EVALUATION OF EXOTIC *SOLANUM* SPP. (SOLANALES: SOLANACEAE) IN FLORIDA AS HOST PLANTS FOR THE LEAF BEETLES *LEPTINOTARSA DEFECTA* AND *L. TEXANA* (COLEOPTERA: CHRYSOMELIDAE)

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Abstract

Tropical soda apple, *Solanum viarum* Dunal, wetland nightshade, *S. tampicense* Dunal, and turkey berry, *S. torvum* Swartz, are considered three of Florida's most invasive plant species. These nonnative perennial broadleaf weeds are disrupting native plant communities in agricultural areas and natural ecosystems. The lack of natural enemies in Florida is thought to be an important factor contributing to their invasiveness. The North American leaf beetles *Leptinotarsa defecta* (Stål) and *L. texana* (Schaeffer) that attack silverleaf nightshade, *Solanum elaeagnifolium* Cav., a native congener of the three nonnative solanums, were evaluated for their potential as biological control agents. The suitability of tropical soda apple, wetland nightshade and turkey berry as host plants for the native *Leptinotarsa* beetles was studied in a quarantine laboratory using single plant and paired plant tests. Neonate larvae of *L. defecta* developed to the pupal stage only on their natural host plant silverleaf nightshade. Feeding damage on turkey berry and wetland nightshade was negligible and no feeding occurred on tropical soda apple. In contrast, development and reproduction of *L. texana* on the nonnative turkey berry were comparable with silverleaf nightshade. These results suggest the nonnative turkey berry may be included in the potential host range of the native silverleaf nightshade beetle *L. texana*.

Key Words: Biological control, weeds, *Solanum viarum*, *S. tampicense*, *S. torvum*, *S. elaeagnifolium*, risk assessment

Resumen

Solanum viarum Dunal, *S. tampicense* Dunal, y *S. torvum* Swartz se consideran como tres de las especies de plantas más invasoras en Florida. Estas malezas perennes no nativas de hoja ancha están perturbando las comunidades de plantas en áreas agrícolas y ecosistemas naturales. Se piensa que la falta de enemigos naturales en Florida es un factor importante que contribuye a su habilidad para ser invasoras. Se evaluaron los escarabajos norteamericanos, *Leptinotarsa defecta* (Stål) y *L. texana* (Schaeffer) que atacan las hojas de *Solanum elaeagnifolium* Cav., una planta nátiva en el mismo género de los tres solanums no nativos, para determinar su potencial como agentes de control biológico. Se estudió si las plantas de *Solanum viarum, S. tampicense* y *S. torvum* podrian ser hospederos adecuados de los escarabajos nativos *Leptinotarsus* en el laboratorio de la cuarentena usando pruebas de plantas individuales y en pares. Se desarrollaron las larvas recién nacidas de *L. defecta* hasta la étapa de pupa solamente en su planta hospedera natural *Solanum elaeagnifolium.* El daño de alimentación en el *S. torvum* y *S.tampicense* fué insignificante y no se alimentó de *Solanum viarum*. Al contrario, el desarrollo y la reprodución de *L. texana* sobre *S. torvum* no nativo, fué similar con los de *S. elaeagnifolium.* Estos resultados suguieron que se puede incluir *S. torvum* no nativo entre los hospederos potenciales del escarabajo de *Solanum elaeagnifolium* no nativo, *L. texana*.

Tropical soda apple, *Solanum viarum* Dunal, wetland nightshade, *S. tampicense* Dunal, and turkey berry, *S. torvum* Swartz, are perennial nonnative invasive weeds that have been identified as candidates for biological control (Cuda et al. 2002). Tropical soda apple was first discovered in Florida in 1988 (Mullahey et al. 1993, Mullahey et al. 1998), and by 1995 infested between 0.25 and 0.5 million ha of prime agricultural and nonagricultural lands (Mullahey 1996a, Mullahey et al. 1998). This invasive weed infests a variety of habitats including improved pastures, natural areas, citrus (*Citrus* spp.), sugar cane (*Saccharum officinarum* L.), sod fields, ditch banks, and roadsides. After establishing in Florida, tropical soda apple continued to expand its range into Alabama, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Pennsylvania, Puerto Rico and Tennessee (Westbrooks & Eplee 1996, Mullahey et al. 1998). The Pennsylvania infestation has since been eradicated (Westbrooks 1998).

The foliage and stems of tropical soda apple are prickly and unpalatable to livestock. However, cattle and wildlife readily ingest the fruits and spread the seeds in their droppings. If left uncontrolled, pasture production declines and stocking rates are drastically reduced (Mullahey et al. 1993). In 1994, production losses to Florida cattle ranchers attributed to tropical soda apple infestations were estimated at US $11 million annually (Cooke 1997). Tropical soda apple also serves as a reservoir for various diseases and insect pests of solanaceous crop plants (McGovern et al. 1994a, 1994b, Medal et al. 1999). A special symposium devoted entirely to various aspects of tropical soda apple and to a lesser extent wetland nightshade's biology, ecology, environmental effects and control strategies was held in Florida in 1996 to address these emerging weed problems (Mullahey 1996b).

Wetland nightshade is a bramble-like plant with spiny tangled stems and leaves that was first reported in Florida in 1983 (Wunderlin et al. 1993, Fox & Bryson 1998). In contrast to tropical soda apple, which dominates upland sites, regularly flooded wetlands are particularly vulnerable to invasion by wetland nightshade (Wunderlin et al. 1993, Fox & Bryson 1998). The largest infestation, approximately 60 ha, occurs in southwest Florida (Fox & Wigginton 1996, Wunderlin & Hansen 2000). 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 the state's wetland habitats thus impeding access to and use of water resources (Fox & Wigginton 1996, Fox & Bryson 1998).

