

Dacryodes excelsa Vahl Tabonuco

Burseraceae Bursera family

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Tabonuco (*Dacryodes excelsa*), also known as gom-mier and candlewood, is the dominant large tree of the native forests that formerly covered the northern lower and middle slopes of the mountains of Puerto Rico. It is distinguished by broad low buttresses, a columnar bole, smooth gray bark, and pinnately compound leaves with five to seven fragrant, dark-green leaflets. When wounded, the tree exudes a clear, fragrant inflammable resin that hardens and turns white on exposure.

Habitat

Native Range

Tabonuco (fig. 1) is native to elevations from 200 to 900 m (660 to 2,800 ft) throughout Puerto Rico. On favorable sites, it may make up 35 percent of the basal area and 80 percent of the timber volume of the forest, commonly termed *Dacryodes*–*Sloanea* association (1). From Puerto Rico, the native range of tabonuco extends into the Lesser Antilles on St. Kitts, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, and Grenada, a gross forest area of about 2300 km² (888 mi²) (24). Other members of the genus are in South America and Africa (5,8).

Climate

Tabonuco in Puerto Rico is found within a mean temperature range of 21° to 25° C (70° to 77° F) and a mean annual precipitation range from 2000 to 4000 mm (79 to 157 in). Precipitation is generally abundant except from February through April, when it may drop to about 75 mm (3 in) per month. At El Verde, on the northwestern slope of the Sierra de Luquillo at an elevation of 420 m (1,380 ft), well within the tabonuco forest range, data collected over 3 years showed the following: mean temperature, 22.6° C (73° F); mean absolute humidity, 18.7 g/m³ (0.02 oz/ft³); mean relative humidity, 91 percent; mean daily insolation, 383 gcal/cm² (383 ly) mean daily pan evaporation, 1.8 mm (0.07 in); mean wind velocity, 4.2 km/h (2.6 mi/h); and mean annual rain-



Figure 1-A mature tabonuco showing spreading crown.

fall, 3700 mm (146 in). Diurnal variations are smaller than some seasonal changes (16).

Soils and Topography

Tabonuco grows on deep, red, acid (pH 4.5 to 5.5), clay soils (Ultisols such as Los Guineos and Humatas) derived from igneous rock. Typically these soils are stony, often with large boulders, and internal drainage is good. Large tabonuco trees tend to be concentrated on upper slopes and ridges, where they may form nearly pure groups whose roots are grafted, thus forming a tree union or clumps of trees. Presumably this reflects the better drainage of soils at such locations or the superior anchorage against hurricane winds that the prominent boulders may offer. Significantly superior diameter growth rates of

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tabonuco on ridges as compared to swales have been reported (22).

Associated Forest Cover

Tabonuco dominates a forest association known locally as the tabonuco type (21). In the French West Indies, the association is described as "forest hygrophytique" (20), and Beard described it as lower montane rain forest, or *Dacryodes-Sloanea* (1). These fall within the broader categories of Tropical or Subtropical Wet Forest life zones (7).

In Puerto Rico this association averages about 50 tree species per hectare (5012.5 acres) larger than 10 cm (3.9 in) in d.b.h. In the Luquillo Mountains close associates include motillo (*Sloanea berteriana*), palma de sierra (*Prestoea montana*), yagrumo hembra (*Cecropia peltata*), yagrumo macho (*Didymopanax morototoni*), and caimitillo verde (*Micropholis garcinifolia*) (21). The forest type has been described in detail (2,15,21). Characteristics of tabonuco stands include a rich mix of 170 tree species in primary and secondary stands (23) with dominants of *Sloanea berteriana*, *Guarea guidonia*, and *Manilkara bidentata*. The relative density of seedlings to that of canopy trees approximates a ratio of 8 while that of saplings is 0.4 (19). On the average, the stand contains 116 trees per hectare (47/acre) 10 to 15 cm (3.9 to 5.9 in) in d.b.h., 100 to 150/ha (40 to 61/acre) larger than 30 cm (11.8 in) in d.b.h., and 63/ha (25/acre) larger than 50 cm (19.7 in) in d.b.h. with a total biomass of 424 t/ha (156 tons/acre) of which 33 percent is in tree boles (14,23). The basal area of the average stand approximates 40 to 46 m²/ha (174 to 200 ft²/acre) and the volume approximates 300 to 345 m³/ha (4,285 to 4,930 ft³/acre) (2). The diurnal gross primary production of a stand with a leaf area index of 6 to 7 in Puerto Rico is reported to average 16 grams of carbon per square meter of ground area (0.052 oz/ft²) (14).

