23 Tropical Soda Apple, Wetland Nightshade, and Turkey Berry

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PEST STATUS OF WEEDS

Nature of Damage

Three non-native species of the genus *Solanum* are considered invasive weeds of agricultural and natural areas in Florida (Langeland and Burks, 1998). Tropical soda apple, *Solanum viarum* Dunal, is more widely recognized as a problem than either wetland nightshade, *Solanum tampicense* Dunal, or turkey berry, *Solanum torvum* Swartz, because it has spread rapidly throughout the southeastern United States after establishing in Florida (Westbrooks, 1998). Tropical soda apple and wetland nightshade were discovered in Florida in the early 1980s and therefore are relatively new introductions. Turkey berry was introduced into Florida more than a century ago but its invasive potential was not recognized until recently (Langeland and Burks, 1998).

All three *Solanum* spp. are on the Federal and Florida Noxious Weed Lists (USDA-APHIS-PPQ, 1999; FDACS, 1999), and are listed as Category I invasive species by the Florida Exotic Pest Plant Council (FLEPPC, 1999). Category I plants "are non-native species that have invaded natural areas, and are displacing native plants or are disrupting natural community structure and function" (FLEPPC, 1999). Although it is unclear why these non-native solanaceous plants have become invasive weeds, lack of host-specific natural enemies in the southeastern United States may have afforded a competitive advantage over native species.

Economic damage. Tropical soda apple typically invades improved pastures, which reduces livestock carrying capacity (Fig. 1). Foliage and stems are unpalatable to livestock, and dense stands of this prickly shrub deny cattle access to shaded areas, which results in heat stress (Mullahey *et al.*, 1998). Stocking rates are drastically reduced and pasture production declines if tropical soda apple is left uncontrolled (Mullahey *et al.*, 1993). In pastures, tropical soda apple forms monocultures that shade out bahiagrass, *Paspulum notatum* Fluegge, a valuable forage species of South American origin. Bahiagrass does not tolerate shade well and productivity declines when it is forced to compete with tropical soda apple. In 1993, a survey of beef cattle operations in south Florida determined the total area of pastureland infested as 157,145 ha, twice the infestation present in 1992 (Mullahey *et al.*, 1994a).

Figure 1. Pasture infested with tropical soda apple, *Solanum viarum* Dunal, in Hendry County, Florida, United States. (Photograph courtesy of Jeff Mullahey.)

Tropical soda apple also serves as a reservoir for various diseases and insect pests of solanaceous crop plants (McGovern *et al.*, 1994ab). At least six plant viruses (cucumber mosaic virus, potato leaf-roll virus, potato virus Y, tobacco etch virus, tomato mosaic virus, and tomato mottle virus) and the potato fungus *Alternaria solani* Sorauer use tropical soda apple as a host and are vectored during the growing season to cultivated crops (McGovern *et al.*, 1996). In addition, the following major crop pests utilize tropical soda apple as an alternate host: tobacco hornworm, *Manduca sexta* (L.); tomato hornworm, *Manduca quinquemaculata* (Haworth); Colorado potato beetle, *Leptinotarsa decemlineata* (Say); tobacco budworm, *Helicoverpa virescens* (Fabricius); tomato pinworm, *Keiferia lycopersicella* (Walsingham); green peach aphid, *Myzus persicae* (Sulzer); silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring; soybean looper, *Pseudoplusia includens* (Walker); and southern green stink bug, *Nezara viridula* (L.) (Habeck *et al.*, 1996; Medal *et al.,* 1999b; Sudbrink *et al.*, 2000).

Turkey berry usually invades disturbed sites such as pastures, roadsides, damp waste areas, and forest clearings (Fig. 2), and is frequently cultivated as a yard plant in South Florida for its bitter-tasting fruits (Morton, 1981; Westbrooks and Eplee, 1989). Recent studies indicate that turkey berry is potentially poisonous to animals (Abatan *et al.*, 1997), and possibly carcinogenic to humans (Balachandran and Sivaramkrishnan, 1995).

Figure 2. Turkey berry, *Solanum torvum* Swartz, growing next to a pasture in south Florida, United States The light green turkey berry dwarfs the cow in the foreground. (Photograph courtesy of Mike Bodle.)

Ecological damage. In addition to causing economic problems, tropical soda apple reduces the biological diversity in natural areas by displacing native plants and disrupting the ecological integrity. The plant invades hammocks, ditch banks, and roadsides, where it out competes native plants (Langeland and Burks, 1998). Wooded areas comprise about 10% of the total land infested by tropical soda apple in Florida. Affected woodlands include oak and cabbage palm hammocks (tree islands surrounded by contrasting vegetation types) and cypress heads (dome-shaped tree islands with tallest trees in the center dominated by cypress, *Taxodium* spp.) (Tomlinson, 1980). Prickles on the plants create a physical barrier to animals, preventing them from passing through the infested area. Tropical soda apple also interferes with restoration efforts in Florida by invading tracts of land that are reclaimed following phosphate-mining operations (Albin, 1994).

Unlike tropical soda apple and turkey berry that are invasive in upland sites, wetland nightshade typically invades regularly flooded wetlands (Coile, 1993; Wunderlin *et al.*, 1993; Fox and Bryson 1998). Approximately 200 to 300 ha of riparian and marsh habitats in southwest Florida have been invaded by wetland nightshade. Once established, it forms large, tangled, dense stands along river margins (Fig. 3), cypress swamps, open marsh, and relatively undisturbed wetlands where it displaces more desirable native species such as pickerelweed, *Pontederia cordata* L. (A. M. Fox, pers. obser.).

