Weed Science 2012 60:42–47

Factors Affecting Silverleaf Nightshade (*Solanum elaeagnifolium*) Germination

Rex Stanton, Hanwen Wu, and Deirdre Lemerle*

Silverleaf nightshade is a widespread, deep-rooted, summer-growing perennial that significantly reduces production in Australian crop and pasture systems. It has an extensive root system, which competes both directly and indirectly with summer and winter pastures and crops through depletion of soil moisture and nutrients. Long-distance dispersal of seeds is an important mechanism for its spread and management. A range of experiments was conducted to determine the factors influencing seed production and seedbank dynamics. Seed production ranged from 1,814 to 2,945 m^{-2}. Diurnally fluctuating temperatures of 25/15 C provided the optimal thermal conditions for germination, with germination not affected by light. Osmotic stress reduced germination, with no germination occurring at −1MPa. Germination was reduced to 5% at 160 mM NaCl, suggesting some salt sensitivity. Germination occurred over a pH range of 4 to 10, but declined with increasing acidity. Viability of buried seed declined to around 20% after 3 yr, with seed buried at 10 cm remaining the most viable. The prolonged seed persistence in the soil indicates a long-term control program is necessary for depleting the soil seedbank.

Nomenclature: Silverleaf nightshade, *Solanum elaeagnifolium* Cav. SOLEL.
Key words: Seedbank, burial, osmotic stress, temperature, salinity, pH.

Silverleaf nightshade is a deep-rooted, summer-growing perennial weed of the Solanaceae family that occurs in the cropping/pasture zone of southern Australia. It spreads by root fragments from cultivation and moving with machinery and by seed movement with fodder, animals, and machinery. Silverleaf nightshade arrived in Australia in the early 1900s as a contaminant of grain and fodder (Parsons and Cuthbertson 2001). Isolated patches of the weed appear to increase in size slowly through cultivation (Moore et al. 1975) and it was not until the 1960s that silverleaf nightshade became an important weed (Cuthbertson et al. 1976) following a series of wet summers.

Surveys report that silverleaf nightshade infested nearly 22,000 ha in southeastern Australia in the early 1970s, with 90% on the infested land being used for agricultural purposes (McKenzie 1976). There was a fivefold increase in the area infested within 20 yr, with 140,000 ha infested by 1992 (Heap and Carter 1999). Modelling prediction has shown that the weed can potentially infest 398 million hectares in Australia (Kwong 2006). Silverleaf nightshade is a declared noxious weed in mainland states of Australia where it occurs and is very difficult to eradicate once established.

Worldwide, silverleaf nightshade is a significant weed of cotton (*Gossypium hirsutum* L.), grain sorghum [*Sorghum bicolor* (L.) Moench] (Boyd and Murray 1982), wheat (*Triticum aestivum* L.), and lucerne (alfalfa) (*Medicago sativa* L.) (Hoffmann et al. 1998), and can cause important economic losses. In Australia, it competes directly with summer species for water and nutrients, and indirectly with winter species (Lemerle and Leys 1991). Grain yield losses of 12% were reported from Australia as a result of an infestation of 9 plants m^{-2} (Leys and Cuthbertson 1977). Yields from North American cotton crops indicate less effect from silverleaf nightshade when irrigated, suggesting that competition for moisture is a significant factor (Green et al. 1988). Silverleaf nightshade currently costs meat and wool producers more than AUD $10 ha^{-1} yr^{-1} and has been estimated to cost South Australian producers more than AUD $10 million (I. Honan, personal communication).

Asexual reproduction is important in perennial weeds to maintain infestations and for local reinfestation. However, seeds are more important than root segments for wider dispersal of silverleaf nightshade (Richardson and McKenzie 1981; Wapshere 1988). Seed can be dispersed by livestock by attachment to fiber or via ingestion, mechanically by attachment to vehicles or machinery, and naturally via wind or water movement.

A recent review (Stanton et al. 2009) summarizes the latest information on silverleaf nightshade. Information on the germination characteristics, or seedbank dynamics, is required to determine future spread under changing climate, where warmer and wetter conditions are likely to exacerbate rates of spread.

Wapshere (1988) reported that high dormancy levels and infrequent germination events may account for the large seedbanks observed in the field. The presence of physiological dormancy has been reported in many *Solanum* seeds (Commander et al. 2008). Seed germination of an Australian native *Solanum* species (*Solanum centrale* J. M. Black) does not vary under constant temperatures, and can occur in saline levels up to 200 mM NaCl (Ahmed et al. 2006), suggesting capacity to establish across a range of climatic and environmental conditions. Silverleaf nightshade appears to require adequate moisture and alternating temperatures for germination to occur (Stanton et al. 2009).

