



Article Demographic Processes Allow *Echinochloa crus-galli* to Compensate Seed Losses by Seed Predation

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Abstract: The effect of weed management that targets the seed stage on subsequent life stages is largely unknown. Post-dispersal seed predation reduces the number of seeds from the soil surface before the seeds contribute to the seedbank. Density-dependent processes can mitigate the effect of seed predation in subsequent life stages. In this study, we tested if (i) targeting the seed stage affects the subsequent seedling stage; (ii) if density-dependent mortality in subsequent life stages partly compensates seedling abundance; and (iii) if the magnitude of final seed production depends on seed predation. We fully parameterized a model for the summer-annual weed *Echinochloa crus-galli* (L.) P. Beauv. Field data from three maize fields in north-eastern Germany were obtained, in the presence or absence of seed predation and different population levels of the weed species. Seeds of *E. crus-galli* were applied in autumn and the number of seedlings, adult plants, and seed production per m² was determined the following season. Seed predation reduced the number of seedlings. Density-dependent mortality during the seedling stage increased fecundity with decreasing seedling density, and, thus, compensated for lower numbers of seedlings. The final level of seed production per m² did not depend on seed predation and initial population densities, but differed among fields. We conclude, solely targeting the seed stage can scarcely limit the population growth of *E. crus-galli*.

Keywords: weed seed predation; density-dependence; constant final seed production; compensation; maize

1. Introduction

The demography of annual plant species that reproduce by seeds can be described by their different life stages. They germinate from seeds, establish flowering adult plants, set seeds that are disseminated on the ground, and die [1]. The primary source of an annual plant population is the weed seedbank. Targeting the seed stage and reducing the size of the seedbank limit the establishment of plants from seeds in the long term [2,3]. Weed management with a focus on the immediate control, however, mainly targets the seedling stage, since seedlings are easy to locate and vulnerable to disturbance [2]. Some seedlings, however, can survive weed control, making weed management less effective. The effectiveness of management depends on both the rate of mortality at the targeted life stage, and its residual effect on escaped individuals. In particular, density-dependent processes in weed populations can compensate for the mortality at any particular life-cycle stage. Thus, to evaluate the population growth, the effects of a specific management strategy on all life stages of an annual weed must be considered.

Post-dispersal seed consumption targets the seed stage, which prevents the contribution of seeds to the seedbank. These seeds are predated as long as they are on the soil surface and not incorporated into the soil [4]. Thus, mortality due to seed predation targets exclusively the top-soil seeds. Annual seed losses by seed predation vary between 8% and



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). 70% [5,6], and depend on weed species [7,8], seed density [9–12], type of seed predator [13], field management [14] and landscape complexity [15,16]. Annual seed losses to seed predation can be substantial, but empirical evidence for the effect on weed population densities is scarce. A modelling approach showed that weed populations decline if annual seed losses are at least 40% [17,18]. To our knowledge, experimental approaches addressing the effect of post-dispersal seed predation on other life stages are limited to the seedling stage [19,20]. Experiments demonstrating the effect of seed predation on other non-target life stages, however, would fill a knowledge gap [21,22]. Understanding the impact of seed predation on each non-target life stage would clarify its potential to control weed species.

While seed predation can cause substantial seed losses, these losses could be compensated by density-dependent processes in the weed population that grow from the seed bank in the soil, and would mitigate the potential of seed predation to manage weeds [23]. In density-dependent processes, mortality rates change with the weed population density [24]. If the weed density is high, then on the one hand mortality is high but on the other hand the survival rate is low. Density-dependence has been recognized to influence different plant population life stages, such as seedling emergence [25], seedling survival [26,27], and fecundity [24,28]. The later means that the fecundity of individual plants within high population densities decreases. Conversely, fecundity increases within low population densities. Then, at least partly, plant populations can compensate for seed losses. Compensation can result in a density-independent seed production per unit area. Weed management identifies solutions to prevent the growth of weed populations by producing new seeds. This requires an understanding of the potential of weed species to compensate for seed losses.

