

Biology, Reproductive Potential, and Winter Survival of Tropical Soda Apple (*Solanum viarum*)

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Field and greenhouse studies were conducted from 1996 to 2000 to determine tropical soda apple fruit size required for mature seed, overwintering survival potential of seeds, and growth and fruit production in a containment area near Stoneville, MS (latitude 33°25'N). Seedling emergence was $\geq 50\%$ from tropical soda apple fruit > 1.8 cm in diameter. Tropical soda apple overwintering emergence was 14, 10, 48, 42, and 13% from seed alone and 86, 83, 48, 41, and 18% for seeds in tropical soda apple fruit overwintering at 100, 0, -5, -10, and -15 cm from the soil surface, respectively. Before frost (early November), average tropical soda apple plant heights were 0.8, 0.6, and 0.7 m; plant diameters were 2.6, 1.7, and 2 m; fruit produced per tropical soda apple plant were 415, 342, 128; and plant weights were 9.9, 9.5, and 4.9 kg at 27 wk after transplanting (WATP) for 1996, 1997, and 1998, respectively. Regeneration from overwintering tropical soda apple roots varied depending on the winter conditions. These results suggest that tropical soda apple plants can survive mild winters.

Nomenclature: Tropical soda apple, *Solanum viarum* Dun. SOLVI.

Key words: Tropical soda apple, Mississippi, overwintering.

Tropical soda apple has become a pernicious weed in pastures, vegetable crops, row crops, forests, urban and natural areas in the southeastern United States (Bryson 1996; Bryson et al. 1995; Coile 1993; Hall et al. 1998; Mullahey et al. 1993). It belongs to the family Solanaceae, section *Ancanthophora*, and subgenus *Leptostemonum* (Nee 1991). In tropical climates, tropical soda apple is a perennial shrub, native to Brazil and Argentina, but has become a weed of other areas of South America, Africa, India, Nepal, West Indies, Honduras, and Mexico (Nee 1991). In the southern region of Brazil, tropical soda apple is found in scattered infestations but is not a major weed problem (Bianco et al. 1997).

Tropical soda apple was first found in Hendry County, FL (ca. latitude 26°07'N), in 1987, and identified as a potential pest in 1988 (Mullahey et al. 1993, Wunderlin et al. 1993). By 1994, tropical soda apple had spread to all 67 counties in Florida infesting over 200,000 ha of agricultural lands, which resulted in an estimated loss of \$11 million to cattle ranchers in Florida alone in 1993 (Mullahey and Cornell 1994). Since its introduction into Florida, tropical soda apple has continued to spread into Alabama, Georgia, Louisiana, Mississippi, North Carolina, Pennsylvania, South Carolina, Tennessee, Texas, and Puerto Rico (Bryson and Byrd 1994; Bryson et al. 1995; Mullahey et al. 1998; TAMU BWG 2006). Tropical soda apple spread is attributed primarily to movement of livestock, contaminated compost manure, and grass seeds from previously infested areas (Coile 1993; Mullahey and Colvin 1993). Once tropical soda apple is established in an area, it is spread by wildlife consuming the fruits and spreading the seeds in their feces (Mullahey 1996).

Because of its rapid spread and threat to U.S. agriculture, tropical soda apple was placed on the federal noxious weed list in 1996 (Bryson et al. 1995). Based on similar temperature and photoperiod requirements for growth, tropical soda apple has the potential to continue to spread in the southeastern U.S. and adjacent regions (Patterson et al. 1997).

In southern Florida and other tropical climates north of the equator, tropical soda apple blooms and produces fruits throughout the year. However, peak bloom and fruit production occurs from September through May (Mullahey et al. 1993). Tropical soda apple bloom and fruit production in Mississippi and other southern states in the United States (subtropics and temperate areas) are primarily from June until frost, with the highest numbers from late August until frost (Bryson and Byrd, unpublished data). The number of seed per fruit varies from 180 to 520; however, most fruits produce 400 to 500 seeds (Akanada et al. 1996b; Bryson et al. 1995; Coile 1993; Mullahey and Cornell 1994; Mullahey et al. 1996). Seed germination ranges from 30 to 100%, though the average germination is about 70% from mature fruit (Akanada et al. 1996a, 1996b; Mullahey 1996). The average period of seed dormancy is about 1 mo, but Pingle and Dnyansagar (1979) reported that tropical soda apple seed may remain dormant for several years.

