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# Effects of environmental factors on seed germination and seedling emergence of common evening primrose (*Oenothera biennis*)

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## Research Article

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## Abstract

There is scant information about seed germination and seedling emergence of common evening primrose (*Oenothera biennis* L.), even though it is a common and widespread weed in North America. This study was conducted to determine the influence of several environmental factors on its seed germination and seedling emergence from three North American populations in autumn. In alternating light (12 h)/darkness (12 h), maximum germination (89.7% to 97.7%) of freshly matured seeds occurred at alternating temperature regimes ≥25/15 C, and germination was lowest (0% to 80.3%) at the coolest temperature regime of 15/5 C. In comparison to seeds incubated with an alternating light/dark photoperiod, germination was lower when seeds were exposed to continuous darkness, indicating that seeds were positively photoblastic. Cold stratification at 4 C enhanced germination, with seed dormancy alleviated after 4 to 8 wk, depending on the study population. For freshly matured seeds, germination exceeded 67% in test solutions ranging from pH 3 to 10, and was highest (80% to 100%) at neutral or near-neutral pH. Germination exceeded 84% in solutions with osmotic potentials ranging from 0 to −0.4 MPa, and germination was observed at osmotic potentials as low as −0.8 to −1.0 MPa, depending on the study population. Seedling emergence was only observed for seeds sown on the surface of soil or buried to depths ≤2 cm. Thus, seeds of *O. biennis* are positively photoblastic and exhibit germination characteristics associated with type 2 non–deep physiological dormancy at maturity, with seeds being capable of germinating under a variety of climatic and edaphic conditions.

## Introduction

Common evening primrose (*Oenothera biennis* L.), also known as yellow evening primrose, is a herbaceous biennial species in the evening primrose family (Onagraceae). The Onagraceae comprises 22 genera and approximately 650 species, most of which occur in temperate and subtropical regions of the world (Wagner et al. 2007). The genus *Oenothera* is one of the major genera of Onagraceae, accounting for 145 species (Wagner et al. 2007). Various species of *Oenothera* have served as model organisms for studying cytoplasmic genetics and plant evolutionary biology since the early 1900s, and many have also been cultivated as oil seed crops and medicinal plants (Greiner and Kohl 2014).

*Oenothera biennis* is native to North America, being widely distributed throughout southern Canada and across most of the continental United States, but less common or absent in the southwestern states (USDA-NRCS 2025). It also has become well established as an introduced species throughout most of Europe and is present in South America, Africa, and Asia, being particularly common in South Africa, Japan, and South Korea. In its native geographic range, *O. biennis* is a common weed of habitats with full sun exposure, such as roadsides and railroads, pastures, hayfields, slopes of drainage ditches, vacant lots, and waste areas (Bryson and DeFelice 2010; Frankton and Mulligan 1970; Hall et al. 1988; Steckel et al. 2019; Voss and Reznicek 2012). In Ontario, Canada, it occurs as a troublesome pest species in winter wheat (*Triticum aestivum* L.) and fall rye (*Secale cereale* L.) fields (Alex and Switzer 1976), and it is considered a weed in vineyards and fruit crops in Europe (Hanf 1983). It also is an early invader of new forest plantations (Miller and Miller 1999). On the other hand, in some regions, including China in particular, *O. biennis* is cultivated as a medicinal plant for its seed oil, which contains very high levels of the polyunsaturated essential fatty acids, linoleic acid (>70%) and γ-linolenic acid (about 9%) (Deng et al. 2001; Timoszuk et al. 2018). These fatty acids are precursors of compounds that yield anti-inflammatory chemicals like eicosanoids that contribute to proper functioning of many human tissues and have been used to treat medical conditions, such as eczema, cancer, multiple sclerosis, and rheumatoid arthritis (Deng et al. 2001).

*Oenothera biennis* exists as a leafy rosette during its first year of growth. In the midwestern United States, second-year plants bolt in late spring to produce either an erect, unbranched stem

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(up to 1.5 m in height) or a stem with few branches bearing bright yellow, four-petalled flowers (Voss and Reznicek 2012). Its flowers are insect pollinated and facultative self-pollinated (Hall et al. 1988). The resulting fruits are 1- to 4-cm-long capsules that dehisce at maturity in late autumn, but the brown 1- to 2-mm-diameter seeds may persist on the plant throughout the winter months (Radford et al. 1968). The number of seeds produced per plant ranges from 5,000 to 118,500 seeds (Hall et al. 1988).

Most reports on the germination requirements for *Oenothera* congeners have focused on the fact that the seeds of many of these species are either light sensitive or possess a light requirement for germination (Kachi 1990; Mihulka et al. 2003; Steiner 1968; Walck and Hidayati 2007). A positive photoblastic response has been reported, too, for germination of *O. biennis* seeds (Andersen 1968; Gross 1985). Studies of how other environmental conditions, such as temperature, pH, osmotic stress, and burial depth, affect germination of *O. biennis* either do not exist or, if available, only consider such factors for a single study population rather than evaluating how they differ in impact among populations (Baskin and Baskin 1994; Mircea et al. 2023). To help understand the broad distribution of *O. biennis* in North America and its introduction and expansion (and potential future spread) in most of Europe and parts of Africa, Asia, and South America, we need to know how its seeds respond to varied edaphic and climatic conditions, all of which may influence seed dormancy states and seed germination timing and success (Baskin and Baskin 2014). Thus, the objectives of this study were to determine the effects of temperature, light, cold stratification, pH, osmotic stress, and depth of burial in soil on the germination/emergence of *O. biennis* seeds/seedlings from several populations across a portion of its native range in North America.

