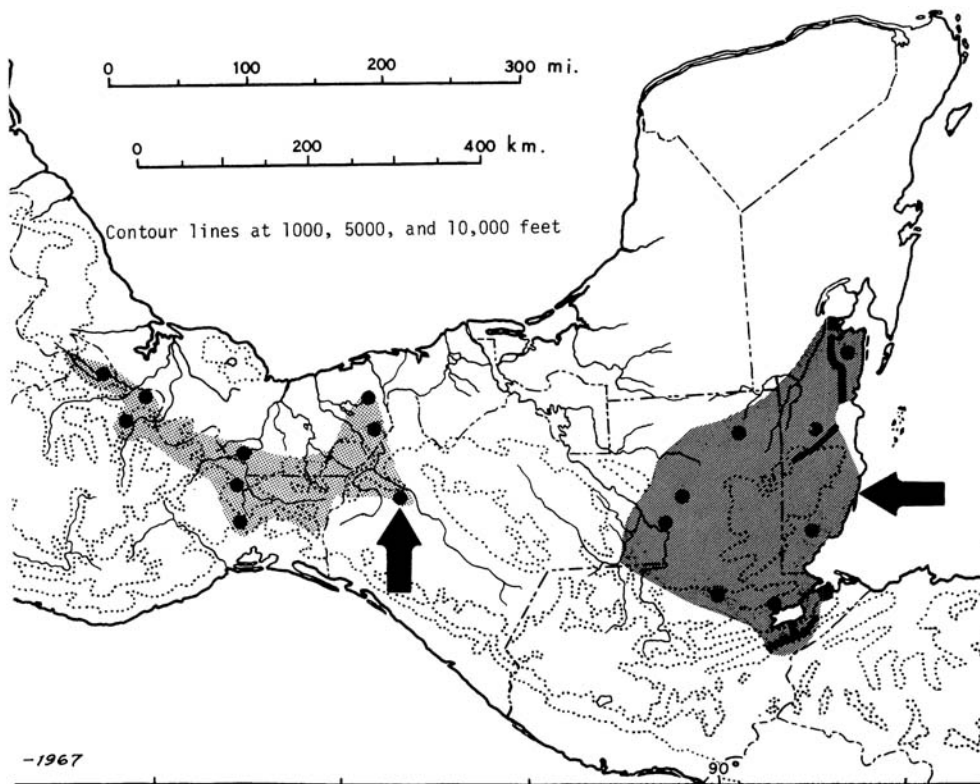


FIGURE 44.—General postulated distribution and collection localities: *A. chiapensis* (stippled area); *A. gentlei* (cross-hatched area).

of *A. allenii*. Several of the occupied sucker shoots in the experiment grew through vine canopies and the ants literally chewed a hole through for the sucker shoot.

5. *Acacia chiapensis* Safford

Acacia chiapensis Safford, 1915:356.

Acacia chiapensis is known only from Mexico (Figure 44) and the type specimen was collected at the same site as the type of *A. collinsii* (site 1). *A. chiapensis* is distinguishable from all other swollen-thorn acacias by the combination of globular inflorescences, multiple and circular petiolar nectaries, semi-indehiscent seed pods, and straight or slightly curved thorns that are circular in cross section. It is easily distinguished from *A. collinsii*, since the latter species has elongate inflorescences and few petiolar nectaries. The type specimen of *A. chiapensis* is representative of its species throughout the range except that the single type A thorn is light brown, while *A. chiapensis* thorns are usually dark brown to black. The immature seed pods on the type specimen are full-sized and display the distinct ridge bordering the margins of the valves, which is characteristic of *A. chiapensis*, and absent from other swollen-thorn acacias.

KEY COLLECTION LOCALITIES (ALL IN MEXICO)

1. San Fernando, Chiapas. VII-12-1907, *G. N. Collins*, no. 164.
2. Shores of lake behind Presa Miguel Aleman, Temascal, Oaxaca (70 m). XI-3-1963, *DHJ*, nc (occasional).
3. Temascal, Oaxaca to La Granja, Veracruz (16 m). All year, *DHJ*, nos. 118, 130, 140, 154, 158, 164, 165, 170, 185, 190, 193, 200, 204, 209, 214, 222, 230, 235, 242, 247, 266, 277, 281 (common in permanently wet sites such as below the dam at Temascal, Rio Chichicazapa, and Arroyo Enmedio, very rare otherwise).
4. 3.4 to 8.5 mi E Papaloapan on Cd. Aleman-Loma Bonita Hgy., Oaxaca (25 m). XI-4-1963, *DHJ*, nc (3 plants).
5. 19.6 mi SW Tuxtepec on Tuxtepec-Oaxaca Hgy., Oaxaca. XI-4-1963, *DHJ*, nc (1 plant).
6. 26.4 mi SW Tuxtepec on Tuxtepec-Oaxaca Hgy., Oaxaca. XI-4-1963, *DHJ*, nc (common).
7. 0.9 mi S Chontalpa on Cardenas-Presa Malpaso Rd., Tabasco (about 80 m). VI-17-1966, *DHJ*, nc (3 plants).
8. 12.6 mi W Cardenas on Hgy. 180, Tabasco (30 m). VI-15-1966, *DHJ*, nc (1 plant), fl.
9. 15.1 mi S and 5.2 to 11.0 mi N turn-off to Matias Romero

on Hgy. 185, Oaxaca (300-160 m). VIII-18-1967, *DHJ*, nos. 1500, 1510 (8 plants).

10. Rio Cascabel, Oaxaca. III-15-1934, *C. D. Mell*, no. 2239 (US 1642830) fl.
11. Upper Rio Coatzacoalcos, Oaxaca. III-8-1930, *C. D. Mell*, no. 600 (US 1492290), fl.
12. Ubero, Oaxaca (30-90 m). IV-1937, *L. Williams*, no. 9124 (US 1741272, F 897560).

NATURAL HISTORY

Acacia chiapensis is the only dry-land lowland, swollen-thorn acacia that could be called rare, un-

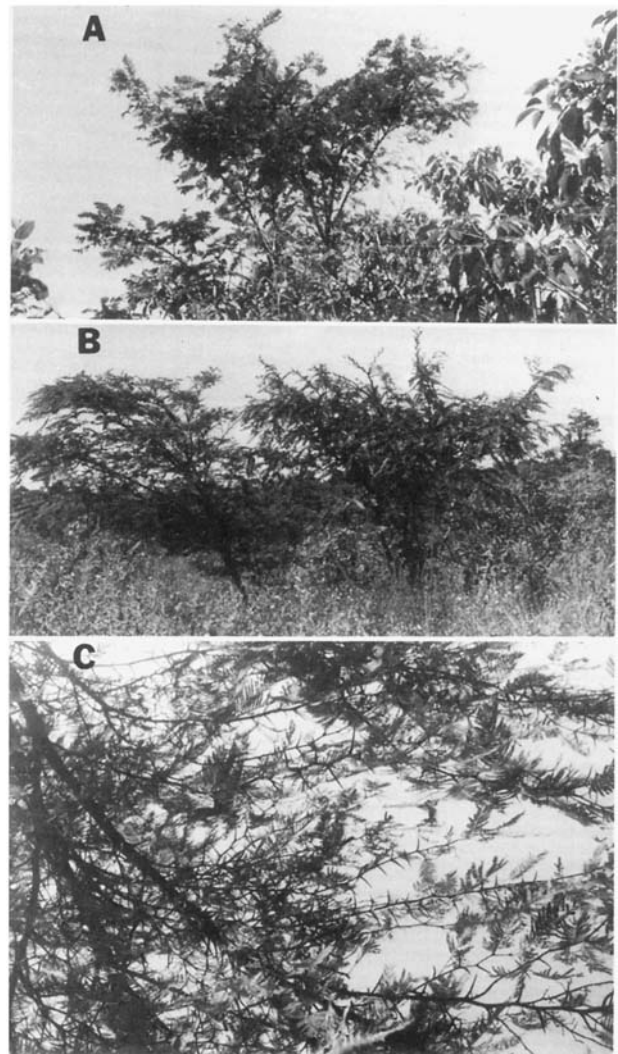


FIGURE 45.—*Acacia chiapensis* (Mexico, site 3): A, emergent crown of an occupied 4-m-tall adult; B, two adults, 2-m tall, in an open field; C, looking up through crown of 5-m-tall adult.

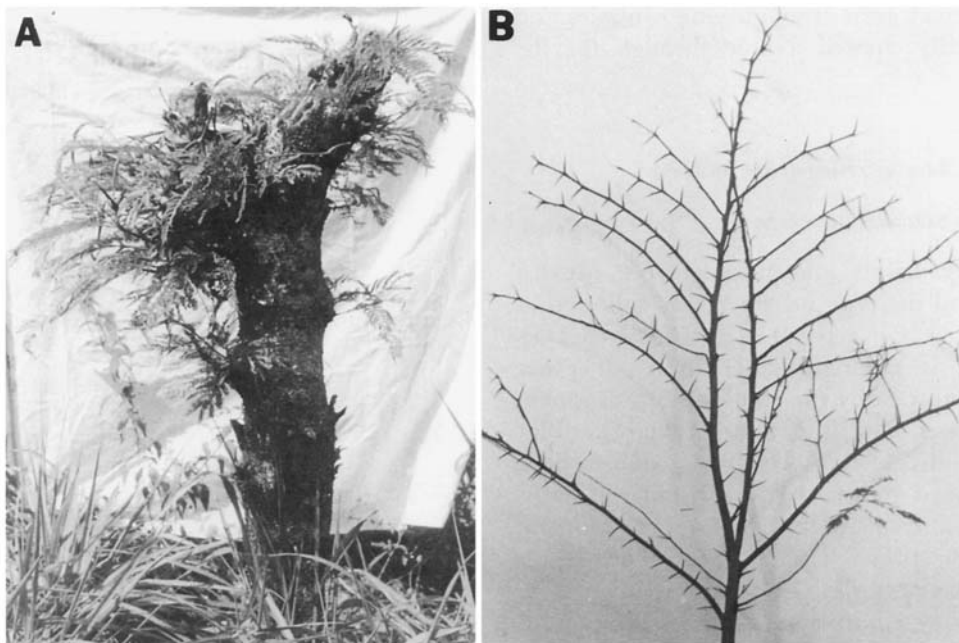


FIGURE 46.—*Acacia chiapensis* (Mexico, site 3): A, stump (4 inches in diameter) with multiple sucker shoots; B, branch pattern of 1.5-m-tall tree.

less it is found that the rare, moist forest species *A. mayana* also occurs regularly in dry sites. It is often represented by only one or two plants where found. At both places where it was common (sites 3 and 5), it was growing along or near watercourses in vegetation heavily disturbed at 2 to 4 year intervals by earth-moving machinery or logging; the sites were subjected to a severe dry season, but the acacias were growing in sites of locally high soil moisture. Based on the general condition of plants growing in a variety of sites, it appears that the pre-Colombian habitat of *A. chiapensis* was the evergreen or semideciduous forest along the edges of foothill streams running through deciduous forest. Road-building machinery appears to have been primarily responsible for movement out of this habitat into human disturbance sites. *A. chiapensis* has not invaded brushy pastures or upland regeneration following clearing for cornfields or logging, in striking contrast to *A. collinsii* and *A. cornigera*, which probably occupied the same pre-Colombian habitat as *A. chiapensis*.

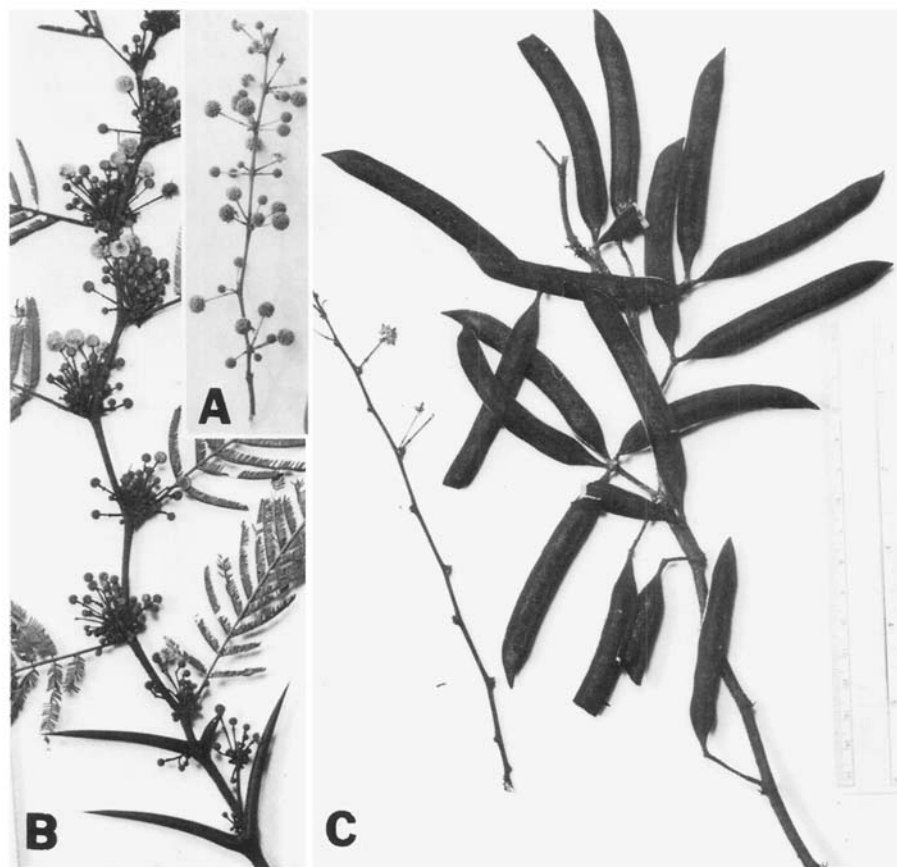
Some of the ecology of *A. chiapensis* at site 3 was discussed briefly as a contrast with *A. cornigera* (Janzen, 1967b) and *A. globulifera* is incorrectly

listed there as a synonym of *A. chiapensis*. A more detailed discussion of *A. chiapensis* is offered here after having seen the plant growing at a variety of sites.

Acacia chiapensis has a life form much like that of dry-land nonant-acacias such as *A. farnesiana* and *A. macracantha* (Figures 45A, B and 46B) but if given ample water will grow into a 8-m-tall tree. When repeatedly cut, a stump of *A. chiapensis* tends to form a large cluster of shoots from one root crown (Figure 46A), rather than also sprouting from lateral roots as the custom with *A. cornigera*. *A. chiapensis* is generally found in the general canopy or slightly emergent to it (e.g., Figure 45A); seedlings in the shade die even faster than those of *A. cornigera* and thus are rarely noticed.

Acacia chiapensis resembles nonant-acacias in another respect. The seeds are surrounded by a dry pulp that is at best only slightly sweet and is probably only rarely eaten by birds. Since the dehiscent pods (Figure 47c) do not open far enough for the seeds to fall out, the pod can either be wind dispersed (perhaps up to 2 or 3 m), water dispersed, or rodent dispersed. None of these methods even approaches being as effective as bird dispersal for

FIGURE 47.—*Acacia chiapensis* (Mexico, site 3): A, flowering branch from a heavily shaded tree; B, flowering branch from a fully insolated tree; C, mature pods on a branch like that in figure A.



rapidly invading newly created patches of young regeneration. All other swollen-thorn acacias, with the possible exceptions of *A. cookii* and *A. ruddiae*, are regularly bird dispersed.

The flowers are pollinated by the wide variety of small bees that are available in deciduous forest habitats and contemporary second growth during the dry season. The inflorescences are borne in very dense clumps in the leaf axils of vegetative branches (as on *A. cookii* in the southern part of its range) produced in the early part of the previous rainy season. At any one site, the number of inflorescences per axil can vary strongly (Figures 47A, B) and the largest numbers are found on branches that are fully insolated and from bushes that are fully insolated. Inflorescences generally set 1 to 5 pods, but may on occasion have as many as 10.

The seedling ecology of *A. chiapensis* has not been examined but the morphology of young bushes indicate that it is more like that of nonant-

acacias than like that of swollen-thorn acacias. It appears that the first swollen thorns often do not appear until the fiftieth or even later leaf, and even in fully insolated bushes, many leaves on lengthening lateral branches are not subtended by swollen thorns. This behavior persists even in very old *A. chiapensis*, resulting in branch segments with many nodes that lack swollen thorns. The canopy section in Figure 45c has about the maximum number of thorns in it to be found in an *A. chiapensis* canopy.

While the large leaves of mature *A. chiapensis* have large numbers of petiolar nectaries (Figure 48A), sometimes making the petiole resemble that of *A. melanoceras*, the leaves on young plants have smaller numbers (e.g., Figure 48B), and I suspect that very young seedlings may only have one or zero petiolar nectaries per leaf. While nectar production of *A. chiapensis* is apparently very high, as with the other swollen-thorn acacias, Beltian body production is clearly reduced as compared with other

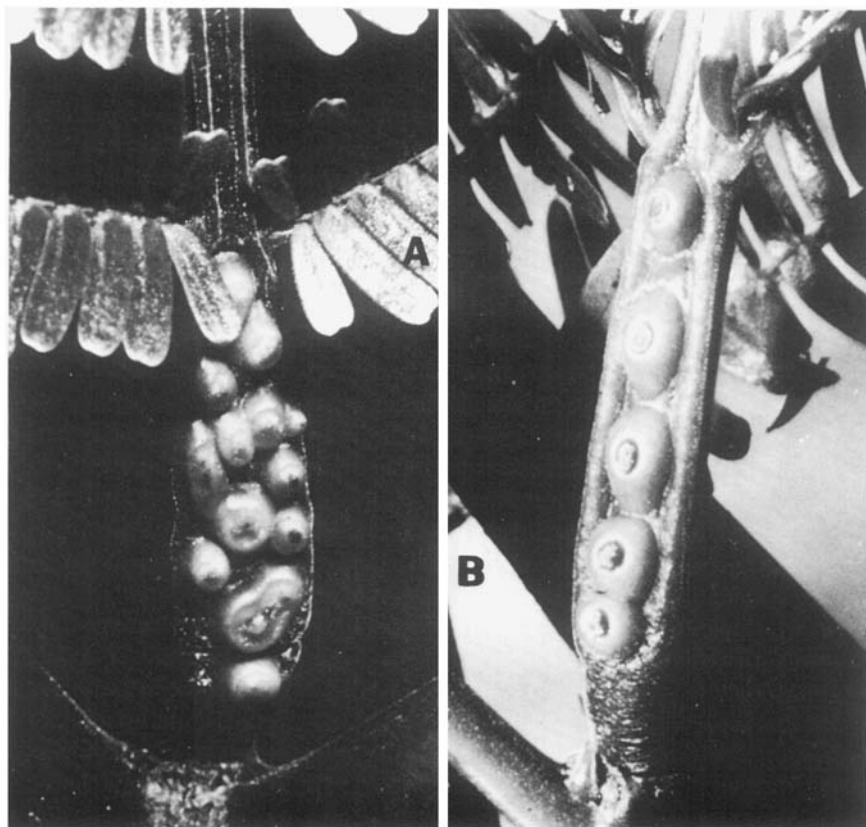


FIGURE 48.—Petiolar nectaries of *A. chiapensis* leaves (Mexico, site 9): A, from fully insolated old crown; B, from a young sapling.

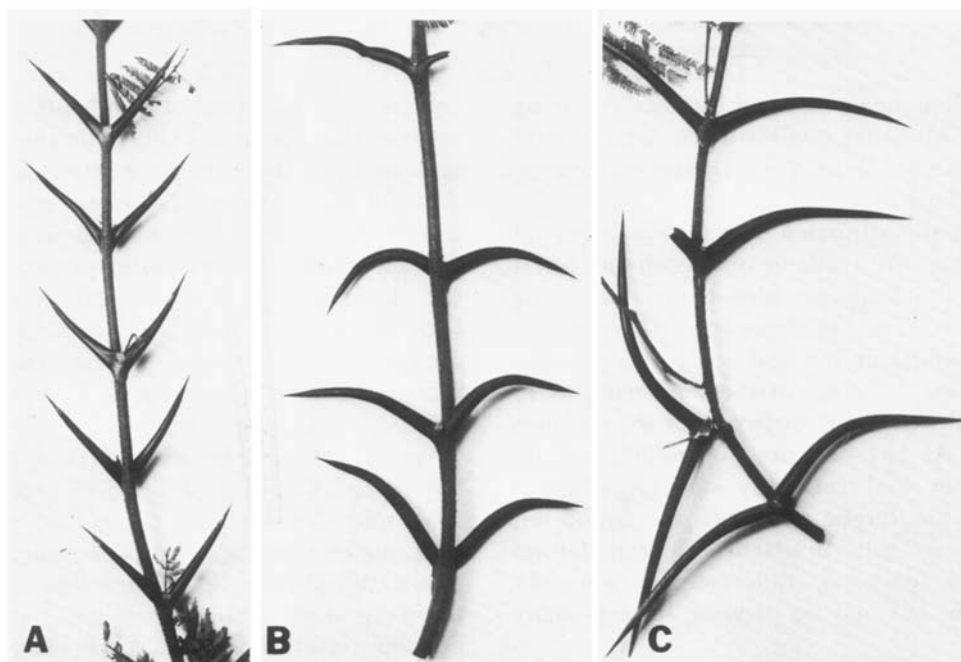


FIGURE 49.—*Acacia chiapensis* (Mexico, site 3): A, type A thorns from lateral branch of adult; B, thorns intermediate between type A and type B on lateral branch from crown of tree in Figure 45c; C, type B thorns from crown of same tree.

dry-land, swollen-thorn acacias such as *A. cornigera*, *A. hindsii*, and *A. collinsii*. *A. chiapensis* leaves on fully mature and well-insolated plants may have Beltian bodies on only half the pinnules of a large leaf subtended by a swollen thorn.

There is strong variation in the degree of herbivore damage to occupied *A. chiapensis*—all occupied plants censused have been occupied by *P. ferruginea* or by a smaller undescribed species of obligate acacia-ant. Even plants with the largest ant colonies to be found on *A. chiapensis* usually have most shoot tips eaten, as with an unoccupied *A. cornigera*. The result is that plants of *A. chiapensis* are generally very shrubby and stunted in appearance. The cause appears to be that with the reduced number of Beltian bodies and reduced number of thorns, almost none of which have a large volume or could be regarded as type B thorns (Figures 49, 50), the ant colony never grows very large. Since the colony may be old, its workers may be very aggressive, but there is too much acacia canopy to patrol effectively. A 2-m-tall *A. chiapensis* such as the one on the left in Figure 3a in Janzen (1967b) may have a maximum colony size of about 2,000 to 4,000 worker *P. ferruginea*, while an adjacent *A. cornigera* of equal size and with an equal number of leaves will have between 5,000 and 10,000 worker ants. Younger plants of *A. chiapensis* characteristically have a colony size reduced to the same degree, with the result that they are slow to gain effective patrolling by ants, and thus have to be on thoroughly cleared ground in order to mature. When roads or dams are built, *A. chiapensis* becomes established on the bare soil where there is no competition from fast-growing suckers from old stumps of woody plants (as would have been the case in areas cleared by fire or machete). At site 6, there was a nearly pure stand of 3- to 6-m-tall *A. chiapensis* covering a gravel island of about 2 acres in the middle of a river; a newly bulldozed site obviously simulates such a situation for primary succession.

If an *A. chiapensis* is growing within 1 to 2 m of an *A. cornigera*, the latter species always contains the queen and the *A. chiapensis* serves as an auxiliary unit to the main colony. This means that during a dry season sufficiently severe to cause the *A. chiapensis* to drop its leaves, the ant colony is very likely to abandon it and retreat into the acacia with the queen. All of these observations suggest

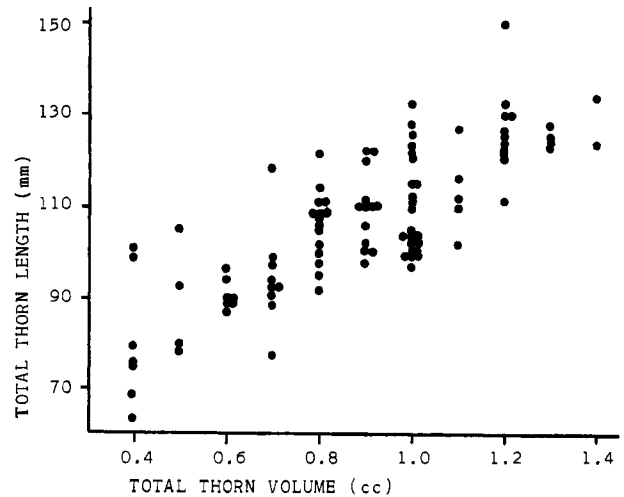


FIGURE 50.—Distribution of 89 cc of thorn volume among 100 type A thorns from an adult occupied *A. chiapensis* (Mexico, site 3).

that *A. chiapensis* is a marginal host for obligate acacia-ants, but that it is still dependent on the ants. However, it may not be as dependent as other dry-land, swollen-thorn acacias since its leaves contain cyanogenic glycosides that are also present in nonant-acacias (*A. farnesiana*) but absent from *A. cornigera* (Rehr et al., 1973).

Not all *A. chiapensis*, however, demonstrate strong susceptibility to insect attack. At site 3, and only at this site, it appears that *A. chiapensis* may be hybridizing with nonant-acacias such as *A. macracantha*. Numerous plants occur there that are intermediate in thorn, leaf, and branching morphology between these two species. A gradient may be recognized between the "typical" *A. chiapensis* life form—dark green large leaves with large pinnules, swollen thorns subtending more than half of the large leaves on lengthening branches, new swollen thorns soft for several days allowing easy entry and with soft inner parenchyma allowing easy cleaning, fast-growing shoot tips, upright-cylindrical life form with a few major branches from a single trunk, and severe herbivore damage to uppermost shoot tips—and a life form like the shrubs in Figures 45A and 45B which tend on all the above characters to be much more like *A. macracantha*. *A. macracantha* is common in the area and shows the opposite traits of those listed above for *A. chiapensis*. It is particularly obvious that the forms intermediate between *A. chiapensis* and *A. macracantha*

are more damaged by herbivores than ordinary nonant-acacias, but they are very weakly occupied, if at all. The lack of damage appears to be due to chemical and morphological defenses, since these only very mildly damaged bushes are often immediately adjacent to heavily damaged more typical *A. chiapensis*.

The large stump of one of these intermediate acacias in Figure 47B is particularly instructive in understanding the poor development of an ant colony in the apparent hybrids. It has produced at least 50 small sucker shoots since it was cut, but only five swollen thorns; sucker shoots of "typical" *A. chiapensis* or *A. cornigera* from an equal-sized stump would have had a swollen thorn subtending almost every new leaf (e.g., Figure 53 in Janzen, 1967b). Not only are there few swollen thorns, but they harden rapidly, and the queen of *P. ferruginea* has a very difficult time hollowing out enough of the inside of the thorn for its own body, to say nothing of enough space for brood and workers.

Many of the new leaves on a stump like this have no Beltian bodies and the nectaries are very poorly developed, again in strong contrast to *A. chiapensis* or *A. cornigera* new sucker shoots. Not only are the suckers slow growing, but dominance is poorly developed with the result that many shoots develop simultaneously. The dense shrub resulting eventually matures in completely insolated sites—as might be expected of dry-land nonant-acacias—but appears incapable of competing with dense vigorous vegetation on land cleared by fire or machete.

In short, there appears to be a gradient in ability to deal with the surrounding vegetation from *A. macracantha* to the apparent hybrid to *A. chiapensis* to *A. cornigera*. Along this gradient, the ant becomes progressively more important to the plant in protecting its faster growing shoot tips that have progressively fewer chemical defenses. Both *A. macracantha* and *A. cornigera* represent adaptive peaks that are successful in vegetation types of great areal extent. The hybrid and *A. chiapensis*

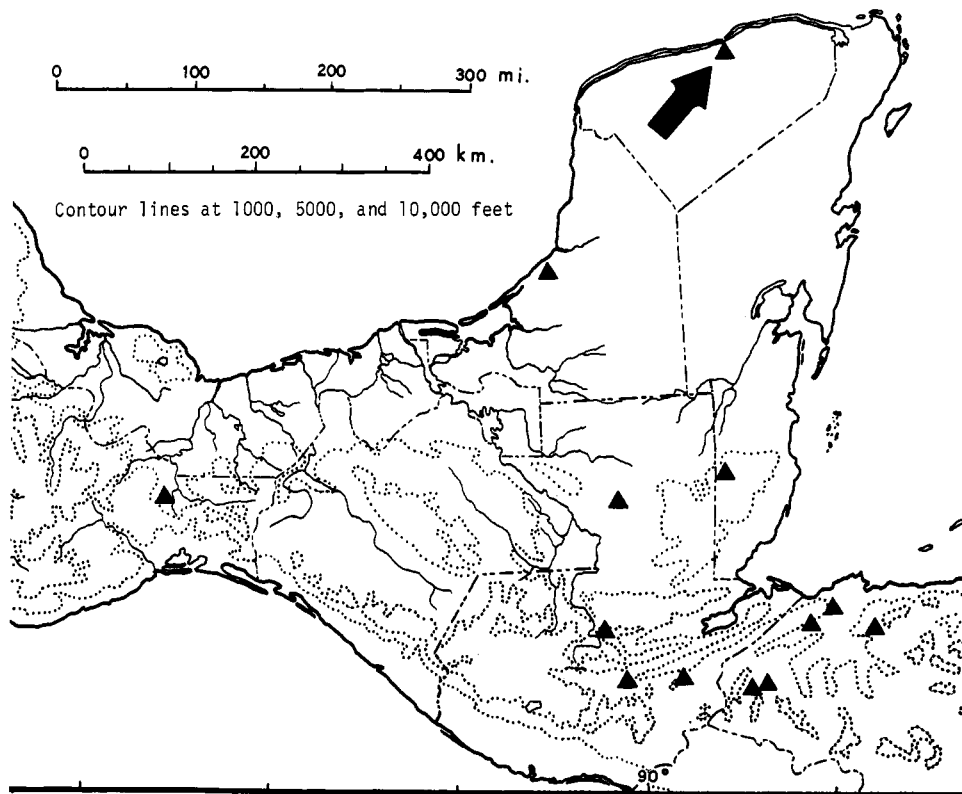


FIGURE 51.—Collection localities of *A. globulifera*; its detailed collection records are too patchy to allow an estimation of the general distribution at this time.

represent adaptive peaks that do well under much rarer combinations of vegetative competition and rainfall. It is not meaningful to say that one is any more or less successful than the other, except in terms of the number of acres of vegetation occupied.

6. *Acacia globulifera* Safford

Acacia globulifera Safford, 1915:360.

Acacia donnelliana Safford, 1915:361.

Myrmecodendrum globuliferum (Safford) Britton and Rose, 1928:93.

Myrmecodendron donnellianum (Safford) Britton and Rose, 1928:93.

Acacia globulifera is easily distinguished from other swollen-thorn acacias by the possession of spherical inflorescences, completely dehiscent pods with valves that curl back on themselves (as with *A. hindsii*), and 2 to 6 circular or oval petiolar nectaries (Figures 6, 7c). Its range (Figure 51) overlaps slightly with that of *A. collinsii*, *A. cornigera*, *A. gentlei*, *A. cookii*, and *A. chiapensis*, but it is very rarely encountered growing side by side with these plants. Herbarium specimens of *A. globulifera* are incorrectly listed as a synonym of *A. chiapensis* in Janzen (1967b), but a comparison of the petiolar nectaries and mature pods—barely indehiscent in *A. chiapensis*, fully indehiscent in *A. globulifera*—will easily separate them. The petiolar nectaries of *A. globulifera* may on occasion be confused with those of *A. collinsii*, but *A. collinsii* has elongate inflorescences. In field studies, failure to examine plants closely may result in misidentifying *A. globulifera* as *A. collinsii* or as *A. gentlei* because it has a very similar life form to either of these when growing in their habitats.

Safford's type specimen of *A. globulifera* (site 1) appears to have been taken from a fully insolated shrub growing in a locally exceptionally dry site, since its thorns are unusually light in color (beige) and short (the largest type A thorns are only 4 cm long), and its leaves only attain 8 cm in length. In the coastal areas of the Yucatan Peninsula such plants are usually found on old beach dunes; the more inland plants have thorns that are nearly black and twice as long, and have leaves up to 20 cm long. The inflorescences on the type specimen are representative of *A. globulifera* throughout its range except that they have peduncles only 10 mm

or less in length, and in wetter areas the peduncles of *A. globulifera* may attain a length of 20 mm.

Safford's type specimen for *A. donnelliana* was collected from that portion of the *A. globulifera* population growing between San Pedro Sula and Santa Rosa, Honduras (site 24), and is representative of the plants in that area growing in very wet habitats (swamps, creek edges); its thorns are nearly black, its leaves are up to 20 cm long, its inflorescence peduncles are up to 18 mm long, and its sexual branchlets are very long (e.g., Figure 52A).

KEY COLLECTION LOCALITIES

Mexico:

1. Type of *A. globulifera*: Silam (Dzilam), north coast of Yucatan. April 1895, *G. F. Gaumer*, no. 1909.
2. 48 mi NE Puerto Real (Isla Aguada) on Mexico 180, Campeche. VI-22-1966, *DHJ*, nos. 611, 615, 617, 623 (occasional), mp.
3. 11.3 mi N intersection of Mexico 185 and 190, on Hgy. 185, Matias Romero, Oaxaca (290 m). VIII-18-1967, *DHJ*, no. 1502 (single plant).
4. 11.8 mi N intersection of Mexico 185 and 190, on Hgy. 185, Matias Romero, Oaxaca (290 m). VIII-18-1967, *DHJ*, nc (occasional plants).
5. 25.8 mi N intersection of Mexico 185 and 190, on Hgy. 185, Matias Romero, Oaxaca (250 m). VIII-18-1967, *DHJ*, nc (very abundant).
6. 26.3 mi N intersection of Mexico 185 and 190, on Hgy. 185, Matias Romero, Oaxaca (240 m). VIII-18-1967, *DHJ*, nc (3 plants).
7. 31.5 mi N intersection of Mexico 185 and 190, on Hgy. 185, Matias Romero, Oaxaca (260 m). VIII-18-1967, *DHJ*, nc (1 plant).
8. Chivelia, Oaxaca, Mexico. III-6-1928, *C. D. Mell* (US 1406953), fl.
9. Silam, Yucatan, Mexico (sea level). IV-1895, *G. F. Gaumer*, no. 655 (US 1267146), fl.
10. Silam, Yucatan, Mexico (sea level). IV-1909, *G. F. Gaumer*, (US 1267508) fl.

Guatemala:

11. Finca San Joaquin, slopes above Rio Negro, near San Cristobal de Verapaz, Alta Verapaz (1080 m). VII-14-1967, *DHJ*, nc (very abundant), mp.
12. 20.5 mi NE Guatemala City on CA9 (980 m). VIII-8-1967, *DHJ*, no. 1565 (occasional), fl., gp.
13. 26.7 mi to 26.9 mi NE Guatemala City on CA9 (700 m). VIII-9-1967, *DHJ*, nc (abundant), gp.
14. 29.6 mi NE Guatemala City on CA9 (850 m). VIII-9-1967, *DHJ*, nc (rare).
15. 23.4 mi SW of turn off to Coban on Hgy. 9, Progreso, Dept. Progreso. VIII-5-1966, *DHJ*, no. 444.
16. 16.2 mi NE Guatemala City on CA9 (870). V-14-1965, *DHJ*, no. 1741 (1 plant).

17. Sanarate, Depto. Progreso (900 m). XI-9-1916, *Popenoe*, no. 720 (US 2089415, US 1319702), mp.
18. La Libertad, Chicbul, Depto. Peten. IV-29-1933, *C. L. Lundell*, no. 3088 (US 1635206, F 738059), fl.
19. Rio Teculután, above Teculután, Depto. Zacapa (250-275 m). I-7-1942, *J. A. Steyermark* (F 1191231) fl., mp.
20. Fallabon-Yaxha Rd., Depto. Peten. III-22-1933, *C. L. Lundell*, no. 2214 (F 740476), mp.
21. Lake Yaxha, Depto. Peten. III-23-1933, *C. L. Lundell*, no. 2208 (F 738041).

British Honduras:

22. Vaca, El Cayo Prov. III-2-1938, *P. H. Gentle*, no. 2275 (F 945039), fl.
23. El Cayo, El Cayo. III-5-13-1931, *H. H. Bartlett*, no. 11992 (US 1493114), fl.

Honduras:

24. Type of *A. donnelliana*: San Pedro Sula, Cortes (200 m). March 1888, *C. Thieme*, no. 5216.
25. 19.4 to 19.9 mi SW San Pedro Sula on Honduras 18 (road to Santa Rosa) Depto. Cortes (160 m). VIII-2-1967, *DHJ*, no. 1682, 1688 (8 plants), fl., gp.
26. 24.6 to 26.0 mi SW San Pedro Sula on Honduras 18 (banks of the Rio Chamelecon; road to Santa Rosa), Depto. Santa Barbara (380 to 420 m). VIII-3-1967, *DHJ*, no. 1604, 1608 (occasional).
27. 28.4 mi SW Sula on Honduras 18 (road from San Pedro Sula to Santa Rosa), Depto. Copan (780 m). VIII-3-1967, *DHJ*, no. 1630 (1 plant).
28. 10.4 to 16.3 mi (Cucuyagua) SW Santa Rosa on Honduras 18 (road to Nueva Ocotepeque), Depto. Copan (980-1180 m). VIII-3-1967, *DHJ*, no. 1634 (occasional), gp.
29. Yoro, Depto. Yoro (850 m). I-26-1934, *J. B. Edwards*, no. P-746 (US 1828182, F 759556), fl.
30. Santa Rosa de Copan, between El Portillo and San Juan Opoa, Depto. Copan (1000 m). IX-23-1963, *A. Molina*, no. 12873 (F 1622365).

NATURAL HISTORY

As with the other widespread swollen-thorn acacias, it is difficult to characterize the contemporary or pre-Colombian habitats of *A. globulifera* in one statement. It is commonly encountered at elevations that represent the upper elevational range of swollen-thorn acacias (e.g., sites 11, 28, 30); however, all of these higher elevation sites are characterized by being dry and dusty even during the rainy season. It is only at these sites that *A. globulifera* is sympatric with no other swollen-thorn acacia, though at some lowland sites *A. globulifera* may be the only riparian species, with *A. cornigera* or *A. collinsii* on the hillsides (e.g., site 26). At lower elevations in the wetter part of the range (e.g., sites

25, 26), it is most commonly encountered in riparian and swamp successional stages and occasionally on the edges of pastures and in roadside right-of-way. At sea level in the drier parts of the range (e.g., sites 2, 3-7) it is found on old sand dunes, rocky slopes, swamp edges, and badly eroded creek edges. No healthy plants have been found in habitats where they are heavily shaded, and almost all reproductive individuals have crowns that are emergent to the general canopy or are growing on nearly bare ground. One is left with the distinct impression that *A. globulifera* can withstand a very wide range of temperature and moisture regimens if it is moderately to heavily insolated. Since the largest individuals encountered have only been 3 m tall, and most are much shorter, this restricts the plant to young stages of succession, or to habitats with low or badly broken vegetative cover. At the higher elevation sites, *A. globulifera* is often associated with pines and oaks, and at sites 11 and 13 became very common—up to 20 adults per acre—in old pastures and regenerating fields formed by clearing mixed pine-oak forest.