Seed predation is likely to contribute to weed management if there is a small weed seedbank and the weed species regenerate by seeds [23]. A large ambient weed seedbank, in contrast, would buffer losses of freshly shed seeds by seed predation. This means seed losses due to seed predation will not reduce the relative number of emerging seedlings from a large seedbank and thus, the influence of seed predators to reduce weed populations is limited.

Echinochloa crus-galli (L.) P. Beauv., a typical summer-annual weed in maize fields in Germany [29], propagates via seeds. This species completes its life cycle within one cropping period. The weed easily adapts to increasing competition by reducing tillers and panicles [30]. One single plant can produce between 2000 and 400,000 seeds [30–32].

The management of *E. crus-galli* relies mainly on chemical control targeting the seedling stage. Herbicide resistance has been found for *E. crus-galli* [33], which calls for the use of additional alternative management strategies. Seed predation may contribute to the management of *E. crus-galli*. The response of *E. crus-galli* to seed predation, however, has not been examined to date.

In this study system, seed predation over the winter was density-independent and seed predation rates were at a high level [12]. Hence, in the presence of seed predation, we assumed that the abundance of weeds in the next season would be reduced. We hypothesized that:

Targeting the seed stage affects the density of the subsequent seedling stage. Density-dependent mortality in subsequent life stages partly compensates seedling abundance. The magnitude of the final seed production depends on seed predation.

2. Materials and Methods

In the present study, we quantified the demography of *E. crus-galli* in relation to whether or not the seed stage was targeted by post-dispersal seed predation. In northeastern Germany, a field experiment was conducted in three intensively managed agricultural fields (continuous maize crops that were minimally tilled) with no seeds of *E. crus-galli* in the seedbank. *Echinochloa crus-galli* populations were introduced to the fields at different densities, and with or without shielding from seed predation. For each population, the currently active life stages were determined. Counts determined for the spring seedbank, seedling stage, adult plant stage, and seed production per unit area and per individual plant were used to estimate the transition probability between life stages as a function of seed density. Next, the effects of density-dependent mortality on the different life stages were estimated.

2.1. Study Sites and Experimental Design

The experiment was carried out in three continuous managed maize fields in northeastern Germany from August 2014 until October 2015. All three fields had a history of at least three years of continuous maize cultivation with minimal tilling. Fields differed in their location, size and soil type; field 1 (53°33' N, 11°08' E) was 11.8 ha in size and had sandy soil. Field 2 ($53^{\circ}97'$ N, $11^{\circ}98'$ E) was 10.1 ha in size and the soil was loamy sand; field 3 ($54^{\circ}02'$ N, $12^{\circ}02'$ E) was 7 ha with sandy loam soil. In each field, the experiment was installed in a randomized block design to measure the demography of *E. crus-galli*. Maize crops grew from May until September or October in 2014 and 2015. The experiment consisted of six blocks (10.5 m \times 13.5 m) with 12 plots (1.5 m \times 1.5 m) where half the plots were surrounded by a plastic frame to prevent the access of seed predators (Figure A1). In the inner 0.5 m \times 0.5 m of each plot the fate of the seeds from *E. crus-galli* was measured. Before the start of the experiment, in each block, 20 randomly chosen soil samples were taken with an auger (2.54 cm) to a depth of 5 cm, stepwise processed using an Elutriator (Elutriator E48X; Disema, Bellvis, Spain; [34]) and indicated that E. crus-galli was absent from the seedbank. In August 2014, in a pure stand of maize crop, *E. crus-galli* seeds were sown once at different densities (300, 600, 1200, 2400 seeds m^{-2} ; seed supplied by Appels Wilde Samen GmbH, Darmstadt, Germany) with each density in two plots per block. In the other four plots per block, no seeds were added for the purpose of a control. The time of seeding coincided with the normal period of seed shedding and the normal seed predation period [4]. The applied densities were within the range of the size of typical ambient seedbanks of *E. crus-galli* in North-West Europe, ranging from 0 to 4050 seeds m^{-2} [35]. The highest applied density is expected to induce density-dependent effects [24].

