

# **Butler University Botanical Studies**

Volume 14

Article 11

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John Pelton

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# **Recommended** Citation

Pelton, John (1964) "A Survey of the Ecology of Tecoma stans," *Butler University Botanical Studies*: Vol. 14, Article 11. Available at: http://digitalcommons.butler.edu/botanical/vol14/iss1/11

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# Butler University Botanical Studies (1929-1964)

Edited by

J. E. Potzger

The *Butler University Botanical Studies* journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana's vegetation in past decades. Authors were Butler faculty, current and former master's degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler's first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal's publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor's degrees and 75 master's degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner, included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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#### A SURVEY OF THE ECOLOGY OF TECOMA STANS

JOHN PELTON

Butler University, Indianapolis, Indiana

#### ABSTRACT

Pelton, John F. (Butler University, Indianapolis, Indiana). A survey of the ecology of Tecoma stans. Butler U. Bot. Studies 14(2):53-88. Illus. 1964 .- Tecoma stans (L.) Juss. ex H.B.K., a shrub or small tree in the Bignoniaceae, is a widely distributed polymorphic complex of the Western Hemisphere tropics and subtropics, and is commonly planted as an ornamental throughout the tropical world. Winter temperature limits its poleward distribution. The species is characteristic of rocky slopes, often limestone outcrops, but also alluvial and other substrata as long as drainage is excellent. In arid regions it occurs in climax xerophytic shrub or thorn forest communities, while in humid areas it is common mainly in deforested and other disturbed sites since it behaves as a heliophyte. The large yellow funnel-form flowers are pollinated by hummingbirds and perhaps also by some insects. The sensitive lobed stigma may favor cross-pollination, and neither dichogamy nor autogamy are usually shown. Extra-floral calyx nectaries which attract ants seem ineffective against corolla-base piercers. A low percentage of fruit is commonly set, drought and pollination failure probably being contributing factors. The pendant capsules contain many paper-thin wind-dispersed winged seeds, which have moderately high viability undiminished even after four years, and no dormancy. The strongly tap-rooted seedlings are often abundant in disturbed sites. The leaflet size class is microphyllous, and the species varies from evergreen to winter-deciduous. It responds to drought partly by leaf abscission, but also by survival of prolonged permanent wilting, unusual for a thinleaved mesomorph. Stump-sprouting is vigorous following cutting or fire, and browsing occurs in heavily-used pastures. No insect parasites or diseases are generally limiting.

Tecoma stans (L.) Juss. ex H.B.K. is a shrub or small tree in the Bignoniaceae having a wide natural distribution in tropical and subtropical parts of the Western Hemisphere. Certain observations made primarily in the summer of 1956 in Jamaica are reported below, together with a review of the literature concerning this species.

Tecoma stans is commonly planted as an ornamental for its yellow flowers and pinnate foliage in warmer climates throughout the world. In Florida, Bailey (1930) remarks, "The value of this shrub . . . cannot be overestimated," and from Texas to California, this species is ". . . classed among the ten best southwestern shrubs by many . . ." (Van Dersal 1942). In Mexico the flowers yield honey, the roots a type of beer, and the plant has supposed diuretic, antisyphilitic, vermifuge, and especially anti-diabetic properties (Guerra 1946; Martinez 1933, 1958; Standley 1926, 1928; Uphof 1959). The anti-diabetic features, however, have recently been experimentally discounted (Miranda 1952; Pesman 1962). The plant is apparently not used medicinally by the negro population in Jamaica (Beckwith 1927). Although the wood is of no commercial value it was formerly used by the Indians in northern Mexico for making bows (Standley 1926), and even now in the South Pacific as stakes upon which to train the vanilla vine (Wilder 1931), and the flexible branches are used in basketry in Peru (Macbride 1961). In the United States, *T. stans* is eaten by mountain sheep (*Ovis canadensis* Shaw) but not by livestock (Dayton 1931; Van Dersal 1938). Observations in Jamaica indicate that *T. stans* is frequently cut, probably mostly for firewood, charcoal, or posts, is moderately browsed by cattle, but uncommon in cultivation.

#### SYSTEMATICS

The systematics of the genus *Tecoma*, as well as of *T. stans* itself, has been subject to diverse interpretations. The most recent world-wide monograph of the Bignoniaceae (Schumann 1895) refers *T. stans* to *Stenolobium* D. Don, not Benth. (Tribe Tecomeae). Although *Stenolobium* is still commonly used by many authors in this sense in order to distinguish the predominantly pinnate-leaved species of *Tecoma* from the palmate-leaved members, the usage is apparently incorrect since *Tecoma* Juss. was emended by Humboldt, Bonpland, and Kunth to exclude digitate types, which are now referred to *Tabebuia* Gomes. (Shinners 1961). Although this interpretation is perhaps the more common among modern authors, the distinction primarily on the basis of leaf compounding has been judged to be rather artificial by Macbride (1961).

By this restricted definition, *Tecoma* Juss. emend. H.B.K. is a Western Hemisphere tropical and subtropical genus of about 16 species of shrubs, of which *T. stans* is the type species. A section, *Eulecoma*, containing *T. stans* and four or five other species has been erected by Melchior (1941). Yet even within this section the taxonomy remains confused and the species are poorly known. This section is best developed in the Andes from Colombia to northern Argentina. The most widely distributed member is *T. stans*, a polymorphic complex often segregated into several species.

What is here referred to as T. stans var. angustatum Rehder (T. incisa (Rose & Standley) I. M. Johnston, T. tronodora (Loes.) I. M. Johnston, T. stans var. apiifolia? Hort., ex A. DC.) has a distinctive range in the United States and northern Mexico with very little overlap with other subspecies (Johnston 1940). It is a dwarf form with narrow incised leaflets among several differences. South of this subspecies (a more appropriate concept here than variety) well into South America are two recognized but intergrading types, the nearly glabrous T. stans var. stans, which seems to be equivalent to var. pinnatum Seeman, and the villous-leaved T. stans var. velutina A. DC. (T. mollis H.B.K., at least in part). Although geographically sympatric in much of their range, there seems to be some altitudinal isolation between T. stans var. stans and var. velutima (see under "Range" below). An additional form has been described from northern Argentina as Stenolobium stans var. multijugum by Fries (1903), apparently incorrectly cited as S. sambucifolia var. multijugum R. E. Fries by Macbride (1961). The latter author, nevertheless, agrees with both Fries (1903) and Herzog (as quoted by Macbride) that this is a form of T. stans. On the other hand, Macbride concurs with Melchior (1941) that T. castaneifolia (D. Don) Melchior, sometimes regarded as a variety of T. stans, probably deserves specific rank. But at least in Peru, Macbride feels that T. stans, T. sambucifolia H.B.K., and T. weberbaueriana (Kränzl.) Melchior are only questionably distinct from one another, and Herzog (1916) agrees with respect to at least T. stans and T. sambucifolia. The need for field studies to clarify the confused taxonomy of Tecoma has been mentioned by Sandwith (1954a), an opinion shared by Macbride (1961). A personal examination of nearly 300 specimens verifies the variability within the T. stans complex and the need for specialized taxonomic approaches.

Both var. stans from Cuba and var. angustatum from Texas are reported to have a chromosome number of 2n = 40 (Bowden 1945), as does *T.* sambucifolium H.B.K. from Peru (Diers, cited in Cave 1962). Although natural hybridization between *T. stans* (in the broad sense) and other species has not been recorded, a reputed artificial hybrid between *T. stans* var. velutina and *Tecomaria capensis* Seem. is in the horticultural trade under the name of *Tecoma imithii* W. Wats. Although this "hybrid" is supposed to come true from seed (Bailey 1930; Chittenden 1951), the chromosome number (2n = 36 in Darlington and Wylie 1956) does not suggest that this is a fertile allotetraploid between *Tecomaria capensis* (2n = 34) and var. velutina, if this latter variety is also 2n = 40. Furthermore, the originator of the hybrid states unequivocally that it does not come true to seed, and that nearly every gradation between the parental types are shown (Smith 1894).

The fact that the greatest variability in *Tecoma* is in the Andean region of tropical South America suggests that this is where the group may have originated. Only one subspecies, var. *stans*, seems to be represented in the West Indies, and the lack of differentiation of the populations among the variou, islands and between the islands and the mainland indicates that this form has not been present for a very long period in the West Indies. *T. stans* var. *apiifolia* (Hort.) ex. A.DC. has apparently been collected from Trinidad (Sandwith 1954b; Seeman 1863) and Guadalupe (De Candolle 1845), but these anomalous collections perhaps originated from cultivated material

of var. angustatum introduced from northern Mexico. Specimens of var. apiifolia have not been seen.