Figure 3. Infestation of wetland nightshade, *Solanum tampicense* Dunal, along riverbank in southwest Florida, United States. (Photograph courtesy of Alison Fox.)

The occurrence of turkey berry as a serious weed problem in seven different countries (Holm *et al.*, 1979) is perhaps the most compelling evidence foretelling its eventual impact on Florida's native plant communities. According to Gordon and Thomas (1997), the best predictor of invasiveness is whether the plant is invasive elsewhere in a similar climate.

Extent of losses. In 1994, production losses to Florida cattle ranchers attributed to tropical soda apple infestations were estimated at $11 million annually (Cooke, 1997), or about 1% of total Florida beef sales. Economic losses from heat stress alone were estimated at $2 million because cattle avoid woods infested with tropical soda apple that provide shade during the summer months (Mullahey *et al.*, 1998).

Production losses were calculated based on several assumptions, including one cow or calf unit per 1.6 ha (4 acres), 50% steer/50% heifer calf crop, and March 1994 market prices for a 500 lb. calf. The number of ha that can be used for production is reduced by the percentage of ha infested with tropical soda apple. The number of calves that could have been produced is likewise reduced because of the decrease in carrying capacity.

Tropical soda apple has been identified as a host for six plant viruses that infect important vegetable crops (McGovern *et al.,* 1994a, 1994b, 1996). Annual sales from vegetable production in Florida approach $1.7 billion. Transmission of the viruses identified in tropical soda apple could represent a significant loss in revenue to vegetable growers. The tomato mosaic virus, which is causing millions of dollars in losses to Florida tomato growers, uses tropical soda apple as a reservoir host (Mullahey *et al.*, 1996). Current practices for managing tropical soda infestations also are expensive. Herbicide applications combined with mechanical control (mowing) cost an estimated $185 per ha for dense infestations of tropical soda apple (Mislevy *et al.*, 1996; Sturgis and Colvin, 1996; Mislevy *et al.*, 1997).

The ability of wetland nightshade to form dense thickets that are difficult for other species to penetrate suggests this noxious weed has the potential to invade and alter many of Florida's wetland habitats as well as impede access to and use of water resources (Fox and Wigginton, 1996; Fox and Bryson, 1998).

Geographical Distribution

Tropical soda apple was first discovered in Glades County, Florida in 1988 (Mullahey *et al.*, 1993, 1998). Initially, the incidence of this plant in Florida was highest in the southern half of the state with infestations concentrated north and west of Lake Okeechobee. Statewide, the total area infested by tropical soda apple in 1990 was approximately 10,000 ha; in 1993, 162,000 ha; and by 1995, the infested area increased to approximately 0.5 million ha (Mullahey, 1996; Mullahey *et al*., 1998). Tropical soda apple now occurs throughout the state in pastures, natural ecosystems, citrus (*Citrus* spp.), sugar cane (*Saccharum officinarum* L.), sod fields, ditch banks, and roadsides.

After establishment was confirmed in Florida, tropical soda apple quickly spread to Alabama, Georgia, Louisiana, Mississippi, North Carolina, Pennsylvania, South Carolina, Tennessee, and Puerto Rico (Bryson *et al.*, 1995; Akanda *et al.*, 1996; Westbrooks and Eplee, 1996; Mullahey *et al.*, 1998). Initial introduction of tropical soda apple into North America probably occurred from seed adhering to people's shoes or it escaped from cultivation (J. J. Mullahey, pers. comm.).

Rapid spread of tropical soda apple throughout the southeastern United States (Fig. 4) occurred inadvertently through the cattle industry (Westbrooks, 1998). The number of infested acres in Georgia, Mississippi, and Alabama was directly related to the number of cattle imported from Florida (Bryson *et al.*, 1995). Extremes in temperature and photoperiod will not prevent tropical soda apple from spreading into adjacent states (Patterson *et al.*, 1997). Tropical soda apple also has invaded other regions outside the United States including the Caribbean, Mexico, Africa, India, Nepal, and China (Chandra and Srivastava, 1978; Coile, 1993; Wunderlin *et al.,* 1993).

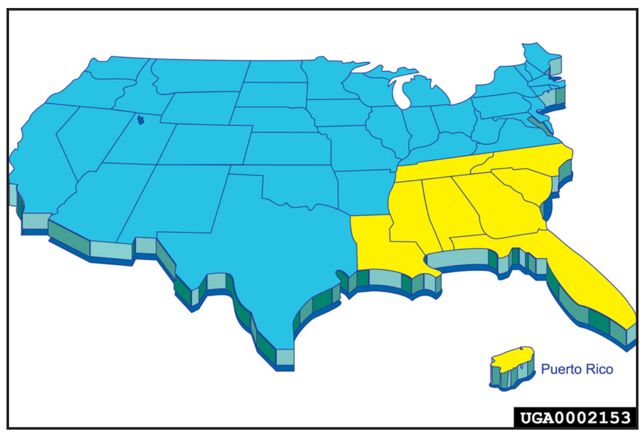

Figure 4. Distribution of tropical soda apple, *Solanum viarum* Dunal, in the United States. Infested region indicated in yellow. (Data from Westbrooks, 1998.)

