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FIRE, VEGETATION STRUCTURE, AND THE ANT X ACACIA INTERACTION IN CENTRAL AMERICA[1]

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Abstract. The effect of fire on swollen-thorn acacias and their tenant obligate acacia-ants in the Central American dry lowlands is discussed. Fires may either consume the entire acacia shoot and ant colony, scorch and kill the acacia but not the ants, or kill neither acacia nor ant colony. Which alternative occurs depends on the structure of the immediately surrounding vegetation which in turn depends on how much of it has been killed by the ant colony and how fast the acacia has grown. The survival of the acacia population in frequently burned areas is almost entirely dependent upon some ant colonies surviving the fire to occupy the new sucker shoots from acacia stumps. The effect of these fires on the evolution of the interaction between the ant and the acacia is discussed.

INTRODUCTION

In view of the increasing interest in fire in the New World as a common environmental factor and as an ecological management tool for vegetation (see Komarek 1962–65), the present paper was prepared to describe the effect of fire on the mutualistic interaction between obligate acacia-ants (*Pseudomyrmex* spp.) and swollen-thorn acacias (*Acacia* spp.) in lowland Central America and Mexico. The interaction requires the cooperation in time and space of two fire-susceptible organisms, and (1) fire has an immediate effect on the interaction; (2) the effect of a fire on the ant and acacia is not independent of other organisms; and (3) the presence of fire may have affected the coevolution of the interaction.

There is little detailed information on the effect of fire on Central American natural communities and their members. Budowski has reviewed the fire ecology literature of forest-savanna succession (1956) and discusses the general effect of fires on tropical forests (1958–59). Johannessen (1963) briefly discusses the prevalence of fire in Honduras. Ross (1966) describes the effect of fire on the interaction between a riodinid butterfly larva (*Anatole rossi*) and its attendant ants (*Camponotus abdominalis*) in the Sierra de los Tuxtlas in southern Veracruz, Mexico; the ants protect the larva from predators and fire by herding it into an underground chamber during the day, where it is safe from the light grass fires that annually sweep the area (see Buechner and Dawkins 1962, Hocking 1964, and Kowal 1966 for discussions of Old World fire ecology). The sole reference to the effect of fire on the ant X acacia interaction is Skwarra's (1934) list of six species of ants living in the thorns of fire-killed *Acacia cornigera* in northwestern Veracruz (Miramar), Mexico.

ANT X ACACIA INTERACTION

The details of the interaction and its coevolution were treated earlier (Janzen 1966*a*, 1966*b*) and are summarized below to provide background. The obligate acacia-ant colony (e.g., *Pseudomyrmex ferruginea, P. nigrocincta, P. spinicola;* taxonomic problems with these ants are discussed by Janzen[2]) lives in the enlarged stipular thorns of a swollen-thorn acacia (e.g., *Acacia cornigera, A. sphaerocephala, A. collinsii, A. hindsii;* for a discussion of taxonomic problems with these acacias see Rudd 1964 and Janzen[3]); the colony obtains nectar from foliar nectaries and eats the nutrient-rich Beltian bodies from the leaflet tips of the same leaves that bear the enlarged stipules (Fig. 1). The production of these morphological traits is independent of the presence of an ant colony. Under natural circumstances, colonies are found only on swollen-thorn acacias. One colony may occupy more than one acacia (species and individual). The workers patrol the surface of the plant and attack nearly all insects and foreign plant matter that contacts the acacia. (In this paper "occupied" refers to worker ants patrolling outside of the thorns, and "unoccupied" has no direct bearing on the thorn content.) The immediate result

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[2] Janzen, D. H. *Unpublished manuscript.* The obligate acacia-ants of Central America.

[3] Janzen, D. H. *Unpublished manuscript.* The swollen-thorn acacias of Central America.

