***Curatella americana* L.** chaparro
DILLENIACEAE

General Description.—Chaparro in English is known as the rough-leaf tree and it is also known as careicillo, peralejo macho, vacabuey, aperalejo, curatela, peralejo, peralejo de sabana, pomme torche, raspa viejo, tlachicón, hoja man, yaha, lengua de vaca, malcajaco, hoja chigüe, raspa, raspa guacal, chumico de palo, hoja chigüe, yahal, saha, chumico, azufre, curata, paricá, chaparro de sabana, chaparro sabanero, chaparro colorado, parica, feuille rude, curatahie, carne de fiambre, caimbe, cajueiro bravo, sambaiba, caimbahiba, cambaiba, sobro, sabaibinha, and chaáco (Liogier 1983, 1990, Standley and Record 1936, Salas Estrada 1993, Siegel and Paguaga 1991, Vargas Ulate 2001, Standley 1920, 1937, Pérez Arbelaez 1978, Record and Mell 1924, Bastos 1984, Kileen and others 1993). *Curatélla* means "plants being used or worked", for example, for polishing weapons and metal (Bailey 1941). It is an evergreen woody shrub less than 50 cm tall to a tree 6 to 10 m in height (Lundell 1937, Liogier 1990, Killeen and others 1993). Its most frequent habit is that of a gnarled shrub or small tree (Sarmiento and Monasterio 1983).

In a family dominated by lianas, chaparro is a twisted, thick-barked shrub/tree with pubescent young branches (Schnee 1960). Leaves are simple, alternate, oval to elliptic oval, 5 to 12 cm wide and 10 to 15 cm long, rounded to emarginated, pinnately veined, hard, pubescent (when young), and with very scabrous surfaces and sinuous margins (Pittier 1926, Gentry 1993, Killeen and others 1993). Leaf borders are dentate. The apex is retuse and the base is decurrent on a short petiole (Schnee 1960). Stipules are deciduous and form small scars on the stem.

Leaf morphology contributes to reduction of heat loads and prevents overheating (Medina 1982). Stomata are slightly elevated and the leaf epidermis is heavily cutinized (Mérida and Medina 1967). Leaves of chaparro are scleromorphic, with low specific leaf area (<100cm^2/g) and low nutrient concentrations (Mérida and Medina 1967, Medina 1977, 1982, Sarmiento and Monasterio 1983).

Throughout its range, chaparro is most commonly associated with the following species: trees such as *Bowdichia virgilioides* and *Byrsonima crassifolia*; and grasses and sedges such as *Leptocoryphium lanatum* and *Trachypogon plumosus*; and species of *Andropogon*, *Axonopus*, *Bulbostylis*, *Paspalum*, and *Rhynchospora* (Sarmiento 1983). In Belize, chaparro grows in pine forests (Standley and Record 1936). Pollen from chaparro appeared in Suriname and Colombia in strata dated at 45,000 years before present at the beginning of the Pleistocene and during glacial times (Van der Hammen 1983). Chaparro pollen was associated with grass pollen and dry periods and has shown cycles of abundance and disappearance in response to climate change. The presence of chaparro pollen in lake sediments established the evolution of savanna vegetation in the Neotropics before the presence of humans (Sarmiento 1983). Chaparro pollen also established the boundary between rain forests and savannas in Bolivia and the southern expansion of the rain forest boundary over the past 3,000 years in response to climate change (Mayle and others 2000), and vegetation changes in southeastern Brazil and Colombia since the Holocene and late Quaternary (Behling 1995, Behling and Hooghiemstra 1999).

Range.—Chaparro has a large geographic range that includes Cuba (Grisebach 1963); Hispaniola; the states of Tepic, Tabasco, Chiapas, Veracruz, Campeche, Oaxaca, and Guerrero of México (Standley 1920); Honduras; Belize (Standley and Record 1936); Nicaragua; Costa Rica; Panamá (Woodson and Schery 1965); Guatemala; El Salvador; French Guiana;

Suriname; Guyana; Trinidad; Venezuela; Colombia (Pérez Arbelaez 1978); Perú (Macbride 1956); Brazil; and Bolivia (Beard 1953, Sarmiento 1983, Liogier 1990, Salas Estrada 1993).

