Weed Science

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Seed Fecundity, Persistence, and Germination Biology of Prairie Groundcherry (*Physalis hederifolia*) in Australia

Hanwen Wu[1], Rex Stanton[2] and Deirdre Lemerle[3]

[1]Principal Research Scientist, Graham Centre for Agricultural Innovation (NSW Department of Primary Industries and Charles Sturt University), Wagga Wagga Agricultural Institute, Wagga Wagga, NSW, Australia, [2]Research Fellow, Graham Centre for Agricultural Innovation (NSW Department of Primary Industries and Charles Sturt University), Wagga Wagga, NSW, Australia and [3]Professor, Graham Centre for Agricultural Innovation (NSW Department of Primary Industries and Charles Sturt University), Wagga Wagga, NSW, Australia

Research Article

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Author for correspondence:
Hanwen Wu, Graham Centre for Agricultural Innovation (NSW Department of Primary Industries and Charles Sturt University), Wagga Wagga Agricultural Institute, Wagga Wagga, Pine Gully Road, NSW 2650, Australia.
(Email: hanwen.wu@dpi.nsw.gov.au)

Abstract

Prairie groundcherry [*Physalis hederifolia* (A. Gray) var. *fendleri* (A. Gray) Cronquist] is an invasive perennial weed with the potential to become a significant summer weed across 409 million hectares in Australia. Current management practices do not provide effective control of established populations. A better understanding of the seed biology is needed to effectively manage this weed. A series of field and laboratory studies were conducted to determine plant fecundity, soil seedbank longevity, and the factors that affect seed germination. *Physalis hederifolia* has the capacity to produce 66 to 86 berries plant^{-1}, 51 to 74 seeds berry^{-1}, and approximately 4,500 seeds plant^{-1}, with the seeds potentially able to persist in the soil seedbank for 20 yr if buried in an intact dry berry pod. The bare-seed component of the soil seedbank can be virtually exhausted within 3 yr if cultivation is minimized to avoid burial of seed. Optimal temperature for germination is diurnal fluctuations of 15 C within the temperature range of 10 and 30 C. Increasing osmotic stress levels reduced the germination under all temperature regimes, with less than 6% germination occurring at −0.96 MPa. *Physalis hederifolia* seed germination was not significantly affected by substrate pH 4 to 10 or salt levels less than 160 mM, while the germination was significantly reduced at NaCl concentrations above 160 mM. These results suggest that *P. hederifolia* can adapt to a range of substrate conditions. Stopping seed set, avoiding grazing plants with viable seeds, and minimizing seed burial in the soil are some effective strategies to control this weed.

Introduction

Prairie groundcherry [*Physalis hederifolia* (A. Gray) var. *fendleri* (A. Gray) Cronquist], previously classified as *Physalis viscosa* L., is one of eight *Physalis* species that occur in Australia (Haegi et al. 1982). It is reportedly native to North and South America (Parsons and Cuthbertson 2001; Symon 1986), although the taxonomic confusion of this genus often makes it difficult to know which species is being referred to in the literature. Whitson and Manos (2005) reviewed the *Physalis* taxonomy and, based on DNA evidence, concluded that the genus contains 75 to 90 species.

Physalis hederifolia in Australia was first recorded in Melbourne in 1909, and the species was considered naturalized by 1914 (Parsons and Cuthbertson 2001). An estimated 24,000 ha of Victorian agricultural land was infested by 1964 (Parsons and Cuthbertson 2001). Grice (2002) reported that 96,000 ha were infested with *P. hederifolia* by 2002. A climatic modeling showed that *P. hederifolia* could potentially infest up to 409 million hectares in Australia (Kwong 2006).

Globally, *P. hederifolia* is a weed in South Africa, Chile, Argentina, Brazil, Uruguay, and the western United States. Within Australia, it is a declared noxious weed in New South Wales, Victoria, and Western Australia. *Physalis hederifolia* has been assessed as a highly invasive weed (Grice 2002; Kwong 2006) with an invasive score of 0.73 out of a possible score of 1. It is a summer-active perennial weed with a deep and extensive rhizomatous root system (Donaldson 1984). The weed is capable of regenerating from the root system, as well as reproducing through seeds. *Physalis hederifolia* seedling emergence and its new shoot emergence from the perennial roots occur in spring/summer. Flowers and fruits are produced in summer (Parsons and Cuthbertson 2001). All aerial growth dies in autumn/winter, while the roots remain alive, producing new shoots in the following spring. The horizontal roots