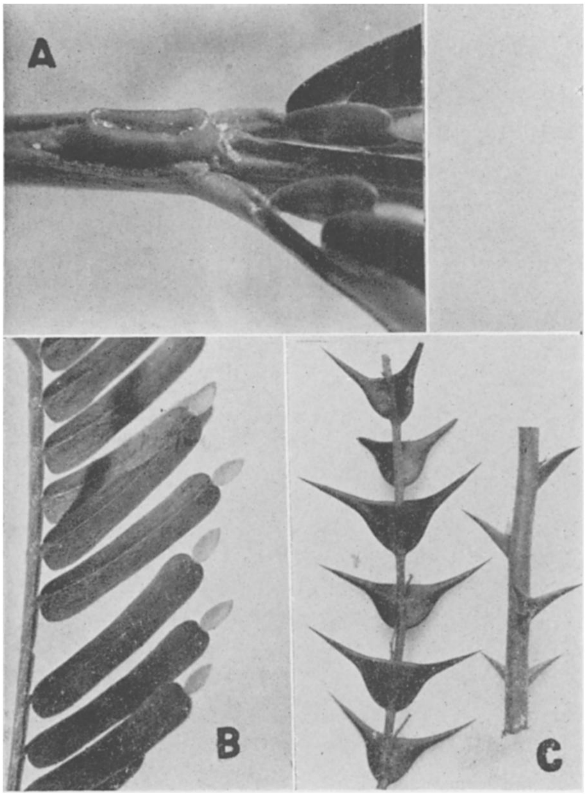

FIG. 1. A. Foliar nectary on dorsal side of distal end of leaf petiole, *Acacia cornigera*. B. Beltian bodies (1.0–1.5 mm long) on tips of pinnules; left pinnules removed, *Acacia cornigera*. C. Swollen stipular thorns occupied by ants; both branches from the same tree, *Acacia hindsii*.

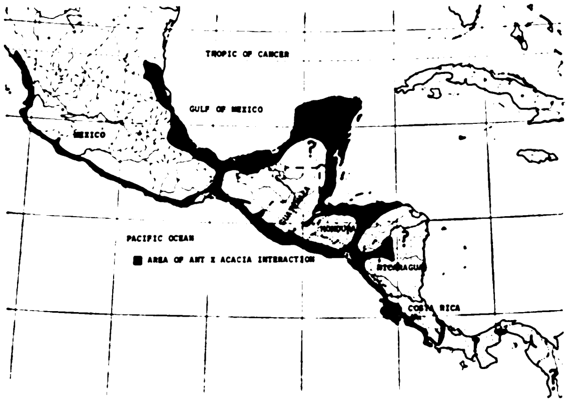

FIG. 2. Distribution of swollen-thorn acacias and obligate acacia-ants in Central America. Question marks indicate areas from which extensive collections are not available, but it is likely that the interaction exists based on scattered reports in the literature. Continuity between actual collection sites (generally at 10- to 100-mile intervals) is based on continuity of vegetation types, rainfall regimes, and topography.

of this protection is that the acacia grows as a normal and common plant in lowland second-growth plant communities. If the ant colony is removed, the swollen-thorn acacia is subject to severe defoliation by insects with subsequent shading by neighboring vegetation; these two factors result in death of the unoccupied acacia within 2–15 months. The swollen-thorn acacia has lost many of the animal and plant deterrents possessed by other *Acacia* spp. and instead maintains a multipurpose deterrent (the obligate acacia-ant) through production of swollen thorns, foliar nectaries, Beltian bodies, and nearly year-round leaf production even in dry areas.

FIRE STATUS OF THE ANT X ACACIA INTERACTION

The swollen-thorn acacias are broadly distributed in lowland areas (up to 1,500 m elevation) of Central America that have a dry season of 1–6 months and mean annual rainfall ranging from 1,500 to 4,000 mm (Fig. 2). When under human influence, these areas are commonly—at times even annually—burned. Fires are both set and escaped; they are most frequent, but not necessarily annual, in young second growth (fallow fields), pastures, roadsides, and newly cleared forest. Distinct patterns and periodicities in these fires are of great importance in the effect of fire on the interaction. The last month of the dry season (April or May) is known as the "quemazones" (time of burning); the air over thousands of square miles of second growth is brown with smoke haze. Prior to Indian activity in lowland Central America, fires were undoubtedly much rarer, but some inferences about their effect can be obtained by examination of present-day uninhabited lowland areas (e.g., central Osa Peninsula, Puntarenas Province, Costa Rica).

The swollen-thorn acacias are plants of disturbed vegetation of many types and therefore are subject to many different types of fires. However, certain parts of the system are held in common. An area clear of foreign vegetation around the base and branches of the acacia is the result of the ants' attack on foreign vegetation (Fig. 3). When a fire burns through this vegetation (1) the acacia may be completely spared due to the size of the clear area; (2) the heat may be enough to kill the shoot but not the ant colony (whereupon the ant colony moves into the regenerating sucker); or (3) the entire shoot and colony may be incinerated or killed. In the latter case, the new sucker normally regenerates without an ant colony and is subject to many mortality factors. The form of the fuel contribution of the surrounding plant community is important in determining which of the three above alternatives occurs.

FIG. 3. A. Bare ground under *Acacia collinsii* is a basal circle made by *Pseudomyrmex nigrocincta* in a heavily grazed pasture in southwestern Nicaragua (early May 1965). Vegetation cleared by the ants killing the shoot tips of plants growing up under the acacia. B. Basal circle under *Acacia cornigera* in ungrazed 1-year-old regeneration. V's mark the margins of the basal circle. Vegetation cleared by *Pseudomyrmex ferruginea*. 5 miles east of Temascal, Oaxaca, Mexico (June 1964).

