Review

The Biology of Australian Weeds
35. *Solanum elaeagnifolium* Cav.

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Name

Solanum elaeagnifolium Cav. is commonly known in Australia as silverleaf nightshade. *Solanum* is from the Latin *solamen*, 'solace' or 'comfort', in reference to the narcotic effects of some *Solanum* species. The species name, *elaeagnifolium,* is Latin for 'leaves like *Elaeagnus*', in reference to olive-like shrubs in the family Elaeagnaceae. 'Silverleaf' refers to the silvery appearance of the leaves and 'nightshade' is derived from the Anglo-Saxon name for nightshades, 'nihtscada' (Parsons and Cuthbertson 1992). Other vernacular names are meloncillo del campo, tomatillo, white horsenettle, bullnettle, silverleaf horsenettle, tomato weed, sand brier, trompillo, meloncillo, revienta caballo, silverleaf nettle, purple nightshade, whiteweed, western horsenettle, desert nightshade, silverleaf bitter apple and devilbush (Boyd *et al.* 1984). In South Africa the plant is known by the Afrikaans name 'Satansbos' (Satan's bush), in testimony to its infamy (Wassermann *et al.* 1988), and in Morocco it is known as morelle jaune (Bouhache, Boulet and El Karakhi 1993).

Description

The following description is from Symon (1981).

> 'An erect, clonal, herbaceous *perennial* to 1 m, often 40–60 cm high, extensive underground root system producing usually annual vegetative growth; stems erect, branching towards top; prickles 2–5 mm long, straight, fine, often reddish, usually present on stems, less often on petioles and leaves, plants sometimes nearly free of prickles; all parts covered with close, dense, tomentum of stellate hairs (sessile or shortly multiseriate-stalked, porrect-stellate with medium or long central ray), general aspect silvery-green, rarely rusty, slightly discolorous. Lower *leaves* c. 10 × 4 cm, oblong-lanceolate, distinctly sinuate-undulate, upper leaves smaller, oblong, entire, venation usually prominent in dried specimens, base rounded or cuneate, apex acute or obtuse; petiole 0.5–2 cm long, with or without prickles. *Inflorescence* a few (1–4)-flowered raceme at first terminal, soon lateral; peduncle 0.5–1 cm long; floral rachis 2–3 cm long; pedicels 1 cm long at anthesis, reflexed and lengthened to 2–3 cm long in fruit. *Calyx* c. 1 cm long at anthesis; tube 5 mm long, more or less 5 ribbed by nerves of 5 subulate lobes, whole enlarging in fruit. *Corolla* 2–3 cm diameter, rotate-stellate, often reflexed, blue, rarely pale blue, white, deep purple, or pinkish. *Anthers* 5–8 mm long, slender, tapered towards apex, yellow, conspicuous, erect, not coherent; filaments 3–4 mm long. *Ovary* pubescent towards summit; style 10–15 mm long. *Fruit* 8–14 mm diameter, globular, first marbled green, later greenish-yellow to orange brown, usually firm, not succulent. *Seeds* 3 × 2 mm diameter, flat or biconvex, light brown, smooth'.

The chromosome number in Australian material examined by Randell and Symon (1976) was n=12. A flowering and fruiting stem is shown in Figures 1 and 2.

There is morphological variability within Australian populations for degree

Figure 1. *Solanum elaeagnifolium*. Flowering and fruiting stem (from Symon 1981).

of spininess, growth habit, petal colour and leaf shape, size and lobing, but the variation is considered to be within the range of the species. The variability is probably the result of multiple introductions, rather than hybridization with related indigenous species (Tideman 1960a, Leys and Cuthbertson 1977).

Silverleaf nightshade is sometimes confused with two native *Solanum* species in Australia, native quena (*S. esuriale* Lindl.) and western nightshade (*S. coactiliferum* J.M. Black). Silverleaf nightshade has a taller, more robust habit, and longer leaves (10 cm cf. 5 cm) than *S. esuriale*, with more wavy margins (Cuthbertson and Leys 1976, McKenzie 1976a). *S. coactiliferum* grows in sandy soils as a relic of native vegetation and is not normally an aggressive weed (D.E. Symon personal communication). *S. karsensis* (Symon), a native perennial that infests irrigated crops in far western New South Wales, is also similar in appearance and behaviour to silverleaf nightshade (Monaghan and Brownlee 1981).

History

Silverleaf nightshade was first reported in Australia at Bingara (New South Wales) in 1901, but the route of introduction is not known. Rapid subsequent records at Tenterfield (1907), North Melbourne (1909), Singleton (1914), Hopetoun (1918) and Cowra (1923), strongly suggest that multiple introductions occurred (Cuthbertson and Leys 1976).

The weed was first recorded in South Australia in 1914 (Kloot 1986), possibly in contaminated hay from the USA (Parsons and Cuthbertson 1992), and was recognized as a potentially serious weed by the late 1940s. Unofficial reports suggest that it has been present in the mid-northern areas of South Australia since 1937. By 1958 it had been recorded from Lameroo, Keith, Owen, Clare, Hilltown, Rhynie, Cleve, Roseworthy, Reynella and in the Upper Murray Irrigation Area. All infestations were thought to be *S. esuriale* until 1958, when it was realized that silverleaf nightshade was also present. The common name ‘tomato weed’ was used to distinguish silverleaf nightshade from native *Solanum* species, commonly known as ‘wild tomatoes’, because farmers were reluctant to change to the name ‘silverleaf nightshade’ (Tideman 1960a,b). Sometime later the name ‘silverleaf nightshade’ was adopted as the official common name for the species in South Australia. By 1978, South Australia had about 16 000 ha (J. Dickenson personal communication) and by 1990 the area exceeded 40 000 ha (South Australian Animal and Plant Control Commission survey, unpublished).

Silverleaf nightshade was first declared under noxious weed legislation in Victoria in 1950 (McKenzie 1980) and by 1973 the State had an estimated 1000 ha, with 90% occurring on six farms (Parsons 1973). Infestations were also increasing in New South Wales and by 1978 there were at least 20 000 ha infested (J. Dickenson personal communication). The weed was of little importance until 1960 when a series of wet summers accelerated spread (Cuthbertson and Leys 1976). It was declared a noxious weed in Western Australia in 1973 (Rutherford 1978) and by 1978 it covered 150 ha, although only 17 ha of this area was densely infested. It arrived in Western Australia before 1921, probably in Sudan grass (*Sorghum sudanense* (Piper) Stapf) from eastern Australia (P.A. Rutherford personal communication).

Figure 2. Flowering shoot of *Solanum elaeagnifolium* growing from a perennial rootstock in cereal stubble.