Genetics.—Comparative flavonoid chemistry of chaparro and other members of the Dilleniaceae family resulted in reticulate distribution of the substances identified and did not permit recognition of taxa beyond the level of genus and family (Gurni and Kubitzki 1981). Woodson and Schery (1965) reported *pentagyna* as a variety of chaparro in Panamá.

Ecology.—Chaparro is a savanna plant with a uniform spatial distribution (San Jose and others 1991). It is adapted to fire, high air temperature, and harsh soil conditions (Pittier 1926, Lundell 1937). Chaparro is among the first invaders after a fire (Salas Estrada 1993). Medina and Silva (1990) describe the savannas where chaparro grows as "steady state (s) regulated by water-fire interactions on a background of low nutrient availability." However, during the early phases of growth, chaparro is susceptible to fire disturbance (San José and Medina 1975). A low allocation of N to leaves--even young ones--reduces photosynthetic capacity, but it is adaptive to fire as only a small amount of N is lost when leaves burn (Medina and Francisco 1994).

Chaparro grows up to 500 m elevation in Bolivia (Killeen and others 1993), and Venezuela (Sarmiento 1983), and it has extended its range in Colombia to up to 500 to 1,500 m due to savannization of forest lands (Cavalier and others 1998). Frost appears to limit its northern and southern distribution, and flooding or soil saturation also limits its distribution (Sarmiento 1983).

High acidity, high clay content, low mineral nutrient concentration, high exchangeable Al, poor drainage, and poor aeration in the deeper soil horizons favor chaparro (Lundell 1937, Gottsberger and Morawetz 1986). Chaparro will grow in depressions. In some sites, chaparro dominates the community and forms dense groves. For example, within a matrix of flooded savannas in Bolivia, chaparro forms groves on ant and termite hills and on hummocks (Killeen and others 1993). *Sahales* is the name used to describe groves of chaparro in northern Petén (Lundell 1937). Chaparro grows in a wide range of moisture conditions from dry to wet savannas. In the Venezuelan Llanos, San José and Medina (1975) report a mean annual rainfall of 1335 mm and a range of 580 to 1990 mm. A "normal" year has a 4 to 6 month dry season. Beard (1953), Sarmiento and Monasterio (1975), Sarmiento (1983), Medina and Silva (1990), and Medina and Huber (1992) report details of the climatic and edaphic conditions of tropical American savannas where chaparro is one of the most common woody species.

Chaparro grows in many soil types. The most favorable are well-drained soils. Examples of soils are red sands, red sandy loams, yellow sands, well drained latosols, hard laterite crusts, ill-drained latosols, deeply weathered quartz gravel and sands, serpentine-derived soils, entisols on well drained sites, entisols on young alluvial surfaces to oxisols on more ancient ones, alfisols, and vertisols (Sarmiento 1983). Vargas Ulate (2001) attributed the presence of chaparro in Guanacaste, Costa Rica, to acid and infertile soils. In Colombia, the loss of the A and B horizons of granitic soils in sierra Nevada have led to savannization and the establishment of chaparro in lands where it normally does not grow (Cavalier and others 1998).

Chaparro has a deep root system reaching the water table in its adult stage. The species is a phreatophyte, so it grows new leaves during the dry season (Sarmiento and Monasterio 1983, Medina and Francisco 1994).

Competition between chaparro and other plants in the savanna occurs in two stages: establishment and subsequent growth. During establishment, grasses may hinder the growth of saplings and constitute a risk because of the high fire frequency. Chaparro roots face water shortages as they grow through the grass root layer, so establishment is favored by sequences of wet years when fire frequency diminishes and soil moisture increases. Eventually, chaparro will out-grow grasses and shade them out (for example in tree groves).

