

UMBUZEIRO (*SPONDIAS TUBEROSA*): A SYSTEMATIC REVIEW

UMBUZEIRO (*SPONDIAS TUBEROSA*): UMA REVISÃO SISTEMÁTICA

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ABSTRACT

Spondias tuberosa Arruda, a fructiferous endemic tree of semiarid Northeast of Brazil, provides several services to its ecosystem as well as to humans. It provides feed for wild animals and domestic ruminants in addition to providing fruits that are rich in vitamins for the human diet. It is an important source of additional income for family farmers and a source for traditional therapeutic medicine. Despite the importance of this tree in northeastern Brazil, limited scientific effort have been accomplished so far towards a better understanding of the tree's physiology and interaction within the ecosystem. Earlier studies about *S. tuberosa* focused on phenology, physiology, population genetics, management practices, and socioeconomic aspects. Due to the lack of breeding and cloning programs, physiological studies and management trials were based on heterogenic plant material, which led to ambiguous results. In order to move forward with *S. tuberosa* research, especially for its genetic conservations and agro-industrial exploitation, basic breeding and intensified genetic research are urgently required. Despite the few publications on *S. tuberosa*, the tree can be considered scientifically neglected, particularly if compared with other members of the Anacardiaceae family.

Keywords: Umbuzeiro; Caatinga; fruit tree; multipurpose tree; ecosystem service.

RESUMO

Spondias tuberosa Arruda, uma árvore frutífera endêmica do semiárido do Nordeste do Brasil, oferece diversos recursos ao seu ecossistema, bem como ao ser humano. Ela fornece alimento a animais selvagens e ruminantes domésticos, além de frutas ricas em vitaminas para dieta do homem. Essa árvore é uma importante fonte de renda extra para propriedades de agricultura familiar, além de ser fonte para um medicamento terapêutico tradicional. Apesar de sua importância no nordeste do Brasil, investiu-se pouco em pesquisa até o momento para compreender melhor a fisiologia dessa árvore, e como ela interage no ecossistema. Estudos anteriores sobre a *S. tuberosa* focaram na fenologia, fisiologia, genética da população, práticas de manejo e aspectos socioeconômicos. Por causa da ausência de programas de reprodução e clonagem, estudos fisiológicos e ensaios de manejo basearam-se em material de planta heterogênea, levando a resultados ambíguos. Para que a pesquisa da *S. tuberosa* se desenvolva, em especial para sua conservação genética bem como para sua exploração agroindustrial, faz-se necessária a condução imediata de pesquisas de reprodução básica e de genética intensificada. Apesar de haver algumas poucas publicações sobre a *S. tuberosa*, é possível dizer que essa árvore tem sido negligenciada do ponto de vista científico, em especial se comparada a outros membros da família das Anacardiaceae.

Palavras-chave: Umbuzeiro; Caatinga; árvore frutífera; árvore polivalente; serviço do ecossistema.

INTRODUCTION

The fructiferous *Spondias tuberosa* known locally as Umbuzeiro or Imbuzeiro belongs to the Anacardiaceae family (LIMA, 1996), which contains several other important tropical and subtropical fruit-bearing trees such as *Mangifera indica* L., *Anacardium occidentale* L., *Pistacia vera* L., *Rhus coriaria* L., *Spondias mombin* L., and *Spondias purpurea* L.. Out of the Anacardiaceae, the genus *Spondias* is one of the most important in the Brazilian context, because of its potential for agro-industrial exploitation (SILVA JUNIOR *et al.*, 2004; ALMEIDA *et al.*, 2007). *Spondias* includes 17 to 18 species with 7 to 9 species occurring in the neotropics (SILVA JUNIOR *et al.*, 2004; MILLER & SCHAAL, 2005). Among these, *S. tuberosa* is endemic to the semiarid northeast region of Brazil, which is covered with deciduous, thorny woodland vegetation called Caatinga (PRADO & GIBBS, 1993; CAVALCANTI *et al.*, 2002a; SILVA JUNIOR *et al.*, 2004; CAVALCANTI & RESENDE, 2006; SANTOS & OLIVEIRA, 2008; REIS *et al.*, 2010; ARAÚJO *et al.*, 2012). The common name Umbuzeiro is derived from the tupi-guarani indigenous word “ymb-u”, which can be translated as “the tree which gives water” (EPSTEIN, 1998; BARRETO & CASTRO, 2010). Its fruit is called Brazilian plum locally known as Umbu, Imbu, Ambu or Ombu (BARRETO & CASTRO, 2010). Umbuzeiro is considered a sacred tree, which is associated with the fact that *S. tuberosa* starts to blossom and subsequently leaves sprout before the onset of the rainy season. The tree is worshipped by indigenous tribes in spiritual rituals owing to these early signs of life in the otherwise dormant Caatinga at the end of the dry season (MACHADO *et al.*, 1997; MONTEIRO, 2007; NADIA *et al.*, 2007; NETO *et al.*, 2010). Due to its early blossom, Almeida *et al.* (2011) claim *S. tuberosa* represents an important feed resource for pollinators and nectar sucking

animals during the dry season. Scientists indicate great economic benefits of *S. tuberosa* for local smallholders and families. Borges *et al.* (2007) found that during the fruit harvest season, fruit picking and selling provide employment and is a major source of income for the dwellers in the semiarid northeast region of Brazil. The fruit of *S. tuberosa* contributes significantly to household income (DRUMOND *et al.*, 2001; REIS *et al.*, 2010; BARRETO & CASTRO, 2010). Moreover, *S. tuberosa* is considered a medicinal plant with high importance for indigenous tribes in the Caatinga (ALBUQUERQUE *et al.*, 2007, 2011). Irrespective of the significance of *S. tuberosa* for local communities and the environment of the Caatinga, the tree faces several natural and man-made threats, which affect its natural regeneration. According to the literature, the problem of natural regeneration and a possible subsequent extinction of *S. tuberosa* seem to be highly multi-factorial.