The aim of this study was to determine the seed production, the longevity of the seed in the soil seedbank, and the factors that affect subsequent seed germination of silverleaf nightshade.

Materials and Methods

A series of experiments was established to examine seed production and factors affecting germination. A randomized complete block design with three replications was used in all experiments.

DOI: 10.1614/WS-D-11-00105.1

* First and third authors: Research Scientist and Director, EH Graham Centre for Agricultural Innovation (an alliance between Charles Sturt University and New South Wales Department of Primary Industries), School of Agricultural and Wine Sciences, Charles Sturt University, Locked Bag 588, Wagga Wagga, NSW 2678, Australia; second author: Senior Research Scientist, EH Graham Centre for Agricultural Innovation, New South Wales Department of Primary Industries, Wagga Wagga Agricultural Institute, PMB, Wagga Wagga, NSW 2650, Australia. Corresponding author's E-mail: rstanton@csu.edu.au

Seed Production. Sampling was conducted in April 2007 in silverleaf nightshade infestations near Leeton (34.4670S, 146.3695 °E), and Culcairn (35.5939 °S147.1688E), New South Wales (NSW) with uniform densities of 7 to 10 stems m^{-2}. At each site, 10 mature stems were randomly chosen at least 2 m apart to minimize the risk of sampling stems arising from the same root system. Total number of fruits was recorded and 10 fruits randomly chosen from each stem to determine fruit diameter and the number of seeds. Further data on fruit size and seed number were determined from 100 fruits randomly collected in April 2006 from silverleaf nightshade infestations near Griffith (34.3350 °S, 146.0327 °E) and Wellington (32.5326 °S, 148.8066 °E), NSW.

Seed Longevity in the Field. Seed was collected in April 2007 from a silverleaf nightshade infestation near Leeton, NSW. Seed burial experiments were commenced in May 2007 a clay loam site near Ganmain (34.894133 °S, 146.989281 °E) and a loamy site near Culcairn (35.593920 °S,147.168820 °E), NSW.

Either 50 bare seeds or four intact fruits were placed in 10- by 10-cm packets constructed of 0.5-mm nylon mesh and then placed at four soil depths (0, 2.5, 5, and 10 cm). A small quantity of soil obtained from the burial location was dry-sieved to eliminate resident weed seed and included in each packet. Packets were recovered after four time periods (6, 12, 24, and 36 mo). Additional seed and intact fruits were stored at ambient room temperature in paper envelopes in the laboratory as a control treatment.

Recovered seeds were counted and placed on Whatman No. 2 filter paper moistened with 4 ml of distilled water in a 9-cm petri dish. In the case of recovered fruits, a total of 50 seeds were randomly chosen for the germination assay. Petri dishes were sealed with Parafilm (Pechiney Plastic Packaging, 289 River St., Menasha, WI 54952) and incubated for 21 d at 25/15 C on a 8/16 h cycle with illumination provided during the 25 C period. Fluorescent lamps with a light intensity of 50 µmol m^{-2} s^{-1} were used as the light source in the incubator.

The number of germinated seeds was recorded and viability of ungerminated seed determined by tetrazolium staining using a modified method of that used for *S. centrale* (Ahmed et al. 2006). Seeds were cut in half and incubated in the dark at 35 C for 5 h in a 0.5% 2,3,5-triphenyltetrazolium chloride (Sigma Aldrich, 2050 Spruce St., St. Louis, MO 63103) solution in petri dishes. Seeds were deemed to be viable but dormant if the radicle was stained red. Total viability of the exhumed seeds included the germinated seeds and the viable but dormant seeds and is expressed as a percentage of seed buried.

Germination Factors. Seed was collected in April 2008 from a silverleaf nightshade infestation near Leeton, NSW. Seed was soaked for 24 h to remove the mucous coating to enhance the germination level (Rutherford 1978), then air-dried and stored prior to use.

Unless stated otherwise, the following protocol was used to determine germination level. Fifty seeds were placed on Whatman No. 2 filter paper moistened with 4 ml of solution in a 9-cm petri dish. Petri dishes were sealed with Parafilm and incubated for 21 d at 25/15 C day/night temperatures with a 12-h photoperiod. Germinated seeds were recorded every 3 or 4 d.

