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# Jacquinia pungens, a Heliophile from the Understory of Tropical Deciduous Forest

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## ABSTRACT

The general ecology of the understory shrub *Jacquinia pungens* is described, with special reference to its behavior of bearing leaves during the dry season (when the overhead forest canopy is deciduous) and being deciduous during the rainy season. The bush is restricted to those stages of lowland deciduous forest succession ranging from 10 to 50 years of age; it appears to starve to death or be competitively excluded from habitats where it is continuously isolated, and from older or wetter forest where it does not receive enough sunlight owing to light obstruction by the deep canopy during the dry season. As expected for a plant that is vegetatively active during the dry season, the plant is especially well protected from herbivores by needle-tipped leaves and toxic compounds in the foliage. Effectively, *J. pungens* has invaded a seasonally available prairie and has the bush life form characteristic of woody plants in such well-insolated habitats.

ALMOST ALL NON-RIPARIAN woody plants in Central American deciduous tropical forest bear leaves during the rainy season and are leafless or vegetatively dormant during the major dry season (January–April). An obvious way for a plant to avoid the intense interspecific vegetative competition of such a forest habitat is to bear leaves during the dry season and to be deciduous during the rainy season. A shrub, *Jacquinia pungens* A. Gray (Theophrastaceae), does this and is thus important in illustrating how the number of species in a habitat can be increased through the invasion by a species that uses resources unused by other members of the habitat.

*Jacquinia pungens* is an understory plant of Central American semideciduous and deciduous forests, where it may attain a density of 0.1 to 60 adult plants per hectare. The highest density is attained in 10- to 50-year-old deciduous second-growth regeneration (old corn fields, pastures, and lumbered areas). Occasional plants are encountered in open pastures; they are ignored by cattle, apparently owing to their needle-tipped and extremely bitter leaves. *J. pungens* and the equally well-protected swollen-thorn acacias (Janzen 1966) are sometimes the only leafy pasture plants avoided by cattle during a severe dry season.

The study reported here deals with a small portion of the large population here identified as *J. pungens*. Under contemporary agricultural disturbance of the dry Central American lowlands, this large population is essentially continuous from the Pacific coast of Panama up to lowland Sonora and northern Veracruz in Mexico. After perusing the large collection of *Jacquinia* in the United States National Herbarium, I would like to suggest that

names such as *J. pungens* A. Gray, *J. aurantiaca* Ait., *J. macrocarpa* Cav., *J. angustifolia* Oerst. (e.g., Standley 1924, 1938), *J. axillaris* Oerst., *J. caracasana* Knuth, *J. flammea* Millsp., etc., are probably all based on type specimens collected from this same widespread population. The range of variation in leaves, fruits, flowers, and habit in these specimens can be found in most subsets of the *J. pungens* population ranging over 100 miles of broken topography and rainfall regimes ranging from one to two meters per year. Willis (1966) notes some 50 species in the neotropical genus, but the Central American ones are probably mostly synonyms. These statements are not intended to apply to the many morphs of *Jacquinia* to be found on Caribbean islands.

## LEAF PRODUCTION AND PHENOLOGY

Adult and juvenile plants of *J. pungens* begin to drop their leaves approximately four weeks after the rains begin, and approximately two weeks after the overhead canopy has completely closed in. Leaf drop is nearly complete within eight weeks after the first heavy rains. In the Cañas area (Guanacaste Province, Costa Rica), for example, the first rains come in late April, and by the end of May the *J. pungens* range from nearly leafless to fully leafed. Nearly the entire population is almost completely leafless by the first week in July (table 1, fig. 1,b). Leafless shrubs are generally inconspicuous but are made obvious at this time by the circular patch of yellow-white dead leaves on the ground below; within about two months these have rotted beyond recognition. Because the shrub is leafless and therefore not noticed during the rainy season, yet obvious during the dry

season, it has earned the common Spanish misnomer of *siempre verde*.