As *S. tuberosa* is not well known (NARAIN *et al.*, 1992), this work aims at raising attention to one of the economically most important native trees of the scientifically neglected semiarid northeast region of Brazil (SANTOS *et al.*, 2011b). Since the late 1980s about 100 articles on *S. tuberosa* were published, which are accessible through Google Scholar, SciELO, ScienceDirect, Scopus, and WorldWideScience. Forty percent of the articles are published only in Portuguese language with an English abstract, which makes it difficult to reach a large scientific audience and may contribute to the fact that neither the general public nor the scientific community is familiar with *S. tuberosa*. We reviewed the majority of the publications mainly on biology, physiology, and management of *S. tuberosa*, which were accessible through the five databases mentioned earlier.

PHENOLOGY, ABUNDANCE, AND REPRODUCTIVE BIOLOGY

S. tuberosa is an up to 9 m tall xerophytic tree with a stunted, and strongly branched trunk of approximately 0.3 to 1.4 m in diameter, and a characteristic umbrella-like crown measuring 10 m in diameter (LIMA, 1996; CAVALCANTI, 2008). The grayish trunk sheds its bark in rectangle shaped plates (LIMA, 1996). The leaves are pinnate and of an uneven number of oval leaflets (LIMA, 1996; EPSTEIN, 1998). Seedlings of *S. tuberosa* develop a taproot system, which is substituted with fibrous

root systems within the first ten years after germination. The horizontal growth of the root system in this period is greater than its vertical development (NETO *et al.*, 2009; CAVALCANTI *et al.*, 2010), thus leading to a shallow root system, which spreads underneath the canopy area and grows up to 1.0 to 1.9 m depth (CAVALCANTI & RESENDE, 2006; CAVALCANTI *et al.*, 2010). As an adaptation to the semiarid climate, *S. tuberosa* forms root tubers, in which the tree is able to store

water, minerals, and organic solutes (LIMA, 1996; EPSTEIN, 1998; DUQUE, 2004; CAVALCANTI *et al.*, 2010). This adaptation of the tree is essential for its survival during the dry season (SILVA *et al.*, 2008a; CAVALCANTI *et al.*, 2010) and for the commencement of flowering before the onset of the wet season (MACHADO *et al.*, 1997; LIMA FILHO, 2007). An adult *S. tuberosa* tree can have several hundred tubers with a mean tuber weight of approximately 2 kg (CAVALCANTI *et al.*, 2002b; CAVALCANTI, 2008). Cavalcanti & Resende (2006) investigated 12 adult *S. tuberosa* and found in average 907 tubers per tree with a mean tuber weight of 1.5 kg. Cavalcanti *et al.* (2010) observed in average 112 tubers per tree with a mean tuber weight of 0.9 kg while exploring the root system of 10 ten-year-old trees. Besides the age of the tree, average annual precipitation is a factor which seems to affect the number of tubers per plant, as Cavalcanti *et al.* (2002b) observed a slight decrease in tubers per tree during the study period from 1995 to 1998 concomitant with and the annual precipitation dropped in the same time on the experimental plot from 348 mm to 147 mm (APAC, 2015).

S. tuberosa is abundant throughout the entire semi-arid Northeast of Brazil, in the states of Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, and in northern Minas Gerais (EPSTEIN, 1998; LIMA, 1996). Santos (1997) assumes the five regions Tanquinho, Jeremoabo, and Ipupira in Bahia, Petrolina in Pernambuco, and Pio IX in Piauí within the Caatinga as the origin of *S. tuberosa* because of the great phenotypic uniformity found within these regions. The tree requires a daily air temperature between 12°C and 38°C, relative air humidity between 30% and 90%, 2,000 to 3,000 insolation hours per year, and 400 mm to 800 mm of precipitation during the wet season from November to February. Deep, free draining soils without stagnant moisture favor its growth (EPSTEIN, 1998). Tree stand density of *S. tuberosa* varies widely within the Caatinga. The theoretical total population of *S. tuberosa* ranges from 21 million to up to 630 million individuals within an area of 845,000 km², which is covered by caatinga. Santos (1997) claims differences in climate and soil types in such a vast area did not influence evolution and phenotypic differentiation of *S. tuberosa*. Neto *et al.* (2012, 2013) confirmed this uniformity in phenotype for areas with different land use and management as well.

S. tuberosa is an andromonoecious tree with white panicle inflorescence ranging from 0.1 to 0.2 m in length (LIMA, 1996; EPSTEIN, 1998; CAVALCANTI *et al.*, 2002a; NADIA *et al.*, 2007). The inflorescence is made of up to 155 flowers on average, of which 40% are hermaphrodite and 60% are male flowers (NADIA *et al.*, 2007). Almeida *et al.* (2011) found a slightly higher number of flowers per inflorescence—176 on average—in *S. tuberosa* located within an anthropogenic influenced site, such as pastures, crop fields and/or corn (*Zea mays* L.), beans (*Phaseolus vulgaris* L.) or cactus (*Opuntia ficus-indica* Mill.) plantations. Sixty percent of the male flowers are located at the base of the inflorescence, whereas 90% of the hermaphrodite flowers are located towards the apex of the inflorescence (NADIA *et al.*, 2007). The inflorescence has a flowering duration of two to seven days (NADIA *et al.*, 2007; LEITE & MACHADO, 2010). Depending on the region blossoms appear from September to April with a peak in November before the onset of the wet season (MACHADO *et al.*, 1997; NADIA *et al.*, 2007; LEITE & MACHADO, 2010; NETO *et al.*, 2013; MENDES, 1990; CAVALCANTI *et al.*, 2000; BARRETO & CASTRO, 2010). Neto *et al.* (2013) stated that the bloom of *S. tuberosa* is negatively correlated with occurrence of precipitation.