produce new shoots each year, which not only recharges the perennial roots with fresh carbohydrates, but also competes directly with summer-growing crops and pastures for moisture, nutrients, and space. *Physalis hederifolia* reduces crop and pasture production and stock-carrying capacity and contaminates grains and hays. It produces cherry tomato–like berries that are palatable to stock, foxes, and birds. Seeds germination is improved after passage through animals. Stock movement after grazing mature berries and long-distance transport of contaminated hay are key mechanisms of spreading the weed within and between paddocks, farms, and regions (Parsons and Cuthbertson 2001).

Physalis hederifolia is relatively hardy, capable of withstanding drought, trampling, and shading. The extensive root system aids vegetative reproduction, with fragments as short as 1.5 cm being viable (Faulkner and Young 2006). Cultivation is therefore not an effective control option due to the regeneration from the fragmented roots and rhizomes. Established populations cannot be readily eradicated using current control techniques.

The information on the physiology and germination of *P. hederifolia* is scarce, which is limiting for the formulation of informed management options. Two related *Physalis* species, cutleaf groundcherry (*Physalis angulata* L.) and smooth groundcherry (*Physalis virginiana* Mill.), prefer alternative temperatures for germination (Bell and Oliver 1979; Thomson and Witt 1987). Both *P. angulata* and *P. virginiana* germinate best at substrate pH levels of 5 to 8, and increasing substrate osmotic potential from 0 to 1.0 MPa can decrease germination rates from above 80% down to 40% for *P. angulata* and to 19% for *P. virginiana* (Thomson and Witt 1987). Similarly, Ozaslan et al. (2017) reported that *P. angulata* and Mexican groundcherry (*Physalis philadelphica* Lam.) also germinated under a wide range of temperature (15 to 40 C), pH (4 to 10), osmotic potential (0 to −1.2 MPa) and salinity (0 to 400 mM NaCl) levels.

Despite the increasing prevalence of *P. hederifolia* as a perennial weed of pastures and arable land, little is known of the seed germination biology of this weed. The aim of this research was to determine seed production levels, the longevity of the seed in the soil seedbank, and the factors that affect germination of *P. hederifolia* seed. The knowledge of germination biology could facilitate the management of this weed.

Materials and Methods

Seed Production

Sampling was conducted in April 2007 on natural *P. hederifolia* infestations near Tocumwal (145.69°E, 35.80°S) and Tarcutta (147.68°E, 35.23°S), NSW, Australia. At each site, 10 mature plants were randomly chosen at least 2 m apart to minimize the risk of sampling stems arising from the same root system. Plant height and total number of berries were recorded, and 10 berries were randomly chosen from each plant to determine berry diameter and the number of seeds.

Seed Longevity in the Field

Seed burial experiments were commenced in May 2007 at two field sites near Ganmain (146.70°E, 34.89°S) and Culcairn (147.17°E, 35.59°S), NSW, using seed collected from a *P. hederifolia* infestation near Tocumwal.

Fifty bare seeds or four intact berry pods were placed in a 10 by 10 cm mesh packet together with a small quantity of sieved soil. The packets were then placed at four soil depths (0, 2.5, 5, and 10 cm) and recovered at four time intervals (6, 12, 24, and 36 mo) in a randomized complete block design with three replicates per site.

Recovered seeds were counted and placed on moistened Whatman No.2 filter paper in a 9 cm petri dish, which was then sealed with Parafilm® and incubated for 21 d under a fluctuating 30/15 C temperature cycle with a 12 h photoperiod. In the case of recovered berries, a total of 50 seeds were randomly chosen for the germination assay.

The number of germinated seeds was recorded, and viability of ungerminated seed was determined by tetrazolium staining. Briefly, seeds were cut in half and incubated in darkness at 35 C for 5 h in a 0.5% 2,3,5-triphenyltetrazolium chloride solution. Seeds were deemed to be viable but dormant if the radical had stained red. Total viability of the exhumed seeds included the germinated seeds and the viable but dormant seeds.

Germination Factors

A series of experiments were conducted to determine factors affecting germination. A randomized complete block design with three replications was used in all experiments. Mature berries were collected in April 2007 from a *P. hederifolia* infestation near Tocumwal, NSW, and washed through a sieve to recover seed, which was then air-dried and stored before 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 under a fluctuating 30/15 C temperature cycle with a 12 h photoperiod.