Tropical soda apple was first collected in Mississippi in 1994, and by 1995, it had been found in 16 sites in seven Mississippi counties (Bryson and Byrd 1995). Currently, tropical soda apple has been recorded and confirmed at 37 sites in 19 Mississippi counties (Bryson and Byrd, unpublished data). However, tropical soda apple was eliminated from many of these sites, especially where single or few plants were observed. In the spring of 1995, following the discovery of tropical soda apple in southern Mississippi in 1994, field observations suggested that both seeds and mature plants could survive winters as far north as Poplarville, Pearl River County, MS (latitude 30°46'N) (Bryson and Byrd 1996). Because tropical soda apple was classified as a tropical perennial, we determined that additional

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research was needed to discover tropical soda apple survival potential north of the frost-free areas of the southern United States. The objectives of these experiments were (1) to determine tropical soda apple seed maturity as related to fruit size, (2) to determine the overwintering survival of tropical soda apple seed, and (3) to determine tropical soda apple growth and reproductive potential.

Materials and Methods

Germination from Differing Fruit Sizes. Tropical soda apple seeds were collected from 10 green fruits of each size, grouped by 0.1-cm increments (0.5 to 3.3 cm diam). Half of the harvested fruits were allowed to ripen in a greenhouse at 25 to 30 C with no supplemental lighting, and then seeds were removed from 10 ripened fruits of each size, grouped by 0.1 cm increments (0.5 to 3.3 cm diam). Parent plants were grown in a confinement field area at Stoneville, MS, in the summer of 1999 and 2000 from seeds collected in pastures southeast of Poplarville, Pearl River County, MS, during the summer of 1994. Fifty seed samples from each fruit were placed in trays on a Bosket sandy loam soil (Mollic Hapludalfs), covered lightly with soil, and allowed to germinate in the greenhouse at Stoneville, MS. Trays were subirrigated to prevent soil disturbance. Emerged seedlings were counted and removed on a weekly basis until emergence ceased (ca. 6 wk/yr). The greenhouse was maintained at 25 to 30 C with no supplemental lighting. The experiment was conducted as a randomized complete-block design with 10 replications (fruit size, 0.5 to 3.3 cm diam) and was repeated. All data were compared with ANOVA, and means were separated by Duncan's New Multiple Range test with $\alpha = 0.05$ and by regression analysis.

Winter Survival. Tropical soda apple seeds and fruit were harvested each autumn from plants that were from the same seed source as described above. Five mature (yellow) fruit of nearly uniform size (3.2 to 3.5 cm diam) or 400 seeds from mature tropical soda apple fruit were placed in nylon mesh bags sealed with hot glue. The first Monday in November of 1995, 1996, 1997, 1998, and 1999, bags of seeds and intact fruit were placed 1 m above the soil surface (suspended by string from a wire), on the surface, or buried in a Dundee sandy loam soil (Aeric Ochraqualfs) at depths of 5, 10, and 15 cm. Bags of seed and fruit were retrieved the first Monday of the following April.

Maximum air temperatures were below freezing on December 10 to 11, 1995; January 8 and 12, February 1 to 5, and December 19, 1996; January 12 to 14, 1997; December 23 to 27, 1998; January 4 to 5, 10, 1999; and December 22, 1999. Freezing temperatures at 5-cm soil depth occurred on February 3 to 8, 1996; January 11 to 14, 1997; December 27, 1998; January 5 to 6 and 11 to 14, 1999; and January 28, 2000. At the 10-cm soil depth, freezing temperatures occurred on February 5 to 6, 1996, and temperatures never reached freezing at soil depths of 15 cm at anytime during the experiment.