Nevertheless, variability of an apparently genetic nature was observed even in the Jamaica material alone. Length of calyx was variable, and at one locality stump sprouts with bluish-green foliage were intermixed with similarly cut shrubs having the normal yellow-green sprouts on the same substrate. One plant had a pubescent calyx and leaf undersurface, unlike var. *stans*. Variety *velutina* has pubescent leaves but only about 10% of the examined specimens had pubescent calyxes. The discovery that a specimen of var. *velutina* had been planted in the Hope Botanical Gardens many years ago suggests that this unusual specimen is either an escape or a backcross or hybrid segregate from the plant of var. *velutina* and the locally abundant indigenous var. *stans*, since the Botanical Gardens are only 2.5 km distant from the anomalous shrub. Vouchers for this and several other populations of *T. stans* have been deposited in the herbaria of the Institute of Jamaica and of Butler University.

The several varieties and subspecies of T. stans doubtless in large part represent ecological races and explain the wide geographic and habitat range of this collective species. For example, there is evidence that cold-hardiness increases in the species with higher latitudes, and that this is correlated with morphological differences, as mentioned under "Climate."

The generic name *Tecoma* comes from Tecomaxochitl, an Aztec name of uncertain application but certainly not used for any *Tecoma* or even Bignoniaceae (Bailey 1883; Shinners 1961); "*stans*" presumably refers to the upright growth of the stems, although spreading growth is also shown. Because of its uses and cultivation throughout the tropical and subtropical world, colloquial names for the species abound in numerous tongues. Standley (1926) lists about 40 such names and the localities where they are used, while Record and Hess (1943) give nearly 60. Kelsey and Dayton (1942) recommend "Yellowtrumpet" as the standardized vernacular English name, but perhaps more common are "Yellow Blossom" and "Yellow-elder" (in reference to the foliage).

#### DISTRIBUTION

## Range

For general orientation, in Fig. 1 is given the approximate natural distribution of T. stans, broadly interpreted as a collective species, based upon the literature and an examination of numerous specimens. A more precise map, distinguishing subspecies and related taxa, especially in South America, must await a critical taxonomic study, not here attempted, of the section *Eulecoma*. The major references consulted in preparing the map which in-

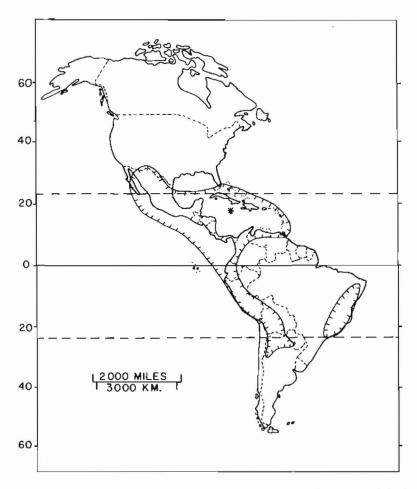


FIG. 1. Generalized map of the natural range of the T. stans complex. Jamaica is indicated by the asterisk.

clude this species within their range are as follows: GENERAL—Schumann 1895; Seeman 1863. UNITED STATES—Benson and Darrow 1945; Johnston 1940; Kearney and Peebles 1942; Macdougall and Sperry 1951; Small' 1913a; Tidestrom and Kittell 1941; Wooton and Standley 1913, 1915. MEXICO AND CENTRAL AMERICA—Brandegee 1891a, 1891b; Calderon and Standley 1941; Durand and Pittier (1891); Gentry 1942, 1949; Goyena 1911; Hemsley 1879-88; Johnston 1924, 1940; Martinez 1958; Millspaugh 1895, 1896; Miranda 1952; Seibert 1940; Shreve 1937, 1939, 1951; Standley 1926, 1928, 1938; Wiggins (in press). SOUTH AMERICA—Bureau and Schumann 1897; Fries 1903; Grisebach 1874;

Herzog 1916, 1923; Hieronymus 1882; Knuth 1926-28; Macbride 1961; Pittier de Fábrega 1939; Schnee 1960; Warming 1892; Weberbauer 1945. WEST INDIES---Anonymous 1893; Arnoldo 1954; Beard 1946, 1949; Boldingh 1909-14; Britton 1918a; Britton and Millspaugh 1920; Britton and Wilson 1923-26; Duss 1897; Eggers 1879; Grisebach 1864; Howard 1952; Leon and Alain 1957; Loveless 1960; Marie-Victorin and Leon 1942; Questel 1941; Roig y Mesa 1928; Sandwith 1954b; Seifriz 1943; Stearns (manuscript); Stehlé 1935; Urban 1920-21; Williams and Williams 1951.

The species is apparently absent in the wild state from Bermuda, British Honduras, and Honduras, and is not included in the indigenous or naturalized floras of the bordering areas of Surinam, British and French Guianas, Uruguay, or Paraguay, nor have specimens been seen from these areas. *Tecoma stans* has, however, been reported for Chile but without locality by Bailey (1930), Chittenden (1951), Hemsley (1879-88), and Seeman (1863), but not in the more detailed flora of Reiche (1910).

Tecoma stans var. stans has the broadest range, nearly coextensive with the distribution on the map, and is the only representative in the West Indies (with the possible exception of var. apiifolia mentioned under "Systematics"), Florida, Venezuela, and Brazil. Gray (1878) questions its indigenous status in Florida, although Small (1913a, 1913b, 1933) implies it is native. As judged by the relative frequency in those collections which have been seen, var. velutina is much less common throughout most of its wide range from Mexico to South America, Variety angustatum represents the complex in northern Mexico and adjacent Texas, New Mexico, and Arizona, although apparently incorrectly reported for Baja California by Martinez (1947). Unlike var. stans, it does not closely approach the coast (Wiggins, in press). Standley (1938) questions whether any forms of T. stans are indigenous to Central America, since the shrub readily escapes from cultivation, and Macbride (1961) similarly has reservations regarding its nativity in Peru, unless the species is defined to "include several variants described as distinct species", such as T. sambucifolia. Certainly the frequent pioneer status of T. stans in secondary vegetation makes the distinction between an indigenous and naturalized condition often difficult. The undisputed nativity of this species (and even of var. stans alone) throughout much of Mexico, the West Indies, and into South America increases the probabilities of its being indigenous to at least parts of Central America, since otherwise a considerable disjunction would occur in its distribution. Even then, the occurrence of the species in southeastern Brazil is peculiarly discontinuous with its distribution in the Cordilleran of South America. Southeastern Brazil, however, is a hilly region providing topographic sites more like those in the rest of the species' range than the great extent of the Amazon basin from which T. stans has not been reported. A small discontinuity also occurs in the Yucatan peninsula

of Mexico, where var. *stans* is present near the very tip of the peninsula, but no form of the species occurs between there and Chiapas. Standley (1930) is uncertain of its nativity in Yucatan as he is for Central America.

In the West Indies, var. stans is almost certainly indigenous to the larger and many of the smaller islands of the Greater Antilles, and also probably all but the northernmost Bahamas and Bermuda. In the Lesser Antilles, on the other hand, Walter H. Hodge (private communication) feels that T. stans may be merely an escape from cultivation on the many islands where it is today growing wild. Beard (1949) describes T. stans only from secondary woodland or abandoned fields on Montserrat, Cannonan, and Antigua, but unfortunately essentially no undisturbed woodlands occur at the elevations where this species might be expected. Nevertheless, T. stans occurs in at least semi-natural xeric plant communities, and not just in ruderal sites, on at least some of the islands of the Lesser Antilles (Duss 1897; Loveless 1960), and is listed as if it were native for many of these islands (Anonymous 1893; Grisebach 1864; Howard 1952; Questel 1941; Seeman 1863; Stehlé 1935; Urban 1920-21). The question of the nativity of this species here, as in Central America, will be difficult to resolve. Tecoma stans is reported as native in Trinidad (Beard 1946; Sandwith 1954b; Williams and Williams 1951) and on the mainland of Venezuela (Knuth 1926-28; Pittier de Fábrega 1939), and could conceivably have entered at least some of the Lesser Antilles by its light wind-dispersed seeds from Venezuela. Yet migration first from Central America across land bridges (which have been summarized by Asprey and Robbins, 1953) to the Greater Antilles is probable for most of the West Indies. The absence of the species today from most of the Yucatan (and Honduras) peninsulas can be explained largely upon topographic (low relief) and vegetational (dense forest) conditions, and is not decisive evidence against past migration across these areas.

In spite of the aggressiveness of T. stans in disturbed communities in many parts of its range, combined with its world-wide cultivation in tropical countries, in the eastern hemisphere tropics it has apparently become naturalized in only certain localities. Perhaps outstanding among these instances are those of southeastern Polynesia (Brown 1935; Setchell 1926; Wilder 1931). Within a period of only 70 years following its introduction into the Tahitian Islands, T. stans had become one of the most vigorous woody invaders in the drier parts of the island. It is naturalized to some degree also in Mauritius (Sauer 1961), India (Seeman 1863), the Netherlands Indies (Talbot in Van Steenis 1928), scarcely so in the Philippines (Merrill 1923) and Indo-China (Le Compte *et al* 1936), and is not mentioned in the other floristic works on the eastern hemisphere which were examined.