Interaction before human presence

Swollen-thorn acacias have been found growing in five different sites in Central America where the vegetation is free from human influence. Natural fires are rare in these sites, but do occur. Man-made fires occasionally spread into them.

Central Osa Peninsula, Puntarenas Province, Costa Rica.—While the Pacific side of the Osa Peninsula has a high incidence of slash-burn farming, there are several hundred square miles of forest on the hills behind Rincon (Golfo Dulce side) which are apparently undisturbed by man in recent times. An undescribed species of swollen-thorn acacia is common (10–20 per hectare) as suppressed seedlings and occasional emergent sexually mature individuals (12–20 m tall) in the forest, on the crests and upper slopes of these hills. The hills experience a 1- to 2-month period with almost no rainfall (February-March). The lower primary forest on the Golfo Dulce side has nearly continuous rainfall, but with several distinctly drier months (January-March); the swollen-thorn acacia is very rare in this forest (probably less than one maturing plant per hectare).

In February 1965 a burn of less than one-half hectare was found on a hillside; it had apparently been started through road-building activities. It had consumed or killed the woody vegetation of less than 2 m height and killed branches of taller trees up to 4 m above the ground. Leaf litter and dead branches on the ground were irregularly consumed; apparently certain areas of the forest floor were damper than others. The young suppressed swollen-thorn acacias, 30–250 cm in height with small ant colonies, had been either completely spared (no burning of litter underneath through local differences in fire pattern) or consumed. Since the ants generally do not remove dead leaves and branches from under the acacia, and this fuel came from the canopy overhead rather than adjacent growing vegetation (the opposite of the case in second growth), the ants had no chance to avert the fire. In the relatively open understory of this forest, very few plants come in contact with the young acacias through normal distribution patterns.

While the light leaf litter around their bases had been consumed, two of the three mature acacias (45–65 cm dbh) in the area of the burn were undamaged. The third tree had leaf litter piled against its base and the cambial layer had been killed by scorching (swollen-thorn acacias have very thin bark). The shoot tips of the acacia canopy were wilted and browning, and small adult cerambycid beetles were feeding on the decomposing bark. Mature leaves had wilted and were falling off. The ants were not patrolling the canopy densely (as would have been the case before the fire), but when the tree was cut they became very active. Heavy patrolling (two to five ants per cm^2) of three new suckers from the root crown indicated that the ants would eventually move the colony into the new sucker shoots. While these suckers will grow slowly in heavy shade, they most likely would not mature unless a natural hole in the canopy occurred. In this type of vegetation (15–25 m high closed canopy, thin understory), reproductive maturity of the acacia by becoming a canopy member confers virtual freedom from fire mortality on the ant colony, but a fire may bring it back down to ground level by killing the aboveground shoot.

Beach dunes of the Veracruz, Mexico, coast.—On new sand dunes, especially between Mocambo

(2 km south of the city of Veracruz) and Alvaredo, *Acacia sphaerocephala* and, more rarely, *Acacia cornigera* are common members of the primary succession. They form a low dense mat (0.5–2.0 m tall) as close as 10 m to the high tide line; inland, both of these acacias become more tree-like (2–5 m tall) and are incorporated into mixed species communities. When in pure stands on the dune, these acacias form a partially to completely evergreen plant community since they do not drop their leaves during the dry season; man-made fires burn into these stands and go out. No evidence has been observed for natural fires at these sites. The low vegetation (1–4 m) of both secondary and primary nature immediately behind the dunes is fully deciduous during the dry season and fires passing readily through this occasionally consume the swollen-thorn acacias. These trees, or at least their tenant ant colonies, are occasionally saved by the bare basal circle free of vegetation under the acacia.

The dune mat of swollen-thorn acacia is relatively unimportant to the obligate acacia-ants because this is one of the few natural sites where the acacias are unoccupied for the most part. Survival of the unoccupied acacias is the result of a lack of phytophagous insects and other plants to shade the slowly growing mat.

Successional stages following mangrove succession.—Near San Blas, Nayarit, Mexico, where relatively undisturbed mangrove succession is common in muddy bays and river mouths, *Acacia hindsii* is occasionally encountered in the vegetation immediately adjacent to the swamp. When these acacias occur as single plants, they have only the bare basal circle to protect them; since the general vegetation is dense and tall, a dry season fire usually consumes the entire plant and ant colony. In two 1-year-old burns of several hectares extent in the San Blas area, there was no sign of survival of individual trees.

However, in these areas *Acacia hindsii* commonly forms very dense stands of shoots of all ages (Fig. 4), and of 1/100 to 1/2 hectare in size (20–1,500 shoots). These are tenanted by huge multiple-queen obligate acacia-ant colonies with as many as several million workers (two undescribed species of *Pseudomyrmex*). The ants kill virtually all other vegetation within the acacia stand, and the ground underneath is nearly bare. These stands remain moderately green during the dry season, and man-made escaped fires commonly burn up to their edge but do not enter, presumably due both to the bare ground and green foliage. The result of such a fire is an area of low regeneration with a clump of *A. hindsii* 4–20 m tall projecting from it.

