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Article

GERMINATION OF *Solanum nigrum* L. (BLACK NIGHTSHADE) IN RESPONSE TO DIFFERENT ABIOTIC FACTORS

*Germinação de **Solanum nigrum** L. (Erva-Moura) em Resposta a Diferentes Fatores Abióticos*

DONG, H.[1]
MA, Y.[2]
WU, H.[3]
JIANG, W.[2]
MA, X.[1,2*]

*** Corresponding author:**
<maxy_caas@126.com>

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ABSTRACT - *Solanum nigrum* L. (black nightshade), an annual to short-lived perennial weed, has become a problem weed in farming systems in central China. Laboratory and greenhouse experiments were conducted to examine the influence of various abiotic factors on seed germination of black nightshade to develop effective weed control programs. Seeds germinated at a range of constant temperatures from 15 to 30 °C, but no germination occurred at temperatures below 10 °C or above 35 °C. Seeds also germinated at alternating temperature regimes from 15/5 to 40/30 °C, with maximum germination (> 93.5%) at the alternating temperatures of 25/15 and 30/20 °C. Germination decreased as osmotic potential became more negative, and no germination was observed at ≤ -0.8 MPa. Moreover, germination was reduced by saline and alkaline stresses and no germination occurred at ≥ 200 mM NaCl or ≥ 150 mM $NaHCO_3$ concentrations. Seed germination was not significantly affected by pH values from 5 to 10. Seedling emergence was significantly affected by burial depth with maximum emergence (93.1%) at 1 cm depth.

Keywords: burial depth, light, osmotic potential, saline and alkaline stress, seed biology, temperature.

*RESUMO - **Solanum nigrum** L. (erva-moura), uma planta daninha perene anual de curta duração, tornou-se uma planta daninha problemática em sistemas agrícolas na China central. Foram conduzidos experimentos em laboratório e em casa de vegetação para examinar a influência de vários fatores abióticos na germinação de sementes de erva-moura para o desenvolvimento de programas eficazes de controle de plantas daninhas. As sementes germinaram em temperaturas constantes de 15 a 30 °C, mas não ocorreu germinação em temperaturas abaixo de 10 °C ou acima de 35 °C. Também foi observada germinação das sementes em regimes de temperaturas alternadas de 15/5 °C a 40/30 °C, com germinação máxima (> 93,5%) nas temperaturas alternadas de 25/15 °C e 30/20 °C. Houve redução da germinação à medida que o potencial osmótico se tornou mais negativo, e nenhuma germinação foi observada a ≤ 0,8 MPa. Além disso, foi observada redução da germinação em função do estresse salino e alcalino, e nas concentrações ≥ 200 mM de NaCl ou ≥ 150 mM de $NaHCO_3$ não ocorreu germinação. A germinação das sementes não foi afetada de forma significativa pelos valores de pH de 5 a 10, porém a emergência de plântulas sofreu influência significativa da profundidade de sementes, com emergência máxima (93,1%) a 1 cm de profundidade.*

Palavras-chave: profundidade de sementes, luz, potencial osmótico, estresse salino e alcalino, biologia de sementes, temperatura.

[1] Tarim University, Alaer, China; [2] State Key Laboratory of Cotton Biology, Institute of Cotton Research of CAAS, Anyang, China; [3] Wagga Wagga Agricultural Institute, Wagga Wagga, Australia.

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INTRODUCTION

Solanum nigrum L. (black nightshade, Solanaceae) is an annual to short-lived perennial weed and widely distributed throughout the world (Defelice, 2003). It is considered troublesome in various crops including: cotton (*Gossypium hirsutum* L.) (Tursun et al., 2016); maize (*Zea mays* L.) (Wang et al., 2019); and grapes (*Vitis vinifera* L.) (Shrestha and Fidelibus, 2005); and causes yield losses, and a reduction in crop quality and value due to its easily crushed berries (Ogg and Rogers, 1989). In contrast, this plant can be beneficial to people (Defelice, 2003) and it has a long history of medicinal usage, dating back to ancient Greece and China (Miraj, 2016).

As a summer-growing plant, black nightshade reproduces sexually and builds up a soil seed bank. Kremer and Kropff (1998) reported that black nightshade had high fecundity and a single plant could produce as many as 10,000 berries with about 60 seeds per berry. The characteristics of weed seed germination and seedling emergence are of vital importance in regulating crop and weed competition. Seeds of black nightshade can emerge over a wide period in spring and summer (Keeley and Thullen, 1983). In the Yellow River cotton production region in China, the emergence of black nightshade seedlings starts in late April and continues through mid October (Ma et al., 2012).