## Materials and Methods

### General Seed Germination Protocols

Seeds of *O. biennis* were collected on November 5 and 6, 2024, from three populations located in (1) a field at the edge of an upland woodland in Malden Park (MP) in Windsor, ON, Canada (42.274° N, 83.062°W); (2) an old field in E. Milo Beck Park (BP), Springboro, OH, USA (39.544°N, 83.258°W); and (3) an old field in Berea (BE), KY, USA (37.563°N, 84.292°W). These populations were chosen with the assumption that differences in selective pressures across a north–south distance of about 540 km would influence the maternal environment during seed development and potentially the dormancy and germination ecology of *O. biennis*. All fruits situated on plants were bulk harvested from 19, 10, and 12 individuals from MP, BP, and BE, respectively. Seeds were separated from fruits and stored in paper envelopes at room temperature (22 C) for 1 wk before the start of experiments. Each experiment was repeated for a total of two trials. For all germination experiments, a single replication consisted of 50 seeds placed on a single sheet of Whatman no. 1 filter paper (Fisher Scientific, Waltham, MA, USA) in a 9-cm-diameter petri dish. Treatments in each trial were replicated three times. Each dish was initially moistened with 4 ml of distilled water or test solution, with a few additional milliliters of water or given solution added as needed to maintain adequate moisture throughout the study period. To minimize desiccation, each dish was sealed with Parafilm® (Fisher Scientific, Waltham, MA, USA). Germination experiments were performed inside environmentally controlled growth chambers. Alternating thermoperiods (daytime high temperature/nighttime low temperature) coincided with a photoperiod of 12-h light/12-h darkness (hereafter light). The growth chamber's fluorescent lighting produced a photosynthetic photon flux of 100 μmol $m^{-2}$ $s^{-1}$. Any dishes assigned to treatments with continuous darkness were wrapped in two layers of aluminum foil. Germination was examined daily over 21 d, except for dark-incubated seeds, which were assessed for germination only on day 21. The criterion for germination was the emergence of the radicle from the seed coat.

### Effects of Temperature and Light

To assess the effects of temperature and light on germination of seeds of *O. biennis* for each study population, freshly matured seeds were placed in petri dishes moistened with distilled water and then incubated in environmental chambers in light at five alternating temperature regimes (15/5, 20/10, 25/15, 30/20, or 35/25 C). Six replicates of 50 seeds were assigned to each of the five chambers, for a total of 30 replicates per population. Three of the six replicates were maintained in continuous darkness by wrapping them in aluminum foil.

### Effect of Moist Cold Stratification

To assess the influence of cold stratification on germination, freshly matured seeds from each population of *O. biennis* were placed in petri dishes with filter paper moistened with distilled water and refrigerated at 4 C. Fifteen replicates, each containing 50 seeds, were assigned to one of four cold stratification periods (0, 4, 8, or 12 wk), for a total of 60 replicates per population. Upon conclusion of a respective chilling period, the 15 replicates were then incubated in light at 15/5, 20/10, 25/15, 30/20, or 35/25 C, as described earlier. Three replicates were assigned to each of the five incubation temperature regimes.

### Effect of pH

To assess the influence of solution pH on germination of freshly matured *O. biennis* seeds from each study population, eight test solutions were prepared with pH values of 3, 4, 5, 6, 7, 8, 9, or 10. To prepare solutions with pH levels of 3, 4, 5, or 6, 0.1 M potassium hydrogen phthalate was used, whereas 25 mM borax was used to prepare solutions with pH levels of 7, 8, 9, or 10 (Shaw et al. 1991). If necessary, 1.0 M HCl or 0.5 M NaOH was used to adjust the buffer solutions to the appropriate pH. For each treatment, petri dishes containing 50 seeds were moistened with a respective pH solution and then incubated in light at 25/15 C. Three replicates were assigned to each of the eight pH treatments, for a total of 24 replicates per population.

### Effect of Osmotic Stress

To investigate the influence of osmotic stress on germination of freshly matured *O. biennis* seeds from each study population, seven test solutions with osmotic potentials of 0 (control), −0.2, −0.4, −0.6, −0.8, −1.0, or −1.2 MPa were prepared by dissolving appropriate amounts of polyethylene glycol (PEG 8000) in 1 L of distilled water according to the equations of Michel (1983). For each treatment, petri dishes containing 50 seeds were moistened with a respective solution and then incubated in light at 25/15 C. Three replicates were assigned to each osmotic stress treatment, for a total of 21 replicates per population.

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**Table 1.** Mean (± SE) germination percentages for seeds of *Oenothera biennis* from three populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at five temperature regimes (15/5, 20/10, 25/15, 30/20, or 35/25 C for 12 h/12 h) with two coinciding light regimes (L/D, alternating 12-h light/12-h darkness; D, 24-h darkness) for 21 d.

| | Germination[a] | | | | | |
|---|---|---|---|---|---|---|
| Temperature regime | MP L/D | MP D | BP L/D | BP D | BE L/D | BE D |
| C | % | | | | | |
| 15/5 | 0Aa$_A$ | 0Aa$_A$ | 36.0 ± 9.9Ab$_B$ | 2.3 ± 0.6Aa$_A$ | 80.3 ± 2.3Ab$_C$ | 10.7 ± 1.7Aa$_B$ |
| 20/10 | 71.7 ± 4.7Bb$_A$ | 22.3 ± 1.1Ba$_A$ | 77.0 ± 1.9Bb$_A$ | 42.7 ± 1.2Ba$_B$ | 91.7 ± 1.4Bb$_B$ | 61.7 ± 1.2Ba$_C$ |
| 25/15 | 94.7 ± 1.8Cb$_A$ | 77.0 ± 1.1Ca$_B$ | 89.7 ± 1.5Cb$_B$ | 69.3 ± 1.4Ca$_A$ | 94.7 ± 0.4BCb$_A$ | 73.7 ± 4.3BCa$_{AB}$ |
| 30/20 | 97.7 ± 0.8Cb$_B$ | 77.3 ± 2.1Ca$_A$ | 93.0 ± 1.8Cb$_A$ | 76.7 ± 2.7CDa$_A$ | 95.3 ± 0.4BCa$_A$ | 78.7 ± 1.2Ca$_A$ |
| 35/25 | 97.0 ± 1.4Cb$_B$ | 90.0 ± 2.0Da$_B$ | 90.0 ± 2.1Cb$_A$ | 79.3 ± 1.7Da$_A$ | 95.7 ± 1.0Ca$_B$ | 89.3 ± 2.4Da$_B$ |

[a]Values followed by different uppercase letters within a column differ significantly among temperature regimes for a given light regime for a respective population. Values followed by different lowercase letters differ significantly among light regimes for a given temperature regime within a respective population. Values followed by different small capital letters differ significantly among populations for a given light regime for a respective temperature regime. Values are significantly different according to Tukey's multiple comparison tests at $P < 0.05$.