FIG. 4. Lower portion of a clustered pure stand of *Acacia hindsii;* note bare ground under the trees. Two miles east of San Blas, Nayarit, Mexico.

Deciduous thorn forest.—On the dry hills 11.4–17.0 miles northeast of Tehuantepec, Oaxaca, Mexico, there is an area where *Acacia collinsii* is a normal member of ravine bottom vegetation. Here it is occupied by *Pseudomyrmex ferruginea, P. nigrocincta,* and an undescribed species. This area is subject to sporadic and widely spaced fires (no agriculture in the immediate area), and unless the acacia has a well-cleaned basal circle, the shoot or the ant colony is normally killed. The situation is much like that on the Osa Peninsula, in that there tend to be large, reproducing trees and small, suppressed trees; however, with the nearly total leaf drop by other plants during the dry season, these small acacias receive some sunlight and grow. These small growing trees have the best developed basal circles and survive ground level fires. Virtually nothing above the ground survives a total (canopy level) fire; there is no clustering effect as with *Acacia hindsii* on the coastal sites.

Island succession in river swamps.—Along the Rio Tonto and Rio Cosamaloapan inland from Cd. Aleman, Veracruz, Mexico, there are occasional old ox-bows and flooded areas that have a natural grass vegetation. Slightly raised patches of ground on these sites are occasionally covered by dense pure stands of *Acacia cornigera* occupied by *Pseudomyrmex ferruginea*. The ground under these stands is nearly bare due to shading and the ants' activity against foreign vegetation. During the dry season the grasses become very dry and are occasionally burned by escaped man-made fires, which burn to the edge of the acacia stand and stop; the acacias are normally green at this time of year.

Interaction after human presence

Prior to man's activities, the ant X acacia interaction was limited to the network of river banks, ravines, and beach dunes, with occasional extrusion into primary forest in the drier areas. Human activities have filled the lacunae in this network with hundreds of thousands of hectares of second-growth vegetation that serves as suitable habitat for the interaction. Aside from its large area and continuity, this new habitat is not grossly different from natural disturbance sites except for one factor. Man-made disturbance sites are subject to frequent fires of both regular and unpredictable periodicity.

Man-made disturbance sites that serve as habitat for obligate acacia-ants and swollen-thorn acacias in Central America usually have vegetation 1–20 years old. It is often arrayed in patches with uniform disturbance histories, but adjacent patches may have quite different disturbance histories. Fire history is one of the important characteristics of these patches and affects their animal and plant species composition, population structure, and physiognomy both at the time of fire and in later years. In the following sections some of the commonest types of disturbance patterns are described in relation to the effect that fires have on the ant X acacia interaction.

Newly cleared old forest, with ungrazed regeneration (roadsides east and south of Rincon, Osa Peninsula, Puntarenas Province, Costa Rica; dry hills, Eskameca, Finca Taboga, 8 miles southwest Cañas, Guanacaste Province, Costa Rica; north shores of Lago de Izabal, east of El Estor, Izabal, Guatemala; vicinity of Temascal, Oaxaca, Mexico).—Throughout the range of the swollen-thorn acacias, when forest of over 30 years' age is cleared, the acacias are occasionally found in the new vegetation. These do not appear to be remnants of populations from previous disturbances, but rather members of a small residual population of seeds (constantly being replaced by birds) and very rare maturing acacias that have entered natural gaps in the canopy. If the regeneration is neither burned nor grazed, it is generally only the suckers from cut acacia stumps (of the maturing trees mentioned above) which grow fast enough and have a large enough ant colony to survive in the new vegetation. Seedlings are usually shaded out. If the site is burned at the time of clearing, all resident obligate acacia-ant colonies and founding queens are killed. If the rainy season then begins immediately, regeneration is so rapid and phytophagous insect damage to the unoccupied acacia seedlings and suckers so great, that there is virtually no recovery by the acacia population. A common case in such sites is, however, for an ant colony living in unburned vegetation adjacent to the newly cleared site to move into the new site and occupy up to 10 new seedlings or suckers (e.g., a single-queen colony of *Pseudomyrmex ferruginea,* Temascal, Oaxaca, Mexico) or as high as 50 (e.g., a multiple-queen colony of an undescribed species of *Pseudomyrmex,* San Blas, Nayarit, Mexico).