S. tuberosa is not especially adapted to a specific pollinator. Up to 19 insect species were observed visiting the entomophily and self-incompatible inflorescence (NADIA *et al.*, 2007; LEITE & MACHADO, 2010; ALMEIDA; ALBUQUERQUE; CASTRO, 2011). The visitors included the following orders: Hymenoptera (Apidae, Pompilidae, Vespidae), Diptera, and Lepidoptera. The Lepidoptera are considered nectar thieves and their visit does not result in pollination (NADIA; MACHADO; LOPES, 2007; ALMEIDA *et al.*, 2011). Barreto *et al.* (2006) investigated the pollen load of pollinators visiting *S. tuberosa* inflorescence. They found the stingless bees *Trigona spinipes* Fabricius and *Frieseome-litta doederleini* Friese. The red paper wasp *Polistes canadensis* Linnaeus are the most important among the pollinators, as they were exclusively loaded with pollen of *S. tuberosa*.

Reported ratios of flowers to fruits per inflorescence of *S. tuberosa* indicate a very low fruit set. Almeida *et al.* (2011) observed 0.55 fruits per flower on average. Leite & Machado (2010) found 0.01 fruits per flower after natural pollination, and this ratio increased

to 0.22 fruits per flower in cross-pollination, whereas Nadia *et al.* (2007) found 0.01 fruits per flower after natural pollination and 0.02 fruits per flower after cross-pollination. They also investigated the effect of a pollen donor and found no significant difference in pollen originated from hermaphrodite flowers or male flowers. As *S. tuberosa* flowers are self-incompatible, and no biparental inbreeding was observed of the outcrossing species, the low fruit set is unlikely a result of reduced offspring fitness due to inbreeding (FRANKHAM, 2005; KELLER & WALLER, 2002; SANTOS *et al.*, 2011a; SANTOS & GAMA, 2013) (Table 1).

The drupe is about 3.2 cm long with a diameter of 2.8 cm, and weighs about 15.4 to 21.2 g (NARAIN *et al.*, 1992; SANTOS, 1997). The form of the greenish-yellow fruit, which contains a greenish-white pulp covered by a thin skin ranges from round to oval or oblong (LIMA, 1996). Fruit weight is made up of approximately 58% pulp, 21% seed, and 21% skin. The pulp pH is about 3.1 with 9.47°Bx, and the content of titratable acids is

1.1%. Hundred gram of eatable portion of the fruit contains 0.3 g ash, 1.5 g iron, 15.6 g calcium, and 27.9 g phosphorus (NARAIN *et al.*, 1992). Additionally, it is a source of several vitamins, such as vitamin B1, B2, B3, A, and C (VIDIGAL *et al.*, 2011), and is one of few native natural vitamin C sources for human consumption in the driest regions of northeast Brazil (ARAÚJO *et al.*, 2001). The dispersal of *S. tuberosa* is exclusively zoochoric by native animals, such as gray brocket (*Mazama gouazoubira* Fischer), black-rumped agouti (*Dasyprocta prymnolopha* Wagler), collared peccary (*Pecari tajacu* Linnaeus), fox (*Dusicyon thous* Linnaeus), yellow armadillo (*Euphractus sexcinctus* Linnaeus), the argentine black and white tegu (*Tupinambis merianae* Linnaeus), greater rhea (*Rhea americana* Linnaeus), white-naped jay (*Cyanocorax cyanopogon*, Wied) as well as by human introduced cattle (*Bos taurus* Linnaeus) and goat (*Capra hircus* Linnaeus) (CAVALCANTI *et al.*, 2009; BARRETO & CASTRO, 2010; AZEVEDO *et al.*, 2013; GRIZ & MACHADO, 2001; CAVALCANTI & RESENDE, 2003).

Table 1 – Floral characteristics of *Spondias tuberosa* according to Nadia *et al.* (2007).

Floral characteristics	Hermaphrodite flower	Male flower
Calyx (sepals)	5	5
Corolla (petals)	5	5
Short stamen/ anther	5/5	5/5
Long stamen/ anther	5/5	5/5
Apocarp	1	0
Ovary per flower	1	0
Pistil	1	1

PHYSIOLOGY

Studies published about the physiology of *S. tuberosa* focus virtually only on its response to mineral fertilization, salt- and water-stress, and its juvenile development.

In a field experiment, Drumond *et al.* (2001) tested the effect of phosphorus and nitrogen fertilization combined with irrigation on *S. tuberosa* seedling growth in the first 40 months after transplanting ten-months-old seedlings. None of the treatments in their exper-

iment showed a significant difference in plant height due to the mineral fertilization or irrigation within their 40 months trial period. In contrast, Melo *et al.* (2005) found a positive response of *S. tuberosa* seedling on phosphorus and nitrogen fertilization on shoot height, shoot diameter, above ground dry matter, leaf area, and tuber diameter in their experiment in a mesh greenhouse and calculated an optimal N and P dose of 99 kg ha⁻¹ and 150 kg ha⁻¹, respectively. Based on a six-month pot experiment, Neves *et al.* (2008a) stated that

the optimal P input for best shoot growth (height and diameter), canopy area, and dry matter of root system of *S. tuberosa* seedlings is approximately 281 mg dm⁻³. They observed a negative effect on all assessed parameters beyond that input level.

Andrade *et al.* (2013) observed in a pot experiment a negative effect of N and K fertilization on the development of *S. tuberosa* seedlings, and on their rootstock and survival. The authors concluded that the N (350 – 2800 mg dm⁻³) and K (1800 – 7200 mg dm⁻³) applied doses reached toxic levels for *S. tuberosa*. Neves *et al.* (2007a, 2007b) observed in a pot experiment the highest dry matter production after application of 286 mg N dm⁻³ and 137–229 mg K dm⁻³. Beyond these doses the authors also observed a negative effect of N and K application on seedling growth. Lacerda *et al.* (2009) observed a negative effect of N application on seedling growth at only 0.65 mg dm⁻³ on their pot experiment. Additionally, they showed an increased seedling growth owing to increased Boron concentration in the growth substrate. The greatest seedling growth in the experiment was achieved when the seedling was supplied with 3 mg B dm⁻³. Since the experiment was conducted with a combined application of N and B, the authors also observed a negative interaction of both. The authors supposed that this might have been the result of an ion antagonism. These experiments mentioned earlier were carried out under different growth conditions—pot versus field experiment, and differ significantly in the growth substrate used. It is difficult to come to a conclusion based on few publications.