Impact of Temperature and Moisture Stress on Germination. The effect of osmotic stress was studied for fixed (10, 20, 30, and 40 C) and fluctuating (25/10, 25/15, and 30/15 C) temperature regimes. Solutions with osmotic pressures of 0, 0.03, 0.06, 0.12, 0.24, 0.48, and 0.96 MPa were prepared by dissolving polyethylene glycol (PEG) 8000(Applichem, Ottoweg 4, D-64291 Darmstadt, Germany) in 80 ml of distilled water using appropriate quantities for each temperature as determined from Michel (1983). In the case of fluctuating temperature regimes, PEG 8000 quantities were determined by the average of the two temperatures. The influence of light was tested at 0 MPa and two fluctuating temperatures (25/10 and 30/15 C) by wrapping petri dishes in aluminum foil during incubation.

Impact of Salinity on Germination. The effect of salinity was studied by incubating seeds at 30/15 C in solutions containing 0, 10, 20, 40, 80, 160, and 320 mM solutions of NaCl (Merck Pty Ltd., 207 Colchester Road, Kilsyth, 3137 Victoria, Australia).

Impact of pH on Germination. To examine the effects of pH on seed germination, buffered solutions of pH 4 to 10 were prepared according to the method described by Chen et al (2009). The seeds were exposed to HCl or NaOH aqueous solutions of pH 4 (10^{-4} mol L^{-1} HCl solution), pH 5 (10^{-5} mol L^{-1} HCl solution), pH 6 (10^{-6} mol L^{-1} HCl solution), pH 8 (10^{-6} mol L^{-1} NaOH solution), pH 9 (10^{-5} mol L^{-1} NaOH solution), and pH 10 (10^{-4} mol L^{-1} NaOH solution), with deionized water as the control (pH 7).

Seeds were placed in petri dishes containing 5 ml of the particular pH solution. Germinable seeds were incubated in growth cabinets under fluctuating day/night temperature cycles (30/15 C).

Statistical Analysis. All germination experiments were repeated, except for germination experiments at 25/15 C, and data were combined as there were no significant differences over time. Germination (%) values at different NaCl concentrations and pH values were fitted to exponential decay ($y = a \times e^{-bx}$) and linear ($y = ax + b$) models, respectively. In all other experiments, means were separated using LSD at $P < 0.05$.

Homogeneity of variance was not improved by transformation; therefore analysis was performed on raw percentage of germination. Data variance was visually inspected by plotting residuals to confirm homogeneity of variance before statistical analysis. Data were analyzed using ANOVA and post hoc Fisher's tests were used to determine statistically different means.

Results and Discussion

Seed Production. Seed production per stem varied between sites, with 2,945 and 1,814 seeds per stem for Culcairn and Leeton, respectively (Table 1). Similarly, fruit number per stem in Culcairn was 64% higher than in Leeton, possibly reflecting the higher total rainfall in 2006 and 2007 (Table 2). The area sampled at each site was less than 0.5 ha; however, the genetic diversity of silverleaf nightshade stems sampled less than 1.3 m apart was similar to stems sampled 50 m apart (Zhu, unpublished data). This suggests that the small

Table 1. Seed production characteristics (± SE) for silverleaf nightshade populations at four sites in Australia.

	Culcairn	Leeton	Griffith	Wellington
Fruits per stem	74 ± 17	45 ± 8		
Fruit diameter (mm)	10.4 ± 0.2	9.5 ± 0.3	11.3 ± 0.2	12.1 ± 0.2
Fruit weight (g)	0.4 ± 0.04	0.5 ± 0.04		
Seeds per fruit	40 ± 4	40 ± 4	38 ± 3	89 ± 5
Seeds per stem	2,945	1,814		

sampling area may have allowed the effects of the genetic diversity of each population to be adequately addressed.

Location had little effect on fruit diameter and weight. The largest mean fruit diameter (12 mm) and highest mean number of seeds per fruit (89) were recorded at Wellington, which had the highest annual and long-term rainfall. Seeds per fruit were consistent across Culcairn, Leeton, and Griffith (40, 40, and 38). Seed production was most likely affected by the severe drought, as total rainfall was less than 50% of the long-term average at all sites in 2006.

Seed Longevity. Combined data are presented because there were no significant differences between field sites. There were significant interactions between duration of burial, depth of burial, and presence of fruit on the germination of silverleaf nightshade seed.

Duration of burial did not affect the percentage of bare seed recovered ($P > 0.05$), with 84 to 100% of bare seed recovered. Burial depth did not affect percentage of seed recovery, apart from bare seed buried at 2.5 cm depth (98%) compared to seed on the soil surface (94%) ($P < 0.05$). There was evidence of in situ germination for bare seed exhumed after 6 mo. Other causes of seed loss were not examined, and could be a function of factors such as soil moisture content (Kegode et al. 2010) or microbial activity (Davis et al. 2006).