Altitudinally, the species ranges from sea level to 3000 m, this latter figure recorded for a presumably wild specimen of var. *velutina* from Peru, and

also mentioned as the upper limit there of this variety by Herrera (1941). The next lower maximum altitude seen for a specimen of this variety was 2439 m in Hidalgo, Mexico. In southern Mexico and Central America var. velutina is most frequent on high mountain slopes (Siebert 1940), which seems also to be true in South America. In fact, Seeman (1863) comments that this form, "... is confined to the higher mountains, never occurring on the coast, where its place seems to be taken by T. stans, and it has not been found in the Isthmus of Panama, where there are no high mountains, though it has an extensive geographical range north and south of that country." Tecoma stans var. angustatum occurs up to 2460 m in Mexico, and to 1680 m in Arizona and Texas, apparently being absent below about 900 m in the United States. Variety stans has been collected up to 2440 m in Hidalgo, Mexico, and to about the same altitude in Peru. It is also common down to sea level, and in the West Indies var. slans seems to occur mostly at rather low elevations. In Guadaloupe, for example, Duss (1897) reports the species to be rare above 350 m, and the highest altitude it was observed by the writer in Jamaica was 750 m at Spur Tree Pass in Manchester Parish. Bruggeman (1957) recommends the species for planting in the tropics up to 3000 m.

A brief reconnaissance of Jamaica showed T. stans in a number of parishes (FIG. 2), often only locally common, and George R. Proctor (oral communication) believes it probably occurs in every parish.

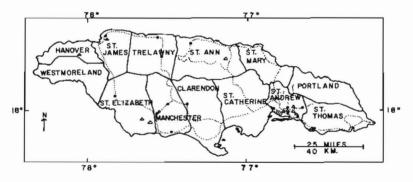


FIG. 2. Map of Jamaica showing stations at which T. stans was observed and the routes which were travelled.  $\bullet =$  sight records;  $\circ =$  voucher collections;  $\bigtriangleup =$  additional localities represented in collections. Kingston is the shaded area in St. Andrew.

#### Climate

The *T. stans* complex is restricted in its natural range to about  $32^{\circ}$  latitude both north and south of the equator (FIG. 1). The range includes Köppen's tropical rainy ("A") types, and the warmer parts of the dry ("B") and humid

mesothermal ("C") climates (Ackerman 1941). A winter isotherm of approximately 15°C (Kendrew 1953) corresponds to the poleward (both north and south) distribution of var. stans. Average (although perhaps not extreme) temperatures reach lower levels, however, where the species occurs at high elevations. Tecoma stans var. velutina from Guatemala is reported to be much less hardy than var. stans, presumably from Florida (Apgar 1910; Bailey 1930). What is probably var. stans is said to recover "from -7°C or less" (Green and Blomquist 1953). The most northerly form, var. angustatum, is the most cold-tolerant, at least of the northern hemisphere races, occurring where the average January mean reaches at least as low as 7°C, and probably even lower at its upper altitudinal limits in the United States. Horticultural experience confirms this conclusion (Bailey 1930; Van Dersal 1942). What is probably var. angustalum in cultivation near Superior, Arizona, was "more or less severely injured" when official temperatures reached -8°C and remained below freezing for 19 consecutive hours (Turnage and Hinkley 1938). Such observational evidence, in conjunction with the isotherm correlation in both northern and southern hemispheres, seems to make plausible the hypothesis that the poleward distribution of the species is conditioned primarily by winter temperature minima, the tolerance of which may vary more or less along latitudinal (and perhaps altitudinal) clines.

Although *T. stans* was introduced into British greenhouses as early as 1730 (Chittenden 1951), very little experimental or horticultural experience is available regarding optimum temperatures for growth. Under glass in England *T. stans* has been reported to grow well with a temperature of 20°C, "but is finest when the thermometer ranges from 24°C to 25.5°C." (Anonymous 1854). A "stove" greenhouse is also recommended by Curtis and Hooker (1832), but Bruggeman (1957) recommends a "cool greenhouse," with a "minimum night temperature of 4.5°C and a day temperature of 10°C to 13°C." This latter environment must be considerably cooler than the species receives within most of its natural range, and seems very doubtfully optimum.

In a considerable portion of its range, the *T. stans* complex is characteristic of dry habitats, where the precipitation-evaporation ratio is low, where a severe dry season occurs, or where drought is edaphic. In the United State and parts of Mexico, *T. stans* is in desert or semidesert climates. In the West Indies it is frequently most abundant on the dry leeward sides of islands, as seems to be the case in Puerto Rico (Britton and Wilson 1923-26), Guadeloupe (Duss 1897; Stehlé 1935), Montserrat, the Grenadines, and Antigua (Beard 1949; Loveless 1960), Trinidad (Beard 1946; Sandwith 1954b; Williams and Williams 1951), and also Jamaica. On the other hand, the species is also widely distributed in humid regions where a high and evenly distributed precipitation prevails, as in parts of Jamaica, but it is probable that deforestation was prerequisite for its general invasion of very humid climates.

In FIG. 3 are climatic data for the year of the study and long-term means at Kingston, near where most of the observations were made. The average yearly precipitation-evaporation ratio here is 0.44, while that of the month of highest evaporation (July) is only 0.20, clearly indicating the aridity of this station. Six consecutive months (November through April) receive less than an average of 10 cm precipitation, which is considered to indicate severe drought in the West Indies (Loveless and Asprey 1957). The area where T. stans was studied most intensively near Kingston (northwestern Loog Mt.) receives 15-25 cm more rainfall than the data of FIG. 3. The species also occurs where the rainfall exceeds 250 cm in Jamaica, but almost certainly only where man has eliminated the original rainforest.

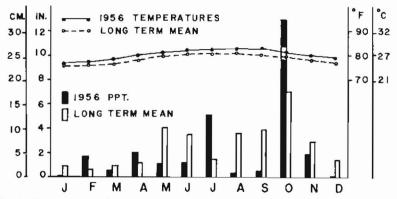


FIG. 3. Temperature and precipitation for Kingston (Palisadoes Airport) during 1956 in comparison with long-term means. Annual precipitation for 1956 totalled 69.8 cm, while the long-term mean is 80.3 cm. Extreme temperatures on record are 13.7°C and 36.6°C. (British Caribbean Meteorological Service 1957; Cover 1952; Matley 1951).

Near Montego Bay, T. stans occurred only 30 m from the sea, and under such conditions would be subject to significant salt spray during storms although no evidence of damage was observed. In Mauritius, T. stans has become naturalized along the shore where it is subject to salt spray and storm waves (Sauer 1961).

## Topography

In much of its range the *T. stans* complex occurs most frequently on irregular and often steep and rocky topography. This is especially true of var. *angustatum* (Bartram 1922; Benson and Darrow 1945; Kearney and Peebles 1942; Palmer 1928; Wiggins (in press); Wooton and Standley 1913; and herbarium sheet notations). Variety *stans* is reported from both relatively

even and rough topographic situations. In Baja California, it very frequently occurs on alluvial fans (Brandegee 1891a; Johnston 1924; Wiggins, in press), and in rocky swales (Gentry 1949). In Sonora, Mexico, var. stans occurs on rocky exposures in the foothills and on barrancas (Gentry 1942). In the Bolivian Andes, *T. stans* (var. unspecified) is a characteristic shrub on steep banks above rivers (Herzog 1923). Of 32 herbarium specimens of var. stans having topographic data, about half occurred in habitats such as "rocky hill," "cliff edge," "dry hillside gully," and half were on relatively level but still well-drained sites, as "alluvial fans," "dry canyon floors," "roadsides," and "clearings." The few specimens of var. velutina bearing data also occurred on dry hills or slopes. Nearly three-fourths of the stations where the species was observed in Jamaica were on distinctly non-level and frequently very rough sites. The writer has also observed *T. stans* occurring abundantly on rocky slopes at the edge of Nassau in the Bahamas.

One possible interpretation of the frequency of T. stans on rough slopes is that the more level areas are under cultivation and the species is thereby excluded from the deeper soils. The restriction of var. angustatum to a narrow altitudinal zone (about 90 m to 1680 m in the United States), however, suggests correlation with moisture at its lower limits, rather than with refuges from human disturbance. In fact, at least in all its more humid territory, T. stans has probably been favored rather than restricted by human activities, as implied above. The relatively tall dense forests on the deep soils which originally prevailed in uniformly rainy areas very likely excluded the shadeintolerant T. stans, and with general deforestation this species has almost certainly increased its density and local distribution on both level and rough sites. The apparent requirement for excellent drainage, moreover, helps explain the prevalence of the shrub on steep slopes and rock outcrops, as well as on coarse sandy or gravelly alluvial fans.

#### Soil

As is expected with widely distributed and genetically variable species, T, stans occurs on a wide variety of substrata. Probably as a reflection of the species' requirements for sun and drainage, the most common soils throughout its range appear to be lithosols or recent coarse alluvium. Deforestation, however, has permitted the shrub to invade many deep soils with mature profiles from which it was most likely formerly excluded by shade, and it also occurs on some deep soils in climax vegetation in arid regions, as in Chihuahau, Mexico (Shreve 1939). Variety angustatum grows on limestone, red sandstone, granite, andesite, and red calcureous gravelly clay, as judged from herbarium specimen data; var. velutina has been collected from limestone, on the few sheets for which data was provided.