Wetland nightshade was originally recorded from the Dry Tortugas in 1974 (Langeland and Burks, 1998) and in mainland Florida in 1983 (Fig. 5) (Wunderlin *et al.*, 1993; Fox and Bryson 1998). The largest infestation of wetland nightshade, approximately 60 ha, occurs in southwest Florida (Fox and Wigginton, 1996; Fox and Bryson, 1998).

Turkey berry was first collected in Columbia County, Florida, in 1899, and has been reported in at least nine counties in peninsular Florida (Langeland and Burks, 1998; J. P. Cuda, pers. comm.), and a new infestation was discovered recently in Glades county (J. J. Mullahey, pers. comm.) (Fig. 5). Turkey berry also is considered a weed in 32 countries and is particularly invasive in parts of Australia and South Africa climatically similar to Florida (Holm *et al.*, 1979).

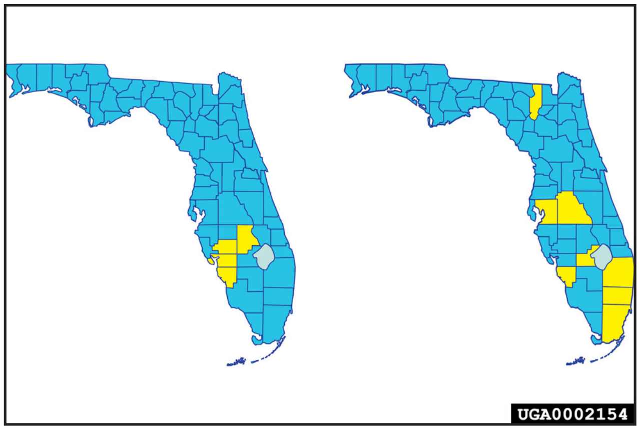

Figure 5. (a) Distribution of wetland nightshade, *Solanum tampicense* Dunal, (left-hand map) and (b) distribution of turkey berry, *Solanum torvum* Swartz, (right-hand map) in Florida, United States. Infested counties indicated in yellow. (Data from Wunderlin *et al.,* 1998.)

BACKGROUND INFORMATION ON PEST PLANTS

Taxonomy

Tropical soda apple, turkey berry, and wetland nightshade are members of the prickly *Solanum* subgenus *Leptostemonum* (Nee, 1991). Tropical soda apple (also called sodom apple, yu-a, or tutia de vibora in Argentina, and joa bravo or joa amarelo pequeno in Brazil) belongs to the section *Acanthophora*. This section includes 19 species characterized by prickly stems, lobed or dented prickly leaves with only simple hairs on the upper surface, and a chromosome number 2n=24 (22 in *Solanum mammosum* L.). *Solanum chloranthum* DC, *Solanum viridiflorum* Schlechtendal, and *Solanum khasianum* Clarke var. *chatterjeeanum* Sen Gupta are synonyms of *Solanum viarum* (tropical soda apple) (Nee, 1991). *Solanum acanthoideum* Jacquin, a species thought to be native to South Africa, is probably synonymous with *S. viarum* (tropical soda apple) (T. Olckers, pers. comm.).

Turkey berry (also known as susumber, gully-bean, Thai eggplant, or devil's fig) is placed in the section *Torva* (D'Arcy, 1972). This section contains approximately 35 species with turkey berry designated as the type species (D'Arcy, 1972; M. Nee, pers. comm.). Langeland and Burks (1998) list *Solanum ferrugineum* Jacquin and *Solanum ficifolium* Ortega as synonyms of *S. torvum* (turkey berry).

Wetland nightshade (or aquatic soda apple, sosumba, ajicón, huistomate, huevo de gato) belongs to the section *Micracantha* that contains approximately 25 species including *Solanum lanceifolium* Jacquin (D'Arcy, 1972; M. Nee, pers. comm.). The close similarity of wetland nightshade to the latter species created some identification and nomenclatural problems (Coile, 1993; Wunderlin *et al.,* 1993; Fox and Bryson, 1998). *Solanum quercifolium* Miller and *Solanum houstonii* Martyn are regarded as valid synonyms of *S. tampicense* (wetland nightshade) (Wunderlin *et al.,* 1993; Langeland and Burks, 1998). *Solanum houstonii* Dunal is occasionally included in the synonymy of wetland nightshade, but *S. houstonii* Dunal is considered an invalid name because it is a later homonym of *S. houstonii* Martyn (Wunderlin *et al.,* 1993).

Biology

Tropical soda apple can be "distinguished in Florida from other prickly *Solanum* spp. by its straight prickles, mixture of stellate and simple hairs with and without glands, clearly petioled leaves with a velvety sheen, terminal (white flowers with recurved petals), and yellow berries that are dark-veined when young." (Langeland and Burks, 1998) (Fig. 6). The plant is readily identified by its immature fruits, which are pale green with dark green veins, and resemble immature watermelons. Tropical soda apple can grow from a seed to a mature plant in 105 days (Mullahey and Cornell, 1994). Petioles and leaves are heavily armed with long straight prickles on leaf veins when exposed to full sunlight, but prickles are fewer in number and less developed on shaded plants (Gandolfo, 1997). Flowers and fruits are produced primarily from September through May in the United States and from November to April (spring to mid-fall) in Argentina (Gandolfo, 1997), with few fruits developing during summer months. A single plant produces about 150 fruits per year. Each mature fruit contains about 400 reddish brown seeds that are moderately flattened and are enveloped in a mucilaginous layer containing the glycoalkaloid solasodine.

Figure 6a.

Figure 6b.

Figure 6c.