### Effect of Planting Depth

To evaluate the influence of depth of seed burial on the emergence of seedlings of *O. biennis* for each study population, freshly matured seeds were buried in plastic pots (8.3 cm by 8.3 cm by 7.3 cm) to six depths below the soil surface: 0, 0.5, 1, 2, 4, or 6 cm. Three pots containing 50 seeds each were assigned to each burial treatment, resulting in a total of 18 pots per population. The soil used for this experiment was a standard, general purpose Pro-Mix® BX potting soil (BFG Supply, Grand Rapids, MI, USA). Pots were placed in a completely randomized design in a growth chamber maintained at 25/15 C with a coinciding photoperiod of 12-h light/12-h darkness. Pots were initially subirrigated, and then subsequently surface irrigated to field capacity and rearranged daily within the growth chamber. Seedling emergence was recorded daily for a period of 30 d.

### Statistical Analyses

All germination experiments were conducted in a randomized complete block design with three replications. Each replication was positioned on a different shelf and considered a block. All experiments were repeated (i.e., two trials). The generalized linear model procedure of the statistical software application Systat v. 13 (Inpixon, Palo Alto, CA, USA) was used to assess significant differences among trials and treatments. We found no significant trial by treatment interactions in any experiment, so data from the two trials were pooled. Mean (±SE) cumulative percentage germination values are reported herein. Cumulative percentage germination values were arcsine square-root transformed to improve homogeneity of variance before analyses. Initial, full models involving three-way ANOVAs were used to assess for (1) the effects of temperature regime, light regime, and study population; and (2) the effects of temperature regime, cold stratification period, and study population on percentage germination of *O. biennis* seeds. Because both models revealed significant three-way interactions, all two-way interactions between pairs of variables were assessed in follow-up analyses. If a two-way interaction was significant, simple main effects were then assessed. Tukey's honest significant difference tests were used to compare treatment means when ANOVAs indicated significant simple main effects.

Nonlinear regression analyses were performed in Systat v. 13 to determine the effect of solution pH and osmotic potential on seed germination, and the effect of burial depth on seedling emergence.

Germination percentages at different pH values were best fit to the quadratic regression:

$$G = ax^2 + bx + c \quad (1)$$

where $G$ represents percentage germination at pH $x$, and $a$, $b$, and $c$ represent the quadratic, the linear, and the constant coefficients, respectively.

Germination percentages at different osmotic potentials were best fit to the three-parameter sigmoid model:

$$G = G_{max}/[1 + \exp(x - x_{50})/b] \quad (2)$$

where $G$ represents percentage germination at osmotic potential $x$, $G_{max}$ represents maximum germination percentage, $x_{50}$ is the osmotic potential required for 50% inhibition of maximum germination, and $b$ represents the slope.

Seedling emergence percentages at different burial depths were best fit to the exponential decay model:

$$E = E_{max} \times \exp(-b \times x) \quad (3)$$

where $E$ represents percentage seedling emergence at burial depth $x$, $E_{max}$ represents maximum seedling emergence, and $b$ represents the slope.

The number of days to 80% germination ($t_{80}$) at different temperature regimes was calculated as: $t_{80} = (H_p - L_p)^{-1} + L$, where $L$ represents the day before 80% germination is reached, $L_p$ is the germination percentage on day $L$, and $H_p$ is the germination percentage when 80% germination is reached on day $L + 1$ (Li et al. 2012).

## Results and Discussion

### Effects of Temperature and Light

A full three-way factorial ANOVA of the effects of population, temperature, and light on germination percentages of *O. biennis* revealed a significant three-way interaction ($F(8, 150) = 15.891$, $P < 0.001$). Germination percentages and follow-up two-way factorial ANOVAs of how these values were affected by (1) temperature and light for each population, (2) population and light for each temperature regime, and (3) population and temperature for each light regime are shown in Tables 1 and 2. Overall, across study populations, seed germination of *O. biennis* increased as incubation temperatures increased for both light regimes, with the highest mean germination percentages (ranging from 89.7% to 97.7%) observed in light at the three warmest temperature regimes (25/15, 30/20, 35/25 C). Germination was lower at the two coldest

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**Table 2.** Results of two-way factorial ANOVAs on germination percentages for seeds of *Oenothera biennis* involving three populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at five temperature regimes (15/5, 20/10, 25/15, 30/20, or 35/25 C for 12 h/12 h) with two coinciding light regimes (L/D, alternating 12-h light/12-h darkness; D, 24-h darkness) for 21 d.