In a liming experiment Neves *et al.* (2008b) demonstrated a positive effect of liming on seedling growth. An increased base saturation because of liming led to an increased content of Ca, Mg, and S in shoot and leaves of *S. tuberosa* seedlings, whereas the content of N, P, K, Cu, Fe, Mn, and Zn decreased (Table 2).

Ferri & Labouriau (1952) and Ferri (1953) were the first authors discussing, inter alia, the internal water balance and stomatal behavior of *S. tuberosa* (LIMA FILHO & SILVA, 1988). Lima Filho & Silva (1988) reevaluated stomatal resistance, transpiration and leaf temperature of *S. tuberosa* at the end of the dry season and after the onset of the wet season. Differences in leaf temperature between dry and wet season could not be observed, and the observed vapor pressure deficit was also similar in both seasons. In both periods the

lowest stomatal resistance was recorded at 7:00 am and was followed by an increase, yet the increase in the dry season was more intense. The stomatal resistance during wet season was maintained at a low value almost until 1:00 pm, when consequently a high transpiration was recorded. Lima Filho (2004) detected a second peak with high stomata conductivity with subsequent high transpiration rates and photosynthesis rates during the wet season at 4:00 pm, in addition to high stomata conductivity in the morning recorded by Lima Filho & Silva (1988). Thus, *S. tuberosa* exhibits a two-peaked daily course of gas exchange. Since the stomatal resistance increased around 1:00 am, with decreased stomatal conductivity, even though environmental conditions were favorable for high transpiration, Lima Filho & Silva (1988) concluded *S. tuberosa* regulates its internal water balance according to a very strict and accentuated stomata behavior, especially under adverse conditions. Later, Lima Filho (2001) stated *S. tuberosa* has two different strategies to maintain favorable internal water balance. Under dry conditions, the author claimed, it maintains its internal water balance by expenses of water stored in the tubers and by restricted transpiration, whereas during the wet season, the internal water balance is maintained by short-term osmotic adjustments, such as uptake of additional inorganic salts or the accumulation of organic solutes (LIMA FILHO, 2001). The very strict and accentuated stomatal behavior reported by Lima Filho & Silva (1988) and Lima Filho (2001, 2004) differs among various phenotypes of *S. tuberosa*, in which some phenotypes appear to be more sensitive than others (SILVA *et al.*, 2009a) (the authors use the term genotype although the accessions in the Germplasm Bank of Umbuzeiro BGU were not categorized on genetic base [see section Population genetics]). Two of the tested phenotypes showed a correlation of stomatal behavior with air temperature, relative humidity, and vapor pressure deficit. One tested phenotype showed correlation with photosynthetic active radiation, whereas one phenotype did not show any correlation of stomatal behavior with the assessed environmental factors. The authors concluded that the observed differences in anatomical alteration in the different phenotypes, such as stomatal density, stomatal index, and stomatal aperture size, could not fully explain the physiological differences among the tested phenotypes. Changes in leaf water potential, concentration of carbohydrates, amino ac-

ids, and proline in leaves and root tubers as a response to intermittent drought differs in different phenotypes as well (SILVA *et al.*, 2009b). The concentration of proteins in *S. tuberosa* leaves and root tubers did not vary either because of induced drought, or because of different phenotypes in the same experiment. Since Silva *et al.* (2009b) observed high leaf water potential even though soil moisture reached the permanent wilting point, the strategy of maintaining favorable internal water balance by water stored in the tubers (LIMA FILHO, 2001) seems factual.

S. tuberosa seedlings show a negative response in growth on salt stress. However, when cultivated in a nutrient solution with a NaCl concentration up to 31 mM,

it proved to be moderately tolerant to salinity (NEVES *et al.*, 2004). The authors assume that this moderate tolerance to salt stress is realized owing to the tubers of the seedlings, which accumulates excess NaCl. Silva *et al.* (2008a) observed negative effects of salinity on the seedling growth if the NaCl concentration exceeded 50 mM. The authors could not detect a decreasing root/shoot ratio as reported by Neves *et al.* (2004). Owing to the increase of root/shoot ratio observed in their experiment, Silva *et al.* (2008a) stated the salinity effects are more severe on the shoot growth than root growth, which implies the root system of *S. tuberosa* is less sensitive towards salt stress than observed in other crops, such as beans (SEEMANN & CRITCHLEY, 1985) or wheat (JBIR *et al.*, 2001).

POPULATION GENETICS

In order to conserve genetic variation of *S. tuberosa*, Embrapa Semiárido (Brazilian Corporation of Agricultural Research) in Petrolina, Pernambuco, Brazil (Embrapa-CPATSA) established in 1994 a germplasm collection (Germplasm Bank of Umbuzeiro [BGU]) in its experimental site in the municipality of Petrolina. Until 2012, it contained 79 accessions with the last addition in 2002 (NASCIMENTO *et al.*, 2002, 2012). The accessions were categorized based on fruit characteristics and tree habit (NASCIMENTO *et al.*, 2002). The first approach studying the genetic variability of *S. tuberosa* was conducted in 2004 using the mixed model methodology—restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) (OLIVEIRA *et al.*, 2004). After evaluating plant height, canopy diameter, basal trunk diameter, and number of primary branches of 42 trees from three different regions, the authors concluded that the greater genetic variability is found within local *S. tuberosa*