Figure 6. Tropical soda apple, *Solanum viarum* Dunal; (a) juvenile plant; (b) typical flower; (c) mature fruits. (Photographs courtesy of Jeff Mullahey.)

Rapid spread of tropical soda apple in the southeastern United States is associated with the plant's tremendous reproductive potential, and highly effective seed dispersal mechanisms. Tropical soda apple also is capable of regenerating vegetatively from its extensive root system (Mullahey and Cornell, 1994; Akanda *et al.*, 1996). One plant can produce on average 45,000 seeds with 70% viability (Mullahey and Colvin, 1993; Mullahey *et al.*, 1997). In one growing season, a single plant can yield enough viable seed to produce 28,000 to 35,000 new tropical soda apple plants. Seeds will not germinate inside the fruit and must be removed from the fruit to dry (aging process) before germination can occur (Akanda *et al.*, 1996). Seed germination occurs following exposure to favorable conditions and is enhanced by scarification (Mullahey *et al.*, 1993). Approximately 20% of the annual seed crop is dormant (Akanda *et al.*, 1996). Seed can remain dormant for months, although average period of dormancy is one month (Pingle and Dnyansagar, 1980). Seed viability increases with fruit diameter, not ripeness (J. J. Mullahey, pers. comm.).

Foliage of tropical soda apple is unpalatable to livestock but cattle and wildlife (deer, raccoons, feral hogs, birds) ingest the fruits and spread the seeds in their droppings (Mullahey *et al.*, 1993; Akanda *et al.*, 1996; Brown *et al.*, 1996). The rapid spread of tropical soda apple is often associated with soil disturbance (Mullahey *et al.*, 1993). Disking a field, cattle congregating around a feeder, cleaning of ditch banks, or feral hogs rooting in a field provide a favorable environment for tropical soda apple establishment and growth. Standing water will stress the plant and even cause death, but once the area begins to dry out new plants will emerge from the seed banks (Mullahey *et al.*, 1993). Cypress heads will harbor tropical soda apple in the center of the head until completely flooded by summer rains that cause the plants to dieback to the outer, drier areas. As water in the cypress head recedes during winter months, tropical soda apple re-infests the inner regions of the cypress head.

Moving water, seed-contaminated hay, grass seed, sod, and machinery also contribute to spreading the plant. In an attempt to alleviate this problem in sod farms, the Florida Department of Agriculture and Consumer Services began charging a fee to sod farmers to certify sod as free of tropical soda apple (Mullahey *et al.*, 1998).

Tropical soda apple contains the glycolalkaloid solasodine in the mucilaginous layer surrounding the plant's seeds (Chandra and Srivastava, 1978). Solasodine, a nitrogen analogue of diosgenin, is used in the production of steroid hormones. These steroids have been useful in treatment of cancer, Addison's disease, rheumatic arthritis, and in production of contraceptives. Maximum content of solasodine in tropical soda apple fruits occurs when fruits change color from green to yellow (Kaul and Zutshi, 1977). Although intensively cultivated as a source of solasodine in Mexico and India (Sahoo and Dutta, 1984), propagation of tropical soda apple for the glycoalkaloid has significantly declined or ceased altogether in these two countries. Apparently, another solanaceous plant was discovered that contains higher levels of solasidine (J. J. Mullahey, pers. comm.).

Solasodine is poisonous to humans with symptoms appearing after consumption of the fruits; a lethal dose requires approximately 200 fruits (Frohne and Pfander, 1983). Mature fruits have a sweet smell similar to a plum or apple when the berry is opened, but the coated seed has a bitter taste (J. J. Mullahey, pers. comm.). Apparently, bitter taste does not prevent wildlife and cattle from consuming the fruits.

Turkey berry can be recognized in Florida " . . . by its treelike habit, (very few) stout prickles, clearly petioled leaves with dense stellate hairs (on both leaf surfaces and on the stem), numerous bright white flowers followed by yellow grape-sized berries, and glandular hairs on the flower stalks. . ." (Langeland and Burks, 1998) (Fig. 7). This prickly shrub can grow up to 3 m in height (Ivens *et al.*, 1978), and forms thickets by sprouting from lateral rhizomes. Turkey berry produces flowers and fruits year-round in tropical and subtropical regions (Adams, 1972), and the seeds are probably bird dispersed (D'Arcy, 1974). The plant is capable of growing in a variety of habitats ranging from wetlands to rocky hillsides (Adams, 1972).

Wetland nightshade is characterized " . . . by its (recurved prickles on the lower surface leaf veins, straight hairs on the upper surface leaf veins) and clusters of up to 11 pea-sized red berries (with no dark markings when green); its petioled longer-than-wide, deeply sinuate leaves; its pubescence of stellate hairs only (no straight or glandular hairs); and its clambering, almost vinelike habit. . ." (Langeland and Burks, 1998) (Fig. 8). The plant will thrive under conditions ranging from full shade to full sunlight but flowers and fruits prolifically from May to January when exposed to the sun (Fox and Wigginton, 1996; Fox and Bryson, 1998). New stems sprout annually from the woody base of the plant and adventitious roots form at the leaf axils. Wetland nightshade can tolerate frost and temporary high water conditions but not permanent flooding. Seeds withstand freezing and drying periods for up to 12 months with little loss in viability (Fox and Wigginton, 1996). More than 90% of the fresh seeds of wetland nightshade will germinate under suitable conditions. In riparian habitats, dispersal of seeds and stem fragments probably occurs downstream (Fox and Wigginton, 1996; Fox and Bryson, 1998).