| Moderator variable | Source of variation | df | *F*-statistic | P-value |
|---|---|---|---|---|
| MP population | Temperature | 4 | 627.0 | <0.001 |
| | Light | 1 | 215.2 | <0.001 |
| | Temperature × light | 4 | 20.2 | <0.001 |
| | Error | 50 | | |
| BP population | Temperature | 4 | 90.2 | <0.001 |
| | Light | 1 | 86.1 | <0.001 |
| | Temperature × light | 4 | 8.2 | <0.001 |
| | Error | 50 | | |
| BE population | Temperature | 4 | 90.8 | <0.001 |
| | Light | 1 | 268.4 | <0.001 |
| | Temperature × light | 4 | 29.4 | <0.001 |
| | Error | 50 | | |
| 15/5 C temperature regime | Population | 2 | 73.4 | <0.001 |
| | Light | 1 | 93.9 | <0.001 |
| | Population × light | 2 | 25.3 | <0.001 |
| | Error | 30 | | |
| 20/10 C temperature regime | Population | 2 | 34.5 | <0.001 |
| | Light | 1 | 222.0 | <0.001 |
| | Population × light | 2 | 4.0 | 0.030 |
| | Error | 30 | | |
| 25/15 C temperature regime | Population | 2 | 10.7 | <0.001 |
| | Light | 1 | 154.7 | <0.001 |
| | Population × light | 2 | 2.2 | 0.134 |
| | Error | 30 | | |
| 30/20 C temperature regime | Population | 2 | 3.1 | 0.060 |
| | Light | 1 | 131.7 | <0.001 |
| | Population × light | 2 | 5.1 | 0.013 |
| | Error | 30 | | |
| 35/25 C temperature regime | Population | 2 | 29.1 | <0.001 |
| | Light | 1 | 17.9 | <0.001 |
| | Population × light | 2 | 3.8 | 0.033 |
| | Error | 30 | | |
| L/D light regime | Population | 2 | 34.3 | <0.001 |
| | Temperature | 4 | 158.9 | <0.001 |
| | Population × temperature | 8 | 39.7 | <0.001 |
| | Error | 75 | | |
| D light regime | Population | 2 | 23.8 | <0.001 |
| | Temperature | 4 | 488.4 | <0.001 |
| | Population × temperature | 8 | 9.7 | <0.001 |
| | Error | 75 | | |

temperature regimes, ranging from 0% to 80.3% at 15/5 C and from 71.7% to 91.7% at 20/10 C. In general, in comparison with seeds exposed to light, germination percentages for the study populations were lower when seeds were kept in continuous darkness. Differences in seed germination were most pronounced between light and dark at 15/5 and 20/10 C, but the differences in germination narrowed with warmer incubation temperatures. No germination was observed at 15/5 C regardless of light regime in the MP population. In each population, the time to the onset of germination and the time to 80% germination decreased as incubation temperatures increased (Table 3). Similarly, low-temperature treatments extended the germination period for the grasses Tausch's goatgrass (*Aegilops tauschii* Coss.) (Wang et al. 2020) and Japanese brome (*Bromus japonicus* Thunb. ex Murr.; syn.: *Bromus arvensis* L.) (Li et al. 2015), which suggests a relationship between germination period and heat accumulation (i.e., growing degree days) in the field.

Based on these results, seeds of *O. biennis* possess non–deep physiological dormancy at maturity. Species with this kind of seed dormancy have seeds that are conditionally dormant at maturity, that is, they germinate readily at high temperatures, but exhibit lower germination or are incapable of germination at cool temperatures (Baskin and Baskin 2014). This finding confirms an earlier assessment of the species' type of seed dormancy first reported by Baskin and Baskin (1994). When exposed to an alternating light/dark photoperiod, freshly matured seeds in their study exhibited primary conditional dormancy, being unable to germinate whatsoever at the coolest temperature regime (15/5 C), but they germinated well at warmer temperature conditions (≥20/10 C). We found similar results for germination of *O. biennis* seeds from the MP population in our study. Under natural conditions outdoors, this means that seeds produced in the autumn are unlikely to germinate until the onset of warmer temperatures during the following spring. Interestingly, percentage germination, time to onset of germination, and time to 80% germination all varied among incubation temperatures for the three North American populations of *O. biennis* in our study. Such intraspecific variability reflects differences in interactions between maternal genotypes and local environmental conditions during seed maturation. Several studies have reported that populations of a given species situated in different locales have different temperature requirements for germination, as well as different degrees of seed dormancy (Bürger et al. 2020; Loddo et al. 2013; Tozzi et al. 2014; Wang et al. 2020). Such intraspecific variability in thermal

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**Table 3.** The time to onset of germination and time to reach 80% germination ($t_{80}$) in seeds of *Oenothera biennis* from three study populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when treated to five different temperature regimes in an alternating photoperiod (12-h light/12-h dark)[a].

| | Time to onset of germination | | | $t_{80}$ | | |
|---|---|---|---|---|---|---|
| Temperature regime | MP | BP | BE | MP | BP | BE |
| C | d | | | | | |
| 15/5 | NE | 5.0 ± 0 | 6.0 ± 0 | NE | NE | 12.9 ± 1.5d |
| 20/10 | 4.0 ± 0 | 4.0 ± 0 | 4.0 ± 0 | NE | NE | 7.1 ± 2.0c |
| 25/15 | 3.0 ± 0 | 2.0 ± 0 | 2.0 ± 0 | 2.0 ± 0 | 5.2 ± 3.2 | 2.0 ± 0b |
| 30/20 | 2.0 ± 0 | 2.0 ± 0 | 2.0 ± 0 | 2.0 ± 0 | 2.0 ± 0 | 1.4 ± 0.4a |
| 35/25 | 1.0 ± 0 | 1.0 ± 0 | 1.0 ± 0 | 1.0 ± 0 | 2.1 | 1.0 ± 0a |

[a]NE (not estimated) represents instances where germination did not occur at all, or where germination values did not reach 80%. Values among temperature regimes within a column followed by different lowercase letters are significantly different according to Tukey's multiple comparison tests at $P < 0.05$.

requirements likely contributes to the successful adaptation of weeds such as *O. biennis* to new regions.

Baskin and Baskin (1994) demonstrated that *O. biennis* seeds experience annual seed dormancy cycles. When they exhumed buried seeds at monthly intervals over a 31-mo period of time and germinated them at five temperature regimes in light or darkness, they determined that seeds were conditionally dormant in summer and autumn, but became nondormant from midwinter to late spring before re-entering dormancy to repeat the seasonal changes in dormancy state. *Oenothera biennis* is one of several species, including two *Verbascum* species, common mullein (*Verbascum thapsus* L.) and moth mullein (*Verbascum blattaria* L.) (Baskin and Baskin 1981), that exhibit similar annual seed dormancy cycles. Interestingly, seed viability testing in Dr. Beal's long-running seed longevity experiment has revealed that seeds of these three species remained viable for a minimum of 80 yr when buried in soil in Michigan, USA (Telewski and Zeevaart 2002). Hence, species with annual dormancy cycles like that reported for *O. biennis* may form persistent, very long-lived seedbanks, contributing to their weediness/invasiveness.