If the fire occurs at the end of the rainy season (e.g., November or December), there is a greater chance for acacia survival. The old acacia stumps produce new suckers within 3 weeks, and founding queens move into them from outside the burned site. By the time the next rainy season starts (May), 5 to 7 of the 9 months necessary for a colony to develop have passed and the young colony may be large enough to protect the acacia during the later part of the rainy season. In addition, the acacia sucker may grow as much as 150 cm during the dry season even when unoccupied because of the lack of phytophagous insects and shading at this time.

Repeatedly cleared 2- to 15-year-old ungrazed regenerating vegetation (occasional roadsides throughout the swollen-thorn acacia range, Fig. 2; crop-fallow systems in areas with high indigenous Indian populations such as around Lago de Izabal, Izabal, Guatemala, and around the lake behind Presa Miguel Aleman, Temascal, Oaxaca, Mexico).—This land is cleared by cutting and burning or just burning, and then planted to corn, squash, and/or beans for 1–4 years. The weeds (grasses, seedlings of ruderals, crown suckers from old stumps) are suppressed by occasional burning, weeding by hand, or cutting with a machete. During the growth of the crop, swollen-thorn acacias are present as unoccupied suckers (the ant colonies having been killed by the fire) and, more rarely, seedlings; there are founding queens in the thorns of these young acacias. Once the field has lain undisturbed for 9–13 months, young obligate acacia-ant colonies begin to appear. Most commonly it is the suckers from old root stocks that are occupied and become members of the new regenerating canopy, but occasionally a seedling does also (ratio of about 10–30 to 1, in the area around Temascal, Oaxaca, Mexico, and Cañas, Guanacaste, Costa Rica).

As regeneration proceeds without cattle grazing or browsing, the general canopy rises and is bound together by a heavy vine mat. The occupied swollen-thorn acacias are part of this canopy or emergent from it, but are free from vine entanglement due to ant attack on foreign vegetation. During the first 1–4 years the acacia grows in a cylindrical area free from other green vegetation; this area is slightly wider than the diameter of the acacia canopy (1–3 m) and projects down to the ground. As the acacia grows taller (over 3–8 m), the clear area on the ground is not maintained by the ant colony, but the ants continue to keep the acacia canopy free of foreign green vegetation.

If, during the dry season, a fire passes through this type of ungrazed regenerating vegetation during the first 2 years (vegetation generally 1–3 m tall, acacias emergent up to 1.5 m), virtually all aboveground parts of the other plants are killed or consumed. Those acacias which are not well cleared of surrounding vegetation or emergent to it are consumed entirely. Those which are clear of the surrounding vegetation are occasionally consumed, but more commonly the shoot is killed but not consumed. In this case, the ant colony sometimes survives the fire. In a few cases, the clear area is so big and/or the acacia is sufficiently emergent that the entire shoot is undamaged. An example of the effect of such a fire is as follows.

On May 19, 1964, about 8 hectares of 15-month-old ungrazed regeneration (from a corn field) was burned 6 km east of Temascal, Oaxaca, Mexico (rainy season started on May 21). On July 11, a 100- by 40-m area in the center of this burn contained 365 standing acacia shoots (*Acacia cornigera* containing *Pseudomyrmex ferruginea*) in the 2- to 4-m height range; the smaller shoots had been completely consumed by the fire and were therefore not counted. Of the 365 shoots, 96 were dead (usually charred), unoccupied, and had no new suckers from the root crown. Twenty-six shoots had not been killed, and all had canopies in full leaf and were occupied. Of these, 21 had well-developed basal circles from 1 to 2.5 m diameter. The remaining 243 shoots had been killed by scorching, but new suckers were growing from old root stocks. Of these, 123 were occupied by portions of mature colonies that had survived the fire; the mean height of these occupied suckers was 59.66 cm (SD = 24.9 cm). The unoccupied 120 suckers had a mean height of 18.08 cm (SD = 11.2 cm). All of the damage to the unoccupied suckers was from phytophagous insects, and both this and shading from the dense stand of grass were responsible for the slowing of their growth. Judging from other similar examples in later stages of growth, only the occupied acacias would go on to become reproductive members of the new regeneration following this fire. This system is discussed in more detail by Janzen (1966*b*).

In ungrazed vegetation 2–5 years old, there is so much fuel that it is only rarely that an acacia is sufficiently protected for the ant colony to survive. However, if it does, it is usually such a large colony (e.g., 20,000–50,000 workers) that it moves out around the acacia after the fire and occupies a number of sucker shoots, and thus exerts a major influence on the presence or absence of maturing acacias in the new regeneration.

The above discussion applies to single-queen colonies (e.g., *Pseudomyrmex ferruginea, P. nigrocincta*). Multiple-queen species often occupy large clusters of acacias (Fig. 4) which, as explained above, can survive severe fires with only some scorching of marginal trees.

