



## Review

Lulo (*Solanum quitoense* Lam.) reproductive physiology: A reviewFernando Ramírez<sup>a,\*</sup>, Jose Kallarackal<sup>b</sup>, Thomas L. Davenport<sup>c</sup><sup>a</sup> Independent Researcher, Bogotá, Colombia<sup>b</sup> Kerala Forest Research Institute, Peechi, Thrissur, Kerala, 680653, India<sup>c</sup> Tropical Research and Education Center, IFAS, University of Florida, 18905 SW 280 St., Homestead, FL, 33031, United States

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## ABSTRACT

Lulo is an important fruit crop, which is considered the “golden fruit” of the Andes. It belongs to the Solanaceae family with two main geographical varieties, *quitoense*, which is spineless and *septentrionale*, bearing thorns. Flowers occur on inflorescences that bear both female-sterile (staminate) and hermaphroditic flowers. Once flowering starts, plants bear buds, flowers, and fruits at different maturity stages throughout the year. Pollen grains are monads and tricolporate. Lulo phenology is influenced by environmental factors such as temperature, altitude and precipitation. More research is required to understand the role of photoperiod. Lulo is mainly pollinated by bumblebees, and insects in the Andes. Self-pollination appears to occur in lulo, but this requires confirmation. Fruit growth and development depends on environmental conditions. Lulo fruit has a sigmoid growth pattern. Hybridization is essential to obtain pest and disease resistant plants. Hybridization programs have been carried out mainly in Colombia and Ecuador achieving successful hybrids resistant to *Fusarium*, nematodes and other diseases. Germplasm collections are essential for maintaining lulo diversity and traits of economic and productive relevance. These are key factors in breeding and hybridization programs. More research is required in all aspects of the reproductive biology of lulo in the tropics. This review is sought to stimulate more research in lulo and to provide the basis for understanding the complexity of its reproductive biology.

## 1. Introduction

Members of this family, comprised of herbs, shrubs, trees and lianas, are cosmopolitan and economically important (Heywood et al., 2007). Economically important species of Andean origin within the family include potato (*Solanum tuberosum*), cape gooseberry (*Physalis peruviana* L.), tomato (*Lycopersicon esculentum*), tree tomato (*Solanum betaceum* Cav.), pepino (*Solanum muricatum*), and lulo (*Solanum quitoense*), etc. (Heywood et al., 2007; Ramírez et al., 2013; Herraiz et al., 2015; Acosta-Quezada et al., 2016).

Lulo is an important tropical fruit species that belongs to the Solanaceae family. Traditionally, Solanaceae is subdivided into two subfamilies, the Solanoideae and the Cestroideae (Heywood et al., 2007). This family is one of the most interesting and largest ones within tropical South America (Schultes and Romero-Castañeda, 1962). *Solanum* sect. *Lasiocarpa* occurs mainly in northern South America (Whalen and Caruso, 1983). The genus *Solanum* is considered one of the largest groups of angiosperms containing more than 1500 species worldwide (Bohs, 2007). The genus contains toxic members and other species that yield edible berries which have been used by local people

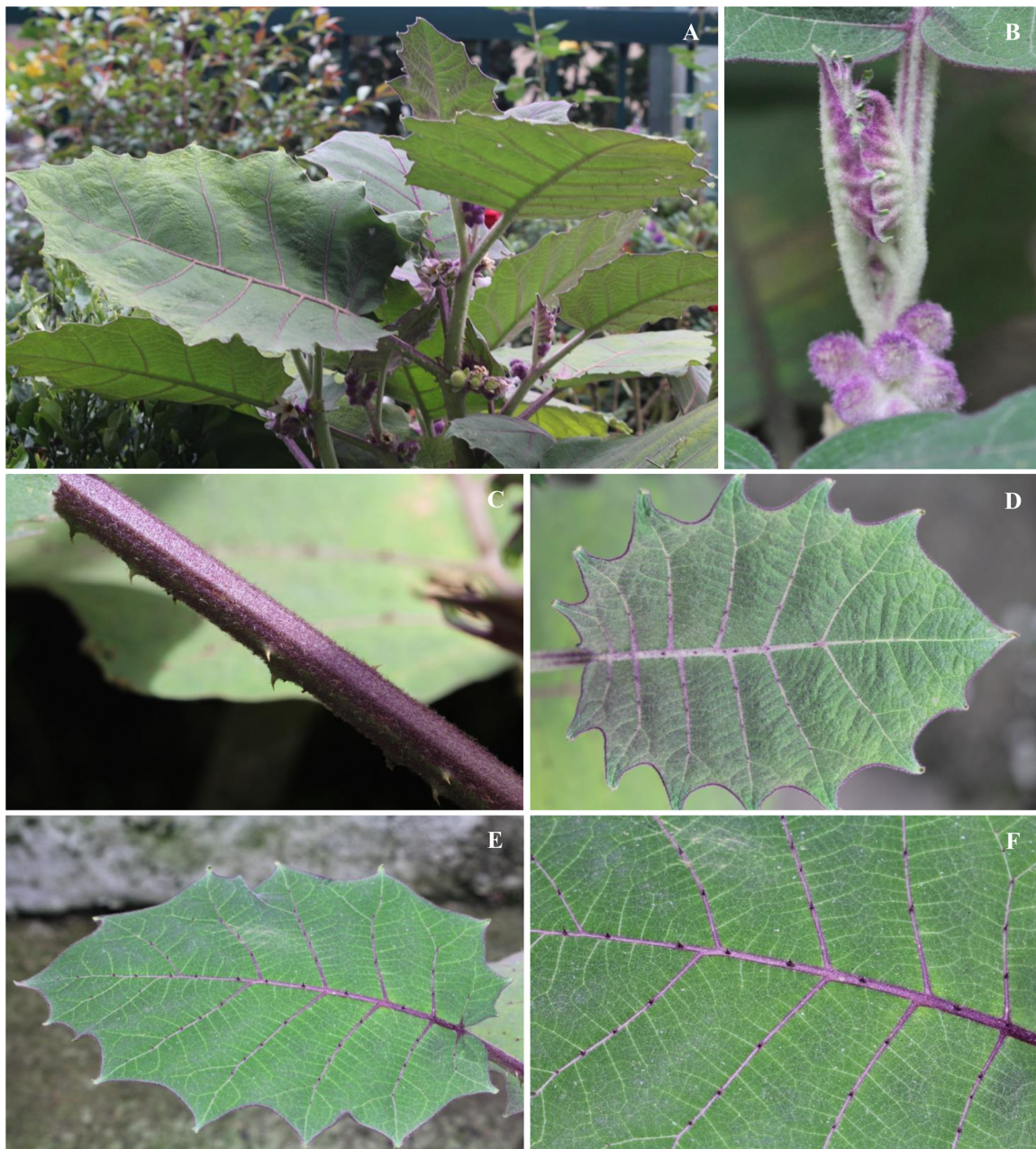
as fruit or to make refreshing beverages (Schultes and Romero-Castañeda, 1962). The *Solanum* genus taxonomy is still in debate due to the high variability in genetic and morphological characters (Pratt et al., 2008).