Distribution

Wapshere (1988) concluded that there is strong evidence that silverleaf nightshade evolved in the Monterrey region in north-eastern Mexico, based on an assessment of the variation, distribution and frequency of its naturally occurring herbivores. Boyd *et al.* (1984) agree that silverleaf nightshade is native to the Americas, but believe that it could be indigenous to either North or South America. They do, however, concede that the likely centre of origin is in south-western United States and northern Mexico. Many of the regions of the world where silverleaf nightshade has established have similar climates to this putative area of origin.

Silverleaf nightshade spread from the Americas to many places, including Australia, Argentina, Brazil, Chile, India, Israel, Greece, Morocco, North America, South Africa and Spain. It has become a major weed problem in Australia, Argentina, Greece, India, Morocco, North America and South Africa (Carretero 1989, Holm *et al.* 1991, Parsons and Cuthbertson 1992, Eleftherohorinos *et al.* 1993). There are 1.4 million ha of land infested with silverleaf nightshade in the southern high plains of Texas alone, including 800 000 ha of cotton (Abernathy and Keeling 1979, Keeling and Abernathy 1985). Over 100 000 ha of irrigated cotton, maize and sesame are infested in central Morocco (Tanji *et al.* 1984). Silverleaf nightshade was first found in South Africa as early as 1905 as a contaminant of seed, but was only officially recorded in 1952 and was declared a noxious weed in 1966. It is now a major weed and infests up to 55% of land in some districts, occurring mainly in the Northern and Northwest provinces, Free State and the Karoo region of the Eastern Cape (Olckers and Zimmermann 1991, Wassermann *et al.* 1988). It is widespread on the semi-arid pampas of South America, but not where crops and pastures provide adequate competition (McKenzie 1980). Potential for invasion of New Zealand is low and a marginally suitable homoclimatic area exists only around the Hawkes Bay region (Panetta and Mitchell 1991).

Silverleaf nightshade occurs in the Australian states of Queensland, New South Wales, Victoria, South Australia and Western Australia. It is a serious weed in South Australia, New South Wales and Victoria, with large infestations occurring throughout the cereal cropping zones. Isolated infestations occur in Queensland and Western Australia (Figure 3). It infests large areas of the southern and central wheat zone, the north-western slopes, and the Murrumbidgee Irrigation Area of New South Wales (Lemerle 1983), with an estimated 140 000 ha affected in 1992, a seven-fold increase since 1977 (Dellow 1993, Hennessy 1995). Infestations occur throughout the Wimmera and Mallee regions in the west and north of Victoria. The worst-affected areas are around Mildura, Hopetoun, Horsham and Pyramid Hill (Anon. 1980). In South Australia, it occurs throughout the cereal cropping zones and is causing most concern in parts of the Upper South East, Mallee, Lower and Mid-North, and Eastern Eyre Peninsula regions. It was first found in 1950 in Western Australia and is established at more than 50 sites in a band running from Perth south-east to Albany. Risk assessment shows that it is established only over a small section of its potential high and medium risk distribution areas (Connell and Panetta 1993).

Habitat

Silverleaf nightshade is adapted to a wide range of habitats, a characteristic that contributes to its weediness in diverse regions around the world. It grows in the warm, temperate regions of Australia with an annual rainfall of 250–600 mm, and grows in a range of soil textures (Parsons and Cuthbertson 1992), although the heaviest infestations occur on sandy soils with low organic matter (Leys and Cuthbertson 1977). For example, in the Wimmera and northern regions of Victoria it grows on heavy clays but is most abundant on the light-textured soils of the Mallee. The largest infestations are on cropping and grazing land, with smaller infestations being found in irrigated pastures, orchards and vineyards, roadsides, channel banks and stockyards (McKenzie 1980). In a study of the potential invasiveness of silverleaf nightshade in New Zealand, Panetta and Mitchell (1991) identified cool summers and high annual rainfall as important factors which may limit its distribution in some regions of Australia which have not been colonized. Although it grows alongside waterways and seeds spread via running water, silverleaf nightshade appears to be susceptible to water-logging. An exceptionally wet winter apparently killed a 2 ha infestation on a heavy clay soil in south-eastern Australia (D.E. Symon, unpublished report). It is sensitive to frost and highly resistant to drought (Wassermann *et al.* 1988).

Silverleaf nightshade grows well on disturbed land such as cultivated fields, roadsides, water furrows and riverbanks, and stock yards in South Africa. It does not normally invade undisturbed pastures, although this has been observed in several districts (Wassermann *et al.* 1988). It invades sandy soils with poor fertility and sparse ground cover in Argentina (Amor 1977), and in the high plains of Texas it has increased in the cropping areas as a result of reduced tillage (Stubblefield and Sosebee 1984).

Growth and development

Silverleaf nightshade is a shrub-like, multi-stemmed plant that grows in summer and autumn. It has a deep, extensive perennial root system (Figure 4). New shoots develop from adventitious buds on the roots and are killed by frosts during late autumn or early winter. Shoots emerge from perennial roots in October to November (spring) in Australia and flowering commences in December and continues through to February or March (summer). The first fruits normally form in January and berries ripen and seeds mature (Figure 5) about 4–8 weeks after fruit set (McKenzie 1980). Soil temperature may influence shoot emergence, because in South Australia in 1975, shoot emergence was delayed by an exceptionally cool spring (J. Dickenson personal communication). New shoots have been observed as late as early May (autumn), after cultivation (Leys and Cuthbertson 1977).

The deep, perennial root system confers drought-resistance (Wassermann *et al.* 1988) and resists most control strategies. Roots have been measured to a depth of 4 m in Australia (D. Creeper personal communication) while in Arizona they extended beyond 3.3 m, 'virtually undiminished' in diameter. Some 45% of roots were in the top 30 cm, and 70% occurred in the top 90 cm (Davis *et al.* 1945). The root system of silverleaf nightshade consists of three main parts: the main or vertical tap root, the portion of the shoot extending from the main tap root to the soil surface, and the lateral structure that connects adjacent shoots. There are three distinct types of tissue specialization in the main tap root: epidermis, cortex, and vascular region. Lateral roots are similar in structure to tap roots, but contain more fibre cells. The structure of the laterals suggests that they are creeping roots, rather than rhizomes (Tisdell *et al.* 1961). Roots increase in diameter through cambial activity and secondary thickening and some branching occurs at depth. Secondary shoots tend to lack secondary thickening and grow up to 2 m horizontally before turning downwards (Cuthbertson 1976).

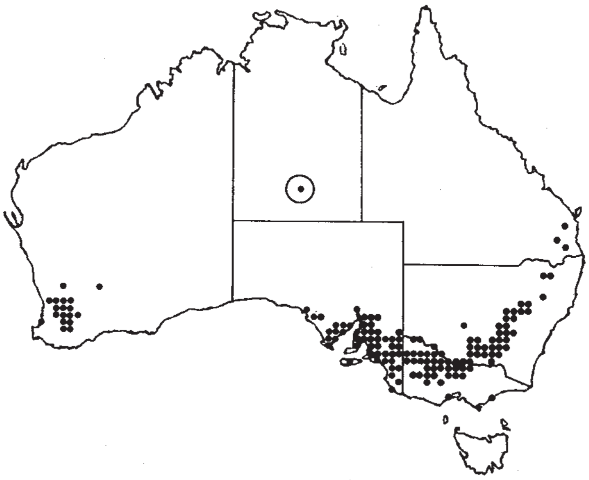

Figure 3. Australian distribution of *Solanum elaeagnifolium* (from Parsons and Cuthbertson 1992).