As a global weed, black nightshade has adapted to a broad range of environmental conditions (Holm et al., 1991). Various of these factors such as temperature, moisture and salinity affect seed germination. Research has shown that black nightshade has the following temperature requirements for germination, from 7.5 to 34 ^{o}C (Del Monte and Tarquis, 1997; Kremer and Lotz, 1998a) with optimum temperatures from 26 to 30 ^{o}C (Taab and Andersson, 2009a). Burial depth is another factor that influences black nightshade seedling emergence. Lati et al. (2012) reported that optimal black nightshade emergence occurred at burial depths of 1-2 cm with minimal emergence at 4-5 cm depth. There was no emergence for black nightshade seeds buried at more than 6 cm depth (Kremer and Lotz, 1998b).

Other environmental factors, such as pH, salinity and osmotic stresses may also regulate weed seed germination and seedling emergence (Asgarpour et al., 2015; Li et al., 2015; Nandula et al., 2006). Soil salinization, for example, has been a persistent ecological issue and a serious threat to global agriculture (Devkota et al., 2015). In recent decades, black nightshade has become an increasingly problematic weed in cotton and corn fields in central China (Jiang et al., 2014). However, no information, to our knowledge, is available on the biology of this weed species under the climatic conditions of this cotton production region, and the response of this weed may vary according to the biotype and environmental conditions (Duddu and Shirtliffe, 2014; Eslami, 2011).

The objective of this study was to evaluate the effects of temperature, light, osmotic and salinity stresses and pH on seed germination, and burial depth on seedling emergence of black nightshade. This information could be used to define more effective management methods for its control and determine its potential spread to new areas in China.

MATERIAL AND METHODS

Seed source and preparation

Black nightshade berries were collected in September 2015 from naturally senescing plants in the experimental field of the Institute of Cotton Research, Chinese Agricultural Academy of Sciences (36.13^{o} N, 114.85^{o} E). The soil was a sandy loam soil (Typic Haplustepts) according to Soil Taxonomy (Soil Survey Staff, 2010); having 40% sand, 25% silt, 35% clay, 1.5% organic matter, pH 8.0 and electrical conductivity of 500 µs cm^{-1}. The mature black berries were crushed, and seeds were washed out and collected on a sieve under running water. The seeds were then air-dried at ambient conditions and stored at room temperature in paper bags. A preliminary germination test in July 2016 (after the 10-month storage) showed that the black nightshade seeds had > 95% germination at 25 ^{o}C, the optimal germination temperature suggested by Defelice (2003).

Germination test

Four replicates of 25 seeds were evenly placed in 90-mm-diam petri dishes on two layers of Whatman No. 1 filter paper moistened with 3 mL of deionized water or treatment solutions. Dishes were sealed with Parafilm to minimize water losses from evaporation. Dishes were then placed in an incubator at diurnal light/dark temperatures of 25/15 °C, unless specified otherwise. The photoperiod was set at 14 h to coincide with the typical day length between July and August and the photosynthetic photon-flux density was 150 μmol m^{-2} s^{-1}. The number of germinated seeds were counted daily and terminated at 10 days after sowing (DAS). Seeds with a radicle of ≥ 2 mm length were considered as germinated. The number of germinated seeds was used to determine germination percentage.

Constant temperature and light

Germination tests were conducted in incubators set at eight constant temperatures of 5, 10, 15, 20, 25, 30, 35 and 40 °C. For germination in complete darkness, the dishes were wrapped in two layers of aluminum foil, and germination was counted once at 10 DAS. However, the germination at the low temperature treatments (≤ 15 °C) was checked again at 20 DAS but there no further germination after 10 DAS.

Alternating temperature and light

Seed germination was evaluated in incubators under six fluctuating temperatures of 15/5, 20/10, 25/15, 30/20, 35/25, and 40/30 °C. The reason for these temperature regimes was that the difference between minimum temperature and maximum temperature in March to November during recent years in the region being approximately 10 °C (Xiong et al., 2018). A set of petri dishes in each temperature was wrapped in two layers of aluminum foil to study seed germination in the dark, and the number of germinated seeds was counted once at 10 DAS.