The plants remain leafless until the rainy season tapers off, and leaf wilt and some leaf drop begins to occur in the forest canopy. Throughout lowland Guanacaste Province this means that the entire new crop of leaves (fig. 1,a) is produced in late November and early December, which is about five months after leaf drop. The leafless *J. pungens* receive a maximum of 20 to 200 foot-candles of light in their most heavily populated habitats during these five months; during the dry season, light intensity in the same crowns ranges from 200 to 6000 foot-candles in late morning on clear days (table 1).

Almost all branch elongation occurs at the time of new leaf production. Only rarely is more than one consecutive new long shoot produced per branch end in a given year, though several long branches often radiate from one cluster of leaf axils. New branches range from 0.1 to 15 cm in length, with two peaks in length frequency. The shorter branches, with an average length of about 0.5 cm, bear one to seven leaves in a tight whorl ( $\bar{X} = 3.6$  leaves for 140 short branches from one plant) and do not expand the volume of the crown. The long branches, with an average length of about seven cm, bear 14 to 15 leaves arrayed along their distal half ( $\bar{X} = 9.3$  leaves for 163 long branches). It is these branches that are responsible for a slight annual increase in crown volume and height. When the 303 branches sampled from this adult plant (fig. 1,a,b) are pooled, they yield an average of 7.34 leaves per new branch (s.d. = 3.30). The new long branches are almost all on the upper surface of the canopy; the range of three to 74 per adult plant in table 1 is representative of the general population.

Flower buds are evident within about one month after leaf production, and nearly all flowers are open within two months (fig. 2,a). The flowers are stiff, waxy, orange-red, and mildly fragrant. They are probably pollinated by hummingbirds. However, during many days and nights of working around these plants, I have observed only two hummingbird visitors and no other potential pollinators. One of these birds visited upwards of 30 flowers on three bushes in the space of a few minutes. As can be seen by comparing the upper and younger flowers in figure 2,a with the lower and older flower, the flowers are not self-pollinated; when the anthers first open, they cover the stigma (the hummingbird's upper bill would then carry pollen at its center). After several days, the anthers move outward and press the pollen-bearing surfaces against the corolla, thus exposing the stigma so as to con-

tact the bird's bill in the same place as the anthers did.

Larger *J. pungens* generally bear more flowers than smaller ones, but there is great variation in the size of the flower crop (table 1). The total number of flowers for an average-sized and shaded shrub (normal habitat) ranges between 100 and 900. In 1969, each adult plant in table 1 set 0 to 15 fruits (fig. 2,b). The low number could be due to lack of cross-pollination (hummingbirds have become extremely rare at this site during the past two years). However, the following observation suggests it is more likely due to a lack of sufficient food reserves to mature the fruits. A four-meter *J. pungens*, with a crown volume of about four times that of the largest tree in table 1, bore 70 fruits in 1969 and was almost in the center of the plot.

Green fruits remain on the tree throughout the dry season and at least three months of the rainy season. Turning sweet during the last three months before the end of the rainy season, the orange fruits are apparently eaten by birds or rodents.

## LIFE FORM

No matter how tall or old, *J. pungens* has a shrub life-form with heavy multiple trunks and branches (fig. 1,b; table 1). This is in strong contrast to adjacent understory woody plants of other species. These characteristically have a few layers of a few large leaves (adults), or are tall and thin "poles" (saplings of canopy-member species). The spherical and bushy life-form of *J. pungens* is very similar to that of fully insolated woody shrubs in arid regions, or to the swollen-thorn acacias that have little lateral canopy competition because of their occupant ants' pruning activities on neighboring plants (Janzen 1966, 1969a). *J. pungens* lives in a seasonally available savanna, as far as insolation is concerned. Just as with other woody plants that are normally fully insolated, it rarely grows more than four meters tall.

The lateral roots of *J. pungens* do not grow into the top 20 to 50 cm of the soil, where most roots of other equal-sized woody plants are encountered. The taproot extends downward at least 0.5 to 1.5 m with less than a 25 percent decrease in diameter. The first few lateral roots are found below this depth, penetrating the sticky gray clay that commonly underlies the rich surface soil of flatland Central American deciduous forests. The taproot penetrates to at least three meters for adult plants two meters tall. This type of "root canopy" is not surprising since the plant is photosynthetically dormant when surface moisture is available; it appears that there is almost no root competition between *J. pungens* and adjacent understory plants.