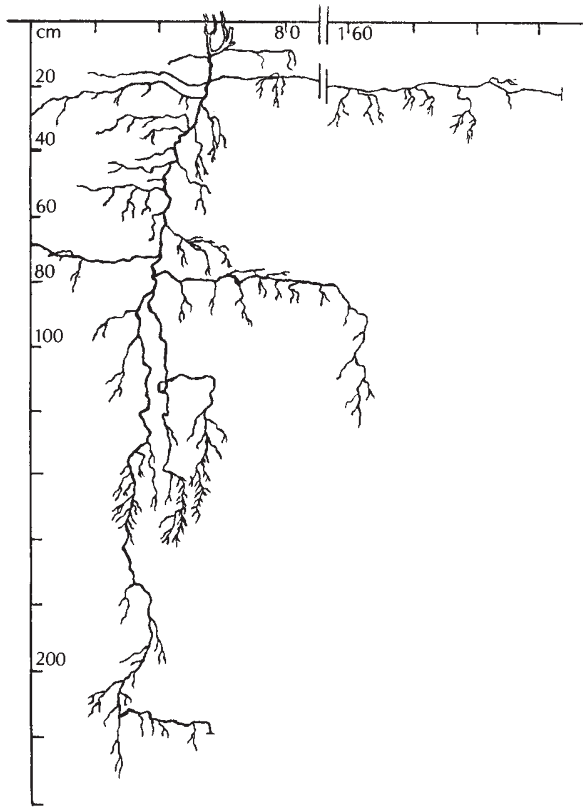

Figure 4. Root system of *Solanum elaeagnifolium* (from Parsons and Cuthbertson 1992).

Total non-structural carbohydrate (TNC) levels are an indication of stored energy reserves and plants are thought to be less able to survive herbicide damage when TNC levels are low. TNC levels were highest in the roots and lower shoot stem. Levels were lowest at flower bud formation and then built up between flowering and fruit maturation, and appeared to be determined by phenological stage rather than soil moisture or humidity (Bouhache, Boulet and El Karakhi 1993). In Texas an increase in TNC was measured in the storage organs of the roots of silverleaf nightshade during late summer and early autumn, coinciding with the green berry stage. TNC levels were highest at full maturity and early senescence, and decreased slightly after senescence, probably as a result of maintenance respiration (Stubblefield and Sosebee 1985).

Reproduction

Floral biology

Flowers first appear in late December to early January, about three weeks after shoot emergence (Moore *et al.* 1975). Flowering and fruiting continue through summer and autumn while conditions are suitable (Cuthbertson and Leys 1976). Flowers are usually bright purple to blue. In most infestations there are subtle differences in flower colour associated with coalescing colonies. Occasionally, white-flowered colonies are found and their occurrence as solid patches amongst predominantly purple-flowering colonies reenforces the relative importance of clonal spread in comparison to spread by seeds. Symon (1981) noted that native Australian *Solanum* species with conspicuous yellow anthers are probably adapted for recognition by pollinating insects. Silverleaf nightshade has conspicuous yellow anthers, and so is likely to be cross pollinated, although there was no literature found describing its breeding system.

Seed production and dispersal

Each stem produces about 60 berries per season in Australia, with each berry containing about 50 seeds (Cuthbertson and Leys 1976). Berries ripen and contain mature seeds about 4–8 weeks after fruit set (Moore *et al.* 1975). There were 24–149 seeds per berry in the USA, depending on sowing date (Boyd and Murray 1982). Viable soil seed banks in heavily infested areas in Morocco were 163 m^{-2} to a depth of 60 cm (Bouhache and Tanji 1985). There were 4000 seeds m^{-2} in the top 10 cm of soil in a dense infestation in north-western Victoria (McKenzie 1980). High dormancy and infrequent germination probably explains why seed bank levels have built up to these levels in dense populations (Wapshere 1988).

Seeds can be dispersed by water, birds, vehicles, machinery and animal faeces (McKenzie 1980, Heap and Honan 1993), as well as infested fodder and seed (Cuthbertson and Leys 1976). Dry berries can spread rapidly over long distances in streams in South Africa (Wassermann *et al.* 1988) and there is strong evidence that this also occurs in Australia. Mature shoots can tumble across the ground when blown by wind, thus spreading berries (Parsons 1973). Boyd *et al.* (1984) observed that the meagre literature on the spread of silverleaf nightshade indicates that it does not spread as rapidly as some species but, once established, it is tenacious.

Seeds can be spread in the faeces of a variety of animals, including cattle, sheep and guinea fowl (Wassermann *et al.* 1988). Sheep readily eat berries in Australia and they appear to be the main vectors. In field studies with sheep in South Australia, excretion began within 24 hours of ingestion and most seeds were excreted within 7–9 days. There were up to 672 seeds kg^{-1} of fresh dung. Single seeds were detected 17 and 31 days after ingestion. Mature berries (on stalks and on the ground) as well as green berries were eaten to exhaustion between January and April (mid-summer to mid-autumn) when alternative feed supplies were low. Much of the excreted seed is viable (Heap and Honan 1993). In another laboratory feeding study with sheep, most seed had been passed by animals by the end of four days, but one seed was detected after six days. Between 8 and 14% of seed was excreted and a quarantine period of at least four days was suggested (McKenzie 1975). Wassermann *et al.* (1988) suggest a quarantine period of at least ten days while the work of Heap and Honan (1993) suggests that 14 days is more appropriate.

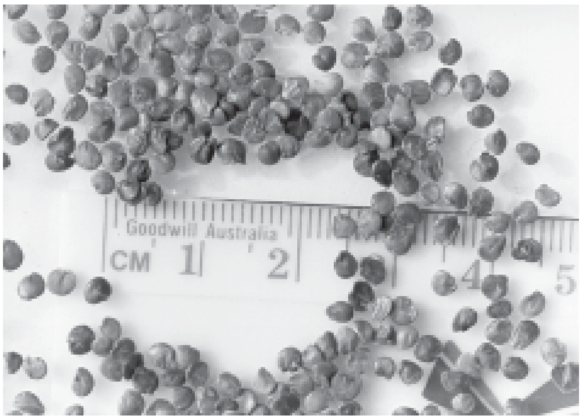

Figure 5. Seeds of *Solanum elaeagnifolium* (scale in cm).