Germination and viability data are presented as a percentage of initial bare seed numbers or, in the case of recovered fruits, a percentage of seed tested. Most viable silverleaf nightshade seed germinated at all burial times and depths when buried as bare seed (Figure 1). Compared to the viability of seed stored in the laboratory for 36 mo (91%), there was a marked decline in viability of buried seed, with 59% of seed buried at 10 cm depth and less than 36% of seed at shallower depths remaining viable. These results suggest that cultivation is likely to extend the life of soil seedbank as a result of seed burial. The rate of decline in viable seed remaining suggests the soil seedbank may be depleted by natural attrition in 6 yr in the absence of seed rain.

The presence of an intact fruit slowed the decline in viable seed numbers. After 6 mo, germination increased with the depth of fruit burial, with maximum germination occurring 12 mo after burial (Figure 2). After 12 mo burial, fruits on the soil surface remained intact and seed from these fruits had

Table 2. Annual rainfall (mm) at locations in Australia during the study.

Year	Culcairn	Ganmain	Leeton	Griffith	Wellington
2006	236	198	190	149	292
2007	546	510	451	312	628
2008	445	391	343	282	664
2009	385	330	289	309	563
2010	891	748	548	605	1,077
30-yr average	601	545	495	423	653

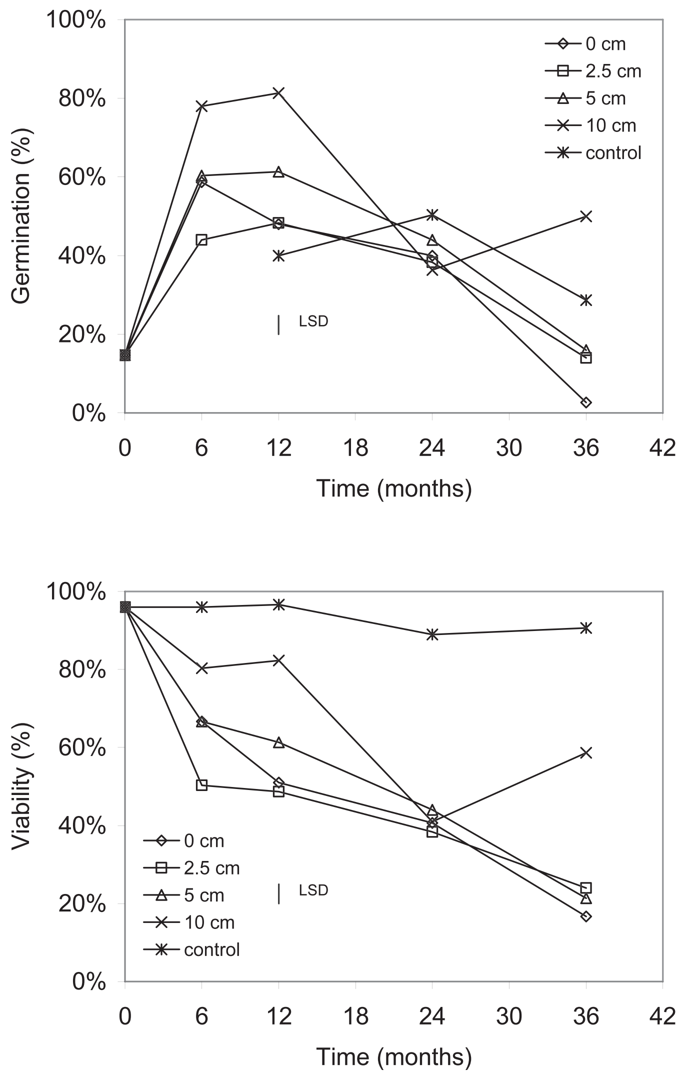

Figure 1. Effect of burial duration (months) and depth (cm) on bare silverleaf nightshade seed (top) germination and (bottom) viability.

16% germination, similar to the 19% germination of seed stored in the laboratory. This is similar to the reported enhanced survival of tropical soda apple (*Solanum viarum* Dun.) seed when fruits were on or above the soil surface compared to fruits that had deteriorated in the soil (Bryson and Byrd 2007).

