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Short title: Knapweed seedling emergence

Seedling emergence of two knapweed (*Centaurea*) species from different soil depths

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Abstract

For many invasive plants, seed dormancy and persistence facilitate population expansion. These traits also complicate control efforts, as new seedlings may continue to emerge for years after the removal of existing plants. The maximum longevity of invasive plant seeds may range from years to decades. However, few seeds emerge after such a long time under field conditions. We conducted a field experiment testing the impact of seed burial depth on emergence of meadow knapweed (*Centaurea* × *moncktonii* C.E. Britton) and spotted knapweed [*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek] over 3 years. For *C.* × *moncktonii*, emergence (raw data corrected for seed viability) was 57% at 0 cm, 28% at 2 cm, 3% at 4 cm, and 0% at 8 cm. For *C. stoebe*, emergence was 84% at 0 cm, 11% at 2 cm, 4% at 4 cm, and 0% at 8 cm. The primary flush of seedlings, averaged over *Centaurea* species and burial depths, occurred during the first few months of the study in fall 2018. Little emergence occurred after spring/summer 2019, although the study continued through spring/summer 2021. Our findings clarify the maximum burial depth from which these *Centaurea* species can emerge and demonstrate that emergence is concentrated in the first year after seed production.

Keywords: Burial depth; *Centaurea*; dormancy; germination; knapweed; longevity; starthistle

Management Implications

Centaurea species, including spotted knapweed [*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek] and meadow knapweed (*Centaurea* × *moncktonii* C.E. Britton), pose an increasing ecological and economic threat in their introduced North American range. These species are highly adaptable and can displace native plants in a variety of environments. One factor complicating *Centaurea* control is the persistent seedbank, from which new seedlings may continue to emerge following control of established plants. The effects of seed burial depth on emergence of *C. stoebe* and *C.* × *moncktonii* were tested using a realistic outdoor experiment in which seeds emerged from a pasteurized field soil. Emergence was tracked for 3 years. Most emergence occurred in the fall immediately after seed burial. Emergence declined with increasing burial depth and was eliminated when seeds were buried at 8 cm depth. Based on these findings, managers could potentially reduce establishment of these *Centaurea* species by inverting the soil so that seeds are buried below 4 cm depth. More generally, these findings suggest that the long potential lifespan of *Centaurea* seeds does not necessarily translate into continued emergence over multiple years in the field if the soil remains undisturbed. This finding underscores the importance of controlling the initial flush of newly emerging seedlings in the year following additions to the seedbank.

Introduction

The genus *Centaurea* within the family Asteraceae includes numerous species that are introduced and invasive in North America (Lejeune and Seastedt 2001; Roché and Roché 2021). These species have invaded millions of grassland hectares in North America and caused major reductions in the productivity of more palatable forages (Lejeune and Seastedt 2001; Roché and Roché 2021). One such species is spotted knapweed [*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek]. This economically harmful rangeland weed capitalizes on nitrogen availability and is not effectively suppressed by neighboring vegetation in North America (Callaway et al. 2011; He et al. 2012). Another *Centaurea* species is meadow knapweed (*Centaurea* × *moncktonii* C.E. Britton), which is a hybrid of black (*Centaurea nigra* L.), brown (*Centaurea jacea* L.), and potentially Vochin (*Centaurea nigrescens* Willd.) knapweeds (Keil and Ochsmann 2006). These invasive knapweeds can achieve rapid population growth in the northeastern United States (Akin-Fajiye and Gurevitch 2020; Molofsky et al. 2023) as well as other areas of the United States (Emery and Gross 2005; Maines et al. 2013). Both species produce numerous seeds, approximately 3 to 3.5 mm long in *C. stoebe* and 2.5 to 3 mm long in *C.* × *moncktonii* (Minnesota Wildflowers 2025).