Seed viability and germination

Factors controlling germination and seedling establishment of silverleaf nightshade are poorly understood. Seeds are highly viable and are long-lived. However, only occasionally are high numbers of seedlings observed, suggesting specific moisture and temperature requirements for germination. Ingestion and excretion of seed by sheep increases germination (Parsons and Cuthbertson 1992). Most seedlings germinate after heavy summer thunderstorms, and survival depends on continued soil moisture during summer in Victoria (Molnar and McKenzie 1976). Following 75 mm of rain in the Mallee in 1973, seedlings were abundant, but few survived to the next growing season (McKenzie 1980). Germination occurs readily in October, when the soil temperature at 30 mm ranges from 10 to 23°C (Leys and Cuthbertson 1977). Seeds harvested at 30, 60, 90 and 360 days after anthesis gave 14.5, 20, 20, and 60.5% germination respectively (Vigna *et al.* 1983). Under favourable conditions, up to 80% of seeds can germinate. In laboratory storage studies in the USA, fresh seed had a germination rate of 29%, 3-year-old seed 72%, and 10-year-old seed 60%. The most favourable conditions for germination are thought to be relatively high temperatures and an abundance of moisture. Seedlings are rarely observed in the Australian Mallee due to dry summers (McKenzie 1980).

Seeds of silverleaf nightshade have a strict germination requirement for alternating temperature (McKenzie and Douglas 1974, Boyd and Murray 1982, Trione and Cony 1990). Optimum conditions for germination in Oklahoma were 20/30°C for 16 h dark/8 h light, producing 57% (Boyd and Murray 1982) and 48% germination (Cooley and Smith 1972). Seeds will germinate equally in light or dark (McKenzie and Douglas 1974, Boyd and Murray 1982, Vigna *et al.* 1983, Trione and Cony 1990). Trione and Cony (1990) found that seeds became sensitive to alternating temperatures five days after the start of imbibition and three cycles of alternation were required for 50% germination. The response to the germinating signal was retained through a dehydration cycle or subsequent incubation at constant temperatures. Germinating seeds were able to withstand periods of extreme temperature and dehydration for several days, and seeds could germinate when immersed in water. Immature seeds broke dormancy under dry storage at room temperature.

Germination was increased significantly by immersion of seeds in running or still water for 1 to 120 h prior to incubation at 20–30°C. Running water increased the rate of emergence but did not affect final germination at 50 days, compared with still water. It was suggested that the mucilaginous substance around the seed inhibited germination, either as a physical barrier, or through inhibitory chemicals (Rutherford 1978). Vigna *et al.* (1983) found that washing in stirred water for 36 h did not alter germination but alternate wetting and drying of seeds in soil accelerated germination. Germination can be increased 50% by treatment for 15 minutes in concentrated hydrochloric acid (Amor 1977). Cooley and Smith (1972) found that mechanical or chemical seed coat treatments did not increase germination. Although experimental results are varied, it seems likely that there is a water soluble substance on seed coats that chemically or physically inhibits germination. Optimum pH for germination was between 6 and 7 and NaCl concentrations in excess of 2500 ppm significantly reduced germination (Boyd and Murray 1982).

Seedling establishment

Seeds of silverleaf nightshade germinate after heavy rains in early autumn or spring, with alternating cool and warm temperatures. Emergence occurs more in disturbed soils than on crusted, compacted or undisturbed soil (Cuthbertson and Leys 1976). Maximum emergence in a glasshouse (33%) was from 30 mm (Cooley and Smith 1972) and few seedlings emerged from below 60 mm (Boyd and Murray 1982). Seedlings clipped at the cotyledon stage are capable of regeneration (Cooley and Smith 1972). Some seedlings are able to regenerate following shoot removal 15 days after emergence; after 30 days 90% recovered from shoot removal (Boyd and Murray 1982). Seedling roots were 190 mm long three weeks after germination (McKenzie 1976a). A newly emerged and 5-week-old seedling are shown in Figures 6 and 7.

Wapshere (1988) postulated that although dispersal and initial establishment must occur by seed, the infrequent emergence and subsequent low survival of seedlings suggest that seeds play a minor role in shoot recruitment in established stands. Circumstantial evidence in southern Australia suggests that seedlings that emerge in late spring or summer rarely survive, due to infrequent rains, despite a potential for root elongation of 1 cm day^{-1} (McKenzie 1980). Spread by seeds is thought to be restricted by drought in South Africa (Wassermann *et al.* 1988). Seedlings that emerge in autumn are probably killed by frost. In regions with significant warm season rainfall, such as in its native range, seedlings are sustained by late spring and summer rainfall and are not normally subjected to frost (Wapshere 1988).

Vegetative reproduction

Silverleaf nightshade has a long, robust tap-root that grows to 2 m. Robust lateral roots branch off from the main tap-root 15–30 cm below the surface (Figure 4). All parts of the root system can regenerate if cut off or damaged by cultivation, thereby aiding spread (Cuthbertson and Leys 1976). The average root depth in the Victorian Mallee was 1.2 m and the deepest measured root was 2.8 m. Plants had an average of five lateral roots which typically arose in the top 60 cm of soil. The laterals were up to 2 m long and sometimes gave rise to daughter shoots. The deepest laterals arose from 143 cm down the vertical root and the shallowest was found at 1 cm (McKenzie 1980, Molnar 1982). Regenerating crowns and lateral roots were observed to arise from as deep as 50 cm in cultivated soils, compared with 1–20 cm for uncultivated soils (Monaghan and Brownlee 1979). Dittmer (1959) excavated root systems in the New Mexico desert and found deep tap roots which gave rise to up to 32 laterals and daughter shoots 40–60 cm from the parent plant. The laterals bearing daughter shoots were 10–16 cm beneath the surface. The older roots were dark brown and only the largest laterals gave rise to tertiary roots. Hairs were abundant on all secondary and tertiary roots and averaged 120 µm long and 8 µm in diameter.

Although most farmers interviewed in southern Australia believed that the spread of silverleaf nightshade within farms was by stock, not cultivation (Tideman 1973), it is clear that vegetative reproduction contributes to spread. This spread is primarily through root growth at the margins of colonies, rather than transport of fragments during cultivation. Large patches of recognizable forms, sometimes isolated, and sometimes interspersed with other forms, indicate extensive spread by root growth in Australia (D.E. Symon unpublished report). In one corner of a paddock in South Australia at least five distinct forms were present (J.W. Heap unpublished data). Grazed colonies increased in diameter by an average of 70 cm per year over three years and the rate of expansion varied greatly with season. In one wet year, colony diameter increased by 3.9 m and in a dry year it decreased by up to 2 m (McKenzie 1980).

When topsoil was removed and replaced by clean soil, regrowth from root systems reached the surface after four months from 50 cm, and after 14 months from 1.25 m. Shoots arising after cultivation were surveyed and 85% had arisen from vertical tap roots, while 15% had arisen from horizontal lateral roots. Of the vertical roots surveyed, 25% had produced more than one new shoot. Ten days after cultivation, the average shoot length was 8 cm (McKenzie 1980). Only 3% of shoots examined in a cultivated fallow in April had arisen from transplanted root fragments (Leys and Cuthbertson 1977).