Furthermore, the experiment was designed to measure the effect of three different factors (intraspecific and interspecific competition, post dispersal seed predation) on the demography of *E. crus-galli*. A factor, intraspecific competition, the competition between *E. crus-galli* without relevant competition with other weed species, was initiated in three blocks by the applied different densities of *E. crus-galli*. In these blocks, the competition with other weed species than *E. crus-galli* was avoided by applying herbicides (not affecting *E. crus-galli*) twice (May and June 2015) and hand weeding (for more details see [32]). The factor of interspecific competition was initiated in three randomly chosen blocks by applying herbicides only once (May 2015). While maize evenly grew within the blocks, here we refer to the interspecific competition as competition between *E. crus-galli* and other weed species. The factor of seed predators' access to half of the plots by a 0.6 m high plastic frame with plots without plastic frame. Each frame was buried 0.2 m deep into the soil. Plastic frames were installed permanently; however, they were taken out short-term for maize harvest in September–October 2014 and maize sowing in May 2015.

Further management was similar in all three fields, including seedbed preparation, maize sowing, and application of fertilizer. The seedbed was prepared by mulching the soil. Maize was sown in rows 0.75 m apart with 9 seeds m⁻². To ensure that the applied *E. crusgalli* seeds did not move from the plots, the soil at the center of each plot ($0.5 \text{ m} \times 0.5 \text{ m}$) was not disturbed either horizontally or vertically. For this reason, the application of manure before maize sowing was omitted. Instead, mineral fertilizer was applied to the crop at the three-leaf stage. The amount of applied fertilizer (field 1, 20 kg/ha N and 40 kg/ha P; field 2, 140 kg/ha N and 60 kg/ha K; field 3, 70 kg/ha N and 70 kg/ha P) was in line with general farming practices. For more details about field management (seedbed preparation, maize sowing, the type and amount of herbicides, and harvest date) and preparation of *E. crus-galli* for sowing see [12].

2.2.1. Spring Seedbank

In March 2015, soil samples were taken from the enclosed plots that excluded seed predation to estimate the depletion of seeds over the winter due to germination or mortality. In the outer 50 cm wide perimeter of each plot, 40 randomly chosen soil samples were taken with an auger (2.54 cm) to a depth of 5 cm. The samples were stored at 4 °C until further processing to retrieve the seeds from the soil. The seeds in the soil samples were separated stepwise from organic material and larger sand particles using an Elutriator (Elutriator E48X; Disema, Bellvis, Spain; [34]), and apparently intact seeds (full and sound) were counted. Analysis showed that the mortality of seeds over winter was affected neither by the three fields nor by the density of *E. crus-galli*. Thus, the values were pooled to obtain a single mean proportion for mortality of seeds during the winter of 0.012 [12].

2.2.2. Seedlings

Emerged seedlings were counted in the central 0.5 m \times 0.5 m of each plot. From May until August 2015, counting was repeated every other week. Except in October and November 2014 and August and September 2015, seedlings were counted once a month. Seedlings that emerged in autumn 2014 died during the winter of 2014–2015. To follow the fate of the seedlings throughout the season, each seedling was marked with a toothpick. In this study, weed seedlings were pooled to a single cohort, because the majority of seedlings that survived to grow to adult plants had emerged within a narrow period between late May and June.

2.2.3. Adult Plants

Adult plants, i.e., plants that survived the seedling stage and developed panicles, were counted prior to maize harvest in October 2015. In the inner 0.5 m \times 0.5 m of each plot, adult plants were cut down to ground level and the panicles separated from the plants.

2.2.4. Seed Production

For each plot, seed production per square meter (m⁻²) and fecundity (number of seeds per plant) was estimated by using the relationship between the number of seeds per panicle dry weight [32]. At the field scale, the relationship of the number of seeds per panicle dry was stable across *E. crus-galli* density, time of seedling emergence, interspecific competition with other weeds, and seed predation [32]. Depending on the field, panicle dry weight explained 95% (field 1), 86% (field 2), and 85% (field 3) of the variability in seeds per *E. crus-galli* panicle. To prepare for estimation of seed production m⁻² and fecundity, seeds were collected by wrapping panicles in a perforated and air-permeable bag (Crispac bag, 150 mm × 300 mm, pores 2 mm diameter, Baumann Saatzuchtbedarf, Waldenburg, Germany) at the beginning of flowering, and the dry weight of the panicle, including seeds, was determined. Field-specific regressions of the number of seeds per panicle dry weight were used to estimate seed production m⁻² based on the total number of seeds produced in the inner 0.5 m × 0.5 m of each plot.