Rates of recruitment from the seedbank help drive population dynamics in *C. stoebe* and *C.* × *moncktonii* (Akin-Fajiye and Gurevitch 2020; Emery and Gross 2005; Maines et al. 2013; Milbrath and Biazzo 2020; Molofsky et al. 2023). Seed dormancy helps determine environmental requirements for germination, the length of time for which viable, non-germinated seeds are likely to remain in the soil, and the likelihood that seeds will eventually germinate at all (Finch-Savage and Leubner-Metzger 2006). Seed dormancy profiles and germination requirements vary both among and within *Centaurea* species in North America (Clements et al. 2010; DiTommaso et al. 2021; Joley et al. 2003; Nolan and Upadhyaya 1988; Pitcairn et al. 2002; Watson and Renney 1974; Young et al. 2005). In *C.* × *moncktonii*, cold-wet stratification reduced dormancy and thereby increased germination (DiTommaso et al. 2021). However, seeds showed germination polymorphism, i.e., variability in different seeds' requirements for the release of primary dormancy. Some seeds did not require stratification to germinate (DiTommaso et al. 2021). Germination polymorphism has been previously reported in other *Centaurea* species including *C. stoebe* (Nolan and Upadhyaya 1988). Warmer temperatures (up to 30:20 C day:night, compared with 15:5 C) and light also stimulated germination of *C.* × *moncktonii* (DiTommaso et al. 2021). In *C. stoebe*, after-ripening and cold-wet stratification may both reduce dormancy (Eddleman and Romo 1988; Nolan and Upadhyaya 1988; Watson and Renney 1974). The degree of dormancy may influence whether *C. stoebe* germination requires light (Nolan and Upadhyaya 1988; Watson and Renney 1974).

An experiment with outdoor germination trays found variable surface germination rates in *C.* × *moncktonii*, which germinated in either autumn or spring (Milbrath and Biazzo 2020). The authors noted that high light availability may have enabled autumn germination under the experimental conditions, whereas existing plants might shade the soil surface during autumn under natural conditions (Milbrath and Biazzo 2020). The same experiment also tested *C. stoebe*, finding that germination mostly occurred in autumn. For both species, survival of dormant seeds on the soil surface was very low (Milbrath and Biazzo 2020). In contrast, buried seeds of *C. stoebe* could remain viable and dormant in the soil for at least one year and potentially more than 8 years (Akin-Fajiye and Gurevitch 2020; Davis et al. 1993). It seems likely that burial reduces germination rates but preserves the viability of seeds in the seedbank.

The objective of this study was to determine the emergence pattern of seedlings of *C. stoebe* and *C.* × *moncktonii* at four soil burial depths over three growing seasons. It was hypothesized that increasing burial depth would reduce emergence of both species and that emergence would be nearly eliminated by 8 cm depth. Emergence was expected to decline with time across the three growing seasons.

Materials and Methods

A trial was established to test the impact of burial depth on emergence of *C. stoebe* and *C.* × *moncktonii* over three growing seasons. The experiment was conducted in an open field area on the Cornell University campus, Ithaca, NY (42.4508°N, 76.4614°W) from 2018 to 2021.

Seed and soil collection

Mature flower heads of *C.*× *moncktonii* were mass collected in 2018 from the Mt. Pleasant Farm, Cornell University, Ithaca, Tompkins County, NY (42.4619°N, 76.3703°W). Flower heads of *C. stoebe* were similarly collected from a private property in Owego, Tioga County, NY (42.0858°N, 76.3078°W). Seeds were cleaned and counted into lots of 200 using a seed counter (Seedburo Seed Counter, Seedburo Equipment Co., Des Plaines, IL). Seeds were stored at room temperature in the laboratory for up to 2 weeks before the start of the experiment. Initial seed viability was estimated by cold-wet stratifying three lots of 200 seeds of each species at 4 C for 3 months. Stratified seeds were germinated in an incubator at a thermoperiod of 25:20 C and a photoperiod of 14:10 h (light:dark). Remaining nongerminated seeds were tested for viability by squeezing the seeds with forceps. Hard seeds were considered viable based on previous assessments with a 1% solution of tetrazolium chloride (98% viable; LR Milbrath and J Biazzo, unpublished data). In contrast, unfilled or dead seeds readily collapsed. The percentage of viable seeds was used as a correction factor when calculating seedling emergence rates in the field: *C.* × *moncktonii* 83.3%, *C. stoebe* 71.2%.

The soil in which the seeds were buried was collected from the Mt. Pleasant Farm to provide the same environment for the two *Centaurea* species. The soil is a very deep, moderately well drained Mardin series (coarse-loamy, mixed, active, mesic Typic Fragiudepts) channery silt loam with pH of 6.3 to 7 (USDA-NRCS 2025). The soil was screened through 1.2-cm hardware cloth to remove stones and large rhizomes, and it was then steam pasteurized at 82.2 C for at least 30 minutes to eliminate contaminating seeds (Baker and Roistacher 1957). This steam pasteurization might have also reduced the incidence of soil-borne pests and pathogens, at least at the beginning of the experiment. However, a pasteurization temperature of 82.2 C would not have completely eliminated all microorganisms nor altered the physical or chemical properties of the soil, i.e., sterilization (Bunt 1988).