Osmotic stress

Germination, as affected by osmotic stress, was determined at water potentials of 0, -0.2, -0.4, -0.6, -0.8, and -1.0 MPa, by dissolving appropriate amounts of polyethylene glycol (PEG) 8000 in deionized water (Michel, 1983). The seeds were incubated at 25 °C. The number of germinated seeds in each dish was recorded daily.

Saline and alkaline stresses

The effect of saline and alkaline stresses on black nightshade germination was determined by incubating seeds in dishes containing sodium chloride (NaCl) or sodium bicarbonate ($NaHCO_3$) solutions of 0, 12.5, 25, 50, 100, 150, 200, 250, and 300 mM. Petri dishes were incubated as described in the osmotic stress study.

pH

To examine the effect of pH on seed germination of black nightshade, buffered solutions of pH 5 to 10 were prepared according to the method described by Chauhan and Johnson (2008). Unbuffered deionized water (pH 6.8) was used as a control.

Seed burial depth

The effect of seed burial depth on seedling emergence was investigated based on the methodologies previously published (Zhou et al., 2005; Nandula et al., 2006). The trial was conducted in a greenhouse at 30±2 / 20±2 °C day/night temperature, 65±5% relative humidity and with a 14-h photoperiod. Fluorescent lamps were used to produce a photosynthetic photon-flux density of 120 μmol m^{-2} s^{-1}. Twenty seeds were buried at seven different depths (0 cm or surface, 1, 2, 3, 4, 6, and 8 cm) in 15-cm-diam by 15-cm-deep plastic pots, filled with a 2:1 mixture of sandy loam and potting soil ($N-P_2O_5-K_2O \geq 2\%$, organic matter ≥ 40%, pH = 6.5±0.5; Huaian Hongyang Agricultural Science and Technology Development Co., Ltd., Jiangsu Province, China). The pots were watered as needed to maintain adequate soil moisture. Seedlings were considered emerged when the two cotyledons were visible at the soil surface. Seedlings were counted 20 days after sowing.

Statistical analyses

A randomized complete-block design with four replications was used in all experiments. Each experiment was repeated twice. Data from repeated experiments were subjected to ANOVA and there was no significant time-by-treatment interaction; therefore, data from two experiments were pooled before further analysis. Neither arcsine, square or log transformation of the data improved the homogeneity of variance; therefore, ANOVA and regression analysis were performed on the non-transformed percentage of germination. Significant differences among treatment means were identified by the Fisher's protected LSD test.

Additionally, regression analysis was used to evaluate the effect of salinity and alkalinity stresses on germination percentage. Data were fitted to a functional three-parameter logistic model (Asgarpour et al., 2015). The applied model was

$$G = G_{max} / \left\{1 + \exp\left[-\left(x - x_{50}\right) / G_{rate}\right]\right\} \quad \text{(eq. 1)}$$

where G is the total germination (%) at different concentrations of salt or alkali potential x, G_{max} is the maximum germination (%), x_{50} is the concentration required for 50% inhibition of the maximum germination, and G_{rate} indicates the slope.

A three-parameter sigmoid model (Chauhan and Johnson, 2008) was used to describe the effects of time (days after sowing) on germination (%). The model fitted was

$$E = E_{max} / \left\{1 + \exp\left[-\left(x - x_{50}\right) / E_{rate}\right]\right\} \quad \text{(eq. 2)}$$

where E is the total germination (%) at time x, E_{max} is the maximum germination (%), x_{50} is the time to reach 50% of maximum germination, and E_{rate} indicates the slope.

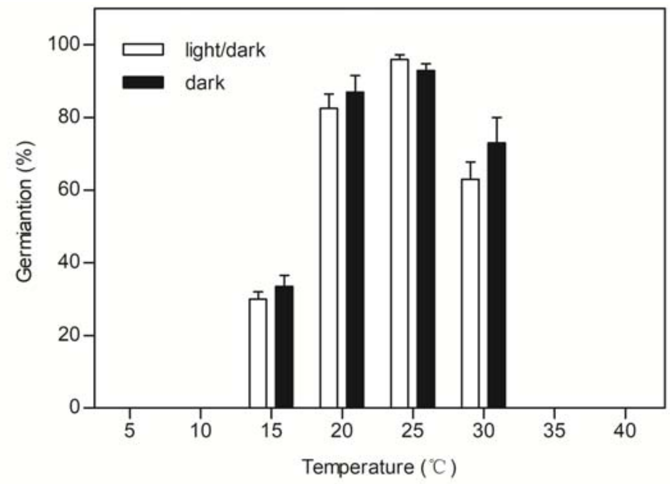
Coefficients of determination (r^2) were calculated for nonlinear regressions and used to determine the goodness of fit of nonlinear models. All probabilities were two-tailed, and the significance level was set at $P = 0.05$. Analysis was performed with the statistical software SPSS 13.0.