Seeds of *O. biennis* exhibited much higher germination in the presence of light than when exposed to continuous darkness regardless of incubation temperatures. Hence, seeds of *O. biennis* clearly displayed a positive photoblastic response. This response to light has been well established in previous reports of seed germination for this species (Andersen 1968; Baskin and Baskin 1994; Ensminger and Ikuma 1987; Gross 1985). In general, the likelihood of a light requirement or positive photoblastism is much higher in species with small seeds than in those with large seeds (Grime et al. 1981; Mahajan et al. 2018; Milberg et al. 2000; Pearson et al. 2002, 2003; Rojas-Aréchiga and Vázquez-Yanes 2000; Vázquez-Yanes and Orozco-Segovia 1993). In particular, Fenner and Thompson (2005) argued that species with seeds weighing less than 2 mg germinated to higher percentages in light than in darkness as opposed to species that do not differ in germination with respect to light versus dark.

In a comparison of seed germination in light versus darkness for 15 non-native *Oenothera* congeners in Europe, Mihulka et al. (2003) reported that 12 of the 15 species had higher germination in light than in dark, whereas only three species had higher germination in darkness than in light. Interestingly, all 12 of the light-germinating species had reported average individual seed mass less than 2 mg (ranging from 0.064 to 0.622 mg), whereas seeds of two of the three dark-germinating *Oenothera* species (tufted evening primrose (*Oenothera caespitosa* Gillies ex Hook. & Arn.) and Missouri evening primrose (*Oenothera macrocarpa* Nutall ssp. *macrocarpa*; syn.: *Oenothera missouriensis* Sims) had average seed mass of 3.805 mg and 20.985 mg, respectively. The sizes (mean ± SE) of the photoblastic seeds of *O. biennis* from our study populations were small (MP: 0.305 ± 0.014 mg, $N = 50$; BP: 0.398 ± 0.015 mg, $N = 50$; BE: 0.270 ± 0.012 mg, $N = 50$) and fell within the range of other positively photoblastic *Oenothera* species (Mihulka et al. 2003). The combination of annual dormancy cycles and a light requirement for seed germination in *O. biennis* contributes to its high seed longevity in a persistent seedbank, thereby potentially spreading germination and establishment over long periods of time.

### Effect of Moist Cold Stratification

A full three-way factorial ANOVA of the effects of population, temperature, and cold stratification on germination percentages of *O. biennis* revealed a significant three-way interaction ($F(24, 300) = 14.610$, $P < 0.001$). Germination percentages and follow-up two-way factorial ANOVAs of how these values were affected by (1) temperature and cold stratification for each population, (2) population and temperature for each cold stratification duration, and (3) population and cold stratification for each temperature regime are shown in Tables 4 and 5. Cold stratification had no effect on the germination of seeds from the BE population, whereas cold exposure enhanced germination of seeds of *O. biennis* from the MP and BP populations, but the magnitude of the effect varied with respect to the duration of chilling and incubation temperature. For the MP and BP populations, seeds incubated at the two lowest temperature regimes (15/5 or 20/10 C) germinated to higher percentages with increased durations of cold stratification, and eventually their germination percentages peaked after 8 wk or 4 wk of chilling, respectively, to similar levels compared with those for the three warmest temperature regimes (≥25/15 C). Seeds from all three study populations incubated at the three warmest temperature regimes germinated to similar, high percentages whether or not they were cold stratified. After 8 wk of cold stratification, germination of seeds incubated at all five temperature regimes was similar (≥ 90%).

Similar germination responses have been observed in other species that set their seeds in late summer/autumn and, according to the Nikolaeva-Baskin classification system (Baskin and Baskin 2021), possess a particular type of seed dormancy known as type 2 non–deep physiological dormancy (An et al. 2022; Hawkins 2019; Peng et al. 2023; Porceddu et al. 2013; Susko 2025; Susko and Hussein 2008; Walck and Hidayati 2007). The seeds of these species were conditionally dormant at maturity in autumn because they could only germinate at high temperatures (which were unavailable at that time of year). Following cold stratification, seeds became nondormant and exhibited a decrease in the minimum

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**Table 4.** Mean (± SE) germination percentages for seeds of *Oenothera biennis* from three populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at five temperature regimes (15/5, 20/10, 25/15, 30/20, or 35/25 C for 12 h/12 h) in an alternating photoperiod (12-h light/12-h dark) for 21 d following four periods of cold stratification at 4 C in darkness (0, 4, 8, or 12 wk).