Turkey berry is a large, prickly shrub that can attain heights of up to 3 m (Ivens et al. 1978). Turkey berry was first collected in Columbia Co., Florida, in 1899, and has been reported in at least nine counties throughout the state (Wunderlin & Hansen 2000, Cuda et al. 2002). This noxious solanum invades disturbed sites such as pastures, crop fields, roadsides, damp waste areas and forest clearings where it competes with desirable plants for moisture, light and nutrients. Although it is frequently cultivated as a yard plant in south Florida (Westbrooks & Eplee 1989), turkey berry is potentially poisonous to animals (Chadhokar 1976, Abatan et al. 1997), and possibly carcinogenic to humans (Balachandran & Sivaramkrishnan 1995). Turkey berry has been reported as a reservoir for *Alternaria solani* Sorauer (Deuteromycetes: Dematiaceae), the causative agent of wilt disease in potatoes and tomatoes (Mune & Parham 1967), and is considered one of the most invasive weeds on other continents, particularly in parts of Australia and South Africa that are climatically similar to Florida (Holm et al. 1979). In the Pacific region, turkey berry was identified as a possible target for classical biological control (Waterhouse & Norris 1987). The occurrence of this plant as an invasive weed in other countries is perhaps the most compelling evidence for predicting its eventual effect on Florida's native plant communities.

Tropical soda apple, wetland nightshade and turkey berry are currently recognized as three of Florida's most invasive nonnative plant species (FLDACS 1999, FLEPPC 1999, Langeland 2001). Although it is unclear why these exotic solanaceous plants have become weeds, the lack of host-specific natural enemies in Florida (the introduced range) may have afforded these plants a competitive advantage over native species (Cuda et al. 2002). Tropical soda apple and wetland nightshade are native to South America (and possibly the West Indies), and Mexico, respectively (Wunderlin et al. 1993), whereas turkey berry is thought to have originated in West Africa (Ivens et al. 1978), Central or South America and the Caribbean region (Morton 1981, Waterhouse & Norris 1987), or Asia (Medal et al. 1999).

Silverleaf nightshade, *Solanum elaeagnifolium* Cav., is a close relative of tropical soda apple, wetland nightshade, and turkey berry that is native to the southern United States, Mexico and possibly Argentina (Goeden 1971, Boyd et al. 1983), and belongs to the same subgenus *Leptostemonum* as the three nonnative *Solanum* spp. (D'Arcy 1972, Nee 1991). Silverleaf nightshade is attacked by many insect herbivores in the southwestern United States and Mexico (Goeden 1971). Two of the most damaging insects attacking silverleaf nightshade in its native range are the defoliating beetles *Leptinotarsa defecta* (Stål) and *L. texana* (Schaeffer) (Jacques 1988). Both *L. defecta* and *L. texana* were released recently in South Africa for biological control of silverleaf nightshade (Olckers et al 1999), and their biologies were summarized by Olckers et al. (1995).

Silverleaf nightshade is considered the natural host plant of *L. defecta* and *L. texana* (Goeden 1971, Neck 1983, Jacques 1988). This solanum defines the actual, realized or field host range of the beetles (Kogan & Goeden 1970, Cullen 1990, van Klinken 2000). Host range encompasses those plants on which an insect completes normal development in nature (Hanson 1983). However, the study by Olckers et al. (1995) demonstrated that under laboratory conditions these two beetles also developed and reproduced on other solanums that do not occur in the insects' native ranges. Similarly, Hsiao (1981) observed *L. texana* developed and reproduced to some extent on eggplant as well as three native plant species—*S. dulcamara* L., *S. carolinense* L. and *S. rostratum* Dunal. These solanaceous plants are not typically exploited by the beetles in nature but are capable of supporting some development and reproduction, and comprise what is considered the insects' potential, physiological or fundamental host range (Kogan & Goeden 1970, Cullen 1990, van Klinken 2000). Horsenettle (*S. carolinense*) and presumably Florida horsenettle (*S. carolinense* L var. *floridanum* Chapm.) are the only potential host plants of *L. texana* that are native to Florida (Wunderlin & Hansen 2000). In spite of its native status in Florida, horsenettle is listed as a troublesome weed by Hall & Vandiver (1991).

Silverleaf nightshade is adventive in Florida, occurring sporadically from the Panhandle to the Keys (Wunderlin 1982, Wunderlin & Hansen 2000). Its natural enemies *L. defecta* and *L. texana* have not spread to Florida (Jacques 1985,1988), presumably because the Gulf of Mexico is an effective barrier to insects like *L. texana* that are incapable of long range aerial dispersal (see Hoffmann et al. 1998). However, a computer model (CLIMEX) that uses various climatic factors to determine whether insects can colonize and persist in new geographic areas (Sutherst & Maywald 1985) predicted that *Leptinotarsa* beetles collected from silverleaf nightshade in the Brownsville area of south Texas could establish and persist in peninsular Florida if tropical soda apple, wetland nightshade or turkey berry were suitable host plants.

The purpose of this research was to determine whether the nonnative and invasive tropical soda apple, wetland nightshade or turkey berry are capable of supporting normal development and continuous reproduction of the North American silverleaf nightshade leaf beetles *L. defecta* and *L. texana*. If these native insects are capable of establishing 'new associations' with the exotic solanums (Hokkanen & Pimentel 1984), they could be introduced into Florida for biological control of these weeds after preintroduction host specificity tests demonstrated they were safe to release.