All fruits on the soil surface remained intact for 12 mo, with only 17% of fruits intact after 24 mo and no fruits intact after 36 mo (Figure 3). Fruits deteriorated with increasing burial depth after 12 mo, with 29, 13, and 6% of fruits remaining intact at 2.5, 5, and 10 cm burial depth. After 24 mo, 4% of fruits remained intact at 2.5 cm, while all fruits buried at 5 or 10 cm were damaged. Seed from silverleaf nightshade fruits buried at any depth in the soil germinated more readily, suggesting that the fruits' deterioration may allow the seed coating to be degraded and increase moisture imbibition. After 24 mo, 94% of viable seed from fruits on the soil surface and 99% of viable seed from fruits buried below the soil surface readily germinated in petri dish assays.

After 36 mo, similar levels of viable seed remained at each burial depth irrespective of the presence of a fruit, except for at 2.5 cm depth, where 65% of seed remained viable when buried in fruits compared to 51% of bare seed. This suggests

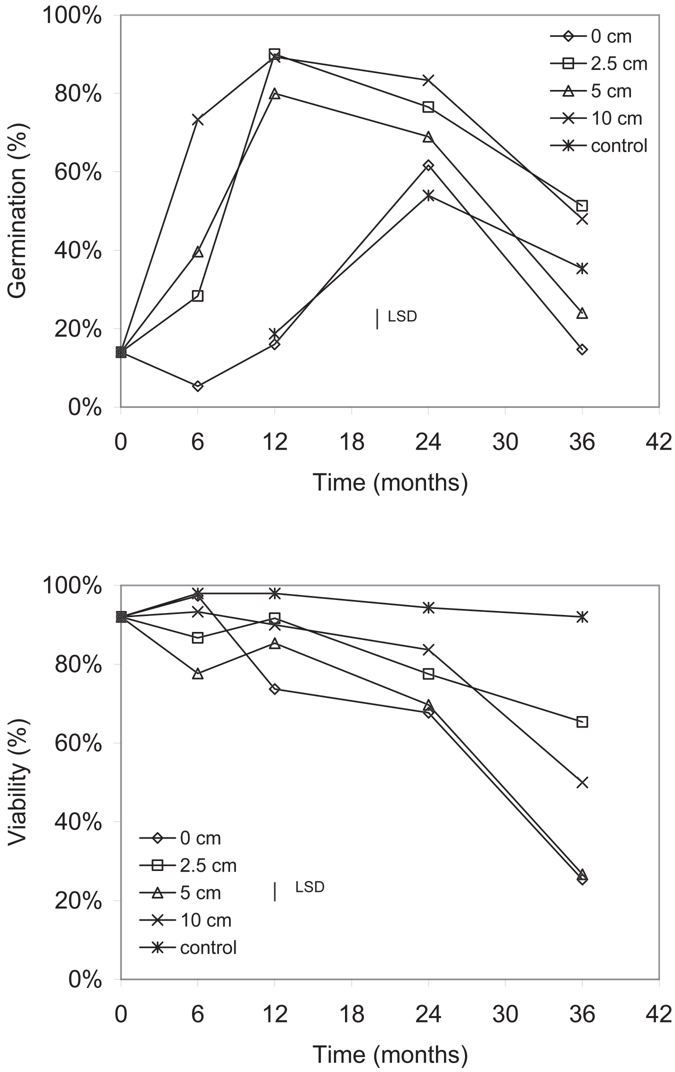

Figure 2. Effect of burial duration (months) and depth (cm) on (top) germination and (bottom) viability of silverleaf nightshade seed buried in intact fruits.

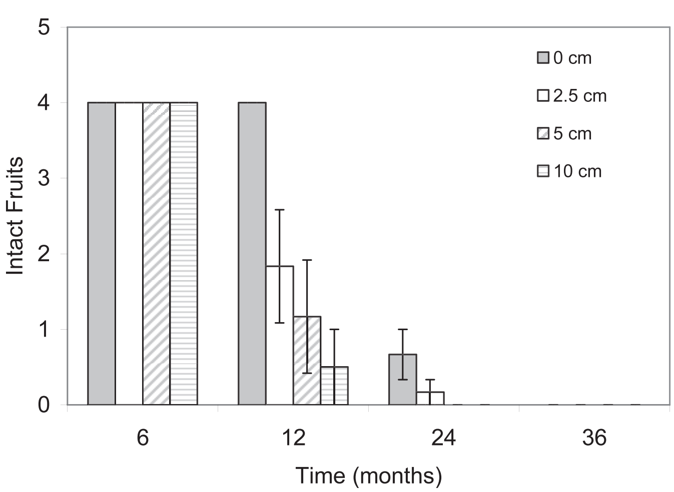

Figure 3. Effect of burial duration (months) and depth (cm) on the number of intact silverleaf nightshade fruits (no. of fruits ± SE).