| Population | Cold duration | Temperature regime | | | | |
|---|---|---|---|---|---|---|
| | | 15/5 | 20/10 | 25/15 | 30/20 | 35/25 |
| | wk | Germination (%) | | | | |
| MP | 0 | 0Aa$_A$ | 81.3 + 4.6Ba$_A$ | 100Ca$_C$ | 97.3 + 0.8Ca$_B$ | 98.3 + 0.3Ca$_B$ |
| | 4 | 36.7 + 2.8Aa$_A$ | 98.0 + 1.0Bb$_B$ | 100Ba$_B$ | 100Ba$_B$ | 98.3 + 1.0Ba$_B$ |
| | 8 | 96.7 + 0.8Ab$_B$ | 98.0 + 1.0Ab$_B$ | 97.7 + 1.0Aa$_B$ | 99.3 + 0.4Aa$_B$ | 96.3 + 1.0Aa$_A$ |
| | 12 | 96.0 + 1.2Ab$_B$ | 97.0 + 1.1Ab$_A$ | 98.7 + 0.4Aa$_B$ | 99.3 + 0.4Aa$_B$ | 96.7 + 0.8Aa$_A$ |
| BP | 0 | 16.7 + 3.7Aa$_B$ | 80.7 + 1.8Ba$_A$ | 87.3 + 0.8BCa$_A$ | 93.3 + 0.8CDa$_A$ | 95.3 + 0.8Da$_A$ |
| | 4 | 73.3 + 0.4Ab$_B$ | 90.0 + 3.8Bb$_A$ | 94.7 + 1.7Bb$_A$ | 90.0 + 3.3Ba$_A$ | 94.7 + 1.3Ba$_{AB}$ |
| | 8 | 90.0 + 0.7Ac$_A$ | 89.7 + 1.5Ab$_A$ | 89.7 + 1.7Aa$_A$ | 91.0 + 1.3ABa$_A$ | 95.7 + 1.3Ba$_A$ |
| | 12 | 88.3 + 2.7Ac$_A$ | 92.0 + 2.1Ab$_A$ | 92.0 + 2.2Aab$_A$ | 92.0 + 1.5Aa$_A$ | 94.7 + 1.3Aa$_A$ |
| BE | 0 | 88.0 + 2.4Aa$_C$ | 94.7 + 1.5Aa$_B$ | 96.7 + 0.8Aa$_B$ | 94.7 + 0.4Aa$_{AB}$ | 95.3 + 0.8Aa$_A$ |
| | 4 | 96.0 + 1.3Aa$_C$ | 96.7 + 1.2Aa$_{AB}$ | 95.3 + 1.1Aa$_A$ | 97.0 + 1.3Aa$_{AB}$ | 91.3 + 2.3Aa$_A$ |
| | 8 | 95.3 + 0.4Aa$_B$ | 93.7 + 2.6Aa$_{AB}$ | 94.3 + 2.3Aa$_{AB}$ | 95.7 + 1.8Aa$_B$ | 94.3 + 1.9Aa$_A$ |
| | 12 | 95.5 + 1.1Aa$_B$ | 94.7 + 1.1Aa$_A$ | 95.3 + 1.1Aa$_{AB}$ | 95.3 + 1.1Aa$_A$ | 95.7 + 1.0Aa$_A$ |

[a]Values followed by different uppercase letters within a row differ significantly among temperature regimes for a given cold-stratification duration for a respective population. Values followed by different lowercase letters differ significantly among cold-stratification durations for a given temperature regime within a respective population. Values followed by different small capital letters differ significantly among populations for a given cold-stratification duration for a respective temperature regime. Values are significantly different according to Tukey's multiple comparison tests at $P < 0.05$.

temperature at which they could germinate. Likewise, we demonstrated that *O. biennis* seed gemination was enhanced by longer durations of cold exposure, particularly for seeds exposed to subsequent cooler incubation temperature regimes.

### Effect of pH

Quadratic regressions best described the relationship between percentage germination of seeds of *O. biennis* and solution pH for populations MP ($G = -0.806x^2 + 10.448x + 65.433$; $R^2 = 0.99$), BP ($G = -1.778x^2 + 22.579x + 19.845$; $R^2 = 0.99$), and BE ($G = -0.933x^2 + 12.163x + 56.045$; $R^2 = 0.99$) (Figure 1). Overall, germination occurred readily and was high over a wide range of solution pH (3 to 10) for populations MP (ranging from 90% to 100%), BP (ranging from 67% to 92%), and BE (ranging from 83% to 96%). For all populations, optimal germination was observed for seeds treated with solutions having neutral or near-neutral pH. Furthermore, germination decreased as solution pH became either more acidic or more alkaline, with germination percentages being lowest at each of the pH extremes (pH = 3 or pH = 10). Germination over a broad range of pH conditions has been reported for many weedy species, with some species, like texasweed [*Caperonia palustris* (L.) A. St.-Hil.] (Koger et al. 2004), American sloughgrass [*Beckmannia syzigachne* (Steud.) Fernald] (Rao et al. 2008), buffalobur nightshade (*Solanum rostratum* Dunal) (Wei et al. 2009), and Asia Minor bluegrass (*Polypogon fugax* Nees ex Steud.) (Wu et al. 2015) germinating about equally well across different pHs, whereas other species, including turnipweed [*Rapistrum rugosum* (L.) All.] (Chauhan et al. 2006), dame's rocket (*Hesperis matronalis* L.) (Susko and Hussein 2008), *B. syzigachne* (Rao et al. 2008), cadillo (*Urena lobata* L.) (Wang et al. 2009), redflower ragleaf [*Crassocephalum crepidioides* (Benth.) S. Moore] (Nakamura and Hossain 2009), feather fingergrass (*Chloris virgata* Sw.) (Fernando et al. 2016), African turnipweed (*Sisymbrium thellungii* O. E. Schulz) (Mahajan et al. 2018), and *O. biennis* exhibit a parabolic response to pH; that is, the highest germination percentage occurs at or near neutral pH, and germination is reduced at more acidic or alkaline conditions. Because *O. biennis* seeds can germinate across a wide spectrum of soil acidities/alkalinities, soil pH is unlikely to be a limiting factor for germination in most soil types.