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 (10/25, 15/25, and 15/30 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 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 from the average for the two temperatures. The influence of light was tested at 0 MPa and two fluctuating temperatures (10/25 and 15/30 C) by wrapping petri dishes in aluminium foil during incubation.

Impact of Salinity on Germination

The effect of salinity was studied by incubating seeds in solutions containing 0, 10, 20, 40, 80, 160, and 320 mM of sodium chloride (NaCl).

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). Seeds were exposed to solutions of pH 4 (10^{-4} mol L^{-1} HCl), 5 (10^{-5} mol L^{-1} HCl), 6 (10^{-6} mol L^{-1} HCl), 7 (deionized water), 8 (10^{-6} mol L^{-1} NaOH), 9 (10^{-5} mol L^{-1} NaOH), and 10 (10^{-4} mol L^{-1} NaOH).

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Statistical Analysis

All germination experiments were repeated, except for moisture stress under constant temperature, and data were combined as there were no significant differences over time. Seedbank persistence was determined by linear regression of seed viability data using square-root transformation of time. Germination (%) values at different concentrations of NaCl were fit to a logistic model:

$$y = a + c / \{1 + \exp[-b * (X - m)]\} \quad [1]$$

where y is the total germination (%) at NaCl concentration X; a, b, c, and m are constants. 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 germination. Data variance was visually inspected by plotting residuals to confirm homogeneity of variance before statistical analysis. Data were analyzed using analysis of variance and post hoc Fisher's tests used to determine statistically different means.

Results and Discussion

Seed Production

Average seed production differed between the two field sites, with 4,911 and 4,371 seeds plant^{-1} for Tocumwal and Tarcutta, respectively (Table 1). Such high quantities of seeds produced by *P. hederifolia* plants are similar to the production of 4,000 seeds plant^{-1} reported in a sister species, *P. angulata* (Travlos 2012). *Physalis hederifolia* at the Tocumwal site produced an average of 66 berries plant^{-1} and 74 seeds berry^{-1}, as compared with 86 berries plant^{-1} and 51 seeds berry^{-1}at the Tarcutta site. Within each site, berry and seed production levels were relatively consistent.

Seed Longevity

Combined data across the two field sites are presented, as there were no significant differences between sites. Both duration and depth of burial significantly reduced ($P < 0.01$) germination and viability of bare *P. hederifolia* seed. There was no interaction between duration and depth of burial. Germination levels for all bare seeds initially rose from 29% to 40%–78% at 6 mo after burial in the field and then steadily decline to 0% to 28% at 36 mo after burial, depending on the burial depth (Figure 1). Seeds exhumed from deeper in the soil profile had higher germination than seeds from shallower depths. The germination of bare seeds stored in the laboratory continued to rise from 0 mo (29%) to 24 mo (92%) after collection and then declined to 72% at 36 mo, indicating the presence of a physiological dormancy mechanism.

Table 1. Seed production characteristics (±SE of the mean) for *Physalis hederifolia* populations at two field sites (Tocumwal and Tarcutta, NSW, Australia) in 2007.

	Tocumwal	Tarcutta
Plant height (cm)	19.5 ±0.8	24.5 ± 1.0
Berries per plant	66 ± 12	86 ± 15
Berry diameter (mm)	12.8 ± 0.7	11.9 ± 0.5
Berry weight (g)	0.50 ± 0.1	0.73 ± 0.5
Seeds per berry	74 ± 10	51 ± 9
Seeds per plant	3,400–6,500	2,700–5,700