Acacia globulifera is distinctly shrubby in life form, and like the other dry-land acacias may bear a large seed crop when only 1 to 2 m tall if well insolated. If growing in full sun continuously, *A. globulifera* generally does not grow over 2 m tall (Figure 53A) but if slightly shaded, it has a slightly more attenuated life form (Figure 53B), and its crown does not expand much laterally until it is emergent to the general canopy or otherwise insolated.

The length of the sexual branchlets of *A. globulifera* appears to be more directly related to the health of the plant than is the case with other swollen-thorn acacias. For example, the very long branchlets in Figure 52A are from a 2.5-m-tall acacia in its third year of sexual reproduction and fully insolated with a large crown and occupied by a very large ant colony. The same is true of the long sexual branchlets bearing immature pods in Figures 54B and 54C. On the other hand, the very short sexual branchlets in Figure 53B are on the healthiest appearing branch in the senescent crown of a 4-m-tall acacia in a swamp. Though fully insolated, this 14-year-old acacia had lost its ant colony and was heavily damaged by herbivores. The extreme differences in number of inflorescences borne by the two branches in Figure 52 are documented in

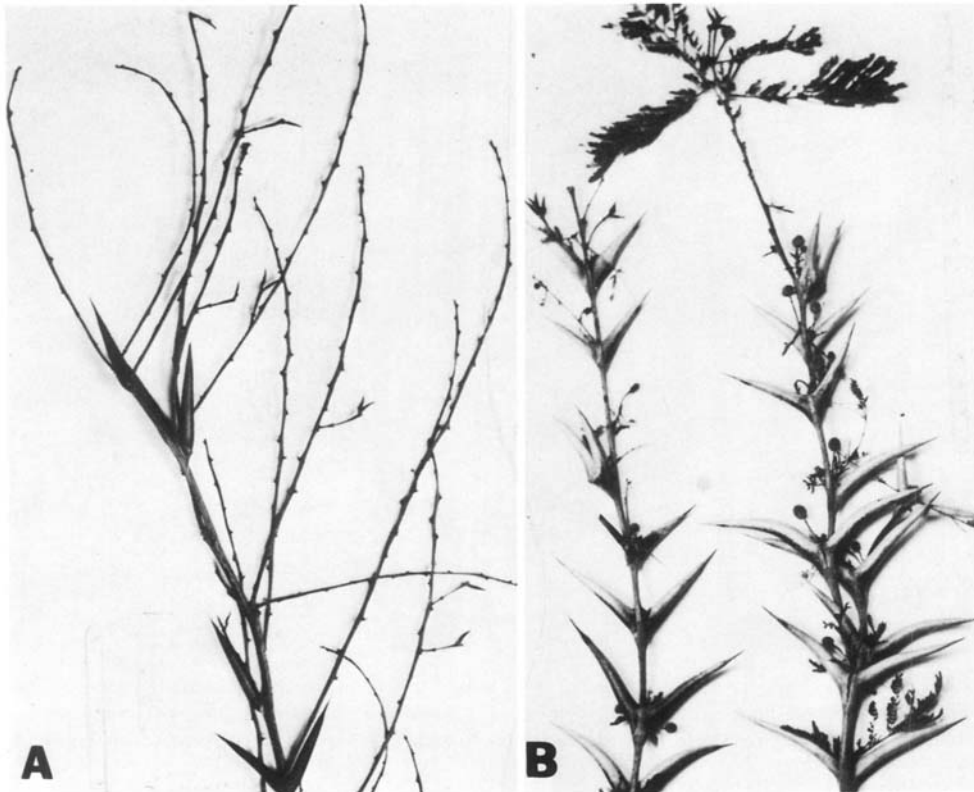


FIGURE 52.—*Acacia globulifera* (Honduras): A, elongate sexual branchlets from a very healthy adult (site 28); B, axillary inflorescences from the crown of a senescent tree (site 25).



FIGURE 53.—*Acacia globulifera* (Honduras): A, heavily insolated subadult (site 26); B, main trunk of subadult growing under intense lateral competition (site 28).

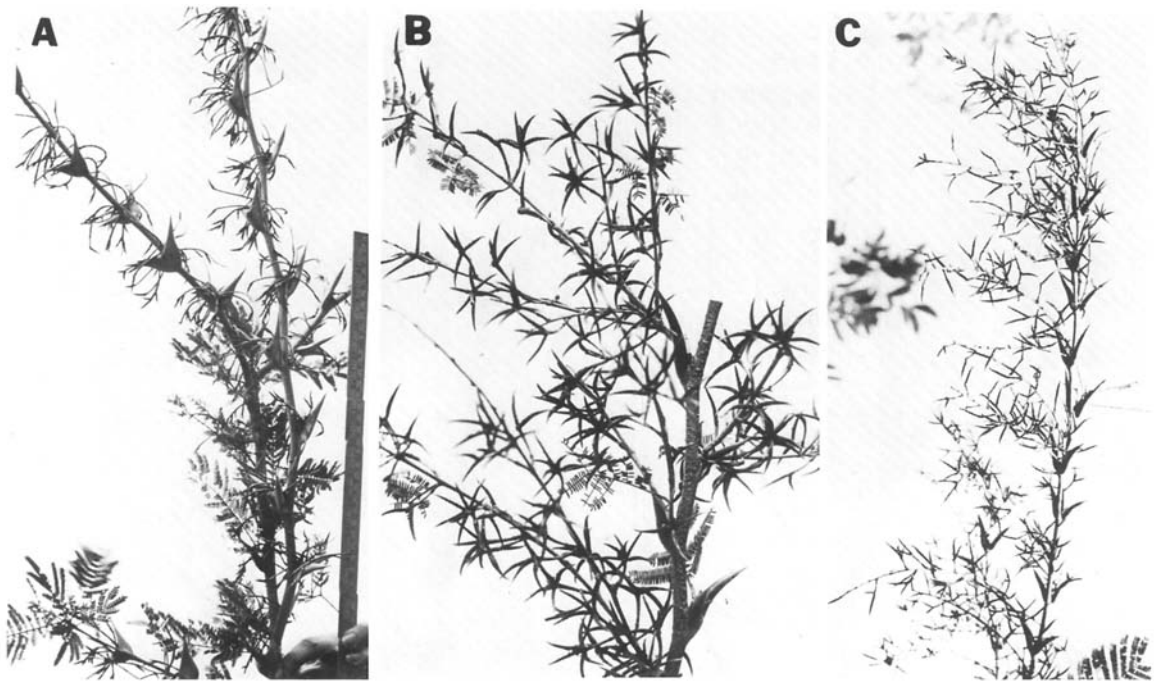


FIGURE 54.—A, lateral branch of *A. hindsii* with large number of immature infructescences (Nicaragua, site 85); B, long sexual branchlets of *A. globulifera* with heavy crop of immature infructescences (Guatemala, site 13); C, the lateral branch bearing the infructescences in Figure B.

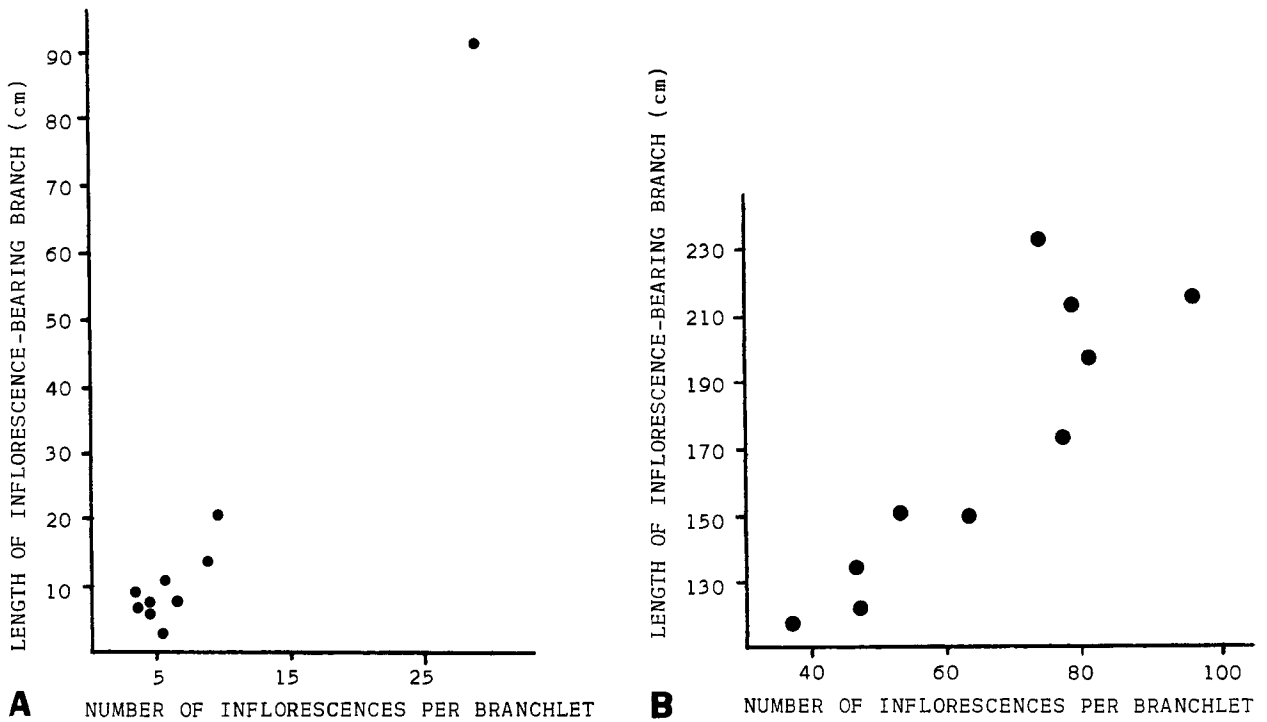


FIGURE 55.—Number of inflorescences per sexual branchlet in *A. globulifera* (Honduras): A, crown of a senescent tree that had an inflorescence crop of about 250 (site 25); B, crown of a healthy adult that had an inflorescence crop of about 12,000 (site 28).

Figure 55; the size of the inflorescence crop is clearly proportional to the condition of the acacia.

Acacia globulifera with many long sexual branchlets usually bear large seed crops (Figures 54B, C, 56). I suspect, however, this means that a large percent of the seeds are killed by bruchid beetles. As with the other dry-land acacias, the young green pods (Figure 112A) remain on the plant throughout the rainy season and do not mature until about the time the new flowers are produced during the following dry season. Mature undehisced pods of *A. globulifera* have not been collected and therefore there is no information available on seeds. Since the pods curl open and yet stay on the tree for several months after all seeds are gone, I suspect that they are bird-dispersed as with *A. hindsii*.

Seedling biology of *A. globulifera* has not been investigated except to note that they develop their first swollen thorns, Beltian bodies, and petiolar

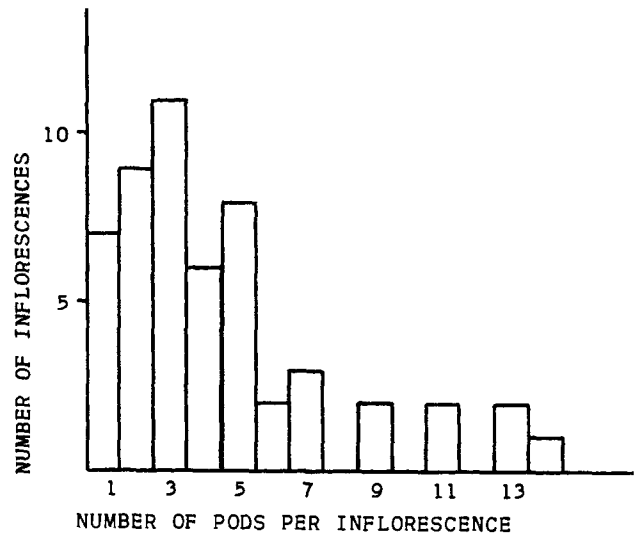


FIGURE 56.—Distribution of 207 immature seed pods among the infructescences from a healthy adult *A. globulifera* (Honduras, site 28).

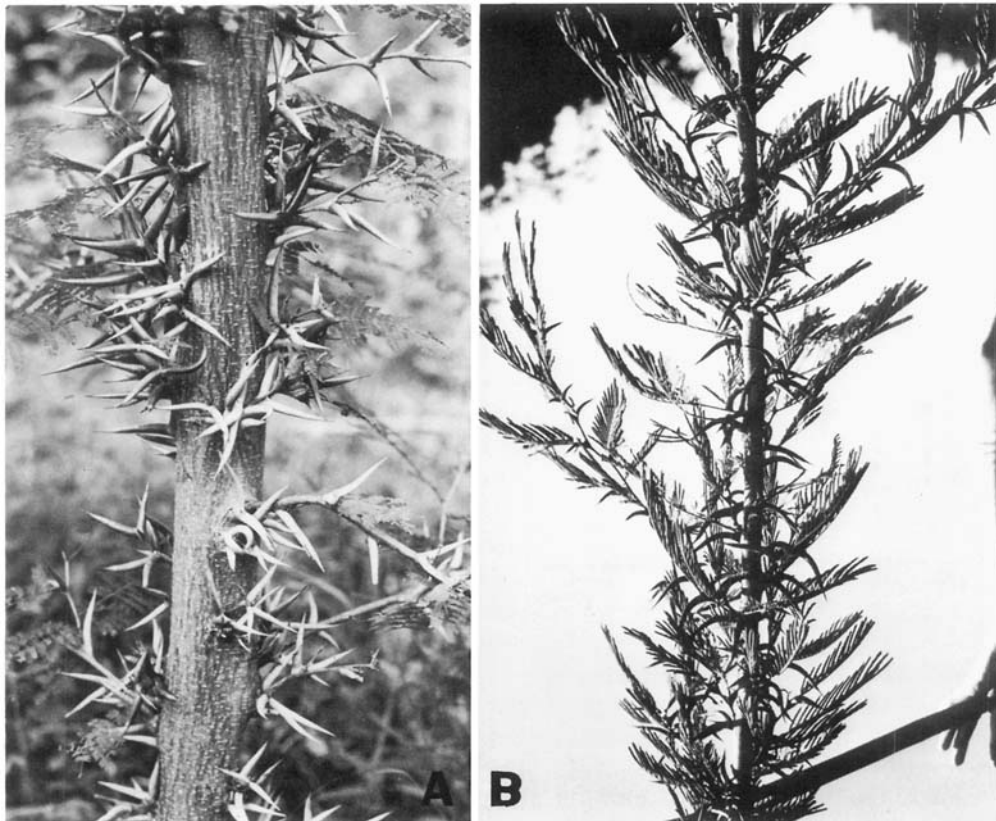


FIGURE 57.—*Acacia globulifera*: A, main trunk covered with type B thorns bleached white by the sun (Guatemala, site 12); B, central axis of subadult with downward curved type A thorns (Honduras, site 28).

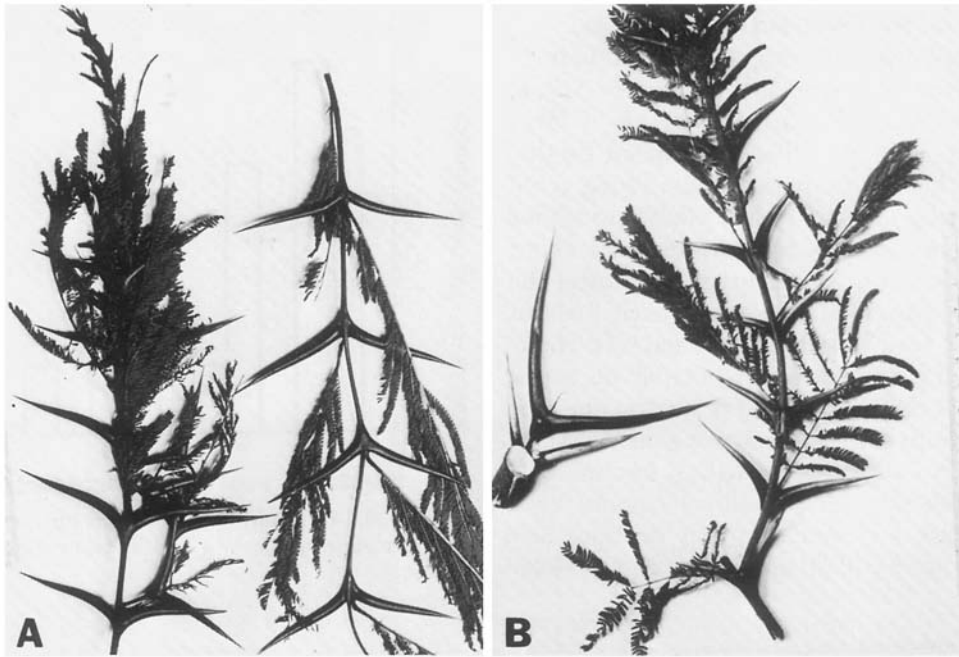


FIGURE 58.—*Acacia globulifera*: A, type B thorns (Honduras, site 26); B, left, type B thorns and on right, type A thorns (Guatemala, site 15).

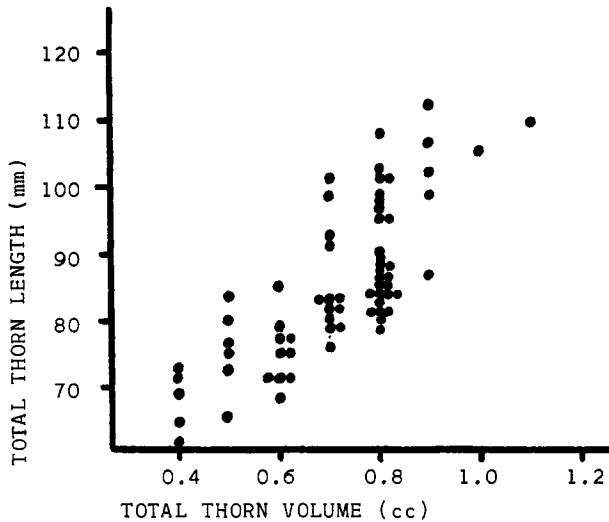


FIGURE 59.—Distribution of 49 cc of thorn volume among 69 type A thorns from lateral branches in the crown of a healthy adult *A. globulifera* (Honduras, site 28).

nectaries very early in development, like other dry-land, swollen-thorn acacias. Also as with other dry-land, swollen-thorn acacias, seedlings of *A. globulifera* appear to die within 1 to 2 years if they are in heavy shade.

Acacia globulifera produces large numbers of swollen thorns early in its development, and continues to do so on all branches. The thorns are exceptional among swollen-thorn acacias in showing extreme differences in color from one habitat to another. Adding to the complexity is the fact that *A. globulifera* thorns bleach exceptionally easily in direct sunlight (e.g., Figure 57A). They are commonly bicolored as well, with lighter tips than bases. Type B thorns are somewhat larger than type A thorns (Figures 57A, 58B, 59, 60), but not spectacularly so. They also do not differ in morphology from type A thorns in any outstanding manner; even the largest type B thorns are usually round in cross section. Type A thorns often curve downward (Figure 57B) or project outward almost at right angles from the branch bearing them (Figure 58).

Acacia globulifera shows greater variation in petiolar nectary morphology than any other species of swollen-thorn acacia. The major factor appears to be in the moisture of the ground where the individual plant is growing; the wetter the site, the longer the leaves. A great deal of the variation in nectary morphology can be viewed as simply the effect of lengthening or shortening the leaf at the

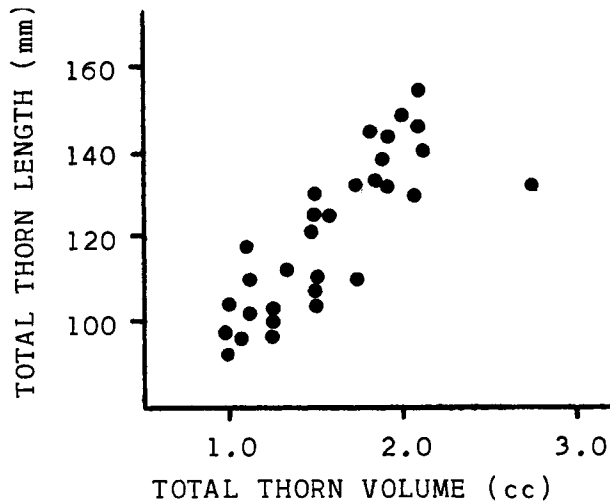


FIGURE 60.—Distribution of 48 cc of thorn volume among 31 type B thorns from the trunk of *A. globulifera* in Figure 57A.

time of formation. The effect of this variation in nectary size and number on the amount of nectar produced per leaf is unknown. There is no evidence that the ants react differently to any of these different forms of nectary.

The impact of herbivore on unoccupied plants of *A. globulifera* has not been examined experimentally, but plants that lose their ant colony through natural causes are badly damaged by insects in the lowlands. At the upper end of the elevational distribution of *A. globulifera*, apparently healthy acacias in reproductive condition are encountered that obviously have been unoccupied for at least a year. They are often tenanted by other arboreal ants in the genus *Camponotus*. At these high elevations, where the weather is often dry, windy, and cool, herbivorous insect populations appear to be much reduced as compared with the lowlands and this is probably the reason why unoccupied *A. globulifera* is relatively free of insect damage at these sites.

7. *Acacia sphaerocephala* Schlectendal and Chamisso

Acacia sphaerocephala Schlectendal and Chamisso, 1830:594.

Acacia veracruzensis Schenck, 1913:362.

Acacia dolichocephala Safford, 1915:355.

Acacia sphaerocephala is easily distinguished

from all other swollen-thorn acacias by having the elongate canoe-shaped petiolar nectaries found also on *A. cornigera* and *A. mayana*, but having a globular or thimble-shaped inflorescence. Sterile specimens of *A. sphaerocephala* are usually distinguishable from *A. cornigera* because the pinnules of *A. sphaerocephala* usually lack readily visible secondary venation (Rudd, 1964). As can be seen from its distribution (Figure 61), *A. sphaerocephala* is probably a dry-land derivative of the widespread *A. cornigera* just as *A. mayana* is probably a wet-forest derivative of *A. cornigera*; the direction of this evolution cannot, however, be stated with certainty.

Schlectendal and Chamisso's type specimen of *A. sphaerocephala* has elongate internodes and moderate-sized thorns, indicating that it was collected a few meters inland from the beach dunes where most of the population of *A. sphaerocephala* now grows (site 1). While its spherical inflorescences are immature, they are representative of those found throughout the population of *A. sphaerocephala* except in the northern part of its range where some plants have more thimble-shaped inflorescences. Rudd (1964) has placed *A. veracruzensis* and *A. dolichocephala* in synonymy with *A. sphaerocephala* and I agree. The small maroon seed pods growing from a globular inflorescence, and the very thick thorns on the type of *A. veracruzensis* identify it clearly as having been collected from the dense mat of *A. sphaerocephala* growing on the dunes immediately above the high-tide line south of the city of Veracruz (sites 2 and 6). At this site, the thorns of *A. sphaerocephala* may attain a diameter of 15 mm (e.g., Figure 65c) while equal-length thorns of *A. cornigera* are only 8 to 10 mm diameter at the base. Also, *A. sphaerocephala* thorns at this site (as at most sites) are bicolored with ivory to beige tips while those of *A. cornigera* are uniformly brown or gray. Safford's type of *A. dolichocephala*, like that of *A. sphaerocephala*, was taken from the population just inland from the dunes and thus has as long internodes and thin thorns as are to be found on *A. sphaerocephala*. Its immature inflorescences are slightly elongate but those of *A. cornigera* at the same site are 3 to 4 times as long.

Acacia globulifera has been commonly misidentified as *A. sphaerocephala* where the former species grows along the dunes sympatric with *A. collinsii* on the Yucatan Peninsula. Careful search has, how-

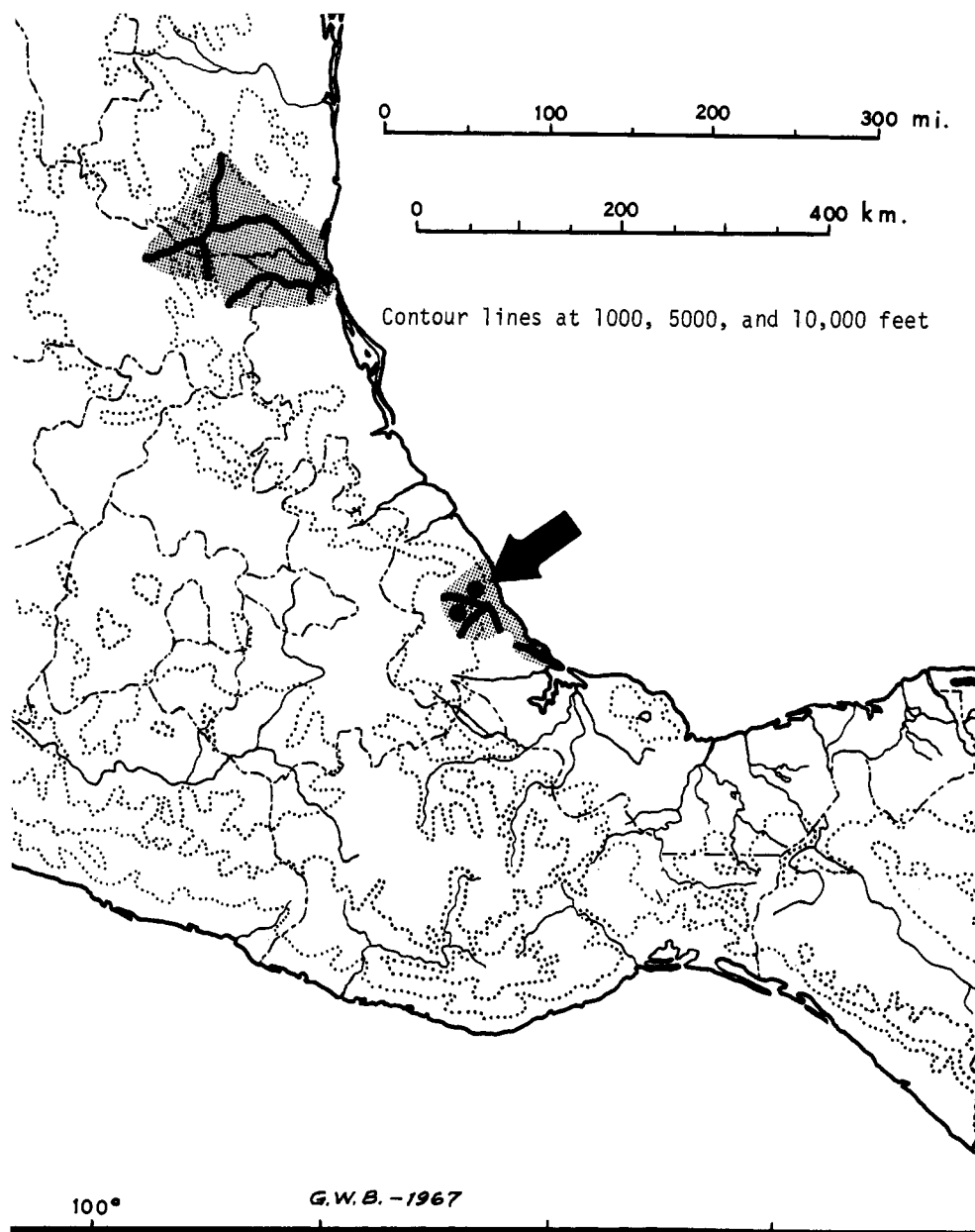


FIGURE 61.—General postulated distribution (stippled area) and collection localities of *A. sphaerocephala*.

ever, located no *A. sphaerocephala* south of Alvarado, Veracruz, Mexico.

KEY COLLECTION LOCALITIES
(ALL IN MEXICO)

1. Type of *A. sphaerocephala*: Actopan, Veracruz (sea level). March, 1820, *Schiede and Deppe*, no. 684.
2. Type of *A. veracruzensis*: sand dunes south of Veracruz, Veracruz (sea level). X-13-1908, *Schenck*, no. 916.
3. Type of *A. dolichocephala*: Along shore north of Veracruz, Veracruz (sea level). I-24-1906, *J. M. Greenman*, no. 87.
4. 5.1 to 38.1 mi SE Jalapa, Veracruz, along Mexico 140. XI-10-1963, *DHJ*, nos. 1921, 1924 (common), mp.
5. 23.5 to 42.0 mi WNW Huatusco, Veracruz, road from Orizaba to Hgy. 140. XI-10-1963, *DHJ*, no. 1920 (common), mp.
6. Within 1-2 km of the ocean beach, from the southern city limits of Veracruz, south to Anton Lizardo (approx-

- mately 15 miles north of Alvarado), Veracruz. *DHJ*, nos. 1922, 1925, 1926, 1927.
7. 26.2 mi N Ciudad Valles to Antiguo Morelos on Mexico 85 (100–300 m). VIII–25–1967, *DHJ*, nc.
 8. Antiguo Morelos to where the Tropic of Cancer crosses Mexico 85 (e.g., 1.8 mi S Llera on Hgy. 85; 22 mi S Ciudad Victoria, Tamps.). VI–10–1964, *DHJ*, no. 505.
 9. Ciudad Mante to Tampico (Mexico 80) (primarily in river beds) and Tampico to the Tamuin area (e.g., 8 mi E Tampico on 110). I–2–1964, *DHJ*, no. 504, Tamps. and SLP.
 10. Antiguo Morelos to Ciudad del Maiz, Tamps. and S.L.P. (occasional populations on dry southeast facing slopes). XII–28–1963.
 11. 10.3 mi NE Ciudad Valles on Mexico 110, S.L.P. I–II–1964, *DHJ*, no. 1923.
 12. Tanquian, Partido de las Valles, Tamcanhuitz Dist., S.L.P. 1908, *L.G. Cuevas*, (US 692167), fl.
 13. Hda. Buena Vista, Tamaulipas, Mexico. VI–15–1919, *E.O. Wooton*; (US 989707).
 14. Between Tula and Tampico. XII–1830, no. 728 (US 40123), fl.
 15. Tampico, Tamaulipas (sea level). I–1–31–1910, *E. Palmer*, no. 133 (US 764678), fl., mp.
 16. Between San Luis Potosi and Tampico (Huasteca Region), 1878, *E. Palmer* (US 764678), fl., mp.
 17. Pueblo Viejo, 2 km S Tampico, Veracruz (sea level). V–23–31–1910, *E. Palmer*, no. 448a (US 463371), fl.
 18. Between Rio de Santa Maria and Rio de los Pescados, Veracruz. X–7–1908, *Schenck*, no. 837 (US 764677).
 19. 1 mi N Cd. Madero, Tamaulipas (sea level). III–1–1961, *R.M. King*, no. 3990 (US 2365430), fl., mp.

NATURAL HISTORY

The distribution of *Acacia sphaerocephala* invariably borders the dry edge of the *A. cornigera* distributions. At sites 2 and 6, it occupies the dunes and only extends inland to the wetter sites occupied by *A. cornigera* as scattered individuals. At sites 4 and 5, *A. sphaerocephala* extends the distribution of swollen-thorn acacias into that part of the state of Veracruz with the most severe dry season. All along the northern part of the range of *A. sphaerocephala*, the northernmost individuals are found in semidesert vegetation while the southernmost individuals are scattered among the northernmost individuals of the *A. cornigera* population. *A. sphaerocephala* is the only species of swollen-thorn acacia that inhabits newly formed dunes, and it occupies some of the driest habitats of any swollen-thorn acacia population. It is the only Central American acacia involved in the early stages of beach succession. In the Isthmus of Tehuantepec on the Pacific side of Mexico, *A. collinsii* is also

found on occasion in extremely dry habitats, but it is not clear if the low density population is reproducing itself or maintained by seed immigration from wetter sites.

For purposes of discussion, the *A. sphaerocephala* population can be divided into two ecotypes: the dune ecotype and the inland ecotype. The dune form occurs only on new dunes in the vicinity of the city of Veracruz (sites 3 to 6), while the inland form occurs throughout the remainder of the range and does not approach the ocean as closely as does the dune form. When seeds of the dune form are grown at well-watered inland sites, the resulting shrub closely resembles the inland ecotype except for having slightly shorter internodes and slightly thicker swollen thorns. On the dune, however, it is a very different plant and worthy of special discussion.

On the dunes closest to the ocean, the dune form of *A. sphaerocephala* forms a dense pure stand from 0.2 to 1.8 m tall that generally crowns the leading edge of the dune (Figure 62b; Figure 10 in Sauer, 1967). The origin of the mat of *A. sphaerocephala* is seed, but most of the plants in the larger mats are from sucker shoots from roots. The branches are so intertwined that the entire mat appears as though it were one crown. The largest mats may be 30 m wide by 200 m long and contain at least 6,000 major stems.

The dune ecotype of *A. sphaerocephala* differs from other swollen-thorn acacias in not being occupied by obligate acacia-ants when it grows on new dunes. Its success as an unoccupied swollen-thorn acacia in this habitat is apparently due to the continuous strong onshore winds, which probably make life very difficult for phytophagous insects and prevent their flying to the acacias in the first place. The absence of other adjacent shrubby vegetation in this barren habitat also removes the source for most of the insects that defoliate unoccupied swollen-thorn acacias. Plants grown at inland sites from dune ecotype seeds are heavily defoliated if unoccupied, just as are adjacent unoccupied *A. cornigera* (experiments conducted 1963–1964, at Cotaxtla Exp. Sta. and Temascal, cf. Janzen, 1967b, for site details). Inland ecotypes of *A. sphaerocephala* interact with ants in the same manner as do *A. cornigera*.

Failure of *Pseudomyrmex ferruginea* (the only obligate acacia-ant at the site) to occupy the dune



FIGURE 62.—A, pasture dotted with young 1–2-m-tall *A. sphaerocephala*; the columnar structure is typical of pasture plants in this area (Mexico, site 9); B, beach dune created by dense mat of *A. sphaerocephala* (Mexico, site 6).

ecotype is due to the following reasons: (1) Searching queens appear to rarely arrive at the dune plants, probably because the prevailing winds blow from the dunes toward the inland swollen-thorn acacias (*A. cornigera* and *A. sphaerocephala*), and because they would have to cross many feet of very hot sand to walk there. Their absence is indicated by the almost complete lack of their characteristic entrance holes in thorns of seedlings and adult plants of the dune ecotype of *A. sphaerocephala*. (2) The dune ecotype produces almost no Beltian bodies and the few that are produced appear to be harvested by colonies of *Crematogaster atrata* Mayr or *C. corvina* Mayr that tenant the thorns in large colonies. These ants cut entrance holes at the base of the thorns, tend mealybugs (Pseudococcidae) and aphids (Aphididae) inside the thorns, and scavenge on the acacia surface. Their foraging is almost entirely nocturnal and very patchy in coverage. There is no evidence that they protect the acacia; inland *A. sphaerocephala* dies as fast from herbivore damage when tenanted by this ant as it does when unoccupied. (3) The *Crematogaster* ants thoroughly harvest the petiolar nectar produced by the dune ecotype of *A. sphaerocephala* and would probably be very severe competitors for the young

queens attempting to start a colony. The total absence of *Crematogaster*, however, from those inland acacias that are producing Beltian bodies and can be found by many searching queens of *P. ferruginea*, indicates that obligate acacia-ants can easily exclude *Crematogaster* in more ordinary habitats. (4) During the latter part of the dry season most of the dune ecotype individuals of *A. sphaerocephala* drop their leaves (e.g., Figure 63c), and this behavior makes colony establishment and maintenance very difficult.

As dune succession proceeds, the dense mats of *A. sphaerocephala* are broken up, and the population consists primarily of very flat-topped scattered individuals that rarely exceed 1.5 m in height (Figure 63b). Once the succession has reached a height of 3 to 5 m, *A. sphaerocephala* disappears completely, though *A. cornigera* may still be common. Birds apparently disperse seeds continually into these inland sites, however, because if they are cleared, both *A. cornigera* and the inland form of *A. sphaerocephala* appear in the early successional stages. In the inland habitat, these two acacias are very difficult to tell apart until they bear flowers.

Seedling development in situ of the dune ecotype has not been examined closely, but leaflet develop-

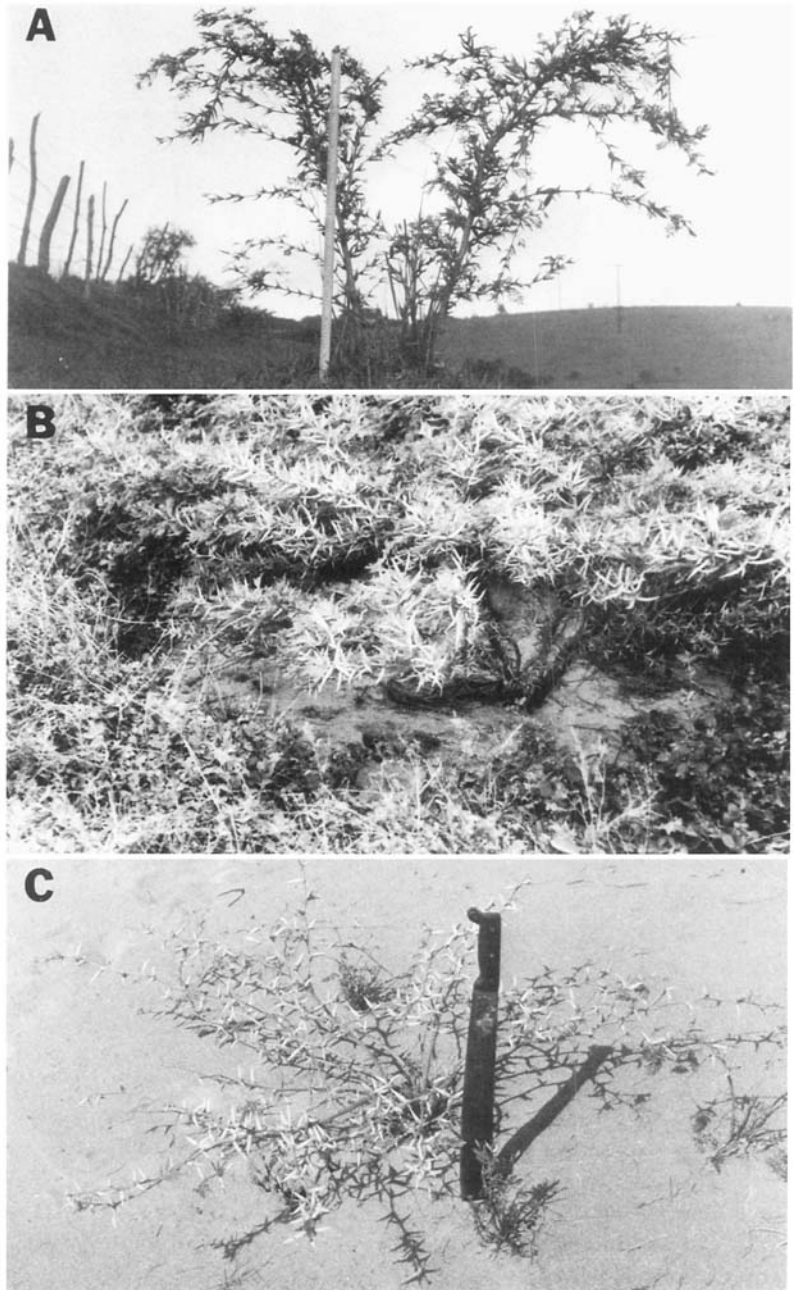


FIGURE 63.—*Acacia sphaerocephala* (Mexico): A, adult in cattle pasture (site 4); B, adult 1 m tall, leafless, in low vegetation several hundred meters behind the high-tide line (site 6); c, leafless subadult on beach dune (site 6).

ment of a representative seedling from an inland plant is depicted in Figure 64. The gradual increase in leaf size and leaflet number with age is representative of dry-land, swollen-thorn acacias. It is characteristic of all the swollen-thorn acacias to have this short period of growth before developing the characteristic traits of a swollen-thorn acacia. In short, the seed probably lacks sufficient reserves

to produce both a small amount of shoot and root, and swollen thorns, nectaries, and Beltian bodies. That these traits increase gradually in quantity indicates that the seedling continues to divide its new photosynthate between conventional vegetative growth and production of resources for the developing ant colony.