Root fragments as short as 10 mm were able to regenerate and the depth of origin had no effect on regenerative capacity. Polarity was strongly maintained in excised fragments with fewer shoots forming on fragments from horizontal roots than from vertical roots (Richardson and McKenzie 1981). Fernandez and Brevedan (1972) found that root fragments regenerated more in light than dark, and that chlorophyll sometimes developed in root fragments incubated in light. Some root fragments survived for 15 months with a capacity for regeneration. Root fragments were strongly polarized so that roots developed on the distal end and shoots on the proximal end. This polarity was lost in some fragments after prolonged storage. Root fragments from at least 1.25 m deep were able to regenerate, with depth of origin having little influence on regeneration. Regeneration from fragments was highest during winter and lowest during summer (Fernandez and Brevedan 1972). In pots, 10 cm long root cuttings failed to grow when planted at 20 cm depth (Babu *et al.* 1995).

Little is recorded on the life-span of individual plants, although it is clear from field observations that individual tap roots produce shoots for at least several years. Tap roots remain alive and new shoots are produced each year in late spring. Shoots are killed by the first frosts of autumn and the dead shoots stand through winter with mature berries on them (Cuthbertson and Leys 1976).

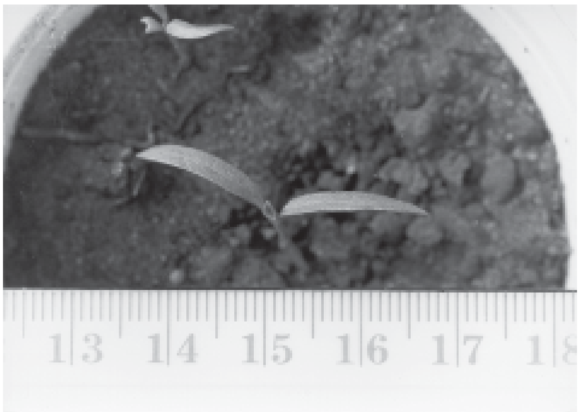

Figure 6. Seedlings of *Solanum elaeagnifolium* (scale in cm).

Figure 7. Seedling rosette of *Solanum elaeagnifolium* at five weeks (approximately 15 cm diameter).

Importance

Detrimental

General. Silverleaf nightshade competes with crops, exudes plant inhibitors, interferes with animal husbandry and harvesting practices, and is an alternative host for phytophagous insects and plant diseases (Boyd *et al.* 1984), but there is little published information on its economic impact. It can reduce management options, such as the use of land and sale of hay (McKenzie 1980). In the 1970s, landowner concern about further spread in Victoria was very strong (McKenzie 1976b), and the greatest economic effect of silverleaf nightshade in eastern Australia was the reduction of land values of both infested and nearby properties (McKenzie 1980, Moore *et al.* 1975). Based on the experience in North America, the weed has the potential to spread to and have a major impact on the summer cropping areas of Australia, especially in the cotton production areas of northern New South Wales and southern Queensland (G.W. Charles personal communication 1997). A low rate of dispersal in the absence of livestock may be the reason that it is not yet a major problem in these areas.

Crops. Silverleaf nightshade competes for water and nutrients in dryland and irrigated crops and soil moisture losses have been measured at depths of up to 150 cm (Green *et al.* 1988). It competes indirectly with winter crops and pastures through moisture and nutrient depletion during the summer fallow period (Cuthbertson and Leys 1976). For example, irrigated and dryland cotton lint yields in Oklahoma were reduced an average 1.5% for each silverleaf nightshade plant per 10 m length of row (Green *et al.* 1987). Yields of dryland crops are reduced over most of its range and competition appears to be most severe in sandy soils and seasons with low rainfall. The greatest unrealized threat to Australian agriculture is widespread invasion of summer-irrigated land (Leys and Cuthbertson 1977). Some farms in western USA have been abandoned due to silverleaf nightshade (Parsons 1973) and on the Eyre Peninsula in South Australia some farmers have discontinued cereal cropping in certain sandy paddocks owing to the competitive effects of silverleaf nightshade (R. Carter unpublished data). It is restricted to being a minor weed in Argentina by intensive cropping (wheat-sorghum-wheat rotation), and the competitiveness of *Eragrostis curvula* (Schrad.) Nees in sown pastures (Amor 1977).

To obtain the same cereal yield as in uninfested crops, extra expenditure on herbicides, cultivation and fertilizers is necessary. In some seasons when berry growth is early and cereal harvest is delayed, there is potential for grain contamination with mature fruits (McKenzie 1980). Yield experiments at 11 sites on the Eyre Peninsula, South Australia, and in New South Wales in 1977 measured cereal yield reductions of 4 to 77% (mean 41%), with the largest loss occurring in low rainfall, sandy sites (J. Dickenson personal communication). Estimated maximum yield reductions in cereals in South Australia at five sites in 1990 ranged from 0–55%. Yield reductions were also highest from dry sandy sites with low rainfall (J. Heap, unpublished data). Research in Victoria suggests that wheat yield can be reduced by up to 50% when infested by silverleaf nightshade, but this varies greatly with seasonal conditions and weed density (McKenzie 1980). Wheat yields at eight sites in the Victorian Mallee were measured over three years in areas with shoot densities between 1.5 and 17.1 plants m^{-2}. Yield reductions ranged from 11 to 43%, with an average of 36% (Molnar 1982). A moderate infestation of nine plants m^{-2} in New South Wales reduced grain yield by 12%. Yield losses were most pronounced in low rainfall years when crops relied more heavily on sub-soil moisture (Cuthbertson and Leys 1976). When silverleaf nightshade was controlled with 2,4-D or glyphosate in New South Wales prior to sowing wheat, yield increases ranged from nil to 69% on a clay-loam soil. The largest increases were recorded in a drought year when moisture limited yield (Lemerle and Leys 1991).

Saponins in the fruits of silverleaf nightshade exert allelopathic effects on cucumbers in Greece (Eleftherohorinos *et al.* 1993), raising the possibility of allelopathic affects on other crops.