2.2.5. Seed Predation

The main seed predators, trapped after sowing *E. crus-galli* in the three experimental fields, were granivorous rodents and carabid beetles. For further details on trapping, we refer to [12]. During seed exposure between August 2014 and March 2015, the response of seed predators did not depend on *E. crus-galli* seed density. The seed predation rates varied between fields (mean \pm sd; field 1, 0.62 \pm 0.28; field 2, 0.38 \pm 0.28; field 3, 0.70 \pm 0.17) [12].

2.2.6. Statistical Analysis

We tested the effect of the three different factors intra- and interspecific competition and seed predation on the fecundity and the transition probability between different life stages. Fecundity was calculated by the quotient of the number of seeds produced per m² and the number of adult plants per m². The life stages include the transition from:

the spring seedbank m^{-2} to seedlings m^{-2} (seedling emergence)

seedlings m^{-2} to adult plants m^{-2} (seedling survival)

adult plants m^{-2} to seed production m^{-2} (seed production m^{-2}).

The best-fitting linear regression models (LM) were selected after log-transformation of count data. Log-transformation is a standard method for count data [36], with results being comparable to those of other studies. Explanatory variables were:

field (1, 2, and 3)

seed predation (+/-) as factor variable

initial density (log) of the relevant life stage and the second-degree polynomial interspecific competition with other weeds (+/-) as factor variable first order interactions.

Model selection was via backward selection by using the *F*-test with $p \le 0.05$ as the test criterion. In preliminary analyses, while data of all fields were analyzed together, transition probability between different life stages did not respond to interspecific competition (seedling emergence, F = 0.326, df = 1, p = 0.207; seedling survival, F = 0.391, df = 1, p = 0.108; and seed production m⁻², F = 0.8623, df = 1, p = 0.355; fecundity, F = 1.121, df = 1, p = 0.291). Therefore, the factor of interspecific competition with other weeds was excluded. Furthermore, analysis on each life transition indicated a significant interaction between field and seed predation for seedling emergence (F = 4.909, df = 2, p = 0.009), fecundity (F = 8.150, df = 2, p < 0.001) and seed production m⁻² (F = 12.162, df = 2, p < 0.001), but not seedling survival (F = 1.162, df = 2, p = 0.327). Similarly, there was an interaction between field and initial density (log) of the relevant life stage for seedling emergence (F = 7.153, df = 2, p = 0.006), but not seed production m⁻² (F = 1.8815, df = 2, p = 0.156) (see Table A1). To avoid threefold interactions that are difficult to interpret, analysis was done field-specifically.

K-value analysis [36]:

k = log(initial density)/log(final density),

was applied to quantify the magnitude of density-dependent mortality in life stages between fields, and in the absence and presence of seed predation. All analyses were carried out in R version 3.1.2 [37].

3. Results

When analyzed per field, the number of seedlings was reduced considerably by seed predation, which ranged from 40% to 50% in field 1, from 26 to 48% in field 2, and from 53 to 69% in field 3 (Figure 1).

Seed mortality was higher in the presence than in the absence of seed predation. Furthermore, seed mortality increased with density (Figure 2). In the presence or absence of seed predation, seedling emergence decreased with increasing seeding density (slope [initial density] < 1; Table 1), except in field 3, where, in the absence of seed predation, seedling emergence increased with increasing seeding density (slope [initial density] > 1; Table 1).



Figure 1. Back-transformed linear regression models showing the responses of transitions between life stages of *Echinochloa crus-galli*, i.e., seedling emergence, seedling survival, seed production m^{-2} , to seed predation (red circles and dashed line) over the winter vs. no seed predation (green circles and solid line) over the winter, as a function of *E. crus-galli* density, in three maize fields in north-eastern Germany (n = 6). Panels labelled (*) indicate a significantly different (p < 0.05) response to seed predation.