RESULTS AND DISCUSSION

Constant temperature and light

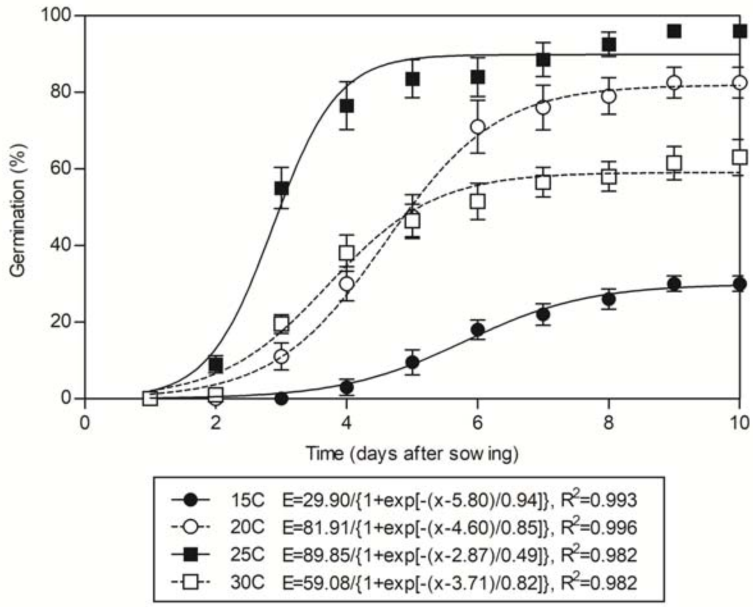
Seed germination of black nightshade was significantly affected by temperature ($P < 0.001$), and seed germination trend under the 14-h photoperiod was similar to that at the complete darkness. Seeds did not germinate at 5 and 10 °C, and had maximum germination at 25 °C, which was followed by a decline in germination at 30 °C. No germination was observed at 35 °C and 40 °C (Figure 1). Light had no significant effect on the percentage of black nightshade seed germination at temperatures between 15 and 30 °C (Mann-Whitney U test, $P > 0.05$).

The optimal temperature (25 °C) not only resulted in the highest germination, but also promoted the onset of germination. The germination at 25 °C started at about 2 days after sowing, as compared to 4 days at 15 °C. Similarly, the days required to achieve 50% germination decreased from 5.80 to 2.87 days with temperature increases from 15 to 25 °C (Figure 2).



Vertical bars represent standard errors of the means.

Figure 1 **-** Effect of constant temperatures and light regimes (light/dark and dark) on black nightshade seed germination.



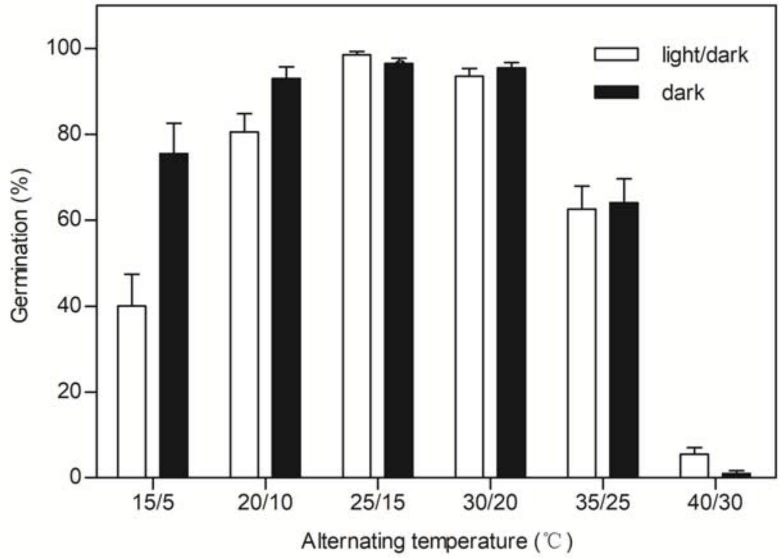
Vertical bars represent standard errors of the means.