Pastures. Silverleaf nightshade competes directly with summer-growing pastures such as lucerne, and occasionally dense infestations restrict access to pasture underneath dense canopies. There is also evidence that annual winter pastures are affected by delayed autumn emergence and lower production, leading to reduced carrying capacity (Cuthbertson and Leys 1976, McKenzie 1980). There is potential to contaminate lucerne hay, and Tideman (1960b) reports that silverleaf nightshade does not seem to be restricted by pastures containing perennials such as phalaris or lucerne. As with many plants, the weed status of silverleaf nightshade as a component of grazed pastures varies. Some graziers in South Africa, who do not crop, consider it to be a valuable pasture species, grazed by cattle and game with no apparent detrimental effects, and it has been pelleted and successfully fed to animals. The crude protein of the shoots is 12.3%, compared with about 20% for lucerne (Wassermann *et al.* 1988). It is, however, more commonly recognized as a weed of pastures due to its poisonous effects on grazing animals. In Texas it poisoned sheep and other livestock (Stubblefield and Sosebee 1984, 1985) and its berries have also been implicated in the poisoning of livestock (Boyd *et al.* 1984). Toxicity to horses has been observed in Argentina (McKenzie 1980). Following an apparently clear case of sheep deaths caused by silverleaf nightshade in Victoria, feeding trials with 2,4-D treated and untreated stems, fruits and leaves failed to produce poisoning (Molnar 1982).

Buck *et al.* (1960) conducted feeding trials in Texas following numerous cattle deaths suspected to be related to silverleaf nightshade. In the field there were typically several dead cattle and several others ill. Cattle that survived for 2–3 days usually recovered. Typical symptoms were rapid, laboured breathing, with an expiratory grunt, salivation and slobbering, nasal discharge, normal to slightly high temperature, and in less acute cases, a yellow discoloration of the skin. Weakness, unco-ordination, trembling of the muscles and back legs, anaemia and accelerated heart rate were also observed. Mature berries were as toxic as green berries. Cattle were more susceptible than sheep and Spanish goats were not affected at ten times the toxic dose for cattle. Rabbits were apparently unaffected.

Silverleaf nightshade density declines to a very much lower level three or more years after a cropping paddock is returned to grazing (Wapshere 1988). Accounts of palatability are varied and somewhat contradictory. It is less palatable after flowering, but this may be overcome by mowing the plants so that they wilt. Sheep will readily eat foliage and berries when pasture reserves are low (McKenzie 1980). Silverleaf nightshade is reported to be unpalatable and generally avoided by stock in Victoria and southern New South Wales, although the fruits are apparently attractive to grazing sheep, which have also been observed grazing buds and flowers. Overall, cattle probably graze it more readily than sheep (D.E. Symon unpublished 1975). One farmer reported that sheep preferentially grazed some biotypes (Tideman 1973). Livestock do not eat it in Arizona and contamination in hay discourages consumption (Davis *et al.* 1945).

Beneficial

Although its significance is overwhelmingly as a weed, silverleaf nightshade also has potential as a source of drugs. It contains the glycoalkaloid solasodine, which is used to produce diosgenine, which is used in the manufacture of pharmaceutical corticosteroidal drugs. There is considerable research and interest in the domestication of silverleaf nightshade for this purpose in India and Argentina. Other compounds are also under study for potential use. Berries yield 3.2% dry weight solasodine and silverleaf nightshade is considered to be the most promising source of the 28 *Solanum* species studied, due to its yield and few thorns (Maiti and Mathew 1967). Silverleaf nightshade is under development for commercial use in Argentina (Chiale *et al.* 1991).

Legislation

Legislation provides for the control of silverleaf nightshade in most parts of Australia. In the Australian Capital Territory there is no noxious weed legislation, while in southern states silverleaf nightshade is required to be controlled. It must be fully and continuously suppressed and destroyed in New South Wales. Similarly, in South Australia, landowners must destroy the plant and inhibit its propagation as far as is reasonably achievable. Landowners in South Australia are also required to notify their local Animal and Plant Control Board if they become aware of the presence of silverleaf nightshade on their land. In Western Australia, it must be eradicated except in one shire, Narrogin, where it must be treated on roadsides and reserves. It is a regionally prohibited weed for much of Victoria, but is a regionally controlled weed in the North Central region and not controlled in Glenelg, Corangamite, Port Phillip West and East, and West Gippsland (D. McKenzie personal communication). Silverleaf nightshade is not allowed to be introduced into Western Australia and South Australia, and in Tasmania it is a noxious weed that is prohibited from introduction to the State and, if found, must be eradicated.

Weed management

Herbicides

Silverleaf nightshade is a major weed on many continents and over the decades a wide array of herbicides have been screened for efficacy. Research into chemical control dates back to at least 1937, when carbon bisulphide was used as a soil sterilant (Davis *et al.* 1945). Although there have been instances of success, there are few weeds which have withstood the onslaught of chemical research as well as silverleaf nightshade. Some herbicides will control seedlings and established plants as a spot-spraying treatment, but there are so far no effective and affordable treatments for control of large and dense infestations (Figure 8). In the absence of such a treatment, the general aim should be to contain and suppress large infestations and to eradicate small patches and colonies (Cuthbertson and Leys 1976).

The exceptional root development of silverleaf nightshade is the reason that it is so difficult to control with herbicides. Chemical control is made more difficult by the range of crops and environmental factors encountered, including the effect of residual herbicides on following crops. Effective control with herbicides relies on effective translocation without root excretion. In South Africa, herbicides were first tried against silverleaf nightshade, unsuccessfully, in 1952 (Wassermann *et al.* 1988). Boyd *et al.* (1984) suggest that silverleaf nightshade has increased in importance in the USA owing to the increased use of soil-applied herbicides. This has reduced competition from annual weeds and reduced the intensity of cultivation, thus favouring silverleaf nightshade growth.

A herbicide that is easily absorbed and very effectively translocated is required to kill the whole root system (Richardson and McKenzie 1981). The three most significant herbicides arising to date are 2,4-D, picloram and glyphosate. McKenzie (1980) observed that herbicide experiments should not be assessed too early because silverleaf nightshade has remarkable abilities to recover, and often emergence in sprayed plots in the following season is merely delayed. Molnar (1982) concluded from the results of 32 field experiments over six years in the Victorian Mallee that 2,4-D ester at 1.2 kg a.i. ha^{-1} was the most effective treatment for short-term suppression of flowering and seedset and that picloram / 2,4-D gave the most consistent long-term control.

Figure 8. Infestation of *Solanum elaeagnifolium* shoots arising from perennial roots in a pasture in early summer.

Picloram. Picloram is most commonly used to treat small infestations of silverleaf nightshade because it remains active in the soil for several years and is moved down the soil profile with wetting fronts. It is often used in a mixture with 2,4-D, which gives rapid control of shoot growth and residual control of regrowth. Spraying shoots and soil for a radius of 2 m was much more effective than treating only shoots (McKenzie 1980). Picloram is not suitable for treating large areas due to cost and the detrimental effect on following broad-leaved crop and pasture species. Molnar (1982) found that picloram at 1.2 kg a.i. ha^{-1} normally gave control for one year. Despite many combinations of rates, timings and sequential picloram applications, at no time was eradication achieved over six years of research. Research in South Africa suggested that picloram / 2,4-D was effective and that autumn applications, when translocation was greater, were more effective than summer applications. There was however, a minimum effective rate of picloram (>264 g a.i. ha^{-1}) which could not be reduced by substitution with increasing rates of 2,4-D (Wassermann *et al.* 1988). Roots were excavated 17 months after picloram application and the average depth of root death was 51 cm, with the maximum depth being 165 cm. The least depth of root death was 8 cm. Picloram was detected 60–100 cm deep 10 weeks after application in November and March, respectively, during periods of moderate to low rainfall. In another study it reached a depth of 1 m within four weeks when rainfall was high, but under dry conditions it remained near the soil surface. Heavy cereal stubbles can prevent picloram from entering and leaching through the soil (McKenzie 1980, Molnar 1982). Root studies from one trial in South Africa suggested that roots were killed to 1.2 m depth by some treatments (Wassermann *et al.* 1988).