Materials and Methods

Collections of the silverleaf nightshade leaf beetles *L. defecta* and *L. texana* were made during the months of June-October 1997 and May 2001 in Starr County, TX, USA, by personnel affiliated with the USDA-Animal and Plant Health Inspection Service, Mission Plant Protection Center, Mission, TX. Parasitoid-free colonies of *L. defecta* and *L. texana* were maintained on potted silverleaf nightshade plants held in screen cages at the laboratory in Mission, TX. Egg masses of *L. defecta* and *L. texana* deposited on silverleaf nightshade were shipped via overnight mail to the Quarantine Laboratory, Entomology & Nematology Department, University of Florida after USDA, APHIS, PPQ issued an importation permit. A shipment of 138 eggs of *L. defecta* and 310 eggs of *L. texana* was received on 8 September 1997. The eggs were deposited in small masses on individual silverleaf nightshade leaves separated by species in petri dishes sealed with Parafilm® to prevent desiccation. The eggs were removed from the silverleaf nightshade leaves with a camel hair brush and transferred to moistened filter paper placed inside another petri dish. This procedure ensured that neonate larvae were not preconditioned by feeding on silverleaf nightshade prior to the host acceptability tests, which would bias the results of the feeding trials.

Percent survival, development time, and amount of feeding for the larval stages of both leaf beetles were measured on each test plant species. Single plant (no-choice) and paired plant (choice) host suitability tests with three replications were conducted with neonate larvae in a quarantine room maintained at a temperature of 24.0 ± 3.1°C, relative humidity of 66.8 ± 6.8% and a 16-h photophase. Leaves used in the experiments were obtained from potted plants fertilized with Peters® 20-20-20 (N: P: K) solution and maintained in a glasshouse or an outdoor shade house. In the single plant tests, five neonate larvae were transferred directly to a freshly excised leaf of each test plant. The leaf was placed inside a large covered petri dish (25.0 cm diam. by 9.0 cm depth) lined with a Seitz® filter disk (25 cm diam.). The filter disk was routinely moistened with deionized water to prevent the leaf from desiccating, and the leaf was replaced each day or every other day until the larvae pupated or died. Leaf consumption was measured by scanning the leaves photometrically before and after exposure to the larvae. The difference in leaf areas was assumed to be the amount eaten by the developing larvae. The single plant larval feeding and development tests were initiated in early September and completed in late November 1997.

Paired plant (choice) tests of the feeding preferences of *L. texana* larvae were conducted with silverleaf nightshade as the control. Four leaf disks (30 mm diam.) were punched from the base of freshly detached leaves of silverleaf nightshade and turkey berry, the test plant species that supported larval development of *L. texana* in the single plant trials (See Results). The leaf disks were positioned alternately by species and equidistantly around the perimeter of the same container used in the single plant trials. Ten neonate larvae were placed in the center of the container and allowed to select their food source when presented with a choice of silverleaf nightshade or turkey berry leaf disks. The amount of feeding on each test plant species in the paired comparison tests was measured by the same procedure used in the single plant trials. The paired plant (choice) larval feeding trials with three replications were initiated in mid-September and were completed by the end of December 1997 when the last larva pupated or died.

On 9 May 2001, a final shipment of 72 adults of *L. texana* (48 males, 24 females) was received from Texas to compare the beetle's reproductive performance on turkey berry with silverleaf nightshade, and larval feeding and development on potato tree, *Solanum donianum* Walpers. Potato tree is a state listed threatened species (Coile 1998), and a critical non-target plant that would be vulnerable to attack by *L. texana* if this insect were approved for release in Florida for biological control of turkey berry.

The beetles were equally divided among whole plants of either silverleaf nightshade or turkey berry in 3.8 liter (1 gal.) pots covered with acrylic cylinders (41 cm height × 14 cm diam.). The tops of the cylinder cages were covered with Nitex® (41 × 42 in. mesh) to prevent the beetles from escaping. Individual leaves with the egg masses intact were removed from the plants daily, and placed in standard petri dishes with moistened filter paper to incubate. When the larvae hatched, a maximum of 10 larvae was transferred to a plastic rectangular container (20 cm × 14 cm × 10 cm) provisioned with leaves of the same host plant from which they originated, and a piece of paper toweling to collect the frass produced by the developing larvae. Each plastic container also had a hardware cloth insert (16 cm × 10 cm × 5 cm) that served as a platform to keep the leaves from coming in contact with the frass at the bottom of the container. By elevating the leaves in this manner, disease problems were avoided. When the larvae stopped feeding, they were allowed to pupate in the same plastic containers filled to a depth of 5 cm with vermiculite.

New adults (F_1 generation) that emerged in the containers were sexed, and exposed to the same species of potted plant (silverleaf nightshade or turkey berry) on which they completed their development. In total, 12 cages of silverleaf nightshade and 12 of turkey berry, each containing 2 males and 1 female of *L. texana*, were maintained inside the quarantine room under the same environmental conditions. Survival of the F_1 females as well as the number of egg masses produced, eggs per mass, and percent larval eclosion on each test plant species were recorded.

A final single plant (no-choice) feeding and development test was conducted to determine the acceptability of potato tree as a host plant for *L. texana*. The experimental procedures and conditions were the same as those described above for the other single plant tests except the neonates used in this test were F_2 generation larvae of *L. texana* obtained from F_1 adults reared on turkey berry, the control plant in this experiment. The adult reproduction and potato tree risk assessment experiments were completed in late December 2001.

Data Analysis

The data on larval development time and leaf consumption were analyzed by ANOVA (SAS 1990). Leaf consumption means were compared with Tukey's Studentized Range (HSD) test. Nonparametric estimates of larval survival data were analyzed using the LIFETEST procedure (SAS 1990), and were compared with chi-square. The TTEST procedure (SAS 1990) was used to compare the effect of plant species (silverleaf nightshade or turkey berry) on adult female reproductive performance, and plant species (turkey berry or potato tree) on larval feeding and development of *L. texana*. Data obtained on larval eclosion (%) were arcsine transformed prior to analysis.