The chlorophyll content of chaparro is low and correlated with low N and high ash concentrations (Medina and Francisco 1994). Leaf photosynthesis rate reached maximum values in mature leaves during the humid season and declined in younger and older leaves and during the dry season (Sobrado 1996b). Young leaves are more efficient in water use than mature leaves.

Stomatal conductance, and water loss, decline during the dry season. Chaparro leaves do not show photoinhibition. Stomatal conductance differences between dry and wet season appear to be responsible for maintaining a homeostatic balance of leaf water and thus maintain xylem integrity in spite of the species vulnerability to embolisms (Sobrado 1996a). Predawn water potential, minimum leaf water potential, and hydraulic resistance of chaparro, did not show significant differences throughout the year. In spite of the scleromorphic

appearance of leaves, chaparro appears adapted only to short-term diurnal deficits (Meinzer and others 1983). The transpiration curves for chaparro during the dry season are always bimodal (Medina 1977, 1982) as plants close their stomata at noontime, independently of water availability (Medina 1967, 1983). Transpiration rates are also low. The dependency of leaf dark respiration on air temperature changes seasonally (Medina 1982). The steepness of the relationship decreases from December, to February, to March, and to September through November, when the relationship is flat.

The fungus *Pseudocercospora curatellae* was isolated from leaves of chaparro (Furlanetto and Dianese 1999). The earthworm *Pontoscolex roraimensis* was associated with chaparro (Guerra Torquemada 1994). Epiphytes are not abundant on chaparro bark, probably due to its flaky deciduous nature (Gottsberger and Morawetz 1993). Leaf herbivory on chaparro was 4.6 percent near Cuiaba, Mato Grosso, Brazil (Nascimento and others 1990).

Reproduction.—The white flowers have a "disagreeable smell" (Grisebach 1963), occur in lateral panicles on defoliated old branches, and are rarely terminal. Flowers are actinomorphic and hermaphroditic. Four to five petals are white or pinkish, 5 to 6 mm, free, and imbricate (Liogier 1990). Four to five green sepals are rounded, 5 mm long, persistent, and externally pilose (Schnee 1960). Stamens are numerous, free, and persistent. The gynoecium has two hirsute carpels of 6 to 7 mm (Liogier 1990) with longitudinal dehiscence (Schnee 1960). They are coned at the base and covered by long and abundant hairs. Follicles are globose, hispid, coned in the lower half, with two seeds (Killeen and others 1993). Flowers and fruits of chaparro are fasciculate and ramiflorous (Gentry 1993). Chaparro flowers between July and November in Bolivia (Killeen and others 1993) and December to February in Venezuela (Montes and Medina 1977). Seeds are oblong, bright, chestnut brown to black, 3 mm long, with a small membranous hilum (Schnee 1960, Liogier 1983). Seeds are long-lived and remain buried until the proper conditions for germination occur (Medina and Francisco 1994). Fire induces germination and sprouting of stems that are too thick to sprout under normal conditions (Foldats and Rutkis 1969). Seeds are dispersed by birds (Salas Estrada 1993), including parrots and parakeets who eat chaparro fruits (Pérez Arbelaez 1978).

Growth and Management.—Chaparro assimilates carbon all year, but its photosynthetic capacity is reduced due to high mesophyll resistance to CO_2 transfer (Medina 1982). Growth is seasonal and its flowering is tardy (Sarmiento and Monasterio 1983). It flowers and produces new leaves during the dry season (Medina 1982). Leaf development takes 45 days (Nascimento and others 1990), and leaf longevity is about 11 months (Montes and Medina 1977). However, young, mature, and old leaves overlap in an individual (Medina and Francisco 1994). Fruiting and seed dispersal may continue for a short time during the rainy season. Fire does not interrupt this cycle as burned leaves fall and within days there is a new flush.