TABLE 1. Ecological statistics for 36 adult and subadult *Jacquinia pungens* growing under 15- to 30-year-old deciduous forest.<sup>a</sup>

Plant number <sup>b</sup>	Number flowers 1970	Number leaves		Foot-candles at bush top		Height uppermost node (cm) 1969	Number new elongating branches 1970	Number major stems 1969	Circumference tallest stem 10 cm above ground 1969 <sup>d</sup>	Number of vines on bush <sup>e</sup>
		1969	1970	1969 <sup>c</sup>	1970					
1	262	0	2320	100	5000	137	54	4	106	5
2	0	0	760	60	4500	135	17	2	66	5
3	524	0	7870	30	3000	185	67	3	259	5
4	348	0	5870	60	4000	145	59	5	96	3
5	38	0	1260	20	800	85	21	1	?	0
6	421	0	1820	60	3500	167	49	1	?	3
7	73	0	140	50	3000	61	22	3	?	0
8	38	1	1360	70	4500	167	52	3	111	3
9	0	1	1840	80	6000	116	52	3	91	1
10	332	1	4220	50	1500	181	74	4	135	4
11	48	2	730	60	3000	106	3	2	59	0
12	43	3	1490	100	2000	162	29	4	88	7
13	0	4	1860	50	6000	139	56	4	75	2
14	0	6	540	70	600	133	16	1	60	3
15	27	10	820	60	500	135	18	3	47	3
16	57	13	760	55	5000	72	38	3	?	0
17	98	19	400	35	2000	82	18	1	?	0
18	0	20	50	30	2000	64	4	1	31	0
19	134	21	4400	60	2000	173	37	7	62	4
20	148	27	1820	30	500	140	51	1	?	0
21	0	31	1360	25	4000	62	12	2	?	0
22	91	34	780	100	4500	69	21	2	?	0
23	0	38	80	20	6000	28	5	6	?	0
24	43	42	730	35	800	85	31	1	?	0
25	53	43	910	70	3500	80	30	1	?	0
26	0	79	1690	110	4000	163	53	3	123	1
27	0	93	1290	110	400	112	20	3	45	1
28	225	103	2410	110	2500	176	86	1	120	3
29	589	115	1530	200	1500	219	43	4	100	3
30	0	136	170	80	200	41	3	2	16	1
31	391	147	2210	65	4500	139	18	3	68	3
32	86	386	1540	70	3000	133	45	2	108	3
33	150	427	2940	40	1500	185	63	7	123	4
34	75	527	1850	100	3000	141	37	5	92	5
35	0	583	1030	105	3000	175	56	2	86	5
36	198	2996	1470	150	400	195	34	3	82	3

<sup>a</sup> Disturbance ranged from light selective to heavy logging 300 m east of main ranch house, Finca La Pacifica, 7 km northwest of Cañas, Guanacaste Province, Costa Rica. Recorded on July 9, 1969 (rainy season) or February 12, 1970 (dry season).

<sup>b</sup>  $6 \times 10^3$  foot-candles in adjacent full insolation, 10:30–11:30 a.m.

<sup>c</sup> Number of different major vine branches using bush as a standard.

<sup>d</sup> Circumference used owing to irregular shape of cross-section.