Experimental design

The factors were species, burial depth, and time. The two *Centaurea* species (*C.* × *moncktonii* and *C. stoebe*) were planted at four seed-burial depths (0, 2, 4, and 8 cm). A preliminary study indicated that seedling emergence was unlikely at depths of 8 cm or deeper (LR Milbrath and J Biazzo, unpublished data). This two-way factorial treatment structure was arranged in a completely randomized design with repeated measures on seedling emergence over time. Each treatment was replicated six times for a total of 48 plots (experimental units) measured over six sub-seasons.

We acknowledge that this multi-year study was not replicated in time, which could have provided more insight into the consistency of seedling emergence patterns. Environmental conditions such as temperature, precipitation, and soil moisture can vary substantially by year, influencing rates of germination and seedling establishment. Replicating the study in time would therefore help determine whether the observed effects of *Centaurea* species and burial depth on seedling emergence are consistent or variable depending on environmental context.

The experiment was conducted in plots consisting of PVC tubes (15-cm diameter, 102 cm long) buried vertically with 10 cm of the tube above the soil surface. Holes were cut into the lower half of the tubes to enhance drainage. Tubes were spaced on 2-m centers in a 7 by 7 grid, i.e., a 12 by 12 m area. The area around the tubes was periodically mowed. The tubes were initially filled with local soil, and the soil in the tubes was allowed to settle for 2 months. The soil is a deep, moderately well drained Williamson series (coarse-silty, mixed, active, mesic Typic Fragiudepts) very fine sandy loam that is strongly acidic (USDA-NRCS 2025). After settling, soil was removed from the top 35 cm of each tube and replaced with a 30 cm deep layer of the pasteurized soil described earlier. Two hundred seeds were sown in each plot in mid-September 2018. *C.* × *moncktonii* and *C. stoebe* were sown in separate plots at the appropriate depths by scattering the seeds over the soil surface and covering with additional pasteurized soil, taking into account settling of the soil based on a pilot study. For the 0-cm depth treatment, seeds were scattered on the soil surface only. A sock sewn from a sheer fabric was secured over the open end of each tube to prevent slug predation and seed contamination. During the winter months, 1.2-cm hardware cloth was added on top of the sock to prevent seed predation by small mammals. The trial was not irrigated.

Emergence rates were calculated over the following 3 years by monitoring seedling emergence twice weekly from late September to early November 2018, then weekly from May through early November each year for the remaining duration of the experiment. Seedlings were counted and removed at the root crown with blunt forceps. Cumulative percent emergence (adjusted for initial viability) was calculated for each plot over six timepoints: fall (September through early November) 2018, spring/summer (May through August) 2019, fall 2019, spring/summer 2020, fall 2020, and spring/summer 2021.

Data analysis

Two plots were excluded from analyses, one from the destruction of the tube by mowing and the second (0-cm treatment) due to extremely poor emergence. Cumulative emergence in the outlier plot was 12% compared with 48% to 76% in the other five replicates, suggesting a non-experimental issue such as loss of the seeds from the soil surface. We have verified that the plot with low emergence is a significant outlier using Grubbs' test on the logit-transformed cumulative emergence (Grubbs 1950).

Results were analyzed using a linear mixed model with a logit-transformed response variable (seedling emergence). The model included repeated measures over time and assumed a compound symmetry covariance structure (PROC MIXED, SAS v. 9.4; SAS Institute, Cary, NC). The fixed effects of species, depth, time, and all interactions were included in a full model. A best-fit model was developed through backward elimination (Montgomery et al. 2021; Quinn and Keough 2002). At each step, the highest-order, least significant interaction term was removed and then the model was rerun. The process ended when all remaining interaction terms were significant. This approach resulted in a best-fit model containing the fixed effects of species, depth, time, and the species by depth interaction. Treatment means were compared using Fisher's protected LSD test and the Bonferroni correction (SAS v. 9.4, SAS Institute, Cary, NC).

Results and Discussion

Monthly average temperatures for 2018 to 2021 are shown in Table 1 (Northeast Regional Climate Center 2025). Total annual precipitation was 106 cm in 2018, 105 cm in 2019, 93 cm in 2020, and 122 cm in 2021 (Northeast Regional Climate Center 2025).