A comprehensive list of vegetative and reproductive characteristics used to distinguish the three non-native species from other prickly solanums occurring in the southeastern United States was compiled by Fox and Bryson (1998).

Figure 7a.

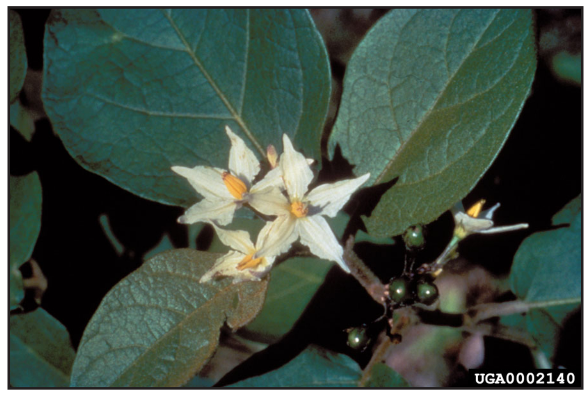

Figure 7b.

Figure 7. Turkey berry, *Solanum torvum* Swartz; (a) juvenile plant; (b) flowers and unripe fruits. (Photographs courtesy of Nancy Coile.)

Figure 8a.

Figure 8b.

Figure 8. Wetland nightshade, *Solanum tampicense* Dunal; (a) stem and leaves with recurved prickles; (b) cluster of berries and typical leaf. (Photographs courtesy of Alison Fox.)

Analysis of Related Native Plants in the Eastern United States

The genus *Solanum* contains more than 30 species that are indigenous to the United States, 27 of these occurring in the southeast (Soil Conservation Service, 1982). The potato tree, *Solanum donianum* Walpers, is found only in the Florida Keys and is listed as a threatened species in Florida (Coile, 1998). Another species potentially at risk is *Solanum pumilum* Dunal, a native plant closely related to *Solanum carolinense* L., once thought to be extinct but now known from a few locations on rock outcroppings in Alabama (M. Nee, pers. comm.) and Georgia (J. Allison, pers. comm.). The genus and family (Solanaceae) also contain economically important ornamental (e.g., petunias) and crop plants closely related to tropical soda apple, wetland nightshade, and turkey berry (Bailey, 1971). Economically important crop species such as pepper (*Capsicum*), tomato (*Lycopersicon*), tobacco (*Nicotiana*), eggplant, and potato (both, *Solanum* spp.) are valuable cash crops that contribute significantly to North American agriculture. In 1991, the combined economic value for production of solanaceous crop plants in Florida alone was reported to be approximately $950 million (Capinera *et al.*, 1994). Clearly, insects or pathogens introduced from the native ranges of the three exotic solanums must be target specific to minimize risk of damage to crops or non-target species (Louda *et al.*, 1997; USDA, APHIS, PPQ, 2000).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Tropical soda apple is native to South America and wetland nightshade to the Caribbean and Central America (Wunderlin *et al.*, 1993), whereas turkey berry is a pantropical weed (D'Arcy, 1974). Tropical soda apple is endemic to southeastern Brazil, northeastern Argentina, Paraguay, and Uruguay (Nee, 1991), and is not considered an important weed in Brazil and Paraguay (Medal *et al.*, 1996). This suggests the plant is regulated by several factors in its native range (possibly natural enemies) that were excluded when tropical soda apple was introduced into Florida in the mid-1980s.

Wetland-nightshade is native to southern Mexico, Guatemala, Belize (Gentry and Standley, 1974), and the Caribbean region (Sauget and Liogier, 1957). It probably also has spread into other areas including the northern part of South America.

The area of origin for turkey berry has not been resolved. It is thought to have originated in either West Africa (Ivens *et al.*, 1978), Central/South America and the Caribbean region (Morton, 1981), or Asia (Medal *et al.*, 1999).

Areas Surveyed for Natural Enemies

Field surveys for native pathogens with potential as biological control agents for tropical soda apple were made in Florida (McGovern *et al.*, 1994ab; Charudattan and DeValerio, 1996; Charudattan *et al*., 2001). Also, several natural enemies associated with silverleaf nightshade, *Solanum elaeagnifolium* Cavanaugh (Goeden, 1971; Olckers, 1996) were collected in south Texas to determine whether they would accept the non-native solanums as novel hosts (Cuda *et al*., 1998; Cuda *et al*., in press). Silverleaf nightshade is native to the southern United States, Mexico, and Argentina (Goeden, 1971; Boyd *et al*., 1983), and belongs to the same infrageneric group (subgenus *Leptostemonum* Dunal) as the three invasive *Solanum* species (D'Arcy, 1972).

A field survey for natural enemies of tropical soda apple in Brazil and northeastern Paraguay in June 1994 identified sixteen insect herbivores and several pathogens (Mullahey *et al*., 1994b; Medal *et al*., 1996). Additional exploratory surveys for insect natural enemies were carried out in northeastern Argentina, Brazil, southeastern Paraguay, and Uruguay (Gandolfo, 1997; Olckers *et al*., 2002).

Natural Enemies Found

More than 75 species of insects were collected from tropical soda apple in the United States (Sudbrink *et al*., 2000). Field surveys in Florida isolated more than 45 pathogens from the foliage, stems, and roots, including fungal isolates of *Alternaria, Colletotrichum, Curvularia, Fusarium, Helminthosporium, Phomopsis, Verticillium*, and bacterial isolates of *Ralstonia (= Pseudomonas) solanacearum* (E. F. Smith) Yabuuchi and *Pseudomonas syringae* van Hall pathovar *tabaci* (Charudattan and DeValerio, 1996). A strain of the tobacco mild green mosaic virus (TMGMV U2) was recently tested in greenhouse and field trials, and found to be lethal to tropical soda apple (Charudattan *et al*., 2001).