Figure 2. K-values to determine the strength of density dependent mortality for seedling emergence (r), seedling survival (s), and seed production per plant (f) of *Echinochloa crus-galli* in the presence ("pred", dashed lines) or absence (solid lines) of seed predation in fields 1, 2, and 3 shown for each log (initial density of *E. crus-galli* [seeds/m²]). Data predicted by using the models (see Table 1) calculate the k-values per log (initial density of *E.crus-galli* [seeds/m²]).

Model	Parameter	Field 1			Field 2			Field 3		
		Estimate	SE	<i>R</i> ²	Estimate	SE	<i>R</i> ²	Estimate	SE	<i>R</i> ²
Seedling emergence _{pred}	Intercept	-1.489	0.848	0.718 *	1.755	0.633	0.605 *	-1.258	0.690	0.777 *
8 - pieu	Slope (initial density)	0.937	0.125		0.543	0.093		0.892	0.101	
Seedling emergence	Intercept	0.003	0.836	0.675	1.068	0.415	0.861	-1.705	0.473	0.918
	Slope (initial density)	0.834	0.123		0.718	0.061		1.102	0.069	
Seedling survival _{pred}	Intercept	0.568	0.384	0.800	1.225	0.582	0.499	1.014	0.281	0.827
I	Slope (initial density)	0.736	0.078		0.502	0.107		0.601	0.058	
Seedling survival	Intercept	0.521	0.582	0.834	1.495	0.504	0.583	1.192	0.412	0.746
	Slope (initial density)	0.769	0.107		0.472	0.085		0.572	0.071	
Seed production _{pred}	Intercept	6.759	0.449	0.674	11.250	0.099		11.648	0.104	
- F	Slope (initial density)	0.726	0.107							
Seed production	Intercept	10.851	0.079		11.530	0.104		11.712	0.121	
Fecundity _{pred}	Intercept	6.759	0.449	0.227^{*}	10.528	1.037	0.307	11.371	0.804	0.481
	Slope (initial density)	-0.274	0.107		-0.817	0.262		-0.928	0.206	
Fecuncity	Intercept	11.051	0.600	0.766	12.427	1.226	0.454	10.983	0.936	0.425
	Slope (initial density)	-1.041	0.122		-1.220	0.285		-0.837	0.208	

Table 1. Log-transformed parameter estimates, standard errors (SE), and R^2 values for linear regression models for *Echinochloa crus-galli* seedling emergence; seedling survival, seed production m⁻² and seeds plant⁻¹ as a function of seed predation (_{pred}) and density of the relevant life-cycle stage in fields 1, 2 and 3.

 R^2 -value with an asterisk (*) indicates that seed predation made a significant difference within the relevant life stage (p < 0.05).

In all three fields, the number of adult plants was not affected by seed predation (Figure 1). Negative density-dependent processes regulated the transition from seedlings m^{-2} to adult plants m^{-2} (Table 1) in all three fields. Seedling mortality was higher in the absence than in the presence of seed predation (Figure 2).

In field 1, fewer seeds were produced per plant in the presence of seed predation. However, fecundity did not differ between fields 2 and 3. In all three fields, fecundity was negatively density-dependent (Table 1). The level of plant mortality was higher in field 1 than in fields 2 and 3. Density-dependent plant mortality was higher in the absence than in the presence of seed predation in field 3 (Figure 2).

Seed production m^{-2} was influenced neither by seed predation nor by the density of adult plants, except in field 1 where seed production m^{-2} was lower in the presence than in the absence of seed predation, and negatively density-dependent (Figure 1; Table 1). The estimated seed production m^{-2} varied between the fields, i.e., lowest in field 1 (51,621 seeds m^{-2}), intermediate in field 2 (101,744 seeds m^{-2}), and highest in field 3 (122,098 seeds m^{-2}).