populations compared to the variability in between populations of different ecoregions. The first study on the genetic level of *S. tuberosa* was conducted by Santos *et al.* (2008), assessing the genetic variability with the amplified fragment length polymorphism (AFLP) method. Their results objected the findings of Oliveira *et al.* (2004), as Santos *et al.* (2008) observed a high variability in between ecoregions, whereas within local populations higher similarities were observed in the resulting dendrogram. The AFLP method was also used to determine the outcrossing rate of *S. tuberosa* (SANTOS *et al.*, 2011a; SANTOS & GAMA, 2013). In both studies, which combined AFLP with the mixed mating model, a high heterozygosity in the offspring generation was observed. This observation shows that *S. tuberosa* is predominantly an outcrossing species. Since the differential of the multilocus outcrossing estimation and the single-locus estimation was small, a parental inbred could not be observed.

Table 2 – Leaf concentration of mineral nutriment if *Spondias tuberosa* seedling is balanced nutrient supplied.

Mineral nutriment	Quantity (mg g ⁻¹ dry matter)	Author
N	25.72–29.48	Neves <i>et al.</i> (2007b)
P	1.52–1.92	Neves <i>et al.</i> (2008a)
K	3.40–6.04	Neves <i>et al.</i> (2007a)
Mg	2.80–3.26	Neves <i>et al.</i> (2008b)
Ca	18.28–21.47	Neves <i>et al.</i> (2008b)

In conclusion, Santos *et al.* (2008) and Santos *et al.* (2011a) recommended numerous protection areas for *in situ* conservation of genetic variability of *S. tuberosa* or broad fruit sampling in various ecoregions

for *ex situ* genetic variability conversations. The latter already exists in form of the BGU of Embrapa even though its accessions are categorized based on phenotype characteristics.

MANAGEMENT PRACTICES

For plantations a density from 39 to 100 plants ha⁻¹ is recommended for *S. tuberosa* with a tree spacing ranging from 10 m x 10 m to 16 m x 16 m (EPSTEIN, 1998). The suggested size of the planting hole is 40 cm x 40 cm x 40 cm or 50 cm x 50 cm x 50 cm and the refill earth should be enriched with 20 l of cow manure, 300 g of simple superphosphate, and 100 g of potassium-chloride - depending on the soil type and soil fertility (EPSTEIN, 1998).

Seeds of *S. tuberosa* have naturally a very distinct dormancy, which remains an obstruction for commercial seedling production. Few, partly antithetical, research works investigated how the dormancy of *S. tuberosa* seeds can be overcome. The effect, which accounts for the natural reproduction and agro-industrial exploration discussed in literature, is the maturation of seeds after the abscission of the fruits. Araújo *et al.* (2001) showed a strong increase in germination after 24 months of seed maturation. This maturation period lead to a germination of 73.6% compared to the germination of 22.8% of freshly harvested seeds. According to the authors, only 12 months of maturation significantly increases the germination to 27.7%. According to Cavalcanti *et al.* (2006) a maturation time of 24 to 48 months leads to the highest germination percentage between 60.0% and 72.5% within 30 days after sowing. Magalhães *et al.* (2007) tested the influence of 13 different maturation periods: 0, 30, 60, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 360 days. After a maturation period of 90 up to 210 days they observed the highest germination of 70% and a decrease in germination beyond a maturation time of 300 days. A fourth work observed the highest germination between 120 and 210 days of maturation (LOPES *et al.*, 2009), which differs only slightly from the work of Magalhães *et al.* (2007) and confirms their findings. Besides the storage period, storage conditions and fruit ripeness affect the germination, which were not consistent in the publications mentioned earlier (compare section "Conclusion").

Methods to break the dormancy of *S. tuberosa* seeds discussed in literature with importance for agro-industrial exploration are mechanical, chemical and thermal scarification, and immersion in water or growth promoting solutions such as gibberellic acid, ethylene, or cytokinin. Chemical scarification and thermal scarification are not appropriate methods to break the dormancy of *S. tuberosa* seeds. Seeds treated with these methods showed a significantly lower germination percentage than the control seeds (ARAGÃO *et al.*, 2008). Lopes *et al.* (2009) did not detect any germination after the seeds were treated with H₂SO₄ for 10 minutes. Neither Lopes *et al.* (2009) nor Melo *et al.* (2012) observed any positive effect on germination owing to treatment with growth regulating solutions. Immersion of the seeds in water for 24 hours slightly increased the germination (ARAGÃO *et al.*, 2008); however, the most appropriate method seems to be the mechanical scarification by a beveled cutting distal of the seed, introduced by Epstein (1998), to allow water to easily soak the seed. Lopes *et al.* (2009) and Aragão *et al.* (2008) observed the highest germination after such treatment. However, Neto *et al.* (2009) and Melo *et al.* (2012) stated even mechanical scarification does not break dormancy of *S. tuberosa* seeds.

According to Cavalcanti *et al.* (2002a), the most suitable substrate for *S. tuberosa* germination and greater shoot height and shoot diameter is the actual Caatinga soil. Growth substrate made of soil and cattle manure (50:50 v/v) lead to the biggest canopy area and subsequent highest dry matter (CAVALCANTI *et al.*, 2002a).