If acacias are cut before being burned, all of the ants and acacia shoots are destroyed since they are lying at ground level when the fire passes through. A strict annual burning program without grazing, or with grazing and cutting, is the only effective means for removing an established population of swollen-thorn acacia root stocks without hand grubbing. In general, it is those areas under this type of burning program for more than 3 years that are free from swollen-thorn acacias during weedy regeneration (cane fields, pure grass pasture). The following example is representative of regeneration following cutting and burning of an ungrazed field with a moderate population of *Acacia cornigera* and *Pseudomyrmex ferruginea*.

On December 1, 1963, 400 m² of 18-month-old woody regeneration 1.5–4 m tall in an old pepper field (red laterite soil) was cut; after 6 days of drying it was burned (5 miles east of Temascal, Oaxaca, Mexico). Six weeks after this fire, 326 sprouting swollen-thorn acacia stumps were found and mapped in this area (Fig. 5). Three seedlings were located as well. The subsequent regeneration through the dry season was almost entirely from old root stocks. The other vegetation very quickly overtopped the swollen-thorn acacias, but, due to the lack of phytophagous insects, these acacias produced a large number of swollen thorns which were in turn entered by founding queens of

FIG. 5. Four-week-old stump sucker of *Acacia cornigera* following a fire on December 1, 1963. The entire previous aboveground shoot with its ant colony was destroyed by the fire, and thus a new colony will have to develop in the new thorns from founding queens of *Pseudomyrmex ferruginea*.

Pseudomyrmex ferruginea. By May 27 (rains started) the general vegetation was 25–60 cm tall, and 100 of the swollen-thorn acacia suckers had a mean height of 32 cm (SD = 26 cm) based on the tallest sucker from each stump. Young ant colonies were developing in the thorns (0–20 workers per colony), but no patrolling of the shoots was evident. In response to the rain, the general vegetation began to grow very rapidly while the swollen-thorn acacias were subject to very severe defoliation. By the end of July, only two of the swollen-thorn acacias were sufficiently patrolled to be growing up with the general canopy (1–2 m tall). The remainder were heavily shaded and despite their small ant colonies did not show signs of becoming emergents. Based on past experience, if there was no subsequent fire, these two might have survived through the rainy season and following dry season, to become reproductives during the following rainy season. Thus, by a cutting and a fire, the resident population of reproductive ant colonies and acacias has been reduced from 326 to a maximum of 2 per 400 m^2.

It is a striking characteristic of these second-growth plant communities that while woody second-growth vegetation over 1.5 years old generally becomes leafless during the dry season (throughout lowland Central America in dry areas, e.g., the area of Cañas, Guanacaste, Costa Rica; Esteli, Esteli, Nicaragua; La Union, La Union, El Salvador; Lago de Izabal, Izabal, Guatemala; Mazatlan, Nayarit, Mexico), newly cut and burned stumps of many species produce leafy and growing suckers at any time during the year, and though their rate of growth is not high during the dry season, they do stay green when less than about 1 year old. Due to their slower rate of growth, however, the unoccupied swollen-thorn acacias following a fire at the beginning of the dry season have more chance to have fully insolated growth than they do if following a fire at the end of the dry season. Thus it is that fires following cutting are progressively less and less effective at removing the acacias as they occur earlier and earlier in the dry season (see discussion above). This is also the case when the vegetation is left standing since the bare area around occupied acacias is more effective in reducing the effect of the fire if the fire is less intense (due to greenness of the vegetation earlier in the dry season).

It is in ungrazed second growth that the apparently random pattern of the fire is of greatest importance. In uniform vegetation, the fire often leaves patches of unburned vegetation, or burns in strips. Those ant colonies whose queens reside in a shoot in the unburned area then move out into the fresh burn to occupy new suckers. This phenomenon was common around the margins of the burn described above in uncut vegetation. If the fire consumes the shoot with the queen in it, but leaves some of the acacias that contain auxiliary parts of the colony, these auxiliary units gradually die out, but during their several months of survival they protect the growing sucker. The above regime results in much variation in height and condition of swollen-thorn acacias in areas that are irregularly burned.

Scorched but unconsumed, dead swollen-thorn acacia shoots support a large population of wood-boring beetles and larvae; these dead shoots are only very weakly patrolled once the ant colony has moved into a new sucker from the old root crown. The larvae of a buprestid, *Chrysobothris* sp. near *basalis*, are very important in killing newly cut but unoccupied stumps throughout the range of swollen-thorn acacias. In frequently burned areas, populations of these beetles are exceptionally high due to their use of scorched shoots as larval substrate. In experimental plots cut during the dry season in the Temascal area, stump mortality due to the mining of these larvae ranged from 30% to 92% after 9 months. These beetles are active as ovipositing females during the dry season as well as rainy season and pose a serious threat to stumps cut at this time when other phytophagous insects are generally absent.