Tropical soda apple seeds from within each treatment were mixed and three 100-seed samples were placed in trays as

described in the experiment above on germination from differing fruit sizes. The experiment was conducted as a randomized complete-block design with three replications (trays) and was repeated five times (years). All data were analyzed by ANOVA, and means were separated by Duncan's New Multiple Range test with $\alpha = 0.05$.

Tropical Soda Apple Growth Potential and Reproduction.

Tropical soda apple plants were established in the greenhouse at Stoneville, MS in 10-cm-diam pots at 25 to 30 C. Plants 10 to 15 cm tall were transplanted into the field 4 m apart in rows 4 m apart in early to mid April of each year (1995 to 1998). Transplanted tropical soda apple plants were maintained in a containment area near Stoneville, MS, on a Dundee silt loam (fine-silty, mixed, thermic Aeric Ochraqualfs) with pH 6.3; 1.1% organic matter; soil textural fractions of 26% sand, 56% silt, and 18% clay; and a cation exchange capacity of 15 cmol/kg. Rainfall during the growing season (April 1 to November 30) was 75, 88.2, 76.4, and 65.2 cm for 1995, 1996, 1997, and 1998, respectively. The 30-yr average rainfall for the corresponding period was 81.1 cm. The numbers of tropical soda apple plants that emerged from surviving rootstock the next year were recorded once every 2 wk from May until mid June. After June, the area was sprayed with glyphosate and disked repeatedly.

Plots were hand-weeded each year to prevent interference by other weed species. Plant height, length along the row, width across the row, and number of fruits were recorded at weekly intervals through October (16 wk after transplanting [WATP]). Tropical soda apple plant weights (fruit included) were recorded in October each year. Fruit greater than 2 cm in diameter (before turning yellow) were counted, removed, and weighed from all plants once every 2 wk throughout the summer. To prevent population persistence, tropical soda apple fruits were incinerated, and plants were burned after data were collected.

The experiment was conducted as a randomized complete-block design with 10 replications (plants) and was repeated four times (years). Data were analyzed by ANOVA, means were separated by Duncan's New Multiple Range test with $\alpha = 0.05$, and tropical soda apple plant heights, diameters, and fruit numbers were subjected to regression analysis.

Results and Discussion

Germination from Differing Fruit Sizes. Tropical soda apple seeds did not emerge when removed from ripened and green fruits that were less than 1 and 1.5 cm in diameter, respectively (Figure 1). The percentage of tropical soda apple seeds that emerged at 35 to 40, 55 to 80, and $\leq 90\%$ from ripened fruit that were 1.6 to 1.8, 1.9 to 2.7, and ≥ 2.8 cm in diameter, respectively. Seeds emerged at 10 to 20, 30 to 80, and $\geq 70\%$ from green fruits that were 1.6 to 1.8, 1.9 to 2.7, and ≥ 2.8 cm in diameter, respectively. These data indicate tropical soda apple seed are sufficiently mature to germinate before the fruit colors change from green to yellow, confirming results previously reported by Mullahey et al. (1996). However, ripened fruits (yellow) provided greater potential for seed germination than from green fruits for fruit

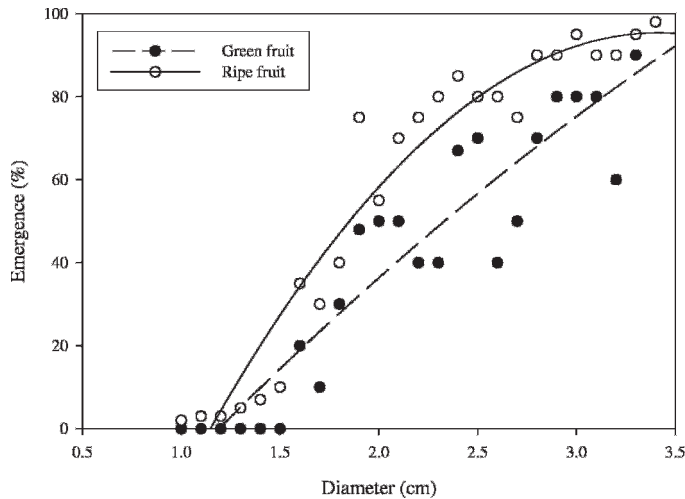


Figure 1. Tropical soda apple seed germination from green and ripened fruit at Stoneville, MS, in 1999 and 2000 (green fruit: $y = -61.44 + 55.56x - 3.3x^2$, $r^2 = 0.9$; and ripened fruit: $y = -121.05 + 126.73x - 18.55x^2$, $r^2 = 0.9$).

