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Growth, Development, and Morphological Differences among Native and Nonnative Prickly Nightshades (*Solanum* spp.) of the Southeastern United States

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Prickly nightshades are troublesome weeds of natural habitats, pastures, feedlots, right-of-ways, and croplands. Native and nonnative invasive weedy species of prickly nightshades were compared to determine growth, development, and morphological differences. Six (*Solanum bahamense*, *Solanum capsicoides*, *Solanum carolinense*, *Solanum dimidiatum*, *Solanum donianum*, and *Solanum pumilum*) of the 18 species of prickly nightshades studied are native to the US. Two species, *Solanum citrullifolium* and *Solanum rostratum*, are annuals; the others are perennials or are short lived perennials or annuals in northern extremes of their range in North America. Tables were developed from new and existing data to differentiate vegetative and reproductive characteristics among 18 species of prickly nightshade found in the southeastern US. In greenhouse experiments, average plant height ranged from 24 and 26 cm (9.45 and 10.24 inch) for *S. carolinense* and *Solanum jamaicense*, respectively, to 100 and 105 cm for *Solanum tampicense* and *Solanum sisymbriifolium*, respectively at 10 wk after emergence (WAE). By 10 WAE, the average number of leaves per plant ranged from < 10 for *S. carolinense* and *Solanum torvum* to > 40 leaves/plant for *S. rostratum* and *S. dimidiatum*. Average number of nodes/plant main stem ranged from 11, 12, and 14 nodes in *S. jamaicense*, *S. torvum*, and *S. carolinense*, respectively, to 54 nodes in *S. rostratum*. Average plant dry weights were collected at 10 WAE and were greatest for *Solanum mammosum* and (> 17 g/plant) (0.6001 oz/plant) and least for *S. carolinense* (1 g/plant). Based on these data, nightshade growth rate and dry weight were variable among some species and variability may be a result of phenology and life cycles, annual or perennial. Plants of *S. rostratum*, an annual, were relatively tall and produced high number of nodes and leaves and had the shortest period from emergence to flower among the prickly nightshades evaluated.

Nomenclature: Bahama nightshade, *Solanum bahamense* L.; buffalobur, *Solanum rostratum* Dunal SOLCU; eggplant, *Solanum melongena* L.; fuzzyfruit nightshade, *Solanum candidum* Lindl.; hairy horsenettle, *Solanum pumilum* Dunal; Himalayan nightshade, *Solanum myriacanthum* Dunal; horsenettle, *Solanum carolinense* L. SOLCA; Jamaican nightshade, *Solanum jamaicense* P. Mill.; mullein nightshade, *Solanum donianum* Walp.; nipplefruit nightshade, *Solanum mammosum* L.; red soda apple, *Solanum capsicoides* All. SOLCI; robust horsenettle, *Solanum dimidiatum* Raf. SOLDM; silverleaf nightshade, *Solanum elaeagnifolium* Cav. SOLEL; sticky nightshade, *Solanum sisymbriifolium* Lam. SOLSI; tropical soda apple, *Solanum viarum* Dunal SOLVI; turkeyberry, *Solanum torvum* Sw. SOLTO; watermelon nightshade, *Solanum citrullifolium* A. Braun SOLCF; and wetland nightshade, *Solanum tampicense* Dunal.

Key words: Solanaceae, invasive weed, invasive nightshades, morphological characterization.

Native and nonnative prickly nightshades (*Solanum* spp.: subgenus *Leptostemonum*) (Weese and Bohs 2007) of the southeastern US include species that are troublesome weeds of pastures, feed lots, right-of-ways, croplands, and natural habitats, while some species require restricted habitats and are rare (Allison and Stevens 2001; Bryson and DeFelice 2009; Fox and Bryson 1998; Mullahey 1996; Wunderlin et al. 1993). In agricultural settings, many prickly

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Management Implications

Many prickly nightshade species are troublesome weeds of natural habitats, feed lots, pastures, croplands, and right-of-ways in the southeastern US. Six (*Solanum bahamense*, *Solanum capsicoides*, *Solanum carolinense*, *Solanum dimidiatum*, *Solanum donianum*, and *Solanum pumilum*) of the 18 species of prickly nightshades studied are native to the US. Two species, *Solanum citrullifolium* and *Solanum rostratum,* are annuals; the others are perennials or are short lived perennials or annuals in northern extremes of their range in north America. Morphological traits of native and nonnative prickly nightshades were compared and charts were developed to distinguish species using vegetative and reproductive characteristics. In greenhouse experiments, basic biological data determined that germination and growth rate, plant height, number of leaves and nodes, plant biomass, and time to flowering varied among 11 of the most troublesome weedy species of prickly nightshade. An annual, *Solanum rostratum*, grew and produced flowers faster than prickly nightshade species that were perennials. These biological and morphological data will be used to determine the most vulnerable stage for effective control strategies and methods of prickly nightshades.

nightshades interfere with crop production and harvest, and reduce yield and feed, fiber, and food quality. For example, *Solanum rostratum* Dunal (buffalobur) and *Solanum elaeagnifolium* Cav. (silverleaf nightshade) are troublesome in cotton production; *Solanum carolinense* L. (horsenettle) is an important weed of corn and peanut production (Armel et al. 2003; Green et al. 1988; Hackett et al. 1987; Mullahey et al. 1993a; Prostko et al. 1994; Rushing et al. 1985; Smith et al. 1990; Whaley and VanGessel 2001); others are highly invasive and difficult to control in pastures (Albert 1960; Gorrell et al. 1981; Mullahey 1996), gardens (Frank 1990) and natural areas (Bryson 1996; Coile 1993; Diaz et al. 2008; Hall et al. 1998; Mullahey and Colvin 1993).