Two geographical varieties of *Solanum quitoense* have been recognized; *quitoense*, (*Solanum quitoense* Var. *quitoense*) which is spineless and found in southern Colombia and Ecuador (Heiser, 1972; National Research Council, 1989) and *septentrionale* (*Solanum quitoense* Var. *septentrionale*) (Fig. 1), which bears thorns, is considered hardier and grows from 1000 to 1900 m in Colombia, Panama and Costa Rica (Heiser, 1972; National Research Council, 1989). *Septentrionale* is possibly more primitive than the spineless variety (Heiser, 1979).

Lulo holds an important historical role in Colombia and Ecuador. It has been described as “the golden fruit of the Andes” and “the nectar of the gods” (National Research Council, 1989). It is locally known in Ecuador as “naranjilla de Quito”, “lulo” in Colombia, “nuqui” in Peru, and the Incas referred to it as *lulum* (Morton, 1987). The origin of lulo remains unknown, but its progenitors could probably be found within Colombia (National Research Council, 1989). Spineless lulo (*S. quitoense* Var. *quitoense*) is possibly indigenous to Southern Colombia, Peru

\* Corresponding author.

E-mail addresses: [fernando.ramirez.lopez.p@gmail.com](mailto:fernando.ramirez.lopez.p@gmail.com), [fermp44@yahoo.com](mailto:fermp44@yahoo.com) (F. Ramírez).



**Fig. 1.** Lulo (*S. quitoense* Var. *septentrionale*) adult plant in Bogotá, Colombia, (A) plant bearing flowers and fruit, (B) emerging leaves, (C) twig with thorns and pubescence, (D) fully opened young leaf, note that it has small spines, (E) Leaf upper side and (F) detail, note the purple veins, and thorns along the veins. Photos by Fernando Ramírez, reproduced with permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

and Ecuador (Schultes and Cuatrecasas, 1953; Morton, 1987). The first records of cultivation are from the mid-1600s in the countries of Colombia and Ecuador (National Research Council, 1989). Its cultivation is common in upland Southern Colombia, Peru, Ecuador, in Venezuela, Guatemala and mountain ranges of Costa Rica (Heiser, 1985; Samuels, 2015) and has also been grown in Panama, Guatemala and Africa (Dennis et al., 1985).

Lulo is a perennial plant reaching heights of 1 to 2 m within 3 to 4 years from seedling (Fig. 1) (Dennis et al., 1985). However, it is known to reach 1.80 to 2 m within a year of sowing at Bogotá Colombia (Ramírez Pers. Obs.). Also, it has been reported to reach 2 m (Schultes and Romero-Castañeda, 1962; Heiser, 1993), 2.5 m (Morton, 1987; Ramsay and Bryan, 2011), or 3 m in height (Almanza Fandiño, 2007; Paull et al., 2012). Lulo is a herbaceous plant with stout, spreading stems,

that become brittle and woody with age. They are covered with thorns and soft stellate-pubescences (Fig. 1) (Ledin, 1952; Schultes and Romero-Castañeda, 1962; National Research Council, 1989; Morton, 1987; Paull et al., 2012). Leaves are alternate having a green color on top, purple on bottom and densely pubescent surfaces (Pérez, 1946; Gargiullo et al., 2008). Leaves have been reported to grow up to 60 cm in length (Dennis et al., 1985), whereas Almanza Fandiño (2007) reported that leaves attain 25 to 30 cm length, with or without blackish thorns depending on variety. Morton (1987) reported that leaves reach 60 cm long by 45 cm wide. Schultes and Romero-Castañeda (1962) described leaves as coarsely membranous with an oblong-ovate shape reaching 50 cm long by 32 cm wide at maturity. The petiole is about 15–18 cm long with densely stellate, soft pubescences (Schultes and Romero-Castañeda, 1962). Veins on leaves can be white or purple in

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