RESULTS

Larval Feeding and Development

Single plant tests. As expected, larvae of both *Leptinotarsa* beetles completed development on their natural host plant silverleaf nightshade (Figs. 1 and 2). The durations of the first, second, third and fourth stadia for *L. defecta* on silverleaf nightshade were 3.7 ± 0.3, 3.7 ± 0.3, 3.7 ± 0.3, and 9.0 ± 1.5 days, respectively (Fig. 3). However, *L. defecta* was unable to develop on any of the non-native solanum species tested (Fig. 1). All larvae on turkey berry, tropical soda apple, and wetland nightshade died by day 7 and none developed to the second instar. The likelihood ratio test for homogeneity of the survival curves was significant (Chi square = 7.9413, df = 3, $p < 0.05$), indicating that differences in survival occurred among larvae fed the different host plant leaves.

In contrast, development of *L. texana* larvae on turkey berry was comparable to that on silverleaf nightshade (Figs. 2 and 4). Durations of the first, second, third and fourth stadia for *L. texana* reared on silverleaf nightshade were 3.0 ± 0.0, 2.0 ± 0.0, 3.0 ± 0.0, and 8.7 ± 1.9 days compared to 2.7 ± 0.3, 3.0 ± 0.0, 3.0 ± 1.0, and 9.5 ± 0.5 days for turkey berry, respectively. Host plant diets of either silverleaf nightshade or turkey berry in the single plant trials did not affect total larval development time. Likewise, the test for equality of the survival curves for *L. texana* reared on silverleaf nightshade or turkey berry was not significant (Chi square = 5.942, df = 4, $p > 0.05$), suggesting that no differences in survival could be detected on these two solanum species.

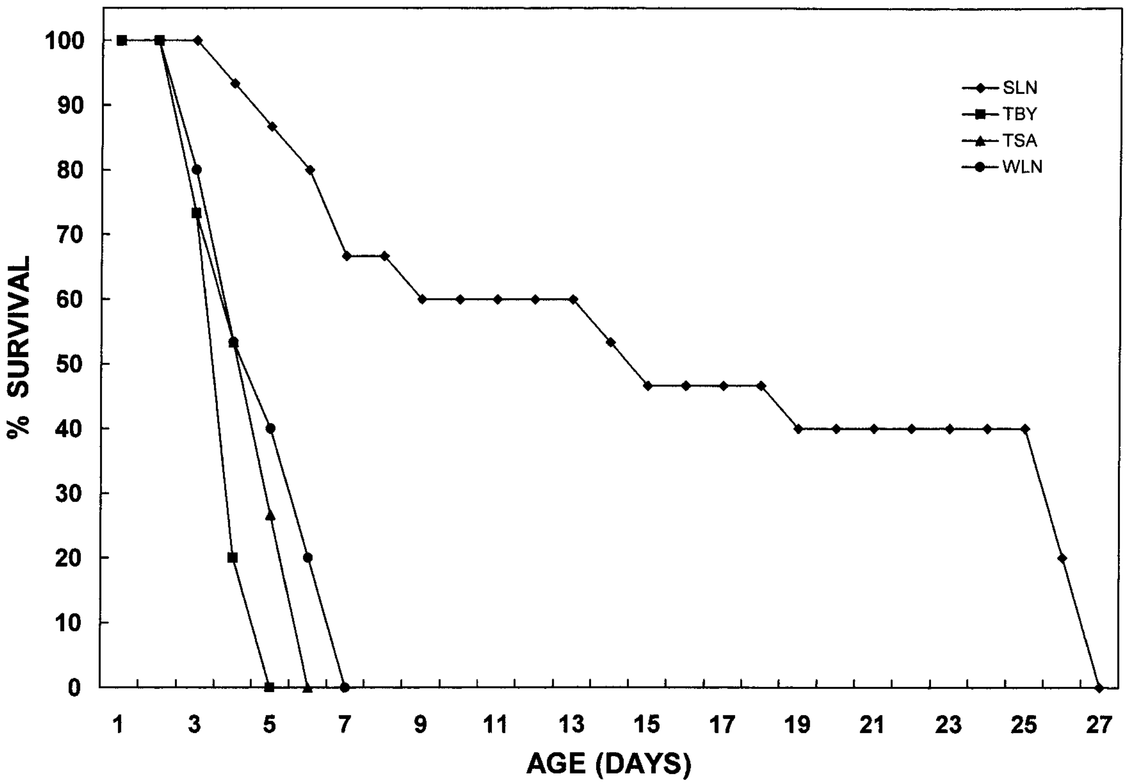

Fig. 1. Survival of larvae of *Leptinotarsa defecta* on four species of the genus *Solanum* in single plant (no-choice) feeding tests in the laboratory. Lines end at larval death or adult emergence. SLN, silverleaf nightshade; TBY, turkey berry; TSA, tropical soda apple; and WLN, wetland nightshade.

The amount of feeding observed on the four solanums by larvae of *L. defecta* and *L. texana* in the single plant feeding trials is presented in Table 1. Larvae of *L. defecta* consumed on average 64.0 ± 9.2 cm^2 of silverleaf nightshade leaf tissue, and mean survival to the pupal stage (≈ day 18) on its natural host plant was 46.7 ± 24.0% (Fig. 1). Although a small amount of feeding occurred on turkey berry and wetland nightshade, all larvae died as first instars. Furthermore, newly hatched larvae confined on tropical soda apple leaves did not feed at all and died within a few days. In contrast, larvae of *L. texana* readily accepted turkey berry leaves as a food source. Larvae ingested 104.5 ± 26.4 cm^2 of turkey berry leaf tissue compared to only 52.3 ± 7.7 cm^2 for silverleaf nightshade (Table 1). Also, larval survival on both plant species was the same for *L. texana*. Survivorship to the pupal stage (≈ day 18) was 40.0 ± 23.1% and 40.0 ± 11.5% for turkey berry and silverleaf nightshade, respectively (Fig. 2).