While many of the prickly nightshades are invasive or troublesome weeds of agricultural production systems, some species are toxic to humans and wildlife or cause mechanical injury to humans, livestock, and native fauna; others are edible and widely cultivated (Bryson and DeFelice 2009; Burrows and Tyrl 2001; DiTomaso and Healy 2007; Mullahey et al. 1993b; Mullahey et al. 1996; Mullahey et al. 1998; Wang et al. 2008). *Solanum mammosum* L. (nipplefruit nightshade) and *Solanum capsicoides* All. (red soda apple) are used for insecticidal and mammal pest control in areas of Central and South America (Nee 1991). Edible species such as *Solanum melongena* L. (eggplant) are cultivated and not considered weedy in the US; however, *S. melongena*'s wild ancestors were garden weeds in southeastern Asia prior to human domestication (Wang et al. 2008). *Solanum torvum* Sw. (turkeyberry) is also cultivated for human consumption, but when it escapes cultivation, it becomes an aggressive perennial and spreads into agricultural and natural areas (Bryson and DeFelice 2009). Three species of prickly nightshades, *Solanum viarum* Dunal (tropical soda apple), *S. torvum*, and *Solanum tampicense* Dunal (wetland nightshade), are currently on the Federal Noxious Weeds List (APHIS 2010). Of these three species, *S. viarum* spread rapidly from its initial introduction point in Florida into other southeastern US through livestock movement. It now infests millions of ha of pasture lands and natural areas (Bryson and Byrd 1994, Bryson and Byrd 1996; Bryson et al. 1996; Everest and Ball 1995; Mullahey et al. 1993a; Mullahey et al. 1998). Development of biological control methods for weedy prickly nightshades using insects and pathogens is made more difficult because each control agent must be host-specific for an individual species or group of weedy species without harming nightshade crops and rare or threatened prickly nightshade species (Medal et al. 2002).

Other prickly nightshades are considered rare natives and are restricted to unique habitats. For instance, *Solanum pumilum* Dunal (hairy horsenettle) was thought to be extinct, but was rediscovered on Ketona Dolomite glades in Bibb County, Alabama (Allison and Stevens 2001). *Solanum bahamense* L. (Bahama nightshade) and *Solanum donianum* Walp. (mullein nightshade) are uncommon natives in extreme southern Florida and are uncommon and are not considered weedy (FL Atlas 2011). *Solanum donianum* is listed as a threatened species in Florida because of lost habitat and low population levels (FL Atlas 2011). *Solanum myriacanthum* Dunal (Himalayan nightshade) is a nonnative reported to occur in Louisiana, though it has not been observed recently (Nee 1979; 1991).

Germination characteristics of *S. viarum* (Akanda et al. 1996b; Pingle and Dyansagar 1979) and biology and growth parameters of *S. viarum* (Akanda et al. 1996a; Mullahey and Cornell 1994; Patterson et al. 1997) and *S. tampicense* (Fox and Wigginton 1996; Fox and Bryson 1998) have been reported; however, little research has been conducted to determine intra- and inter-species growth and development parameters of all prickly nightshades in the southeastern US. Likewise, there is no comprehensive diagnostic tool to identify these prickly nightshades in the vegetative and reproductive growth stages. The objectives of this research were 1) to determine diagnostic characteristics that separate 18 weedy and nonweedy prickly nightshades of the southeastern US and 2) to quantify growth parameters among eleven of the most common and troublesome weedy prickly nightshades.

Materials and Methods

Comparative Morphological Evaluations. Fruits of *S. bahamense*, *S. rostratum*, *S. melongena*, *Solanum candidum* Lindl. (fuzzyfruit nightshade), *S. pumilum*, *S. carolinense*, *Solanum jamaicense* P. Mill. (Jamaican nightshade), *S.*

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Table 1. Collection locations for herbarium and seeds of 17 prickly *Solanum* species used to evaluate morphological characteristics and growth parameters in lab and greenhouse studies at Stoneville, MS.

Species		State	County	Latitude and Longitude
Scientific name	Common name			
S. bahamense	Bahama nightshade	Florida	Monroe	24 38.42N 81 19.56W
S. rostratum	Buffalobur	Mississippi	Bolivar	33 40.28N 91 01.38W
S. melongena	Eggplant	Mississippi	Washington[a]	33 24.14N 90 54.34W
S. candidum	Fuzzyfruit nightshade	Florida	Alachua[b]	29 38.31N 82 18.25W
S. pumilum	Hairy horsenettle	Alabama	Bibb	33 01.50N 87 08.33W
S. carolinense	Horsenettle	Mississippi	Leflore	33 25.17N 90 14.10W
S. jamaicense	Jamaican nightshade	Florida	Collier	26 24.35N 81 22.18W
S. donianum	Mullein nightshade	Florida	Alachua[b]	29 38.31N 82 18.25W
S. mammosum	Nipplefruit nightshade	Puerto Rico	San Sebastián	18 20.13N 66 59.26W
S. capsicoides	Red soda apple	Georgia	Berrien	31 13.06N 83 15.36W
S. dimidiatum	Robust horsenettle	Oklahoma	Canadian	35 38.26N 98 17.12W
S. elaeagnifolium	Silverleaf nightshade	Mississippi	Washington	33 23.46N 90 50.44W
S. sisymbriifolium	Sticky nightshade	Mississippi	Harrison	30 29.53N 89 07.43W
S. viarum	Tropical soda apple	Mississippi	Pearl River	30 45.00N 89 29.12W
S. torvum	Turkeyberry	Florida	Dade	25 26.59N 80 30.27W
S. citrullifolium	Watermelon nightshade	New Mexico	Catron	33 17.19N 108 52.46W
S. tampicense	Wetland nightshade	Florida	DeSoto	27 13.22N 81 52.34W

[a] Plants grown in garden.

[b] Plants grown at University of Florida, Alachua County for research.