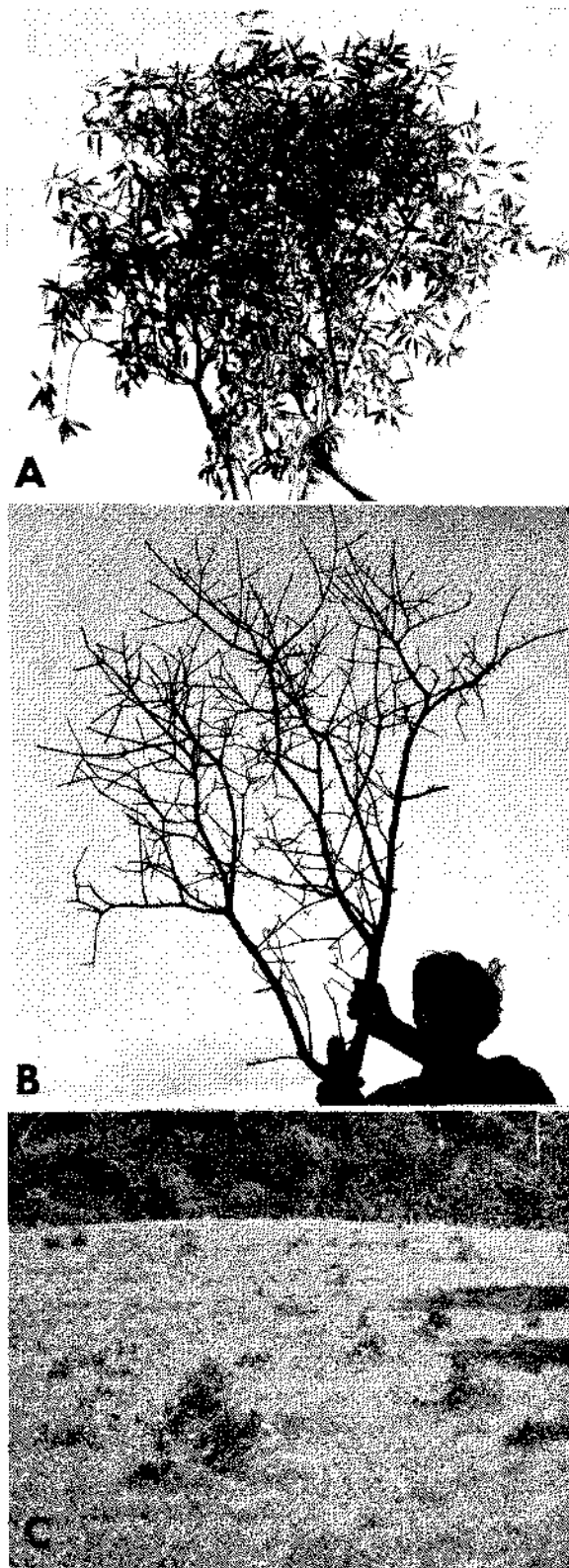
<sup>e</sup> Plants chosen by picking a 1–2 acre area and censusing all *J. pungens* present.

## FOOD STORAGE

Just as with plants that are dormant during the dry season, *J. pungens* must store enough energy reserves to carry it through the inimical (rainy) season and produce a leaf crop in November–December. At the time of leaf drop (early rainy season), the twigs, branches, trunks, and thick taproot of *J. pungens* have an extremely high starch content. Dilute solutions of I<sub>2</sub> in KI stain at least 90 percent of the surface area of cross-sections very dark black, and the starch granules are obvious in parenchymatous cells. About one month after the new crop of leaves and at the time of first flower production (January of the following year), cells throughout the plant stain only pale gray with very strong KI; obvious starch granules are gone from the cells. The plant reserves are probably lowest at this time.

## HABITATS OCCUPIED BY *J. PUNGENS*

The fate of *J. pungens* in various habitats illustrates the many environmental challenges that are involved in controlling its relative abundance. *Jacquinia pungens* is absent as a reproducing adult from microhabitats that are insulated year-around. This can be partly explained by examining pasture habitats. When the forest is cut such that *J. pungens* adults are insulated year-around, the top of the bush dies back at such a rate that in about three years there are only a few 10- to 50-cm sprouts remaining of a once-large bush. The upper branches appear to be starving to death. At the time of leaf drop, these insulated bushes appear to have the same amount of starch in them as their shaded neighbors. About 2.5 months later tissues of the insulated upper branches show virtually no staining reaction with



iodine, while tissues from *J. pungens* branches in the adjacent forest stain dark black. The midday air temperatures in the open are only 1 to 3° C higher in the open than in the shade. However, the insolated branches of *J. pungens* may attain surface temperatures of 33 to 38° C during the five or six midday hours; while shaded branches in the adjacent forest are at air temperature (27 to 30° C) during the same hours. It is possible that the metabolic rate in the insolated branches is so high that they are depleted of food reserves before the time of new leaf production.