Potato tree, which is considered a threatened species in Florida, was not an acceptable host plant for *L. texana*. Although the leaves sustained some feeding damage, average leaf consumption by the larvae was significantly lower on potato tree (17.8 ± 17.8 cm^2) compared to turkey berry (98.06 ± 22.33 cm^2) ($t = 2.81$, df = 4, $p < 0.05$). More importantly, no larvae of *L. texana* restricted to a diet of potato tree leaves survived beyond the second instar on this high risk species whereas seven out of 15 larvae, or 47%, experienced normal development and pupation exclusively on a diet of turkey berry leaves. The amount of turkey berry leaf tissue consumed by larvae in this test was not statistically different ($t = 0.239$, df = 4, $p > 0.05$) from that observed for turkey berry in the earlier single plant test shown in Table 1.

Paired plant tests: Paired comparison tests were conducted only with *L. texana* because the single plant trials demonstrated this insect was capable of completing its development to the pupal stage on turkey berry in the absence of its natural host plant silverleaf nightshade. When offered a choice between leaf disks of silverleaf nightshade and turkey berry as a food source, the larvae did not exhibit a clear preference for silverleaf nightshade over turkey berry (Table 1). Although average leaf consumption on silverleaf nightshade was 76.2 ± 6.69 cm^2 compared to 40.0 ± 12.9 cm^2 for turkey berry, the observed differences were not significant ($t = 2.49$, df = 4, $p >$

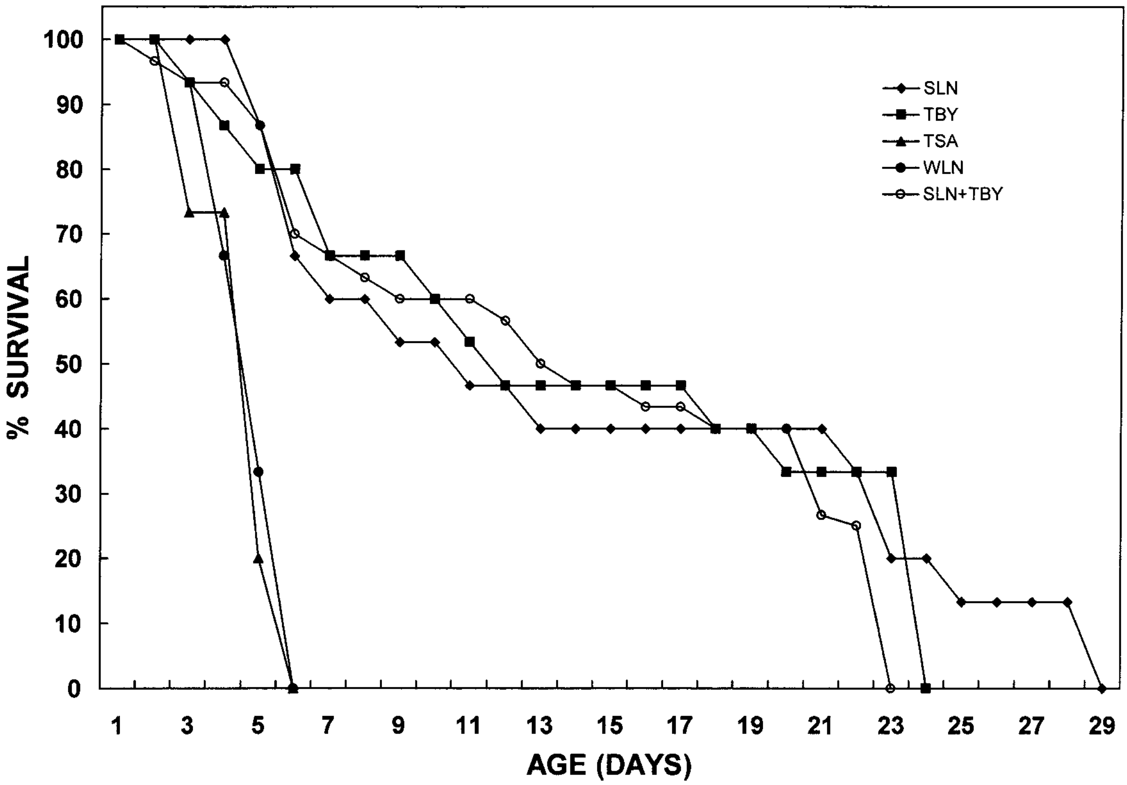

Fig. 2. Survival of larvae of *Leptinotarsa texana* on four species of the genus *Solanum* in single plant (no-choice) and paired plant (choice) feeding tests in the laboratory. Lines end at death or pupation of larvae. SLN, silverleaf nightshade; TBY, turkey berry; TSA, tropical soda apple; WLN, wetland nightshade; and SLN + TBY, silverleaf nightshade + turkey berry.

0.05). Survival and development of *L. texana* to the pupal stage (≈ day 18) in the choice tests were virtually identical (40.0 ± 5.8%) to that observed in the single plant trials (Fig. 2).

Adult Female Survival and Reproduction

In total, eight out of 12 females (67%) of the F_1 generation survived and reproduced on silverleaf nightshade compared to only three F_1 females (25%) on turkey berry. However, the surviving females on average lived as long on turkey berry (58.0 ± 18.3 days) as they did on their natural host plant silverleaf nightshade (58.1 ± 22.4 days) (t = 0.00, df = 9, $p > 0.05$) (Table 2).

Adults of *L. texana* caged on potted turkey berry plants exhibited an unusual feeding behavior not observed on the silverleaf nightshade plants in this study. Beetles often completely stripped the turkey berry plants of their leaves by feeding on the petioles where they were attached to the stem. This feeding behavior resulted in complete defoliation of the turkey berry plants even at the low adult densities (1 to 3 beetles per plant) maintained in this study. Hoffmann et al. (1998) observed a similar phenomenon on silverleaf nightshade but only when *L. texana* reached high densities following its release and establishment in South Africa for biological control of this weed.