donianum, *S. mammosum*, *S. capsicoides*, *Solanum dimidiatum* Raf. (robust horsenettle), *S. elaeagnifolium*, *Solanum sisymbriifolium* Lam. (sticky nightshade), *S. viarum*, *S. torvum*, *Solanum citrullifolium* A. Braun (watermelon nightshade), and *S. tampicense* were collected from Alabama, Florida, Georgia, Mississippi, New Mexico, Oklahoma, and Puerto Rico (Table 1) and the number of seeds were counted for 20 fruits for each species, with the exception of *S. pumilum* (3 fruit). Seeds of each species were placed on surface of a 7 cm deep 1:1 mixture of potting media (Jiffy mix, Jiffy Products of America Inc., Batavia, IL 60510) and soil (Bosket sandy loam, fine-loamy, mixed thermic Mollic Hapludalfs) and covered lightly with the soil mixture in 25 by 40-cm trays. Trays were subirrigated as needed. *Solanum carolinense* and *S. dimidiatum* trays were placed inside clear plastic bags to increase temperature and humidity to promote seed germination (Mike Chandler, personal communication). Plants were grown in a glass greenhouse at Stoneville, MS, until the first fruit was mature with the exception of *S. citrullifolium* and *Solanum myriacanthum* Dunal (Himalayan nightshade). Data were obtained from herbarium specimens of *S. citrullifolium* collected in New Mexico and *S. myriacanthum* collected from Mexico (vouchers at Missouri Botanical Gardens) and data from Nee (1979). Plants and fruit were harvested, dried on a plant dryer at 40 ± 3 C (104 F) for 2 weeks, and preserved as a herbarium specimen. Vouchers were deposited in the Crop Production Systems Research Unit herbarium (SWSL) which is now on permanent loan to the Mississippi Museum of Natural Science (MMNS) in Jackson, MS. Various plant measurements, parameters, and characteristics were recorded, compared to available literature, and used to construct interspecies comparative morphological characteristic tables. Many of these characters, such as seeds per fruit, were unavailable for most species of these prickly nightshades. All measurements smaller than 10 cm were obtained with a Mitutoyo digital plastic caliper (Forestry Supplier, Inc., 205 West Rankin Street, Jackson, MS). Origins and morphological characteristics of prickly nightshade species were obtained from various sources (Bryson and DeFelice 2009; Correll and Johnston 1979; D'Arcy 1974; DiTomaso and Healy 2007; McGregor and Barkley 1986; Nee 1991; Radford et al. 1968; Small 1933; Standley 1924; Steyermark 1963).

Differential Growth and Development Studies. Fruits of *S. rostratum*, *S. carolinense*, *S. jamaicense*, *S. mammosum*, *S. capsicoides*, *S. dimidiatum*, *S. elaeagnifolium*, *S. sisymbriifolium*, *S. viarum*, *S. torvum*, and *S. tampicense* were collected (Table 1) and seeds were removed after the fruit had fully ripened and begun to wither. Seeds were germinated in soil mixture as mentioned above in the comparative morphology evaluation study during early June in a glass greenhouse at Stoneville, MS. Planting dates were staggered because seed germination period varied in preliminary

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Table 2. Origin and vegetative characteristics for 18 native and nonnative prickly *Solanum* species from the southeastern US.

Species	Origin	Roots/life cycle	Stems	Leaves
S. bahamense	Native of Caribbean islands and southern Florida	Taproot; perennial	Shrub 1.0–3.8 m tall; prickles sparse	Lanceolate; trichomes stellate
S. rostratum	Native of Central America	Taproot; annual	Herb 0.3–0.8 m tall; prickles straight, dense	pinnatifid, lobes rounded at apices, petiole 1/2 as long as blade; prickles, dense; trichomes scattered
S. melongena	Native of Asia, cultivated for fruit	Taproot; annual as a vegetable crop	Herb 0.5–1.5 tall; prickles hooked, sparse	Ovate, irregularly sinuate; trichomes dense
S. candidum	Native of Central America	Taproot; perennial	Shrub 0.3–1.0 m tall; prickles dense	Ovate to elliptic-lanceolate, irregularly sinuate lobed, prickles purple, up to 3.0 cm long, on veins; trichomes dense
S. pumilum	Native of North America, rare endemic of Alabama and Georgia	Taproot with lateral rhizomes; perennial	Shrub 0.2–0.3 m tall; prickles few, small, scattered	Ovate to oblong ovate, entire or shallowly sinuate, prickles very few, trichomes dense
S. myriacanthum	Native of Central America	Shallow taproot with lateral rhizomes; perennial	Shrub 0.5–1.5 m tall; prickles slender, straight, slightly curved or stout recurved, scattered	Suborbicular or broadly ovate, shallowly lobed; trichomes, simple and stellate (below), glandular, dense
S. carolinense	Native of North America	Deep taproot with lateral rhizomes; perennial	Shrub 0.3–1.0 m tall; prickles scattered	Ovate to elliptic-lanceolate, irregularly sinuate; prickles scattered; trichomes stellate
S. jamaicense	Native of Central America	Taproot; perennial	Shrub 0.5–1.0 m tall; prickles dense, hooked, stout	Ovate, sinuate–irregularly lobed, triangular, large and small leaf paired, subacute; petiole winged; prickles, dense, hooked; trichomes dense
S. donianum	Native of Caribbean islands and Florida	Taproot; perennial	Shrub 1.0–3.0 m tall; prickles sparse	Lanceolate, trichomes sparse
S. capsicoides	Native of North and South America	Taproot; perennial	Shrub 0.3–1.0 m tall; prickles dense	Ovate-triangular, sinuate-lobed, subobtuse or subulate; prickles, dense, trichomes scattered, stellate
S. dimidiatum	Native of North America	Deep taproot with lateral rhizomes; perennial	Shrub 0.5–1.2 m tall; prickles scattered	Ovate to elliptic-lanceolate, irregularly sinuate lobed or parted; prickles scattered; trichomes stellate
S. mammosum	Native of Central and South America	Shallow taproot with fleshy lateral rhizomes; perennial	Shrub 0.5–1.2 m tall; prickles hooked and straight, scattered	Ovate-triangular, sinuate-lobed, lobes subobtuse or subacute; prickles straight scattered; trichomes dense
S. elaeagnifolium	Native of South America	Deep taproot with lateral rhizomes; perennial	Shrub 0.5–1.2 m tall; prickles thin, scattered	Linear to oblong ovate, entire or shallowly sinuate; prickles sparse, straight; trichomes dense, stellate
S. sisymbriifolium	Native of South America	Deep taproot with lateral rhizomes; perennial	Shrub 0.4–1.5 m tall; prickles straight, dense	Pinnatifid, lobes with mucros, acute or obtuse at apices; petiole < 1/2 as long as blade, prickles straight yellow to orange, dense; trichomes glandular, sticky
S. viarum	Native of South America (Brazil and Argentina)	Shallow taproot with lateral fleshy rhizomes; perennial	Shrub 0.5–2.0 m tall; prickles hooked and straight, scattered	Ovate-triangular, sinuate-lobed, lobes subobtuse or subacute, prickles straight, scattered; trichomes viscid, dense, straight or stellate
S. torvum	Native of South America	Taproot with lateral rhizomes; perennial	Shrub 0.4–3.0 m tall; prickles sparse	Elliptic, oval, ovate or oblong, entire or irregularly lobed, acute or obtuse, highly variable; prickles straight or few hooked; trichomes dense, stellate