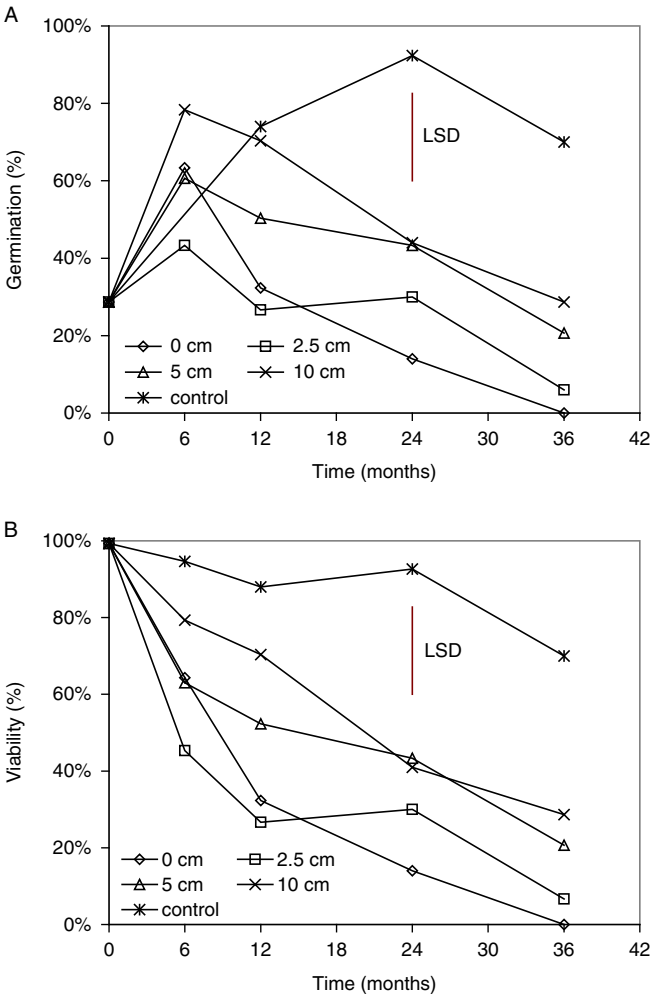

Figure 1. Effect of burial duration and depth on bare *Physalis hederifolia* seed (A) germination and (B) viability. Combined data from two field sites (Ganmain and Culcairn) are presented.

The viability of buried bare seeds rapidly decreased during the first 12 mo after burial, after which there was a steadily declining trend (Figure 1). No viable seed remained on the soil surface (0 cm) after 3 yr, and only 29% of bare seed remained viable at the 10 cm depth compared with 70% viability of seed stored in the laboratory. Linear regression indicated that bare seed buried up to 10 cm in the soil profile may persist for 6 yr.

Germination and viability of seed in intact berry pods also declined with duration and depth of burial ($P < 0.01$); however, these levels were similar to those of seed stored in the laboratory (Figure 2), indicating the protective role of intact berry pods on maintaining seed viability under natural conditions. The exception was the seed recovered from intact berries on the soil surface, which had only 3% of seed remaining viable after 3 yr. It is estimated that seed buried in intact berry pods has the potential to persist in the soil seedbank for up to 20 yr unless the integrity of the dried berry is disrupted.

Temperature and Osmotic Stress

Without osmotic stress, *P. hederifolia* seed germinated between constant temperatures of 20 C and 40 C, with optimal germination (26%) at 30 C constant temperature. No germination was recorded at 10 C constant temperature (Figure 3). Diurnal

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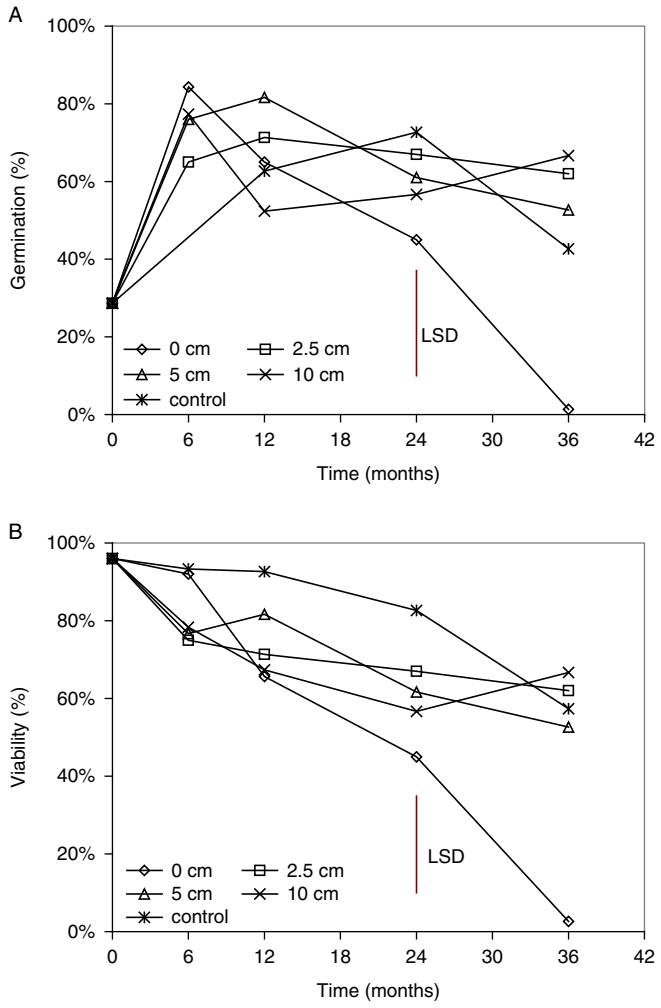