The reproductive performance of female *L. texana* on potted turkey berry plants was similar to silverleaf nightshade in this study (Table 2). The number of egg masses deposited by the surviving females on silverleaf nightshade was 18.9 ± 3.8 compared to 9.7 ± 6.7 on turkey berry, but the difference was not significant (t = 1.24, df = 9, $p > 0.05$). Also, the number of eggs laid in each mass by females confined to each of these test plants was similar. The number of eggs per mass averaged 22.6 ± 1.8 for silverleaf nightshade compared to 16.0 ± 3.0 for turkey berry (t = 1.96, df = 9, $p > 0.05$). More importantly, the viability of the eggs produced by the F_1 females reared exclusively on a diet of either silverleaf nightshade or turkey berry leaves was the same. Average percent eclosion of F_2 generation larvae from eggs deposited on silverleaf nightshade and turkey berry

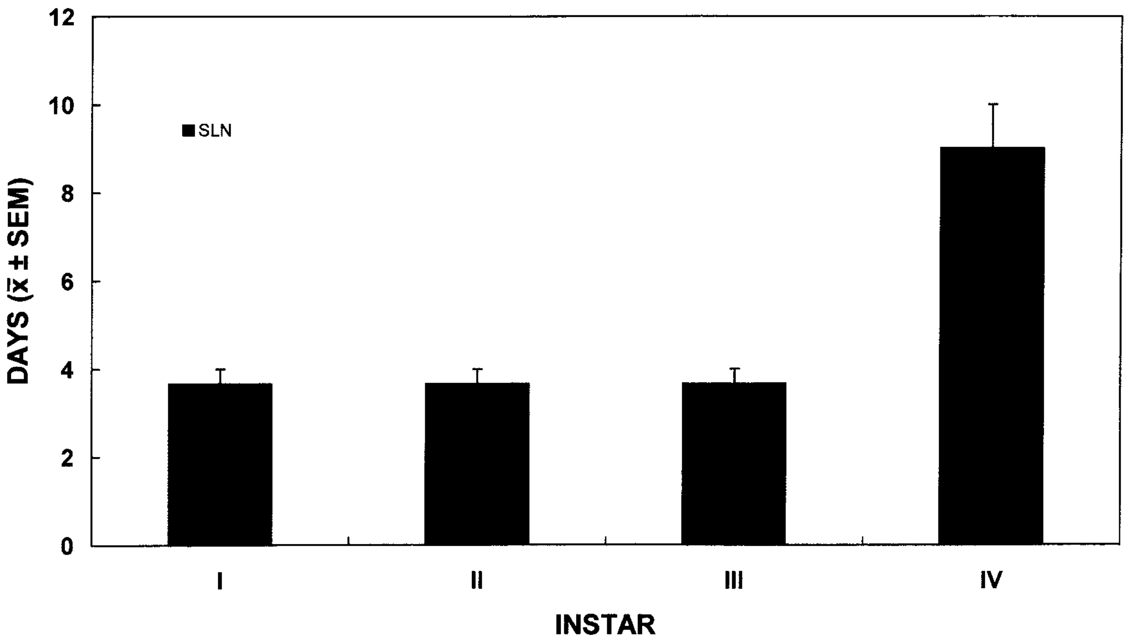

Fig. 3. Average stadial length (in days) of each larval instar of *Leptinotarsa defecta* on *Solanum elaeagnifolium* (silverleaf nightshade, SLN) in single plant (no-choice) feeding tests in the laboratory.

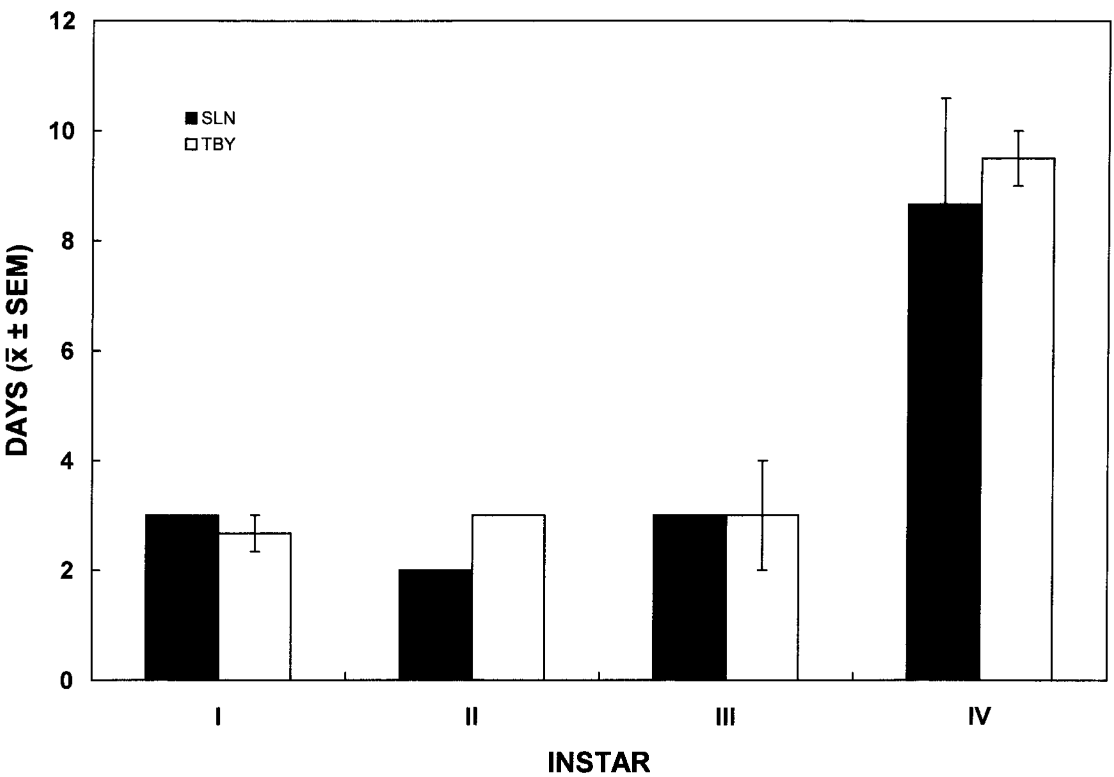

Fig. 4. Average stadial length (in days) of each larval instar of *Leptinotarsa texana* on *Solanum elaeagnifolium* (silverleaf nightshade, SLN) and *Solanum torvum* (turkey berry, TBY) in single plant (no-choice) tests in the laboratory.