Table 2. Continued

Species	Origin	Roots/life cycle	Stems	Leaves
S. citrullifolium	Native of Central America	Taproot; annual	Herb 0.2–0.8 m tall; prickles straight, dense	Pinnatifid, lobes rounded at apices, petiole 1/2 as long as blade; prickles dense; trichomes scattered
S. tampicense	Native of Central and South America	Taproot; perennial	Sprawling or clambering shrub, 1.0–5.0 m long; prickles hooked	Ovate lanceolate, irregularly sinuate-lobed; prickles straight abaxial and hooked adaxial scattered; smooth or trichomes sparse

germination studies. For example, average days from planting to seedling emergence were 7 to 8 d for *S. rostratum*, *S. elaeagnifolium*, and *S. viarum* while average *S. carolinense* seedling emergence was 23 d after planting. When all species germinated, plants at the first true leaf stage were selected and one plant per species was transplanted into a 30-cm-diam plastic pot filled with the previously mentioned mixture of potting media and soil. Plants were maintained in a greenhouse set to 30/22 C (± 3 C) day/night temperature. Light was supplemented with sodium vapor lamps to provide 14 h of photoperiod. Plants were subirrigated as needed and were grown in the greenhouse until final measurements were taken. Plant height, number of nodes on the main stem, and number of leaves were recorded for each plant for 10 WAE, and the above ground portion of the plants was harvested, placed in paper bags, dried on a plant dryer at 40 ±3 C for two weeks, and dry weights recorded.

Statistics. The differential growth and development greenhouse experiment was established as a randomized complete block with species as treatments and seven plants (pots) of each species as replications. The experiment was repeated in separate greenhouse bays with experiment initiation at 3 wk apart. Because there were no time by treatment (species) interaction, data were combined and subjected to analysis of variance, and means were separated at the 5% level of significance by Fisher's protected LSD test using SAS (Statistical Analysis Systems (SAS) software, Version 9.1. SAS Institute Inc., Box 8000, SAS Circle, Cary, NC). The box plots for plant dry weights were constructed with Sigma Plot (Sigma Plot 10.0, Systat Software Inc., San Jose, CA).

Results and Discussion

Comparative Morphological Evaluations. Origin and vegetative characteristics of species evaluated in this study are presented in Table 2 and the reproductive characteristics are presented in Table 3 and illustrated in Figures 1 and 2. To our knowledge, this is the first report of selected characteristics and parameters of these prickly nightshades. Likewise, these are the first comprehensive diagnostic charts to compare and contrast these species within the context of a single publication. For instance, the numbers of seeds per fruit were reported for *S. viarum* and *S. tampicense* (Bryson and DeFelice 2009; Fox and Bryson 1998; Mullahey and Cornell 1994), but this information was lacking for other prickly nightshades of the southeastern US.

Origin. Six of the 18 species of prickly nightshades listed here are reported to be natives of the US and they are *S. bahamense*, *S. capsicoides*, *S. carolinense*, *S. dimidiatum*, *S. donianum* and *S. pumilum* (Table 2). Two species, *S. citrullifolium* and *S. rostratum*, are annuals; the others are

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Table 3. Reproductive characteristics for 18 native and nonnative prickly *Solanum* species from the southeastern US.

Species	Flowers	Fruits	Seeds
S. bahamense	1.5–2.5 cm wide; corolla violet-blue to white, deeply lobed; petals narrow, anthers same length	0.6–1.0 cm diam, round, green, turning red at maturity	0.5–1.0 mm wide, compressed, tan or light brown, 20–60 per fruit
S. rostratum	2.0–2.5 cm wide; corolla bright yellow, shallowly lobed, star-shaped, rotate, apex rounded; one anther longer than others	1.5–2.0 cm diam, dry berry completely enclosed prickled calyx; prickles covering calyx	1.8–2.5 mm wide, compressed, shiny brown to black, pitted, 20–60 per fruit
S. melongena	2.0–5.0 cm wide; corolla lavender to purple, shallowly lobed; petals 5, recurved, anthers same length	7.0–30.0 cm diam, elongate or obovoid, pale green with dark green veins, turning light green or dark purple at maturity	2.0–3.0 mm wide, compressed, yellowish-orange to tan, 300+ per fruit
S. candidum	3.5–4.0 cm wide; corolla white, shallowly lobed, star-shaped, anthers same length	2.5–5.0 cm diam, round, pale yellow, turning orange at maturity, covered with golden-yellow trichomes	1.5–2.5 mm wide, compressed, yellowish brown, 75–330 per fruit
S. pumilum	1.8–2.4 cm wide; corolla white, shallowly lobed, star-shaped, anthers same length	1.4–1.8 cm diam, round, green with light green mottling, turning yellow at maturity	1.5–2.5 mm wide, compressed, glossy yellowish-orange or brown, 16–40 per fruit
S. myriacanthum	0.7–1.5 cm wide; corolla yellowish green to white, deeply lobed; petals 5, recurved; anthers same length	2.0–3.0 cm diam, round, pale green with dark green veins, turning yellow at maturity	2.7–3.1 mm wide, compressed, brownish tan, 200–320 per fruit
S. carolinense	2.5–3.0 cm wide; corolla white or lavender, shallowly lobed, star-shaped, anthers same length	1.8–2.0 cm diam, round, green with light green mottling at calyx end, turning dull yellow at maturity	2.0–3.0 mm wide, compressed, glossy yellowish-orange or brown, 40–120 per fruit
S. jamaicense	1.0–1.25 cm wide; corolla white, deeply lobed; anthers same length	0.7–1.0 cm diam, round, green with dark green veins, turning yellow then reddish orange at maturity, lustrous	0.8–1.2 mm wide, compressed, tan or light brown, 20–60 per fruit
S. donianum	1.0–1.6 cm wide, corolla white, deeply lobed; anthers same length	1.0–1.5 cm diam, round, green, turning yellow then red-orange at maturity	2.0–3.0 mm wide, compressed, tan to light brown, 18–20 per fruit
S. mammosum	1.8–3.0 cm wide; corolla lavender to purple, deeply lobed; recurved, anthers same length	0.5–7.0 cm diam, ovoid or ellipsoid, nipples 1–5, proximal and/or one terminal, pale green with dark green veins, turning yellow to orange-yellow at maturity, lustrous	2.8–3.2 mm wide, compressed, dark brown, lustrous, 200–460 per fruit
S. capsicoides	0.5–2.5 cm wide; corolla white, deeply lobed; anthers same length	2.0–5.0 cm diam, round, pale green, turning yellow then persimmon red to scarlet at maturity	3.0–6.0 mm wide, compressed, tan to dark brown, winged, margins hyaline, 160–420 per fruit
S. dimidiatum	3.0–5.0 cm wide; corolla bluish violet to lavender, rarely white, shallowly lobed, star-shaped; anthers same length	2.4–3.0 cm diam, round, green with light green mottled, turning yellow at maturity	2.5–3.5 mm wide, compressed, yellowish-orange or brown, glossy, 40–120 per fruit
S. elaeagnifolium	2.0–2.5 cm wide; corolla bluish violet to violet, shallowly lobed, star-shaped, anthers same length	1.5–2.0 cm diam, round, green with light green mottled, turning yellow at maturity	2.5–4.0 mm wide, compressed, yellowish-orange or brown, lustrous, 40–120 per fruit