Repeatedly cleared 1- to 15-year-old regenerating vegetation with grazing and browsing (brushy pastures and crop-field regeneration throughout the swollen-thorn acacia range).—The major part of the swollen-thorn acacia population in Central America exists under these circumstances. As cattle density increases, species density and vegetational solidarity decrease, the result of selective feeding activities of the cattle, and trampling. Vines in the Convolvulacae, Pasifloraceae, Menispermaceae, and Papilionaceae are quickly eaten, and those in the Asclepiadaceae, Bignoniaceae, and Gleicheniaceae are trampled from between clusters of woody shrubs and herbaceous plants that are not eaten (e.g., *Jatropha urens, Acacia cornigera, Calliandra houstoniana, Bixa orellana, Bauhinia* spp., *Cassia* spp., etc.). Favored woody plants are eaten from between these clusters (e.g., *Guazuma ulmifolia, Enterolobium cyclocarpun, Cordia alliodora,* etc.). This opens the vegetation and allows grasses and herbs to grow between the clusters of woody vegetation. As the woody vegetation gets older, it is harder for the cattle to influence it, but they always affect seedling regeneration.

During the dry season, fires occasionally pass through these sites and burn only the areas between the clusters of trees and bushes. Gradually, through trampling and occasional burning of the margins of the clusters, the grassy areas become larger and the clusters smaller (Fig. 6). However, new clusters are constantly being formed in the grass, through the successful establishment of plants not eaten by cattle, and the woody vegetation around such plants gradually increases. Intensive grazing and browsing pressure can convert a solid second-growth plant community (1–2 m tall) to such a structure in one rainy season and the ensuing dry season. However, this process usually takes many years and the pasture represents a type of "permanent" community (e.g., around the Cotaxtla Experiment Station, Veracruz, Mexico; northwestern El Salvador; much of lowland Guanacaste, Costa Rica, especially in the area from Cañas to Liberia and Filadelfia). Each island of vegetation is a separate microsuccessional community, and these islands are only rarely destroyed in toto by fire in exceptionally dry years.

FIG. 6. A. Heavily grazed pasture 12.5 km south of Liberia, Guanacaste, Costa Rica, during the rainy season. *Acacia collinsii* shoots are scattered along the margins of the islands of vegetation. B. Same pasture as in A. above, during the dry season after the usual grass fire; note the patches of pale unburned vegetation around the bases of the vegetation islands.

Swollen-thorn acacias are found in both the grassy areas and in the woody clusters, or islands, of vegetation. When the woody vegetation is less than 8–10 years old, the acacias are often scattered through it as canopy members and emergents and are quite free from fires unless the pasture is ungrazed for a year and much grass fuel builds up. As these communities become older, the original acacias in the cluster die out and only seedlings and suckers around the margin become reproductively active. The bare basal circle around the base of these acacias often extends out into the grass and very often one colony occupies a number of acacias. Only rarely does a grass fire get hot enough to scorch the acacia across the 0.5- to 1.5-m radius of the bare basal circle.

Unoccupied swollen-thorn acacias growing in the open grass are in grave danger from the grass fires, which usually consume these young shoots. They are, however, free from shading and thus survive longer than in the woody vegetation provided there is no burning. If they are allowed to grow long enough for an ant colony to become established, or one moves in from a neighboring plant, and a basal circle develops, the colony generally survives a grass fire, even if the shoot is scorched. In areas such as southwestern Nicaragua, western Honduras, and eastern lowland Mexico, natural or planted grass pastures are frequently encountered that have almost no other woody plants besides swollen-thorn acacias and grass (Fig. 7). The acacias are either clustered or single, and often have very large and bare basal circles; they may be as old as 15 years and these old plants undoubtedly have weathered many fires.

Effect of fire on seed pods

The canopy of most swollen-thorn acacias is 3–20 m above the ground when seed pods mature

FIG. 7. Ungrazed grass pasture with almost no other woody plants besides *Acacia sphaerocephala* occupied by *Pseudomyrmex ferruginea;* each of the shoots that is heavily occupied has a basal circle. A fire passing through such a site would probably kill about two-thirds of the acacia shoots and one-third of the ant colonies. (December 1963, 30 miles south of Panuco, Veracruz, Mexico.)

(during the dry season, a year after flowering). In those species with indehiscent pods (*Acacia cornigera* and *A. sphaerocephala*), the pods hang on the tree until opened by a bird or the seeds are destroyed by bruchids. Fires which merely scorch the trunk or leaves generally do not damage the pods. The seeds will even germinate after the outer pod has been slightly charred. Seeds of *Acacia cornigera* germinate readily after a fire has passed over them on the ground, but need to be scarified with a knife or file beforehand. Dehiscent pods (e.g., *Acacia hindsii, A. collinsii*) present their seeds to birds, or they drop to the ground. In either case, the fire generally passes over them while on the ground and apparently has no effect on them.