### Effect of Osmotic Stress

Three-parameter sigmoid models best described the relationship between the germination of seeds of *O. biennis* and water stress for populations MP ($G = 99/\{1 + \exp[-(x - 0.567)/0.074]\}$; $R^2 = 0.98$), BP ($G = 96/\{1 + \exp[-(x - 0.768)/0.087]\}$; $R^2 = 0.98$), and BE ($G = 96.7/\{1 + \exp[-(x-0.746)/0.098]\}$; $R^2 = 0.96$) (Figure 2). For each study population, germination was characterized by a decreasing sigmoidal curve with germination being highest in distilled water (ranging from 96% to 99%), but it remained high at osmotic stress levels between −0.2 to −0.4 MPa (ranging from 89% to 98%). Germination exceeded 37% for MP at −0.6 MPa and BP and BE at −0.8 MPa. Seeds germinated at osmotic stress levels as low as −0.8 MPa for MP (3%), and −1.0 MPa for BP (2%) and BE (3%), respectively, and no germination occurred at −1.2 MPa for seeds from any population. Previously reported seed germination responses to water stress appear to be quite variable. Some species are very sensitive to osmotic stress. Seeds of species such as redvine [*Brunnichia ovata* (Walter) Shinners] (Shaw et al. 1991), trumpetcreeper [*Campsis radicans* (L.) Seem. ex Bureau] (Chachalis and Reddy 2000), and *U. lobata* (Wang et al. 2009) failed to germinate at osmotic potentials below −0.25 MPa. Such species with a limited tolerance to water stress require moist soil conditions for germination. On the contrary, seeds of other species, such as *R. rugosum* (Chauhan et al. 2006), Venice mallow (*Hibiscus trionum* L.) (Chachalis et al. 2008), *S. rostratum* (Wei et al. 2009), and sand hornwort (*Ceratocarpus arenarius* L.) (Ebrahimi and Eslami 2011) are quite tolerant to osmotic stress and can germinate at very low osmotic potentials (−1.0 MPa or below). These species often occupy drier habitats with well-drained soils. Mircea et al. (2023) found that germination of *O. biennis* from a single European population exceeded 80% when seeds were sown under water-stressed conditions at osmotic potentials ranging from −0.25 to −0.75 MPa. Similarly, our study demonstrated that *O. biennis* seeds can germinate well under moderately water-stressed conditions, suggesting that seeds should be able to germinate in a fairly wide range of soil conditions, from

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**Table 5.** Results of two-way factorial ANOVAs on germination percentages for seeds of *Oenothera biennis* involving three populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at five temperature regimes (15/5, 20/10, 25/15, 30/20, or 35/25 C for 12 h/12 h) in an alternating photoperiod (12-h light/12-h dark) for 21 d following four periods of cold stratification at 4 C in darkness (0, 4, 8, or 12 wk).

| Moderator variable | Source of variation | df | *F*-statistic | P-value |
|---|---|---|---|---|
| MP population | Temperature | 4 | 242.657 | <0.001 |
| | Cold stratification | 3 | 94.398 | <0.001 |
| | Temperature × cold stratification | 12 | 73.178 | <0.001 |
| | Error | 100 | | |
| BP population | Temperature | 4 | 51.263 | <0.001 |
| | Cold stratification | 3 | 30.010 | <0.001 |
| | Temperature × cold stratification | 12 | 16.910 | <0.001 |
| | Error | 100 | | |
| BE population | Temperature | 4 | 1.234 | 0.301 |
| | Cold stratification | 3 | 1.125 | 0.343 |
| | Temperature × cold stratification | 12 | 1.403 | 0.177 |
| | Error | 100 | | |
| 15/5 C temperature regime | Population | 2 | 270.609 | <0.001 |
| | Cold stratification | 3 | 465.173 | <0.001 |
| | Population × cold stratification | 6 | 111.127 | <0.001 |
| | Error | 60 | | |
| 20/10 C temperature regime | Population | 2 | 11.287 | <0.001 |
| | Cold stratification | 3 | 9.756 | <0.001 |
| | Population × cold stratification | 6 | 2.884 | 0.016 |
| | Error | 60 | | |
| 25/15 C temperature regime | Population | 2 | 42.457 | <0.001 |
| | Cold stratification | 3 | 2.525 | 0.066 |
| | Population × cold stratification | 6 | 2.517 | 0.031 |
| | Error | 60 | | |
| 30/20 C temperature regime | Population | 2 | 31.830 | <0.001 |
| | Cold stratification | 3 | 1.869 | 0.144 |
| | Population × cold stratification | 6 | 0.780 | 0.589 |
| | Error | 60 | | |
| 35/25 C temperature regime | Population | 2 | 5.876 | 0.005 |
| | Cold stratification | 3 | 0.073 | 0.974 |
| | Population × cold stratification | 6 | 1.145 | 0.348 |
| | Error | 60 | | |
| 0-wk cold stratification | Population | 2 | 96.346 | <0.001 |
| | Temperature | 4 | 412.895 | <0.001 |
| | Population × temperature | 8 | 92.732 | <0.001 |
| | Error | 75 | | |
| 4-wk cold stratification | Population | 2 | 7.746 | 0.001 |
| | Temperature | 4 | 48.795 | <0.001 |
| | Population × temperature | 8 | 22.208 | <0.001 |
| | Error | 75 | | |
| 8-wk cold stratification | Population | 2 | 21.535 | <0.001 |
| | Temperature | 4 | 1.060 | 0.382 |
| | Population × temperature | 8 | 1.558 | 0.152 |
| | Error | 75 | | |
| 12-wk cold stratification | Population | 2 | 19.450 | <0.001 |
| | Temperature | 4 | 1.336 | 0.264 |
| | Population × temperature | 8 | 1.205 | 0.308 |
| | Error | 75 | | |

moist, poorly drained soils to moderately dry soils. Asghari (2019) and Sharma (2022) have demonstrated that mature plants are, at a minimum, tolerant of mild to moderate water stress and salinity stress.