Figure 2 **-** Effect of constant temperatures on cumulative germination of black nightshade seeds under light/dark condition.

Taab and Andersson (2009b) tested the seed germination of black nightshade at a range of constant temperatures from 6 to 38 °C and found that germination occurred from 18 to 34 °C, with a maximum germination at 26-30 °C. In this study, seed germination started at 15 °C and maximum germination occurred at 25 °C, which is consistent with previous studies (Kremer and Lotz, 1998a). Moreover, these studies have also showed that extreme higher temperatures, e.g. 35 °C and 40 °C in this study, were not conducive to the germination of black nightshade seeds. Roberts and Lockett (1978) found that high temperatures in late summer could induce secondary seed dormancy in black nightshade.

Alternating temperature and light

Germination was favored at the alternating temperature regimes of 25/15 °C and 30/20 °C under both light/dark and dark conditions and declined at 35/25 °C. Only 5.5% germination occurred at light/dark temperature regime of 40/30 °C (Figure 3). Germination did not differ



Vertical bars represent standard errors of the means.

Figure 3 - Effect of alternating temperatures and light regimes (light/dark and dark) on black nightshade seed germination.

between the two temperature regimes of 25/15 °C and 30/20 °C. At the temperatures 15/5 °C and 20/10 °C, germination was greater in the darkness (75.5 and 93.0%) than in the light/dark treatment (40.0 and 80.5%; Mann-Whitney U test, $P < 0.05$). However, the germination at 40/30 °C was only 1.0% in the dark as compared to 5.5% in the light/dark treatment ($P = 0.02$). There was no significant difference in germination between the light/dark and darkness treatments at 25/15, 30/20, and 35/25 °C ($P > 0.05$; Figure 3).

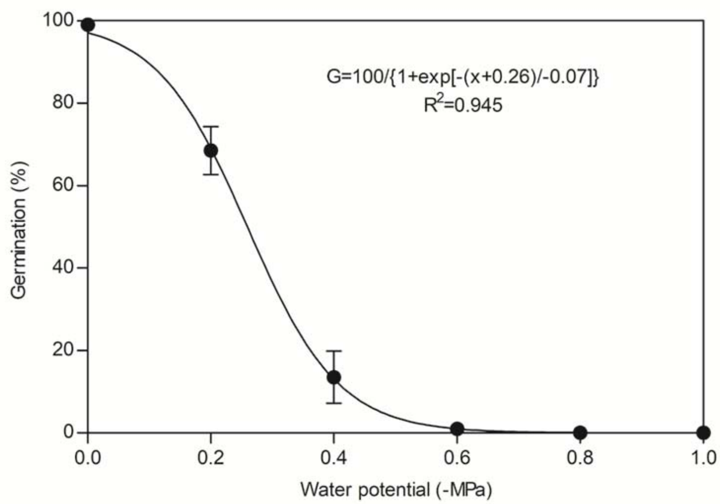
Temperature determines the time of weed emergence. In the Yellow River cotton production region in China, the emergence of black nightshade seedlings starts in late April and continues through to mid-October, coinciding with the cotton growing period (Ma et al., 2012). Such an emergence pattern is well supported by the average monthly temperatures of 15.2 °C and 15.9 °C in April and October, respectively, based on the climatic data between 2011 and 2015 in this region (Xiong et al., 2018).

The results of this study show that black nightshade seeds can germinate over a wide range of conditions when temperatures fluctuate. Germination at 15/5 °C and 20/10 °C in darkness reached 75.5% and 93.0%, respectively, but only 33.5% at constant 15 °C. Similarly, no germination was observed at constant temperatures 35 °C or 40 °C, but seeds of black nightshade could still germinate at 40/30 °C in both light and dark conditions. The results of previous studies were in agreement with this trend, that alternating temperatures were an important stimulus for germination of black nightshade (Roberts and Lockett, 1978), eastern black nightshade (*S. ptycanthum*) (Zhou and Deckard, 2005), and muskweed (*Myagrum perfoliatum*) (Honarmand et al., 2016). Thompson et al. (1977) found that in some species a fluctuation of 1 °C was enough to promote germination. On the contrary, relatively stable temperatures were more suitable for seed germination than alternating temperatures in Japanese brome grass (*Bromus japonicus*) (Li et al., 2015).