Life History

Reproduction and Early Growth

Flowering and Fruiting-Male and female flowers appear on different trees, making this a dioecious species. Flowers are greenish, about 4 mm (0.16 in) across, and develop in lateral, much-branched panicles. The fruit, a one-seeded oblong-ovoid drupe about 19 mm (0.75 in) in diameter, has a corrugated surface when dry (19). The seed is fleshy, with folded cotyledons (5,17).

Flowering peaks between May and November, with most fruit falling from October to December. There

is some flowering and fruiting at other times and considerable annual variation. Empty fruits commonly fall earlier than those that are fertile. At one period during the autumn of 1963, two-thirds of the crop was composed of empty fruits, although a second smaller crop of viable seeds appeared later. Gamma radiation stress reportedly has led to earlier and increased fruit fall (6). Fruits are generally found in abundance beneath the crowns of the parent trees.

Seed Production and Dissemination-Of the fruits that fall, those dark in color were found to be heavier, with 60 fruits per kilogram (27/lb) compared to 73 per kilogram (33/lb), and more viable, up to 22 percent compared to up to 5 percent, than green fruits. Completely developed fruits tend to sink when immersed in water. Of those that float, most are hollow, although as many as 33 percent may still be viable. The period of viability under natural conditions is short but not precisely known. A few seeds are known to have survived 5 weeks storage exposed to the air.

Germination is epigeal and takes place within a few days under humid, shady conditions. Under direct exposure to the sun, germination is less than in the shade, 11 percent compared to 28 percent in one test.

Seedling Development-In nature the seedlings grow best on steep slopes under low light intensities (0.07 to 0.05 gcal/cm² min or 0.07 to 0.05 ly). They are fragile and root within the litter layer. At an age of 4 months they attain an average height of 16 cm (6.3 in) and typically have six leaves. In some areas there may be as many as four seedlings per square meter (0.4/ft²). Few seedlings grow beyond this stage, only half surviving beyond 8 months. Continued growth of the remaining seedlings under intermediate light intensities is slow. Net photosynthesis is low (60 mg of carbon per m².h or 0.08 gr/ft².h), and the ratio of net photosynthesis to respiration is 0.78 (12).

In the nursery it has been found that seedlings during their first month will not withstand direct exposure to the sun. Under shady conditions seedlings attained 22 cm (8.7 in) in 6 months. Like many other large-seeded tree species, tabonuco does not survive bare root transplanting. In contrast, 85 percent survival has been attained by the use of containers with an intact ball of earth about the roots. At 9 years, trees were 3.0 to 4.3 m (10 to 14 ft) in height and 3.8 to 5.0 cm (1.5 to 2.0 in) in d.b.h. (13).

Direct sowing in the forest has yielded germination as high as 33 percent but subsequent problems such

as leaf fall, drought, and vines precluded successful establishment, so planting is recommended.

Vegetative Reproduction-There is no evidence of vegetative reproduction.

Sapling and Pole Stages to Maturity

Growth and Yield-Mature tabonucos in Puerto Rico may reach 35 m (115 ft) in total height and 180 cm (71 in) in d.b.h. The age of large trees is estimated at up to 400 years. Unpublished preliminary volume tables exist for the species, and a composite table for tabonuco type forest has been published (2). Because of the mixed nature of the forests in which tabonuco is found, growth and yield of tabonuco per unit of forest area are somewhat meaningless.