Figure 2. Effect of burial duration and depth on (A) germination and (B) viability of *Physalis hederifolia* seed in buried dried berries. Combined data from two field sites (Ganmain and Culcairn) are presented.

alternating temperatures significantly increased germination up to 80% under the 30/15 C temperature regime. The two treatments of 30/15 C and 25/10 C, which had a diurnal temperature fluctuation of 15 C, had higher germination than the treatment at 25/15 C with a diurnal temperature fluctuation of 10 C. Increasing osmotic stress levels reduced the germination observed under all temperature regimes, with less than 6% germination occurring at −0.96 MPa. At 20 C constant temperature, no germination occurred, even at −0.24 MPa. These results suggest that *P. hederifolia* prefers warm and moist conditions for optimal seed germination.

Light

Significantly more ($P < 0.05$) *P. hederifolia* seed germinated when exposed to 12 h of light compared with germination in complete darkness at 30/15 C (81.3% and 70.0%, respectively), with a similar trend apparent when seeds were incubated at 25/10 C (Figure 4).

Salt

Physalis hederifolia seed germination declined gradually when NaCl concentrations were less than 160 mM (Figure 5). However,

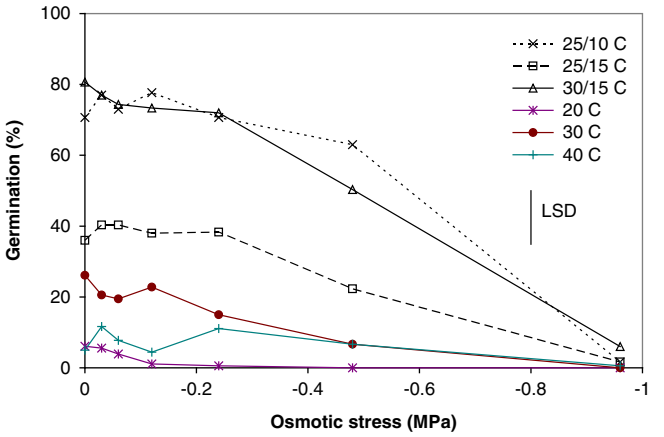

Figure 3. Effect of osmotic potential on *Physalis hederifolia* seed germination after 21 d of incubation in constant or fluctuating day/night temperatures with a 12 h photoperiod. No germination recorded at 10 C constant temperature.

a sharp decline in germination occurred at higher salt concentrations, with less than 15% and 6% of seed germinating when exposed to 240 and 320 mM NaCl, respectively. Logistic regression accounted for 91.4% of variance ($y = 0.05 + 0.72/\{1 + \exp[0.05*(X - 197.51)]\}$).

$$\{1+\exp[0.05*(X-197.51)]\}$$

pH

More than 72% of *P. hederifolia* seed germinated at all pH levels examined (Figure 6). No significant trend was apparent across pH levels, suggesting that substrate pH levels do not impact *P. hederifolia* germination.

Persistence of weed populations in the absence of seed production relies on the longevity of the soil seedbank. The dried *P. hederifolia* berry appears to afford protection to the enclosed seed against loss of seed viability. In comparison with bare seed, seed enclosed within a dried berry pod has the potential to persist three to four times as long in the soil seedbank. However, if the