Light had no effect on the seed germination of black nightshade between 15-30 °C and at the alternating regimes of 25/15-35/25 °C. Roberts and Lockett (1978) also found that the effect of light on seed germination of black nightshade depended on the surrounding temperature and germination at favorable temperatures was similar irrespective to the absence or presence of intermittent exposure to light. Varied germination responses to light have been reported among different weed species of the Solanaceae family. Seed germination of hairy nightshade (*S. physalifolium*) was not sensitive to photoperiod and seeds germinated equally well under a 14-h photoperiod or continuous darkness at 30 °C (Zhou et al., 2005). However, enhancement of seed germination by light has been reported in eastern black nightshade (Zhou and Deckard, 2005).

Osmotic stress

Black nightshade seed germination decreased from 99.0 to 1.0% as water potentials decreased from 0 to -0.6 MPa. Germination was completely inhibited at the water potentials less than -0.8 MPa. The water potential that caused 50% inhibition of the maximum germination was -0.26 MPa, and germination substantially reduced to 68.5% and 13.5% when water potential was -0.2 and -0.4 MPa, respectively (Figure 4).



Vertical bars represent standard errors of the means. Seeds placed in an incubator at 25 °C with a 14-h photoperiod for 10 days.

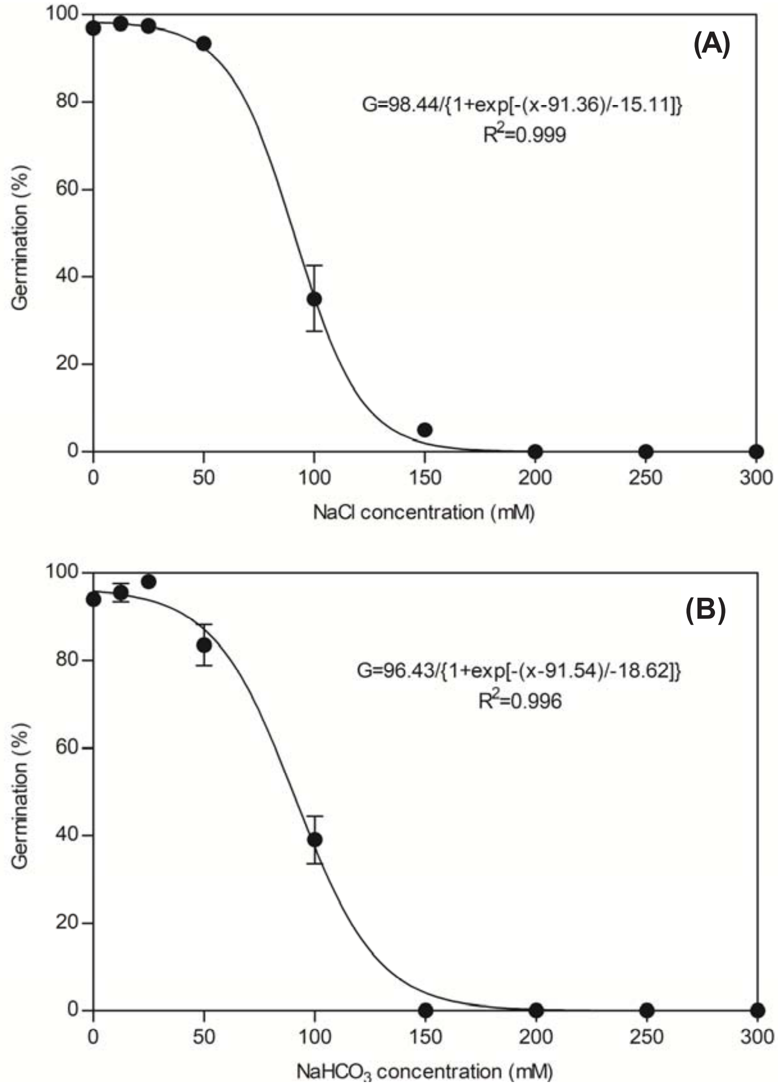
Figure 4 **-** Effect of water potential on seed germination of black nightshade seeds.