No matter in what habitat it is growing, a young

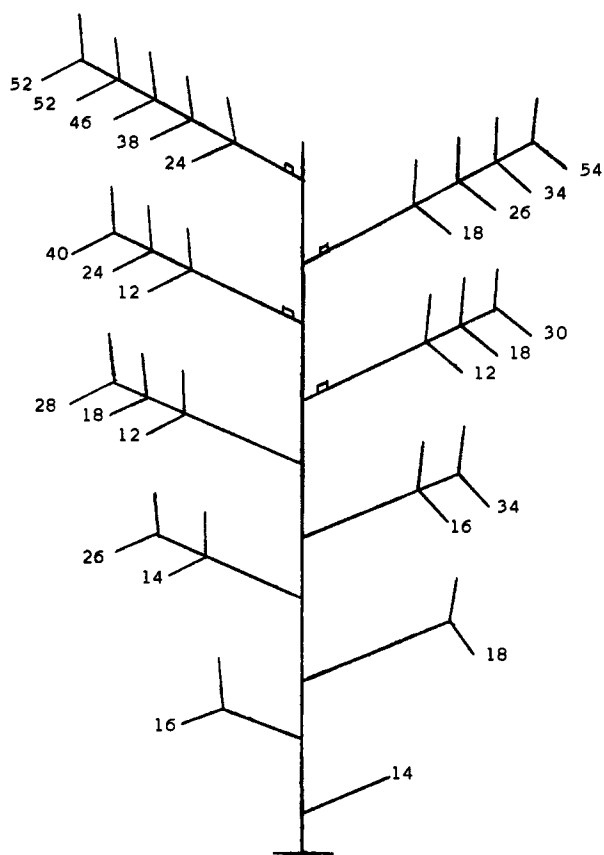


FIGURE 64.—Schematic representation of 46-day-old *A. sphaerocephala* seedling; the number of pinnules for each pinna are recorded on the figure and the first petiolar nectary appeared on the 7th leaf with the first swollen thorn and Beltian bodies at the 11th node. A fully mature leaf on the 50th or later node may have as many as 20 pinnae with 50-70 pinnules on each (Mexico, site 6).

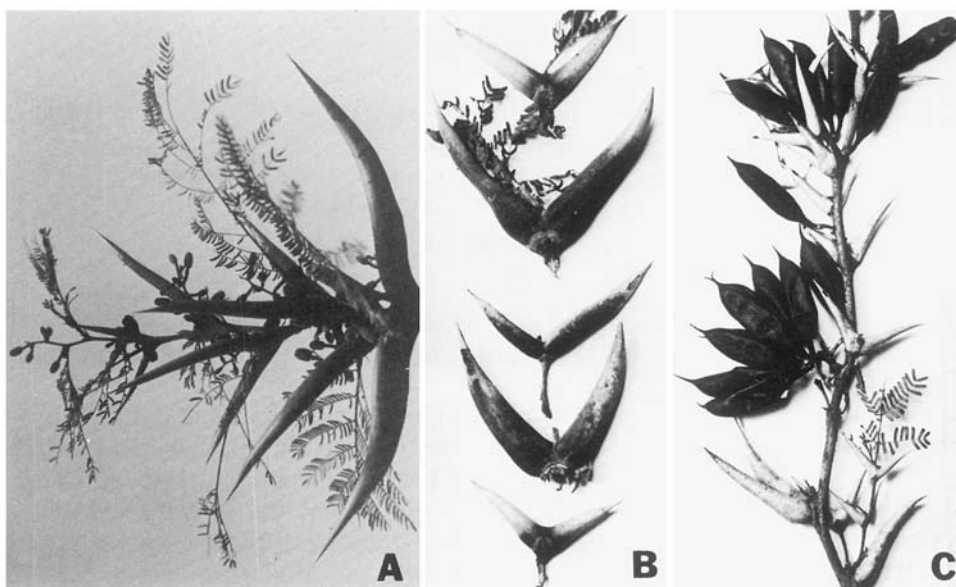


FIGURE 65.—*Acacia sphaerocephala* (Mexico): A, sexual branchlet with type B thorns (site 9); B, type B thorns (two very large thorns) and type A thorns from the plants found on beach dunes (site 6); C, fruits and type A thorns (site 6).

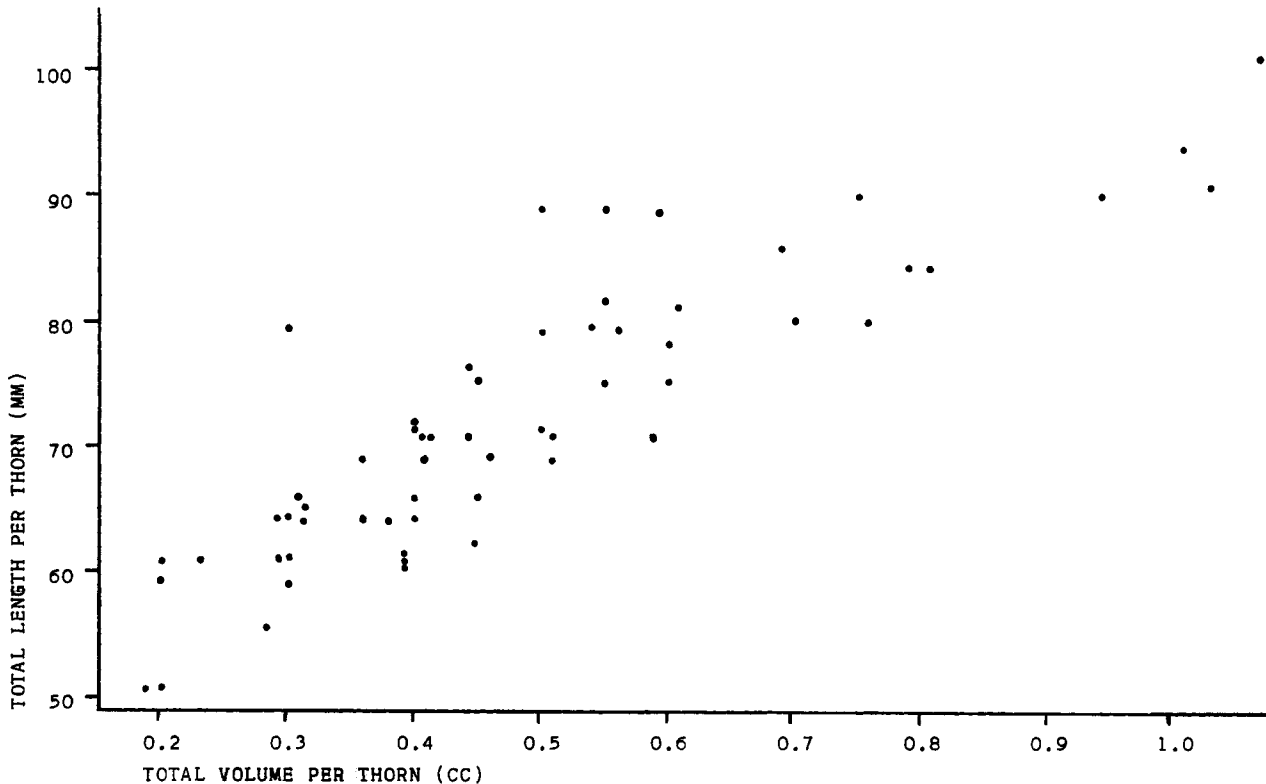


FIGURE 66.—Distribution of 30 cc of thorn volume among the 59 thorns on a 50-cm-tall *A. sphaerocephala* from the mat of shrubs on beach dunes (Mexico, site 6).

A. sphaerocephala starts out with a single major trunk (e.g., Figure 62A), as with *A. cornigera*. These plants, however, are generally in dry and, therefore, relatively well-insolated sites and thus rapidly spread out laterally (Figure 63A). *A. cornigera* in the same sites tends to grow taller and more slender. Within 2 to 4 years after first becoming occupied by obligate acacia-ants, the young *A. sphaerocephala* bears flowers. It is generally one year ahead of *A. cornigera* growing at the same site. After flowering, *A. sphaerocephala* rarely increases in height much in later years. The pods (Figure 65c) are produced in dense clusters, again as with *A. cornigera*, but generally have very thin walls—easily crushed between one's fingers—in contrast to the stiff and tough walls of *A. cornigera* at the same sites. *A. cornigera* has a morph with thin pod walls, but it is not sympatric with *A. sphaerocephala*.

In an effort to document the thorn volume of *A. sphaerocephala*, and its relationship to external thorn dimensions, the swollen-thorns of three dif-

ferent plants were measured. The young seedling (Figure 66) has the very small thorns (as compared with those of the adult in Figures 67 and 68) characteristic of young plants; in general, the larger the thorn, the higher it was up on the plant. For the inland ecotype (Figures 65A, 69A, B), the maximum thorn volume is 3.5 to 4.5 cc and probably represents the maximum possible inside thorn diameter for optimal ant brood care. The great increase in thorn volume found in the dune ecotype (Figures 65B, 69C) would be negatively adaptive for plants occupied by obligate acacia-ants, since it is produced by inflating the thorn rather than increasing its length. It is very difficult for the ants to organize and care for brood in thorns where the thorn walls are more than about 4 to 6 mm apart. The ants of *Crematogaster*, however, that normally tenant these thorns are accustomed to living in large cavities in plants and build carton partitions in the thorns to keep the brood separate. One may envision this as the first possible step in the development of an

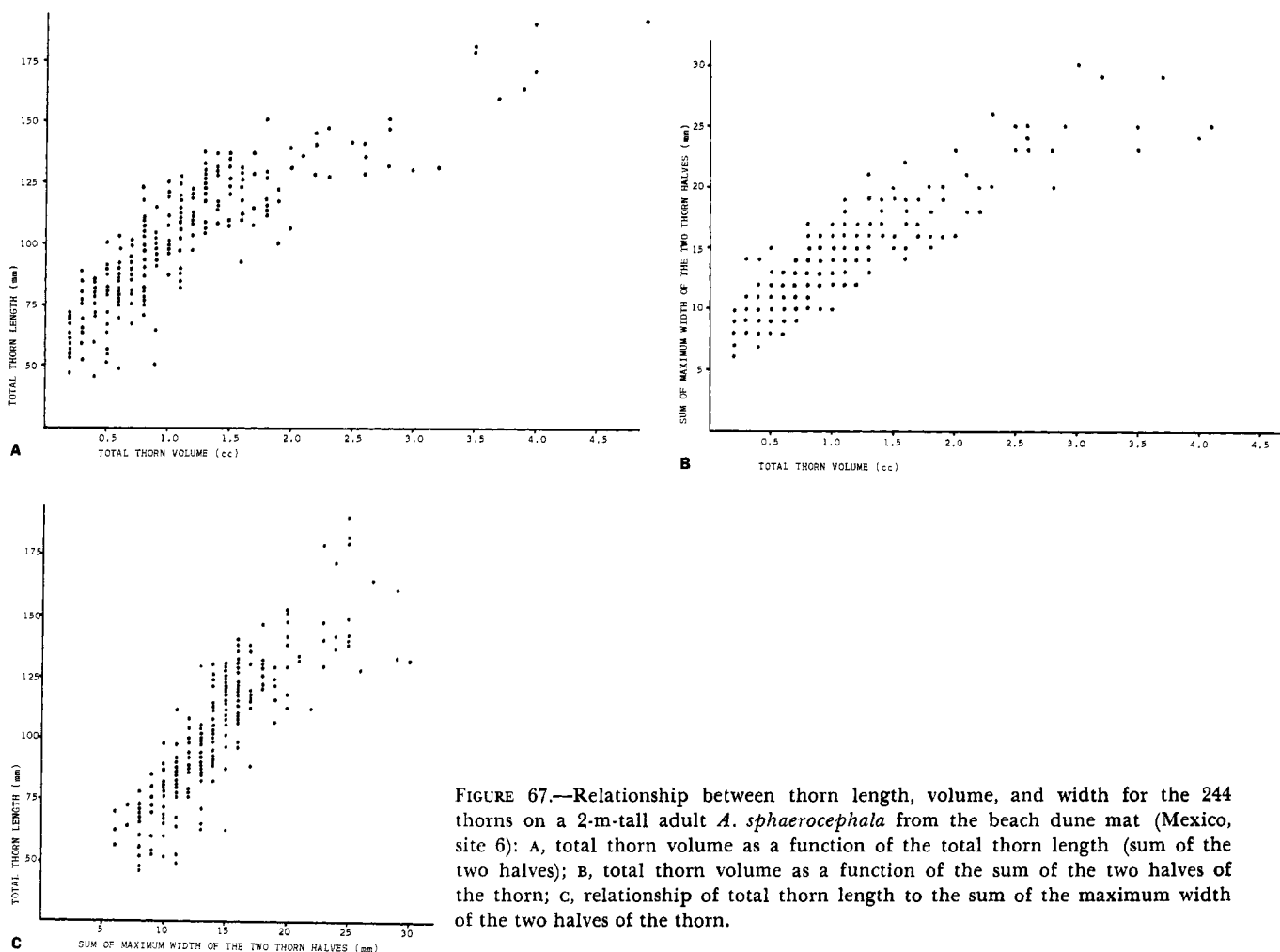


FIGURE 67.—Relationship between thorn length, volume, and width for the 244 thorns on a 2-m-tall adult *A. sphaerocephala* from the beach dune mat (Mexico, site 6): A, total thorn volume as a function of the total thorn length (sum of the two halves); B, total thorn volume as a function of the sum of the two halves of the thorn; C, relationship of total thorn length to the sum of the maximum width of the two halves of the thorn.

interaction in the New World as has evolved between the African swollen-thorn acacias and *Crematogaster*.

8. *Acacia cornigera* (L.) Willdenow

Acacia cornigera (L.) Willdenow, 1806:1080.

Mimosa cornigera L., 1753:520.

Acacia cornigera var. *americana* Dc., 1825:460.

Acacia spadicigera Schlechtendal and Chamisso, 1830:594.

Acacia cubensis Schenck, 1913:360.

Acacia nicoyensis Schenck, 1913:360.

Acacia hernandezii Safford, 1914:358.

Acacia jurcella Safford, 1914:359.

Tauroceras spadicigerum (Schlechtendal and Chamisso) Britton and Rose, 1928:85.

Tauroceras cornigerum (L.) Britton and Rose, 1928:86 [excluding synonymy].

Acacia interjecta Schenck, 1913:361.

Acacia rossiana Schenck, 1913:361.

Acacia campecheana Schenck, 1913:361.

Acacia turgida Safford in Wheeler, 142:plate 45.

Acacia cornigera is the best known of the swollen-thorn acacias. It is readily distinguished from all other swollen-thorn acacias by the unique combination of elongated "canoe-shaped" petiolar nectaries (Figure 8B), very elongated inflorescences (Figure 12A), thorns usually round in cross section, and completely indehiscent seed pods.

Linnaeus' type specimen of *A. cornigera* is a sterile branch representative of the eastern Mexican portion of the total population; it was collected from a cultivated plant in Holland, presumably grown from Mexican seed (Rudd, 1964). Rudd has compared pinnules of the type with those of *A. sphaerocephala* and found that the pinnules of the type have the readily visible secondary venation lacking on *A. sphaerocephala*

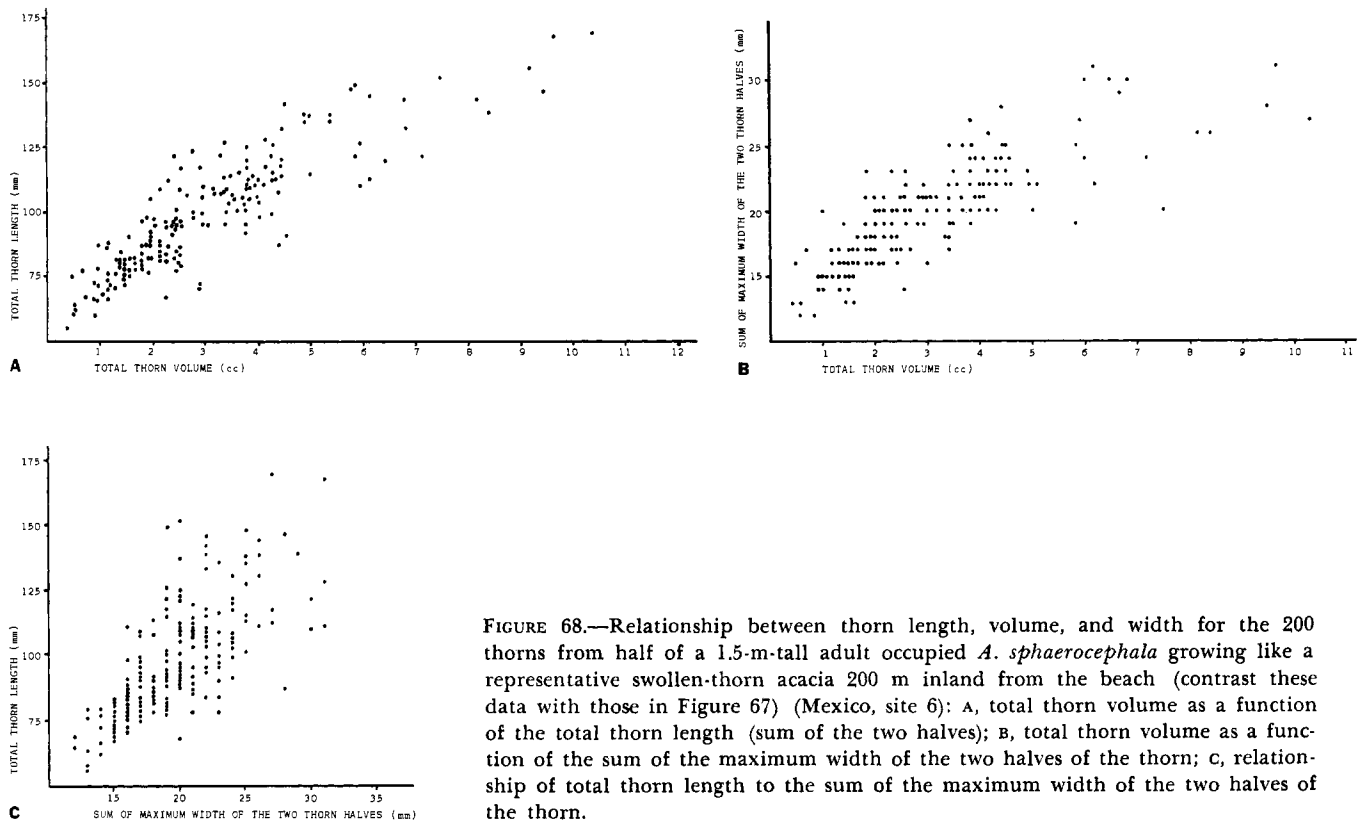


FIGURE 68.—Relationship between thorn length, volume, and width for the 200 thorns from half of a 1.5-m-tall adult occupied *A. sphaerocephala* growing like a representative swollen-thorn acacia 200 m inland from the beach (contrast these data with those in Figure 67) (Mexico, site 6): A, total thorn volume as a function of the total thorn length (sum of the two halves); B, total thorn volume as a function of the sum of the maximum width of the two halves of the thorn; C, relationship of total thorn length to the sum of the maximum width of the two halves of the thorn.

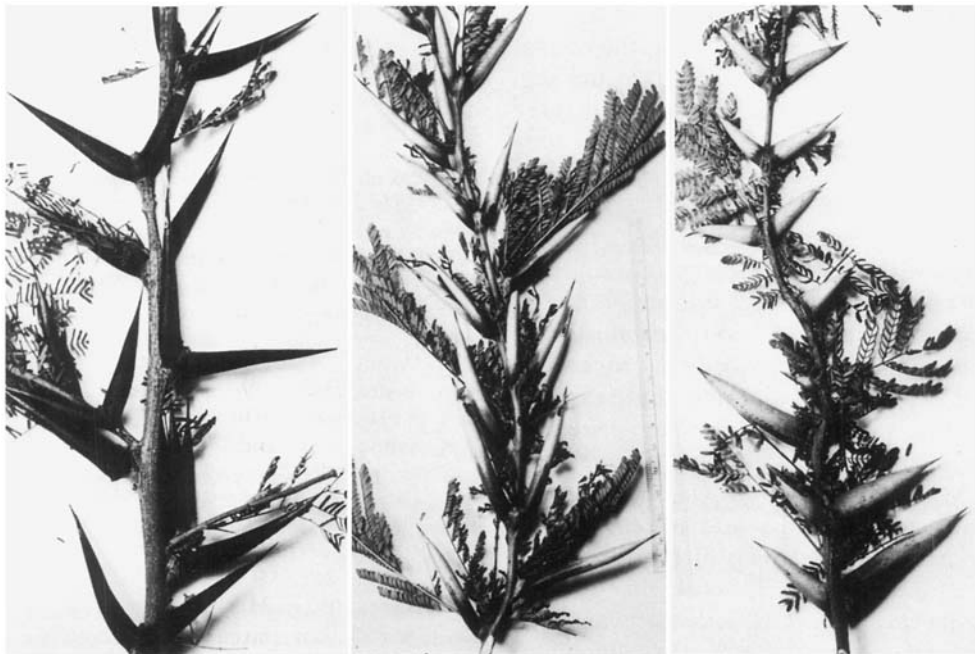


FIGURE 69.—*Acacia sphaerocephala* (Mexico): A, black type A thorns on lateral branch (site 5); B, bicolor type A thorns from a lateral branch of an inland adult (site 6); C, bicolor type A slightly inflated thorns of plants growing in the dune mat (site 6).

leaflets. Owing to the peculiar thorns of *A. mayana*, there is no doubt that the type does not belong to that species.

The type specimen of *A. spadicigera* (site 1) is easily identified as *A. cornigera* because of its elongate inflorescences and thorns round in cross section. Its straight short thorns are representative of *A. cornigera* from lowland wet sites in Veracruz. Safford's type specimen of *A. hernandezii* is unmistakably from the northern wet lowlands portion of the *A. cornigera* population. *A. cornigera* is the only species of swollen-thorn acacia in the Rascon area (site 2). Safford's leafless type specimen of *A. furcella* is representative of the *A. cornigera* population in the Lake Catemaco region (site 3). The type has the very dark brown thorns and widely spread type B thorns characteristic of high-elevation, eastern Mexican *A. cornigera*. The inflorescences of the types of both *A. hernandezii* and *A. furcella* are representative of *A. cornigera* inflorescences.

Schenck's type of *A. rossiana* (site 4) is representative of that portion of the *A. cornigera* population inland from Minatitlan, Veracruz, Mexico. I have been unable to locate his type specimen for *A. campecheana*; possibly it was destroyed at Berlin. He states that its leaves are like those of *A. spadicigera* and *A. rossiana*, and it was therefore most likely collected from that part of the *A. cornigera* population that extends along the coastal lowlands from Veracruz to Yucatan. Its name suggests that it was collected in Campeche, and there appear to be no swollen-thorn acacias in that area that could be confused with *A. cornigera*. Schenck described *A. interjecta* from material growing in the Singapore and Kew botanic gardens; the description agrees with that of *A. cornigera* and the seed probably came from Mexico, since that appears to have been the source of most introduced *A. cornigera* seed. Schenck described *A. nicoyensis* from material representative of the southern end of the geographic range of *A. cornigera* (site 77). His type specimen has the white and slightly flattened type A thorn found on Costa Rican *A. cornigera* growing in very dry and insolated sites. The inflorescences and seed pods of the type of *A. nicoyensis* are unmistakably *A. cornigera*.

Schenck's type specimen of *A. cubensis* was taken from a cultivated plant (site 82); the white and partially recurved type B thorns indicate that the seed came from the *A. cornigera* population some-

where north of Guatemala. *A. cornigera* apparently occurs only in gardens in Cuba and its presence unlikely is due to natural introduction by birds or other means. The absence of ant entrance holes in the thorns of the type specimen of *A. cubensis* indicates that the ants have not yet been introduced to Cuba.

Since *A. turgida* is supported only by a photograph (Wheeler, 1942), it probably represents a name that Safford intended to propose. I cannot find the locality (site 5) for the specimen, but it appears to have been collected from that rather distinctive portion of the *A. cornigera* population growing where the Pan-American highway crosses the Guatemala-Mexico border.

KEY COLLECTION LOCALITIES *

Mexico:

1. Type of *A. spadicigera*: La Laguna Verde, Veracruz, Mexico. March 1820, *Schiede*, no. 685.
2. Type of *A. hernandezii*: Rascon, S.L.P., Mexico. VII-19-22-1905, *E. Palmer*, no. 669.
3. Type of *A. furcella*: Catamaco, Veracruz, Mexico (300 m). IV-26-1894, *E.W. Nelson*, no. 427.
4. Type of *A. rossiana*: Santa Lucrezia, Isthmus of Tehuantepec, Veracruz, Mexico. X-8-1906, *H. Ross*, no. 918.
5. "Type" of *A. turgida*: Herba Santa, Chiapas, Mexico (see plate 45 in Wheeler, *Bull. Mus. Comp. Zool. Harvard*, 90:1-262).
6. Guatemala-Mexico border (near Ciudad Cuahatemoc) to 19.0 mi N on Hgy. 190, Chiapas (720-600-780 m). VIII-7-1966, *DHJ*, no. 499; VIII-16-1967, *DHJ*, nc (common to rare).
7. 2.6 mi NE to 0.9 mi W Chiapa de Corzo on Hgy. 190, Chiapas (580-475 m). VIII-17-1967, *DHJ*, nc (common to rare).
8. 9.7 mi W Tuxtla Gutierrez to 8 mi NE Cintalapa on Hgy. Chiapas 190 (860-1090-570 m). VIII-18-1967, *DHJ*, nc (common to rare to occasional).
9. 13.5 to 9.0 mi E of intersection of Hgy. 190 and 185 (La Ventosa), Oaxaca (80 m). VIII-18-1967, *DHJ*, nc (common to rare).
10. 9.9 to 23.4 mi N of intersection of Hgy. 190 and 185 (La Ventosa), Oaxaca (210-290-250 m). VIII-18-1967, *DHJ*, nc (common to occasional).
11. 33.3 mi N of intersection of Hgy. 190 and 185 (La Ventosa) to Acayucan, Oaxaca-Veracruz (230-40 m). VIII-18-1967, *DHJ*, nc (common).

* Hundreds of collection records of *A. cornigera* in the U.S. National Herbarium and elsewhere are included within the inclusive localities given here. For the sake of brevity, only type localities or collections made in sites not visited in this study are cited.

12. Near Salina Cruz, Oaxaca (sea level). X-3-1965, *DHJ*, nc (occasional).
13. Coatzacoalcos to Veracruz on Hgy. 180, Veracruz (0-350-0 m). III-21-1964, *DHJ*, no. 1935; VI-15-1966, *DHJ*, nc (occasional to common).
14. 8.3 mi SE bridge over Rio Coatzacoalcos, Veracruz, to Cardenas, Tabasco, on Hgy. 180 (0-40 m). VI-15-1966, *DHJ*, nc (very rare, about 1-2 plants per 2 miles).
15. Cardenas to 37.1 mi S, Tabasco (40-100 m). VI-17-1966, *DHJ*, nc (rare to common).
16. Cardenas to Paraiso, Tabasco (40-10 m). VI-17-1966, *DHJ*, nc (rare).
17. Cardenas to Ciudad del Carmen, Tabasco-Campeche (40-0 m). VI-22-1966, *DHJ*, no. 494 (rare, and only on well drained sites), fl.
18. Campeche to Ruinas Edzna (29 mi E on Hgy. 180), Campeche (0-50 m). VI-22-1966, *DHJ*, nc (very rare to occasional).
19. Hopelchen to Ticul on Hgy. 180, Campeche-Yucatan (50-80). VI-28-1966, *DHJ*, nc (very rare to occasional).
20. 12.2 mi S Peto (Santa Rosa) on Hgy. to Cd. Chetumal, Yucatan-Quintana Roo (50-80 m). VI-29-1966, *DHJ*, nc (common), fl.
21. Cd. Chetumal to 69.6 mi NW on Hgy. to Peto, Quintana Roo (0-20 m). VI-30-1966, *DHJ*, nc (common), fl.
22. 30 mi S to Campeche on Hgy. 180, Campeche (0-80-0 m). VI-25-1966, *DHJ*, no. 491; VII-8-1966, *DHJ*, nc (rare to common).
23. 3.2 mi E Cruz Grande to 19.1 mi NW Puerto Escondido on Hgy. 200, Guerrero-Oaxaca (50-250-70 m). VI-18-1967, *DHJ*, nc (rare to common to occasional).
24. 9.3 mi N Playa Pie de la Cuesta to 16.5 mi SE Papanoa on Hgy. 200, Guerrero (0-20 m). VI-17-1967, *DHJ*, nc (very common in swamps, absent on dry hills).
25. Alvarado to Tlacotalpan to Cd. Aleman to Las Tinajas to Paso del Toro, Veracruz (0-100-0 m). Throughout the year, *DHJ*, no. 1939 (common), flower February-May.
26. Tierra Blanca to La Granja to Temascal, Veracruz-Oaxaca (20-70 m). Throughout the year, *DHJ*, nos. 1966, 1967, 1968, 1969, 1970, 1971, 1972, 1973, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981 (very common).
27. Shores of the lake behind Presa Miguel Aleman, Temascal, Oaxaca (70 m). X-20-1963, *DHJ*, no. 1937; XI-3-1963, *DHJ*, nc (occasional to very common).
28. Cd. Aleman to Loma Bonita to Rio Playa Vicente, Veracruz-Oaxaca-Veracruz (50-100 m). XI-4-1963, *DHJ*, no. 1938 (common to very rare on red clay hills).
29. Cd. Aleman, Veracruz to Valle Nacional, Oaxaca, on Hgy. to Oaxaca, XI-6-1963, *DHJ*, nc (common to occasional).
30. 22.8 to 27.5 mi SW Conejos (turn off of Hgy. 140 to Huatusco) on Hgy. to Huatusco to Cordoba, Veracruz. XI-10-1963, *DHJ*, nc (common to rare).
31. 4.3 mi E Cordoba, Veracruz on Hgy. 150, Veracruz (800-0 m). X-16-1963, *DHJ*, nc (rare to very common).
32. Hgy. 150 SE to San Ignacio de la Llave, Veracruz (60-10 m). X-16-1963, *DHJ*, nc (common).
33. Tampico to Tuxpam on Hgy. 105, Veracruz (0-100-0 m). I-2-1964, *DHJ*, nos. 1942, 1943; VI-13-1966, *DHJ*, nc (common to rare).
34. Tuxpam to 1.2 mi S Villa A. Camacho on Hgy. 130, Veracruz. I-2-1964, *DHJ*, no. 1940; VI-13-1966, *DHJ*, nc (occasional to rare).
35. Poza Rica to Nautla on Hgy. 180, Veracruz (50-0 m), I-20-1964, *DHJ*, nc (occasional to rare).
36. 6 mi SW Tamazunchale to Cd. Valles on Hgy. 85, San Luis Potosi (500-100 m). I-1-1964, *DHJ*, no. 1936; XII-31-1963, *DHJ*, nc (rare to common).
37. 36.6 mi E Rio Verde to Cd. Valles on Hgy. 86, San Luis Potosi (1140-100 m). VIII-24-1967, *DHJ*, nc (rare to common).
38. Cd. Valles to 6.4 mi N Antiguo Morelos on Hgy. 85, San Luis Potosi-Tamaulipas (100-250 m). VIII-24-1967, *DHJ*, nc (rare).
39. Antiguo Morelos to 20 mi NW Cd. del Maiz, Tamaulipas-San Luis Potosi (250-? m). XII-31-1963, *DHJ*, nc (common on wetter hillsides).
40. Cd. Valles to Tampico on Hgy. 70, San Luis Potosi-Veracruz (100-10 m). VI-11-1966, *DHJ*, nos. 496, 497; VIII-24-1967, *DHJ*, nc (common to occasional).
41. Pt. Talisman (Guatemala-Mexico border) to 3 mi N Arriaga on Hgy. 200, Chiapas (50-150 m). I-11-1965, *DHJ*, no. 1047 (common).
42. Presa Benito Juarez, near Jalapa de Marquez on Hgy. 190, Oaxaca (200 m). IX-7-1968, *DHJ*, nc (1 plant).
43. Pichucalco, Chiapas. I-1907, *G.N. Collins* and *C.B. Doyle*, no. 260 (US 692169) mp.
44. 3 mi S Pinola Las Rosas along road to Soyatitan, Venustiano Carranza (W of Comitán), Chiapas (1400 m). VII-27-1965, *D.E. Breedlove*, no. 11367 (US 2484541), fl.
45. Zacualpan, Veracruz (1000 m). VII-1917, *C.A. Purpus*, no. 7748 (US 884536), fl., and IX-1908, *H. Schenck*, no. 836 (US 764665).
46. Fortuño, Rio Coatzacoalcos. III-1937, *L. Williams* (F 897476), fl.
- British Honduras:
47. Sta. Elena to Belize on main Hgy. (5-0 m). VI-30-1966, *DHJ*, nc (rare to occasional), fl.
48. El Cayo, El Cayo Prov. V-5-1931, *H.H. Bartlett*, no. 13007 (US 1493273), mp.
- Guatemala:
49. Escuintla to Taxisco along Hgy. CA-7, Depto. Escuintla-Santa Rosa (330-100 m). I-13-1965, *DHJ*, nc (occasional).
50. Escuintla, Depto. Escuintla, to Puente Talisman, Depto. San Marcos (Guatemala-Mexico border) on Hgy. CA-7 (330-50 m). VII-16-1966, *DHJ*, no. 466; I-11-1965, *DHJ*, nos. 1045, 1046 (common to occasional), fl.
51. Retalhuleu SW to Champerico, Depto. Retalhuleu (200-0 m). VIII-1-1966, *DHJ*, nc (occasional).
52. Retalhuleu to 14.0 mi NE on Hgy. S, Depto. Retalhuleu (200-900 m). VII-28-1966, *DHJ*, no. 464 (common to rare).
53. Escuintla to 7.4 mi NE on Hgy. 3, Depto. Escuintla (330-880 m). VIII-13-1967, *DHJ*, nc (common to occasional).
54. 0.3 mi SW to 4.1 mi NE Los Amates on Hgy. CA-9 (150-110 m). VIII-9-1967, *DHJ*, nc (common).
55. Finca San Joaquin, Slopes above Rio Negro, near San

- Cristobal de Verapaz, Depto. Alta Verapaz (1420-1080 m). VIII-14-1967, *DHJ*, nc (rare to common).
56. 14.9 mi SE to Guatemala-Mexico border (near Ciudad Cuauhtemoc), Depto. Huehuetenango (900-1000-720 m). VIII-16-1967, *DHJ*, nc (common).
57. Patalul, Depto. Solola. II-14-1906, *W.A. Kellerman*, no. 5915 (US 578841), fl.
58. Finca Sepacuite, Depto. Alto Verapaz. IV-1905, *O.F. Cook* and *R.F. Griggs*, no. 8 (US 590344), mp.
59. 1-2 mi N Ocos, Depto. San Marcos (sea level). III-15-1940. *J.A. Steyermark*, no. 37867 (F 1035247).
- Honduras:
60. 12.5 to 19.5 mi NW Siguatepec on Tegucigalpa-Puerto Cortes Hgy., Depto. Comayagua (910-540 m). VII-31-1967, *DHJ*, nc (common to very rare).
61. 0.7 mi N Rio Lindo to 18.6 mi S Puerto Cortes on Tegucigalpa-Puerto Cortes Hgy., Depto. Cortes (90-10 m). VIII-2-1967, *DHJ*, nc (common to occasional).
62. San Pedro Sula to 8.1 mi SW on Hgy. to Santa Rosa, Depto. Cortes (90-130 m). VIII-2-1967, *DHJ*, nc (occasional along streams).
63. 20.6 mi NE to 28.4 mi SW Sula on San Pedro Sula-Santa Rosa Hgy., Depto. Santa Barbara (260-780 m). VIII-3-1967, *DHJ*, nc (common to rare), fl.
64. Vegas del Rio Agua, 3 km from Yoro, Depto. Yoro (1000 m). V-8-1956, *A. Molina*, no. 6807 (US 2412019), fl.
- El Salvador:
65. From 11.2 to 26.3 mi N (Depto. Cuscatlan) San Salvador on San Salvador-Nueva Ocotopeque Hgy. (420-590 m). VIII-4-1967, *DHJ*, nc (common to rare).
66. 6 mi E San Salvador on Interamerican Hgy., Depto. San Salvador (650 m). I-14-1965, *DHJ*, nc (occasional), fl.
67. 29.7 to 31.6 mi E La Libertad on La Libertad-La Union Hgy., Depto. La Paz (50-80 m). VIII-5-1967, *DHJ*, nc (rare).
68. Intersection of Hgy. from La Herradura with La Libertad-La Union Hgy., Depto. La Paz (20 m). VIII-5-1967, *DHJ*, nc (1 plant).
69. 15.2 to 10.2 mi SE Santa Ana on Interamerican Hgy., Depto. Santa Ana (440-700 m). VIII-6-1967, *DHJ*, nc (common).
70. San Vicente, Depto. San Vicente (350-500 m). III-2-1922, *P.C. Standley*, no. 21687 (US 137448, US 1137096), fl.
71. Ateos, Depto. La Libertad. IV-17-1922, *P.C. Standley*, no. 23360 (US 1139047), fl.
72. San Martin to Laguna de Ilopango, Depto. San Salvador. IV-1-1922, *P.C. Standley*, no. 22580 (US 1138317), fl.
- Nicaragua:
73. Peñas Blancas (Depto. Rivas) to 7.2 mi NW on Hgy. 2 (50 m). VII-25-1967, *DHJ*, nc (common along rivers).
74. 3.4 mi SE Leon on Hgy. 12, Depto. Leon (20 m). VI-27-1967, *DHJ*, nc (30 acre patch), fl.
75. 1.2 mi W Matagalpa to 3.6 mi N on Hgy. 3, Depto. Matagalpa (650-880 m). VII-28-1967, *DHJ*, nc (common), fl.
76. 8 mi S Esteli on Hgy. 1 (940 m). VII-28-1967, *DHJ*, nc (1 plant).
- Costa Rica:
77. Type of *A. nicoyensis*: Shores of the Gulf of Nicoya, Guanacaste, Costa Rica (sea level). February 1900, *Tonduz*, no. 13538.
78. 20 mi NW turnoff of Interamerican Hgy. to Puntarenas, to Peñas Blancas (border of Costa Rica and Nicaragua) on Interamerican Hgy., Guanacaste Prov. (10-100 m). January-September, periodically in 1963-1967, *DHJ*, nc (rare to common, patchy distribution and associated with wet spots), fl., February-April.
79. Liberia to Playa Coco along Hgy. 21, Guanacaste Prov. (100-0 m). January-September, periodically in 1963-1967, *DHJ*, nc (rare to very common, primarily in wet spots), fl. and mp., in February.
80. Hda. Palo Verde, COMELCO, Bagaces, Guanacaste Prov. (sea level). IV-2-1966, *DHJ*, nc (occasional).
81. Filadelfia, Guanacaste Prov. III-2-1946, *Echeverria*, no. 279 (F 1442853), mp.
- Cuba:
82. Type of *A. cubensis*: North coast of Cuba. IV-21-1963, *C. Wright*, no. 2402.