Effect of fire on obligate acacia-ants

When the vegetation around an occupied swollen-thorn acacia is burning, the ants remain in the thorns. The walls of the thorns are 1–3 mm thick and do not catch fire readily, though once burning, they burn quickly. If a rapid fire is passing through, thorns must offer some protection from the heat to the ants. When a thorn is passed through an open flame, with a thermistor probe inside the thorn, it takes 5–20 sec for the temperature to reach 125°F., the air temperature at which the ants are driven out of their thorns on hot days. The ants do not hesitate to cross ash after the fire to communicate between two acacias (two parts of the colony).

When a fire is hot enough to kill the ant colony, but not to consume the acacia, other ants often use the thorns of the unoccupied acacia for domatia. *Crematogaster, Azteca, Solenopsis, Camponotus,* and other *Pseudomyrmex* are the most commonly encountered genera. These ants are sometimes removed by an invading obligate acacia-ant colony at a later date.

DISCUSSION

There are five immediate effects of a fire on an individual swollen-thorn acacia with its ant colony: (1) If neither the shoot nor the colony is killed, due to the size of the clear area around the acacia, the acacia then grows in a fully insolated position. (2) If the shoot but not the colony is killed, then the new sucker shoots are occupied by the colony and grow rapidly in the new regeneration cycle. (3) If both shoot and colony are killed, then the new sucker shoots must grow unoccupied for 7–9 more months (length of time necessary for a new colony to grow in situ), and most likely the acacia will not become reproductive. (4) If the shoot but not the colony is killed, the colony is still brought down to ground level and is much more susceptible to a fire during the following dry season. (5) Since the very young shoots with founding queens in them are usually destroyed in a fire, new queens must migrate into the site shortly after. Evidence of all these effects are often found in an area following an irregularly burning fire.

If the swollen-thorn acacia grows in clusters, with large obligate acacia-ant colonies, then the evergreen habit and freedom from other dry plant matter makes the cluster relatively free from fire damage. Other acacias not associated with ants in Central America generally are plants of less dense vegetation (drier sites) than the swollen-thorn acacias, and appear to be more fire hardy. This latter trait is associated with thicker bark (1–3 mm cork layer on the main trunk as contrasted with less than 0.5 mm cork layer on swollen-thorn acacias) and less heat-sensitive leafless branches during the dry season.

As one progresses from the most dense and complex regeneration (no grazing) to pure grass pastures, the acacia with a well-developed basal circle and clear area around the canopy becomes progressively less and less susceptible to fires. When the acacia is emergent or a member of a high canopy, fires passing underneath may or may not kill the shoot by scorching the trunk, but whatever the case, the ant colony is generally out of reach of the fire.

It seems likely that the major, and probably original, selective value of the obligate acacia-ants maintaining a basal circle and clear area around the acacia canopy was (1) to reduce shading in the dense second-growth plant communities in which the swollen-thorn acacias do so well, and (2) to reduce the rate of insect invasion from the surrounding vegetation (Janzen 1966*a*). Its behavioral basis appears to be simply a manifestation of the attack reaction for any foreign object on the acacia. However, with man's entrance into the Central American ecosystem, fire has become a commonplace phenomenon in lowland second-growth plant communities. The clear area around the acacia has a definite beneficial value to both the acacia and the ant colony in the face of fire, and it seems probable that some selection for enlargement and cleaning of the clear area has occurred. Likewise, there may be some selection for clustering of the acacias and the necessary subsequent evolution of multiple-queen colonies to avoid dilution of worker-patrolling efficiency through having too large an area for a single-queen colony to patrol.

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FACTORS AFFECTING THE DISTRIBUTION OF SHRUB LIVE OAK (*QUERCUS TURBINELLA* GREENE)[1]

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Abstract. The disjunct distribution, reproduction, and rooting habits of *Quercus turbinella* in the Arizona chaparral were studied on quartz diorite, sedimentary, and volcanic substrata. The oak was less dense on the sediments and volcanics than on quartz diorite. Lower densities on the bedded sediments resulted from restricted root penetration which prevented access to deep soil moisture; on the volcanic substratum heavy clay soils gave an overall poorer moisture regime than soils developed from the quartz diorite. Shrubs growing on the less favorable sedimentary and volcanic substrata probably were more susceptible to damage by drought and fire, and low mobility and low seedling production tended to eliminate the species from these areas. It is suggested that the *Q. turbinella* "islands" within large areas of grassland are relicts rather than evidence of invasion.

Introduction

Quercus turbinella, a small evergreen shrub, is a dominant member in much of the Arizona chaparral where it occurs in the semi-arid zone between the grassland and woodland types at elevations from 4,000 to 5,000 ft. Its distribution is often affected by factors that prevent its establishment on local grass-covered areas that are surrounded

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