Variety stans, the most widely distributed subspecies, has been reported

or collected from soils described as rocky, gravelly, sandy, coral, granitic, loam, clay, coarse alluvium, volcanic sand and especially often, limestone outcrops or derived soils. In cultivation it does well on either sandy or heavy soils (Hume 1951), or well-drained loam (Bruggeman 1957). In Jamaica, the species occurs mostly on limestone or the resulting residual soils, but the correlation is misleading since these substrata cover two-thirds of the island. At the edge of Nassau in the Bahamas T. stans was also observed to be abundant on shallow residual soils over limestone. On Long Mt. in Jamaica, where the species is abundant, the limestone bedrock weathers into a characteristically jagged "honeycomb" pattern. Tecoma stans grows to large size in small crevices in this substrate even though soil is absent. In the more level spots, in depressions, and near the base of the slope a porous brick-red infertile "terra rossa" latosolic soil in which the shrub also occurs has accumulated from the limestone. Observations along road cuts and from soil pits indicate that the roots penetrate deeply into the bedrock beyond the accumulated soil. Also, the fact that there may be no difference in size between shrubs growing on bare limestone and adjacent ones in pockets of soil suggests that the mass of the root system is in the bedrock crevices in either case. A humus layer here is absent, but the small amount of humus in the terra rossa nevertheless accounts for all the exchangeable bases (Innes 1951). In a few localities on Long Mt. where soil occurs on nearly level areas adjacent to limestone outcrops, T. stans favors the outcrops even where the vegetation is but little denser on the soil, perhaps because of its requirement for excellent root aeration. At higher elevations here the species was frequent on a 23 cm terra rossa which was becoming brown with humus in the top 15 cm. Even here a humus layer was absent and the roots penetrated deeply into the parent limestone.

Elsewhere in Jamaica, T. stans was observed in several sites, both with and without soil, very similar to Long Mt. Where the vegetation is denser and the ground more level a better-developed litter layer and browner color develops, as the northern station in Trelawney (FIG. 2). Two stations occurred on alluvial soil, both on old river terraces 6-23 m above the present river channels in St. Andrew parish. In both cases the soil seemed well drained, coarse in one case and finer textured in the other, with considerable humus incorporated into the upper portion. At another site but on a steep slope in this parish T. stans was on residual soil derived from shale. Where the species occurred along mountain roads, it was usually most abundant and largest on the fill side, although it always occurred also on the soilless cut bank. Only two out of ten soils tested with HCI failed to show free carbonates, one from a river terrace in St. Andrew and one from terra rossa in Manchester.

In large areas of the island the terra rossa soils are bauxitic, and T. stans

occurs in secondary forest and pastures both on deep bauxitic soils and on adjacent limestone outcrops in St. Ann and St. Elizabeth parishes (Howard and Proctor 1957a, 1957b). The surface soils here exhibit a pH of 6.1, an organic content of 7.2% and have adequate nitrogen and trace elements but are very deficient in phosphorus, potassium, and calcium.

#### Communities

Over its 64° latitudinal range, *T. stans* occurs in physiognomically and floristically diverse communities. Variety *angustatum* in Arizona and New Mexico is present in the "Lower Sonoran Zone" (Wooton and Standley 1915), the "Larrea and grass belts" (Tidestrom and Kittell 1941), and the "upper part of the desert, the desert grassland, and the lower oak woodland" (Benson and Darrow 1945). Some associated species in Arizona have been listed by Bailey (1914) and Shreve (1951). For the Sonoran Desert in general this form is described by Wiggins (in press) from mainly the Lower Sonoran Zone but ranging into the Upper Sonoran Zone.

Herzog (1916, 1923) places T. stans (variety unspecified) in the mesic soft-leaved shrub formation or thickets of the warmer portions of the Bolivian Andes. In Mexico, the species as a whole is characterized as being from well-drained areas in both the "Mesquite-Grassland Zone" and the "Deciduous Tropical Forest" (Pesman 1962), and it is abundant in thickets in Chiapas (Miranda 1952). Shreve (1937, 1939, 1951) describes several shrub and thorn forest communities in which T. stans is important in the Sonoran Desert. In Costa Rica and Panama, Standley (1928, 1938) reports the species "In the thickets and hedges." In western Nicaragua, it is important in seral and frequently burned low woodland 5 to 8 m high on the slopes of recently active volcanoes (Taylor 1963).

Variety *velutina* occurs in the evergreen riparian bush forests of the Peruvian Andes (Weberbauer 1936, 1945), and specimens of this subspecies have been seen which were collected in *''Juniperus* woodland'' in Hidalgo, Mexico, and it is ''common on dry brushy slopes'' in Guatemala.

Tecoma stans var. stans occurs in both the Lower Sonoran and Tropical Zones in the Sonoran Desert (Wiggins, in press). It is also described from Sonora in "Short-tree forest" and "with lower oaks... Except for its cultivation in gardens as an ornamental this species is rare in the Rio Mayo region and makes up no appreciable part of the natural vegetation as it does in neighboring Baja California." (Gentry 1942). What is probably this form is very common in "brush lands" in Yucatan (Millspaugh 1896). Herbarium specimens from Mexico record var. stans from "cleared overgrown slope, common" (Guerrera), "moist places in dry canyon thorn scrub" (Durango), "small tree in forest" (Yucatan), "juniper woodland" (Hidalgo), "with Agave, Yucca, mesquite" (Coahuila), "with Jatropha, Pachycereus, and various shrubs" and "with Lysiloma candida, Ulmus, and Erythea" (Distrito del Sur, Baja), and "semi-desert roadside" (San Luis Potosi). In Colombia, var. stans has been collected along an "old road on brushy slope," and at the "edge of mangrove swamp" (probably on adjacent outcrop). In Venezuela, it has been collected in "second growth along roadside," and "in hedges, woods, pastures, and savannas," and in Bolivia from a "stony roadside."

In Florida and the Keys, var. stans occurs in hammocks, waste places, woods, and thickets (Small 1913b, 1933). Marie-Victorin and Leon (1942) and Seifriz (1943) list some of its associates in Cuba, where it often is in "thickets." In Puerto Rico, T. stans occurs in the "Borders of woodlands" (Millspaugh 1900), and in "Waste places, scrub lands, and borders of coppices" in the Bahamas (Britton and Millspaugh 1920). In the Virgin Islands, this shrub is listed as a dominant in the "Eriodendron (Ceiba) vegetation" (Harshberger 1911), in "thickets" (Britton 1918a), and on St. Croix in "open places, very common" (Millspaugh 1902) or "in thickets, often gregarious" (Eggers 1879). It is frequent in the usually seral "Deciduous Seasonal Forest" in Trinidad (Beard 1946), and occurs in "Dry Scrub Woodlands," a secondary type in the Deciduous Seasonal Forest on Montserrat, Grenadines, and Antigua (Beard 1949, Loveless 1960). Sauer (1961) describes the open upper beach vegetation in which T. stans is naturalized in Mauritius. Herbarium specimens bear data such as "hillslopes above pine" (Dominican Republic), dry rocky roadsides (Haiti; Barbados), "Deciduous Seasonal Forest" (Grenada), "edges of clearings" (Cuba), and dry woods, thickets, waste places, and cleared areas (Grenadines, Bahamas, Grand Cayman).

In Jamaica, T. stans occurs in "open sunny places and thickets" (Stearns, manuscript), in "Dry Limestone Scrub Forest" (Asprey and Robbins 1953), and in "waste land" (herbarium specimen notation). In the present study, the shrub was observed as isolated specimens along roadsides, scattered in open pastures (FIG. 4A), and in thickets. In western Manchester parish for about a 300 m altitudinal zone below Spur Tree Pass, the shrub is an important component of the secondary thickets and pastures, but becomes more restricted to roadsides below this zone and near the top of the pass at 750 m. Near the coastal part of Trelawny parish T. stans was locally abundant also in quite dense second-growth thickets and in pastures. It was either very local or considerably less common at most of the other stations where it was observed (Fig. 2), often being largely or entirely restricted to roadsides. Where the species is a dominant on Long Mt. (the lower elevations), the physiognomy resembles Beard's (1955) "Evergreen Bushland," the main upper stratum being about 4.5 m with occasional emergents. Tecoma stans also occurs here in taller vegetation best classed as "Dry Evergreen Thicket," or "Deciduous Seasonal Forest."