NATURAL HISTORY

Acacia cornigera (Figure 70) and *A. collinsii* have the greatest geographic and ecological range of all the swollen-thorn acacias. The riparian and swamp habitats that were occupied by *A. cornigera* previous to human interference are in lowland areas that are ideal for slash-burn milpa agriculture. *A. cornigera* has probably been common in lowland agriculture fallow fields as long as Indians have lived in the Central American lowlands. Since occupied *A. cornigera* may reach reproductive maturity in 3 to 4 years, and since birds, people, and cattle distribute its seeds widely in second growth vegetation, *A. cornigera* populations have expanded widely into pastures, roadsides, and short-fallow fields generated by contemporary agricultural practices. At many locations, *A. cornigera* is found in all types of disturbance sites, from creek bottoms to hilltops. Only *A. sphaerocephala* and *A. collinsii* are on occasion found in drier habitats than *A. cornigera*. The natural history of *A. cornigera* in eastern Mexico has been described in detail (Janzen, 1967b), and the comments in the remainder of this section are designed to highlight the way it differs in other parts of its range from that portion of the population.

Local short-distance dispersals of *A. cornigera* by

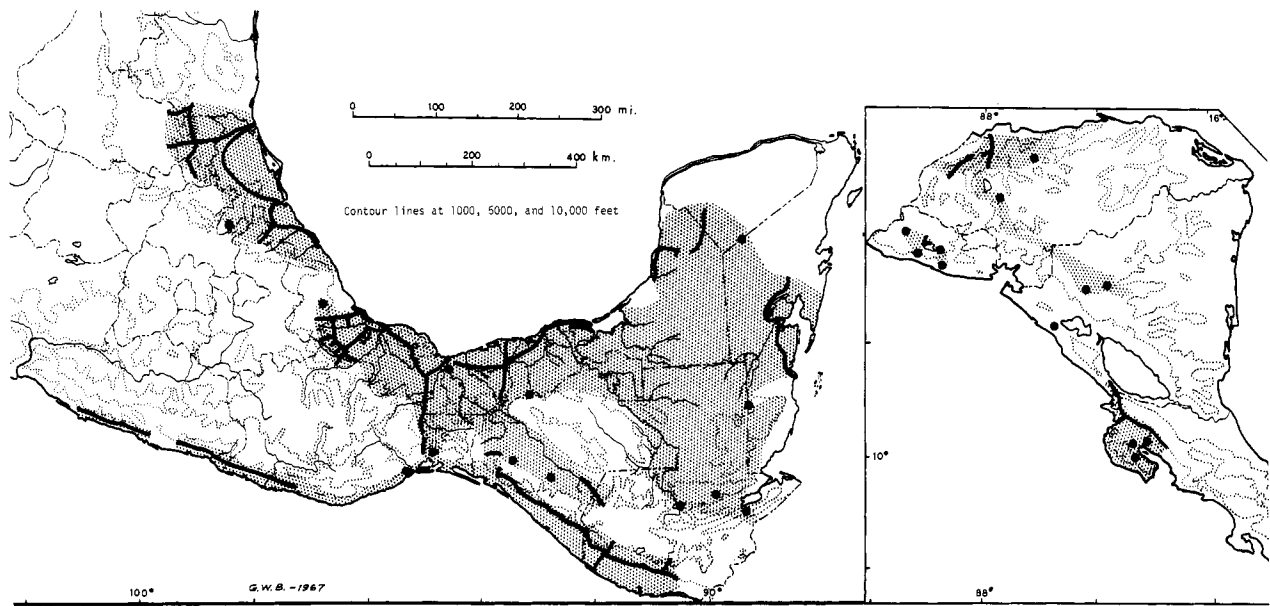


FIGURE 70.—Postulated general distribution (stippled area) and collection localities for *A. cornigera*.

humans make it difficult to understand its pre-Columbian range. For example, at site 42 in western Mexico, a single *A. cornigera* was found growing by a new hydroelectric dam. The closest native population of *A. cornigera* is several hundred miles away in the Isthmus of Tehuantepec and along the west coast in the Acapulco region (sites 23, 24) (also an introduction?). This plant probably arrived by either road-building machinery or through humans; farmers and Indians often eat the sweet pulp around the seeds and ingest many seeds simultaneously (Janzen, 1967b). The work crews on public construction in Mexico often come from several hundred miles away. If more than one plant was introduced in the area of the dam, it is likely that viable seeds will be produced. The bruchids that normally kill most *A. cornigera* seeds will be absent, at least at first, and this swollen-thorn acacia will likely spread down the watercourse away from the dam. It will probably not spread around the lake since the general area of the lake is extremely dry and water levels will fluctuate greatly. The single plant was occupied by *Pseudomyrmex ferruginea*. The queen probably came from the population of *A. collinsii* about 25 miles to the south or the population of *A. hindsii* 50 miles to the northwest. As a second example, in the central Yucatan Peninsula, *A. cornigera* is only common around small

settlements, cattle corrals, and old Indian ruins (sites 18 to 21). These small sites are also usually the wetter habitats in the region (the outlying areas are heavily occupied by *A. collinsii*), and it is impossible to know if the presence of *A. cornigera* is due to recent and frequent introduction by humans and cattle, or by natural dispersal by birds.

Deliberate long-distance introduction of *A. cornigera* may have some interesting repercussions in the future. Introduced to the southern tip of Florida as a garden plant, *A. cornigera* has occasionally escaped to form feral populations (e.g., Oneco and Chapman Field, US 1433083 and US 764685 in the U.S. National Herbarium). These plants are severely damaged by the frosts that occasionally damage orange orchards, but they do flower and set fertile seeds if there are several together. Obligate acacia-ants have not been introduced, but it would be interesting to examine the interaction of occupied swollen-thorn acacias with the subtropical communities of southern Florida. Reproductively isolated from the Mexican parent genotype, *A. cornigera* might even develop a frost-resistant population in Florida. *A. cornigera* has also escaped on Martinique, Guadeloupe, and Cuba in the Caribbean (US 2229384, US 1714928, US 764657). Here, with a climate not unlike that of some parts of eastern lowland Mexico, the popula-

tions (again without their ants) have a chance to expand into the native vegetation just as many other species of introduced trees have done on Caribbean islands. The central question here is whether the herbivore pressure in the island communities is strong enough to require occupation by obligate acacia-ants for the survival of a large breeding population of *A. cornigera*. All introductions to the Old World tropics appear to have been to botanical gardens, and I have no information on their escape into natural habitats.

Acacia cornigera and *A. collinsii* occupy adjacent habitats over much of their range. Always *A. cornigera* is in the wetter creek bottoms and swamp edges while *A. collinsii* is on the drier hillsides (e.g., Guanacaste Province, Costa Rica). In the wetter parts of the range, *A. hindsii* and *A. cornigera* often occur together (e.g., Pacific foothills of Guatemala) and here, *A. cornigera* is the drier hillside plant with *A. hindsii* along the watercourses. The distinctiveness of these separations by habitat was probably once very clear. Current agricultural practices have rendered wetter habitats drier and more isolated by clearing the vegetation, with the consequence that the formerly separated swollen-thorn acacias now grow side by side.

In the southern part of its range, the *A. cornigera* population is much more broken up into subpopulations than in eastern Mexico where it is found in all sorts of disturbance and climatic regimes from sea level to 1200 m, and from areas with a 7-month dry season to areas with almost no obvious dry season. In habitats where one expects to find *A. cornigera* in the northern part of the range, one instead encounters *A. collinsii* and *A. hindsii*. To determine the role of competitive exclusion in this system, we need much more information on the parasites and predators (specifically, bruchid beetles) that these species have in common, and the ability of each to grow and maintain the largest possible obligate acacia-ant colony in the shortest period of time.

Why *A. cornigera* has stopped its southward movement in Guanacaste Province in Costa Rica is very enigmatic. *A. collinsii* continues south to Colombia with a nearly continuous population that occupies many habitats similar to those occupied by *A. cornigera* further north. It may well be that it has not stopped at all, but rather that it is in the process of slowly moving southward. The only

possible ecological explanation that comes readily to mind is that the Guanacaste plants of *A. cornigera* are specialists at surviving the severe dry season there and therefore cannot advance slowly through the wet-forest area immediately down the coast from Puntarenas. What is needed is a long-distance dispersal of more than one seed simultaneously from Guanacaste to the dry Pacific coast of Panama.

The dependency of *A. cornigera* on a colony of obligate acacia-ants for survival to reproductive maturity has been well documented for lowland eastern Mexican habitats (Janzen, 1967a). Judging from the badly damaged condition of naturally unoccupied *A. cornigera* throughout its range, this dependency is the general case. It is clear, however, that the intensity of damage to unoccupied *A. cornigera* varies from one habitat to another, just as it did from one season to another in the lowlands of eastern Mexico. High-elevation sites subjected to wet, cool, and windy weather (e.g., site 75) produce the healthiest appearing unoccupied *A. cornigera*, but even here it is doubtful if an unoccupied tree can survive until reproductive maturity unless growing in a cluster of acacias in a large and well-grazed cattle pasture. In central highland Guatemala (e.g., site 53) and on the highland Atlantic side of Honduras (site 60), *A. cornigera* is occasionally "occupied" by a large colony of *Camponotus planatus* which appear to compete directly for thorns with the obligate acacia-ants colony. The *C. planatus* patrol the acacia quite effectively and the plants are healthy in appearance. How long an acacia can be occupied by *C. planatus* and survive is not clear. On some occasions, a colony of *C. planatus* and one of obligate acacia-ants occupy the same acacia, but usually in different branches. *C. planatus* occurs throughout much of the range of swollen-thorn acacias but in other areas does not appear to offer any protection to the acacia. It also lives in hollow twigs in many other species of tree.

Acacia cornigera has gained the same "freedom" from herbivorous insects gained by *A. hindsii* in areas of intense agriculture (e.g., site 74 in El Salvador); however, it is much rarer than *A. hindsii* in these sites and will probably become extinct in the near future. Seedlings are almost never encountered. Without the ants to keep the vines off, the stiff and upright young shrub of *A. cornigera*



FIGURE 71.—*Acacia cornigera* (Mexico, site 26): A, unoccupied seedling from heavily shaded site; B, unoccupied seedling from strongly insolated site.

makes an excellent vine standard leading to its death by shading. The young plants of *A. hindsii* are more shade tolerant and less rigid than *A. cornigera* of the same age.

As with *A. hindsii* and *A. collinsii*, the seedlings of *A. cornigera* are scattered throughout the habitat occupied by the parents. As stressed earlier (Janzen, 1967b), they attain the height of 10 to 50 cm and die after 1 to 2 years if not occupied by a colony of obligate acacia-ants. When in heavily shaded sites, the seedlings tend to produce few swollen thorns (Figure 71A), while in fully insolated sites thorn production is much greater (Figure 71B). Once occupied, a variety of different shrub life forms may develop. In dry areas, about as much wood goes into the central trunk as into branches (e.g., Figure 72A), and the shrub ends up being very bushy in appearance (Figures 73A, B). Only very rarely does *A. cornigera* become a large tree 10 to 15 m in height; however, such trees are normally found in natural disturbance sites along rivers and

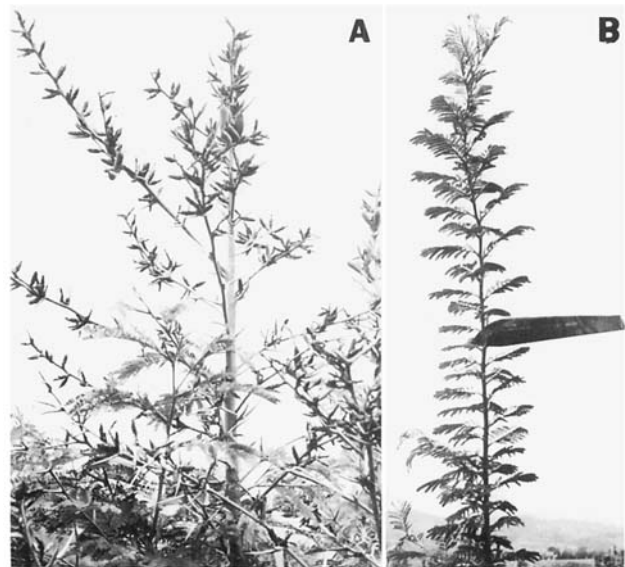


FIGURE 72.—*Acacia cornigera*: A, crown of healthy adult after losing its leaves during the last part of the dry season (Nicaragua, site 75); B, crown of healthy subadult growing in marshy pasture (Honduras, site 61).

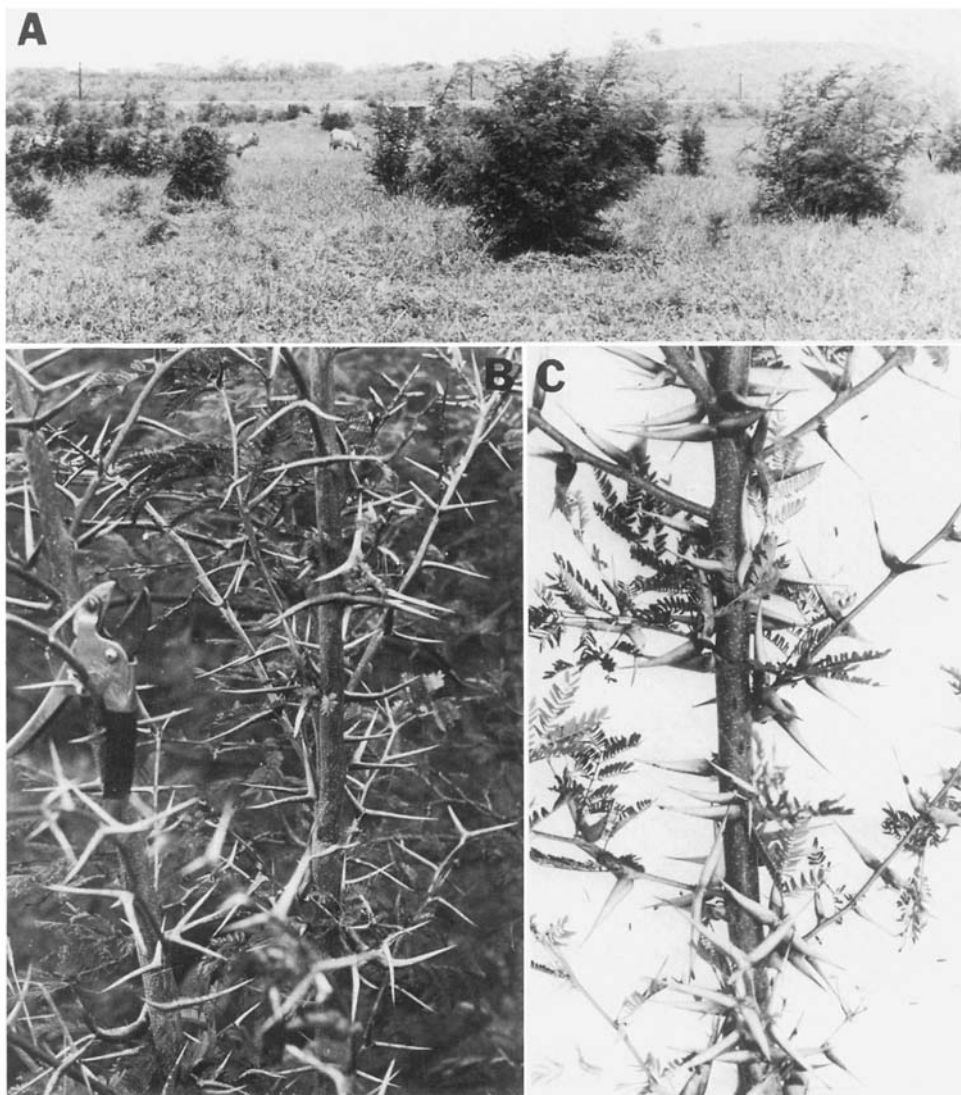


FIGURE 73.—*Acacia cornigera*: A, pasture with adult (Mexico, site 23); B, type B and type A thorns in center of crown of adult (Nicaragua, site 75); C, type B thorns on main trunk of adult (Mexico, site 24).

may at one time have made up a much larger proportion of the reproducing population than at present.

Over most of the distribution of *A. cornigera*, sexual branchlets and their products are rather uniform; however, wetness of the habitat does appear to influence this. In the Pacific foothills of Guatemala (site 50) the sexual branchlets may be 20 to 50 cm long (Figure 74A). In contrast to the situation at this wet site, most populations of *A.*

cornigera produce sexual branchlets 1 to 10 cm long (Figure 74c). The inflorescence itself is not influenced by the amount of moisture at the site, except that at some of the driest sites, some of the shortest inflorescences were found (again suggesting that *A. sphaerocephala* is a dry-land offshoot of *A. cornigera*). The number of florets per inflorescence is poorly correlated with the length of the inflorescence (Figure 75) at any one site but over a variety of sites shows a weak correlation (Figure 76).

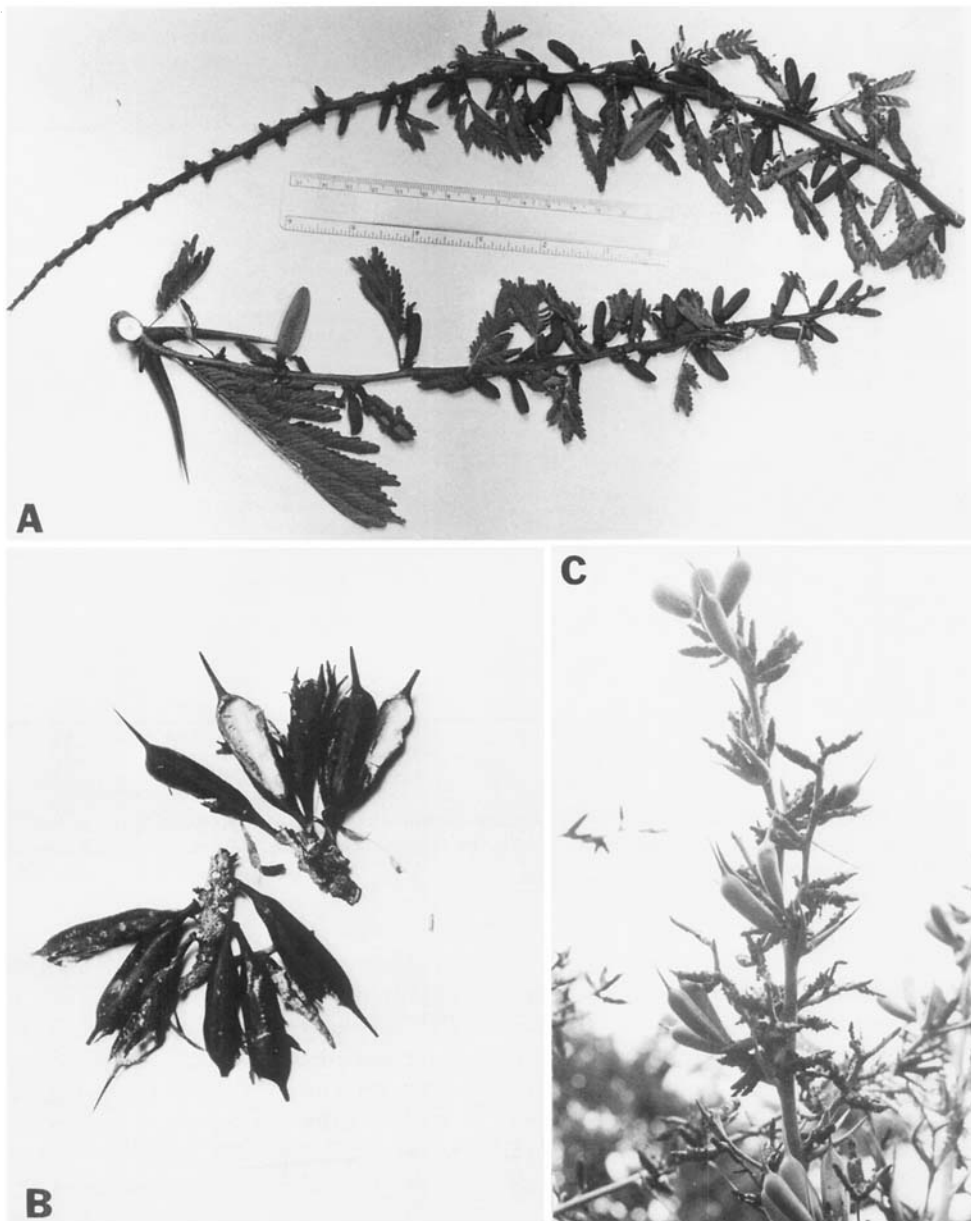


FIGURE 74.—*Acacia cornigera*: A, exceptionally long sexual branchlets (Guatemala, site 50); B, mature pods ripped open by birds (Guatemala, site 50); C, last year's pods and this year's inflorescences on short sexual branchlets in the crown of an adult (Nicaragua, site 75).

The indehiscent pods of *A. cornigera* are split open by birds (Figure 75B) and the seeds dispersed by birds that frequent second-growth vegetation (Janzen, 1967b). Over most of the range of *A. cornigera*, the pod walls are thick and hard to break between ones fingers. They tend to have sharp

and stiff long points on the end (Figures 74B, c); however, in riparian habitats at site 26, the pod walls are very thin and even split of their own accord when drying. The plants on the adjacent dry hills have the usual thick-walled pods. This difference is genetic as shown by a lack of intermediates

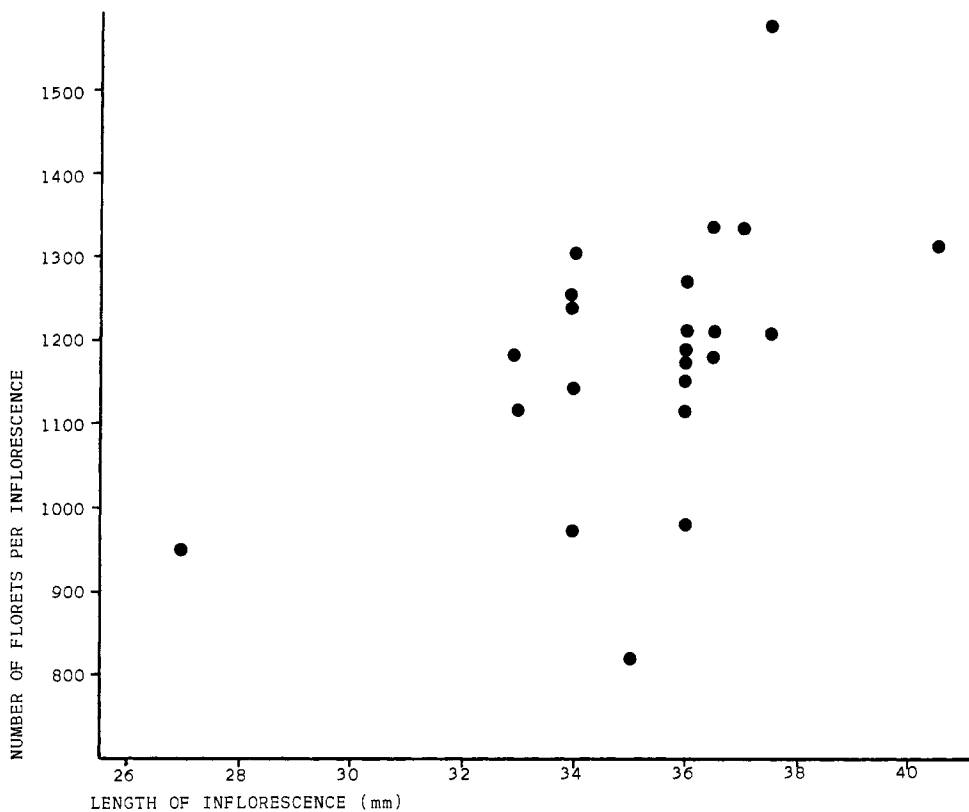


FIGURE 75.—Distribution of 27,262 florets among 23 inflorescences from a single adult *A. cornigera*; the inflorescences averaged about 35 mm in length (excluding peduncle) and 8.9 mm in width (Mexico, site 26).

and occasional plants bearing the "wrong" type of pods for the habitat where the plant is encountered. It is interesting that this site is only about 80 miles from that portion of the *A. sphaerocephala* population below the city of Veracruz that also has very thin pod walls. The number of seeds in *A. cornigera* pods is representative for dry-land, swollen-thorn acacias (Figure 77) but nearly all the seeds are killed by bruchid beetles. The very high predation on *A. cornigera* seeds by these beetles may be due to the high concentration of pod crops to be found in fields and roadsides; when the plants were widely spaced in natural disturbance sites, the bruchids might have a much more difficult time locating the pod crops.

The thorns of *A. cornigera* display every color found in swollen-thorn acacias, but there is little intertree or intratree variation at any one site. In general the thorns in very hot and dry lowlands are

white, ivory, or pale gray. At high elevations they are often very dark brown or nearly black. Though the correlation is not perfect, it is tempting to interpret these differences as being adaptive in respect to the ant colony. In lowland areas, temperatures in fully insolated thorns can be high enough to drive out the ants, and light-colored thorns may reflect radiation and slightly lower the temperature inside the thorn. It is perhaps significant in this connection that *A. collinsii* also has very light-colored thorns in dry and hot areas and dark thorns in high and wet sites. The dark thorns of *A. cornigera* could aid in warming up the ant colony on cool days and thereby increase the degree of patrolling by ants. It is significant in this respect that *A. sphaerocephala* has very dark thorns at the one high (cool) and dry site where it occurs, in strong contrast to the light-colored thorns it bears in dry lowland areas. All of the wet-forest swollen-

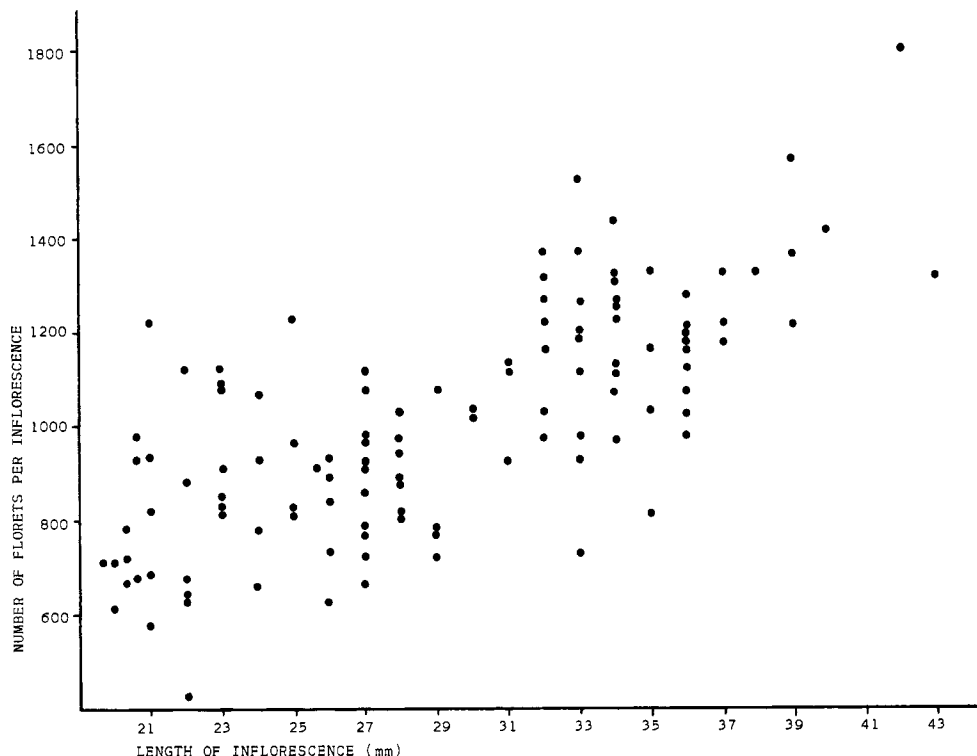


FIGURE 76—Distribution of 125,773 florets among 122 inflorescences from 16 adult *A. cornigera* from throughout the range of *A. cornigera*; there was no evidence of a geographical trend in size of inflorescence or number of florets per inflorescence.

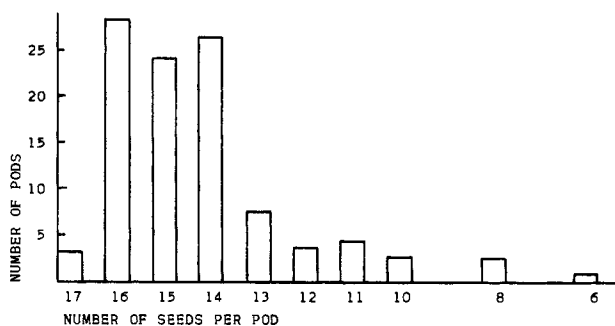


FIGURE 77.—Distribution of 1436 seeds among 100 pods from an adult *A. cornigera* with a normally heavy seed crop of about 500 pods (Mexico, site 26).

thorn acacias have very dark brown thorns, and this may be important in warming the thorns by occasional direct insolation. Bicolored thorns (Figure 78c) are somewhat puzzling in this respect. They are most prominent in the small and insulated population of *A. cornigera* on the west coast of

Mexico; here *A. cornigera* grows only in swamps, with *A. collinsii* on the extremely dry and hot adjacent hillsides.

The spectacular "bull's horns" swollen-thorns of *A. cornigera* are extremely variable in shape, but in a consistent and often clinal manner. Many sites are characterized by a particular thorn type, and many of these thorn types resemble thorns found on other species of swollen-thorn acacia (though often not sympatrically). Type A thorns of *A. cornigera* (Figures 78, 79) are usually round or nearly so in cross section and form a shallow to steep "V" with the branch wearing them. When flattened so that they superficially resemble *A. hindsii* thorns (Figure 80b), they are still easily distinguished by having very thick and rough walls. Type B thorns (Figures 80, 81) are highly variable in form, but all are much larger in volume than type A thorns. There is no part of the range of *A. cornigera* where it is consistently occupied by multiple-queen species of obligate acacia-ants, so

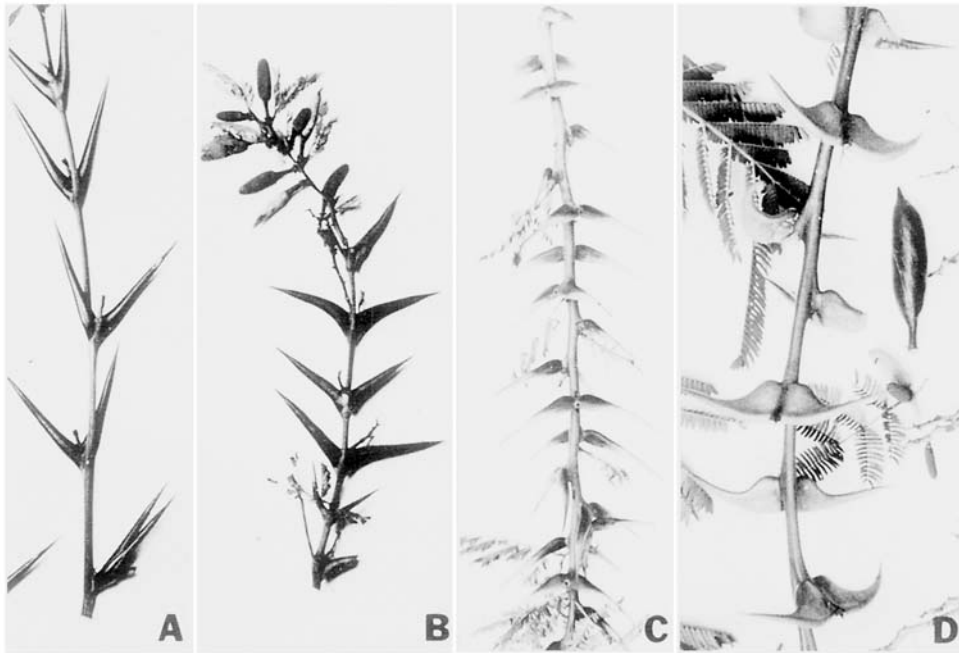


FIGURE 78.—Geographic variation in type A thorns from occupied adult *A. cornigera*: A, Mexico, site 33; B, Mexico, site 40; C, Mexico, site 24; D, Guatemala, site 56.



FIGURE 79.—Geographic variation in type A thorns from occupied adult *A. cornigera*: A, Mexico, site 33; B, Mexico, site 36; C, Mexico, site 33.

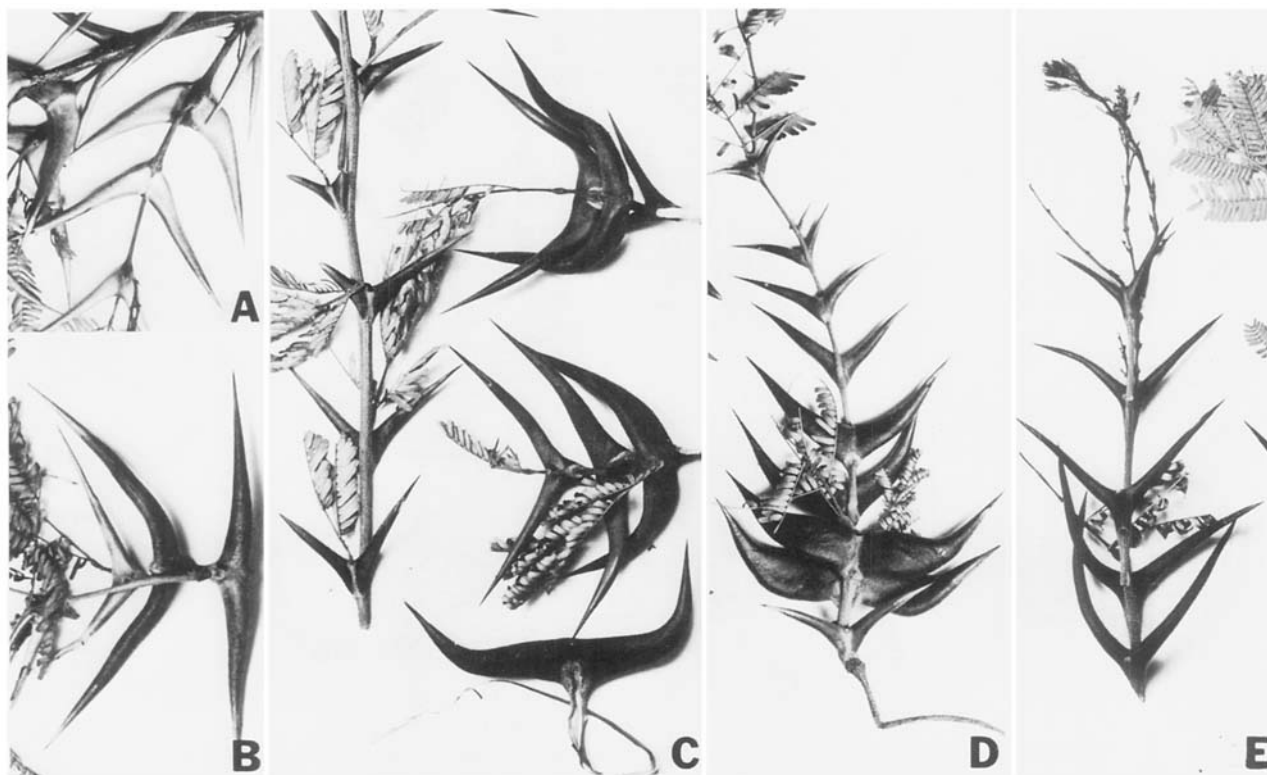


FIGURE 80.—Geographic variation in type B thorns from occupied adult *A. cornigera*: A, Mexico, site 33; B, Guatemala, site 52; C, Mexico, site 34; D, Guatemala, site 56; E, Mexico, site 35.

selection for large type B thorns is omnipresent. Type B thorns of *A. cornigera* are the hardest to break into of any of the swollen-thorn acacias. Several are often twisted together, making it difficult to even pull one off the acacia.

9. *Acacia mayana* Lundell

Acacia mayana Lundell, 1937:210.

Acacia mayana (Figure 17) is the most easily recognized of the swollen-thorn acacias, owing to the pair of bladelike longitudinal flanges extending from the thorn base to tip. The type specimen is representative of the other specimens examined, though it should be noted that there are only 6 specimens at hand of this exceptionally rare swollen-thorn acacia. The leafless isotype of the U.S. National Herbarium was collected from the upper part of the canopy of a mature plant that has been reproducing at least 2 years, since it bears both flowers and fruit. The fruits and flowers of *A.*

mayana are similar to those of *A. cornigera* and *A. sphaerocephala* (and therefore very different from the other 9 species of swollen-thorn acacia), but the fruits differ from those of these two species by being longer, thinner, and having a long thin base or stalk before swelling out around the seeds. The inflorescences differ from those of *A. cornigera* and *A. sphaerocephala* in that they taper to a point, rather than having a blunt end. More specimens of *A. mayana* are needed for study.