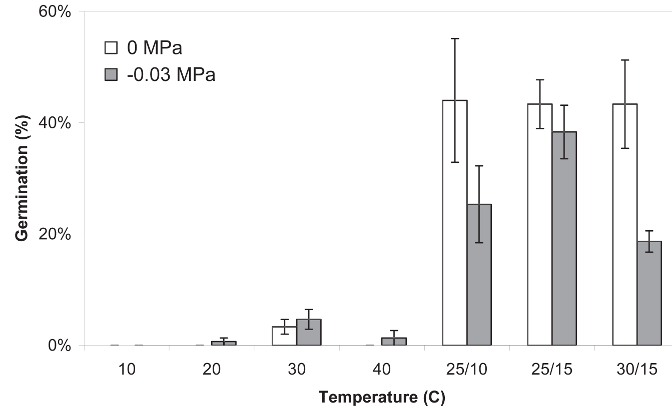

Figure 4. Effect of constant or fluctuating day/night temperatures on silverleaf nightshade seed germination after 21 d incubation in a 12-h photoperiod.

that the fruits provide some initial protection for up to 24 mo, however the subsequent rate of decline of the viable soil seedbank is not affected.

Temperature. Silverleaf nightshade seed did not germinate at a constant temperature of 10 C and only 0.7% of seed germinated at 20 C and −0.03 MPa osmotic stress (Figure 4). Germination was less than 5% at constant temperatures of 30 and 40 C. Alternating temperature regimes increased germination, with germination at −0.03 MPa highest (38%) at 25/15 C.

Osmotic Stress. Germination decreased with increasing osmotic stress for all alternating temperature regimes, with 26% germination significantly higher ($P < 0.01$) for 25/15 C at −0.24 MPa (Figure 5) than for other alternating temperature regimes for that level of osmotic stress. Similar germination levels and trends were present between the alternating temperature regimes of 25/10 C and 30/15 C. At −0.48 MPa, 2% germination occurred at these temperature regimes, as compared to 17% germination at 25/15 C. These results suggest that silverleaf nightshade requires diurnal temperature fluctuation to promote seed germination. At the optimum temperature regime of 25/15 C, seed can germinate with less-favorable moisture conditions.

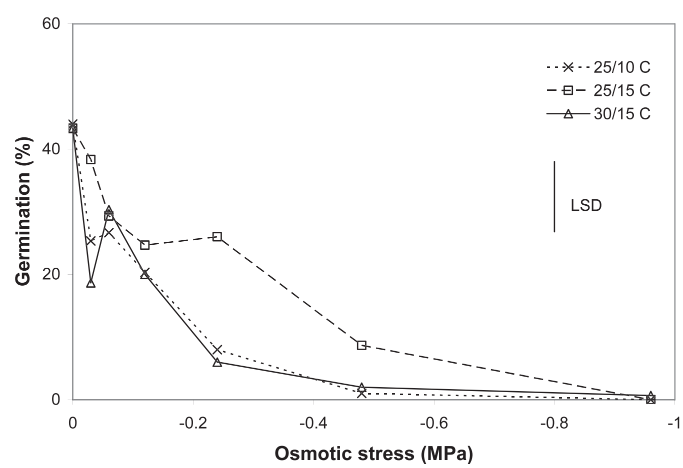

Figure 5. Effect of osmotic potential on silverleaf nightshade seed germination after 21 d incubation in 25/10, 25/15, and 30/15 C day/night temperatures in a 12-h photoperiod.

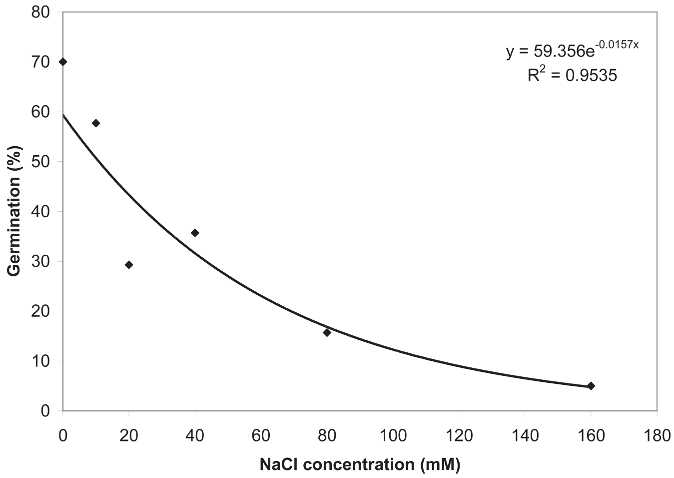

Figure 6. Effect of NaCl concentration on silverleaf nightshade seed germination after 21 d incubation in 25/15 C day/night temperatures in a 12-h photoperiod.