size ≤ 2.9 cm in diameter (Figure 1). Seed germination did not differ between green and ripened fruits ≥ 3 cm in diameter. Mullahey (1996) reported that white tropical soda apple seed did not germinate and that seed germination was not linked to fruit maturity (color), but rather to fruit size (Mullahey et al. 1996). Thus, tropical soda apple plants with fruit < 1.0 cm. in diameter can be hand-removed or mowed without special treatment to destroy fruits or seeds.

Winter Survival. No significant ($\alpha = 0.05$) treatment-by-year interaction occurred for tropical soda apple seed emergence; therefore, data were combined for all years. An average of 14, 10, 48, 42, and 13% of tropical soda apple plants emerged from exposed seeds overwintered without fruit at 100, 0, -5, -10, and -15 cm in relation to the soil surface, respectively at Stoneville, MS (Figure 2). An average of 86, 83, 48, 41, and 18% emerged from seeds overwintered

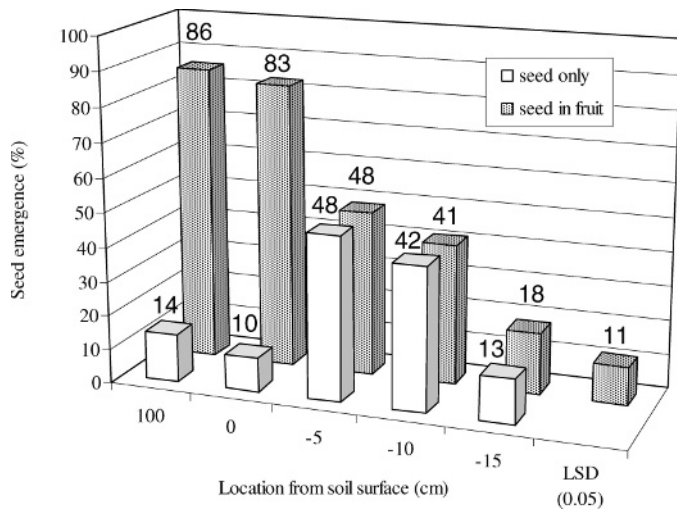


Figure 2. Tropical soda apple winter survival of seeds exposed or retained within fruit at Stoneville, MS, from 1995 to 1999.

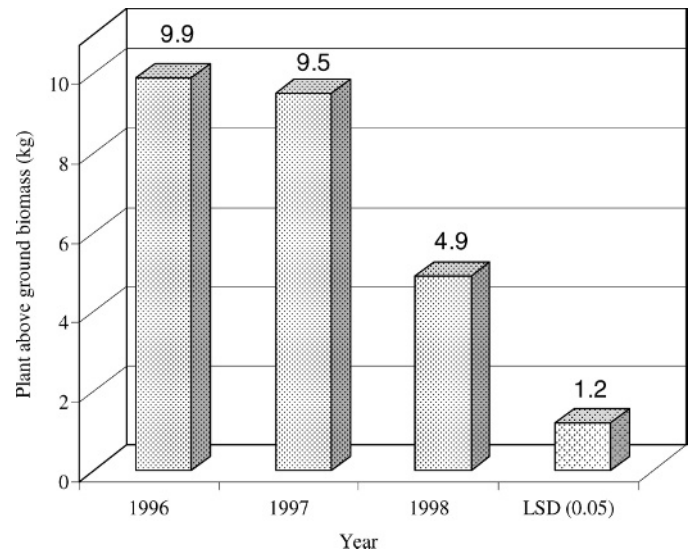


Figure 3. Tropical soda apple dry weights from field-grown plants in 1996, 1997, and 1998 at Stoneville, MS.

within fruit at 100, 0, -5, -10, and -15 cm in relation to the soil surface, respectively. Overwintering tropical soda apple seed within intact fruits at, or above, the soil surface enhanced seed survival rates. Germination rates for seeds overwintered in fruits at or below the soil surface were equivalent to those of exposed seeds overwintering without fruits at the same depths. Fruit deterioration through the winter at or below the soil surface may explain why seedling emergence rates were similar regardless of whether seed were inside or outside the fruit.