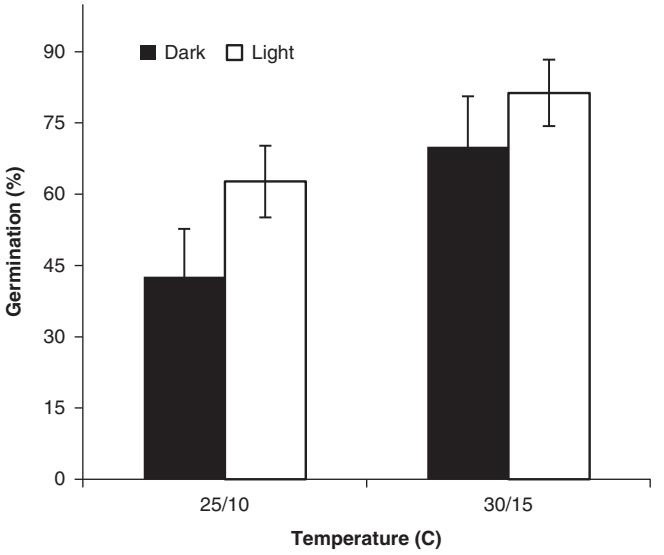

Figure 4. Effect of exposure to light on *Physalis hederifolia* seed germination after 21 d of incubation in fluctuating temperatures with a 12 h photoperiod. Vertical bars represent standard error of the mean.

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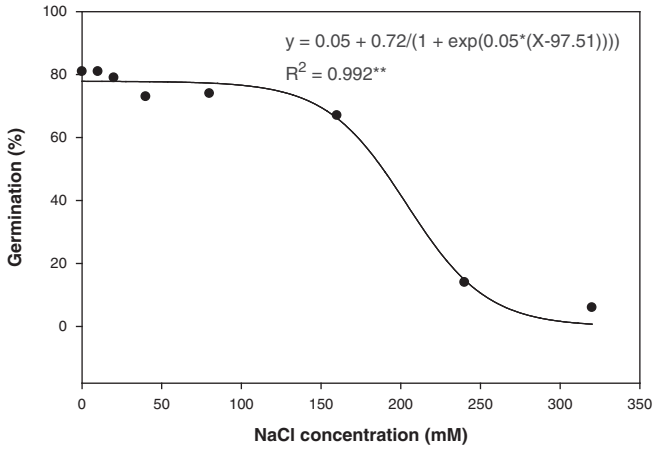

Figure 5. Effect of NaCl concentration on *Physalis hederifolia* seed germination after 21 d of incubation in 30/15 C day/night temperatures in a 12 h photoperiod.

berries and seeds are left on the soil surface, seed persists for a shorter period of time, due to greater fluctuations in temperature and moisture under natural conditions. These results suggest that eradication of this weed will take many years of vigilant control, and that it is highly important to have seed set (berry set) control strategies in place to minimize the replenishment of seeds into the soil seedbank. Berries present on stems could contaminate hays or could be grazed by livestock and other animals, providing opportunity for seeds to be dispersed and potentially incorporated into the soil seedbank in a previously weed-free field. Given *P. hederifolia*'s seedbank persistence and the vegetative reproduction capacity of its root system (Faulkner and Young 2006), cultivation is not recommended, as it will not only trigger new shoot emergence regenerated from the perennial roots, but will also contribute to the enforced burial of seeds in the soil, resulting in prolonged persistence of *P. hederifolia*. Maintaining seeds on or near the soil surface through zero or minimum tillage would assist in depleting the soil seedbank.

Physalis hederifolia germinates best when exposed to either diurnally fluctuating temperatures or a constant 30 C. These results are in agreement with the reported influence of temperature regimes on the germination of *P. angulata*, *P. virginiana*, and *P. philadelphica* (Ozaslan et al. 2017; Thomson and Witt 1987), for which maximum germination occurs with alternating temperatures. The temperature change during the diurnal cycle appears to be more important than the minimum and maximum temperatures of the cycle, as germination under the 10 C temperature fluctuation was lower compared with germination under the two 15 C fluctuation treatments, despite the similarity in temperature maxima and minima.

The increased persistence of seed down the soil profile, combined with the requirement for diurnal temperature fluctuations of 15 C within the temperature range of 10 and 30 C, suggests that conventionally tilled fields provide optimum conditions for the establishment and persistence of this weed.

The increased germination levels when seed was exposed to light are consistent with the findings of Thomson and Witt (1987) that germination of *P. angulata* and *P. virginiana* seed is reduced in the dark. Similarly, Ozaslan et al. (2017) found that the seeds of *P. angulata* and *P. philadelphica* exhibited higher germination when incubated in a 12 h light/12-h dark photoperiod than under continuous-dark treatments.