The gall-making nematode *Ditylenchus phyllobius* (Thorne) Filipjev (Parker, 1991) and the defoliating leaf beetles *Leptinotarsa defecta* (Stål) and *Leptinotarsa texana* (Schaeffer) (Jacques, 1988) were screened as potential "new associates" of the non-native solanums (Cuda *et al*., 1998; Cuda *et al*., in press). These species severely damage their natural host plant silverleaf nightshade, but do not harm economically important solanaceous crops (Olckers *et al*., 1995). Although silverleaf nightshade is reported from Florida (Wunderlin *et al.*, 1998), its natural enemies do not occur there (Esser and Orr, 1979; Jacques, 1985). However, climate models indicate their potential to persist in Florida if tropical soda apple, turkey berry, or wetland nightshade were suitable host plants.

The tingid *Corythaica cyathicollis* (Costa) and the membracid *Amblyophallus maculatus* Funkhonser were the two most common insects found during surveys on tropical soda apple in Brazil and Paraguay (Medal *et al.*, 1996). Leaf-feeding beetles of the genera *Metriona*, *Gratiana*, and *Platyphora* as well as the nymphalid butterfly *Mechanitis lysimnia* Fabricius severely defoliate the plant in its native range (Medal *et al.*, 1996; Gandolfo, 1997). The defoliating leaf beetles *Metriona elatior* Klug and *Gratiana boliviana* (Spaeth) are both promising candidates because they complement each other (D. Gandolfo, pers. comm.). *Metriona elatior* prefers larger plants in shaded areas whereas *G. boliviana* favors plants growing in open areas. The flower bud weevil *Anthonomous tenebrosus* Boheman, collected during surveys in Argentina and Brazil (Gandolfo, 1997), is another promising biological control candidate attacking the flower buds, which reduces seed production.

Host Range Tests and Results

In a host range trial using 31 *Solanum* spp. and five strains of *R. solanacearum*, all test plant species were either mildly or highly susceptible to one or more strains of the bacterium (Charudattan and DeValerio, 1996). This finding suggests that if *R. solanacearum* is developed commercially as a bioherbicide for use against the non-native solanums, the potential for non-target damage due to drift must be considered.

The nematode *D. phyllobius*, a species collected from silverleaf nightshade, failed to induce leaf or stem galls on either tropical soda apple or wetland nightshade (Cuda *et al.,* 1998); turkey berry was unavailable for testing.

Leptinotarsa defecta did not feed and develop on any of the three invasive species tested, but *L. texana* may have some potential as a control agent for turkey berry (Cuda *et al.*, in press). Development and reproduction of *L. texana* on turkey berry were comparable with its normal host plant silverleaf nightshade, and larvae did not exhibit a feeding preference when given a choice between the two species in paired plant tests (Cuda *et al.*, in press).

In screening tests with the nymphalid butterfly *M. lysimnia* conducted in Argentina, it was found that this insect was not sufficiently host specific to warrant further consideration as a biological control agent (Gandolfo, 1997).

The leaf-feeding tortoise beetle *M. elatior* exhibited a broad host range under laboratory conditions (Hill and Hulley, 1996; Medal *et al.*, 1999b), but this insect fed and oviposited only on tropical soda apple in surveys and open field experiments conducted in the insect's native range (Medal *et al.*, 1999a; Olckers *et al.*, 2002). Contradictory results obtained with critical solanaceous test plants may be explained by the conditions under which the screening studies were conducted (Medal *et al.*, 1999ab).

Gratiana boliviana, another leaf-feeding chrysomelid beetle, developed completely albeit poorly on eggplant and three South American *Solanum* spp. in no choice laboratory feeding trials (Gandolfo, 1998; Gandolfo *et al.*, 2000ab; Medal *et al.*, in press). However, surveys and open field experiments conducted in Argentina, Brazil, Paraguay, and Uruguay since 1997 clearly demonstrate that *G. boliviana* does not attack eggplant in South America, even when tropical soda apple plants are growing intermixed or adjacent to egg plant fields (Gandolfo, 1999; Medal *et al.*, 1999a; Gandolfo *et al.,* 2000ab; Olckers *et al.*, 2002; Medal *et al.*, in press). Apparently, the high density of stellate trichomes on the leaves of eggplant act as a physical barrier to the neonates of *G. boliviana* (Gandolfo, 1998; Gandolfo, 2000).

Releases Made

No insect natural enemies have been released for classical biological control of tropical soda apple in the United States as of March 2002. An application for permission to release *M. elatior* against tropical soda apple in the United States was submitted to the Technical Advisory Group for Biological Control Agents of Weeds (TAG) in October 1998, but the request for release from quarantine was denied because of the perceived risk to eggplant. The TAG recommended additional field-testing in South America to resolve discrepancies that often occur between laboratory and open field tests.