KEY COLLECTION LOCALITIES

1. Type: Rio Pasion, San Diego, Peten, Guatemala. VI-10-1935, *M. Aguilar*, no. 495 (US 1688106), mp.
2. Forest S of Finca Yalpemech, near Alta Verapaz-Peten boundary, Depto. Alta Verapaz, Guatemala (100-150 m). III-23-1942, *J. A. Steyermark*, no. 45184 (F 1188721), mp.
3. 3 mi W Cardenas, Tabasco, Mexico (20 m). VI-18-1966, *DHJ*, no. 458.
4. Fortuño, Coatzacoalcos River, Veracruz, Mexico (30-50 m). III-1937, *L. Williams*, no. 8425 (F 896540).
5. Retiro, Tenosique, Tabasco, Mexico. VI-19-25-1935, *E. Matuda*, no. 3410 (F 1027159) ("shrub in virgin forest").

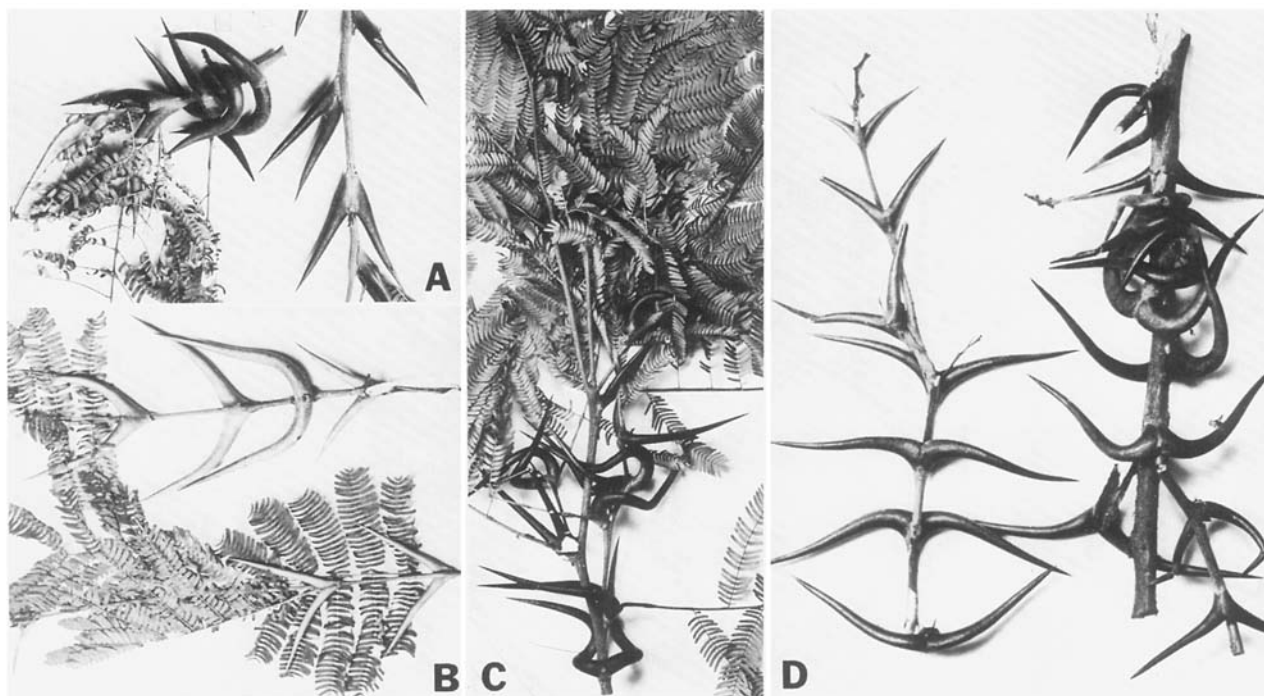


FIGURE 81.—Geographic variation in type B thorns from occupied adult *A. cornigera*: A, Mexico, site 26; B, Mexico, site 28; C, Mexico, site 26; D, Mexico, site 41.

6. Rio Icuolay, NNW Finca Cubilquitz to Quebrada Diablo, Depto. Alta Verapaz, Guatemala (300–350 m); III-6-1942, J. A. Steyermark, no. 44726 (F 1148694).

NATURAL HISTORY

Acacia mayana is by far the rarest of the swollen-thorn acacias. If the small number of collections represents the true density and spatial distribution of the species, it may well be self-pollinated in contrast to the other swollen-thorn acacias. The only specimen that I have been able to find (site 3) was growing in the same type of old second-growth cornfield regeneration that commonly harbors *A. cornigera*, but with one exception. The forest was about 15 m tall and the single *A. mayana* was heavily shaded, yet growing very well; an *A. cornigera* in the same shade regime would have been spindly with undersized thorns. It is possible that *A. mayana* is a species of primary forest, such as *A. melanoceras* and *A. allenii*; Matuda recorded it at site 5 as a "shrub in virgin forest." If this is the case, then its rarity in areas under heavy agricultural pressure probably means that it will become extinct in the lowlands.

If the above hypothesis is correct, then *A. mayana* is a mature and wet-forest edition of *A. cornigera*. It is interesting in this context that *A. cornigera* has perhaps produced both a beach-edge species (*A. sphaerocephala*) and a wet mature forest species.

It is tempting to view the oddly shaped thorns of *A. mayana* as the result of a long past hybridization with a sword-thorn acacia such as *A. macracantha*. When *A. macracantha* hybridizes with *A. chiapensis*, the result is often a "roundish" thorn in cross section, with longitudinal shallow-sided ridges down each side of the thorn. On the other hand, *A. mayana* displays no other traits suggesting a history of introgression with other acacias.

Whether the ridges are the result of introgression, or a novel mutation, they have a possible adaptive value. *A. cornigera* thorns on heavily shaded shoots have weak walls and are easily opened by birds for the ant brood inside; apparently the starving shoot does not have the energy to make the thick-walled thorns that effectively protect the ant colony in more insulated microhabitats. The longitudinal ridges on *A. mayana* thorns may be a way to solve the strengthening problem without

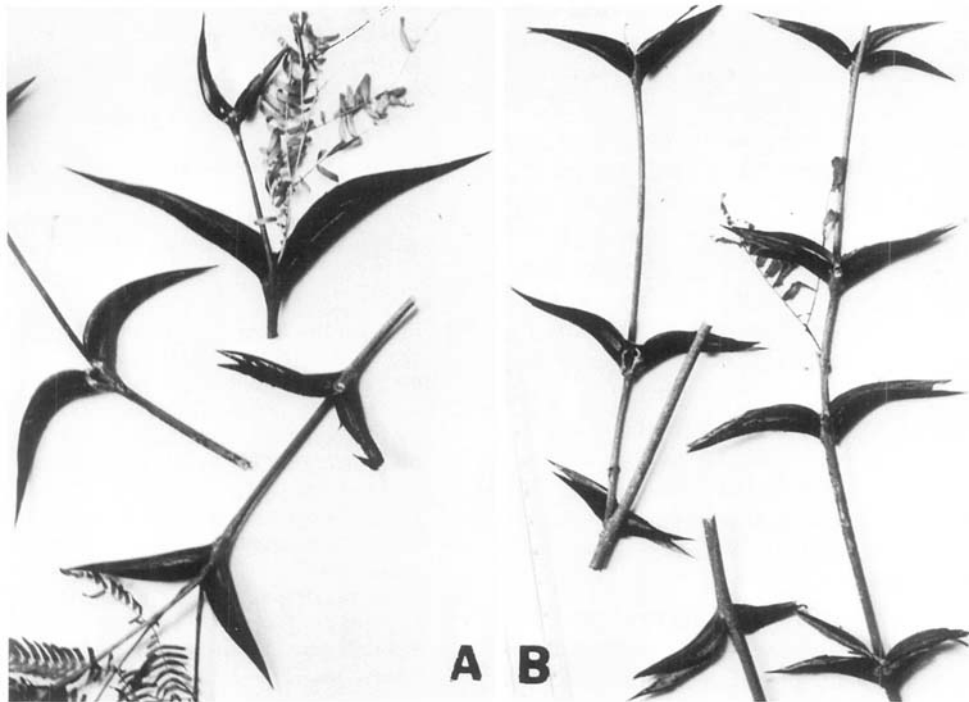


FIGURE 82.—*Acacia mayana*: A, type B thorns (the two largest), the largest thorn contained the ant colony queen; B, type A thorns split by birds in search of ant brood (Mexico, site 5).

putting a lot of bulk into the thorn wall (this bulk is also adaptive as insulation in heavy insulated sites) in a heavily shaded habitat. First, it is important to note that the ant colony grows slowly at a comparatively large cost to the acacia in the shaded habitat, and the loss of thorns with brood will be proportionately larger to the acacia than in an insulated site. Second, the slow replacement rate of thorns in shaded sites, observed on all forest species of swollen-thorn acacias, means that the birds have a longer time per thorn to locate the tree and go after its ants. Figure 82 shows that birds can be a threat to the ant colony in *A. mayana*, and it is important to note that they opened all the thorns on the shoot except the few largest ones.

All specimens of *A. mayana* examined have been occupied by mature colonies of *P. ferruginea*. In view of the small sample size, however, this should not be taken to indicate that it is a suitable host for only this species of obligate acacia-ant. The colony in the specimen at site 3 was as normal as can be expected of a colony that has just lost about three-fourths of its brood and workers to a bird. While the petiolar nectaries of *A. mayana* are

nearly twice as long as those of *A. cornigera* and *A. sphaerocephala*, it should not be assumed that the ant colony gets twice as much nectar per leaf from the shaded plant. There are no data to show a correlation between nectary size and nectar production.

A total of 12 pods from herbarium sheets was examined and there was no attack by bruchids. Owing to the small sample size, and the small sizes of the crops from which the pods were taken, this should not be taken as an indication that *A. mayana* is free from predispersal seed predation. On the other hand, if in fact it does occur as widely scattered individuals in mature forest, it is possible that the bruchids that commonly infest *A. cornigera* and *A. sphaerocephala* cannot cope with the very low prey density that such a rare population of swollen-thorn acacias presents (as with *A. melanoceras* and *A. allenii*).

10. *Acacia gentlei* Standley

Acacia gentlei Standley, 1940:77.

Acacia gentlei is the common acacia of wetter

sites in British Honduras and lowland northern Guatemala (Figure 44). It is easily distinguished from other swollen-thorn acacias by the combination of elongate inflorescences, one or at the most two elongate petiolar nectaries, and a large number of very thin thorns. Where it is sympatric with *A. collinsii* and *A. cornigera* in northern British Honduras, it is easily distinguished from both by attaining heights of 3 to 8 m, while they are generally 1.5 to 3 m in height when reproductive, and by having much darker green foliage that strikingly contrasts with the rust-red bark. Both are generally found in the drier sites, while *A. gentlei* is generally in the wetter sites. Where the distribution of *A. gentlei* overlaps with that of *A. ruddiae* and *A. cookii* in northern Guatemalan wet forest, *A. gentlei* is again easily distinguished from the former by being occupied by obligate acacia-ants and by having Beltian bodies on the new foliage. It is distinguished from the latter by having oval petiolar nectaries and elongate inflorescences. Some specimens of *A. globulifera* have oval petiolar nectaries as well, but the spherical inflorescence of *A. globulifera* is very easily distinguished from the elongate one of *A. gentlei*.

Standley's type specimen of *A. gentlei* was obviously collected from the upper part of the crown of a large acacia such as the one in Figure 83A, and it is representative of the population whose distribution is plotted in Figure 44. The thorns on the type are slightly redder than most thorns in nature from British Honduras; they look more like those common on the north side of Lake Izabal. The seed pods on the type specimen are not mature but are nearly full length (19 to 20 cm).

KEY COLLECTION LOCALITIES

British Honduras:

1. Type of *A. gentlei*: British Honduras. *P. Gentle*, no. 185.
2. 13.5 mi S Sta. Elena, Corozal Prov., to 43.8 mi SE Orange Walk (on road to Belice), Belice Prov., British Honduras (10–30 m). VI–30–1966, *DHJ*, nos. 582, 575 (occasional to common) fl., mp.
3. 17.9 to 36.1 mi SW Belice (on road to Cayo), Cayo Prov., British Honduras (50–100 m). VII–3–1966, *DHJ*, nc (common).
4. 2 mi S Sta. Elena, Corozal Prov., British Honduras (sea level), VII–4–1966, *DHJ*, nc (3 plants).
5. Gallon Jug, British Honduras. III–5–1938, *D. A. Lancaster*, no. 31 (US 2219935) fl., mp.

6. Maskall, British Honduras. I–31–1934, *P. H. Gentle*, no. 1121 (US 1635002), mp.
7. Little Cocquericot, Belize River. III–27–1933, *C. L. Lundell*, no. 4406 (F 738238).
8. Valentin, El Cayo Prov. VI–1936, *C. L. Lundell*, no. 6328 (F 894493).
9. Camp 6, El Cayo Prov. III–9–1938, *P. H. Gentle*, no. 2311 (F 945128).
10. Rio Grande (southern B. H.) (80 m). III–20–1933, *W. A. Schipp*, no. 1142 (F 669139) ft.

Guatemala:

11. El Zapotillo, 1 km E El Estor, Depto. Izabal, Guatemala (10 m). V–16–1965, *DHJ*, nos. 657, 659, 665, 667, 671, 690 (common), fl., mp.
12. 16.1 mi SW (Puente El Lobo) Los Amates to 29.4 mi NE (Santa Rosa) Los Amates on CA–9, Depto. Izabal, Guatemala (200 to 50 m). VIII–9–1967, *DHJ*, nc (common but scattered).
13. 1.0 to 9.4 mi SE Mariscos (S side Lake Izabal), Depto. Izabal, Guatemala (100 m). V–13–1965, *DHJ*, nc (common).
14. Uaxactun, Depto. Peten, Guatemala, IV–21–1931, *H. H. Bartlett*, no. 12676 (US 1493227, US 1493228), fl., mp.
15. Aguacaliente, Depto. Santa Rosa. I–25–1908, *W. A. Kellerman*, no. 7710 (F 224606) (locality doubtful).
16. La Libertad, Depto. Peten. IV–1–1933, *C. L. Lundell*, no. 2379 (F 738067) fl.
17. N of Sebol, between Sebol and Carrizal, Depto. Alta Verapaz (200–300 m). IV–18–1942, *J. A. Steyermark*, no. 45762 (F 1180368, F 1180419).
18. S of Sayaxche, Laguna Petexbatum. (Laguna Mexico), Depto. Peten (50 m). V–3–1942, *J. A. Steyermark*, no. 46221 (F 1180409).
19. 2–4 mi W Livingston, Depto. Izabal. IV–16–1940, *J. A. Steyermark*, no. 39546 (F 1038624).
20. Fallabon-Yaxha Road, Depto. Peten. III–1933, *C. L. Lundell*, no. 2195 (F 739642).
21. 2.8 mi W Puerto Matias de Galvez (on road to Escobas), Depto. Izabal (10 m). VIII–10–1967, *DHJ*, nc.

NATURAL HISTORY

While *A. gentlei* is clearly a plant that was originally associated with wetter forest than extreme dry-land species such as *A. cornigera*, *A. hindsii*, and *A. collinsii*, it has survived very well in the face of human disturbance, in contrast to *A. allenii*, *A. melanoceras*, and *A. ruddiae*. Wherever the forest is cut with at least a 15 to 20 year fallow rotation period, *A. gentlei* becomes very common, and has even become a roadside plant in the wetter parts of British Honduras. It is very common in fallow Indian milpas in the Izabal region of Guatemala. In Guatemala, it is commonly encountered in swamps and river-edge vegetation in forest undisturbed by man for a long time.



FIGURE 83.—*Acacia gentlei* (Guatemala, site 12): A, crown of 5-m-tall emergent adult; B, type B thorns on main trunk of adult.

The obvious success of *A. gentlei* in moving from natural disturbance sites is probably due to two factors. First, the seeds are surrounded by a white and sweet pulp that is readily picked from the semidehiscent pods by birds such as kiskadees (*Ptangus sulpheratus*) and saltators (*Saltator* spp.). These, and other birds of second-growth vegetation, are probably responsible for frequent dispersal of seeds into newly cleared sites. Second, as will be discussed later, *A. gentlei* is quickly occupied and heavily patrolled by obligate acacia-ants.

While *A. gentlei* adults in reproductive condition are only occasionally encountered in primary forest (but slightly more often than are *A. allenii* or *A. melanoceras*), their seeds are probably moderately common. *A. gentlei* seeds are very hard, like those of other dry-land acacias, and remain viable at least 5 years and probably much longer. The presence of *A. gentlei* seeds in the forest litter is suggested as the effect of the hurricane that leveled large expanses of wet forest to the southwest of

Belice, British Honduras (site 3), in the late 1950s. In the woody regeneration that followed, by 1966 *A. gentlei* was scattered over the area at a density of about 10 reproducing adults per acre. There had clearly been enough seed and seedlings present to do this, despite the fact that the average density of *A. gentlei* in this type of forest, when undisturbed, is about 0.1 tree per acre.

Reproductive details of *A. gentlei* have not been recorded, but it sprouts very well from cut stumps. Seedlings grow well in very dense shade but appear to require a slight break in the general canopy before they can grow large enough to reproduce. Seed crops are large and therefore comparable in size with the other dry-land acacias when fully insolated and mature. Adults are difficult to age because they show the least clear growth rings of any of the swollen-thorn acacias. Based on size, they probably live up to about 20 or 25 years and rarely have a trunk diameter in excess of 15 cm.

Trees of *A. gentlei* are usually very heavily oc-

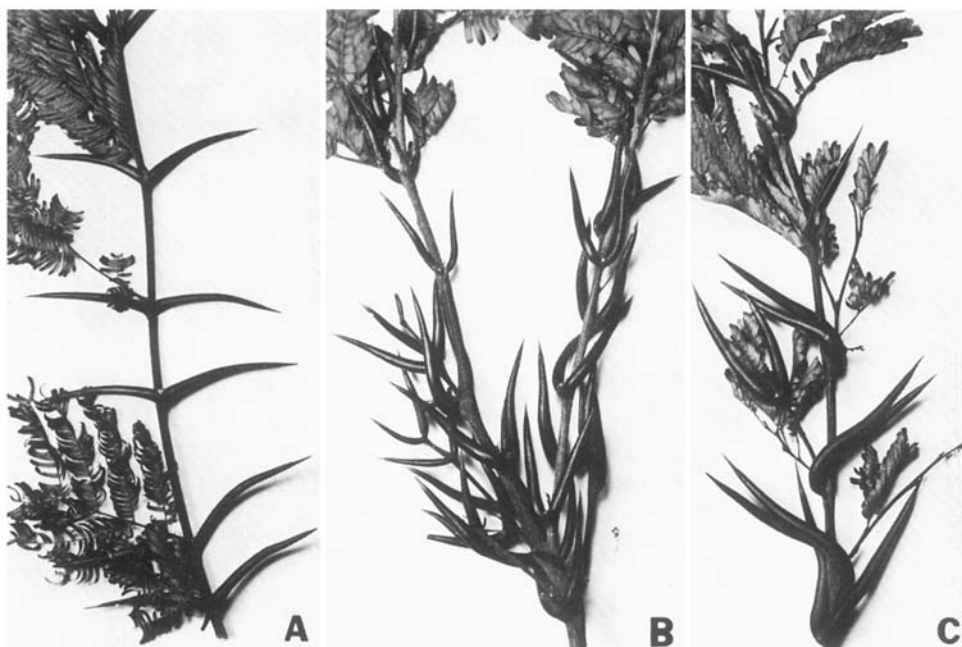


FIGURE 84.—*Acacia gentlei*: A, type A thorns from a lateral branch from the crown of a mature tree (Guatemala, site 11); B, type A thorns from the crown of a mature tree (British Honduras, site 2); C, type B thorns on the base of a lateral branch (British Honduras, site 2).

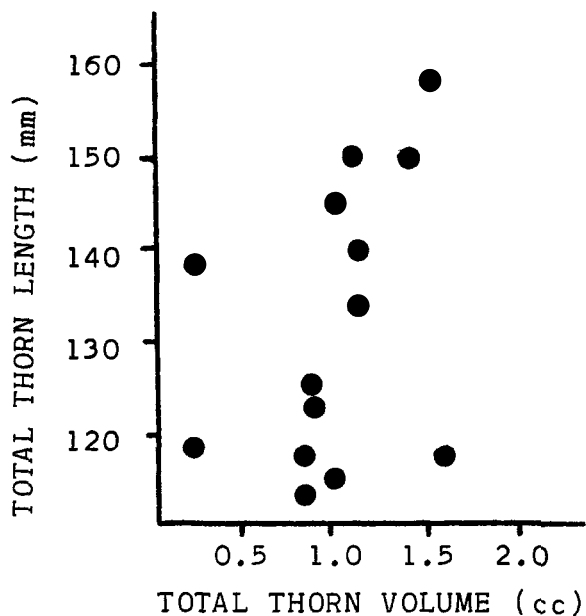


FIGURE 85.—Distribution of 15.4 cc of thorn volume among 14 very large type A thorns from one *A. gentlei* (Guatemala, site 13).

cupied by *P. ferruginea* or one of the two undescribed species of obligate acacia-ants found within its range. The young single-queen colonies appear to have little trouble becoming established—though in roadside areas of British Honduras, an unusually aggressive black morph of *Pseudomyrmex gracilis* often takes over young acacias. While the dark green foliage of *A. gentlei* closely resembles that of *A. chiapensis* in texture, color, and taste, *A. gentlei* lacks the herbivore damage so characteristic of *A. chiapensis*. This lack of herbivore damage is apparently because the ant colonies grow very large in *A. gentlei*; a single-queen colony of 15,000 workers is not uncommon in a 3-m-tall tree.

Acacia gentlei shows that thin thorns (Figure 83B, 84) alone do not lead to poor growth of an ant colony. As can be seen in Figure 85, even the very longest thorn has a very small thorn volume. Many thorns are only 1.5 to 3 mm inside diameter, barely allowing the worker ants to pass through. As a consequence there is a very small amount of brood per thorn, but the very large number of thorns per tree probably means that the total thorn volume available to the colony is about the same in equal-



FIGURE 86.—Football-sized carton nests of *Azteca* ants in the crowns of 12-m-tall *A. gentlei* (Guatemala, site 12).

sized trees of *A. gentlei* and other swollen-thorn acacias. The other thin-thorned species, *A. cookii*, does not appear to have an excessive number of swollen thorns, but the slightly larger diameter of *A. cookii* thorns may compensate for the lower number as contrasted with *A. gentlei*.

Large senescent trees of *A. gentlei* growing in undisturbed (by humans) habitats are occasionally heavily tenanted by an unidentified species of ant in the genus *Azteca*. This ant genus, better known for its species occupying *Cecropia* and *Cordia*, is arboreal, predaceous on insects, and very aggressive to animals that shake the foliage near the nest. In *A. gentlei* the ants live both in the thorns previously opened up by the obligate acacia-ants and in hanging carton nests (Figure 86). While they do not systematically patrol the acacia leaves, they do forage on them, which probably results in the senescent tree living longer than normal. The obligate acacia-ant colony generally does very poorly in a senescent acacia since the ants have to have Beltian bodies and nectar in large quantities to maintain a colony large enough to effectively patrol the acacia.

11. *Acacia collinsii* Safford

- Acacia collinsii* Safford, 1910:677.
Acacia yucatanensis Schenck, 1913:361.
Acacia nelsonii Safford, 1914:363.
Acacia costaricensis Schenck, 1913:361.
Acacia penonomensis Safford, 1914:363.
Acacia panamensis Schenck, 1913:362.

Myrmecodendron collinsii (Safford) Britton and Rose, 1928:92.

Myrmecodendron costaricense (Schenck) Britton and Rose, 1928:93.

Acacia collinsii is easily distinguished from all other swollen-thorn acacias by its unique broadly dome-shaped petiolar nectaries. It has elongated inflorescences and fully dehiscent pods (which it has in common only with *A. hindsii*). *A. hindsii* and *A. collinsii* may be distinguished at almost all localities by their thorns, since type A thorns from mature *A. hindsii* are always strongly flattened while type A thorns of *A. collinsii* are round in cross section. Of all the swollen-thorn acacias, *A. collinsii* and *A. cornigera* have the widest geographical and ecological distributions (Figure 87).

Safford's type specimen of *A. collinsii* offers a classic example of the inadequacy of type specimens at representing an entire population. While Safford's type specimen is representative of the population of *A. collinsii* at site 1, the Chicoasen population of *A. collinsii* is quite different from *A. collinsii* over the remainder of its range. The type specimen appears to have been taken from a large adult tree in a partially shaded riparian site. Its leaves are as long as any found on *A. collinsii* (up to 16 cm long with the 10 pinnae spaced up to 3 cm apart). The leaves have the unusually large number of 5 to 6 petiolar nectaries with the distal ones being as far as 2 mm apart (this makes one suspect a bit of introgression with *A. globulifera*, which also occurs at this site). The sexual branchlets are up to 8 cm long (normal maximum) and the peduncles of the mature inflorescences range up to the exceptional length of 33 mm. The peduncles are also nearly 2 mm thick, while on most *A. collinsii* they are 1 mm or less thick. The thin type A thorns are round in cross section but twisted around the branch; this is characteristic of the *A. collinsii* population only in Chiapas, Mexico.

Schenck's type of *A. yucatanensis* (site 2) is representative of most of the population of *A. collinsii* in drier habitats, and especially the Yucatan portion of the population. The small leaves are specially characteristic of *A. collinsii*. His type of *A. costaricensis* is not available (apparently destroyed in Berlin) but a paratype from Costa Rica (site 66) is clearly drawn from that portion of the *A. collinsii* population at dry intermediate elevations in Costa Rica. If it were useful to designate a lectotype, this

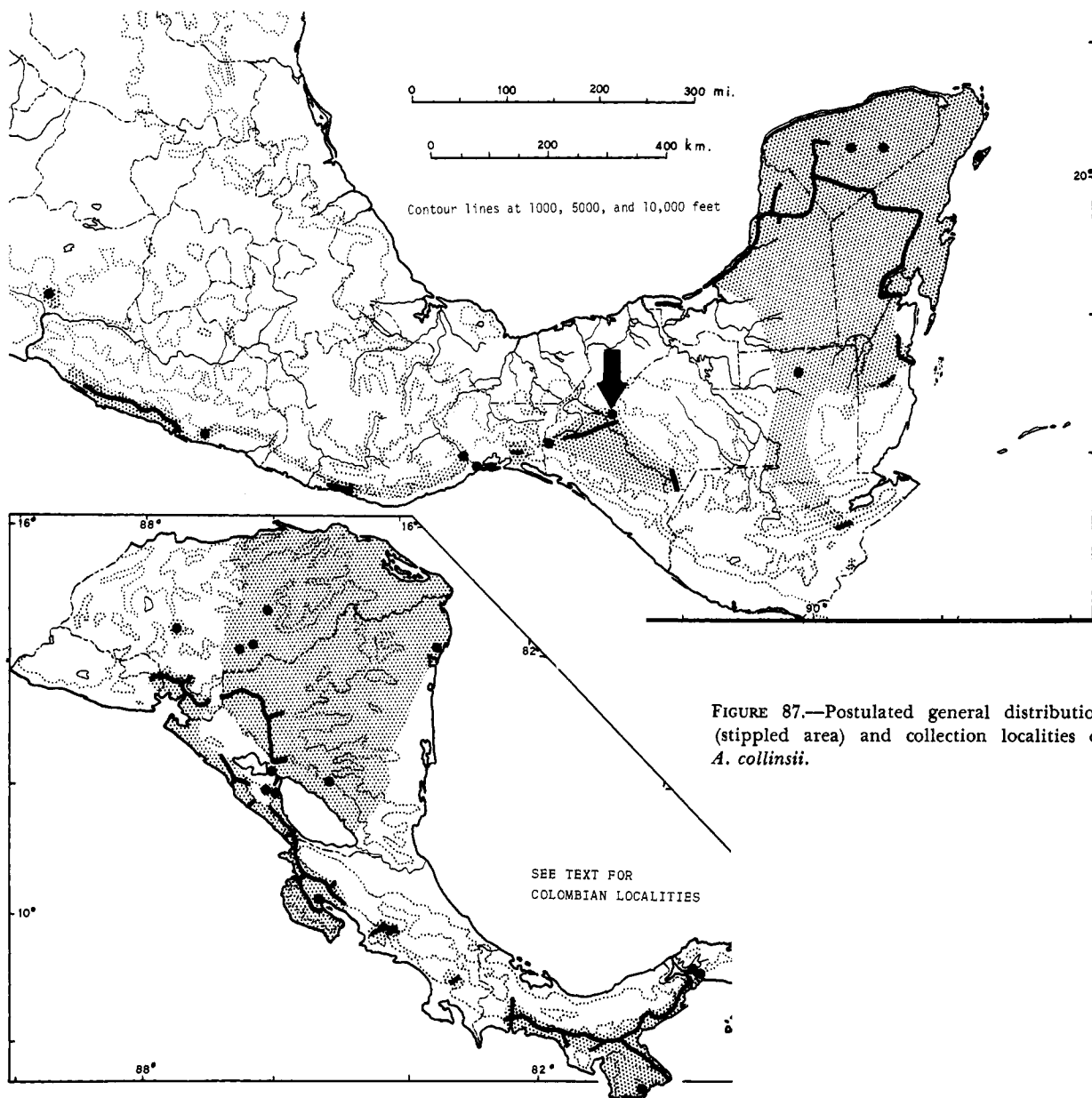


FIGURE 87.—Postulated general distribution (stippled area) and collection localities of *A. collinsii*.

would be the appropriate specimen. Schenck's description of *A. costaricensis* applies unmistakably to *A. collinsii* and is very different from the other Costa Rican swollen-thorn acacias (*A. cornigera*, *A. allenii*, *A. ruddiae*). Britton and Rose (1928) refer to the type locality of *A. costaricensis* as "Lagarto, Costa Rica" but do not give the source of these data; there is a "Lagarto" in Puntarenas Province and *A. collinsii* is abundant there (sites 67 and 75).

Acacia panamensis is clearly based on two species of plants. The description of the thorn and leaf-

bearing branch clearly applies to *A. collinsii* (not to *A. melanoceras*, the only other central Panamanian species of swollen-thorn acacia). Schenck (1913) notes that he is not sure that the inflorescences belong to the sterile branch; the globular inflorescences could be from *A. melanoceras* (unlikely owing to their very thin peduncle) or, more likely, from one of the other nonant-acacias that grow commonly in the drier parts of Panama along with *A. collinsii*. A final complication is that the exact locality is given as "Aljahuela" and I cannot

locate such a site in Panama. This site most likely represents Alajuela in Alajuela Province, Costa Rica, which was a favorite collection site for German collectors around the turn of the century. *A. collinsii* is the only swollen-thorn acacia in the Alajuela region (sites 68, 69, 74).

Safford's type of *A. nelsonii* (site 3) is representative of the *A. collinsii* population in the area north of the Isthmus of Tehuantepec, Mexico, but differs from more southerly populations in having large pinnules (up to 11 mm long and 3 mm wide) and somewhat flattened thorns (2 to 3 times as wide as deep in cross section). Flattened thorns are, however, even better developed in the *A. collinsii* population from central Costa Rica to Panama. The inflorescences of the type of *A. nelsonii* are normal, but the thorns on the same branch have been weathered gray rather than being the usual beige color of younger thorns from western Mexico. Safford's type of *A. penonomensis* (site 76) differs from the remainder of the *A. collinsii* population on the dry Pacific side of Panama in that its type A thorns are not quite as flattened as are those on many *A. collinsii* at sites 82 to 84. The seed pods on the type of *A. penonomensis* are representative of those found in the drier parts of the range of *A. collinsii*; these pods have stiff woody valves that only curl a slight amount during dehiscence.

KEY COLLECTION LOCALITIES

Mexico:

1. Type of *A. collinsii*: (between San Fernandino and) Chicoasen, Chiapas, Mexico (320 m). I-13-1907, G. N. Collins and C. B. Doyle, no. 180 (US 692159).
2. Type of *A. yucatanensis*: Yucatan, Mexico. 1895, G. F. Gaumer, no. 353 (US 571618).
3. Type of *A. nelsonii*: Acapulco, Guerrero, Mexico (sea level). IV-30-1903, E. W. Nelson, no. 7024 (US 399366).
4. 3.6 mi NW, border station between Mexico and Guatemala (La Mesilla) to 8.4 mi S La Trinitaria on Hgy. 190, Chiapas (680-720-600-1060 m). VIII-7-1966, DHJ, nos. 441, 443; VIII-17-1967, DHJ, no. 1713 (very common to occasional).
5. 11.8 mi E (near turnoff to Villa Hermosa) Chiapa de Corzo to 13.8 mi SW Tuxtla Gutierrez on Hgy. 190, Chiapas (1090-450-1090 m). VIII-17-1967, DHJ, nos. 424, 435 (common to occasional).
6. 13.8 mi SW, Tuxtla Gutierrez to 17.9 mi SW Las Cruces (turnoff to Arriaga) on Hgy. 190 (1090-530-820 m), Chiapas. VIII-18-1967, DHJ, nc (common to exceedingly rare).
7. 1-2 mi N Gabriel Zamora on Hgy. 37, Michoacan (820 m). VI-10-20-1968, DHJ, nc (very common).
8. 13.4 to 23.5 mi E Zanatepec on Hgy. 190, Oaxaca (50 m). VIII-18-1968, DHJ, nc (very rare to common), fl.
9. 42.1 mi E Zanatepec on Hgy. 190, Oaxaca (60 m). VIII-18-1967, DHJ, nc (1 plant).
10. 3 mi N Soyalo on Tuxtla Gutierrez-Villa Hermosa Hgy., Chiapas (\approx 1100 m). VII-10-1966, DHJ, nc (common), fl.
11. 10 to 14 W Tehuantepec (Hgy. 190), Oaxaca (100 m). I-10-1965, DHJ, nos. 1845, 1950. IX-3-1965, DHJ, nos. 1779, 1780, 1783 (common).
12. Puerto Escondido to 3.5 mi N on road to Oaxaca, Oaxaca (10-120 m). VI-19-1967, DHJ, nc (common to very rare).
13. Puerto Escondido to 18.4 mi NW (Hgy. 200), Oaxaca (10-80 m). VI-19-1967, DHJ, nc (common to very rare).
14. Hills in and around Acapulco, Guerrero (0-100 m). VI-18-1967, DHJ, nc (occasional).
15. Acapulco to 1.3 mi SE Papanoa, Guerrero (0-30 m). VI-16-1967, DHJ, nc (common on dry hillsides, absent from swamps).
16. 48 mi NE Isla Aguada (across from Puerto Real, Campeche) to Merida (Yucatan), on Hgy. 180 (0-30 m), VI-22-1966, DHJ, nos. 428, 431, 433, 438, 606 (occasional to very abundant).
17. Ruinas Edzna north to Hgy. 180 (east of Campeche), Campeche (15-40 m). VI-25-1966, DHJ, nc (rare to occasional).
18. Becal south to Hgy. 180, Campeche (15-40 m). VI-26-1967, DHJ, nc (rare to occasional).
19. Merida to 14.2 mi E (Hgy. 180), Yucatan (10-20 m). VI-28-1966, DHJ, no. 455 (rare).
20. Muna (Yucatan) to Felipe Carillo Puerto (road to Cd. Chetumal), Quintana Roo (10-20 m). VI-29-1966, DHJ, nc (very rare).
21. Felipe Carillo Puerto to Cd. Chetumal, Quintana Roo (20-0 m). VI-30-1966, DHJ, no. 453 (very rare to occasional).
22. 9.6 mi E San Marcos on Hgy. 200, Oaxaca (50 m). VI-18-1967, DHJ, nc (1 plant).
23. La Ventosa, 7 km E Salina Cruz, Oaxaca (sea level). VII-3-1959, R.M. King, no. 1302 (US 2362102), fl.
24. Petatlan, Montes de Oca, Guerrero. VI-17-1937, G. B. Hinton, no. 10333 (US 1805541, F 959109).
25. Tuxpeña, Campeche. II-2-1932, C. L. Lundell, no. 1279 (US 1494445), mp.
26. Sudzal, Yucatan. IV-21-1956, O. G. Enriquez, no. 564 (US 2448079).
27. Chichen Itza, Yucatan. V-30-1929, J. Bequaert, no. 2 (US 1477467), fl., mp.
28. Isla Cozumel, Quintana Roo. XII-5-1966, V. E. Rudd, no. 2036 (US 2518023).
29. San Vicente, Chiapas. IV-16-1904, E. A. Goldman, no. 862 (US 470663), mp.
30. Berriozabal, on road to San Fernando, Chiapas (950 m). XII-18-1949, F. Miranda, no. 5847 (US 2367591), mp.
31. Chorreadero de Tuxtla, 5.6 mi E Chiapa de Corzo (800 m). II-16-1965, D. E. Breedlove, no. 9018 (F 1627187), fl.