The germination of *P. angulata* and *P. virginiana* declined gradually to 40% and 19%, respectively, under a simulated osmotic stress level of −1.0 MPa (Thomson and Witt 1987). In comparison, germination of *P. hederifolia* seed declined to less than 6% at −1.0 MPa, suggesting a greater sensitivity to moisture stress. Decreasing germination under drier conditions suggests that good soil moisture conditions must be present for a *P. hederifolia* germination event to occur.

Physalis hederifolia germinates across a broad range of pH 4 to 10, which is in contrast with the responses of *P. angulata* and *P. virginiana* (Thomson and Witt 1987), for which decreased germination levels occurred at pH 4. Similarly, seeds of *P. angulata* and *P. philadelphica* had optimal germination at a substrate pH 7 to 8, and germination was reduced at highly acidic or alkaline pH (Ozaslan et al. 2017).

Substrate salinity reduces germination of *P. hederifolia*, which is consistent with the suppressive effect of saline environments on the germination of *P. angulata* and *P. philadelphica* (De Souza et al. 2016; Ozaslan et al. 2017). The germination and seedling growth of tomatillo (*Physalis philadelphica* Lam.) and Peruvian groundcherry (*Physalis peruviana* L.) were also affected by varying levels of NaCl treatments, with seedling emergence and growth being more sensitive to salt stress than seed germination (Yildirim et al. 2011). Our results suggest that *P. hederifolia* is less sensitive to soil pH than other *Physalis* species, but has a similar lack of tolerance to saline conditions.

Results from these experiments provide insight into the seed production, longevity, and germination requirements of *P. hederifolia*. The capacity of this species to germinate under a range of substrate conditions suggests that the spread of this weed may not be limited by soil type. Producers and land managers need to be vigilant in monitoring all areas for the occurrence of new infestations. Monitoring for seedlings should be undertaken when soil temperatures are above 15 C and after rainfall events, as *P. hederifolia* requires warm and moist conditions for seed germination. Any seedlings should be promptly controlled before the formation of viable seeds to achieve complete seed set control.

Seedlings of *P. hederifolia* are much easier to control than established plants, which have an extensive root system. Therefore, new infestations should be managed before the plants are able to establish. Good stock, grain, and machinery hygiene will minimize the risks of spread. Some PRE and POST herbicide

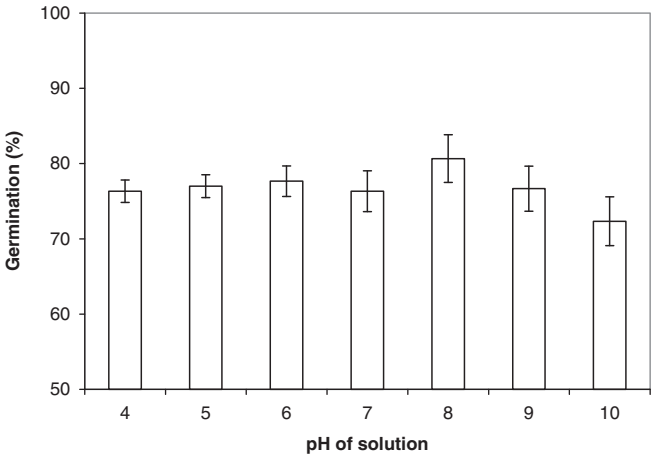

Figure 6. Effect of pH level on *Physalis hederifolia* seed germination after 21 d of incubation in 30/15 C day/night temperatures in a 12 h photoperiod. Vertical bars represent standard error of the mean.

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treatments are effective in reducing the berry production of *P. hederifolia* and *P. angulata* (Donaldson 1984; Price et al. 2013), thereby minimizing the replenishment of the seedbank. More field studies are needed to determine the optimum control timing and effective herbicide options to stop berry production and reduce the viability of the perennial root system. A previously proposed "dual-action" approach for the effective management of another perennial solanum species, silverleaf nightshade (*Solanum elaeagnifolium* Cav.) (Wu et al. 2016) could be evaluated, with the first action targeting the seed set and the second action targeting the roots.

This study suggests that land managers need to ensure that berry production is minimized as much as possible and that management practices are implemented to reduce movement of seeds away from the site of infestation via livestock, machinery, grain, or fodder. Long-term commitment is required to manage *P. hederifolia* due to the perpetual seedbank and the extensive perennial root system.

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