TABLE 1. FEEDING (CM^2) BY LARVAE OF *LEPTINOTARSA DEFECTA* AND *L. TEXANA* ON *SOLANUM* SPP. IN THE LABORATORY.

	L. defecta	*L. texana*
Test/Plant Species[1]	Mean (±SEM)	Mean (±SEM)
Single Plant[2]		
SLN	64.00 (9.2) a[4]	52.30 (7.7) b[4]
TBY	0.02 (0.01) c	104.50 (26.4) a
TSA	0.00 (0.0) c	0.00 (0.0) d
WLN	0.17 (0.04) b	0.08 (0.4) c
Paired Plant[3]		
SLN	—[5]	76.20 (6.69) b
TBY	—	40.00 (12.9) b

[1]SLN = silverleaf nightshade; TBY = turkey berry; TSA = tropical soda apple; WLN = wetland nightshade.
[2]Amount of feeding per n = 3 groups of 5 larvae; each group of larvae exposed to only one test plant species. Values for leaf consumption were based on the number of larvae surviving in each trial.
[3]Amount of feeding per n = 3 groups of 10 larvae; each group of larvae exposed to both plant species simultaneously. Values for leaf consumption were based on the number of larvae surviving in each trial.
[4]Means followed by the same letters within columns are not statistically different ($p > 0.05$) according to Tukey's Studentized Range (HSD) test.
[5]Not tested.

was 78.9 ± 6.4% versus 78.0 ± 7.1%, respectively ($t = 0.08$, df = 9, $p > 0.05$). Taken together, these data strongly suggest that *L. texana* is capable of continuous reproduction on turkey berry.

DISCUSSION

Risk assessment has been a cornerstone of the practice of weed biological control since its inception because of safety concerns for crop species (Strong & Pemberton 2000). Clearly, any insect introduced for the biological control of a weed must not itself become a plant pest. The rigorous screening process ensures that non-specialist insects capable of reproducing on economically important, or environmentally sensitive species that are close relatives of the target weed, are dropped from further consideration. In recent years, risk assessment has focused less on crop species and more on native plant species related to the target weed, and the ecological consequences of "environmental spillover"—when a non-target species is attacked by the insect after its introduction (Tisdell et al. 1984). The ecological risks associated with releasing an insect for weed biological control with a host range that includes non-target native species (especially those threatened with extinction) are high, and it is unlikely that the effects will be reversible once the insect is introduced (Strong 1997, Louda et al. 1997, Strong & Pemberton 2000, Louda & O'Brien 2002).

Environmental risks can be reduced by selecting weed targets for classical biological control that (a) are nonnative invasive plant species, and (b) have few native relatives in the United States that could become host plants of the introduced insects (Center et al. 1997, Strong & Pemberton 2000). From this premise, it follows that selecting the nonnative solanum species tropical soda apple, wetland nightshade and turkey berry as candidates for classical biological control raises questions about the potential effects of imported insect herbivores on the numerous nontarget cultivated and native representatives of the genus *Solanum* in North America.

The genus *Solanum* contains over 30 species that are indigenous to the United States, 27 of these occurring in the southeast (Soil Conservation Service 1982). Two native species that are especially vulnerable to attack are the potato tree in Florida (Coile 1998), and *S. pumilum* Dunal, a diminutive species once thought to be extinct yet persists in a few sites in Alabama and Georgia (C. T. Bryson, personal communication). In this study, the potato tree was found to be an unacceptable host plant for *L. texana*.

The genus and family (Solanaceae) also contain economically important crop plants closely related to tropical soda apple, wetland nightshade, and turkey berry (Bailey 1971). Species such as bell pepper (*Capsicum*), tomato (*Lycopersicon*), tobacco (*Nicotiana*), eggplant and potato (both *Solanum* spp.) contribute significantly to Florida's economy. For example, the combined economic value for Florida's solanaceous crop plants in 1998 was reported to be over US $920 million (FLDACS 1998).

To reduce the risk of non-target damage, insect natural enemies imported from the native range of the nonnative solanaceous plants should use only the target weeds as host plants. However, the high degree of host specificity that must be demonstrated in order to obtain federal and state approval for release of these insects in the United

TABLE 2. LABORATORY SURVIVAL AND REPRODUCTIVE PERFORMANCE OF FEMALE *LEPTINOTARSA TEXANA* ON *SOLANUM TORVUM* COMPARED TO ITS NATURAL HOST PLANT *S. ELAEAGNIFOLIUM*.

	SLN[2]	TBY
Parameter[1]	Mean (±SEM)[3]	Mean (±SEM)
Longevity (days)	58.1 (22.4)	58.0 (18.3)
Egg Masses	18.9 (3.8)	9.7 (6.7)
Eggs/Mass	22.6 (1.8)	16.0 (3.0)
% Larval Eclosion	78.9 (6.4)	78.0 (7.1)

[1]Data in each category derived from 8 ovipositing females in the *S. elaeagnifolium* tests, and 3 females in the tests with *S. torvum*. Adults were obtained from neonate larvae reared through one generation on each of the test plants before the experiment was initiated.

[2]SLN - silverleaf nightshade, *S. elaeagnifolium*; TBY - turkey berry, *S. torvum*.

[3]Means within a row compared by *t*-test; none were statistically different ($p > 0.05$, df = 9).