Diameter growth of individual trees is most rapid on slopes and unexposed ridges and for specimens that are large in size and dominant in crown position (0.15 cm/yr, 0.06 in/yr, for dominant crowns in mature stands vs 0.10 cm/yr, 0.04 in/yr, for suppressed crowns). Growth rates are slow when compared to planted exotics, but what the potential growth of tabonucos would be if planted under comparable conditions is not known.

Rooting Habit-The observed preference of tabonuco for upper slopes and ridges and its obvious successful survival of frequent hurricane winds that break crowns rather than uprooting trees point to a strong and presumably deep root system. Root grafts among trees of this species are common and can be seen in stumps that remain alive and continue to develop callus over the cut surface for decades. Anywhere from 10 to 20 individual trees can form a union as a result of root grafts. Dense and deep root-mats develop near the bases of some large trees, presumably where unusually large amounts of litter are trapped on the surface.

Reaction to Competition-Overall, tabonuco may be classed as intermediate in tolerance to shade. Seedlings are very tolerant. Only a tiny proportion of the seeds that fall produce trees that reach maturity. Competitive factors include light, moisture, mechanical damage resulting from the falling of litter or other trees, and smothering by vines. For best survival, seedlings need to be free of competition until they are at least 3 or 4 m (9.8 to 13 ft) tall.

Growth rates of established trees can be accelerated if the trees are released from competition (i.e., from 0.15 cm/yr, 0.06 in/yr, in mature stands to 0.66 cm/yr, 0.26 in/yr, in cutover stands). However, even mature trees will suffer shock if severely ex-

posed to the intensive rays of the sun, due in part to scalding of previously shaded bark. Trees severely isolated in residual stands after logging have been observed to exhibit crown deterioration and will be lost, within 10 years.

Damaging Agents-The success of tabonuco in the mountains of the West Indies speaks for its capability for dealing with hurricanes. Many trees do not survive, and many of those that do, suffer crown breakage and subsequent heart rot. Despite this, most of the mature trees in Puerto Rico have sound butt logs. A few trees exhibit bark swelling and cankers that provoke an abundance of resin exudation. The pathogen is unknown. Abortion of the fruits is a common and possibly an important phenomenon whose causes are unknown. The significance of fertile seed removal by parrots, other vertebrates, and invertebrates is not known either.

Special Uses

Tabonuco wood is used for all types of furniture, cabinet work, interior trim, general construction, and carpentry. The wood is also useful for crates, boxes, shingles, and small boats. It is a substitute for mahogany in a variety of uses. The wood itself is moderately heavy, with a specific gravity of 0.53 (19). It air-seasons easily and satisfactorily, undergoes moderate and uniform shrinkage during seasoning, and holds its place well after manufacture. Tabonuco is a moderately good machining wood; it cuts and saws easily but will dull saw teeth due to its high silica content. Tabonuco lumber yields good surfaces when planed, sanded, mortised, or shaped (turning and boring are more difficult). It is easily glued, holds nails well, takes stain well, and finishes beautifully with varnish or lacquer. The wood is only slightly resistant to decay, lasting 3 years or less in the ground, and is difficult to impregnate with preservatives by either pressure or nonpressure methods (11,12,18). Tabonuco wood compares favorably with mahogany and birch (24).

Early settlers used the resin of tabonuco for making candles and torches, for caulking boats, for incense, and for medicinal purposes. The endangered Puerto Rican parrot feeds on tabonuco seeds.

Genetics

Wood cutters in Puerto Rico have recognized two races of tabonuco based on the degree of red color and other visible properties of the wood. Other variations, such as the shape of the fruit, have been ob-

served. The genetic significance of these traits, if any, is unknown. *Dacryodes excelsa* has a nuclear volume of 52.6 μ^3 (9) and shade leaves appear to contain less DNA than sun leaves, 590 compared to 715 Mg/g (3).

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