When the *J. pungens* bushes are cut with the forest, the effect on the population depends on the time of year. If cut shortly after the leaf and flower crop has been produced, *J. pungens* disappears from the habitat. Not only are its reserves for the production of a new canopy extremely limited at this time, but most of its woody neighbors will respond to the cutting with many leafy suckers that heavily shade the new *J. pungens* sprouts. The other species of plants are operating on the reserves that had been stored for dry-season maintenance metabolism, flowering (Janzen 1967), etc. If cut at the beginning of the rainy season, *J. pungens* generally persists in the community (fig. 1,c) for two to 10 years, especially if the site is heavily grazed by cattle. The *J. pungens* stumps usually remain dormant through the rest of the rainy season and then sprout vigorously at the onset of dry weather. However, the effect of direct insolation during the following rainy season, coupled with poor photosynthesis during that first dry season (owing to the common failure of other woody plants to drop their foliage from young sucker shoots), is probably what causes the eventual death of the branches. The more heavily grazed the site, the more photosynthesis can occur during the dry season. However, grazing also leads to more direct insolation on *J. pungens* during the rainy season.

In pastures, the 10- to 50-cm sucker shoots of *J. pungens* retain their leaves during the rainy season, so that insolation at this time may be of value during the very early stages of succession. However, by the second rainy season they adopt the adult behavior of rainy-season deciduousness.

Reproductive adults of *J. pungens* are totally

FIGURE 1, a-c. a. Representative crown of *Jacquinia pungens* (at least eight years old) during the dry season. b. Same crown as in a, but with 1970 leaves and twig growth removed to simulate rainy season (1969) appearance (a and b are to same scale). c. Lightly grazed pasture dotted with one-year-old sucker shoots of *J. pungens* from old root stock left when land cleared eight years previously. All photos, February 13, 1970; 7 km northwest of Cañas, Guanacaste Province, Costa Rica.

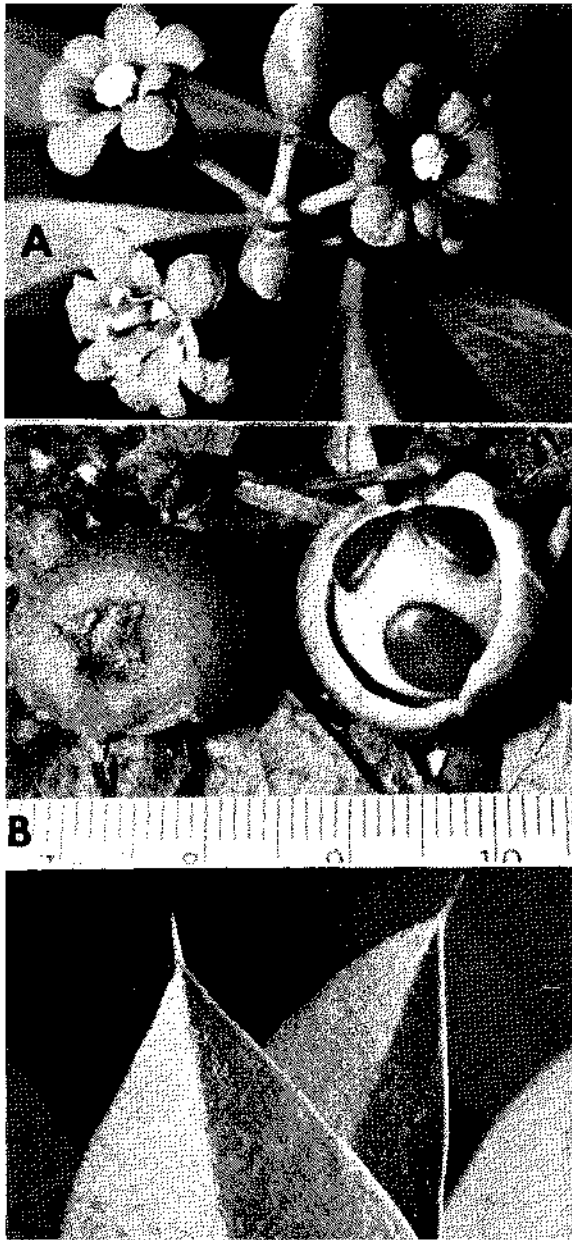


FIGURE 2. *a-c.* *a.* Upper two flowers of *J. pungens*, younger, with anthers closed over stigma in center of flower; lower flower, older, with anthers flexed outward and stigma exposed. *b.* Broken fruit of *J. pungens* with mature seeds partially implanted in sweet pulp (hull on left). *c.* Needle tips on leaves of *J. pungens*. All photos same site and date as in figure 1.