Seedling emergence varied by burial depth, with percent emergence (averaged over time) showing some minor variation between *C.* × *moncktonii* and *C. stoebe* (Species by Depth interaction, $F_{3,38} = 5.01$, $P = 0.005$; Table 2; Figure 1). Emergence of seedlings was greatest at 0 cm and generally decreased with increasing depth of burial, including no successful emergence at 8 cm (Figure 1). For *C.* × *moncktonii*, emergence (raw data corrected for seed viability) was approximately 57% at 0 cm, 28% at 2 cm, 3% at 4 cm, and 0% at 8 cm. For *C. stoebe*, emergence (raw data corrected for seed viability) was 84% at 0 cm, 11% at 2 cm, 4% at 4 cm, and 0% at 8 cm.

These findings contrast with some studies in which surface-sown seeds had reduced emergence compared to other shallow-buried seeds, typically in larger-seeded species (DiTommaso et al. 2017; Froud-Williams et al. 1984). In diffuse knapweed (*Centaurea diffusa* Lam.), shallow burial (0.5 cm) increased emergence relative to surface-sowing (Meiman et al. 2009). However, our finding is consistent with a study on *C. diluta* that reported a 54% reduction in emergence when seeds were buried at 2 cm compared with 0 cm (Sousa-Ortega et al. 2024). Successful seedling emergence typically declines as seeds are more deeply buried (DiTommaso et al. 2017; Froud-Williams et al. 1984; Roberts and Chancellor 1979; Roberts and Feast 1972). Seedlings of species that possess larger-sized seeds can emerge from deeper depths than smaller-seeded species (DiTommaso et al. 2017; Froud-Williams et al. 1984). Because the seeds of the two *Centaurea* species we tested are similar in size (average 1.9 mg per seed; J. Biazzo, unpublished data), we would not expect an interspecific difference in emergence patterns with burial depth.

Similar to our findings, other studies involving *Centaurea* species have also observed reduced emergence from deep burial depths. For instance, a growth chamber experiment found that seedling emergence of *C. diluta* and *C. cyanus* was reduced by 92% and 90%, respectively, when buried at 9 cm compared with 2 cm (Sousa-Ortega et al. 2023). A greenhouse experiment found that seedling emergence of *C. iberica* was 78% at the soil surface, 22% at 1 cm burial depth, and 0% at 4 cm burial depth (Nosratti et al. 2017). Combined with our findings, these results demonstrate that it is possible but atypical for *Centaurea* species to emerge from below approximately 5 cm burial depth.

Because we did not exhume seeds annually, it is unclear how much fatal germination may be occurring, i.e., seedlings dying before reaching the soil surface (e.g., DiTommaso et al. 2017). Based on previous research as well as an on-going companion seedbank study, most buried seeds of *Centaurea* species appear to remain intact and dormant for several years (Davis et al. 1993; LR Milbrath et al., unpublished data). Deeper burial is known to promote dormancy in various weed species (Benvenuti 2003; Benvenuti et al. 2001). In *Centaurea* species including *C.* × *moncktonii*, light limitation reduces germination rates (DiTommaso et al. 2021), likely contributing to low emergence of deeply buried seeds. However, these species also show evidence of germination polymorphism (DiTommaso et al. 2021). This phenomenon might help explain why some studies have reported occasional emergence from deep burial depths (Sousa-Ortega et al. 2023).

The primary flush of seedlings, averaged over *Centaurea* species and burial depths, occurred during the first few months of the study in fall 2018 (Time, $F_{5,225} = 5.73$, $P < 0.001$; Table 2; Figure 2). For *C.* × *moncktonii*, percentage emergence in fall 2018 (out of all seeds emerged during the experiment for each burial depth) was approximately 95% at 0 cm, 61% at 2 cm, and 67% at 4 cm. For *C. stoebe*, percentage emergence in fall 2018 (out of all seeds emerged during the experiment for each burial depth) was approximately 99% at 0 cm, 86% at 2 cm, and 97% at 4 cm. Significant but lesser emergence occurred the following season (spring/summer 2019), but little (spring/summer 2020) to no (all other time periods) emergence was otherwise observed (Figure 2).