Rehydration of seeds is an important initial step towards germination. The seed imbibition rate decreases with reducing water potential (Bewley and Black, 1978) and, subsequently, the germination rate decreases. Guillemin et al. (2013) estimated that the base water potential for black nightshade germination was -0.89 MPa, which was higher than the other 9 weed species in the study (from -3.31 to -0.95 MPa). Our study showed that seed germination of black nightshade was completely inhibited at the water potentials less than -0.80 MPa. These results indicated that seed germination of black nightshade was more sensitive to moisture stress and drought was unfavorable for seed germination. However, in central China, the annual precipitation is 600-1600 mm with rains mostly occurring from May to August, which coincides well with the seedling emergence of black nightshade. Moreover, crops are often irrigated in low-rainfall years. Thus, moisture stress or drought generally is not a limiting factor in the spread of black nightshade in agricultural production areas in central China.

Salinity and alkalinity stress

Seed germination of black nightshade was significantly reduced in both NaCl and $NaHCO_3$ treatments ($P < 0.001$). Germination at ≤ 50 mM NaCl was ≥ 93.5%, and it declined to 35.0% and 5.0% at 100 and 150 mM NaCl, respectively, being completely inhibited at ≥ 200 mM NaCl (Figure 5a). Seed germination at ≤ 50 mM $NaHCO_3$ was ≥ 83.5%, and reduced to 39.0% at 100 mM $NaHCO_3$, with complete inhibition at $NaHCO_3$ concentration ≥ 150 mM (Figure 5b). The salt concentrations required for 50% inhibition of the maximum germination were 91.4 mM for NaCl and 91.5 mM for $NaHCO_3$.

Excessive salt and alkali accumulation in soils is one of the most important environmental problems in the world and is particularly serious in the arid and semi-arid and coastal regions of China (Zhao et al., 2016). Different cations and anions, e.g. Na^+, chloride (Cl^-), and bicarbonate (HCO_3^-), in the soil play important roles in governing the changes in soil salt-alkalization (Zhao et al., 2014). Therefore, NaCl and $NaHCO_3$ were used to determine the effect of salt and alkali stresses on seed germination of black nightshade.



Seeds placed in an incubator at 25 °C with a 14-h photoperiod for 10 days.

Figure 5 **-** The relationship between sodium chloride (NaCl, A) or sodium bicarbonate ($NaHCO_3$, B) concentration and seed germination (mean ± SE) of black nightshade.

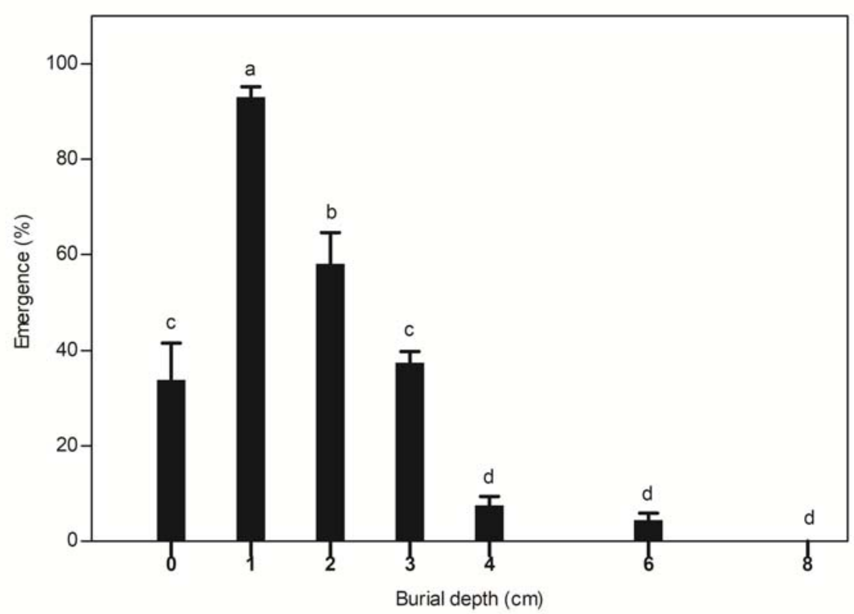
Most of the studies exploring the effects of saline stress on seed germination of weed species were focused on NaCl, and the salinity tolerance of black nightshade was similar to spotted spurge (Asgarpour et al., 2015), with 36.5% germination at 120 mM NaCl and no germination at 160 mM NaCl. To our knowledge, no attention to date has been paid to alkaline stress on seed germination of weed species, although there were several studies on the impact of NaCl, Na_2SO_4, Na_2CO_3, and $NaHCO_3$ on the germination of crop and pasture species, e.g. sweet sorghum [*Sorghum bicolor* (L.) Moench] (Zhao et al., 2014), sunflower (*Helianthus annuus* L.) (Liu et al., 2010) and *Leymus chinensis* (Trin.) Tzvel. (Lin et al., 2014). Salt solutions have both water potential and specific salt effects on seed germination (DiTommaso, 2004), and in alkaline solutions these may be more related to pH than to salt effects. Therefore, further research is needed to understand the combined effects of salinity and osmotic stresses and alkaline and pH stresses on seed germination.