Light. Silverleaf nightshade seed germination was not influenced by absence of light during incubation, with 44 and 45% germination in dark and light conditions, respectively ($P > 0.05$). This result is similar to that reported by Zhou et al. (2005) of hairy nightshade (*Solanum sarrachoides* Sendtner) germinating under both light and dark conditions.

Salt. Silverleaf nightshade seed germination was inhibited by increasing NaCl concentrations ($y = 59.356 \times e^{-0.15x}$, $r^2 = 0.954$), with germination reduced from 70% in deionized water to 5% at 160 mM NaCl (Figure 6). This suggests that silverleaf nightshade seed germination may be reduced by saline soil that occurs in the current distribution range in southern Australia.

pH. At least 51% of silverleaf nightshade seed germinated at all pH levels tested (Figure 7), with germination increasing linearly with pH ($y = 3.71x + 40.28$, $r^2 = 0.795$). Germination was only significantly higher at pH 10 compared to pH 4 ($P < 0.05$), suggesting that soil pH within the range examined is not likely to limit germination. Similarly, seeds of little mallow (*Malva parviflora* L.) readily germinate across a broad pH range (Chauhan et al. 2006).

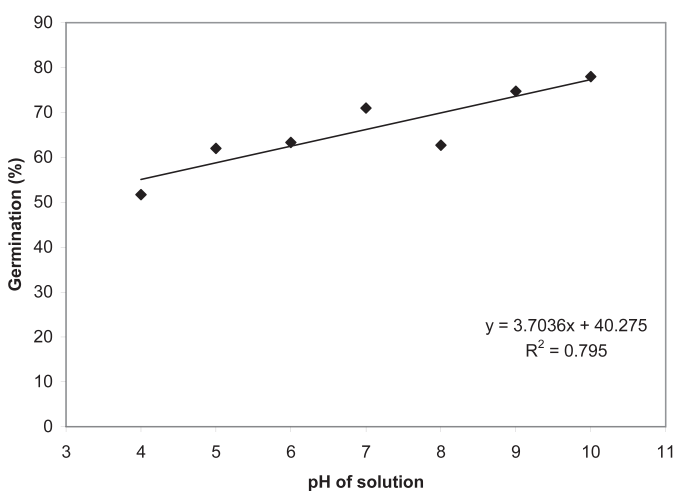

Figure 7. Effect of pH level on silverleaf nightshade seed germination after 21 d incubation in 25/15 C day/night temperatures in a 12-h photoperiod.

Approximately 20% of silverleaf nightshade seed remains viable after 3 yr of burial. Seed germination appears to be limited during the first 12 mo when buried in fruits; however, germination rates of 40 to 80% occurred for bare seed. Burial at 10 cm depth is likely to increase seed survival in the soil.

Silverleaf nightshade requires diurnally fluctuating temperature to germinate, and is not photoblastic, as germination was not affected by the absence of light. Commander et al. (2008) also reported that alternating temperatures improved the germination of a range of *Solanum* species. Germination was reduced with increasing osmotic stress, suggesting that good soil moisture conditions must be present for a significant germination event to occur. This may assist in management by allowing monitoring for seedling emergence to be targeted to after good rainfall events in spring/early summer and autumn. Germination may be less likely to occur in saline soils as sensitivity to salt stress was observed.

Acknowledgment

The authors gratefully acknowledge the financial support of Meat and Livestock Australia.

Literature Cited

Ahmed, A. K., K. A. Johnson, M. D. Burchett, and B. J. Kenny. 2006. The effects of heat, smoke, leaching, scarification, temperature and NaCl salinity on the germination of *Solanum centrale* (the Australian bush tomato). Seed Sci. Tech. 34:33–45.

Boyd, J. W. and D. S. Murray. 1982. Growth and development of silverleaf nightshade (*Solanum elaeagnifolium*). Weed Sci. 30:238–43.

Bryson, C. T. and J. D. Byrd, Jr. 2007. Biology, reproductive potential, and winter survival of tropical soda apple (*Solanum viarum*) Weed Tech. 21:791–795.

Chauhan, B. S., G. Gill, and C. Preston. 2006. Influence of environmental factors on seed germination and seedling emergence of rigid ryegrass (*Lolium rigidum*). Weed Sci. 54:1004–1012.