absent from evergreen riparian forest. Seedlings are very rarely encountered along the interface of hillside deciduous forest with riparian forest; they mature only when under large trees that are deciduous, even if growing on moderately wet soil [e.g., under *Enterolobium cyclocarpum* (Jacq.) Griseb.].

Adult *J. pungens* are generally present but extremely rare in totally undisturbed deciduous forest. These scattered plants are usually in the spaces left by old windthrows that involved several large trees, or under a major dip in the general canopy surface. Under fully developed deciduous forest canopies, the increase in insolation during the dry season is not nearly as striking as in 10- to 50-year-old regeneration (as in table 1). The complex of branches and vines, coupled with occasional evergreen trees (e.g., *Hymenaea courbaril* L.), obstructs much of the sunlight. The large old trees may also provide severe root competition at the normal depths of *J. pungens* taproots.

The effect of fire is strongly dependent on its periodicity and on habitat structure. Annually burned sites are lacking *J. pungens* unless the fire comes just before the rains; in the latter case, enough reserves have been stored to allow stump sprouts. The grasses in annually burned sites die back during the dry season so that the sprouts are insulated (in contrast to the woody succession following widely spaced fires). However, these plants never attain reproductive status (fig. 1,c). When ground fires pass under deciduous forest, the pre-fire density of adult *J. pungens* appears to be regained within about five or six years. Understory vegetation does not sprout heavily after fire, and thus provides little dry-season competition for the maturing *J. pungens* stump sprouts.

## VEGETATIVE DEFENSES

Being green throughout the dry season, *J. pungens* may be expected to exhibit substantial defenses against leaf eaters. The tips of the stiff sclerophyllous leaves are armed with an extremely sharp spine (fig. 2,c). With the multiple layers of inflexible leaves pointing in all directions (fig. 1,a), the plant is effectively a cactus with spines five to 10 cm long. Neither tame brocket deer (*Mazama americana* Erxleben) nor white-tailed deer (*Odocoileus virginiana* Zimmermann) will eat the leaves of *J. pungens*, even if the spines are clipped from the leaf ends and the animal has starved for a day (brocket deer test done in Veracruz, Mexico, June 1964; white-tailed deer test done on Finca La Pacifica, 7 km north of Cañas, July 1969). The hispid cotton rat (*Sigmodon hispidus* Say and Ord) will not eat the leaves even if starved for two days (test in Veracruz, Mexico, June 1964). The leaves taste extremely bitter and are ground up for fish poison in lowland Veracruz, Mexico. Standley (1924, 1930) implies that this is a generic trait. Of significance in recognizing the toxic compound(s) as primarily defensive is the observation by Mexican fishermen that the freshly dehiscid

leaves lack the toxic principle, indicating clearly that it is not a waste product to the plant.

Being the only member of its family in the habitat, there is not a large community of insects on congeneric species to serve as potential herbivorous threats. The entire leaf crop of many individual bushes often remains *totally* undamaged throughout the dry season. This is so in spite of the fact that the early part of the dry season has a large community of insects that pass the dry season as active leaf-eating adults. They use a wide variety of "greenery" for water and some nutrition (insects in reproductive diapause are generally much less specific about their host plants than are reproducing adults). In striking contrast to *J. pungens*, adjacent woody plants of many species characteristically suffer heavy damage to any new foliage produced during the early part of the dry season.

An unidentified moth larva, that eats the epidermis and adjacent cells off the leaf, is found on about one out of every five bushes. It normally destroys four to 10 leaves while maturing. It is probably host specific to *J. pungens*, at least on a seasonal basis.