32. Chichen Itza, Yucatan. V-30-1929, *J. Bequaert*, no. 2 (F 710846).
33. Izamal, Yucatan. II-21-1906, *J. M. Gaumer*, no. 379 (F 189844), fl.
34. Salina Cruz, Oaxaca (sea level). IV-28-1910, *Orcutt*, no. 3451 (F 280154), mp.
- British Honduras:
35. 23.6 mi S Orange Walk to Belize, Belize Prov. (10-0 m). VII-2-1966, *DHJ*, nc (rare to common).
36. 10.1 to 34.4 mi SW Belize on road to El Cayo, Belize Prov. (30-100 m). VII-3-1966, *DHJ*, nc (rare to occasional).
37. Duck Runn, Pine Ridge, El Cayo Prov. II-17-1931, *H. H. Bartlett*, no. 11546 (US 1493376, US 1493375), mp.
- Guatemala:
38. 2.6 mi SW Puente Rio Hondo on Hgy. CA-9 (near turnoff to Zacapa), to 1.8 mi NE Puente El Lobo on Hgy. CA-9, Depto. Zacapa (200-100 m). VIII-9-1967, *DHJ*, nos. 1794, 1797 (very common to occasional).
39. "District of Peten." IV-8-1933, *C. L. Lundell*, no. 2614 (F 738050).
- Honduras:
40. El Espino (Nicaragua) to 0.4 mi W on Honduras-Nicaragua border on Interamerican Hgy., Depto. Choluteca (880-930 m). VII-29-1967, *DHJ*, nc (4 plants).
41. 21.6 mi W San Marcos de Colon on Interamerican Hgy., to Choluteca, Depto. Choluteca (450-10 m). VIII-31-1965, *DHJ*, no. 1788; V-11-1965, *DHJ*, no. 1807; VII-29-1967, *DHJ*, nc (very common).
42. Choluteca (Depto. Choluteca) to Jicaro Galan (Depto. Valle) on Interamerican Hgy. (10-40 m). VII-29-1967, *DHJ*, no. 1803 (common to rare).
43. Jicaro Galan to 3.8 mi NE (Hgy. 1), Depto. Valle (40-80 m). VII-29-1967, *DHJ*, nc (rare).
44. Comayagua to 3 mi S on Hgy. 1, Depto. Comayagua (550 m). VII-31-1967, *DHJ*, nc (rare to common), fl.
45. Jicaro Galan to El Amatillo (Honduras-El Salvador border) on Interamerican Hgy. (40-200 m). I-15-1965, *DHJ*, no. 1841; V-12-1965, *DHJ*, nc (occasional to rare), fl.
46. Juticalpa, Depto. Olancho. III-5-16-1949, *P. C. Standley*, no. 17580 (F 1378910), mp.
47. Rio Guayambre, Valle Jamastran, Depto. El Paraiso (350 m). III-13-1956, *A. Molina*, no. 7364 (F 1599625).
48. Danli, Depto. El Paraiso (700-800 m). II-11-23-1949, *P. C. Standley*, no. 16506 (F 1378924).
- El Salvador:
49. El Amatillo (Honduras-El Salvador border) to 7.1 mi W (on road to La Union), Depto. La Union (200-190 m). V-12-1965, *DHJ*, no. 1801 (rare), fl.
- Nicaragua:
50. Peñas Blancas (Depto. Rivas) to Jinotepe (Depto. Carazo) (Hgy. 2) (50-500 m). V-9-1965, *DHJ*, no. 1822; I-16-1965, *DHJ*, nos. 1830, 1932; VII-26-1967, *DHJ*, nc (occasional to very common).
51. La Virgin to San Juan del Sur (Hgy. 16), Rivas Prov. (50-0 m). V-10-1965, *DHJ*, nos. 1814, 1815, 1819, 1921 (common), fl, mp.
52. Masachapa to 14.7 mi NE (Hgy. 8), Depto. Managua (0-480 m). VII-26-1967, *DHJ*, nc (common to rare).
53. 15.2 mi SW Interamerican Hgy. (Depto. Managua) on road to Chinandega (Hgy. 12) to 5 mi SE Leon (Depto. Leon), (30-450 m). VII-27-1967, *DHJ*, nc (occasional to rare).
54. Puerto Somoza to 6.4 mi NE (junction with Hgy. 12), Depto. Leon (0-30 mi S Tipitapa on Hgy. 1, Depto. Managua (50 m). V-10-1965, *DHJ*, no. 1812; VII-28-1967, *DHJ*, nc (1 unoccupied plant).
56. 4.2 mi N Tipitapa on Hgy. 1, Managua (75 m). VII-28-1967, *DHJ*, nc (1 unoccupied plant), fl.
57. San Benito (N of Tipitapa on Hgy. 1) to 16.7 NE (Hgy. y) (100 m). VII-28-1967, *DHJ*, nc (extremely common).
58. San Benito (Depto. Managua) to Sebaco (Depto. Matagalpa) on Hgy. 1 (100-420-350-500 m). VII-28-1967, *DHJ*, nc (very common to very rare at 420 m to common), fl.
59. Sebaco to 1.6 mi N Matagalpa (Hgy. 3), Depto. Matagalpa (500-730 m). VII-28-1967, *DHJ*, nc (common to occasional), fl.
60. Sebaco (Depto. Matagalpa) to Esteli (Depto. Esteli) on Hgy. 1 (500-1040-850 m). VII-28-1967, *DHJ*, nc (common to very rare at 1040 m to common).
61. Esteli (Depto. Esteli) to El Espino on the Honduras-Nicaragua border (Depto. Madriz) on Hgy. 1 (850-530-880 m). I-15-1965, *DHJ*, no. 1825; V-11-1965, *DHJ*, no. 1808, 1810; VII-29-1967, *DHJ*, nc (common).
62. Laguna de Masaya, Depto. Masaya (300 m). VII-6-1923, *W. R. Maxon*, no. 7739 (US 1181452), fl.
63. Granada, Depto. Granada (250 m). VII-2-1923, *W. R. Maxon et al.*, no. 7597 (US 1181308); IV-21-1916, *J. D. Mandragou* (US 764653 and US 764655), fl; and II-12-1903, *C. F. Baker*, no. 2546 (US 862954), fl.
64. La Libertad, Depto. Chontales, V-29-VI-1-1947, *P. C. Standley*, no. 8826 (F 1288080).
65. Braggman's Bluff (Puerto Cabezas), Yulu Village, Depto. Zelaya (100 m), (F 585006).
- Costa Rica:
66. Potential lectotype of *A. costaricensis*: Alajuela, Alajuela, Costa Rica (920 m). 1896, *J. D. Smith*, no. 6488 (cf. Schenck, 1913).
67. 18.4 mi to 21.4 mi E Palmar Norte, Puntarenas Prov. (90 m). V-23-1965, *DHJ*, no. 1832; VI-26-1967, VIII-23-1965, V-15-1965, III-21-1966, VII-21-1963, *DHJ*, nc (occasional), in fl.
68. Escazu to 3.6 m W Santaigo de Puriscal (Hgy. 7), Alajuela Prov. (1000-600 m). VII-17-1967, II-15-1965, *DHJ*, no. 1862; III-2-1965 (fl), *DHJ*, nc (occasional to rare).
69. Along the electric railroad from Antonio to Orotina, Alajuela Prov. (900 to 50 m). VIII-1963, *DHJ*, nc (occasional).

70. 15.0 mi NW turnoff of Interamerican Hgy. to Puntarenas, to Peñas Blancas (Border of Costa Rica and Nicaragua), Guanacaste Prov. (10–100 m). January–September, periodically in 1963–1967, *DHJ*, nos. 1757, 1759, 1762, 1763, 1826 (rare to exceedingly common), fl. January to April.
71. Liberia to Playa Coco (Hgy. 21), Guanacaste Prov. (100–0 m). January–September, periodically in 1963–1967, *DHJ*, no. 1858 (occasional to very common), fl. January to April.
72. Hda. Palo Verde (about 18 mi S. Bagaces), Guanacaste Prov. (sea level). IV–2–1966, *DHJ*, nc (common), fl.
73. Cañas to 6 mi NE Guanacaste Prov. (80–300 m). IV–15–1965, *DHJ*, nc (occasional), fl.
74. Alajuela Prov. (920 m). III–1896, *J. D. Smith*, no. 6488 (US 943274), fl.
75. Lagarto, Puntarenas Prov. (sea level). XII–1891, *Tonduz*, no. 4810 (US 943276).

Panama:

76. Type of *A. penonomensis*: Penome, Cocolé, Panama (15–300 m). II–23–1908 to III–22–1908, *R. S. Williams*, no. 113.
77. 4.8 mi NE Tucuman Airport on Panama-Chepo Hgy., Panama Prov. (20 m). VII–1–1967, *DHJ*, no. 1704 (very rare), gp.
78. Vicinity of Madden Dam, Madden Lake (50 m). VII–3–1967, *DHJ*, no. 1653 (common), gp, fl.
79. Miraflores Locks to Paraiso and Corozal area, Canal Zone, VII–8–1967, *DHJ* and *Wheeler* (1942), nc (rare).
80. Arraijuan to 4.1 mi E on Interamerican Hgy., Canal Zone. VII–9–1967, *DHJ*, nc (occasional).
81. 3.2 mi SW La Chorrera, Panama Prov. (100 m). VII–1–1967, *DHJ*, nc (rare).
82. 5 mi N. Bejuco (Panama Prov.) to Santiago (Veraguas Prov.) along the Interamerican Hgy. (10–50 m). VII–1–1967, *DHJ*, nos. 1698, 1700, 1702 (rare to occasional).
83. Interamerican Hgy. (Herrera Prov.) to 3.1 mi S Pedasi (Los Santos Prov.) on Azuero Peninsula (5–25 m). VI–30–1967, *DHJ*, no. 1695 (occasional to common).
84. Santiago (Veraguas Prov.) to David (Chiriqui Prov.) along Interamerican Hgy. (50–200 m). VII–11–1967, *DHJ*, nc (very rare to occasional).
85. 2.1 mi NE Sona to Santiago, Veraguas Prov. (50 m). VI–29–1967, *DHJ*, nc (rare).
86. Remedios (Chiriqui Prov.) to 19.9 mi NW Jorones (Veraguas Prov.) on Sona-Remedios Road. VI–29–1967, *DHJ*, no. 1666 (occasional).
87. David to Pedregal, Chiriqui Prov. (0–30 m). VI–29–1967, *DHJ*, nc (rare).
88. David to 8.5 mi S Boquete, Chiriqui Prov. (30–620 m). VI–28–1967, *DHJ*, nc (rare to occasional), gp.
89. David to 2.7 mi NW on Interamerican Hgy., Chiriqui Prov. (90 m). VI–28–1967, *DHJ*, nc (rare to occasional).
90. Along Quebrada Ocho Paso, Río Tonosi, Tonosi, Los Santos Prov. (20 m). II–26–1963, *W. L. Stern et al.*, no. 1831 (US 2490276), fl., mp.

Colombia:*

* Colombian localities are not included in Figure 87.

91. Streams of Usiacuri and Pital, in mountains SW of Baranquilla, Depto. Atlántico. V–26–1928, *E. Niemeyer* (US 1496168).
92. Malambo to Sabanagrande, Depto. Atlántico (60 m). I–1936, *A. Dugand*, nos. 117, 404 (US 1619541).
93. Megua, Depto. Atlántico (50 m). I–13–1941, *A. Dugand* and *Jaramillo*, no. 2796 (US 1799137).
94. Usiacuri, Baranquilla, Depto. Atlántico (250 m). VII–1927, *B. Elias*, no. 245 (US 1342535), fl.
95. Arroyo Jubilado, Depto. Atlántico (50–60 m). XII–24–1933, *A. Dugand*, no. 117a, 40u (US 1573571).
96. Cartagena, Depto. Bolívar. 1919, *B. Heriberto*, no. 39 (US 1041093).
97. Isla de Providencia (Caribbean Sea). IV–29 to V–9–1948, *G. R. Proctor*, no. 3430 (US 1979268), fl., mp.; I–24–1967, *S. Anderson*; VIII–23 to VIII–29–1970, *DHJ*, nc (very common).
98. Providence Island (Caribbean Sea). VII–19–26–1966, *J. H. Torres R.*, no. 238 (COL 112189).
99. Juanmina, Baranquilla Dist., Depto. Atlántico (20 m). VII–5–1963, *H. S. McKee*, no. 10433 (COL 98405).
100. Valencia de Jesús, Valledupar, Magdalena (30 m). II–14–1948, *R. Romero-Castañeda*, no. 793 (COL 44486).
101. Arroyo de Megua, Depto. Atlántico (50 m). I–13–1941, *A. Dugand* and *R. Jaramillo*, no. 2769 (COL 05500).

NATURAL HISTORY

Over its wide geographical and ecological range (Figure 87), *A. collinsii* is found in habitats ranging from moderately wet to very dry, but the majority of the population is found in habitats that appear generally too dry for other swollen-thorn acacias (except *A. sphaerocephala* with its peculiarly local distribution). These habitats are often too dry for agriculture on hillsides (8 month dry season), and as a result, the majority of the contemporary population of *A. collinsii* lives in shrubby vegetation that is overgrazed by cattle and goats (Figure 88). In the moister parts of its habitat, the natural vegetation has been almost entirely destroyed to plant cornfields, but where this is done with a 5 to 25 year fallow period (e.g., sites 67 and 88), *A. collinsii* is a common part of the regeneration. In the very dry parts of its range, such as the east side of the Yucatan Peninsula and the Tehuantepec area, *A. collinsii* probably grows in vegetation similar to that occupied before the advent of European agriculture except for grazing by goats.

Wherever *A. collinsii* and other species of swollen-thorn acacias occur in the same general area, *A. collinsii* is always in the driest subhabitat (and thus mixed in with several nonant-acacias). This is particularly striking at a place such as site 15 where it



FIGURE 88.—Typical pasture habitat of *A. collinsii* (Nicaragua, site 60).

is common on the dry ridges that extend into the swampy coastal flatland occupied by *A. cornigera*. Also, in the very dry lowlands in northeastern Guatemala (site 38), *A. collinsii* occupies the dry rocky pastures, while *A. hindsii*, *A. gentlei*, and (rarely) *A. cornigera* occupy the swamps and stream bottoms and banks. Since much of the Yucatan Peninsula lacks surface watercourses, it would lack swollen-thorn acacias in most of the eastern drier area if it were not for *A. collinsii*. While *A. collinsii* is apparently sympatric with either *A. cornigera* (e.g., site 17) or *A. globulifera* (e.g., site 16), the latter two species are always in a local wet site, such as a lagoon running along the beach or the site of a cenote or well.

Acacia collinsii appears rarely to be moved about by contemporary human activities, and the geographic distribution recorded in Figure 87 is probably little changed since Europeans began disturbing Central American vegetation. Like *A. cornigera* and *A. hindsii*, however, *A. collinsii* is probably much more common now than in pre-Columbian times, since it grows very well in the dry and shrubby pastures that have replaced much of lowland Central America's deciduous forests. The failure of humans to move the seeds of *A. collinsii* is probably due in part to the fact that the pods dehisce so that the edible pulp is either taken by a bird or drops to the ground (in contrast to the

indehiscent pods of *A. cornigera* that can be easily harvested, and carried about). Also, *A. collinsii* lives in habitats that are so dry that earth-moving equipment is less likely to pick up mud with seeds in it than is the case for either *A. cornigera* or *A. hindsii*. Finally, and perhaps most important, *A. collinsii* appears to occupy virtually all the suitable habitats in the dry lowlands on both coasts of Central America. The conspicuous exceptions to this statement are the dry northern portions of the east and west coasts of Mexico, occupied by *A. cornigera* and *A. sphaerocephala*, and by *A. hindsii*, respectively; human-movement patterns in these parts of Mexico are not at all favorable to contemporary transport of *A. collinsii* further north than at present.

The failure of *A. collinsii* to spread throughout the dry lowlands of Colombia is the most perplexing aspect of its distribution. There are two possibilities, neither of which can be discussed fully with the data at hand. It may be a relatively recent introduction from Panama or further north along the coast; old coastal ports such as Acapulco, La Libertad, Puntarenas, and Panama City are well within the range of *A. collinsii*. On the other hand, the twin dry seasons in Colombia may be inimical to the development of *A. collinsii*. Jesus Idrobo (personal communication) reports that it is most commonly found in swamps in Colombia, a habitat rarely occupied by *A. collinsii* in Central America.

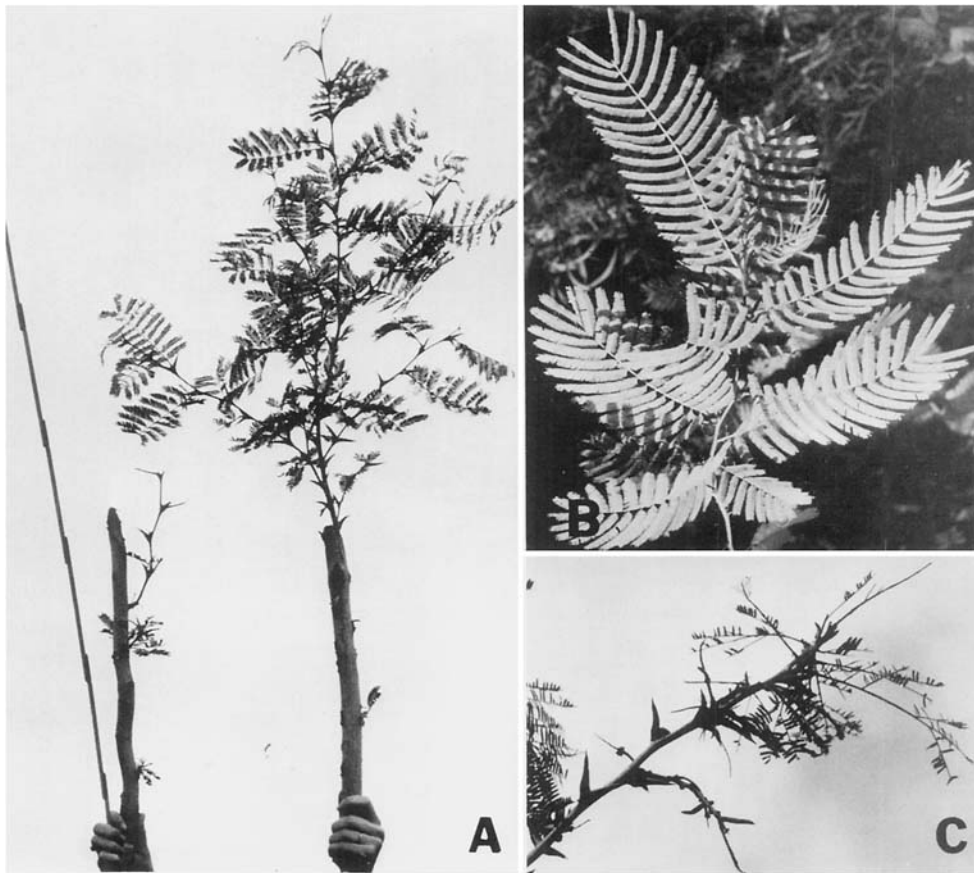


FIGURE 89.—*Acacia collinsii*: A, left, unoccupied sucker regeneration and on the right, occupied sucker-shoot regeneration of the same age (Costa Rica, site 70); B, occupied lateral branch end; contrast with Figure C (Costa Rica, site 67); C, unoccupied lateral branch end growing near Figure B.

While swollen-thorn acacias may reach immediately offshore islands (e.g., occupied *A. collinsii* on Isla Cozumel, site 28), there is only one case where the ant \times acacia interaction appears to have become naturally established on an island far from the Central American coast. *A. collinsii* is a common member of the flora of Isla Providencia (sites 97 and 98) where it is occupied by *Pseudomyrmex ferruginea*. This island is about 100 miles off the Caribbean coast of Nicaragua, and even though the acacia is completely wild, there is no guarantee that it was not introduced by post-Colombian human activities. Isla Providencia has been in contact with Europeans for at least 200 years. Even if the acacia was recently introduced, it is most likely that the ants got there of their own accord; even the most

avid gardener is unlikely to bring an acacia with an ant colony on a boat from the mainland to Isla Providencia. The Isla Providencia population of *A. collinsii* is morphologically representative of the mainland population, with the exception that the seed pods are the smallest I have seen. Not only are they very heavily woody (like those on the dry Pacific side of Panama) but range from 2 to 3 cm long and 4 to 8 mm thick. Almost all of the vegetation on Isla Providencia has been cut many times and is repeatedly disturbed by livestock and cultivation; however, even in equally disturbed sites on the mainland, the population density of adult *A. collinsii* is higher on this island than I have ever encountered in mainland sites of comparable land use. This high abundance is probably attributable

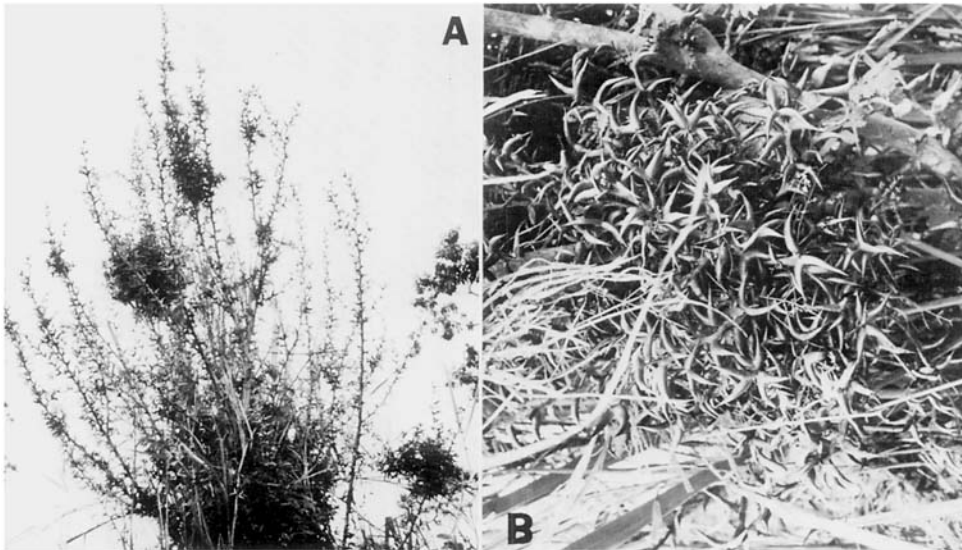


FIGURE 90.—*Acacia collinsii* (Panama, site 85): A, crown of adult with clumps of type A thorns caused by an unknown disease; B, close-up of the thorn cluster from the crown.



FIGURE 91.—*Acacia collinsii*: A, two seedlings (compound leaves) with their first pair of leaves (Costa Rica, site 70); B, sucker sprout from burned stump (Costa Rica, site 70); C, unoccupied 2-4-year-old seedlings (Panama, site 88).

to several factors: (1) Based on two small seed samples taken in August 1969, the bruchids that kill a high percentage of the mainland seeds have not arrived on the island; each of the seeds produced is therefore still alive when dispersed. (2) Based on sweep samples taken during the rainy season (late August 1969) the herbivorous insect density on the island is far lower than found in any mainland lowland habitat during the rainy season; this means that the primary environmental challenge that unoccupied seedlings face is competition from other plants. (3) Since the number of plant species is very low on the island, most of the usual competitors with *A. collinsii* are absent from the habitat; in particular, vines are missing. The ants appeared to be as aggressive as their mainland counterparts and attacked vegetation contacting the *A. collinsii* crown as usual. The only major herbivore on *A. collinsii* that appears to have arrived on Isla Providencia is the noctuid moth (*Cocina hadenoides*) whose larva can protect itself against the ants and eats the shoot tips of occupied swollen-thorn acacias (Janzen, 1967b). On the mainland, this larva invades the acacia often enough to cause occasional multiple branching in the shrub's development. On Isla Providencia, its damage was intense, causing nearly all the acacias to take on a shrubby life form.

While *A. collinsii* lives in a drier habitat than *A. cornigera*, it appears to have a dependence on obligate acacia-ants as great as that of *A. cornigera*. A brief test of this was conducted with the hilltop portion of the *A. collinsii* population two miles southeast of Cañas, Guanacaste Province, Costa Rica (site 70). While there are three species of obligate acacia-ants in the area (*P. ferruginea*, *P. belti*, *P. nigrocincta*), only those plants occupied by *P. belti* were used in the experiment. The hilltop site was covered with regenerating pasture shrubs (*Bauhinia*, *Croton*, *Cassia*, *Luhea*, *Acacia*, etc.) and about 40 adults of *A. collinsii* to the acre. On February 16, 1967, 52 plants of *A. collinsii* in the 2 to 3 m class (3 to 4 years of occupied growth) were cut off 60 cm above the ground. The acacia crown was left next to 25 of the stumps, and for 27 stumps the crown was dragged at least 10 m away. After the usual movements of *P. belti* colonies following this disturbance, 9 of the stumps in the control plot lost their colonies and none of those in the experimental plot gained one (if this ex-

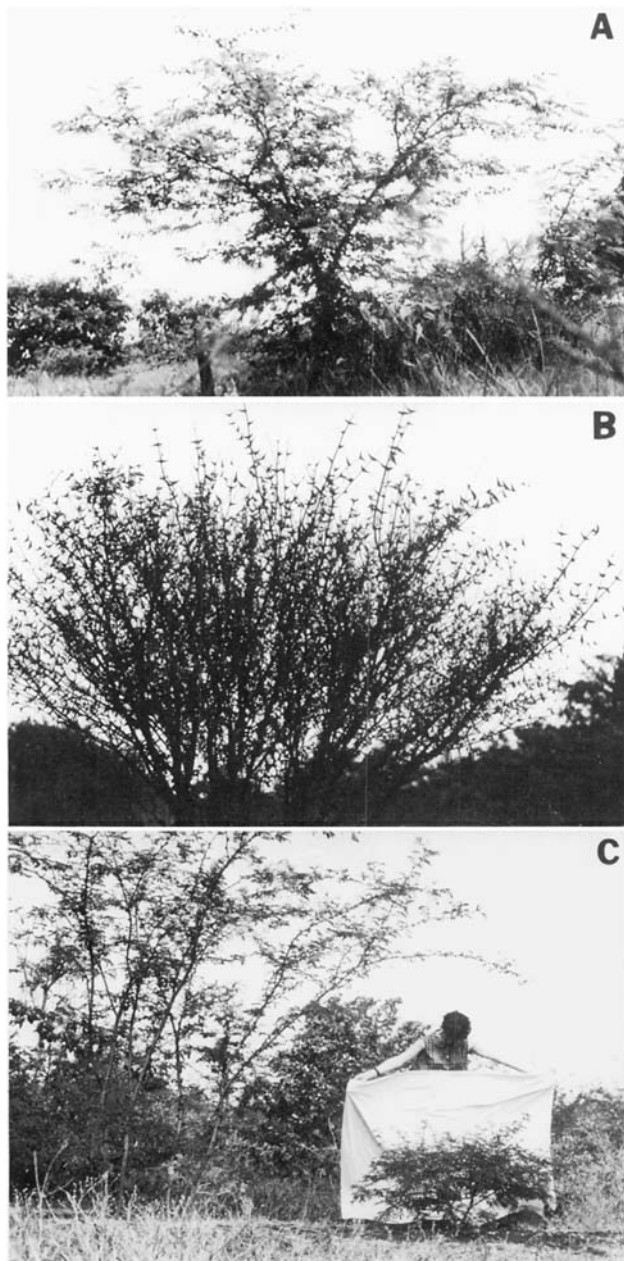


FIGURE 92.—*Acacia collinsii*: A, ten-year-old adult (Panama, site 83); B, crown of adult (Nicaragua, site 54); C, left, 7-year-old clump occupied by *Pseudomyrmex belti*; right, 7-year-old tree occupied by *Pseudomyrmex ferruginea* (Nicaragua, 57).

periment had been conducted during the rainy season, when colonies are larger and the ground is not so hot, 5 to 10 of the stumps in the experimental plot would have regained their colonies despite the

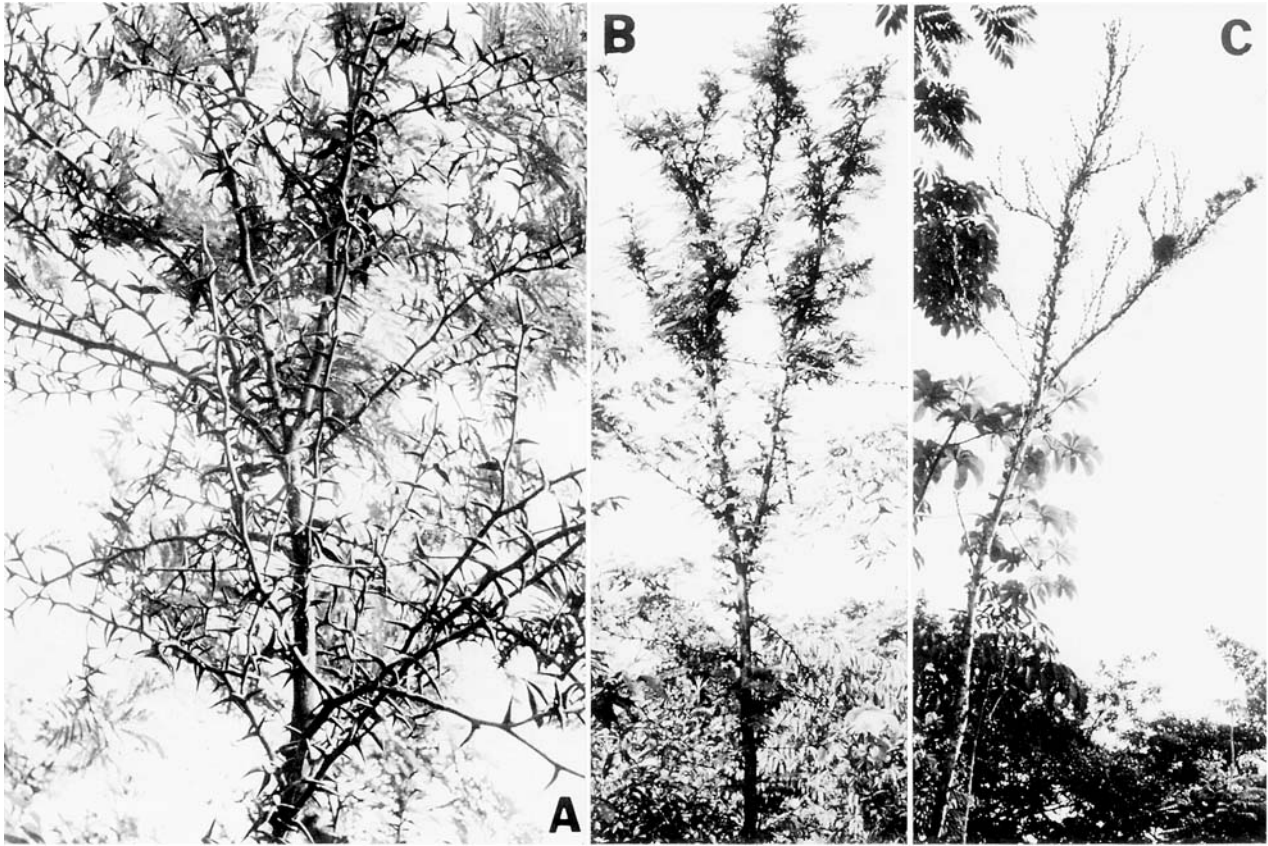


FIGURE 93.—*Acacia collinsii* (Panama): A, central crown of adult (site 78); B, crown of 10-m-tall tree (site 88); C, senescent crown of 10-m-tall tree (site 88).

distance to which they were removed). By July 19, 1967, about five months later, the mean length of the longest sucker shoot from each of the 25 stumps in the control plot was 25.1 cm (s.d. 10 cm) while the same measurement was 5.1 cm (s.d. 4 cm) in the experimental plot. These differences are highly significant (Mann-Whitney U test) and differ in no major way from the results obtained with occupied and unoccupied sucker regeneration of *A. cornigera* and *P. ferruginea* in eastern Mexico (Janzen, 1967b). If we consider only the 16 members of the control plot that were occupied, the results are more dramatic; the mean length of the longest sucker shoot is 36.4 cm (s.d. 14 cm). The 9 unoccupied suckers of the control plot also had a mean length of 5.1 cm (s.d. 12 cm). Figure 89A illustrates a representative shoot from each of the occupied and unoccupied stumps of this date. Figures 89B and C compare the branch ends of large lateral branches

from naturally occupied and unoccupied adult acacias in a much wetter habitat in southern Costa Rica (site 67).

Since nearly all the regeneration was during the dry season, this low total amount of sucker-shoot development was expected. That no stump died during the course of the experiment suggests strongly that substantial energy reserves were stored in the lower stump and root system. One year later, on July 12, 1968, only 4 of the stumps unoccupied on July 19, 1967, were still alive; all the plants that had been occupied in 1967 were still alive. By July 14, 1969, all the occupied shoots had approximately regained their original height (1967) or grown taller, and there was no trace of the 36 stumps unoccupied on July 19, 1967.

Acacia collinsii has a small number of leaf and stem galls just as do other swollen-thorn acacias. At site 86 in Panama, however, the population of

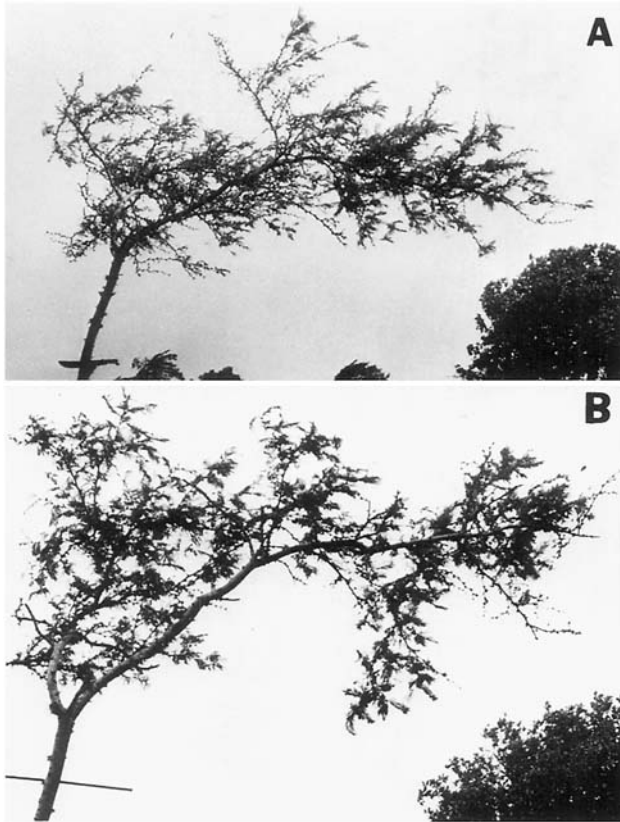


FIGURE 94.—*Acacia collinsii* (Costa Rica, site 68): A, adult growing in open pasture, August 1, 1963; B, same tree crown, July 1, 1967; the lack of change is due to lack of interplant competition.

A. collinsii is afflicted with an outstanding disease. Almost all the acacias have thick clusters of swollen thorns scattered through the crown (Figure 90). These are the consequence of some agent that causes extreme branch proliferation, yet each internode is extremely short. The number of thorns produced by the acacia is far greater than the ants can use, with the consequence that many of the thorns in the cluster have no entrance holes. The potentially negative effect of this excess of thorns on seed production has not been examined. Young seedling and sucker shoot development of *A. collinsii* is very similar to that of *A. cornigera* and *A. hindsii*. The bird-dispersed seed germinates at the beginning of each rainy season (Figure 91A) and, if fully isolated, forms into a small bush that produces its first swollen thorn on the 12th to 17th leaf (about two months old). Suckers from stumps in recently



FIGURE 95.—*Acacia collinsii*: A, crown of adult growing in area with very severe dry season (Nicaragua, site 54); B, crown of tree growing in area with very mild dry season (Costa Rica, site 67).

burned areas do the same (Figure 91B), but the larger the stump, the more the first foliage resembles that of the mature plant. As the months pass without a new colony developing in the young plants, they gain in height at the rate of about 10 cm per year and suffer very heavy damage from defoliating insects (Figure 91c). In most open habitats, *A. collinsii* grows into a bushy shrub once occupied (Figures 92A, B). If it is in dense regeneration, it may become a small tree that gradually loses crown size and senesces when 15 to 20 years old (Figure 93). It may retain this shape for many years (Figure 94).

There is considerable variation in branching pat-

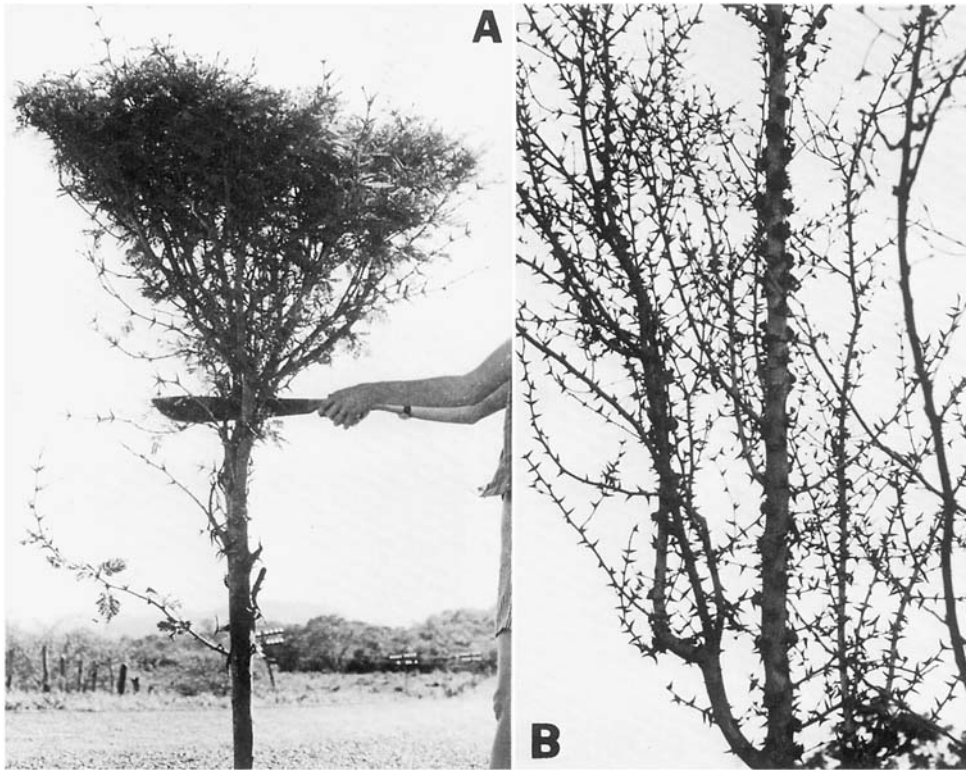


FIGURE 96.—*Acacia collinsii* (Nicaragua): A, dense crown of adult caused by shoot damage by *Pseudomyrmex ferruginea* (site 57); B, diffuse crown of adult occupied by *Pseudomyrmex nigrocincta* (site 51).

terns of *A. collinsii* in fully insolated habitats. In the very driest sites, where *A. collinsii* may almost be regarded as a member of the "climax" forest, the plant has only a few major branches, and the new leaves each year are produced in axillary tufts or on very short new branches (Figure 95A). In the wettest sites, the canopy is uniformly dense owing to the production of a large number of small lateral branches (Figure 95B). A second type of crown variation is produced by the interaction between the eastern Nicaraguan portion of the *Pseudomyrmex ferruginea* population and *A. collinsii*. This species of ant in this area prunes the shoot tips of the swollen-thorn acacia it occupies. The consequence is that two adjacent *A. collinsii* of the same age—one occupied by *P. ferruginea* and the other by *P. belti* or *P. nigrocincta*—will be extremely different in height (Figure 92c). If the shoot is not occupied by *P. ferruginea* until it is 1 to 2 m tall, it produces a "lollypop" life form

(Figure 96). As discussed in Janzen (1969c), one possible explanation for the ants' behavior is that birds preying on ant brood cannot get into the dense crown to get the queen-thorn; in this area, *A. collinsii* does not have the well-developed type B thorns which are normally adequate to protect the queen from birds.

Acacia collinsii, like *A. cornigera*, bears its first flowers at the end of three years of occupied growth. Seeds therefore appear in the fourth dry season after the plant is occupied, meaning that *A. collinsii* can exist as a reproducing population in cultivated sites with only four years fallow. Its long inflorescences are normally born in short axillary clusters (Figure 98A) but in very wet sites may be produced on long sexual branchlets (Figure 97A). There appears to be a general cline in increasing inflorescence length from the northern to the southern end of the range of *A. collinsii*. The woody pods are usually born 1 to 6 per inflorescence; upon



FIGURE 97.—*Acacia collinsii*: A, exceptionally well-developed sexual branchlet (Mexico, site 4); B, type A thorn at base of leaf with three droplets of nectar from petiolar nectaries (Costa Rica, site 67); C, newly grown type B thorns and fully developed branch on tree in Figure B.

dehiscing, the seeds drop partly out and are wrapped in sweet yellow pulp which is picked off by birds in flight. This dispersal mechanism is common to the entire population, but there is considerable variation as to how woody the pods are and how much they curl upon opening. In no areas do the pods curl as extremely as those of *A. hindsii* and *A. globulifera*.