### *Effect of Planting Depth*

Exponential decay models best described the relationship between seedling emergence and depth of seed burial in soil for populations MP ($E = 46.3*\exp(-8.48x)$; $R^2 = 0.98$), BP ($E = 53.9*\exp(-2.97x)$; $R^2 = 0.98$), and BE ($E = 73.0*\exp(-1.82x)$; $R^2 = 0.90$) (Figure 3), with seedling emergence being greatest for seeds sown on the soil surface. The lower germination of seeds sown on soil versus seeds sown on filter paper in petri dishes at similar temperature and light conditions is likely the result of poor seed–soil contact and lower hydraulic conductivity in the former (Ghorbani et al. 1999). Seedling emergence was restricted to a burial depth between 0 to 0.5 cm for MP and 0 to 2 cm for BP and BE. No emergence of seedlings was observed for any seeds sown at depths greater than 2 cm. Furthermore, no seedlings were observed upon exhumation of soil within pots. Similarly, Chauhan and Johnson (2009) and Mahmood et al. (2016) reported that nearly all germination was restricted to, or near, the soil surface for the seeds of two positively photoblastic weeds, common purslane (*Portulaca oleracea* L.) and green galenia [*Galenia pubescens* (Eckl. & Zeyh.) Druce]. Baskin and Baskin (2014) noted that the availability and quality of light and the size of seeds typically limit seedling emergence in photoblastic seeds. Given that light typically only penetrates the first few millimeters of soil (Woolley and Stoller 1978), restricted light availability is likely the principal reason for the nonemergence of buried *O. biennis* seeds. Furthermore, Gross (1985) showed that seed germination did not occur or was severely reduced when *O. biennis* seeds were exposed to

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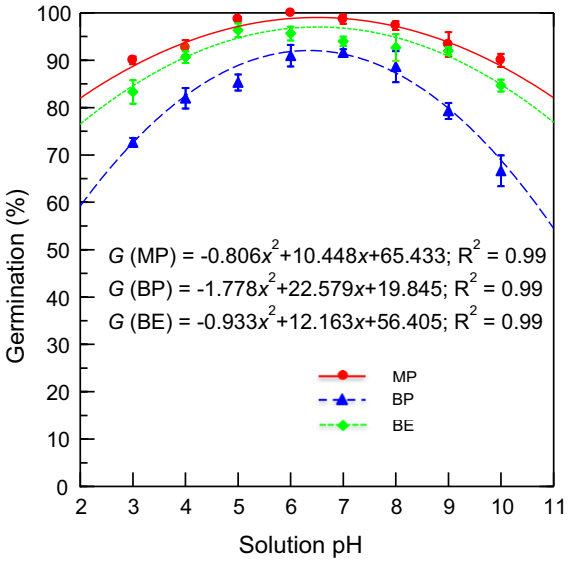



**Figure 1.** The relationship between solution pH and mean percentage germination (±SE) of seeds of *Oenothera biennis* for three study populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at 25/15 C in an alternating photoperiod (12-h light/12-h dark) for 21 d.

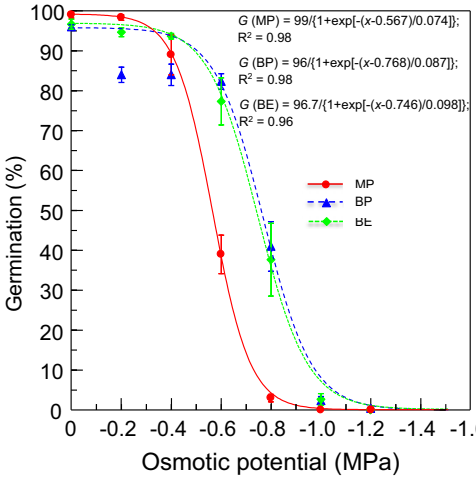



**Figure 2.** The relationship between osmotic potential and mean percentage germination (±SE) of seeds of *Oenothera biennis* for three study populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at 25/15 C in an alternating photoperiod (12-h light/12-h dark) for 21 d.

filtered light with lower red:far-red light beneath several types of leaf canopies. An ecological benefit of this type of positive photoblastic response may be that it allows for the germination of *O. biennis* seeds that either settle on or, through disturbance, are brought to the soil surface and exposed to full sunlight, provided appropriate temperature conditions are available. In the case of the small, light-sensitive seeds of *O. biennis*, their germination will be inhibited by burial in soil, by being covered with leaf litter, or by being situated beneath a leaf canopy. The inability of seedlings to emerge when buried in soil could not be attributed to low seed viability, as tetrazolium tests indicated that >95% of freshly harvested seeds were viable for each population.

In conclusion, seeds of *O. biennis* possess type 2 non–deep physiological dormancy at maturity, with freshly matured seeds

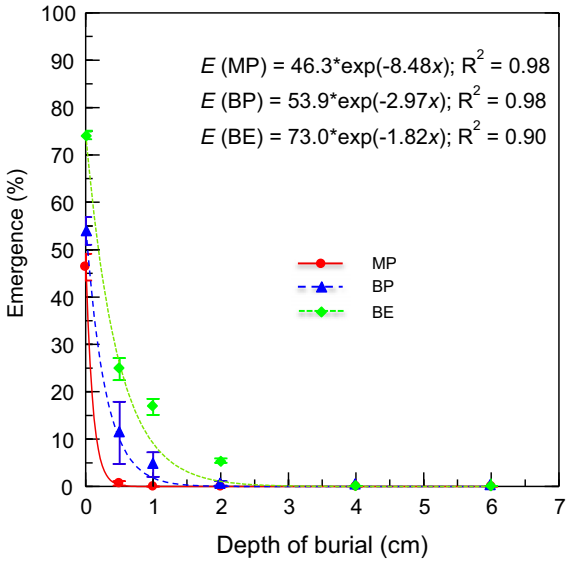



**Figure 3.** The relationship between depth of burial in soil and mean percentage emergence (±SE) of seedlings of *Oenothera biennis* for three study populations (MP, Malden Park, Windsor, ON, Canada; BP, Beck Park, Springboro, OH, USA; BE, Berea, KY, USA) when incubated at 25/15 C in an alternating photoperiod (12-h light/12-h dark) for 30 d.

initially germinating primarily at warmer temperatures, but seeds emerging from dormancy after prolonged periods of cold stratification. Germination of freshly matured seeds occurred over a broad range of solution pH and osmotic stress, indicating that the seeds are capable of germinating in a variety of soils with varying levels of acidity and moisture. The positively photoblastic seeds failed to germinate when buried in soil at depths exceeding 2 cm, suggesting that (1) seeds that are buried in soil or remain shaded on the soil surface may persist in the soil seedbank for long periods of time; and (2) management practices in agricultural settings, such as no-till or minimum-tillage agriculture, may favor seedling emergence of *O. biennis*.

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