The temporal dynamics observed in our study demonstrate that, in the absence of disturbance, emergence can be highly concentrated in the first season after seeds enter the seedbank. For this reason, focusing exclusively on a seed's maximum longevity can be misleading. Many *Centaurea* seeds have a relatively long maximum longevity. For instance, buried yellow starthistle (*Centaurea solstitialis* L.) seeds could remain viable for 6 years (plumeless) or 10 years (plumed) (Callihan et al. 1993). In *C. stoebe*, more than 50% of buried seeds remained viable and dormant after 5 years and 25% remained viable and dormant after 8 years (Davis et al. 1993). However, many seeds have more limited dormancy (DiTommaso et al. 2021) or fall victim to pathogens and predators. Milbrath and Biazzo (2020) reported that survival of dormant, shallow-buried *C. stoebe* and *C.* × *moncktonii* seeds was very low across multiple sites in New York State. Even seeds that remain viable may still be losing vigor over time, possibly limiting invasion potential. For instance, *C. stoebe* seeds were reported to germinate more slowly (lower rate of radicle elongation) after burial for 12.5 months (Chicoine 1984).

Overall, these findings demonstrate strong impacts of burial depth on emergence in *Centaurea* species, as well as the steep decline in emergence over time. Management practices that expose *Centaurea* seeds to soil-surface or near-surface conditions would tend to stimulate emergence, whereas practices leading to deeper burial in soil or litter would reduce emergence. Our results also suggest that controlling the initial flush of seedlings following seed introduction is a crucial step in the process of *Centaurea* control, although it does not obviate the need for continued follow-up in subsequent years.

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Competing Interests

The authors declare none.

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Table 1. Monthly average temperature (C) for Ithaca, New York (Northeast Regional Climate Center 2025).

	2018	2019	2020	2021
January	–6.9	–6.1	–1.7	–3.5
February	–1.1	–3.4	–3.1	–5.6
March	–1.9	–1.6	3.1	2.0
April	3.5	7.1	4.8	7.1
May	15.7	12.7	12.2	12.4
June	17.3	17.3	18.3	19.6
July	21.4	21.7	22.6	20.1
August	21.4	18.9	20.8	21.5
September	17.8	15.4	15.1	16.8
October	9.1	10.0	9.8	13.2
November	1.2	1.2	6.1	2.9
December	–0.8	–1.8	–0.8	1.3

Table 2. Type 3 Analysis of Variance (ANOVA). Seedling emergence was measured for two *Centaurea* species, four burial depths, and six timepoints. The fixed effects of species, depth, time, and the species by depth interaction were analyzed using a linear mixed model with a logit-transformed response variable. The model included repeated measures over time and assumed a compound symmetry covariance structure (PROC MIXED, SAS v. 9.4; SAS Institute, Cary, NC).

Effect	Numerator df	Denominator df	F	P
Species	1	38	0.64	0.4288
Depth	3	38	339.38	<.0001
Time	5	225	5.73	<.0001
Species by depth	3	38	5.01	0.0050