Type A thorns on *A. collinsii* are easily distinguished from those of all other swollen-thorn acacias, but the differences are difficult to characterize. *A. collinsii* bears the shortest type A thorns to be found on a mature swollen-thorn acacia. They are usually round in cross section and give the impression of being "fat" (Figures 98, 99). When flattened (Figures 98A, 99E) like *A. hindsii*, they still have much thicker walls than would an *A. hindsii* thorn of the same size. *A. collinsii* probably shows the most extreme variation on type A thorn morphology of any of the swollen thorn acacias.

Most of the population of *A. collinsii* bears thorns that are ivory to beige, but in wet or high elevation sites they are often dark brown with a maroon or reddish cast. There is usually a prominent bump on the inner wall of each thorn near the base; this may aid the ants in making use of the large volume of space at the base of the "fatter" thorn types (e.g., Figure 98B).

Type B thorns of *A. collinsii* (Figures 100–103) are easily as variable in shape as those of *A. cornigera* and *A. hindsii*. As is the case with these latter two species, there is little intrapopulation variation in this trait, but of course there is rather great variation associated with the age of the acacia. Type B thorns are generally produced at the expense of the leaf they subtend (Figure 97c) and are produced very rapidly once branch elongation starts. It is common to find all the type B thorns on a short branch to be at approximately the same stage in hardening. While type B thorns may appear



FIGURE 98.—Geographic variation in type A thorns from occupied adult *A. collinsii*: A, Costa Rica, site 68; B, Nicaragua, site 61; C, D, Mexico, site 16.

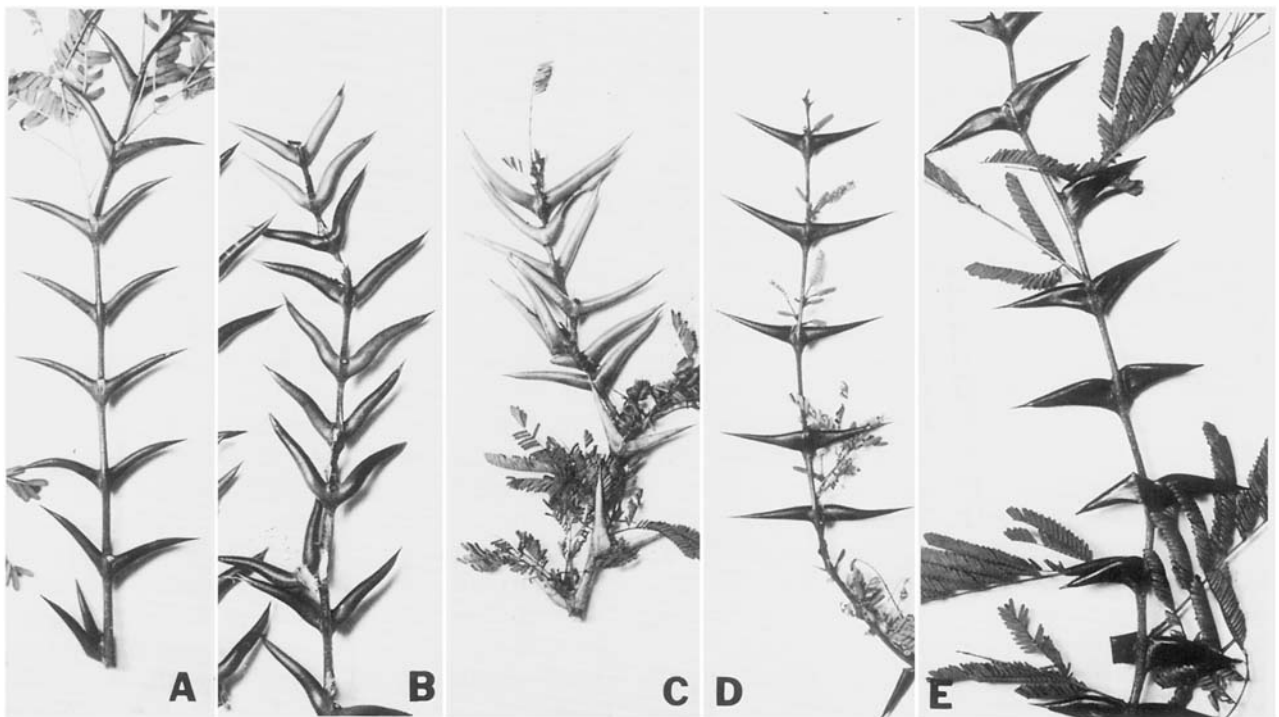


FIGURE 99.—Geographic variation in type A thorns from occupied adult *A. collinsii*: A, Mexico, site 11; B, C, Mexico, site 16; D, Nicaragua, site 61; E, Panama, site 86.

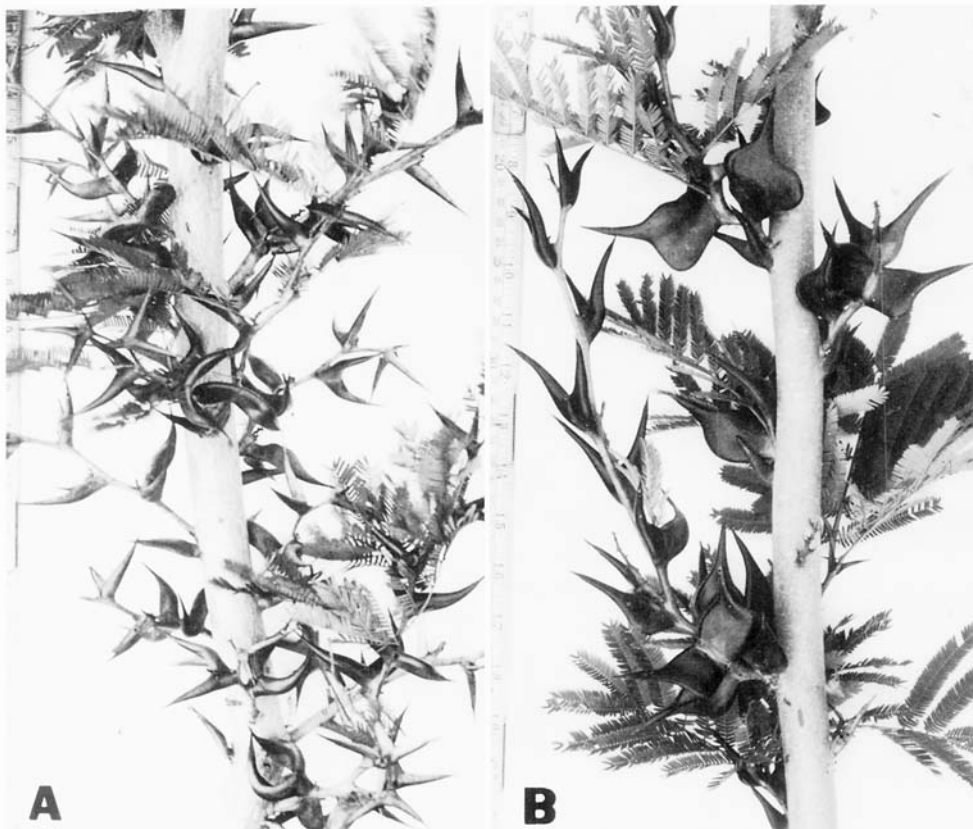


FIGURE 100.—Type B thorns around main trunk of *A. collinsii*: A, Panama, site 88; B, Costa Rica, site 67.

to converge on those of *A. cornigera* or *A. hindsii*, *A. collinsii* is not sympatric with those species where this occurs. While the very largest type B thorns to be found on *A. collinsii* (Figure 104) have a large volume and are therefore similar to the largest on *A. hindsii*, in general both type A and type B thorns of *A. collinsii* are small in volume when compared with swollen-thorn acacias in general.

12. *Acacia hindsii* Benth

Acacia hindsii Benth, 1842:504.

Acacia bursaria Schenck, 1913:363.

Acacia tepicana Safford, 1914:366.

Acacia sinaloensis Safford, 1914:365.

Myrmecodendron hindsii (Benth) Britton and Rose, 1928: 91.

A mature *Acacia hindsii* is distinguished from all other swollen-thorn acacias by its very flat and dis-

tended thorns. On occasion the thorns of *A. collinsii* display superficially similar distension, but *A. hindsii* has small diameter petiolar nectaries rather than broad dome-shaped ones as on *A. collinsii*. *A. hindsii*, *A. collinsii*, and *A. cornigera* are the three most widely distributed swollen-thorn acacias. *A. hindsii*, however, is essentially a plant on the Pacific lowlands and foothills (Figure 105).

I was unable to examine the type specimen of *A. hindsii*, but *A. hindsii* is the only species of swollen-thorn acacia in the Manzanillo Bay area (site 1), and the type description agrees closely with the swollen-thorn acacia population in that area. The northernmost record of *A. collinsii* (*A. collinsii* site 7) is from slightly to the south of site 1, but at this site it has cylindrical thorns and is not sympatric with *A. hindsii*. *A. hindsii* is not to be confused with its hybrids with nonant-acacias such as *A. pennatula*, e.g., *A. oaxacanum*, *A. hirtipes*, and *A.*

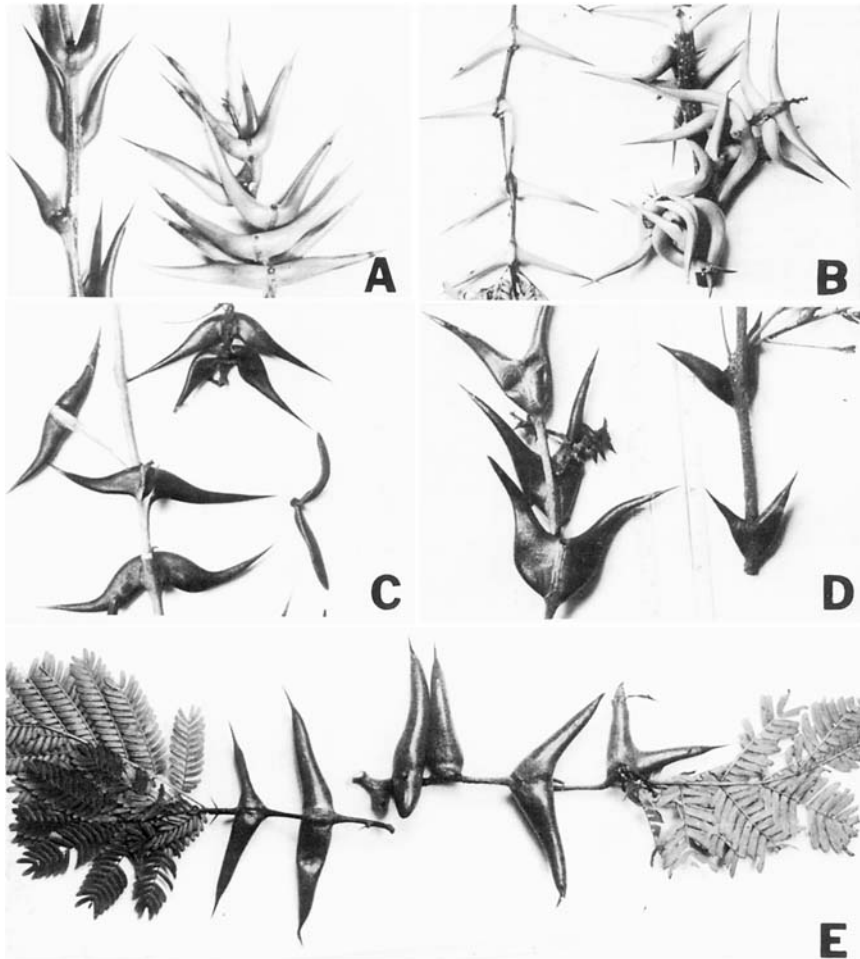


FIGURE 101.—Geographic variation in type B thorns of occupied adult *A. collinsii*: A, B, Mexico, site 4; C, Nicaragua, site 51; D, Costa Rica, site 67; E, Mexico, site 11.

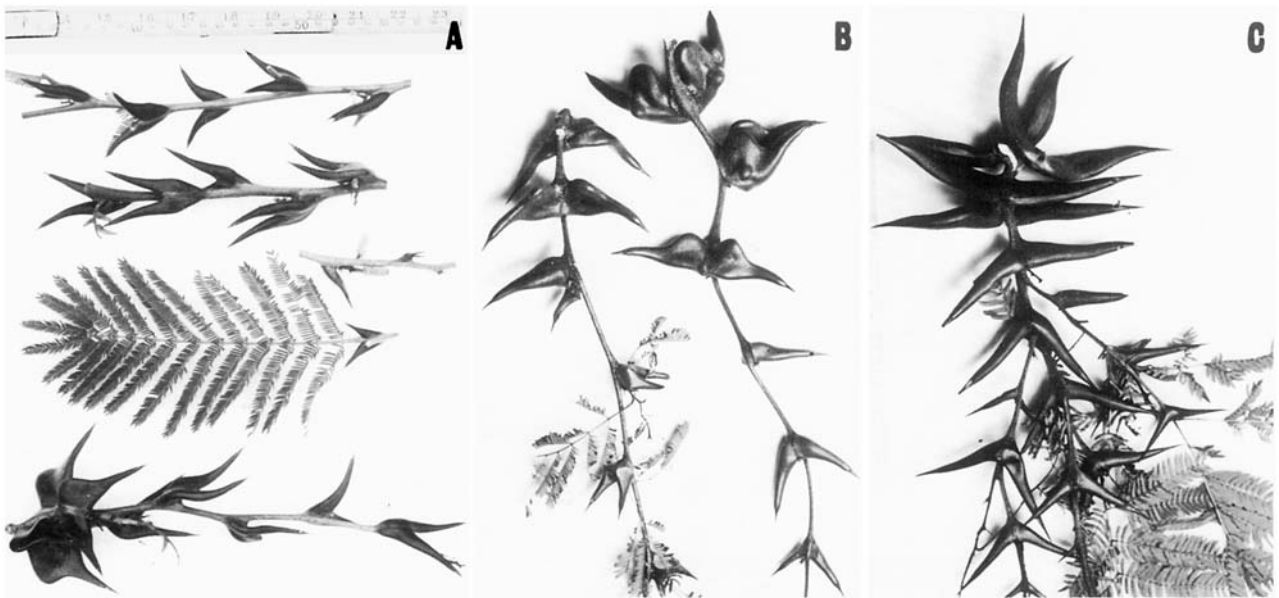


FIGURE 102.—Geographic variation in type B thorns of occupied adult *A. collinsii*: A, Costa Rica, site 67; B, Nicaragua, site 51; C, Mexico, site 4.

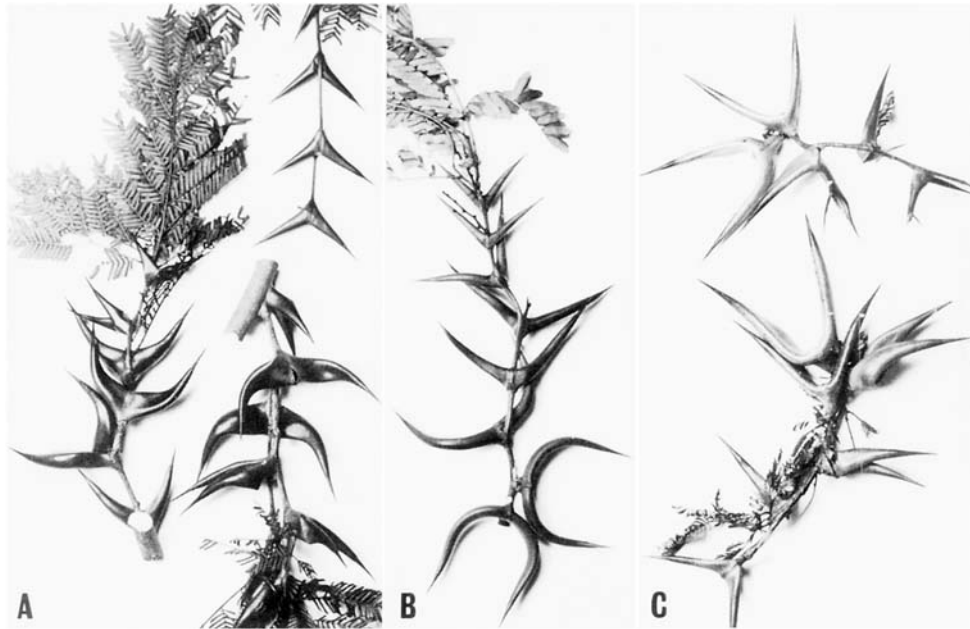


FIGURE 103.—Geographic variation in type B thorns of occupied adult *A. collinsii*: A, Panama, site 82; B, Mexico, site 11; C, Guatemala, site 38.

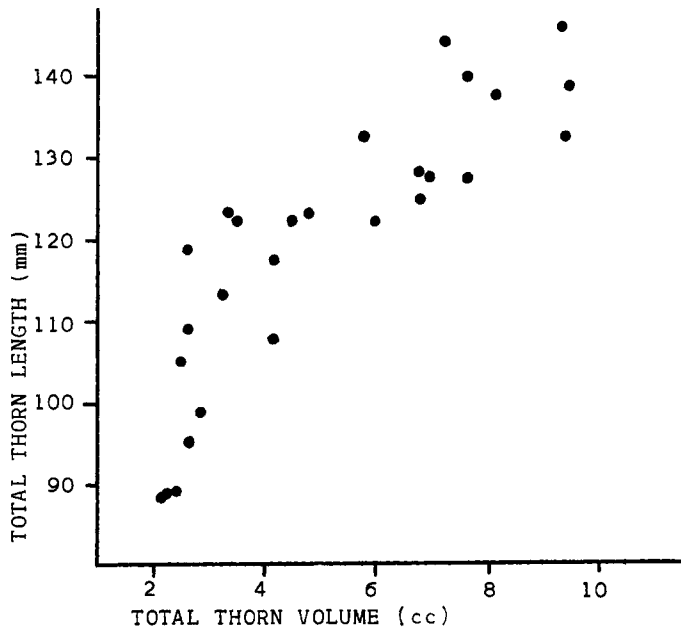


FIGURE 104.—Distribution of thorn volume among the largest type B thorns of *A. collinsii* (Costa Rica, site 67).

standleyi. None of the hybrids has a full complement of Beltian bodies, large nectaries or fully developed swollen thorns.

Shenck's description of the type of *A. bursaria* applies without doubt to the *A. hindsii* population at site 49, rather than to *A. cornigera*, which is the only other swollen-thorn acacia at the type locality. The thorns on the type specimen of *A. bursaria* are exceptionally large type A thorns, of the kind often found on large and very healthy *A. hindsii* in the wetter parts of Guatemala.

The vegetative branch chosen for the type specimen of *A. tepicana* is a representative young sucker shoot or central axis from a young seedling before it became occupied by obligate acacia-ants. The thorns are not flattened, but this is the case with most young *A. hindsii*. Their very light color is also representative of young *A. hindsii* in areas where the adults have very dark colored thorns. The peduncle with mature fruits accompanying the type specimen was taken from a representative mature *A. hindsii*. *A. hindsii* is the only swollen-thorn acacia found as far north as Acaponeta in western Mexico (site 2).

Safford's type specimen for *A. sinaloensis* is a representative branch from the upper crown of a normal mature *A. hindsii* of the form common at the type locality (site 3). Type A thorns of all degrees of flattening occur in such a crown and the

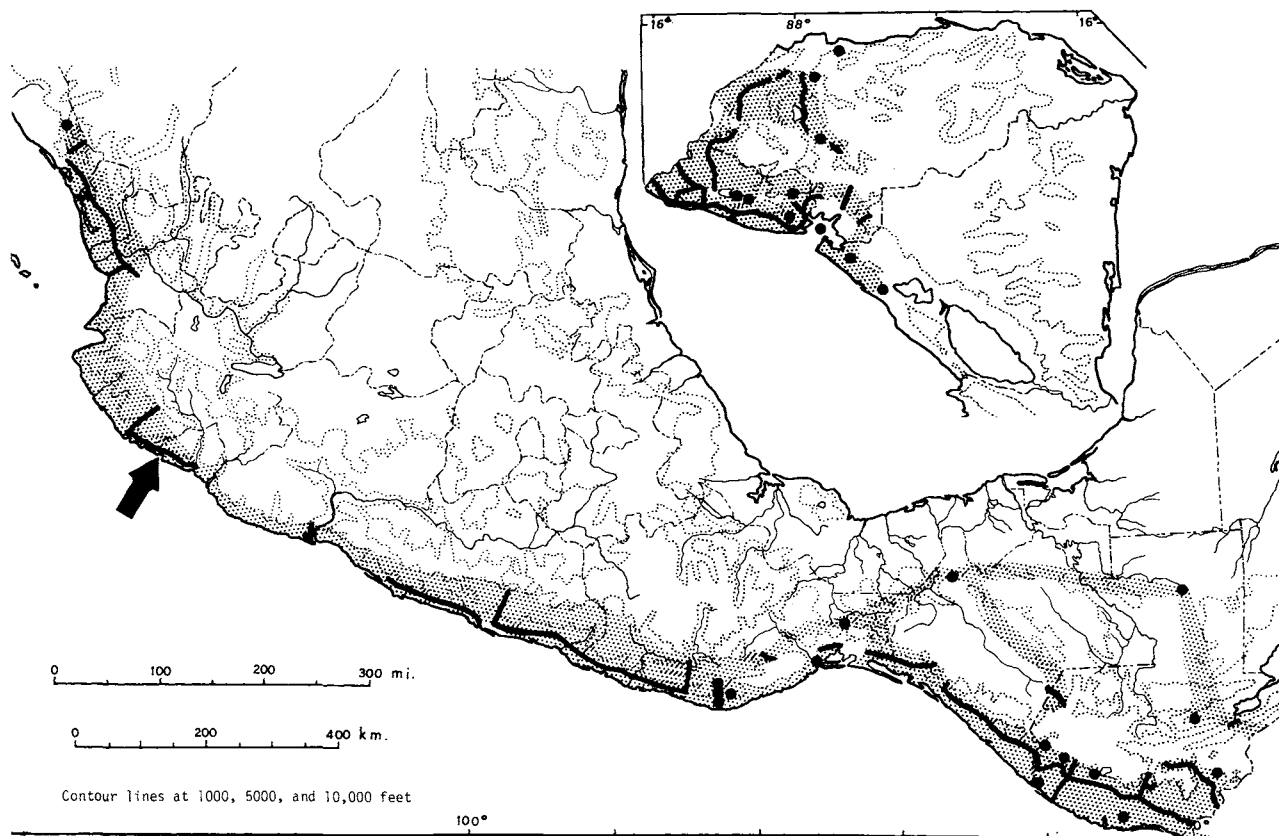


FIGURE 105.—Postulated general distribution (stippled area) and collection localities of *A. hindsii*.

type specimen has thorns representing the smaller end of the spectrum. The seed pod accompanying the type is a normal *A. hindsii* pod. *A. hindsii* is the only swollen-thorn acacia found as far north as Villa Union, Sinaloa, Mexico.

KEY COLLECTION LOCALITIES

Mexico

1. Type of *A. hindsii*: Shore of Manzanillo Bay, Colima, Mexico (sea level). 1836-39 (or 1841; Sir George Taylor, in litt.), *R. B. Hinds*, no. 248.
2. Type of *A. tepicana*: Acaponeta, Nayarit, Mexico (30 m). IV-10-1910. *J. N. Rose*, *P. C. Standley*, and *P. G. Russell*, no. 14357.
3. Type of *A. sinaloensis*: Villa Union, Sinaloa, Mexico (10 m). IV-2-1910, *J. N. Rose*, *P. C. Standley*, and *P. G. Russell*, no. 13972.
4. Arriaga to 13.2 mi N on Hgy. 200, Chiapas (10-550 m). I-9-1965, *DHJ*, nc (common).
5. Tehuantepec to 21.2 mi E on Hgy. 190, Oaxaca (10-30 m). I-10-1965, *DHJ*, no. 1041; IX-2-1965, *DHJ*, nc; VIII-7-1966, *DHJ*, no. 415 (occasional to rare).
6. Near Salina Cruz, Tehuantepec, Oaxaca (sea level). IX-1-1965, no. 1934 (occasional to common).
7. Tapilula to 3 mi E, Chiapas (700 m). VII-10-1966, *DHJ*, nc (occasional).
8. 12.2 mi SW El Camaron to 10.2 mi W turn into Tequisistlan on Hgy. 190, Oaxaca (925-735 m). I-10-1965, *DHJ*, nos. 1033, 1034.
9. Puerto Escondido to 36.9 mi N on Hgy. to Oaxaca, Oaxaca (sea level to 940 m). VI-19-1967, *DHJ*, nc (occasional to rare).
10. Las Cruces (just inland from Acapulco) to Puerto Escondido on Hgy. 200, Guerrero-Oaxaca (20-300-10 m). VI-18-1967, *DHJ*, nc (common to occasional).
11. 14.0 mi S Chilpancingo to Las Cruces, Guerrero (1175-30 m). I-7-1965, *DHJ*, nos. 1031, 1035; *DHJ*, nc (common).
12. Playa de Pic de la Cuesta (just W of Acapulco) to 13.6 mi SE Papanoa on Hgy. 200, Guerrero (sea level). VI-17-1967, *DHJ*, nc (common to very rare, only along upper edges of swamp sites).
13. 21.6 mi SW Autlan to Barra de Navidad, Jalisco (450-0 m). I-5-1965, *DHJ*, nos. 1026, 1027, 1028, 1029, 1030 (common to rare, only in wetter sites).
14. Barra de Navidad to Tecoman, Jalisco-Colima (50-0 m). I-5-1965, *DHJ*, nc (rare-common).
15. 12 mi NW Tepic to 28.4 mi SE Mazatlan on Hgy. 15,

- Nayarit-Sinaloa (700-5-70 m). IX-14-1963, *DHJ*, no. 1745; I-2-1965, *DHJ*, no. 1011; VI-8-1967, *DHJ*, nc (rare to common to rare), fl.
16. Hgy. 12 to San Blas on Hgy. 46, Nayarit (200-0 m). I-13-1965, *DHJ*, nos. 1019, 1020, 1021, 1022, 1023, 1024, 1025.
17. 23.5 mi SW El Palmito to 9.0 mi SW, Concordia on Hgy. 40 (1085-10 m). I-2-1965, *DHJ*, nos. 1005, 1006, 1012, 1013, 1014, 1015, 1016, 1017; VI-6-1967, *DHJ*, nc (common to rare).
18. Palo Blanco, San Ignacio, Sinaloa (340 m). IV-18-1918, *M. N. Montes and H. E. Salazar*, no. 286 (US 1035197).
19. Puerto Angel, Oaxaca (sea level). IV-12-1933, *C. V. Morton and E. Makrinus*, no. 2614 (US 1585606), fl.
20. Cafetal Concordia, Oaxaca (400-650 m). IV-15-1933, *C. V. Morton and E. Makrinus*, no. 2427 (US 1585440), fl.
21. Pochutla, Oaxaca (50 m). IV-19-1917, no. 3146, *C. Conzatti* (US 763852), fl.
22. Huatulco, Oaxaca (150 m). II-1941, *B. P. Reko*, no. 6010 (F 1510963), fl.
23. 13.7 mi NE La Mira to Playa Azul and to Melchor Ocampo on Hgy. 37, Michoacan (200-0 m). VI-12-1968, *DHJ*, nc (common).
24. Guatemala-Mexico border (near Ciudad Cuauhtemoc) to 3.6 mi N on Hgy. 190, Chiapas (720-680 m). VIII-6-1966, *DHJ* no. 416; VIII-16-1967, *DHJ*, nc (common to rare).
25. 5.1 mi SW Cintalapa (Chiapas) to 20.9 mi W Tapanatepec (Oaxaca) on Hgy. 190 (610-820-110 m). VIII-18-1967, *DHJ*, nc (common to rare).
- 25a. 23.3 mi S Pichucalco, on Villa Hermosa-Chiapa de Corzo road, Chiapas (1000 m). VII-10-1966, *DHJ*, no. 420, 564.
26. 29.3-35.0 mi W Tapanatepec, Oaxaca (100-20 m). VIII-18-1967, *DHJ*, nc (occasional).
27. 6.8-4.1 m S of turn into Matias Romero, on Hgy. 185, Oaxaca (250 m). VIII-18-1967, *DHJ*, nc (3 plants).
28. Guatemala-Mexico border (Pte. Talisman) to Arriaga on Hgy. 200, Chiapas. I-10-1965, *DHJ*, nc (common).
- Guatemala:
29. 6.8 mi SW (1370 m) Guatemala City to Escuintla, Depto. Esquintla on Hgy. 2. I-12-1965, *DHJ*, no. 1050; VIII-12-1967, *DHJ*, nc (common).
30. Shores of Lake Amatitlan and surrounding hills (1300-1350 m). Depto. Guatemala. VIII-11-1967, *DHJ*, nc (common).
31. Escuintla, Depto. Escuintla (330 m) to Guatemala-Mexico border (Pte. Talisman), Depto. San Marcos (50 m). I-12-1965, *DHJ*, nos. 1048, 1049 (rare to common).
32. Retalhuleu SW to Champerico, Depto. Retalhuleu (200-0 m). VIII-1-1966, *DHJ*, nc (occasional to rare).
33. Retalhuleu to 15.2 mi NE on Hgy. 9S, Depto. Retalhuleu (200-1000 m). VII-18-1966, *DHJ*, no. 400; VII-16-1966, *DHJ*, no. 404; VII-28-1966, *DHJ*, nc (common to rare).
34. 16.5 mi SE to Guatemala-Mexico border (Ciudad Cuauhtemoc), Depto. Huehuetenango (900-1000-720 m) on Interamerican Hgy. VIII-16-1967, *DHJ*, nc (common).
35. 9.5 mi SW to 6.2 mi NE Puente El Lobo on Hgy. 4, Depto. Zacapa (150 m). V-14-1965, *DHJ*, nos. 1929, 1930; V-20-1965, *DHJ*, no. 1931; VIII-9-1967, *DHJ*, nc (very rare except as clumps on river banks).
36. Guatemala-El Salvador border (25 m; Pijije), Depto. Jutiapa to Escuintla (330 m), Depto. Escuintla on Hgy. 6E. I-13-1965, *DHJ*, nc (rare to common), fl.
37. Guatemala-El Salvador border (San Cristobal), Depto. Jutiapa to 15.8 mi SE Guatemala City on Hgy. 2, Depto. Guatemala (520-1250 m). VII-7-1967, *DHJ*, nc (common to rare to common).
38. Tikal, Depto. Peten (100-500 m). IV-2-1922, *O. F. Cook and R. D. Martin*, no. 170 (US 1084640), mp.
39. San Carlos, Depto. Retalhuleu (650 m). III-22-1921, *Rojas*, no. 241 (US 1014948), fl.
40. Santa Barbara, Depto. Solola (400 m). VIII-1891, *W. C. Shannon*, no. 578 (US 943298).
41. Pancajche, Depto. Alta Verapaz (360 m). IV-5-1939, *P. C. Standley*, no. 70648 (F 978766), fl.
42. Barranca Hondo, lower slopes Volcan de Fuego, Depto. Sacatepequez (1800 m). XII-16-1938, *P. C. Standley*, no. 60262 (F 994870), gp.
43. Ocos, Depto. San Marcos (sea level). III-15-1940, *J. A. Steyermark*, no. 37779 (F 105266).
44. Between Finca Pirineos and Finca Soledad, lower south-facing slopes of Volcan Santa Maria, between Santa Maria and Calahuache, Depto. Quezaltenango (1300-1400 m). I-5-1940, *J. A. Steyermark*, no. 33599 (F 1051210).
45. Near Calahuache, Depto. Quezaltenango (1020 m). III-1-1939, *P. C. Standley*, no. 67107 (F 987673), mp.
46. Rio Chiquimula, 1.5 mi NE Chiquimula, Depto. Chiquimula (400 m). X-21-1939, *J. A. Steyermark*, no. 30123 (F 1038583).
47. Finca El Porvenir, Rio Cabus, SW slope Volcan Tajumulco, Depto. San Marcos (1000-1300 m). III-12-1940, *J. A. Steyermark*, no. 37550 (F 1049161).
48. Along Rio Gaucalate, Depto. Escuintla (500 m). XI-28-1938, *P. C. Standley*, no. 58188 (F 993751), gp.
49. Type of *A. bursaria*: San Felipe, Retalhuleu, Guatemala (300 m). February, 1878, Bernouilli and Cario, no. 1129 or Laguna Amatitlan, Depto. Guatemala, Guatemala (1100 m). 1890, *J. D. Smith*, no. 2304 (Sir George Taylor, in litt.).
- Honduras:
50. 13.1 mi W San Marcos de Colon (850 m) to 11.6 mi NE Choluteca (330 m) on Interamerican Hgy., Depto. Choluteca. I-14-1965, *DHJ*, no. 1053; V-11-1965, *DHJ*, nos. 1928, 1933; VII-29-1967, *DHJ*, nc (rare to common to rare).
51. 9.4 mi NE Choluteca on Interamerican Hgy., Depto. Choluteca (300 m). VII-29-1967, *DHJ*, nc (1 plant).
52. 4.3 mi NE Jicaro Galan, Depto. Valle (70 m) to 21.6 mi S Tegucigalpa, Depto. Francisco Morazan (1000 m) on Hgy. 1. VII-30-1967, *DHJ*, nc (rare to common to rare).
53. Honduras-El Salvador border (El Amatillo) to 15.5 mi E on Interamerican Hgy., Depto. Valle (50-100 m). I-15-1965, *DHJ*, nc (very rare).
54. 13.1 mi W Zambrano, Depto. Francisco Morazan (830 m) to 7.8 mi SE Villa de San Antonio, Depto. Comayagua

- (750 m) on Tegucigalpa-Puerto Cortes Hgy. VII-31-1967, *DHJ*, nc (common).
55. 7.8 mi SE to 4.7 mi N (550 m) Villa de San Antonio on Tegucigalpa-Puerto Cortes Hgy., Depto. Francisco Morazan. VII-31-1967, *DHJ*, nc (occasional to very rare).
56. 5.3 to 6.3 mi NW Comayagua on Tegucigalpa-Puerto Cortes Hgy., Depto. Comayagua (510 m). VII-31-1967, *DHJ*, nc (rare).
57. 13.2 mi NW Comayagua on Tegucigalpa-Puerto Cortes Hgy. (850 m). VII-31-1967, *DHJ*, nc (1 plant).
58. 10.7 mi NW (820 m) Siguatepec, Depto. Comayagua to 16.4 mi S (50 m) San Pedro Sula, Depto. Cortes on Tegucigalpa-Puerto Cortes Hgy. VIII-2-1967, *DHJ*, nc (common to occasional).
59. 4.6 mi SW (90 m) to 12.9 mi SW (150 m) San Pedro Sula, Depto. Cortes on road to Santa Rosa. VIII-2-1967, *DHJ*, nc (occasional).
60. 24.4 mi SW (240 m, bank of Rio Chamelecon) San Pedro Sula, Depto. Cortes to 10 mi N Santa Rosa. VIII-2-1967, *DHJ*, nc (occasional to very rare).
61. 4.4 mi SW Santa Rosa, Depto. Copan (940 m). VIII-3-1967, *DHJ*, nc (1 plant).
62. 4.4 mi NE (1310 m) Nueva Ocotepeque to Honduras-El Salvador border (850 m) on Santa Rosa-San Salvador Hgy., Depto. Ocotepeque. VIII-4-1967, *DHJ*, nc (rare to common).
63. Amapala, Isla Tigre, Depto. Valle (less than 250 m). II-14-1922, *P. C. Standley*, no. 20738 (US 1136566, US 1136557), fl.
64. Siguatepec, Depto. Comayagua (1080-1400 m). II-14-27-1928, *P. C. Standley*, no. 56333 (US 1409186), fl.
65. Las Limas, Depto. Comayagua (1000 m). IV-16-1932, *J. B. Edwards*, no. P-89 (F 713842), fl.
66. Vicinity of Siguatepec, Depto. Comayagua (1080-1400 m). II-14-27-1928, *P. C. Standley*, no. 56333 (F 581757), fl.
67. La Lima, Depto. Cortes (30 m). IV-11-20-1947, *P. C. Standley* and *J. Chacon*, no. 7548 (F 1268530), fl.
68. Near Lancetilla, Depto. Atlantida. VIII-10-1934, *T. G. Yuncker*, no. 5099 (F 749502).
- Union Hgy., Depto. La Union. V-12-1965, *DHJ*, no. 1932; I-15-1965, *DHJ*, nc (rare).
75. La Libertad, Depto. La Libertad to El Salvador-Guatemala border (La Hachadura), Depto. Ahuachapan. I-14-1965, *DHJ*, no. 1051 (common to rare).
76. Sonsonate (280 m) SE to Interamerican Hgy., Depto. Sonsonate. VIII-6-1967, *DHJ*, nc (common to occasional).
77. Sonsonate through Armenia to San Salvador-Guatemala Hgy. (280-920-450 m). VIII-6-1967, *DHJ*, nc (occasional to rare).
78. Intersection of San Salvador-Guatemala City Hgy., with Sonsonate-Armenia Hgy. to Guatemala-San Salvador border (San Cristobal), Depto. Santa Ana (450-810-520 m). VIII-6-1967, *DHJ*, nc (very rare to common to occasional).
79. San Martin de Laguna Hopango, Depto. San Salvador. IV-1-1922, *P. C. Standley*, no. 22622 (US 1138360), fl.
80. 2 km NW Monte Cristo, 15 km NE San Miguel, Depto. Morazan (150 m). XII-7-1941, *J. M. Tucker*, no. 486 (US), mp.
81. Laguna de Olomega, Depto. San Miguel (75 m). II-20-1922, *P. C. Standley*, no. 21027 (US 1136842).
82. San Vicente, Depto. San Vicente (350-500 m). III-2-11-1022, *P. C. Standley*, no. 21291 (US 1137447), fl.
83. Ahuachapan, Depto. Ahuachapan (700-1100 m). I-16-1925, *P. C. Standley* and *E. Padilla*, no. 2497 (F 1256801).
84. 2 km NW Monte Cristo, 15 km NE San Miguel (150 m). XII-7-1941, *J. M. Tucker*, no. 486 (F 1492748).

Nicaragua:

85. 3.4 mi SE Leon on Hgy. 12, Depto. Leon (20 m). VII-27-1967, *DHJ*, nc (30 acre patch), gp.
86. 4.9 mi SE Leon on Hgy. 12, Depto. Leon (20 m). VII-27-1967, *DHJ*, nc (1 plant).
87. Ameya (near Pto. Morazan) Depto. Chianandega (sea level). VI-19-21-1923, *W. R. Maxon et al.*, no. 7176 (US 1180890).