Tropical Soda Apple Growth Potential and Reproduction.

In 1998, tropical soda apple plant weights were about half those in 1996 and 1997, presumably because of fewer and smaller fruit and a dryer and hotter summer (Figure 3).

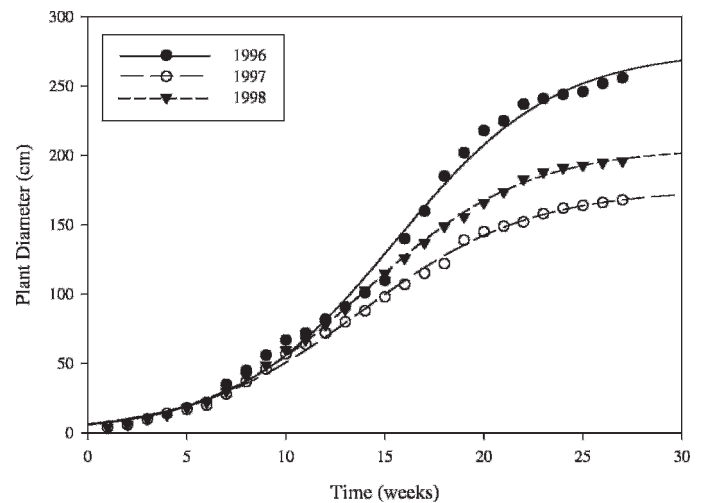


Figure 4. Tropical soda apple mean plant diameters for field-grown plants in 1996, 1997, and 1998 at Stoneville, MS (1996: $y = 275.85/[1 + \exp\{-(x - 15.52)/4.04\}]$, $r^2 = 0.99$; 1997: $y = 175.54/[1 + \exp\{-(x - 13.83)/4.25\}]$, $r^2 = 0.99$; and 1998: $y = 205.43/[1 + \exp\{-(x - 14.03)/4.04\}]$, $r^2 = 0.99$).

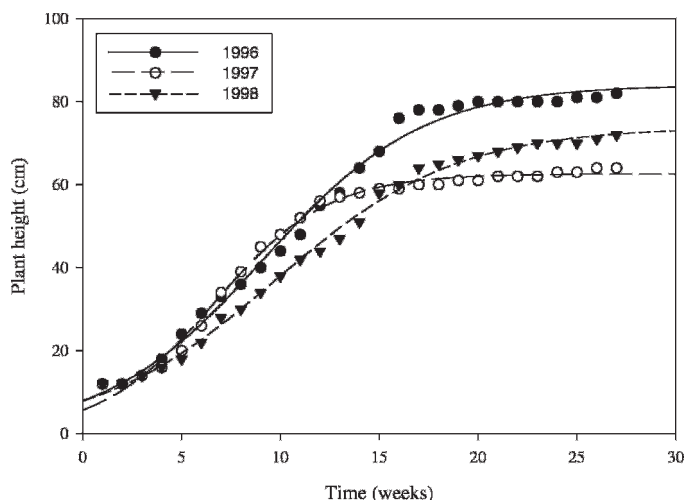


Figure 5. Tropical soda apple mean plant heights for field-grown plants in 1996, 1997, and 1998 at Stoneville, MS (1996: $y = 83.99 / \{1 + \exp[-(x - 9.14) / 4.04]\}$, $r^2 = 0.99$; 1997: $y = 62.59 / \{1 + \exp[-(x - 6.62) / 2.87]\}$, $r^2 = 0.99$; and 1998: $y = 73.82 / \{1 + \exp[-(x - 9.73) / 4.57]\}$, $r^2 = 0.99$).