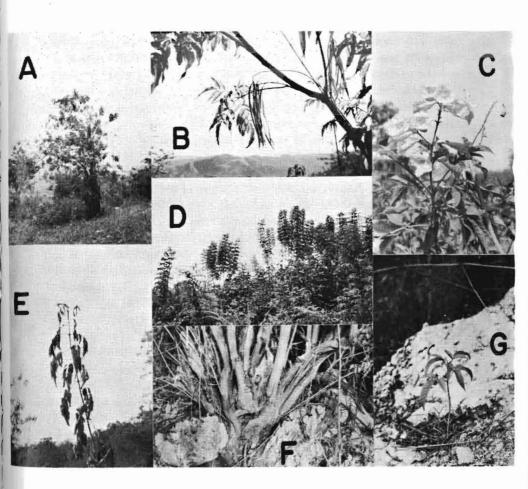


FIG. 4. (A) An isolated 3.8 m tall *T. stans* with a single trunk in a pasture just below Spur Tree Pass, Manchester Parish. (B) Pinnate foliage and pendant habit of mature fruits. Long Mt., St. Andrew. (C) Inflorescences in which fruits are not forming, the one on the right having abscissed all but one flower. Long Mt. (D) Characteristic sprouts 2 m tall resulting from cutting. Edge of field, near Redgate, St. Elizabeth. (E) Typical permanent wilting behavior during drought. Even the youngest leaves are collapsed and the shoot tip is pendant, although all leaves are flexible and green. Long. Mt. (F) Base of large shrub growing in crevice in solid limestone. The largest nearly erect stems are about 5 cm diameter. Long. Mt. (G) Seedling 10 cm tall showing trifoliate juvenile foliage, growing in limestone crevice in clearing. Long Mt.

The species everywhere was observed only in vegetation which had been considerably disturbed by fire, cutting, grazing, or road work, and this seems to be characteristic of var. stans (but not var. angustatum) throughout much of its range as is implied above. Variety stans probably occurred originally in climax stands of xeric thicket vegetation in Jamaica such as occurs on Long Mt. now modified by cutting and burning. The fact that it is not reported by Lewis (1943) or Loveless and Asprey (1957) from the least disturbed stands of this type (on Portland Ridge), however, suggests that the species was uncommon even in the drier parts of the island, and that it has increased markedly since Spanish settlement. In the less accessible and more humid higher elevations (to over 300 m) on Long Mt. T. stans is even now infrequent within the dense thickets except adjacent to roads. It may well tend to increase with occasional burning; at the edge of Nassau in the Bahamas, T. stans was observed to be one of the dominants of a frequently burned open shrub-savanna, and Taylor (1963) reports it as abundant in frequently burned woodland in Nicaragua.

No particular vascular plants were found to be consistently associated with *T. stans* in Jamaica. The following species, however, were frequent in at least two stations and on the same substrate as adjacent shrubs of *T. stans:* Bursera simaruba Sarg., Cordia spp, Coccoloba tenuifolia L., Guaiacum officinale L., Haematoxylon campechianum L., Acacia spp, Cassia spp, Croton linearis Jacq., Tabebuia spp, Morinda royoc L., Cassieria spp, Pissonia aculeata L., Lantana camara L., Urechites lutea (L.), Britton, and Agave sp. Other associates in Jamaica can be found in the lists of Asprey and Robbins (1953), Baxter (1942), Howard and Proctor (1957b) and Swabey (1942).

Although T. stans occurs on cut-over forest and pasture lands in St. Ann and St. Elizabeth parishes to be strip-mined for bauxite, it is not an invader of newly-mined areas, even though seed sources are available from adjacent limestone outcrops (Howard and Proctor 1957b). The explanation for its lack of aggressiveness here may be an intolerance of non-porous substrata. It is not listed as abundant in secondary vegetation on the bauxite soils even before the mining operation begins (Howard and Proctor 1957a), and the heavy leveling machinery which is used subsequent to the mining probably greatly compacts the substrate. Leveling coal strip-mined land in the United States usually reduces subsequent tree growth and survival owing to compaction (Limstrom 1960), and an analogous effect may be present on the admittedly very different bauxite soils in Jamaica.

The maximum density of mature shrubs of *T. stans* observed in Jamaica was measured in a  $4 \times 65$  m transect on Long Mt., on honeycomb limestone in "Evergreen Bushland" with *T. stans* as a leading dominant. An average of seven shrubs of 10-40 cm diameter (measured 15 cm above the substrate) occurred per 100 sq. m. The lack of reproduction was striking, only

one plant smaller than 10 cm diameter occurring in the transect. In an adjacent clearing, on the other hand, seedlings were abundant (FIG. 4G).

It is therefore evident that the T. stans complex occurs primarily in relatively open communities where light intensity is high. Even in what appears to be dense secondary thickets or low forest, the individual shrubs probably became established in a more open earlier successional stage and do not appear to be reproducing now. In the denser vegetation in which T. stans was observed in Jamaica, sunlight reached from 20-50% of the ground in July, even though this is not the season of greatest deciduousness of the component species. In cultivation, full sun is probably preferable (Bruggeman 1957), but the shrub will bloom in partial shade (Anonymus 1958; Greene and Blomquist 1953).

#### LIFE HISTORY

#### Flowering

Flowering varies from year-long to seasonal. Variety angustatum flowers from May to September (Kearney and Peebles 1942; Van Dersal 1942). Pesman (1962) states that in Mexico T. stans flowers profusely from August to November, but often twice a year; variety stans has been collected there in bloom, however, in nearly every month of the year (Seibert 1940). This variety flowers from November to April in Costa Rica (Allen 1956), and September to January in Colombia (note on herbarium specimen). In Florida, it can bloom either from spring to September (Apgar 1910), primarily in the fall (Bailey 1930; Menninger 1962; Van Dersal 1942; Watkins and Wolfe 1954), twice a year (Menninger 1953), or all year (Small 1933). In Puerto Rico, var. stans flowers most profusely in winter, although some flowering continues throughout the year (Hume 1951), and in the Grenadines it blooms heavily during the dry season, approximately January through April (Howard 1952). Under glass in England, var. stans flowers only rarely, and then in August (Curtis and Hooker 1832). In cultivation in India, the species is stated to flower practically throughout the year (Bor and Raizada 1954). In coastal California it blooms primarily in the summer and fall (Van Rensselaer 1948), although the writer has seen what is probably var. velutina flowering vigorously in January in the desert under cultivation in this state. Variety velutina in Australia is in bloom about five months of the year (Smith 1894), while in Florida under cultivation it flowers in July (Menninger 1953).

Herbarium specimens indicate that var. angustatum blooms later in the fall (through November) than reported above, and that var. stans lacks a distinct floral season in most of its range. Of nine flowering specimens seen collected in Jamaica all were approximately coincident with the winter dry season, perhaps partly because of the greater activity of collectors then. On Long Mt., Martyn (1948) reports that this species can nearly always be found in flower. The writer observed many shrubs in full bloom in July on the island, but flowering was not then general and was absent entirely at some stations.

In the Sonoran Desert, both var. stans and var. angustatum tend to flower after rains (Wiggins, in press), suggesting water as a controlling factor in the drier parts of the species' range. This observation is strikingly similar in certain respects to that by Corner (1940), who has noted that *T. stans* in Malayan gardens flowers several times a year, apparently after dry spells, and suggests that it may be a "temperature tree," responding by gregarious flowering to sudden drops in temperature such as accompany a storm.

In summary, the major controls of flowering in T. stans appear to differ with race and geography. The preponderance of summer and fall blooming near the shrub's northern boundary in the United States, or under cultivation here, suggests inhibition by winter temperatures. Rains and their accompanying temperature changes also may be important factors, especially in the driest areas. The fact that at a latitude of  $32^{\circ}$  day lengths vary from 11 to 15 hours (United States Naval Observatory 1959) suggests the possibility at least of a photoperiodic response in the extra-tropical races of this widely distributed species. In the warmer and tropical parts of its range, however, the species often tends to bloom most profusely during the winter dry period, although far from being restricted to this season. The dry season may be more favorable for pollination and hence fruiting, as observations in India suggest (see Fruiting). The nature of the stimulus, however, is unknown.

The yellow flowers are borne in loose terminal racemes or panicles (FIG. 4C). To the writer (and to Neal 1948) they are only slightly fragrant, although Palmer (in Vasey and Rose 1890) notes the flowers (presumably of var. stans) to be "very fragrant" in Mexico. Variety velutina, in contrast, is reported to lack odor (Apgar 1910; Bailey 1930). Flowers produce a sweet nectar which collects in barely visible quantities in the shallow cupuliform hypogenous disk subtending the ovary. The wide-mouth funnelform corolla, although abruptly contracted above the base, permits a variety of visitors to reach the nectar (FIG. 5). In the United States the flowers are visited by "hummingbirds and insects" (Bailey 1930), "hummingbirds and bees" (Byers, in Menninger 1962), and by "hummingbirds, ... butterflies, moths, bees, and other insects" (Van Dersal 1942), and one specimen from Mexico is annotated, "attracts bees." In Jamaica, the Vervain hummingbird (Mellisuga minima L.) and the Jamaican Mango hummingbird (Anthracothorax mango L.) were observed to visit flowers, but other effective pollinators were not seen. In Argentina, however, Fries (1903) reports only a

single visit by a hummingbird (on T. stans var. multijugum). Honey bees (Apis mellifera L.) have been observed by the writer to actively work flowers of var. velutina cultivated in the California desert, and the nectar has been reported to be good bee food (Standley 1926; Vines 1960), but Apis is too small to regularly contact the anthers or style; a hummingbird also made one visit. Whether or not, therefore, T. stans should be considered to possess primarily hummingbird-pollinated flowers is still in doubt, but as yet no insect visitor has been recorded by anyone who also reports effective pollen transfer by this means; hummingbirds, by contrast, seem structurally well-fitted for pollen transfer.