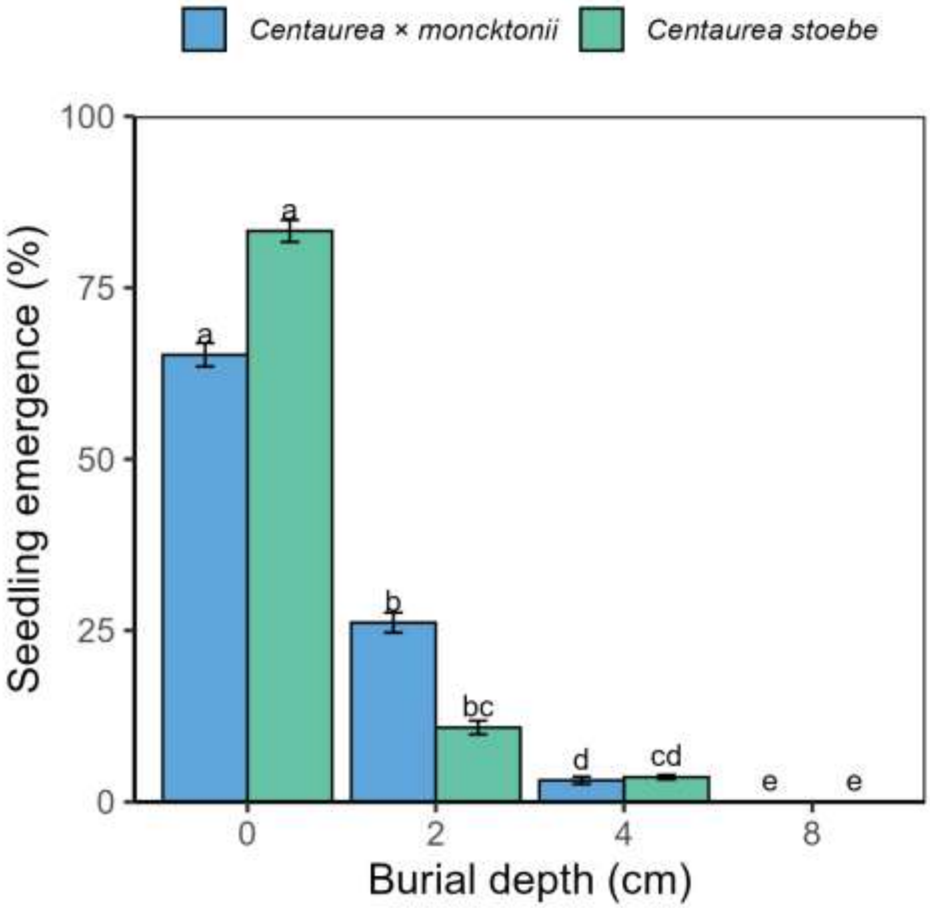

Figure 1. Seedling emergence of two *Centaurea* species at four burial depths, averaged over time. Raw data are shown (mean ± SE, $n = 36$). Bars denoted by the same letter are not different (Fisher's protected LSD test with Bonferroni correction at $\alpha = 0.05$, analyses performed on a logit scale).

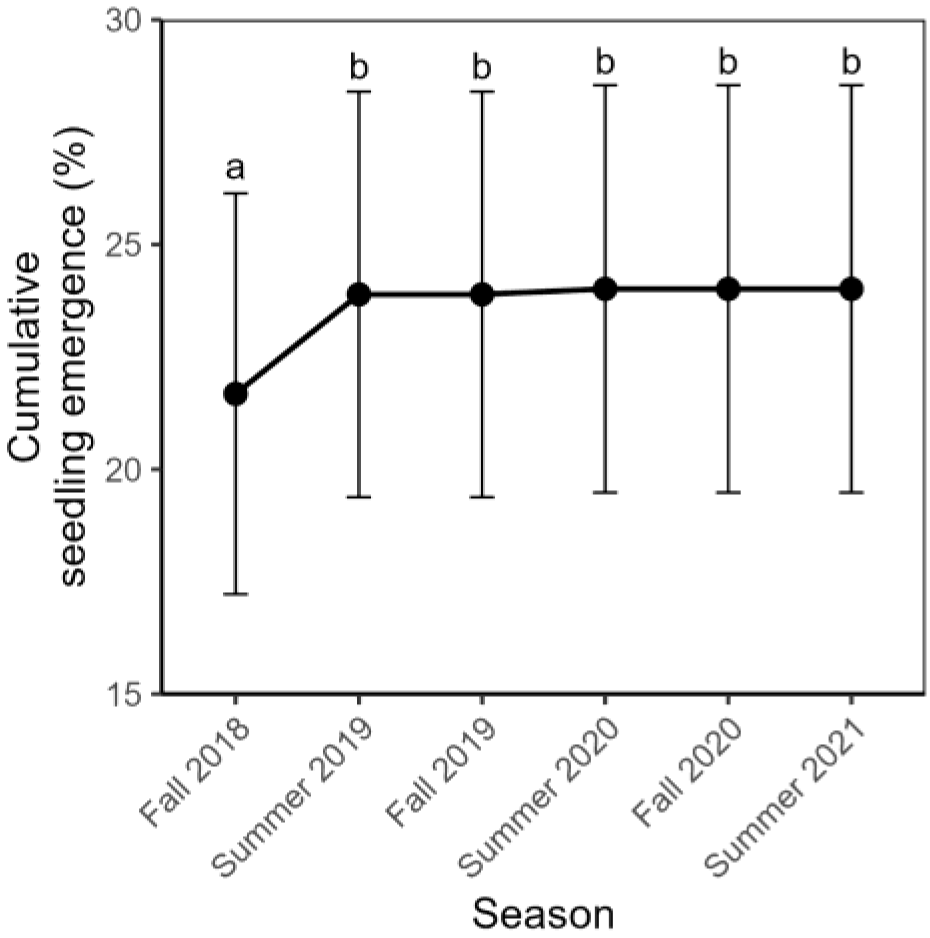

Figure 2. Cumulative seedling emergence over time, averaged over *Centaurea* species and burial depth. Raw data are shown (mean ± SE, $n = 48$). Points denoted by the same letter are not different (Fisher's protected LSD test with Bonferroni correction at $\alpha = 0.05$, analyses performed on a logit scale).