Chen, G. Q., S. L. Guo, and Q. S. Huang. 2009. Invasiveness evaluation of fireweed (*Crassocephalum crepidioides*) based on its seed germination features. Weed Biol. Manag. 9:123–128.

Commander, L. E., D. J. Merritt, D. P. Rokich, G. R. Flematti, and K. W. Dixon. 2008. Seed germination of *Solanum* spp. (Solanaceae) for use in rehabilitation and commercial industries . Aust. J. Bot. 56:333–341.

Cuthbertson, E. G., A. R. Leys, and G. McMaster. 1976. Silverleaf nightshade—a potential threat to agriculture. Agric. Gaz. N. S. W. 87:11–13.

Davis, A. S., A. I. Kathleen, S. G. Hallett, and K. A. Renner. 2006. Weed seed mortality in soils with contrasting agricultural management histories. Weed Sci. 54:291–297.

Green, J. D., D. S. Murray, and J. F. Stone. 1988. Soil water relations of silverleaf nightshade (*Solanum elaeagnifolium*) with cotton (*Gossypium hirsutum*). Weed Sci. 36:740–46.

Heap, J. W. and R. J. Carter. 1999. The biology of Australian weeds. 35. *Solanum elaeagnifolium* Cav. Plant Prot. Q. 14:2–12.

Hoffmann, J. H., V. C. Moran, and F.A.C. Impson. 1998. Promising results from the first biological control programme against a solanaceous weed (*Solanum elaeagnifolium*). Agric. Ecosyst. Environ. 70:145–150.

Kegode, G. O., G. Nazre, and M. J. Christoffers. 2010. Germination ecology of biennial wormwood (*Artemisia biennis*) and lanceleaf sage (*Salvia reflexa*) Seeds. Weed Sci. 58:61–66.

Kwong, R. 2006. Feasibility of Biological Control of Solanaceous Weeds of Temperate Australia; Silverleaf Nightshade, *Solanum elaeagnifolium* Cav. and Prairie Ground Cherry, *Physalis viscosa* L. North Sydney, Australia: Meat and Livestock Australia. 148 p.

Lemerle, D. and A. R. Leys. 1991. Control of silverleaf nightshade increases the grain yield of wheat. Aust. J. Exp. Agric. 31:233–36.

Leys, A. R. and E. G. Cuthbertson. 1977. *Solanum elaeagnifolium* Cav. (silverleaf nightshade) in Australia. Proc. South. Weed Sci. Soc. 30:137–41.

McKenzie, D. N. 1976. Silverleaf nightshade—another perennial problem. Pages 3.9–3.10 *in* Proc. of the Australian Weeds Conf. Melbourne: Australian Weeds Committee.

Michel, B. E. 1983. Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. Plant Physiol. 72:66–70.

Moore, R. M., W. T. Parsons, J. Strang, and A. F. Tideman. 1975. Silver-leaf nightshade (*Solanum elaeagnifolium* Cav.). Aust. Weeds Res. Newsl. 22:5–13.

Parsons, W. T. and E. G. Cuthbertson. 2001. Silverleaf nightshade, white horesnettle. Pages 609–612 *in* W. T. Parsons and E. G. Cuthbertson, eds. Noxious Weeds of Australia. 2nd ed. Melbourne: CSIRO.

Richardson, R. G. and D. N. McKenzie. 1981. Regeneration of, and toxicity of 2,4-D to, root fragments of silver-leaf nightshade (*Solanum elaeagnifolium* Cav.). J. Aust. Inst. Agric. Sci. 47:48–50.

Rutherford, P. A. 1978. Effect of time of immersion in running and still water on the germination of silver-leaf nightshade. Pages 372–378 *in* Proc. of the First Conference of the Council of Australian Weed Science Societies. Melbourne: Council of Australian Weed Science Societies.

Stanton, R. A., J. W. Heap, R. J. Carter, and H. Wu. 2009. *Solanum elaeagnifolium* Cav. Pages 274–293 *in* F. D. Panetta, ed. The Biology of Australian Weeds. Volume 3. Melbourne: R. G. and F. J. Richardson.

Wapshere, A. J. 1988. Prospects for biological control of silverleaf nightshade, *Solanum elaeagnifolium*, in Australia. Aust. J. Agric. Res. 39:187–97.

Zhou, J., E. L. Deckard, and W. H. Ahrens. 2005. Factors affecting germination of hairy nightshade (*Solanum sarrachoides*) seeds. Weed Sci. 53:41–45.

Received June 23, 2011, and approved August 27, 2011.