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Table 3. Continued.

Species	Flowers	Fruits	Seeds
S. sisymbriifolium	2.0–2.5 cm wide; corolla white, shallowly lobed, star-shaped; anthers same length	1.6–2.0 cm diam, round, green, turning yellow then bright red at maturity; calyx prickly, loosely surrounds fruit until maturity, then splits to expose fruit	1.2–2.5 mm wide, compressed, tan to light brown, 18–60 per fruit
S. viarum	0.7–1.5 cm wide; corolla white, deeply lobed, petals recurved; anthers same length	2.5–4.5 cm diam, round, pale green with dark green veins, turning dull yellow at maturity	1.8–2.5 mm wide, compressed, light brown, minutely rough, 180–420 per fruit
S. torvum	2.0–2.5 cm wide; corolla white, shallowly lobed, star-shaped; anthers same length	1.0–1.5 cm diam, round, green, turning yellow then orange or brown at maturity	1.2–2.5 mm wide, compressed, light brown, 80–240 per fruit
S. citrullifolium	1.5–2.0 cm wide; corolla violet or lavender, shallowly lobed, star-shaped, apex rounded, rotate; one anther longer than others	1.0–1.5 cm diam, dry berry completely enclosed prickled calyx; prickles covering calyx	1.4–2.5 mm wide, compressed, shiny, dark brown, 20–60 per fruit
S. tampicense	0.5–1.5 cm wide; corolla white to creamy-white, deeply lobed, petals straight or slightly recurved; anthers same length	0.8–1.0 cm diam, round, green, turning yellow then red at maturity, lustrous	1.8–3.0 mm wide, compressed, light brown to light yellowish brown, 18–50 per fruit

perennials or are short lived perennials or annuals in northern extremes of their range in north America. The native range of *S. elaeagnifolium* may be the southwestern US and Mexico or Central and South America, where it was subsequently transported by early Spanish explorers (Boyd et al. 1984). Most of the introduced prickly nightshades are from Central and South America or from the Caribbean Islands and have also been introduced within the past two centuries (Mullahey and Cornell 1994; Wunderlin 1998). The first records of *S. jamaicense* were recorded around 1930 (Mulvania 1930), while *S. viarum* is a more recent introduction in 1980s (Mullahey and Cornell 1994). A number of these species have been introduced into Asia, Africa, and Europe. For example, *S. elaeagnifolium* has become a problematic weed in South Africa (Boyd et al. 1984).

Root System and Life Cycle. *Solanum rostratum*, *S. melongena*, and *S. citrullifolium* are annuals, while all the other prickly nightshades of the southeastern US are perennials (Table 2). Most of the perennial species of prickly nightshade possess deep taproots with shallow lateral rhizomes that enable plants to persist for years.

Stems. Of these prickly nightshades, *S. pumilum* is the shortest and forms a rosette with an erect flowering and fruiting stems to 3 cm (1.18 inch) tall (Table 2). In contrast, *S. tampicense* plants are the tallest among these prickly nightshades and can grow to 5 m (16.4 ft) height. All others can grow as tall as 0.3 to 3 m. The type and number of prickles and trichomes are variable among these prickly nightshades. For instance, the stems of *S. bahamense*, *S. melongena*, and *S. torvum* possess few prickles, whereas, the stems of *S. jamaicense* are covered by dense thick, broad-based, hooked prickles and dense yellowish stellate trichomes. Stem prickles of *S. viarum* are of two types, thin straight and broad-based retrorsely hooked.

Leaves. Leaf shape and texture among the prickly nightshades of the southeastern US is highly variable (Table 2). Leaf shape varies from simple linear to oblong ovate in *S. elaeagnifolium*, a perennial to the deeply lobed leaves of *S. rostratum* (annual), *S. sisymbriifolium* (perennial), and *S. citrullifolium* (annual). Prickles on leaf surfaces are usually restricted to the veins and may be sparse or absent in *S. bahamense* to elongate prickles (up to 4.0 cm long) on the leaves of *S. candidum* (also commonly known as ''bed of nails''). Leaf trichomes range from sparse to dense, straight to stellate, and glanded or glandless. Often, more than one type of trichome is found on leaves of a species, e.g., *S. viarum* leaves are covered with trichomes that are straight and stellate and glanded or glandless.