## SEED DEFENSES

The immature fruits, green throughout, taste "soapy-bitter" like the leaves, but with much greater intensity. Just touching the juices of a crushed fruit to one's tongue is an extremely unpleasant experience. Standley (1924) reports their use as fish poisons in western Mexico. *J. pungens* is among a minority of tropical woody plants in having virtually no predation on its immature or newly matured seeds by insects or vertebrates. Of 143 full-sized fruits, with nearly mature seeds borne by 81 plants in early June, 1969 (in the general area of the *J. pungens* in table 1), only one had been bored into. This was done by the same caterpillar mentioned above that feeds on the leaves (it killed three of the seven seeds in the fruit). Once mature, however, the fruit turns yellowish and the inner pulp is then extremely sweet. The hard seeds (fig. 2,b) appear as though they would pass through a bird gut undamaged. They germinate in about 14 days without scarification. Green fruits are rejected by tame pacas (*Cuniculus paca* L.), squirrels (*Sciurus variegatoides* Ogilby), coatis (*Nasua narica* L.), white-tailed deer (*Odocoileus virginiana*), and agoutis (*Dasyprocta punctata* Gray); all of these are potential predators on green fruits in the usual habitats of *J. pungens*. They are also potential seed-dispersal agents inasmuch as they eat fruits readily. The rodents either spit the seeds out or appear to swallow them intact.

Since there is almost no seed predation, *J. pungens* places as many viable seeds in the habitat as do many other plants of similar size, but it only produces a tiny fraction of the number of seeds that they do. A neighboring representative of *Acacia collinsii* Safford (bird dispersed with seeds almost identical to those of *J. pungens*), two meters tall, loses about 95 percent of its seed crop to bruchid beetle larvae that eat seeds. Its total seed crop usually ranges between 500 and 3000, and escape is by predator satiation (Janzen 1969b). *J. pungens* bushes of equal size produce about nine to 90 seeds (based on a sample of 102 fruits of *J. pungens*, with average of 9.56 seeds per fruit, s.d. = 2.76). Seven *J. pungens* seeds had an average weight of 0.0598 grams.

## DISCUSSION

In contrast to some herbaceous plants of temperate hardwood forests which carry out most of their photosynthesis during the few spring weeks before the overhead canopy leafs out (e.g., Sparling 1967), *J. pungens* is restricted to an intermediate stage in forest succession. Even in undisturbed forest, reproducing adults are limited to micro-successional communities associated with breaks in the general canopy. Most of the contemporary population is to be found in 10- to 50-year-old secondary succession. Prior to the introduction of European agriculture and lumbering methods, *J. pungens* was probably much rarer than now. Not only was there much less total acreage of suitable habitat, but, since it was highly fragmented, many seeds probably failed because they had landed in forest unsuitable only in respect to successional stage. In the large tracts of rather uniformly disturbed forest presently common in the dry lowlands of Central America, a much higher fraction of the seed crop will land in suitable habitat. In view of the lack of competition with other plants, *J. pungens* could be expanding its population at close to an exponential rate in appropriate habitats. It is relevant that there is no empirical evidence that predation or parasitization rates by herbivores will increase with increased density of adult *J. pungens* or their fruit crops (cf., Janzen 1970 for a discussion of the more usual opposite case).

There is one major unknown in the system, however. The number of 20- to 50-cm-tall seedlings in habitats containing reproductive adults is easily less than 1 percent of the viable seeds that these adults have produced during the previous three years. Something is killing a large number of the very young seedlings. Older seedlings and adults appear to be essentially immune to predation, parasitization, and disease. It is perhaps relevant that *J. pungens* seedlings grow extremely slowly. Well-watered, un-

crowded, and fully insolated seedlings in the greenhouses of the University of Chicago grew 0.5 to 3 cm tall in five months following germination. It may well be that seed reserves are not adequate for the deep taproot development that must be needed to get through the first dry season. In this case only the occasional seed that landed over a very local rise in the water table would survive. Temporal habitat heterogeneity could help here; the seedling could pass its first dry season in very local heavy shade, but then grow out of it in later dry seasons. The ideal test site would be one that had been held at an intermediate successional stage for many years. It is significant that the highest density of *J. pumgens* appears to be in the old brush lots with scattered large trees.