States may be an unrealistic expectation. For example, *Leptinotarsa undecemlineata* Stål, a congener of the two leaf beetles whose host plant relationships were examined in this study, is purported to be monophagous on turkey berry in Cuba (Ballou 1928, Pospisil 1972). In reality, *L. undecemlineata* is actually oligophagous, attacking several different host plants in the genus *Solanum* (Hsiao and Hsiao 1983, Jacques 1985). This particular example is relevant not only because it concerns the same group of insects and one of the plants that were the subject of this study, but clearly illustrates that most plant-feeding insects feed on a small group of closely related plants instead of a single species (Pemberton 1996).

The risk assessment process is further complicated by the fact that herbivorous insects that are screened as candidates for weed biological control projects often exhibit expanded host ranges under confined laboratory conditions (Cullen 1990, Blossey 1995, Olckers et al. 1999). For example, several candidates for classical biological control of tropical soda apple and other solanaceous weeds usually developed in laboratory studies on eggplant, *Solanum melongena* L., potato, *Solanum tuberosum* L. and tomato, *Lycopersicon esculentum* Mill., and other solanums that were not attacked in nature (Olckers et al. 1995, Hill & Hulley 1996, Olckers 1996, 1999, Gandolfo 1997, Medal et al. 1999, 2002).

An alternative to classical biological control—the importation of natural enemies from the native range of the target weed—is to select native insects from North American congeners, and attempt to establish 'new associations' between these native insects and the nonnative *Solanum* spp. (Hokkanen & Pimentel 1984). This approach differs from classical biological control in that the natural enemies have not played a major role in the evolutionary history of the host plant, and are therefore considered "new associates" (Hokkanen & Pimentel 1984). In theory, insect natural enemies from closely related plant species growing in similar climates but different geographical areas from the target plant are potentially more damaging than co-evolved natural enemies. The target weed is more likely to experience greater damage by the "new associates" because it lacks the appropriate defense mechanisms to resist attack (Hokkanen & Pimentel 1984). The 'new association' approach for selecting plant-feeding insects as biological control agents has been critically examined and supported by some practitioners of biological control of weeds (Dennill & Moran 1989, DeLoach 1995), but has been criticized as being based on faulty data by other specialists (Goeden & Kok 1986).

Although there are risks associated with releasing an insect in Florida from a congener of the nonnative *Solanum* spp. that occurs in another geographical region of North America ecoclimatically similar to Florida (e.g., south Texas), the risk of collateral attack on non-target species may be acceptable. The only known potential host plants for *L. texana* in Florida are eggplant and horsenettle. In the unlikely event that eggplant were to be attacked by *L. texana*, insecticides used for crop production in Florida would be an effective feeding deterrent (Nesheim & Vulinec 2001). Likewise, minor damage to horsenettle could be viewed as beneficial as this native solanum is regarded as a weed in Florida (Hall & Vandiver 1991). More importantly, the 'new association' approach has been attempted in the United States against Eurasian watermilfoil, *Myriophyllum spicatum* L. (Haloragaceae), (Buckingham 1994, Sheldon and Creed 1995) and more recently English cordgrass, *Spartina anglica* Lois. (Poaceae) (Wu et al. 1999) without harming native plant communities.

The results of this study indicate that the native leaf beetle *L. texana*, which attacks silverleaf nightshade, is capable of using the nonnative turkey berry as a host plant whereas none of the nonnative solanums supported development in the laboratory of its congener *L. defecta.* The inclusion of turkey berry in the potential host range of *L. texana* was not entirely unexpected. Studies by Hsiao (1981) and Olckers et al. (1995) showed the potential host ranges of *L. defecta* and *L. texana* are much broader than their actual host ranges would indicate. In these laboratory studies, both beetles exhibited limited reproduction on several native *Solanum* spp. as well as on cultivated eggplant. However, the study by Olckers et al. (1995) also showed these beetles would not attack other members of the plant family Solanaceae that are vital to Florida agriculture, including potato, tomato, or bell pepper, and would not survive on plants outside the genus *Solanum*.

The acceptance of eggplant as a host plant in laboratory tests by candidate natural enemies of solanaceous weeds appears to be the rule rather than the exception (Olckers 1996, Medal et al. 1999, 2002). Eggplant apparently is devoid of certain feeding deterrents (chemical or physical) that normally play a role in host plant selection, and often produces false positives in a laboratory setting. However, *L. texana* never has been recorded on eggplant in south Texas even though this economically important solanum is often cultivated extensively in the vicinity of its natural host silverleaf nightshade. Furthermore, eggplant crops in Florida would be chemically protected from attack by *L. texana*. Thus, the risk to eggplant from damage by *L. texana* would be low if the insect were approved for released in Florida for biological control of turkey berry.

If *L. texana* were approved for release, this "new associate" might provide substantial control of one of Florida's most invasive solanaceous weeds. Sustained defoliation by *L. texana* could severely stress turkey berry and perhaps make it less competitive with native plants. More importantly, the ecological risks associated with the release in Florida of *L. texana* may be acceptable because of the behavior exhibited by the beetle following its introduction and establishment on silverleaf nightshade in South Africa. Hoffmann et al. (1998) reported that *L. texana* attained high densities and had well-developed wings, but was unable to fly or reluctant to do so. The beetle remained in the release area until the food supply was exhausted and only dispersed by crawling en masse to adjacent plants. Because it appears that *L. texana* is incapable of flight, the beetle could be confined to a small area during the initial release and establishment phase where appropriate mitigation procedures would be implemented if post release surveys indicated that non-target plants were vulnerable to attack.

Although *L. texana* is native to North America, and would be exempt from the rigorous screening and approval process required by the federal Technical Advisory Group on the Introduction of Weed Biological Control Agents (TAG) (Lima 1990), other nonweedy members of the genus *Solanum* that are native to Florida could be attacked. The risk to these non-target species should be thoroughly assessed and the appropriate state agencies consulted to obtain their approval before releasing *L. texana* in Florida for biological control of turkey berry.

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