pH

Black nightshade seed germination was not affected by the tested levels of pH ($P = 0.19$) and germination was > 95% over the pH range from 5 to 10. This characteristic has been observed in silverleaf nightshade (*S. elaeagnifolium* Cav., Stanton et al., 2012). In contrast, the optimum pH range for hairy nightshade germination was between 6 and 8 and a marked decrease in germination occurred when pH was outside this range (Zhou et al., 2005). In the soils of central China, the pH range is commonly 7-8. Thus, the soil pH should not be a limiting factor for black nightshade seedling emergence, with such a wide tolerance of pH a useful trait in helping this weed species colonize various habitats.

Seed burial depth

Burial depth had significant effect on the emergence of black nightshade ($P < 0.001$). Only 33.8% germination occurred when seeds were sown on the soil surface. The highest seedling emergence (93.1%) was observed when seeds were sown at 1 cm depth, and emergence decreased significantly from 1 to 4 cm depth. At deeper burial depths (4 and 6 cm) emergence was only 4.4-7.5%. No seedlings emerged when seeds were sown at 8 cm (Figure 6).



Vertical bars represent standard errors of the means. Bars with the same letters are not significantly different ($P = 0.05$).

Figure 6 **-** Effect of seed burial depth on seedling emergence of black nightshade.

Black nightshade seedlings emerged over a range of burial depths, with the optimal emergence at 1 cm burial, followed by a rapid decline in response to the increasing burial depths. This emergence pattern in relation to soil burial depth is consistent with previous reports, showing that seedling emergence decreased with an increase in sowing depths and that highest emergence was observed when seeds were sown on or near the soil surface (Nandula et al., 2006; Li et al., 2015). In this study, the emergence of black nightshade seeds sown at the soil surface was lower than that at 1 cm or 2 cm soil depth. The poor emergence from the soil surface is likely due to a combination of the loose soil contact with the seed and the restricted access to moisture on the surface. The present study showed that black nightshade seedling emergence occurred mostly from the top 4 cm soil layers, suggesting that black nightshade has the potential to become a problematic weed under no-tillage farming systems, widely adopted by farmers in central China.

In summary, the results of this study indicate that black nightshade germination is affected by various environmental factors. Black nightshade germinated over a wide range of temperature regimes from 15 to 30 °C and 15/5 to 40/30 °C, with optimum germination occurring at 25, 25/15, and 30/20 °C. Light and pH (5-10) had little effect on seed germination of black nightshade. Germination decreased as water stress and salt and alkali concentration increased, but germination occurred over a broad range of water potentials (> -0.80 MPa), salt and alkali concentrations (NaCl < 200 mM; $NaHCO_3$ < 150 mM), indicating its tolerance to dry, saline and alkaline conditions. Seeds of black nightshade could emerge from on or near the soil surface (with a burial depth less than 8 cm). These results suggest that the environmental conditions in central China, e.g. temperature, rainfall (600-1600 mm in May-August) and soil pH (7-8) are suitable for black nightshade emergence. Therefore, it is imperative to control black nightshade in this region due to favorable climatic and edaphic conditions for its emergence and spread. Application of suitable herbicides during the peak emergence period is one effective option for black nightshade control. Application of soil-applied herbicides, such as oxyfluorfen or pendimethalin, has been suggested for the season-long control of black nightshade. Post-emergent herbicides, such as trifloxysulfuron or glyphosate, can be used to control black nightshade at the seedling stage in cotton and in corn fields. Soil tillage, especially shallow ploughing/harrowing, is an effective strategy to encourage the emergence, which could be subsequently controlled by post-emergent herbicides. On the other hand, deep inversion plough could be used to bury seeds to prevent the emergence. In conclusion, the results determining the germination and emergence patterns and timing of black nightshade in the field can be used to develop strategies for the effective management of this weed in agricultural production areas in China.

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