Flowers. The most common flower color for prickly nightshades is white followed by blue, lavender, and purple in *S. bahamense*, *S. melongena*, *S. mammosum*, *S. dimidiatum*, *S. elaeagnifolium*, and *S. citrullifolium* (Figure 1, Table 3). *Solanum rostratum* is the only prickly nightshade with yellow flowers in the southeastern US. Flower shape

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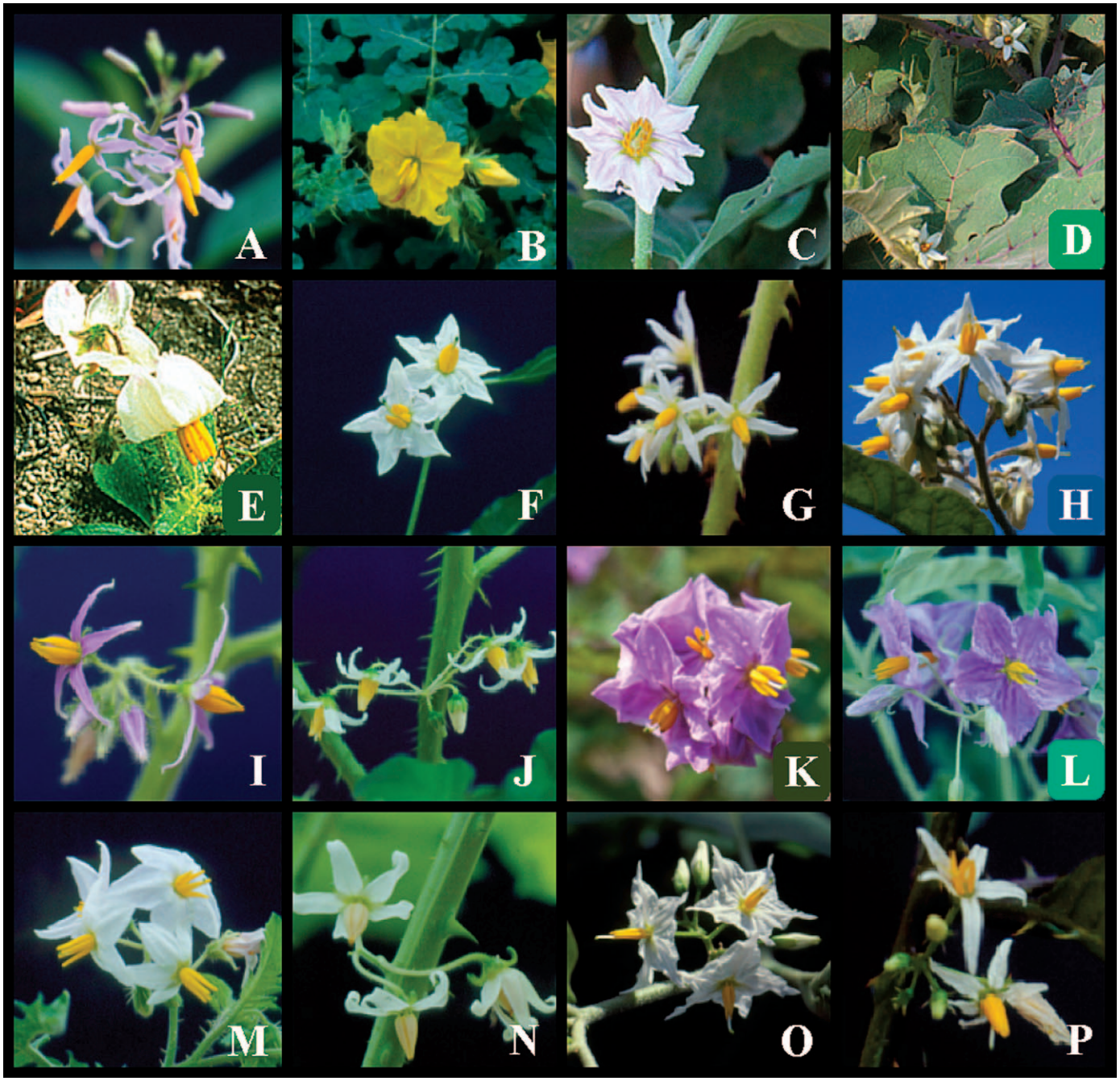

Figure 1. Flowers of prickly *Solanum* species: A - *S. bahamense*; B - *S. rostratum*; C - *S. melongena*; D - *S. candidum*; E - *S. pumilum*; F - *S. carolinense*; G - *S. jamaicense*; H - *S. donianum*; I - *S. mammosum*; J - *S. capsicoides*; K - *S. dimidiatum*; L - *S. elaeagnifolium*; M - *S. sisymbriifolium*; N - *S. viarum*; O - *S. torvum*; and P - *S. tampicense* (photos by Charles T. Bryson).

varies from star-shaped with petals fused about half their length in *S. rostratum, S. melongena, S. candidum, S. pumilum*, *S. carolinense, S. dimidiatum, S. elaeagnifolium, S. sisymbriifolium, S. torvum*, and *S. citrullifolium* while *S. bahamense*, *S. myriacanthum, S. jamaicense, S. donianum, S. mammosum, S. capsicoides, S. viarum*, and *S. tampicense* possess flowers with narrow, deeply lobed petals. The anther length is uniform in each species, except for the two annual nonnative species, *S. rostratum* and *S. citrullifolium*, where one anther is longer than the others. Calyx shape and size varies from narrow to wide and from glabrous and covered with trichomes and with or without prickles.

Fruit. Shape, size, and color of fruit vary among prickly nightshades in the southeastern US (Figure 2, Table 3). Fruit in most of these prickly nightshades are round or