In uptake and translocation studies with silverleaf nightshade, uptake of picloram reached 50% by 6 h and ceased after 72 h, when 75% of the applied herbicide had been absorbed. Picloram was rapidly translocated throughout the root system within 24 h. The concentration in the roots halved between 24 and 168 h after treatment due to redistribution within the plant or exudation. A concentration of 4.5×10^{-9} mmoles mg^{-1} dry weight of picloram in root fragments prevented regeneration. Picloram (1×10^{-9} mmoles mg^{-1} dry weight) had been translocated 1.5 m down the root system by 6 hr. The concentration in the first 20 cm of roots was about four times higher than in the 20–150 cm zone. The concentration in the roots reached a peak after 24 h and then declined. It was concluded that for effective control it is essential to kill all parts of the root system that can regenerate. In field studies of picloram translocation, root fragments collected 6 h after treatment produced fewer shoots than fragments collected 24 h or 8 days after treatment. For some reason there is a decline in picloram concentration after the first 24 hours after treatment (Richardson 1979a,b).

Field experiments suggested that picloram / 2,4-D was effective but one application of herbicide, even at a very high rate, was not sufficient to eradicate colonies, and that successive applications of picloram / 2,4-D were required to kill the root system. Time of picloram application had little influence on control, except that plants treated in November sometimes regrew in the same season, while those treated in February did not regrow. Cultivation before or after picloram / 2,4-D application has little effect on control (McKenzie 1980).

2,4-D. Ester or amine formulations of 2,4-D are used to suppress shoot growth and to reduce flowering and seed set in silverleaf nightshade but there is little evidence that roots are damaged. 2,4-D ester at 1.12 kg a.i. ha^{-1} was effective at preventing seed set and maintaining a clean summer fallow, but two to four applications were needed over the six month growing season (McKenzie 1980). A concentration of 7.5×10^{-8} mmoles mg^{-1} dry weight of 2,4-D in root fragments was sufficient to prevent regeneration (Richardson and McKenzie 1981).

Glyphosate. Glyphosate gives variable control of silverleaf nightshade in Australia, but results in some other countries are good. Efficacy is probably determined by factors such as drought stress, dustiness of leaves and air humidity, and research suggests that growth stage is also important. Spot treatments are used at 3.6 to 7.2 g a.i. L^{-1}. Under dry Mallee conditions, glyphosate was not effective, with regrowth and seed set occurring frequently after treatment (McKenzie 1980). Glyphosate applied as a single or sequential spot treatment at various timings in Texas resulted in 6 to 98% control, illustrating the variable efficacy of this herbicide (Westerman and Murray 1994). Glyphosate applied at the green berry stage, when there was a strong flow of assimilates to the roots, was most effective (Stubblefield and Sosebee 1985). Control with glyphosate ranged from 0 to 69% in Greece (Eleftherohorinos *et al.* 1993). Glyphosate applied with a rope wick wiper in Australia was equally as effective as boom-spray applications, but although less herbicide was used, some short and dusty plants were not controlled (Lemerle 1982). Glyphosate at 0.21 kg a.i. ha^{-1} applied with a rope-wick applicator in Texas gave over 95% control (Abernathy and Keeling 1979). South African studies suggested that roots were killed to 1.2 m when glyphosate was applied at 2.16 kg a.i. ha^{-1} (Wassermann *et al.* 1988) and glyphosate at 2.13 kg a.i. ha^{-1} gave greater than 80% control 460 days after treatment in Morroco (Bouhache *et al.* 1993b).

Other herbicides. Some other herbicides with reported efficacy against silverleaf nightshade include bromacil, clopyralid, ethidimuron, fluoroxypyr, hexazinone, imazapyr, karbutilate, tebuthiuron and terbacil (Molnar 1982, Bouhache, Boulet and Mounir 1993, and G.M. Fromm personal communication). Tebuthiuron was applied in South Africa at 2–6 kg a.i. ha^{-1} without complete control (Wassermann *et al.* 1988) but at one site in Australia, 4 kg a.i. ha^{-1} gave over 99% control six years after application (J. Heap, unpublished data).

Molnar (1982) reported inadequate control in the Victorian Mallee after one year from clopyralid, dicamba, cyanatryn, triclopyr, dicamba/2,4-D, fosamine, asulam, atrazine, 2,4-DB, terbutryn, isoproturon, metribuzin, 2,4,5-T ester, 2,4-D ester, metoxuron, dichlobenil, glyphosate, bromacil and oxyfluorfen. In Greece, triclopyr gave almost no control (Eleftherohorinos *et al.* 1993).

Amor (1977) reported that in Texas, blade ploughs fitted with herbicide injectors were used to apply sub-surface bands of dinitroanaline herbicides (dinitramine, profluralin and trifluralin) for suppression of silverleaf nightshade. The triazine herbicides atrazine, terbutryn, and propazine were boom sprayed and incorporated to achieve moderate levels of short-term control.

Other treatments

Before the advent of modern herbicides, Davis *et al.* (1945) conducted crop competition, cultivation, hoeing and burning experiments in irrigated crops in Arizona over three years. Weekly, fortnightly and monthly cultivation during the silverleaf nightshade growing season for three years eradicated the weed. Shade from summer-growing crops, such as cotton, was important to the success of cultivation, but shade alone was ineffective. Oats grown during winter, followed by monthly cultivation eradicated silverleaf nightshade by the end of the third year. Lucerne grown for hay did not reduce silverleaf nightshade when the lucerne was cut at 25 or 50% flower, or when cutting coincided with silverleaf nightshade flowering. Weekly hoeing and burning during the silverleaf nightshade growing season for two years did not give satisfactory control. The successful control methods of Davis *et al.* (1945) described above were applied very successfully in South Africa. In regions with sufficient rainfall, dense crops also effectively suppressed silverleaf nightshade by shading (Wassermann *et al.* 1988). Shoot growth, berry production and carbohydrate production were progressively and greatly reduced by 47–92% shading (Boyd and Murray 1981).