NATURAL HISTORY

El Salvador:

69. Honduras-El Salvador border (850 m) to 10 mi S (1170 m), Depto. Chalatenango on Santa Rosa-San Salvador Hgy. VIII-4-1967, *DHJ*, nc (occasional to very rare).
70. 11.7 mi S (1130 m) Honduras-El Salvador border (Depto. Chalatenango) to 9.3 mi N San Salvador (580 m) on Santa Rosa-San Salvador Hgy. VIII-4-1967, *DHJ*, nc (rare to very common to rare).
71. Intersection just E of La Libertad (sea level) to 11.8 mi N on Hgy. to Interamerican Hgy. (910 m), Depto. La Libertad. VIII-5-1967, *DHJ*, nc (rare to very common).
72. La Libertad, Depto. La Libertad to La Union, Depto. La Union (sea level to 30 m) on La Libertad-Zacatecoluca-Usulután-La Union Hgy. VIII-6-1967, *DHJ*, nc (common to occasional to rare).
73. La Herradura to La Libertad-Zacatecoluca Hgy., Depto. LaPaz. VIII-6-1967, *DHJ*, nc (very rare).
74. 41.5 mi SE San Miguel to La Union on San Miguel-La
- Being widespread geographically (Figure 105) on soils and in climates very suitable to seasonal agriculture, *A. hindsii* is difficult to characterize ecologically since nearly all the semideciduous and deciduous forests that it occupied before the advent of European agriculture have been destroyed. As McVaugh (1966) has stressed, when both of these forest types are cleared, *A. hindsii* is a common member of the shrubby regenerating vegetation. In contrast to those swollen-thorn acacias that live in natural disturbance sites in wet or rain forests (*A. allenii*, *A. melanoceras*, perhaps *A. mayana*), the *A. hindsii* population density has very likely increased greatly since the advent of European agriculture, except in those areas where Indian slash-burn agriculture was common on a system with at

least ten years fallow per field. Based on examination of *A. hindsii* throughout its contemporary range, I suspect that its pre-Colombian ecological distribution was the following. The plant was extremely common along rivers and mangrove swamps in deciduous and semideciduous forests and formed large thickets where occupied by multiple-queen species of obligate acacia-ants (Janzen, 1967a, 1973). Scattered large trees surrounded by sucker shoots from lateral roots occurred on dry hillsides, becoming progressively rarer the more intense and the longer the dry season. Along the wetter margins of its range (usually higher as well) it was found only along watercourses and other natural disturbance sites. In the very driest parts of its range (e.g., where the Tropic of Cancer crosses western Mexico), it occurred only along watercourses and in the foothills where the slightly cooler weather compensated for a lack of rain equal to that in the well-drained parts of the coastal plain. In no places did it occur as a shrub in the semidesert conditions as *A. collinsii* may do on rare occasions. In short, *A. hindsii* was a plant of locally wet sites in the drier habitats of the Pacific side of Central America between Nicaragua and the Tropic of Cancer. Throughout this range it invaded wet sites, as wet as those occupied by *A. gentlei*, *A. cookii*, *A. mayana*, *A. globulifera* on the Atlantic coast. Like these four swollen-thorn acacias, it was restricted to natural disturbance sites such as river banks in the wetter habitats. The wetter sites on the Pacific side, however, tend to experience a much more severe dry season than do sites on the Atlantic side with roughly equal annual rainfall. That the plant had to be able to survive this dry season, and thus could move into drier sites fairly readily, had been instrumental in preventing the very widespread population of *A. hindsii* from differentiating into many species. In other words, drying of the general weather would not be so likely to split that population of *A. hindsii* into as many small and isolated populations as it would a species widely distributed along the wetter Atlantic side of Central America.

The restriction of *A. hindsii* to the Pacific side of Central America is very puzzling. It has been collected east of the Continental Divide at only 7 sites, and 5 of these (sites 7, 27, 35, 55, 56) could well be the result of seed dispersal via road building machinery; at these sites the population is restricted in the area within a mile of the highway. At Tikal

and Lancetilla (sites 38 and 68) there has been much traffic by biologists from other parts of Central America, and the collections could well be recent introductions. *A. hindsii* is certainly not the common swollen-thorn acacia at these sites; however, there were reproducing trees at each of the 5 sites that I examined, and if they are not very recent introductions, it is most enigmatic that they have not spread from these sites over much of Caribbean Central America. Even if these 7 sites represent recent introductions, it is puzzling that the many natural introductions that must have occurred in the past have not resulted in established populations of *A. hindsii* on the Atlantic side of Central America. Being bird dispersed, the seeds surely must have been carried across the Continental Divide. Since isolated greenhouse plants of *A. hindsii* never set seed despite the fact that they flower profusely, it is likely that they are self-sterile. Successful establishment across the Continental Divide would then be exceedingly difficult except with simultaneous multiple-seed dispersal as could easily occur via the mud caked on road-building equipment. Low-income workers on the roads also eat the sweet pulp around the seeds and may have dispersed some seeds in this manner.

The dependency of *A. hindsii* on obligate acacia-ants for survival to reproductive maturity appears no different from that of *A. cornigera*, though experiments have not been conducted. Naturally unoccupied plants of *A. hindsii* are heavily damaged by herbivorous insects except under two circumstances: one natural and the other artificial. At the upper elevation limits of their distribution (e.g., sites 8, 37) in windy cool habitats, it appears that herbivorous insect pressure is low enough so that only during the warmest months of the year are unoccupied *A. hindsii* subject to severe defoliation. *A. hindsii* is one of the small number of species of woody second-growth plants that has managed to survive along the well-traveled dirt roads on lowland coastal El Salvador (site 72). These roads lie between cotton fields that are frequently sprayed with parathion and other very toxic insecticides. Not only have all the insects been eliminated from the roadside strips of vegetation by the combination of dust and insecticides, but the colonies of obligate acacia-ants have been gone so long that a large *A. hindsii* can show no sign of ever being located by searching queens. The thorns only stay on the



FIGURE 106.—*Acacia hindsii*: A, unoccupied 1-year-old sucker shoot (Mexico, site 6); B, unoccupied 2-year-old seedling (Mexico, site 9); C, occupied 2-year-old sucker shoot (Honduras, site 59); D, lateral branch from crown of occupied adult (Mexico, site 6).

acacia for a maximum of about 4 years, so this means that the ants have been missing at least that long. Since these fields are 10 to 30 years older than that, I suspect that the ants and most other insects have been missing equally long. The dust along other Central American roads is generally not as bad, since those with as much traffic as El Salva-

doran roads are usually paved. Despite the absence of herbivorous insects, the *A. hindsii* do very poorly because they are frequently used as vine standards by wild plants. At site 85 in Nicaragua, the southernmost local population of *A. hindsii* displays an extreme case of insecticide protection. This 30-acre patch of nearly pure *A. hindsii* (with scattered *A.*

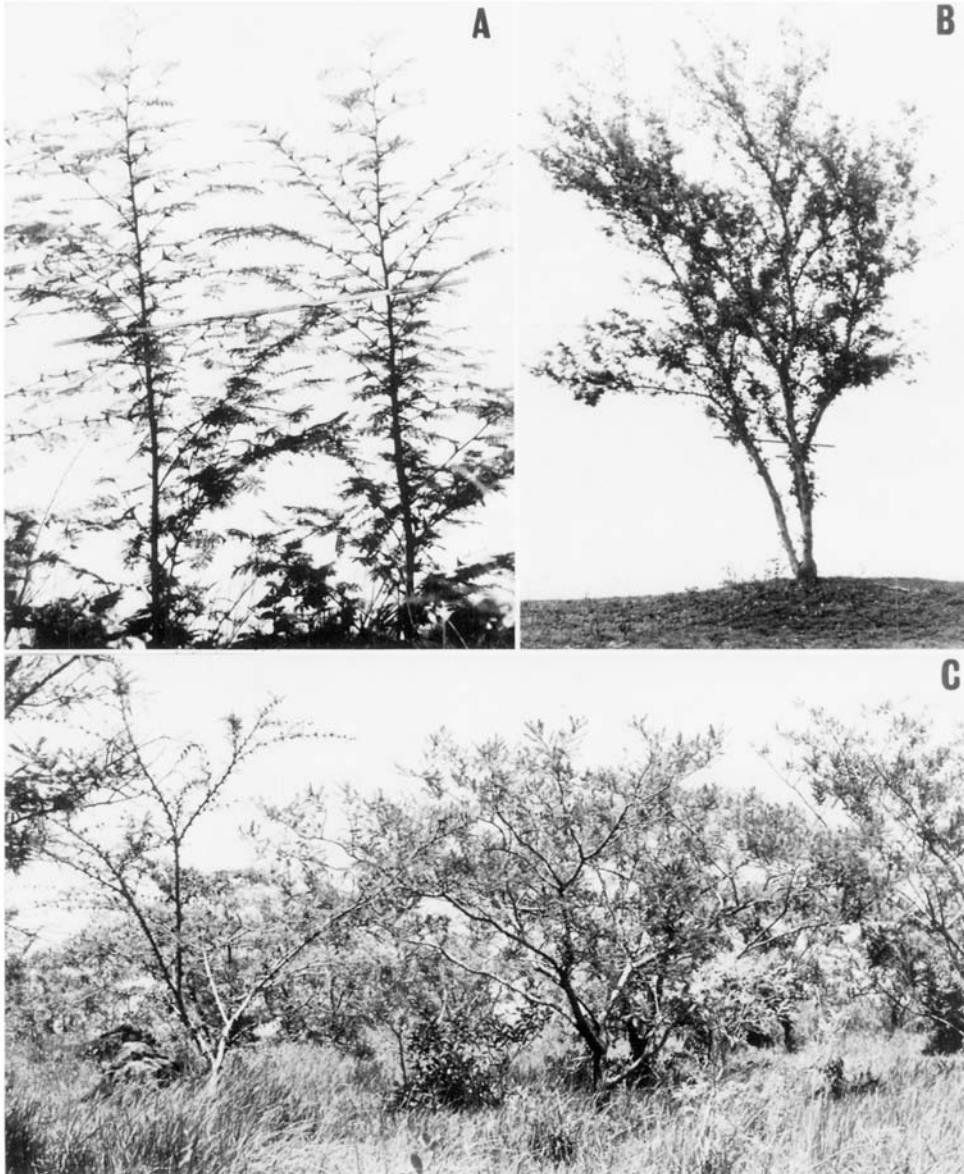


FIGURE 107.—A, B, *Acacia hindsii* (Mexico, site 6) : A, pair of 2-m-tall subadult occupied sucker shoots; B, adult 4-m-tall occupied tree, with the life form characteristic of open pastures; C, brushy pasture with a 3-m-tall occupied *A. hindsii* on the left and *A. pennatula* at right of center (Guatemala, site 37).



FIGURE 108.—*Acacia hindsii*: A, looking up through the crown of an occupied adult (Mexico, site 17); B, fully leafed crown of an occupied subadult (Guatemala, site 35).

cornigera) was almost certainly established from seed brought by man and is an island in the center of many hundreds of acres of cotton. The acacias are of all ages and many are reproducing. Three species of obligate acacia-ants are in the foothills 25 miles east, but after searching for 2 hours at site 85 I could find no evidence that any searching queen had located the patch during the past 4 years. If any did, they were killed by insecticide before they could attempt to cut an entrance hole in a thorn. There were almost no other insects in this patch of vegetation, and almost every plant had no herbivore damage; cotton in this area is almost uneconomical to grow because of the severity of insect damage.

Seedlings of *A. hindsii* in natural disturbance sites, and in brushy pasture, tend to attain a height of 10 to 40 cm over 1 to 3 years of growth unoccupied by obligate acacia-ants. Such unoccupied seedlings are very stunted in appearance (Figures 106A, B) with damaged leaves and many short branches that grew a few cm before having the shoot tip eaten off by an insect. In contrast to the heavily shaded unoccupied seedlings of *A. allenii* and *A. melanoceras*, whose slow growth is as much

from a lack of sunlight as defoliation, the slow growth of unoccupied *A. hindsii* seedlings can be attributed almost entirely to defoliation by insects. It appears that somewhat less than 1 percent of the seedlings of *A. hindsii* ever become occupied; most die within the first 4 years. cursory examination of habitats where they are common indicated that the fully insolated unoccupied seedlings live longest, despite the dryness of the site. This indicated that once established, energy relationships during the wet season are more important than desiccation during the dry season.

Once occupied by a single-queen colony, the young seedling often produces a small intact bush (Figure 106c) with multiple branches but quickly one of the vertical branches becomes the central trunk (Figures 107A, c). The central trunk grows rapidly upward; there may be 1 to 2 m of vertical elongation during a 5-month rainy season. During the second and third years of occupied growth, the crown begins to fill in with small branches (Figures 107c, 108B) if not under strong lateral competition from the crowns of other plants. If there is much adjacent woody vegetation, the vertical elongation



FIGURE 109.—A clump (clone?) of adult *A. hindsii* occupied by a multiple-queen species of obligate acacia-ant (Mexico, site 16).

of the central trunk may continue until the tree is 6 to 12 m tall. Lateral branches are long and bear large leaves and swollen thorns (Figure 106b). Old *A. hindsii* almost invariably have dense crowns (Figures 107b, 108a). The development described for *A. hindsii* is very similar to that for *A. cornigera*.

In areas where multiple-queen species of obligate acacia-ants are primary occupants of *A. hindsii*, the development is somewhat different. Here, most new

plants are sucker shoots from lateral roots of older acacias and are occupied by part of the colony in the parent shoot. This produces a dense thicket (Figure 109) of *A. hindsii* that can cover as much as several acres. In a new habitat, where the *A. hindsii* is becoming established through seeding, the early stages of shoot development are not much different from the case with single-queen obligate acacia-ants, but within a few years, the thicket be-

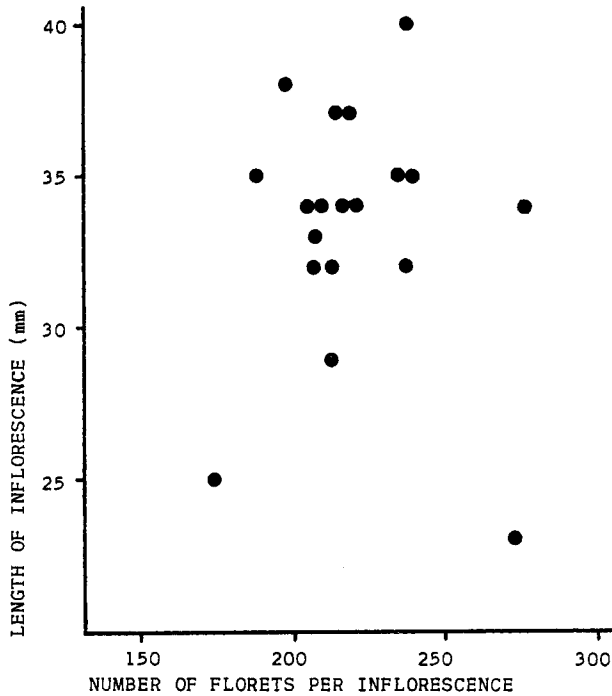


FIGURE 110.—Distribution of 4314 florets among 20 inflorescences from one adult *A. hindsii* (Mexico, site 5).

gins to form. The multiple-queen situation prevails in areas with particularly severe dry seasons coupled with wet seasons very favorable to acacia growth, as in western Mexico.

Acacia hindsii does not bear flowers until the fifth to seventh year after becoming occupied, and

many trees occupied by multiple-queen species do not produce their largest seed crops until they are 10 to 30 years old. In contrast, *A. cornigera* and *A. collinsii* bear flowers in the fourth to sixth year of occupied growth and have their heaviest seed crops when 6 to 15 years old. The inflorescences of *A. hindsii*, like those of other dry-land acacias, are visited by many species of small wild bees. The inflorescences vary greatly in length, but not so greatly in the number of florets per inflorescence, (Figure 110), but a maximum of 8 pods per inflorescence (Figures 111A, 112B) is observed in most pod crops. When more than 2 pods develop on a single inflorescence, they become so tangled when they dehisce (Figure 14B) that not all the seeds are externally visible to the birds that disperse them. The number of seeds per pod (Figure 111B) is representative of acacias in general and swollen-thorn acacias in particular. As with other dry-land acacias, these seeds are heavily attacked by bruchid beetles.

The swollen thorns of *A. hindsii* show very high variation in volume, as do those of *A. collinsii*. The volume of type A thorns (Figure 113) tends to be about the same throughout the range. In areas where there are only multiple-queen ant colonies, all thorns are type A and rather monotonous in form. Where single-queen colonies are present, however, and *A. hindsii* is represented primarily by well-defined individual trees, there is great variation in thorn volume. The volume for some of the largest type B thorns encountered are graphed in

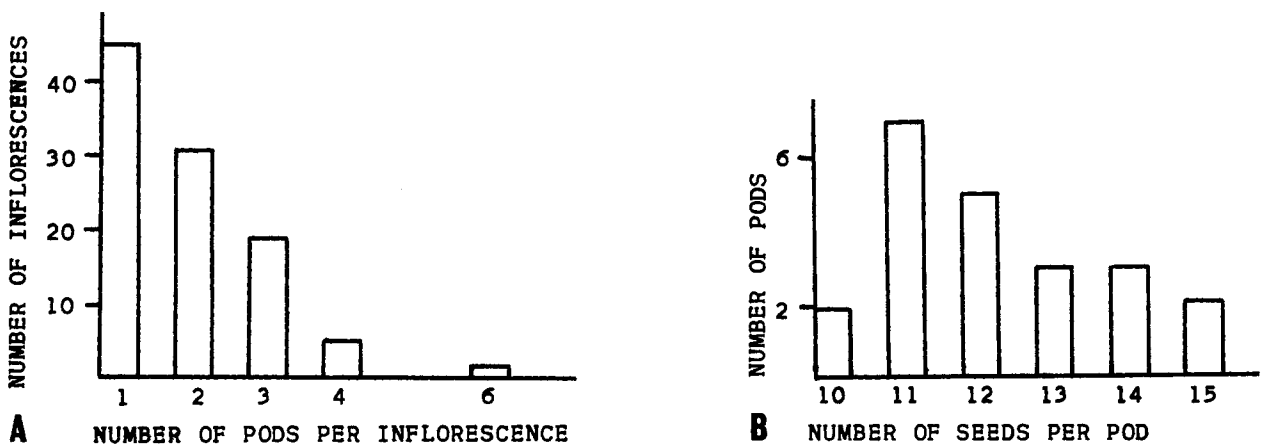


FIGURE 111.—*Acacia hindsii* (Guatemala, site 29): A, distribution of 187 mature seed pods among 100 inflorescences on one tree; B, distribution of 268 seeds among 22 of the mature pods.

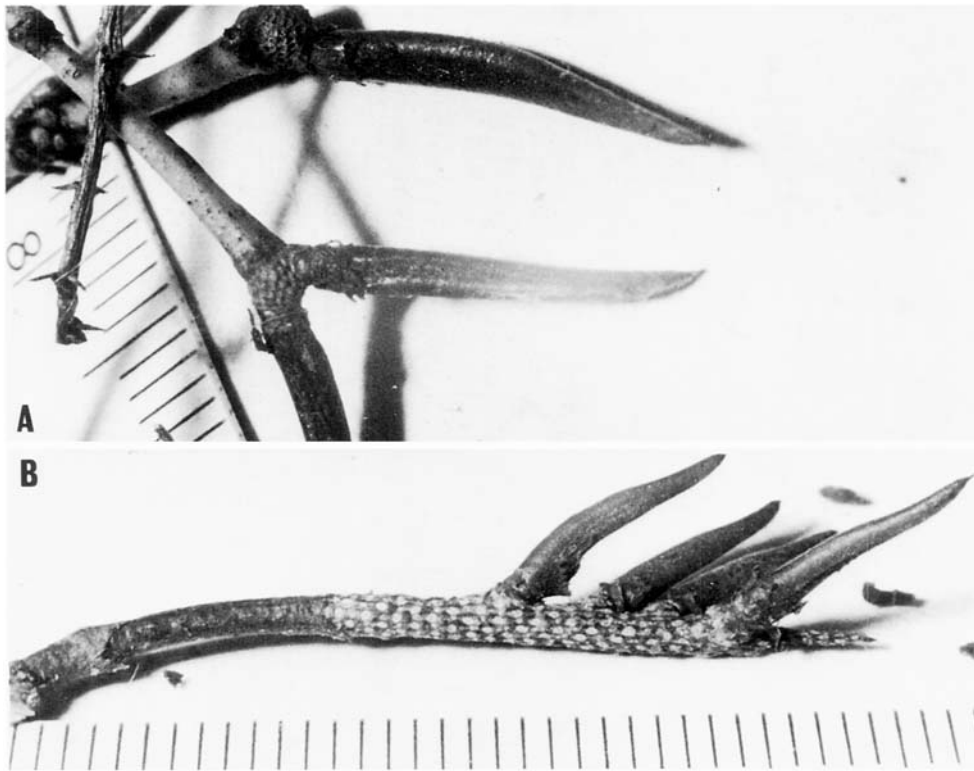


FIGURE 112.—Infructescences with immature pods: A, *A. globulifera* (Guatemala, site 13); B, *A. hindsii* (Honduras, site 59).

Figure 114, and in contrast to the large volumes for the dune ecotype of *A. sphaerocephala*, the large space is all useful to the ants because the thorn is flattened such that the thorn walls are only 2 to 4 mm apart.

The thorns of *A. hindsii* are highly variable in shape, as are those of *A. cornigera* and *A. collinsii*. Almost all seedlings have thorns that are cylindrical or only slightly flattened in cross section (e.g., Figure 106B). Thorns on young sucker shoots are the same (Figure 115A, middle). This difference between young and old thorns is probably associated with maximizing thorn volume and wall strength with a fixed small amount of energy to be expended on the thorn. Type A thorns in the crowns of mature *A. hindsii* show strong geographic variation (Figures 82B, 83c, 115, 116, 117, 118B, c) but have low variation at any particular locality. Their geographic variation in morphology is as great as that displayed between different species of more geographically restricted swollen-thorn acacias.

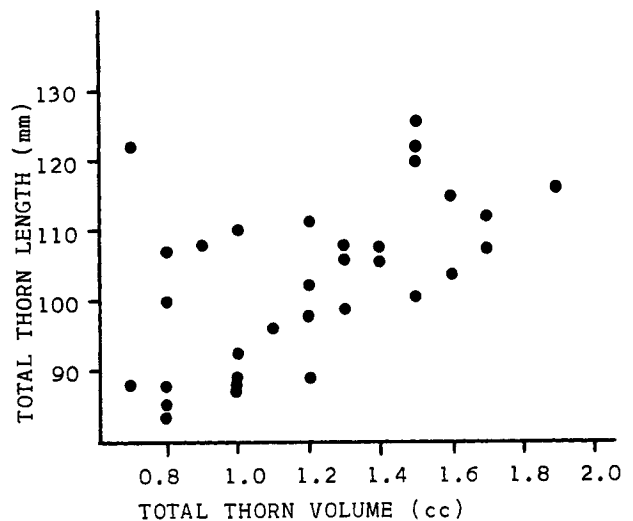


FIGURE 113.—Distribution of thorn volume among type A thorns from representative lateral branches in the crown of an adult occupied *A. hindsii* (Mexico, site 17).

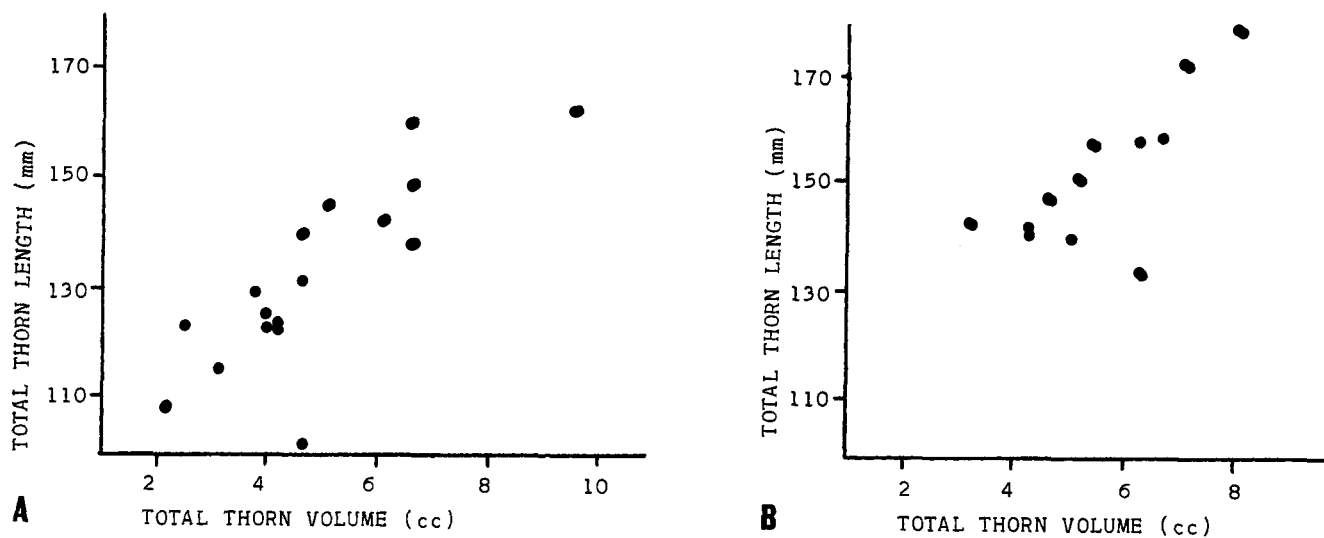


FIGURE 114.—*A. hindsii* (Mexico): A, distribution of 84 cc of thorn volume among 17 of the largest type B thorns on an occupied adult (site 9); B, distribution of 62 cc of thorn volume among 11 of largest type B thorns on an occupied adult (site 11).

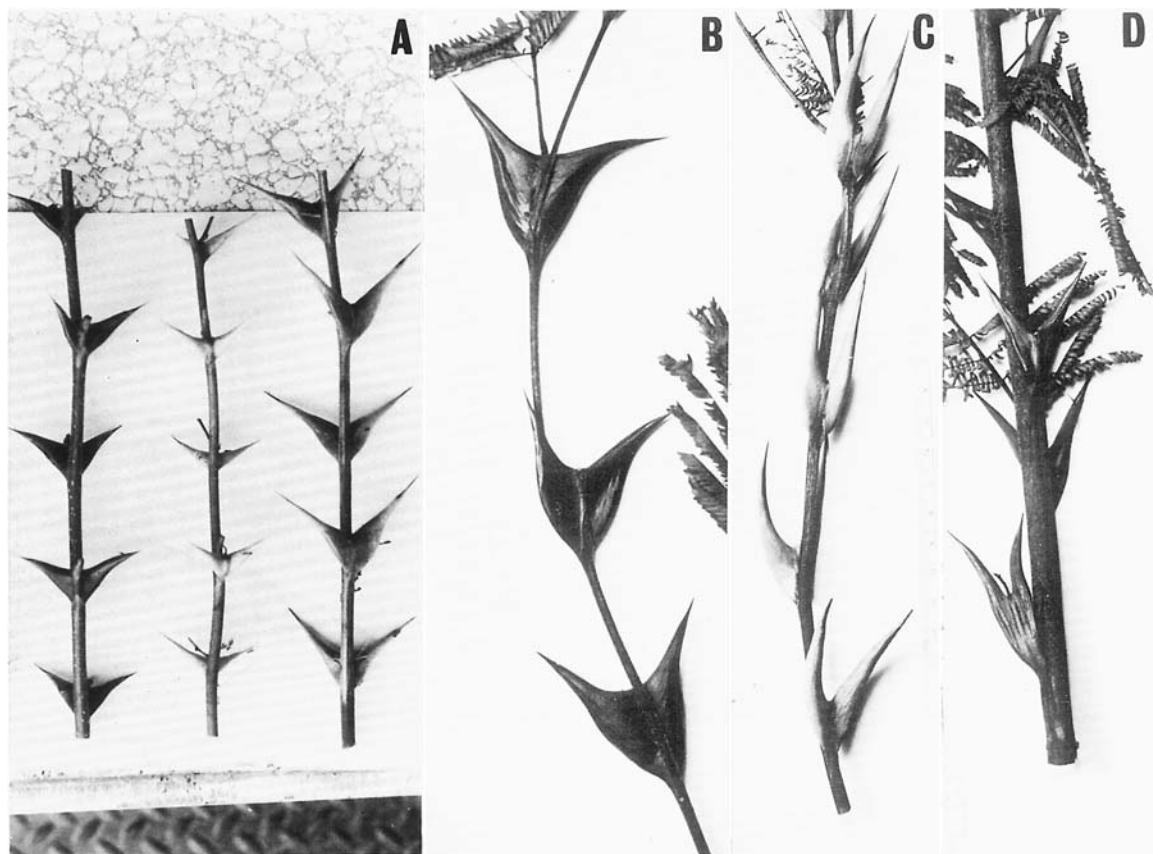


FIGURE 115.—Geographic variation in type A thorns from occupied adult *A. hindsii*: A, Mexico, site 17; B, Guatemala, site 33; C, Honduras, site 50; D, Guatemala, site 25A.

FIGURE 116.—Geographic variation in type A thorns from occupied adult *A. hindsi*: A, Mexico, site 11, B, Mexico, site 13; C, Guatemala, site 33.

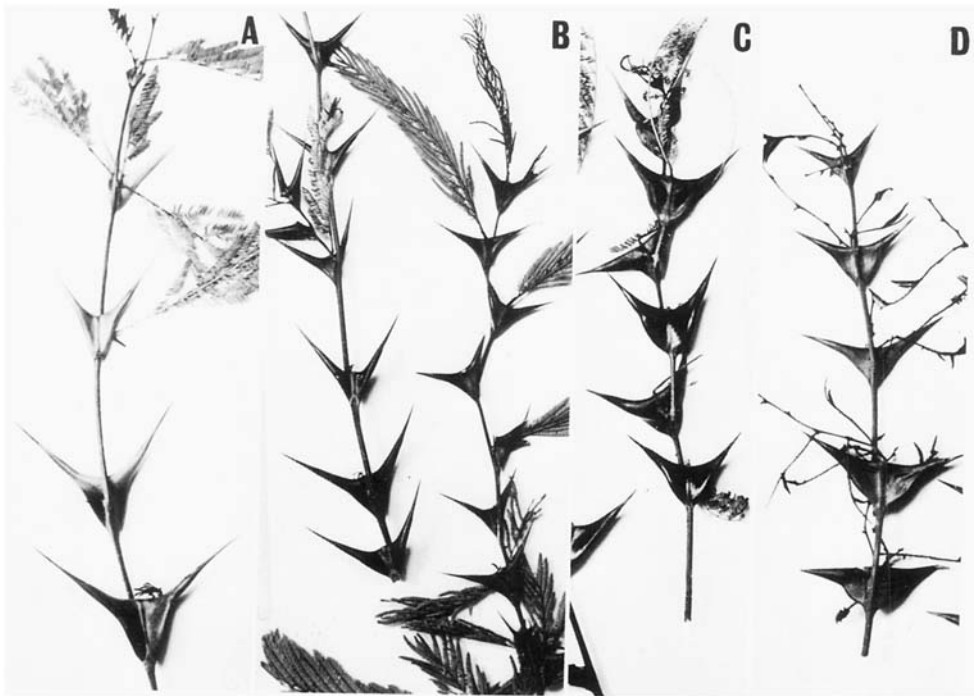
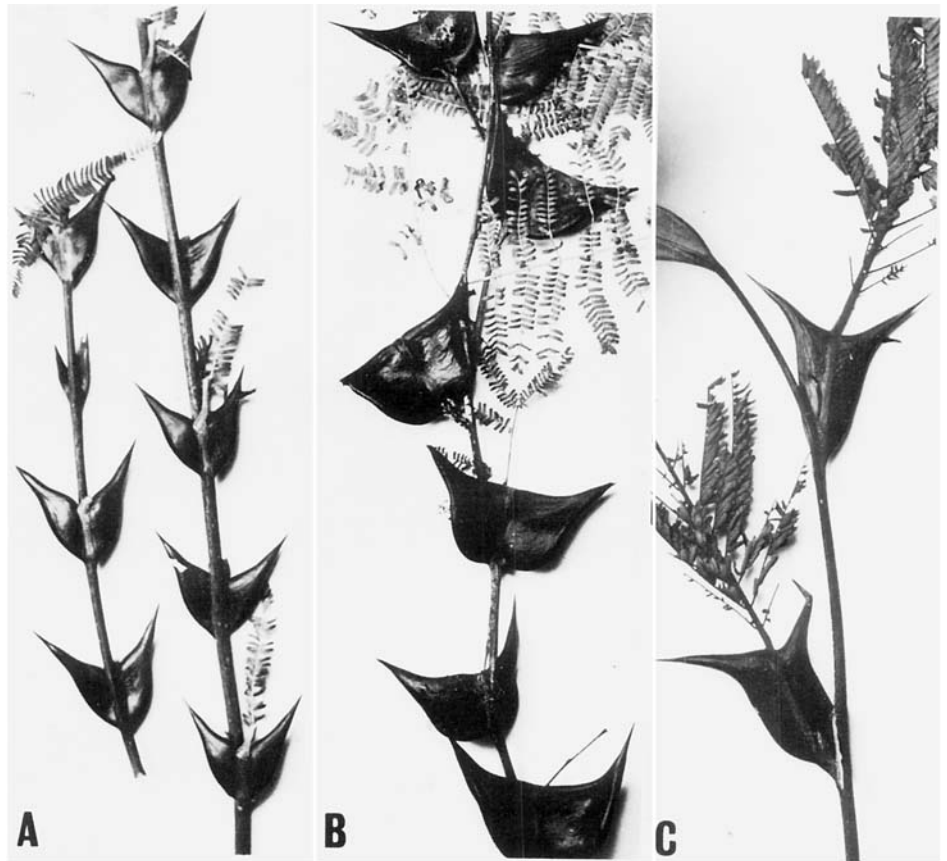


FIGURE 117.—Geographic variation in type A thorns from occupied adult *A. hindsi*: A, Mexico, site 8; B, Guatemala, site 35; C, Mexico, site 13; D, Guatemala, site 35.



FIGURE 118.—*Acacia hindsii* (Mexico): A, type B thorns on short lateral branches from main trunk of an occupied adult (site 9); B, white type A thorns on main trunk and lateral branches of occupied subadult (site 17); C, black type A thorns on main trunk and lateral branches of occupied subadult (site 17).

Much of the variation is probably adaptive in the context of the developmental physiology of the lateral branch, rather than the ant colony. It is possible that the details of the thorn shape are nonadaptive, but unlikely, since so much of it is clinal in nature. The production of type B thorns

appears highly adaptive in the context of multiple-queen colonies; the single-colony queen lives in the type B thorns. There is, however, a great deal of geographic variation in type B thorn shape (Figures 118A, 119) that probably had the same basis as that displayed by type A thorns.

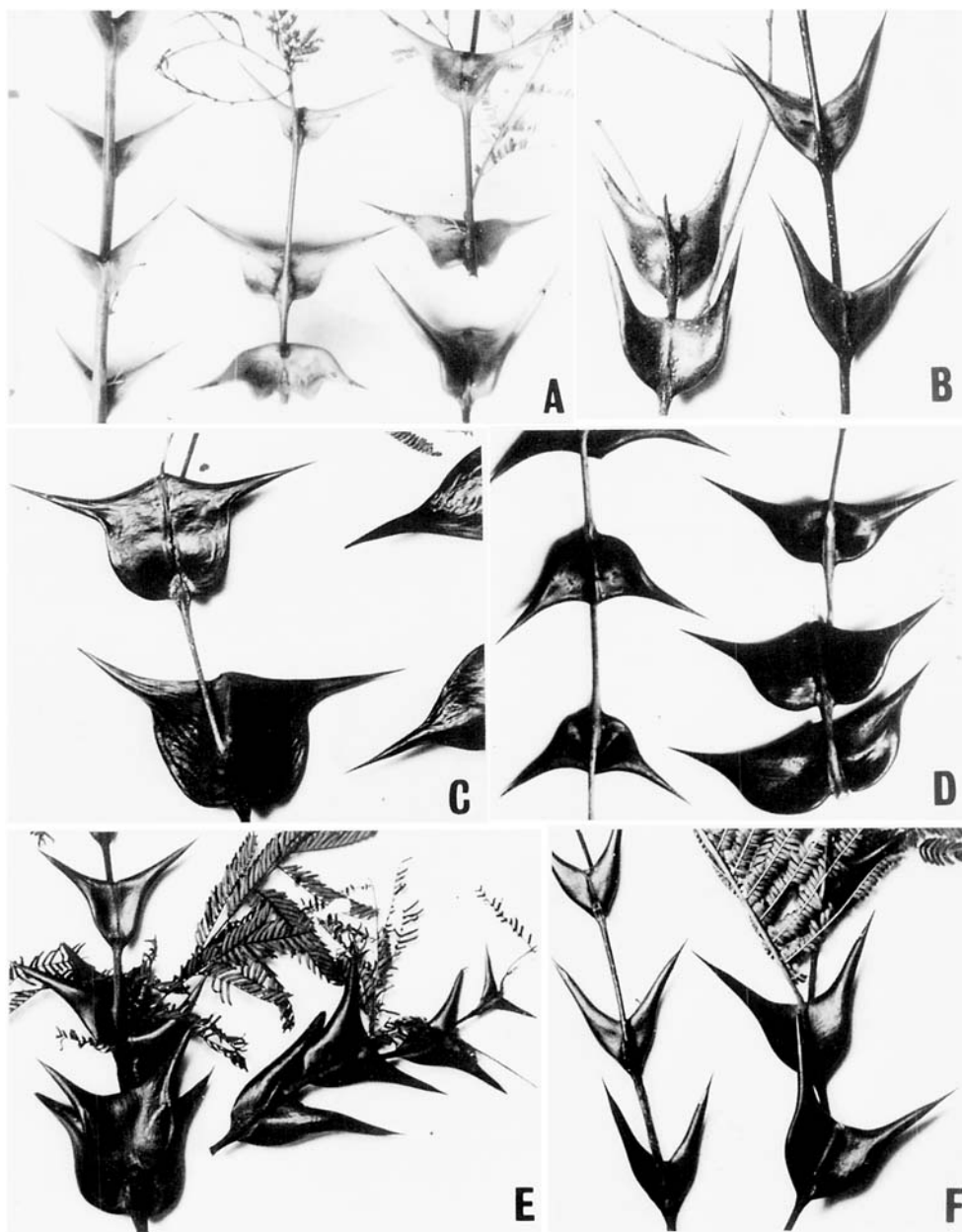


FIGURE 119.—Geographic variation in type B thorns from occupied adult *A. hindsii*: A, B, F, Mexico, site 11; C, Guatemala, site 31; D, Mexico, site 13. E, Type B thorns of *A. collinsii* that are convergent in shape on those of *A. hindsii*.

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