Besides the generative propagation, *S. tuberosa* can be propagated by vegetative reproduction with stem cuttings (EPSTEIN, 1998; LIMA, 1996), which is of interest for the agro-industrial use of *S. tuberosa* since the uncertain and time demanding germination will be skipped. *S. tuberosa* propagated by stem cutting is not prone to form root tubers and it is not recommended to plant such trees in areas with limited soil water availability (LIMA FILHO, 2007), unless such trees are

placed in a plantation with additional irrigation. Melo *et al.* (1997) experimented a different form of vegetative propagation to produce living germplasm for genetic conservation of *S. tuberosa*. They succeeded with micro-propagation of nodal segments of one-year-old seedlings on a Murashige and Skoog medium (MS0) (MURASHIGE & SKOOG, 1962) with 0.1 mg/l BAP (6-Benzylaminopurine, C₁₂H₁₁N₅) to obtain 2.2 new sprouts on average after one week of cultivation. In the control treatment, 1.5 shoots sprouted. They also tested IBA (C₁₂H₁₃NO₂), which seemed to hamper sprouting as did higher doses of BAP. Dutra *et al.* (2012) found IBA did not have a positive effect on growth of *S. tuberosa* in their experiment as well. Even though they claim IBA promotes root growth when used to propagate *S. tuberosa* by air layering, they could not show a significant effect of IBA concentrations on the development and growth of root tissue.

In 1990 and 1991, two works were published on successful grafting of *S. tuberosa* (MENDES, 1990; PEDROSA *et al.*, 1991), which seems to be a promising method for commercial seedling production, as grafted seedlings start to produce fruits after four years, whereas non-grafted seedlings bear fruits only after 10 years (MENDES, 1990; NASCIMENTO *et al.*, 1993). Espindola *et al.* (2004) tested how two different size classes (7–9 mm; 4–6 mm) of the scion, cleft graft, and splice graft affect the development of the grafted seedling. The viability of the seedlings after 15 days did not differ between the two grafting methods and the different methods had no influence on the development of the seedlings within the first 45 days. However, the authors observed that larger scions significantly formed more sprouts than the smaller ones. A similar effect of diameter was noted by Gomes *et al.* (2010), who investigated the effect of rootstock diameter and grafting method on seedling development. They observed a positive

effect in larger diameter rootstock on the growth of grafted seedlings within the first 120 days regardless of the grafting method. In their experiment, the success of the grafting was dependent on the method chosen. The fixation of the scion was significantly higher if the splice graft was conducted regardless of the rootstock diameter. This was already observed by Araújo & Neto (2002) in their experiment. Additionally, the author stated neither the physiological nor phenological state of a tree the scion is taken from, has influence on the success of grafting, which allows grafting throughout the entire year. Six months after germination, *S. tuberosa* seedlings can already be used as rootstock for grafting, and the ability will not change until the rootstock exceeds six years of age. After six years, the success rate of grafting reduces gradually (REIS *et al.*, 2010). The effect of grafting on the tuber production of *S. tuberosa*, as seen under stem cutting conditions, has not yet been investigated.

Narain *et al.* (1992) identified an absence of plantations of *S. tuberosa*. The fruit production of Brazilian plum is limited to extractivism. Neto *et al.* (2010) observed the management of *S. tuberosa* is limited to tolerance of native trees, fruit picking, and in particular cases, protection manners against an abundant epiphyte, *Tilandsia* sp. In addition, little is known about pest and diseases of *S. tuberosa* and its fruits. Pests and pathogens associated with *S. tuberosa* are *Phasmatodea* spp., *Diabrotica speciosa* Germar, *Megalopyge lanata* Stoll, *Cryptotermes* spp., *Pinnaspis* spp., *Elsinoë* spp., *Sep-toria* spp., *Glomerella cingulata* (Stoneman) Spauld. & H. Schrenk, and *Guignardia* spp. (FREIRE & BEZERRA, 2001; NEVES & CARVALHO, 2005; TAVARES *et al.*, 1998). Two fruit flies, *Ceratitis capitata* Wiedemann, and *Anastrepha obliqua* Macquart, are associated with the Brazilian plum and are considered as postharvest pests (ARAUJO *et al.*, 2005; SILVA *et al.*, 2008b).

ECONOMIC ASPECTS

S. tuberosa is considered a multipurpose tree whose foliage is used for animal feed, and its fruits and root-tubers contribute to human diet. It also generates fuelwood, and its bark, bast and resin are utilized for therapeutic practices (LIMA, 1996; EPSTEIN, 1998; ALBUQUERQUE *et al.*, 2007; NETO *et al.*, 2010; SILVA *et al.*, 2009c). To ban the utilization of *S. tuberosa* as fuelwood, a draft law (Law Project Nº 3.548) to

prohibit felling the tree was introduced in 2004 (DUARTE, 2004).

The fruit itself is the most important product of *S. tuberosa*. It is consumed in Brazil *in natura* or processed as juice, sweet, jam, ice cream, and *umbuzada* (fruit pulp boiled with milk and sugar) (NARAIN *et al.*, 1992; NETO *et al.*, 2010). Frozen industrial processed fruit

pulp is also exported to several European countries (NARAIN *et al.*, 1992). The reported annual yields of *S. tuberosa* vary largely. Santos (1999) observed annual yields in 16 trees ranging from 4.2 kg to 184.0 kg of fresh fruits per tree, with a mean of 61.5 kg. Cavalcanti *et al.* (2008) reported annual yields ranging from 206.9 kg to 531.2 kg of fresh fruits per tree with a mean of 323.6 kg based on 66 trees. As Cavalcanti *et al.* (2011) noted an increase of fruit production owing to additional irrigation, the observed wide range in fruit yield may primarily be due to the great variation in precipitation throughout the Caatinga. Especially the precipitation in the beginning of the rain season from November to December is very important for yield formation (CAVALCANTI *et al.*, 2011). Fruit yield per tree increases in strong correlation to the canopy diameter

(SANTOS & NASCIMENTO, 1998). Thus, the variation in yield seems to be primarily defined by climatic factors and tree age (Table 3).

Family farmers involved in Brazilian plum harvest in 2007 generated an averaged additional income of 670 BRL within 55 days of harvest, which equals about two minimum wages (CAVALCANTI, 2008). If harvesting farmers or cooperatives additionally process the fruits, their benefits could increase approximately 1,025%, owing to adding value (BARRETO & CASTRO, 2010). In 2012, 7,979 t of Brazilian plum were harvested, which generated a monetary value of approximately US\$ 3,820,500 (Table 4). This underlines the economic importance of the Brazilian plum commercialization for the rural communities, especially if processing is done in the communities. Using the root tubers of *S. tuberosa*

Table 3 – Chemical composition of 100 g of the eatable portion of Brazilian plum, modified from Narain *et al.* (1992).