A request for the release of *G. boliviana* from quarantine was submitted to the TAG in April 2000 (Medal *et al.*, 2000). The TAG recommended that *G. bolviana* be approved for use as a biological control agent of tropical soda apple in April 2002. The release of this insect for classical biological control of tropical soda apple is anticipated in the Spring of 2003.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Pathogens

Ralstonia solanacearum is a ubiquitous soil-borne bacterium that is pathogenic to tropical soda apple (Charudattan and DeValerio, 1996). Chlorosis, necrosis, systemic wilting, and rapid plant mortality characterize the disease. *Ralstonia solanacearum* can survive in the soil for a long time even in the absence of a host. As a soil-borne pathogen, *R. solanacearum* does not spread readily unless contaminated soil and tools, infected plant parts, or contaminated irrigation water are involved. The bacteria can survive for several years in certain types of soils. However, use of resistant crop varieties, proper sanitation, rotation with nonhost crops, soil solarization, or soil fumigants can control the disease.

The U2 strain of the tobacco mild mosaic virus causes foliar lesions, systemic necrosis of the petioles, and systemic wilt of tropical soda apple plants within 14 days post-inoculation (Charudattan *et al.*, 2001). Unlike the U1 strain that induces only mosaic or mottle symptoms, the U2 strain causes hypersensitive mortality of tropical soda apple (Charudattan *et al.*, 2001).

Leptinotarsa texana (Coleoptera: Chrysomelidae)

The biology of *L. texana* on silverleaf nightshade was recently summarized by Olckers *et al.* (1995). In the laboratory, females laid clusters of 20 to 40 eggs on the lower leaf surfaces (Fig. 9), while in the field egg batches may exceed 100 eggs. The cream-colored eggs of *L. texana* are larger than the yellow eggs of *L. defecta*. Females, which live longer than males, may oviposit more than 2,000 eggs in their life span of three to four months in the laboratory. Adults readily cannibalize each others eggs, especially under crowded conditions in cages.

Larvae hatch after four to five days and consume the eggshells before feeding on the plant. Larvae feed in groups, and pass through four instars in 10 to 14 days. Mature larvae burrow into the soil to pupate; adults emerge 10 to 14 days later.

Figure 9. Adult and egg mass of *Leptinotarsa texana* (Schaeffer) on silverleaf nightshade, *Solanum elaeagnifolium* Cavanaugh. (Photograph courtesy of Gary Bernon.)

Figure 10. Adults of *Metriona elatior* Klug feeding on leaf of tropical soda apple, *Solanum viarum* Dunal. (Photograph courtesy of Julio Medal.)

Larvae of *L. texana* have orange head capsules from the third instar onwards and are easily differentiated from *L. defecta* larvae, which have black head capsules. The period from larval eclosion to adult emergence in these trials was 22 to 26 days. Adults commence feeding immediately after emergence and are able to oviposit after seven to 10 days. Adults of *L. texana* have four black stripes along each elytron (Fig. 9), and easily are distinguished from *L. defecta* adults, which have two elytral stripes. The adults undergo a reproductive diapause before winter, burrowing into the soil as the plants senesce in autumn, and emerge the following spring. Adult quiescence is induced by poor host plant quality, particularly senescing leaves rather than photoperiod.

Metriona elatior (Coleoptera: Chrysomelidae)

The biology of *M. elatior* was studied on *S. sisymbriifolium* by Hill and Hulley (1996) and on tropical soda apple by Gandolfo (1997). Adults have a nearly circular body shape (Fig. 10). Pronotum and elytra are mostly green, but occasionally are pale red. Ventrally, the body is shiny black with a pale reddish or greenish lateral margin on the posterior abdominal segments; legs are shiny black.

Females deposit 31 to 109 egg masses, each containing 5 to 13 eggs, on lower surfaces of leaves. Larvae hatch in six or seven days at 25°C. First instars feed individually on the same leaf where the egg mass was deposited. There are five instars, and the pale yellow larvae carry the exuviae and feces dorsally. At high densities, larvae can induce leaf abscission. Mature larvae stop feeding and attach themselves to the lower surface of a leaf with an abdominal secretion to pupate. Pupae are yellow and black in color, and the duration of the pupal stage is five to eight days. Development from the egg to the adult stage is completed in approximately 35 days.

Gratiana boliviana (Coleoptera: Chrysomelidae)

Gandolfo (1998) and Gandolfo *et al.* (2000b) studied the biology of *G. boliviana.* Adults of *G. boliviana* are elliptical in shape and light green in color (Fig. 11a). Females produce an average of 300 eggs during their lives, deposited individually on the leaves or petioles. Eggs are white initially but turn light green during incubation. Larvae hatch within five to seven days at 25°C. There are five instars and the larvae usually feed on the underside of younger leaves (Fig. 11b). The larval stage is completed in 15 to 22 days. Like *M. elatior*, the larvae carry the exuviae and feces on their backs. Mature larvae cease feeding, and attach themselves by the last abdominal segment to the underside of the leaves near the insertion of the petiole to pupate. Pupae are green and flex their bodies when disturbed. The pupal stage usually lasts 6 to7 days.

Anthonomus tenebrosus (Coleoptera: Curculionidae)

The anthonomine weevil *A. tenebrosus* was collected on tropical soda apple during initial surveys in Argentina and Brazil, but was misidentified as *Apion* sp. (Gandolfo, 1997). Adults are black (Fig. 12), approximately 2 mm in length, and feed on tender shoots, buds and flowers of tropical soda apple. The larvae destroy the contents of the flower buds as they

Figure 11a.

Figure 11b.

Figure 11. *Gratiana boliviana* (Spaeth) shown with feeding damage on leaves of tropical soda apple, *Solanum viarum* Dunal; (a) adult, (b) larvae. (Photographs courtesy of Julio Medal.)