Two hundred randomly selected trees of chaparro growing in the seasonal savannas of western Venezuela had a mean stem diameter at ground level of 8.3 cm. The largest recorded diameter was 39.8 cm (Sarmiento and Monasterio 1983). Chaparro wood has no growth rings and its sapwood is not clearly defined (Record and Mell 1924).

Under a regime of annual burning, chaparro will experience die back of all its annual growth shoots, and growth will start the next season from adventitious buds that develop from vascular cambium of older branches (Sarmiento and Monasterio 1983). As a result of this response, "the tree behaves as a mechanical structure supporting a crop of annual branches" (Sarmiento and Monasterio 1983). The vascular cambium assumes the role of apical meristem as the main replacement tissue. Chaparro can maintain itself as a hemixyle--with annual shoots and woody underground structures--and even complete the reproductive process in this growth form (Sarmiento and Monasterio 1983). Chaparro can develop new individuals from injured roots (Foldats and Rutkis 1975). Usually, saplings that develop from injured roots have higher water potentials than normal saplings because they are already connected to the water table. Injury to roots will stimulate vegetative regrowth, which in turn also facilitates formation of groves (San Jose and others 1991).

The mineralization of nitrogen, soil organic matter, soil exchangeable Ca, Mg, and K, and total soil nitrogen were higher in soils under chaparro trees than soils under savanna grasses. For soil organic matter, K, and cation exchange capacity, chaparro exceeded values measured under deciduous trees in savannas (García Miragaya and others 1994, Sánchez and others 1997). Although chaparro is not an aluminum accumulating plant, it exhibits seasonal variation in its nutrient concentration (Villela and de Lacerda 1992). Potassium, Fe, Cu, and Zn were highest in August, Ca and Mg in November, and Al and Mn in May. The Al and Mn concentration of mature chaparro leaves

is 171 and 105 parts per million, respectively (Medina 1977).

Benefits.—Chaparro produces good wood with a reddish hue and specific gravity of 0.85. Record and Mell (1924) and de Matos Araujo and de Matos Filho (1977) contain wood anatomy information for chaparro. Small stem sizes limit wood utilization of shrubs and trees. However, the wood is durable and used for charcoal, fuelwood, posts, small cabinetwork, and for turning (Record and Mell 1924, Standley and Record 1936, Killeen and others 1993, Salas Estrada 1993). Termites do not attack chaparro wood (Pérez Arbelaez 1978). Wood utilization increases where trees or shrubs become locally abundant and grow in groves (Pittier 1926). People use dry leaves as substitutes for sand paper and for cleaning kitchen utensils or polishing metals (Killeen and others 1993). Chaparro bark produces tannins that provide a gray color when used for dying pelts (Killeen and others 1993). Ground seeds mixed with chocolate flavors the drink in Oaxaca, México (Standley 1920). Chaparro was one of the most abundant pollens in honey samples during the months of January, February, and March from an apiary north of Roraima State, Brazil (da Silva and Absy 2000). Siegel and Paguaga (1991) suggested using chaparro twigs and pods for prospecting for gold in Costa Rica. In Venezuela, Clamens and others (1999) evaluated chaparro for industrial gum production and found the species promising.

Pharmaceuticals.—Chaparro is a medicinal plant used extensively in folk medicine throughout its range. Infusions from leaves and stems are used for arthritis, diabetes, and to lower blood pressure (Killeen and others 1993, Liogier 1990). Guerrero and others (2002) found that a dose of 20 mg/kg of ethanolic extracts of chaparro showed significant antihypertensive activity in rats. In Brazil, chaparro is used for treatment of inflammation and ulcer. Anti-inflammatory and analgesic tests with hydroalcoholic extract of bark were successful in mice (Alexandre Moreira and others 1999). Cooked leaves are used to mitigate skin eruptions, for dressing wounds, and the water for purifying blood (Liogier 1990).

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