Only four days were required for several marked buds to pass from stage A through C in FIG. 5, and two more days to the fully open stage D. The corolla changes from green to yellow between stages B and C. The four functional stamens lie appressed against the upper lip of the corolla, one pair slightly above the other but both pairs well inserted. The anthers are villous, and following dehiscence pollen sticks to the hairs. As the buds approach anthesis, the two lobes of each anther begin diverging, until by the time of dehiscence the divergence approaches 180° so that the sacs of one anther form a straight line about 6 mm long oriented parallel and adjacent to the style. The anthers dehisce introrsely by a longitudinal slit, the upper pair dehiscing first, approximately at the time the corolla opens. The connective is crowned with a small flat projection, and a small apparently functionless staminode is present. The large whitish pollen grains are spherical, smooth but sticky, with three pores. Only 10  $\pm$  3.0% of the grains examined were shrivelled or failed to stain with acetocarmine.

The style and stigma are located close to the upper lip of the corolla in a groove between the members of each pair of stamens. As in many other Bignoniaceae the stigma consists of two large lamelliform lobes, the inner surfaces of which are sensitive and close together when touched. The greenish lobes are minutely papillate-hairy on the inner surface, and smooth on their outer surfaces. The lobes close within 10-30 seconds of being touched on their inner surfaces in warm weather, returning to normal in 5-10 minutes. Newcombe (1922) agrees with his predecessors that this behavior favors cross-pollination by receiving pollen from an insect entering the corolla but closing before the insect can dust the receptive inner stigma surfaces with pollen from the same flower. At least in the case of hummingbird visits to T. stans, however, the rapidity of the response seems insufficient.

No evidence of dichogamy was obtained. East (1940), however, reports protandry occurs in many Bignoniaceae, and that self-incompatibility occurs in several unnamed *Tecoma* species although true self-sterility is probably absent from the family. Although the stigma and anthers of *T. stans* both lie against the upper corolla lip, the former is usually (in Jamaica) slightly

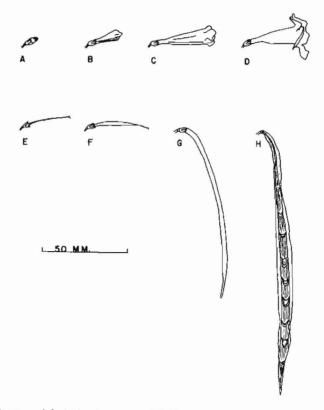


FIG. 5. Flower and fruit development and dehiscence.

more extended (by 1-3 mm), and since only the upper stigmatic surfaces are probably receptive, autogamy of open flowers is unlikely. Bud autogamy is also probably rare since usually the stigma lobes are closed and the anthers do not dehisce until the corolla opens. On the other hand, in flowers of var. *velutina* cultivated in California autogamy seems quite possible, since the stigma was on the same level as the dehiscing anthers in a substantial proportion of the flowers, and often only 1 to 2 mm distant.

Only a small proportion of flowers set fruit in the localities studied. Drought was a major factor in promoting abscission of flower buds. Injury by insects chewing buds and flowers was of less importance. Pollination failure also may have been important. Few floral visitations were observed, perhaps because the period of study was not the main flowering season for the species. Furthermore, nectar-stealing through slits in the corolla tube just above the calyx was extremely common. Some inflorescences showed slits on all open flowers and advanced buds. A *Bombus* species was observed to consistently visit the slits and never the mouth of the corolla. In addition, the Vervain hummingbird visited the slits more frequently than the mouth, and also ants. Taylor (1955) reports that both of the above species of hummingbirds regularly puncture the base of long-tubed flowers to reach the nectar. *Bombus* spp also frequently rob nectar from many plants by biting through the corolla (Kerner 1895; Pilj 1960), and 90% of the flowers of *T. stans* cultivated in Java observed by Burck (in Knuth, Appel, and Loew 1905) were pierced.

Certain features of the flower may function in discouraging visits by small insects which could feed upon nectar but not touch the anthers or stigma. The inner surfaces of the outer tube and corolla lobes are minutely glandular-sticky, and the bases of the filaments and adjacent areas above the nectary are glandular pubescent. The calyx also usually has extra-floral nectaries, which are depressed multicellular saucer-shaped glands (Seibert 1948; Govindu 1951). These exude visible droplets of liquid which is avidly eaten by at least two kinds of ants in Jamaica, and by honeybees in California. The writer is inclined to agree with Brown (1960) and Pilj (1960) that such extra-floral nectaries probably evolved as adaptations protecting (by the presence of ants) against certain insects or browsing animals. In Jamaica, however, the ants seem to have no effect in deterring flower-base piercers, and the glands may well serve no function here far from the place and time of evolution of these structures. Where *T. stans* is cultivated in Java, the glands attract but few ants (Burck, in Knuth, Appel, and Loew 1905).

## Fruiting

The fruit of *Tecoma* is an elongate flattened two-valved dehiscent capsule (FIG. 5). In Jamaica *T. stans* was once observed bearing fruits when only 46 cm tall, but even sucker sprouts from cut stumps only occasionally fruit at less than a meter (in contrast to the dwarf var. *angustatum*). In Cuban gardens, var. *stans* will begin to bloom at a height of about 60 cm (Anonymous 1958), and under glass in England var. *velutina* has come into flower in nine months from seed (Anonymous 1854). In spite of this apparent success in English greenhouses, within less than 50 years this form apparently disappeared from cultivation there for unknown reasons (Watson 1893).

As discussed above, the percentage of flowers maturing fruits was found to be low in Jamaica. Counts of several old inflorescences on four vigorous plants on Long Mt. showed only 209 fruits had matured from a total of 1422 flowers, or  $14.7 \pm 0.9\%$ . The opened fruits are retained on the plant at least a year, until thoroughly weathered, since an abscission layer is not formed, and the flowers which have not matured capsules are recognizable by the persistent pedicels on the now woody rachis. Fruits of three flowering cycles were compared on these plants. The older cycle, probably of the preceeding winter or even earlier, as judged by the chocolate-brown color, weathered exterior, and almost complete absence of seeds, resulted in  $18.1 \pm 2.0\%$  fruit set, while a more recent cycle on which the fruits were still of a light tan color set  $13.4 \pm 1.1\%$ . Counts of still green and immature fruits showed a fruit set of  $13.2 \pm 3.0\%$ . A t-test suggests that the middle and oldest groups are barely significantly different at the 5% level, perhaps a consequence of fruit production having a higher percentage of success at one season or in one year than another. Herbarium specimens from the West Indies and the mainland indicate that fruit set is usually no higher elsewhere.

The percentage of fruit set or matured does not give any information regarding the average or maximum fruit production per plant. The greatest fruit production observed was a count of 350 capsules (all ages combined) on one occasionally cut vigorous 4 m high shrub growing on an open roadside on Long Mt. Counts of eight other nearby plants in apparently similar habitats gave an average of only  $26 \pm 6.7$  full sized fruits of all ages, ranging from 5 to 55 per plant. Under conditions of competition in the interior of the scrub thicket at the same location about half the shrubs were fruiting only somewhat more poorly than this average, while the remainder bore few or no fruits.

At only a few of the widely distributed localities visited in Jamaica was fruit production significantly better than the average of 26 for open sites on Long Mt. Below Spur Tree Pass, where moisture conditions are probably quite favorable, fruiting was superior on the average to that on Long Mt. In St. Thomas parish plants were observed fruiting well in a ravine but poorly on the adjacent hillslopes, again suggesting the limiting nature of moisture in the area. At most remaining stations fruiting was no better and often much lower than on Long Mt. At several localities some individual shrubs would bear well and others not at all for no evident reason.

In India, Bor and Raizada (1954) report that capsules are produced on cultivated plants only during the winter dry season, even though the plant flowers throughout the year, but this behavior has not been reported elsewhere. A tally of occurrence of fruits on 65 herbarium specimens suggests that var. *angustatum* fruits mainly in summer and fall, but that var. *stans* has a good chance of being collected with both flowers and nearly or completely mature fruit any month of the year. The species is reported to set fruit abundantly in cultivation in Malaya (Corner 1940) and where naturalized in Polynesia (Brown 1935).

An average of  $42 \pm 9$  seeds per capsule, with a range of 31 to 44, occurred in a small sample from several plants on Long Mt. The "average seed output" (Salisbury 1942) would be  $42 \times 26$  or 1092, the "average reproductive capacity" is  $1092 \times 67\%$  (viability as determined below), or 732 viable seeds per plant. Seed output of *T. stans* would be similar to that of herbaceous species of unshaded habitats in Great Britain, a low reproductive capacity considering the size of the plant and weight of the seed. "Average reproductive weight" is then  $732 \times 0.00840$  g (average fresh weight of 100 viable seeds), or 6.1 g per plant. The seed weight of *T. stans* is much less than the average of 21 shrub species reported for Great Britain (Salisbury 1942); this difference is understandable, however, since the shrubs listed for Great Britain are woodland species of shaded habitats dispersed by animals. In contrast, *T. stans* probably infrequently colonizes any but initially semi-open sites, a habit which most likely favors the evolution of light-weight wind-dispersed seeds.