Constituents	
Moisture [g]	87.25
Fat [g]	0.85
Protein [g]	0.31
Crude fiber [g]	1.04
Total sugars [g]	5.38
Starch [g]	1.41
Tannin [g]	0.12
Ascorbic acid [mg]	15.80

Table 4 – Quantity and value of Brazilian plum harvest in 2012 (IBGE, 2015). 1 BRL ≈ 0.50 USD in 2012.

Federal State	Quantity (t)	Value (1,000 BRL)
Piauí	56	55
Ceará	38	53
Rio Grande do Norte	231	453
Paraíba	83	59
Pernambuco	403	281
Alagoas	34	25
Bahia	7,010	6,615
Minas Gerais	124	100

seedlings to produce pickles could generate further income for family farmers. Pickles produced of 120 days old seedlings, cultivated in washed sand and pickled with salt and ascorbic acid show a high consumer acceptance (CAVALCANTI *et al.*, 2004). To produce the needed seedlings, the authors suggested using seeds that remain from pulp or juice production, as they are already available.

A further branch of commercial exploration of *S. tuberosa* might be the oil obtained from seed kernels. The oil content of the kernels, approximately 56%, is very high compared to cashew nut (46%) or sesame seeds (49%) (BORGES *et al.*, 2007). The authors observed a favorable ratio of the oleic and linoleic fatty acids, and a high content of minerals. They suggested the oil of *S. tuberosa* may be an edible oil for food enrichment and even utilized as frying oil. Screening the oil for toxins or allergenic factors was not carried out (Table 5).

The foliage of *S. tuberosa*, which is utilized for animal feed, has a slightly higher content of crude protein during the wet season compared with other native Caatinga species, which makes it an interesting alternative animal feed (LIMA, 1996; CAVALCANTI *et al.*, 2004). The crude protein content of the foliage drops by 31% during dry season and, consequently, the *in vitro* digestibility drops from 46% to 40%. Cavalcanti *et al.* (2004) quantified the amount of foliage consumed by Caprinae during wet and dry season per *S. tuberosa*. The authors observed that Caprinae consume approximately 19 kg foliage per tree during the wet season and approximately 39 kg foliage per tree during the dry season and concluded that *S. tuberosa* is a very important alternative food source for animal husbandry in the semi-arid Northeast of Brazil. During fruit season, *S. tuberosa* contributes considerably to animal nutrition too, as one goat consumes more than ten thousand fruits per fruit season, which equals to approximately 131 kg of Brazilian plum (RESENDE *et al.*, 2004).

Table 5 – Fatty acids composition of Brazilian plum kernel and other oil plants, compiled from Borges *et al.* (2007), Ivanov *et al.* (2010), Wang *et al.* (2012), and Were *et al.* (2006).

	Fatty acids composition (%)					Ratio oleic/linoleic acid
	16:0	18:0	18:1	18:2	20:0	
Brazilian plum kernel oil	19.4	11.3	34.4	33.7	0.6	1/0.98
Sesame seed oil	8.2	4.9	37.6	47.8	0.5	1/1.27
Peanut oil	11.0	3.3	43.2	35.0	1.6	1/0.81
Soybean oil	17.0	5.2	16.0	47.6	1.4	1/2.98

SPONDIAS TUBEROSA, A MEDICAL PLANT

Among the dwellers and indigenous tribes of the Caatinga, *S. tuberosa* is considered a medical plant (ALBUQUERQUE & OLIVEIRA, 2007; ALBUQUERQUE *et al.*, 2007, 2011; ALMEIDA *et al.*, 2010; NETO *et al.*, 2010; FERREIRA JÚNIOR *et al.*, 2011). Interviews with local communities reveal that in traditional therapeutic practices, bark, bast, leaves, fruits, roots, and resin of *S. tuberosa* are used to treat numerous symptoms, such as conjunctivitis, ophthalmia, venereal diseases, digestive problems, colic, diarrhea, diabetes, menstrual disturbances, renal infection, throat afflictions, kidney inflammation, tooth pain, and “not healing cut” (ALBUQUERQUE *et al.*, 2011; FERREIRA JÚNIOR *et al.*, 2011).

None of the publications above mentioned which plant parts are used for which purposes and whether the plant parts are utilized *in natura*, as extraction or infusion. The therapeutic efficacy of *S. tuberosa* drugs may be a result of the high content of tannins and flavonoids detected in bark and fruit, which are considered as wound-healing and anti-inflammatory active (ARAÚJO *et al.*, 2008). The content of tannin and antioxidant activity varies in plants owing to environmental and genotypic factors, and plant age as summarized by Araújo *et al.* (2012). The same authors investigated whether different habitats influence the tannin content and antioxidant activity in *S. tuberosa*. They observed a sig-

nificant difference in antioxidant activity owing to the collection site, whereas the tannin concentration did not show significant difference. Since other studies showed a correlation between tannin concentration and antioxidant activity (HE *et al.*, 2011; AOUDIA *et al.*, 2013), Araújo *et al.* (2012) concluded that the antioxidant activity of *S. tuberosa* might be influenced by other metabolites, whose production and accumulation is more sensitive to differences in habitat.