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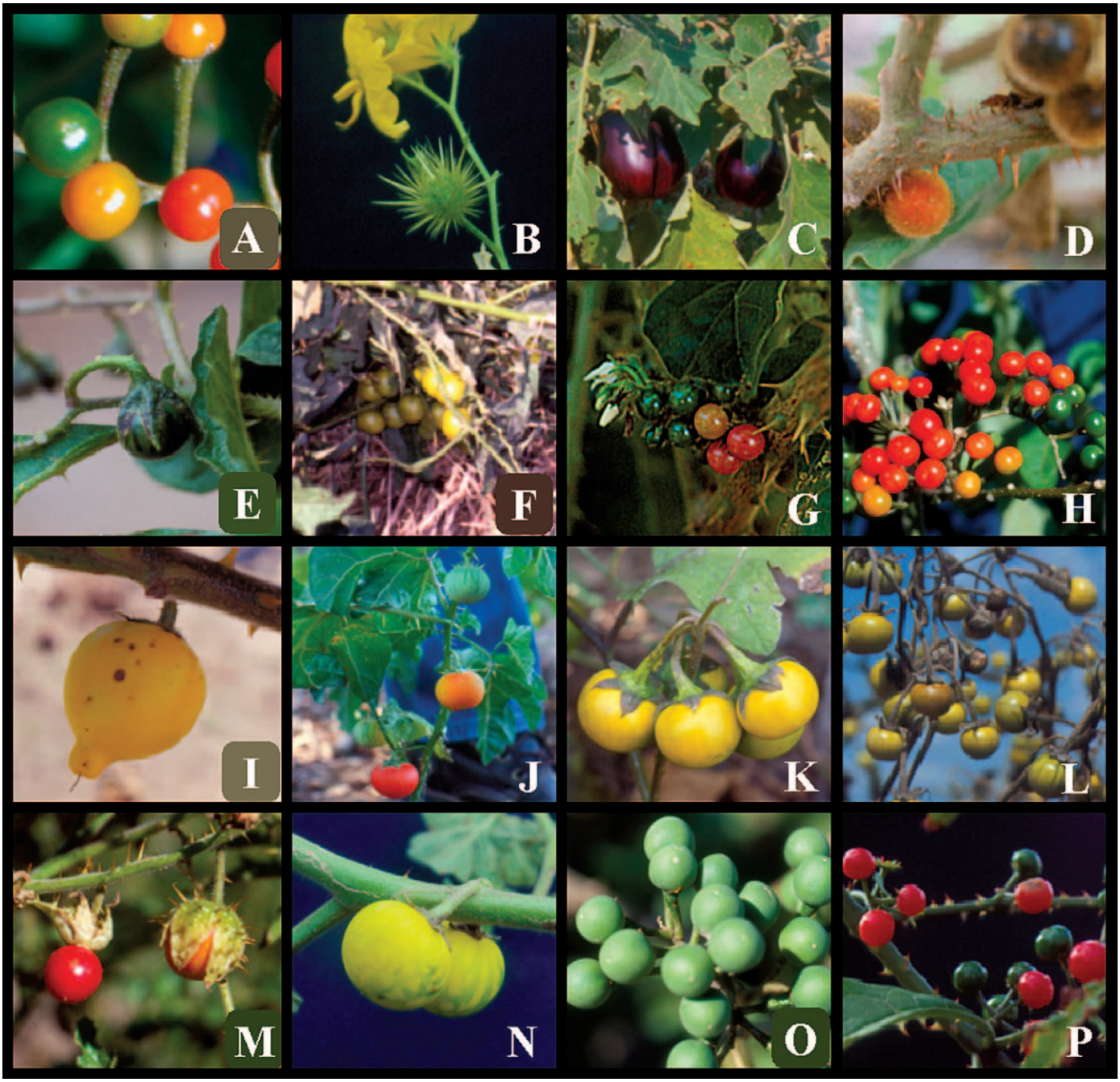

Figure 2. Fruit of prickly *Solanum* species: A - *S. bahamense*; B - *S. rostratum*; C - *S. melongena*; D - *S. candidum*; E - *S. pumilum*; F - *S. carolinense*; G - *S. jamaicense*; H - *S. donianum*; I - *S. mammosum*; J - *S. capsicoides*; K - *S. dimidiatum*; L - *S. elaeagnifolium*; M - *S. sisymbriifolium*; N - *S. viarum*; O - *S. torvum*; and P - *S. tampicense* (photos by Charles T. Bryson).

nearly round; however, the fruit of *S. melongena* is elongate or ovoid while the fruit of *S. mammosum* are ovoid or elliptical and usually with several nipples on the proximal end or a single nipple on the distal end, thus the common name *S. mammosum*. *S. melongena* and *S. mammosum* fruit are the largest while fruits of *S. tampicense* are the smallest (0.8 to 1.0 cm diam). *Solanum candidum* is the only species among this group with trichomes on the fruit. The fruit of the other prickly nightshades in the southeastern US are glabrous with the exception of *S. candidum*, *S. rostratum* and *S. citrullifolium*. The dry fruit of the two annual species *S. rostratum* and *S. citrullifolium* are surrounded by a prickly calyx that splits to disperse seed. *Solanum sisymbriifolium* fruits are also covered by a prickly calyx; however, the calyx splits exposing the smooth lustrous fruit as it matures. The calyx of *S. elaeagnifolium* possesses thin

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Table 4. Average time (d) from planting to emergence; average number of leaves and nodes per main stem; height; and time (d) to first flower from emergence for 11 native and nonnative prickly *Solanum* species from the southeastern US.

Species	Planting to emergence	Leaves	Nodes	Height	First flower
	(d)	(number/plant)		(cm)	(d)
S. rostratum	8	44	54	97	34
S. carolinense	23	7	14	24	-[a]
S. jamaicense	10	21	11	26	-[a]
S. mammosum	8	15	21	85	65
S. capsicoides	10	34	32	62	49
S. dimidiatum	12	53	24	47	65
S. elaeagnifolium	8	38	42	97	63
S. sisymbriifolium	8	37	38	105	43
S. torvum	17	8	12	47	-[a]
S. viarum	7	25	25	57	67
S. tampicense	13	25	26	100	58
LSD (0.05)	2	7	11	18	9

[a] no plants flowered within 70 d after emergence.

green or orange prickles; however, the fruits are not enveloped like those of *S. sisymbriifolium*.

Seed. Prickly nightshade seed are all compressed, but the seed sizes vary from 0.5 to 1.0 mm (0.0197 to 0.0394 inch) wide for *S. bahamense* to 3.0 to 6.0 mm wide for *S. capsicoides* (Table 3). *Solanum capsicoides* is the only species with seed margins winged and these wing margins are hyaline (whitish), which make the seed easily distinguishable from the other prickly nightshades in the southeastern US. Seed number per fruit is dependent on fruit size, thus fruits of *S. melongena* and nipple fruit nightshade possess the most seeds (> 300 seed per fruit) compared to a *S. tampicense* (18–50 seed per fruit) with smaller fruit. Seed color and texture varies among these prickly nightshades from dark brown to almost black pitted seed of *S. rostratum* to the yellowish-orange or brown, lustrous seed of *S. elaeagnifolium*.

Greenhouse Differential Growth and Development Studies. The time between planting and emergence, growth parameters, and time from emergence to first bloom varied among some of the 11 species of prickly nightshades (Table 4). The average shortest times between planting and emergence (7 to 8 d) were observed for *S. rostratum*, *S. mammosum*, *S. elaeagnifolium*, *S. sisymbriifolium*, and *S. viarum* (Table 4). Average days after planting to emergence were 10 to 13 d for *S. jamaicense*, *S. capsicoides*, *S. dimidiatum*, and *S. tampicense*, while emergence for *S. torvum* and *S. carolinense* was 17 and 23 days, respectively. The data for the number of days between planting and emergence is lacking for these prickly nightshades; however, *S. viarum* germination times are similar to those observed by Akanda et al. (1996b).