#### Dispersal

As in many other Bignoniaceae, the dispersal unit of *Tecoma* is the conspicuously winged seed (Fig. 6). Viable seeds, including wings, averaged  $24.2 \pm 1.1$  mm in maximum length and  $5.4 \pm 0.2$  mm in maximum width. The two extremely thin whitish wings, which are outgrowths of the outer seed coat, compose two-thirds of the length of the seed ( $67.4 \pm 2.9\%$ ). At right angles to their long axis, the wings form only a narrow border, constituting  $24.7 \pm 1.9\%$  of the total seed width. At their ends the wing margins are usually irregular, often lacerate or fimbriate, and even when smooth are ciliate (Fig. 6).

The seeds fall slowly in still air, spinning rapidly, usually in a horizontal position. Strong winds and especially hurricanes are capable of blowing them for possibly hundreds of miles. The weight of filled seeds given above (.00840 g) is but slightly smaller than the .00972 recorded for the species by Guppy (1912), who states that they "... weigh just about the same as a piece of newspaper cut to the same size." Guppy notes that the wings constitute about 14% of the weight of the seed, and is likewise convinced as to their efficacy in wind dispersal.

Wind, consequently, could conceivably be the sole reason for the wide distribution of T. stans in the West Indies, since many of the islands have been above the sea for a considerable period (since middle Miocene for Jamaica). On the other hand, the several land bridge connections of Jamaica and the Greater Antilles to Central America hypothesized by many biographers (Asprey and Robbins 1953) more likely have been at least the initial source of the species. It is probable that the shrub reached the United States by two different routes, var. stans into Florida by wind via the West Indies, and the progenitors of var. angustatum into Texas, New Mexico, and Arizona from adjacent Mexico.

The seeds readily float on the surface of still water for days or even weeks, but it is doubtful that they can withstand sea water. Occasional transfer by streams, downslope rainwash, mammals, or birds could occur, but survival would be possible only if the seeds lodged in a well-drained site. The capsules dehisce shortly after they lose their green color, and the seeds sift out gradually over a period of time. Even some of the oldest weathered and darkened fruits which had probably dehisced months previously sometimes still had a few filled seeds. The seeds which are retained for any extended period in the opened capsules, however, are mostly defective. Consequently, the season of dispersal in Jamaica is probably coincident with the entire year, since dehiscing fruits may be found in every month on the island as a whole.

#### Germination

The seed of *Tecoma* is exalbuminous, with large foliaceous emarginate cotyledons, which are clearly visible through the semi-transparent coats in *T. stans* (FIG. 6). Germination is epigeous, and the cotyledons soon expose a relatively large photosynthetic surface. The sequence from A to F in FIGURE 6 required about 15 days in moist terra rossa soil at Kingston in July. Much variation in seedling emergence and growth was evident. For example, anthocyanin pigments became conspicuous in certain seedlings by the time they developed their second pair of epicotyledonary leaves.

Germination tests were performed by placing recently matured seeds from Long Mt. between moist towelling, others in Petri-dish germinators between filter paper, and most successfully, by simply floating the seeds on water. No difference between diffuse light or dark was obtained, and essentially no dormancy was exhibited. Four years of open room-temperature storage did not result in any reduction in germinability, even though the moisture content of filled seeds at the end of this time was only 7.2%. Peak germination rates (as determined by emergence of the radicle) occurred within two days on tap water in normal July room temperatures in Kingston. Seeds simultaneously planted in soil required an average of eight days to break the surface.

Up to an average maxium of  $90.5 \pm 2.1\%$  "real germination" (based upon seeds with embryos larger than one-half full size and not discolored or soft at the end of the test) was obtained on both fresh and four-year-old seeds. The "apparent germination," based upon both defective and normal-appearing seeds, ranged up to  $66.6 \pm 3.6\%$ . Approximately one-third of the defective-appearing seeds were empty, the remainder having embryos which were discolored, disintegrating, or smaller than one-half size. Seeds with one-half or smaller sized embryos, or those which are dark at the beginning of a test, are not usually viable.

For artificial propagation, Bailey (1930) recommends the use of seeds, although greenwood cuttings will root, but Chittenden (1951) suggests cuttings of partly ripened shoots, or layering.

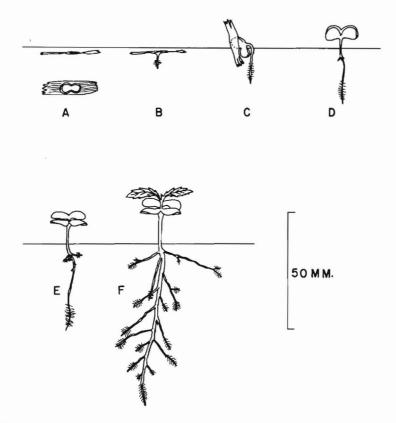


FIG. 6. Germination sequence, showing the flat seed in two views, the emarginate cotyledons, and the simple juvenile leaves.

#### Establishment

Seedlings are distinctly tap-rooted, a trait retained on at least juvenile plants as well. Plants grown in moist chambers produced 16 mm of short (0.5 mm) hairs behind 2 mm of root tip; in water, only 2 mm of hairs were formed, and these occurred only near the water surface. Leaves remain simple or only trifoliate for some time on slowly growing individuals (FIG. 4G). In pot tests, germination and growth were inhibited in a finertextured brown alluvial soil in Kingston with slow internal drainage in contrast to the porous terra rossa in which the species was so common on nearby Long Mt.

Seedlings were abundant in disturbed areas from the base to the top of Long Mt. They superficially resemble juvenile plants of a *Bidens* species, but differ in nodal morphology and pubescence. All age classes are often present in open habitats, but seedlings and juveniles are rare in closed thickets. Elsewhere in Jamaica, seedlings were abundant at about half of the Tecoma stations visited, although none were seen at a few localities. Northwest of Kingston seedlings were abundant on crushed limestone used for the road shoulders but absent on the adjacent fine-textured alluvial river terrace.

Greenhouse tests at Butler University have shown that under favorable conditions seedlings grow rapidly. Yet in such natural sites as Long Mt. the semi-annual drought greatly inhibits seedling growth and survival even in open sites. One juvenile plant in the open there was only 6.4 cm high, and yet the very woody narrow stem had 32 closely crowded nodes, all barren except three which bore only simple leaves less than 2 cm long. A strong tap root penetrating deeply into bedrock which could not be excavated was almost invariably found here. An inability to compete in closed vegetation and susceptibility while still young to fire are probably other important limiting factors on Long Mt.

Under cultivation in Florida (Bailey 1930) and in India (Bor and Raizada 1954) T. stans frequently produces hundreds of seedlings around mature plants.

#### Growth

*Tecoma stans* var. *stans* is usually a microphanerophyte, but var. *angus-tatum* is a nanophanerophyte (Raunkaier 1934). Several stems usually separate at least by a height of 15 cm from the ground (FIG. 4F). Occasionally a single trunk exists for a short distance (FIG. 4A); the largest plant observed with such a tree habit had a trunk 46 cm high before branching, and 20 cm in diameter at this height. Seibert (1940) reports the trunk to reach 25 cm in diameter in Mexico, Hieronymus (1882) to 20 cm in Argentina, and one herbarium sheet of var. *stans* from Venezuela reports, "Tree to 23 cm diameter." In Polynesia it only becomes 10 cm (Brown 1935).

Two herbarium specimens were seen (var. *stans* from Mexico and var. *velutina* from Colombia) with the notations "climbing shrub" and "shrubby vine", respectively, but this must be very unusual. The flowers, however, have been said to give the impression in the forest "... that they belong to a vine that has draped itself over a bushy shrub" (Anonymus 1958), and possibly in shady sites the wand-like sucker shoots require support by adjacent plants. That there may well be some genetic forms which tend to be scandent has been noted from horticultural experience (Watson 1893).

The growth habit of open-grown plants is moderately spreading, although the vigorous sucker shoots tend to be erect as the specific name "stans" implies. The peripheral branches tend to grow almost horizontal in full sun as they become top-heavy; sucker shoots arise from their upper sides, these in turn bending, with strong vertical shoots arising from their top surface. The growth pattern partly results from the inflorescence terminating a vegetative shoot, succeeding growth necessarily developing from axillary buds some distance behind the tip. In dense thicket vegetation the habit is similar but the peripheral stems tend to grow much more erect. The leaves and buds are oppositely arranged, but often only one bud develops at a node, or if two develop one tends to die back, resulting in an assymetrical growth habit.