Figure 12. *Anthonomus tenebrosus* Boheman, flower bud weevil of tropical soda apple, *Solanum viarum* Dunal. (Photograph courtesy of Stephan McJonathan.)

develop and pupate inside the buds. This type of damage can inhibit fruit production, which reduces spread of the plant. There are no previous host records for this species but a close relative (*Anthonomus sisymbrii* Hustache) that is known from *S. sisymbriifolium* (Clark and Burke, 1996), also attacks tropical soda apple (Olckers *et al*., 2002). The specimens collected on tropical soda apple were tentatively identified as *A. tenebrosus* as some specimens seem to fall somewhere between *A. tenebrosus* and *A. sisymbrii* (W. E. Clark, pers. comm.). Host specificity studies with the flower bud weevil *A. tenebrosus* have been initiated in U.S. quarantine (Medal and Cuda, 2001).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

As of March 2002, no arthropod natural enemies have been released for classical biological control of tropical soda apple in the United States. However, the TAG recommended the release of *G. boliviana* from quarantine in April 2002.

Suppression of Target Weed

A combination of mowing and herbicide application is currently recommended for controlling tropical soda apple in pastures (Mullahey and Colvin, 1993; Mislevy *et al.*, 1996). Hence, a post-mowing application of *R. solanacearum* or mowing with a simultaneous application of *R. solanacearum* were considered rational methods for field application of this bacterium.

Initial trials were done on 187-day-old plants by clipping the main stem 3 cm above the soil and swabbing the cut surface with a 1-day-old bacterial suspension of *R. solanacearum* Race 1, Biovar 1. The inoculum was applied at two rates, 0.74 and 1.74 A at 600 nm. After 12 weeks post treatment, 100% of the plants subjected to the high inoculum level were killed and the shoot biomass was reduced in the low inoculum level treatment.

As a novel method of application, the Burch Wet Blade™mower system (BWB) also was used to deliver the bacterial pathogen *R. solanacearum* (Fig. 13).

Figure 13a.

Figure 13b.

Figure 13c.

Figure 13. (a) Burch Wet Blade Mower™ used for applying the bacterial pathogen *Ralstonia solanacearum* (E. F. Smith) Yabuuchi to tropical soda apple, *Solanum viarum* Dunal; (b) wilted tropical soda apple plant exhibiting disease symptoms; (c) field plots in Immokalee, Florida, United States, showing control of tropical soda apple two months post-treatment in 1998. The bacterial pathogen *R. solanacearum* was applied using the Burch Wet Blade Mower™ to plots visible on left side that were previously infested with tropical soda apple. (Photographs courtesy of R. Charudattan.)

The BWB is commonly used to deliver chemical herbicides to target weeds during mowing, but it had not been tested to deliver a biological control agent. The bacterium *R. solanacearum* Race 1, Biovar 1 was suspended in sterile water and applied to tropical soda apple growing in a pasture located in Hendry County, Florida, with the BWB. The bacterium applied with the BWB reduced the ground cover of tropical soda apple to approximately 1% after 67 days (Fig. 13). Thus, *R. solanacearum* applied during mowing or as a post-cut treatment is an effective way to integrate biological with mechanical control of tropical soda apple under field conditions (DeValerio and Charudattan, 1999; DeValerio *et al.*, 2000).

Recovery of Native Plant Communities

In field trials, pasture grass regrowth after treatment of tropical soda apple with *R. solanacearum* applied with the BWB mower system was comparable to surrounding areas where the weed did not occur. Furthermore, symptoms of bacterial wilt were not observed on any of the pastures grasses exposed to the bacterium.

RECOMMENDATIONS FOR FUTURE WORK

Because the leaf beetle *L. texana* accepted turkey berry as a host plant in laboratory tests (Cuda *et al.*, in press), a request should be submitted to state regulatory officials to obtain approval to introduce the insect from Texas into Florida for biological control of turkey berry. However, additional species of the genus *Solanum* that are endemic to Florida would have to be tested prior to release to determine whether native species are at risk for non-target damage by *L. texana*. For example, the native potato tree that is considered a threatened species in Florida would not be attacked by *L. texana* because the beetle failed to complete its development on this critical test plant in no choice laboratory tests (J. P. Cuda, unpublished data).

Additional screening tests with the tropical soda apple leaf beetle *M. elatior* were completed in the Florida quarantine laboratory as recommended by the TAG, and a petition for field release was resubmitted in December 1999. The supplemental petition requesting release of *M. elatior* from quarantine was denied until open field experiments and surveys are undertaken in South America to resolve the discrepancies observed in development of the insect on eggplant, potato, and tomato in the laboratory larval feeding tests (Hill and Hulley, 1996; Gandolfo, 1997; Medal *et al*., 1999a).

Five additional natural enemies of tropical soda apple have been identified in South America (Medal and Cuda, 2000; Medal *et al.*, 2000b). Specificity tests with another leaf beetle *Platyphora* sp. (Coleoptera: Chrysomelidae), a leafroller (Lepidoptera: Pyralidae), a leaf-tier (Lepidoptera: Oecophoridae), and a stem-mining fly (Diptera: Agromyzidae) should be initiated.

Wetland nightshade is an ideal target for classical biological control. This species tends to form extensive impenetrable thickets in remote, periodically flooded areas. The extreme conditions that characterize this habitat make controlling the plant by conventional means a difficult task. Field surveys in Florida and in the native range would need to be conducted to discover potential biological control candidates for wetland nightshade.

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