Tropical soda apple plants were larger in 1996 than in 1997 and 1998 (Figures 4 and 5). Also in 1996, tropical soda apple plant diameters were greater by late October and late August, respectively, than in 1997 and 1998. In 1996, the largest tropical soda apple plant was about 2 m across and produced about 900 fruit in a single season (data not shown). Larger tropical soda apple plants may be a result of more-frequent rainfall events in 1996 than in 1997 or 1998; however, tropical soda apple fruit production in 1996 and 1997 did not differ significantly (Figure 6). Tropical soda apple fruit production was greatest from early September (19 WATP) until frost (Figure 6). Unlike Florida populations, which produce the majority of fruit between September and May (Mullahey et al. 1993), tropical soda apple produce the majority of fruit between September and November, and tropical soda apple fruit productions ceased at Stoneville, MS, following the first freezing temperatures each autumn.

No tropical soda apple plants emerged from rootstocks of the previous year in 1996 and 1997, but 85% of tropical soda apple plants survived the winter of 1997 to 1998. The winter of 1997 to 1998 was warmer than normal for Stoneville, MS (0 d with maximum temperatures below freezing), and warmer than the winters of 1995 to 1996 and 1996 to 1997, with 4- and 2-d periods with maximum temperatures below freezing, respectively. Akanda et al. (1996b) reported that tropical soda apple seed production was 24% greater in plants that overwintered from rootstock (72,435 seeds) than from seedling plants (50,770 seeds). Our data on plant growth and survival of overwintering seed indicate tropical soda apple can persist through a mild winter, resulting in higher population levels the following spring and can function as a facultative annual when seedling emergence is early enough for plants to produce fruit before frost.

Results of this research indicated that tropical soda apple seeds survived the winters of 1995 to 1999, and tropical soda apple plants were able to survive winter conditions near Stoneville, MS, in only 1 of 3 yr. It is apparent that tropical

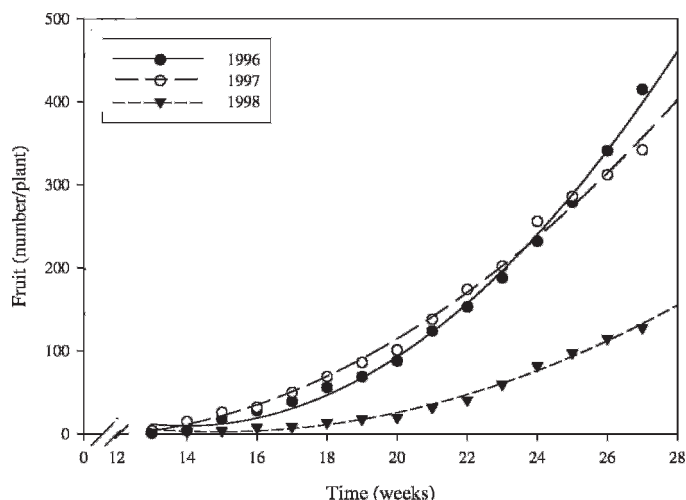


Figure 6. Tropical soda apple mean fruit and plants from field-grown plants in 1996, 1997, and 1998 at Stoneville, MS (1996: $y = 18.72 - 9.11x + 2.3x^2$, $r^2 = 0.99$; 1997: $y = -1.48 + 3.78x + 1.34x^2$, $r^2 = 0.99$; and 1998: $y = 9.9 - 5.14x + 0.9x^2$, $r^2 = 0.99$).

soda apple plants have the ability to survive warmer-than-normal winters (all maximum temperatures ≤ 0 C) at 33°N latitude and that tropical soda apple will persist as an annual in areas where it cannot survive winters as a perennial. Seeds from intact fruits exhibited higher levels of germination than exposed seeds. Survival modes of tropical soda apple seeds and rootstocks should be taken into account in formulating best-management practices for this pernicious, invasive weed.

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