In height, the species (var. unspecified) is stated to rarely reach 7.1 m in the wild (Record and Hess 1940, 1943); in Peru it on rare occasions is 8 m (Macbride 1961), and commonly is 6 m in Argentina (Hieronymus 1882). Tecoma stans var. multijugum in Argentina is 5-8 m tall (Fries 1903). Variety angustalum is usually less than a meter in height, but one specimen seen from Mexico was labeled 4.6 m. Vines (1960) reports var. angustatum to reach 7.3 m, but this almost certainly refers to var, stans or velutina. Under cultivation var. stans in Bermuda reaches 9.1 m (Britton 1918b), in Puerto Rico 4 m (Stahl, in Cook and Collins 1903), nearly 4 m in Hawaii (Rock 1917), 4.5 m in Cuba (Anonymous 1958), and 3-5 m in Malaya (Corner 1940; Van Steenis 1927). In Florida, this form develops into a dense mass 5.5-7 m high and equally wide under cultivation (Bailey 1930), or even to 9.1 m (Menninger 1953), and to 8 m in the wild (Small 1933). In the Malaya region of Mexico var. stans is 1.5-9 m tall (Seibert 1940), in east central Baja California Sur 2-3.5 m (Johnston 1924), or commonly 5-8 m in the Sonoran desert as a whole (Wiggins, in press), 3-11 m in Costa Rica (Allen 1956), or even up to 12 m (Standley 1938) or 15 m (herbarium specimen notation) there. On the other hand, var. stans is only 0.9-1.8 m in the Grenadines (Howard 1952). Presumably wild specimens in Cuba reach 9 m (Leon and Alain 1957), and where it is naturalized in Polynesia var. stans averages about 4 m (Brown 1935).

In Jamaica, the tallest plants seen reached about 7.1 m, this being not uncommon on favorable sites. At some stations the maximum height was only 3-3.7 m, often as a consequence of recent cutting. Stearns (manuscript) describes the Jamaican populations as mostly under 4 m although occasionally to 8 m. An unburned arboreous specimen observed along a roadside near Nassau in the Bahamas was 4.3 m tall and 13 cm in trunk diameter. Growth rate under cultivation is usually rapid (Bailey 1930; Bruggeman 1957; Van Rennselaer 1948).

Axillary buds are often in superposed pairs (Trelease 1931). Two pseudostipular bud scales, which soon become brown and scarious at their tips but are for a while green and fleshy below, develop even before bark forms; eventually the scales become brown and scarious throughout. The young green stems soon develop conspicuous lenticels, and somewhat later a more continuous grayish corky bark, which becomes shallowly and irregularly fissured longitudinally on older stems and sloughs off readily. On a 10 cm diameter stem the bark averaged 2 mm thick, reaching 3 mm in places.

The wood is moderately hard and heavy, and growth rings are present (Record and Hess 1940; 1943). Whether or not the rings are seasonal or correlated with alternating cycles of shoot growth and flowering is uncertain. The stems 13 mm in diameter with three layers of wood seemed to show only two cycles of length growth and flowering, but another pair of stems which were examined had the same number of growth layers as apparent cycles of length growth.

The leaves of mature shrubs are imparipinnate with usually three pairs of leaflets, although leaflet number varies greatly through the range of the species and is much affected by age and environment. Planimeter measurements of leaflet areas of several Jamaican specimens averaged 516 square mm, when the larger terminal leaflet was included in its normal proportional occurrence to the laterals. The species therefore is a microphyll in leaflet size class (Raunkiaer 1934). It is also a heliophyte, and the leaf is thin and apparently mesomorphic. Vigorous shoots sometimes bear leaves for up to 1.5 m (FIG. 4D). "The sterile bush most strikingly resembles a young ash" (Johnston 1924). In most sites examined in July in Jamaica, however, even sucker sprouts retained leaves only near the top.

*Tecoma stans* is described as "deciduous" by Trelease (1931), and also by Asprey and Robbins (1953) for Jamaica. It is at least partly so in cultivation in Australia in winter (Smith 1894). Judged by herbarium specimens and the lack of comments by other writers, however, it seems that the species is evergreen in much of its range, or at least partly so; this is implied for Arizona by Bartram (1922) and for Florida by Menninger (1953). A very few herbarium specimens were seen from Mexico which bore no leaves at all or only new growth, a result perhaps of extreme drought or of frost, but since the species does not seem to flower while leafless, such specimens would not be frequently expected in collections. In spite of some leaf abscission, the shrubs remained leafy during the severe July drought in Jamaica. The writer has not visited the natural range of this species in the winter, which is the normal leaf-fall season for deciduous species in Jamaica, but var. *velutina* in cultivation has been seen repeatedly only in full leaf in January in the southern California desert.

Although at least partial leaf abscission is one response by T. stans to drought, a much more striking behavior is the permanent wilting of the leaves for extended periods. The leaves have a remarkable physiological resistance to permanent wilting not to be seen in typical mesomorphic species. Plants on Long Mt. during the height of the July drought were just as wilted in early morning in the shade as they were in the late afternoon sun. During the period of the study the July drought was probably as severe as

it normally is, although the July total recorded in FiG. 3, coming mostly late in the month, is much higher than average. Furthermore, official data for the Hope Laboratory suggests that July precipitation was much closer to normal on Long Mt. than at the Palisadoes Airport in 1956.

During drought, the thin leaflets droop, curl irregularly, and even the tip 2-5 cm of young shoots becomes pendant (FIG. 4E). Dieback of leaflet edges or tips seems uncommon. Sucker sprouts from cut stumps also wilt, but less severely owing to a larger root-shoot ratio. Plants in the dense thicket vegetation wilted more severely than those on road fill on Long Mt., but even shrubs growing on apparently identical limestone in the thicket showed great variability in occurrence of wilting. Prompt recovery of permanently wilted shoots followed heavy rains, but lighter showers had little effect, probably owing to the occurrence of absorbing roots primarily at deep levels in the limestone crevices. This drought behavior of T. stans contrasts markedly with its many xeromorphic or completely drought-deciduous associates in the dry thicket vegetation of Jamaica.

Length growth ceases completely during drought even in the absence of wilting. Four shoots of differing vigor were measured periodically for a three week period. No growth at all was detected for two weeks of drought. Then within one week following significant rains, the four shoots lengthened by 6 mm, 34 mm, 15 mm, and 20 mm. The first two were not wilted initially, but the latter two were permanently wilted.

A significant amount of water seems to be absorbed by the roots of permanently wilted plants. Shoots excised and left in the sun still have only a few young green leave after four days, while intact but permanently wilted controls survived unthanged.

Tecoma stans does not normally multiply by vegetative means, but does spront vigorously from cut stumps or after fire. Sucker sprouts often reach 4.5 m high while only 2 cm in diameter at breast height (FIG. 4D). Experimentally cut shrubs produced sprouts to 13 cm long from axillary buds within 18 days. Shrubs in a recently burned area near Nassau in the Bahamas were observed actively resprouting from the ground.

No enerally important injurious insects or diseases were observed on T. stan in Jamaica or are reported by others. Scale insects (Coccoidea) cultured i g ants were frequent but not serious on both mature plants and seed-lings 1. some localities, and the shrubs are heavily infested with mealybugs (Eriococcidae) in the Butler University greenhouse. Leaf chewing insects produled considerable damage in eastern St. Andrew parish and were present but not important at all other stations visited. *Cuscuta* parasitizes the plant and sometimes killed entire branches on Long Mt., and *C. australis* R. Br. attacks this species in Malaya (Van Steenis 1954). The following fungi have been listed for *T. stans* by Seymour (1929): *Cyphospilea* 

polylopha Syd., Puccinia tecomae Sacc. & Syd., P. maligna Dict., P. transformans Arth., and Tryblidiella rubula Spreng. In addition, Olive (1958) reports Septobasidium alni Torr. on T. stans in Tahiti, and Silveira (1943) has collected Prospodium appendiculatum on this species in Brazil, and this autoecious rust also occurs on T. stans in Florida and Texas (Westcott 1960). The latter author also lists the shrub as being susceptible to the ubiquitous root rots, Clitocybe tabescens in Florida and Phymatotrichum omnivorum in Texas.

Physiological diseases were not observed, except for some conspicuous chlorosis of lower leaves on otherwise vigorous sprouts in St. Elizabeth near Redgate in a limestone area. Browsing by livestock is an important factor in pastured areas, primarily through its inhibition of seedling survival but also by the maintenance of open habitats which *Tecoma* can invade if the grazing pressure is temporarily released.

#### ACKNOWLEDGMENTS

The writer wishes to express his thanks to C. B. Lewis, Director of the Institute of Jamaica, who kindly provided research facilities. All plant determinations, along with valuable suggestions, were given by G. R. Proctor and Dulcie Powell of the Institute. Acknowledgment for help is also extended to R. P. Bengry and T. H. Farr of the Institute, to A. R. Loveless of the University College of the West Indies, and to M. T. Hall and Lorraine Gustafson at Butler University. W. T. Stearns of the British Museum provided the manuscript for his forthcoming volume containing the Bignoniaceae of Jamaica, and has provided information on Jamaican specimens in the British Museum. In addition, the cooperation of the British Caribbean Meteorological Service, the Geological Survey Department of Jamaica, and of the Curators of the herbaria at Stanford University, the New York Botanical Garden, and the Missouri Botanical Garden is gratefully acknowledged. I am particularly indebted to my wife, Jeanette S. Pelton, for much help and advice.

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