We may visualize *J. pumgens* as having invaded/evolved into its present temporal and spatial habitat from either of two quite different habitats. It could have been an ordinary deciduous forest understory shrub that retained its leaves longer into the dry season (accompanied by sclerophylly, needle-tipped leaves, very toxic defensive compounds). When it reached the point where further specialization for a leaf active in the dry season (desiccation resistant, requiring high insolation) made that leaf uneconomical during the very heavily shaded rainy season, a mutant with rainy-season leaf drop was favored. Or, the plant could have produced its leaves progressively earlier before the first rains and then dropped them when the rains finally came. Many trees leaf out one to four weeks before the rainy season begins.

On the other hand, it could have been a dry-land plant that found water conditions during the dry season in deciduous forest to be roughly equivalent to wet-season conditions in drier areas. Here again, the selective pressure for leaf drop would be the inefficiency of a heavily shaded leaf that is specialized for high insolation.

The distribution of other members of the genus is not helpful in deciding which of these two alternatives to choose. The possible other Central American species are either from very dry areas such as the Yucatan peninsula or wet areas such as Panamanian wet forest. The many Caribbean island species could be derived from a single emigration of *J. pumgens* from the Central American mainland, or by island-hopping from Trinidad by one of the South American species so similar to *J. pumgens*. On the other hand, the whole complex could have evolved first as dry-land Caribbean endemics, one of which later immigrated to Central or South America.

It is not clear why the leafing behavior of *J. pumgens* is not displayed by many species of deciduous forest understory plants, just as there are many species of springtime herbaceous plants in temperate hardwood forests. All other plants in the forest occupied by *J. pumgens*, with the exception of an occasional columnar cactus, have their major vegetative growth period during the rainy season. A few of these photosynthesize during the dry season, but this likely produces only a small fraction of the annual photosynthate (e.g., green-barked *Bursera simaruba* (L.) Sarg.; evergreen *Hymenaea courbaril*, *Curatella americana* L., *Byrsonima crassifolia* (L.) Rich., *Acacia collinsii*, etc.).

*J. pumgens* affords an opportunity to touch briefly on several general questions of community structure. Should *J. pumgens* be regarded as a member of the general community if its presence has little or no effect on the presence of other plants in the habitat? At best it is a peripheral member, inasmuch as its flowers may support a tiny part of the hummingbird complex and frugivorous bird or mammal complex. We may also ask if the resources it uses are really unavailable to the other plants in the habitat. In one sense they are available, just as all resources are potentially available to all organisms in the community. However, in specializing to harvest, sequester, and disperse any resource, the organism automatically cuts itself off from other resources. In this sense then, all other plants in the habitat are too specialized to be able to use the resources that *J. pumgens* harvests. Finally, we may ask if this is still the same community if *J. pumgens* is added to the species list for this spatial/temporal habitat. A habitat is probably about as similar to the original habitat (pre-*J. pumgens*) after the addition of this new species as is possible, and clearly represents the opposite end of the gradient that terminates with the extreme change that would be brought about by adding another large tree species such as *Enterolobium cyclocarpum* to the general canopy.

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## LITERATURE CITED

- STANDLEY, P. C. 1924. Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. 23(4):849-1312.
- . 1930. Flora of Yucatan. Publ. Field Mus. Nat. Hist. Bot. Ser. 3:157-492.
- . 1938. Flora of Costa Rica. Publ. Field Mus. Nat. Hist. Bot. Ser. 18:1-1616.
- SPARLING, J. H. 1967. Assimilation rates of some woodland herbs in Ontario. Bot. Gaz. 128:160-168.
- JANZEN, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249-275.
- . 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620-637.
- . 1969a. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology 50:147-153.
- . 1969b. Seed eaters versus seed size, number, toxicity, and dispersal. Evolution 23:1-27.
- . 1970. Herbivores and the number of tree species in tropical forests. Amer. Naturalist 104: (in press).
- WILLIS, J. 1966. A dictionary of the flowering plants and ferns (Revised by H. K. Airy Shaw). University Press, Cambridge.