Cultivation is reported to be ineffective in Australia because most of the roots are below the depth of cultivation and new plants may arise from transplanted fragments. Under dry conditions, deep cultivation may reduce but not eradicate an infestation (Parsons and Cuthbertson 1992). Silverleaf nightshade recovered rapidly after slashing and flowers developed close to the ground even when plants were slashed every 2–3 weeks. Cultivation every 3–5 weeks was required to obtain acceptable control. This frequency of cultivation is expensive and damaging to soil structure, and there is evidence that shoot density increased as wounded roots produced multiple shoots. The combination of slashing or cultivation and herbicide application did not improve control above the level of 2,4-D or picloram/2,4-D treatments alone (McKenzie 1980).

Natural enemies

The inability of cultural or chemical methods to control silverleaf nightshade has made it a major candidate for biological control in many countries, including the USA, South Africa and Australia. There have been extensive searches for agents in western and central USA but so far no agents suited to Mediterranean regions have been found. In a survey of the USA 22 insect species were found on silverleaf nightshade in California, on the extremities of the plant's range, and 90 species in Texas, part of the probable centre of diversity for the species (Goeden 1971).

It was recognized during the 1970s that there was a case for direct Australian participation in biological control investigations (Moore *et al.* 1975). Successful agents in Australia will need to be adapted to autumn-sown wheat cultivation under predominantly winter rainfall. The two most important aspects for selection of potential agents are the absence of silverleaf nightshade aerial vegetation from autumn to spring, and regeneration primarily from established rootstocks. Most agents identified in Central America would be severely limited by cultivation associated with wheat production. No agents that attacked roots were detected. It is concluded that the summer drought which occurs in most areas infested in Australia would not be suitable for the agents found in Central America. However, some regions in northern New South Wales and southern Queensland which receive reliable summer rainfall may support some promising species (Wapshere 1988). Similarly, Goeden (1971) concluded that transfer of agents from Central America to regions of California with a Mediterranean climate would be unlikely to succeed.

Wassermann *et al.* (1988) concluded that unless an extremely effective herbicide became available, biological control should be given serious attention in South Africa. Silverleaf nightshade has virtually no natural enemies in South Africa. A range of eight agents has been evaluated in South Africa since 1972 including a snout beetle from Argentina (*Conotrachelus bisignatus* (Boh.)), tortoise beetles from Texas and Argentina (*Gratiana lutescens pallidula* (Boh.) and *G. lutescens lutescens* (Boh.)) and a bug from Argentina (*Arvelius albopunctatus* (De Geer)), but most of these have been rejected due to lack of specificity or rearing problems. A fruit-boring gelechiid moth from North Mexico (*Frumenta nephelomicta* Meyrick) was cleared for introduction but failed to establish (Wassermann *et al.* 1988, Olckers and Zimmermann 1991, Olckers 1997). A gall-forming parasitic nematode from Texas (*Orrina phyllobia* (Thorne) Brzeski) which attacks silverleaf nightshade has been identified (Parker 1986) and was imported for specificity testing in South Africa in 1982. Pre-release evaluation studies were continuing in 1991 (Olckers and Zimmermann 1991). This nematode showed initial promise for release in Australia, but it has not been successful due to specificity problems and climatic restrictions (Field 1990). A stink bug, thought to be *Nezara viridula* (Linnaeus), destroyed up to 95% of seeds on plants in some regions of South Africa (Wassermann *et al.* 1988). Other agents identified by Goeden (1971) and Zimmermann (1974) with potential were *Trichobaris texana* (Le Conte), *Leptinotarsa defecta* (Stal) and *Anthonomus* spp. Neser (1985) also identified the beetle *Leptinotarsa texana* (Schaeffer) as a promising agent. *L. defecta* and *L. texana* (Chrysomelidae) were released in South Africa in 1992, despite a suggestion that eggplant (*Solanum melongena* L.) was at risk. These beetles have damaged silverleaf nightshade plants at release sites and are contributing to integrated control. *L. texana* has multiplied significantly, in contrast to *L. defecta,* and insects have been harvested from the field for secondary release at other locations. Silverleaf nightshade plants are defoliated in waves, leaving only skeletons of stems almost without bark, thus reducing plant density and spread. So far *L. texana* has been successfully established in the Eastern Cape, south-western Cape, Free State, Gauteng, Northern Province and Northwest Province. Establishment has been predominantly in non-crop areas, where plants are not disturbed by herbicide application or cultivation. This is the first time that biological control agents have been successfully released against a member of Solanaceae anywhere in the world (Olckers *et al.* 1996, Olckers 1997).

There have been periodic reports of a range of native agents attacking silverleaf nightshade in Australia. Fruits were frequently attacked by insect larvae in Victoria and New South Wales and one form of a virus was almost universally present, causing small, narrow leaves. A second virus was abundant on one property, causing a proliferation of the inflorescence and virescence of the flowers. Both viruses completely suppressed flowering but vegetative vigour was not obviously affected. One large irregularly-circular bare patch was reported by a farmer to have been caused by a root-boring larvae (D.E. Symon, unpublished report). On a property near Parkes, New South Wales, plants had apparently been killed by the root-feeding larvae of a native Gelechiid moth, identified by the CSIRO Division of Entomology as *Scrobipalpa leucocephala* Low. (Moore *et al. 1*975). A report of larval feeding on silverleaf nightshade roots was received from near Parilla in South Australia in 1995 and is currently under investigation by the authors. Larvae were found mining in the upper tap roots of perennial silverleaf nightshade plants and in most cases the shoots wilted and senesced. Provisional identification of the larvae suggest that they also belong to the family Gelechiidae. McKenzie (1980) reported that three native moths, one of which feeds on the roots and two on the seeds, have little permanent effect on the weed. In 1978/79, Rutherglen bugs (*Nysius vinitor* (Bergroth)) and a shield bug caused extensive damage to silverleaf nightshade and other species near Hopetoun, Victoria, but plants soon recovered.

Co-ordinated control

A major government-sponsored eradication program of silverleaf nightshade, based on the use of picloram, began in South Africa in 1968. Picloram is not the ideal herbicide because residual effects can continue for several years. The program, involving subsidies to landowners, lasted until 1972. The campaign was abandoned due to high costs and poor results, although control appeared to be better on shallow soils than on deep, arable soils which allowed deeper root growth. The program failed because of inadequate knowledge of the weed and herbicide efficacy, as well as poor farmer co-operation. Despite intensive research, no herbicides were specifically registered against silverleaf nightshade and by 1988 recommendations had reverted to using 2,4-D to restrict growth and prevent seed formation (Wassermann *et al.* 1988). Wassermann *et al.* (1988) concluded that silverleaf nightshade was impossible to eradicate in any practical way. Smith (1975) mapped the distribution of silverleaf nightshade in South Australia and proposed a control strategy to limit spread. Carter (1992) demonstrated that co-ordinated control programs involving publicity, extension and enforced control reduced the rate of spread of silverleaf nightshade in the Eyre Peninsula region of South Australia. The study highlighted the need to detect new infestations early, and to ensure that they were controlled, rather than concentrating on large, established infestations.

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