Average number of leaves per plant at 10 WAE was least for *S. carolinense* and *S. torvum* (7 and 8 leaves per plant, respectively) when compared to the average number of leaves per plant in *S. rostratum*, *S. jamaicense*, *S. capsicoides*, *S. elaeagnifolium*, *S. sisymbriifolium*, *S. viarum*, *S. dimidiatum*, and *S. tampicense* (21 to 53 leaves per plant) (Table 4). Average number of leaves per plant differed between *S. carolinense* (7 leaves per plant) and *S. mammosum* (15 leaves per plant). The average numbers of leaves per plant were highest for *S. dimidiatum* (53 leaves per plant) compared to the other 10 prickly nightshade species.

The average numbers of nodes on the main stem per plant at 10 WAE was highest for *S. rostratum* (54 nodes per plant) when compared to the other 10 prickly nightshade species (< 42 nodes/plant), while the least number of nodes were observed in *S. jamaicense*, *S. torvum*, and *S. carolinense* (10, 12, and 14 nodes per plant, respectively) (Table 4).

Average height of prickly nightshade plants at 10 WAE ranged from 24 cm for *S. carolinense* to 96 to 105 cm for *S. elaeagnifolium*, *S. sisymbriifolium*, and *S. tampicense* (Table 4). These results are not surprising because *S. carolinense* is usually a smaller statured plant than *S. tampicense*, which may grow to 4 m in natural settings (Bryson and DeFelice 2008; Fox and Bryson 1996).

Average plant dry weights for prickly nightshade plants at 10 WAE ranged from 1 g (0.0353 oz) per plant for *S. carolinense* to 17 and 18 g/plant for *S. rostratum* and *S. mammosum*, respectively (Figure 3). Average dry weights did not differ and ranged from 10 to 13 g per plant among *S. jamaicense*, *S. capsicoides*, *S. elaeagnifolium*, *S. viarum*, *S. torvum*, *S. dimidiatum*, *S. sisymbriifolium*, and *S. tampicense*.

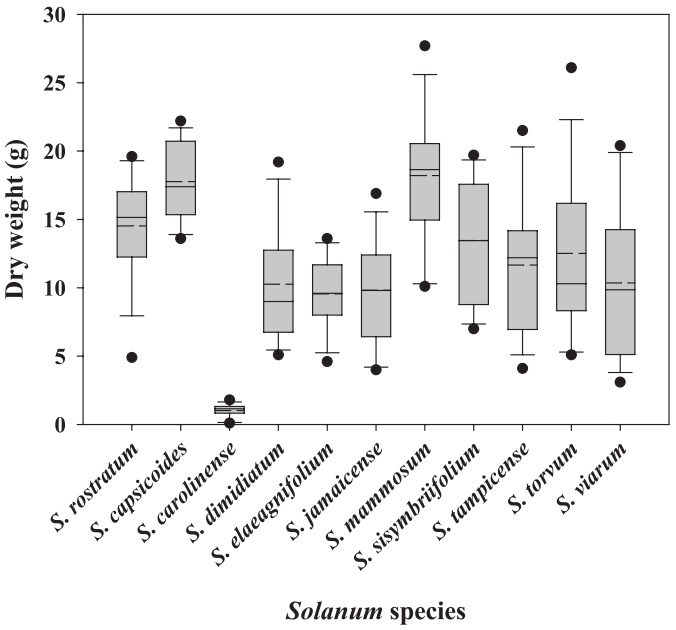

Figure 3. Box plot of average above soil surface plant dry weights for 11 prickly *Solanum* species grown in greenhouse for 10 wks after emergence at Stoneville, MS. Species include: *S. rostratum*; *S. capsicoides*; *S. carolinense*; *S. dimidiatum*; *S. elaeagnifolium*; *S. jamaicense*; *S. mammosum*; *S. sisymbriifolium*; *S. tampicense*; *S. torvum*; and *S. viarum* The boundary of the box closest to zero indicates the 25th percentile, a solid line within the box marks the median, a dashed line within the box indicates the mean, and the boundary of the box farthest from zero indicates the 75th percentile. Error bars above and below the box indicate the 90th and 10th percentiles, and solid dots indicate outliers. The number of independent observations was 14.

Average number of days from emergence to first bloom varied among prickly nightshade species. The shortest time between emergence and first flower was 34 d for *S. rostratum*, an annual species (Table 4). Average time between emergence and first bloom was similar in *S. sisymbriifolium* and *S. capsicoides* (43 and 49 d, respectively). *S. jamaicense*, *S. tampicense*, *S. elaeagnifolium*, *S. mammosum*, robust nightshade, and *S. viarum* took a longer time to first flower and ranged from 58 to 67 days. *S. carolinense* and *S. torvum* did not flower within the 70 day period between emergence and harvest of plants to obtain dry weights.

Solanum rostratum plants were the tallest and produced the highest numbers of nodes and leaves among the prickly nightshades, while *S. carolinense* plants were the shortest and produced fewer leaves and nodes among these prickly nightshade species. Likewise, the time between plant emergence and first flower differed between these two species. The time between emergence and first flower for *S. rostratum*, an annual, was the shortest for the prickly nightshade species, while for *S. carolinense*, a perennial, it was the longest between plant emergence and first flower. As annuals and perennials, these factors are critical for the survival of these nightshade species and a characteristic that make both weedy, as generally described for many annual and perennial weed species by Radosevich and Holt (1984).

These biological and morphological data can be used to help determine the most vulnerable stage to develop the most effective methods and strategies for control of *S. rostratum*, *S. carolinense*, *S. jamaicense*, *S. mammosum*, *S. capsicoides*, *S. dimidiatum*, *S. elaeagnifolium*, *S. sisymbriifolium*, *S. viarum*, *S. torvum*, and *S. tampicense*. Additional research is needed to determine seed longevity, germination rate, time required to become a perennial, reproductive potential, dispersal mechanisms, and other parameters.

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