Besides traditional therapeutic practices, *S. tuberosa* became the focus of academic medicine as well. In 1997, 75 Brazilian plant species, including *S. tuberosa*, were screened for antitumor active extracts (MORAES *et al.*, 1997; PESSOA *et al.*, 2006). Moraes *et al.* (1997) reported an inhibition of Walker's tumor growth of 18% after treating with a crude hydroalcoholic extract of *S. tuberosa* bark. As the authors considered the extracts active if the inhibition exceeded 40%, the extract of *S. tuberosa* was not considered antitumor active. *S. tuberosa* may provide a breakthrough for the development of an anti-dengue virus agent. The recently

developed and tested anti-dengue virus vaccine—the Sanofi Pasteur dengue vaccine—provides protection against dengue virus type 1, 3, and 4 but does not provide significant protection against dengue virus type 2 (DENV 2) (BÄRNIGHAUSEN *et al.*, 2013). *S. tuberosa* research may not provide a solution for the vaccination dilemma, but it shows promising results for developing an anti-dengue virus agent. Silva *et al.* (2011) tested secondary metabolites, phenolic compounds, of *S. tuberosa* and *Spondias mombin* for their antiviral activity against DENV 2. The authors identified two flavonoids in the leaf extract of the two *Spondias* species with antiviral activity—rutin and quercetin—and only in *S. tuberosa* both were present (Table 6). Rutin and quercetin showed *in vitro* a viral inhibiting effect of DENV 2 in C_{6/36} cells of 68.42% and 50%, respectively. In conclusion, the author stated that rutin and quercetin extracted from *S. tuberosa* leaves have potential for the development of an anti-DENV 2 agent. However, further studies with other cell lines and *in vivo* survey are required to affirm the effectiveness of these flavonoids against DENV 2 (SILVA *et al.*, 2011).

Table 6 – Quantities of flavonoids in *Spondias* species, modified from Silva *et al.* (2011).

Components	<i>S. mombin</i> (mg/g extract)	<i>S. tuberosa</i> (mg/g extract)
Rutin	n.d.*	53.38
Quercetin	41.56	169.76

*not detected

CONCLUSION

To date *S. tuberosa* is hardly domesticated (NETO *et al.*, 2012), and all experiments were virtually conducted with wild types. Additionally, no homogeneous plant material is available. The highest uniformity in plant material was achieved by grafting *S. tuberosa* seedlings at Embrapa Semiárido. Even though the scions are obtained from the same tree as well as the seeds, which formed the rootstock, the grafted seedlings are not genetically identical. Because seeds from the same stock plant are genetically heterogeneous, which is caused by self-incompatible and outcrossing feature of the reproduction system of *S. tuberosa*. In addition, some publications use the term clone or genotype erroneously for grafted *S. tuberosa* seedlings from

Embrapa Semiárido. To the best of our knowledge, neither cloning nor breeding was successfully executed to date. Owing to the lack of clones or hybrids, physiological studies conducted on *S. tuberosa* seedlings are difficult to interpret since observed outcomes may have resulted from the genetic diversity and not from applied treatments. Moreover, grafting of *S. tuberosa* is the key method for its commercial propagation in tree nurseries to obtain refined seedlings for a fast fruit production.

Besides the heterogeneity of the used plant material, comparing existing results with each other faces further constraints, which we want to illustrate with the results from the P fertilization experiments and the

seed maturation experiments. Consulting literature for the optimal P fertilization is a difficult task owing to the lack of methodological consistency among the studies. On the one hand, there are field experiments, and on the other hand, pot experiments using different bases for calculating the fertilizer dose: per plant versus per hectare versus per soil volume. Whereof the calculation based on weight per volume is rather unorthodox. Therefore, it is difficult to compare the results concerning the response of *S. tuberosa* seedlings on P fertilization. This shows a dilemma in *S. tuberosa* research, as only few studies, which are hardly comparable owing to the lack of standardization on the units used in the fertilizer application, are available. A unit, which can be supposedly deduced from the three P fertilization experiments published, is g plant⁻¹. This unit is not precise, in addition to being unserviceable.

The partly opposing findings on germination after seed maturation may result from the inconsistent conditions of the seeds storage during maturation. Araújo *et al.* (2001), Magalhães *et al.* (2007), and Lopes *et al.* (2009) stored the seeds under controlled conditions with 10°C, 22.5°C, 25°C, respectively. Only Cavalcanti *et al.* (2002a) stored the seeds under ambient conditions in dry soil, which comes close to natural conditions seeds encounter in the Caatinga. The antithetical findings may also have occurred owing to differences in the maturation of the fruits. Souza *et al.* (2005) observed a significant effect of degree of ripeness of the fruit itself on the germination of *S. tuberosa* seeds. The other authors mentioned previously did not comment on degree of ripeness of their experimental material or neglected this information. Therefore, the results are again difficult to compare owing to different experimental setups and to the lack of methodological consistency.

S. tuberosa research in general is not yet very advanced and lacks accessibility. For instance, Scopus shows only 58 hits for *S. tuberosa* in the time period between 1980 and 2015, whereas other wider distributed and economically more important members of the family Anacardiaceae, such as mango and cashew, generated 522 and 521 hits respectively in the same period. The lack of scientific work was also noted by Neves & Carvalho (2005) in their publication. The scarce availability of studies about *S. tuberosa* is present in all aspects of its research, and only a few researchers and research groups worked on *S. tuberosa*, which is reflected in the little number of different authors and their recurrence. Despite its economic and medical potential for northeast region of Brazil, we consider *S. tuberosa* scientifically neglected to date. In order to progress in *S. tuberosa* research, we suggest focusing on following research fields:

- Vegetative propagation/ cloning;
- Breeding and establishing cultivars;
- Management practices;
- Utilization as medical plant and oil source;

To increase the understanding of *S. tuberosa*, especially for its further agro-industrial exploitation and its medical use, scientific effort is still required. To avoid a depletion of the natural *S. tuberosa* population, efforts are required in breeding and management practices in order to shorten the time between germination and first fructification to make *S. tuberosa* plantations profitable. Simultaneously, efforts are required to understand *S. tuberosa* in its habitat, with its problematic reproduction in mind, in order to maintain and protect its genetic diversity.

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