4. Discussion

4.1. Targeting the Seed Stage Affects the Density of the Subsequent Seedling Stage

As expected in the first hypothesis, mortality at the seed stage affected the subsequent seedling stage. In addition, the high mortality of seeds due to seed predation (\leq 77%) seeds removed from experimental plots [12]) limited seedling emergence by 26 to 69%. These patterns are in contrast to the findings of Blubaugh & Kaplan [20]. Blubaugh and Kaplan [20] followed the fate of *Chenopodium album* L. seeds in the presence of seed predators. They found that in the presence of seed predators, seedling emergence was limited by 38% only. Our study, and the one of Blubaugh and Kaplan [20], differed in the size of the ambient seedbank. We measured the effect of seed losses on the seedling stage exclusively with freshly applied seeds, as there was no ambient seedbank of *E. crus-galli* in our experimental fields. This is the case when maize is introduced to the crop sequence. Here, weed species communities alter immediately, and especially E. crus-galli benefits [29]. Blubaugh and Kaplan [20], in contrast, conducted their experiment in a field that carried an ambient seedbank of 15,000 C. album seeds m^{-2} . Thus, seedlings emerged from both newly-shed seeds and older seeds in the ambient seedbank, which were protected from seed predation which happens on the soil surface. This implies that mortality at the seed stage limits seedling emergence, but the strength of the limitation depends on the size of the ambient seed bank.

4.2. Density-Dependent Mortality Compensates a Low Abundance of Seedlings

Seedling abundance was partly compensated by density-dependent mortality in subsequent life stages. As expressed in our second hypothesis, mortality at the seed stage limited the abundance of seedlings ($\leq 69\%$), but this effect was mitigated in subsequent life stages, namely adult plants, seed production per unit area (except in field 1), and fecundity. These results are similar to those from a study demonstrating the life cycle of an invasive plant species (*Centaurea solstitialis* L.) in the presence of pre-dispersal seed predation that targeted seeds on the plant before seed-shed [38]. Garren and Strauss [38] showed that seed losses were compensated in the subsequent vegetative period.

The summer-annual weed species *E. crus-galli* compensated seed losses through density-dependence in seedling emergence, seedling survival and fecundity. Density-dependent regulation in *E. crus-galli* in these life-stages is in line with findings in other annual weed species, i.e., *Veronica hederifolia* L., *Papaver rhoeas* L., *Fumaria officinalis* L., and *Capsella bursa-pastoris* (L.) Medik. [39]. In our study, plant populations responded to seed losses by different mortality rates in subsequent life-cycle transitions. The latter means in terms of seedling mortality, that the mortality of seedlings in *E. crus-galli* populations without seed loss through seed predation was higher than in populations with seed loss. Finally, seed production m⁻² was constant in all populations of *E. crus-galli*.

In summary, although the number of seedlings, adult plants, and seed production m^{-2} differed between the fields, density-dependent seedling survival and fecundity regulated the populations of *E. crus-galli* and lead to a constant final seed production in all three maize fields.

4.3. The Amount of the Final Seed Production Did Not Depend on Seed Predation

In contrast to what we had expected in our third hypothesis, the final seed production in *E. crus-galli* populations did not depend on a high level of seed losses by seed predation. Demographic processes compensated the losses in *E. crus-galli* populations in maize fields. Analysis in field 1, however, showed that seed losses by seed predation in autumn and winter effect the final seed production of *E. crus-galli* in the subsequent year. If seed predation were the reason, we would expect that seed predation would effect life stages prior to seed production, namely seedling and adult plant life stages. Thus, the number of seedling and adult plants would have been lower in the presence of seed predators. In field 1, however, the number of adult plants differed neither in the presence nor in the absence of seed predators. This suggests that seed predators did not cause differences in seed production. The differences in seed production in field 1 could rather be a consequence of given conditions due to the prevailing soils in the field. From field 1 over field 2 to field 3, the soils differed from sand over loamy sand to sandy loam. The different quality of the soils can be the reason for the varying amount of the constant final seed production of *E. crus-galli* between the fields. The constant final seed production increased from field 1 to field 3. In each field, the *E. crus-galli* population fits through the level of seedling mortality and the per capita seed number. In field 1, seedling mortality was low, while individual plants set a comparably low number of seeds. In fields 2 and 3, in contrast, both seedling mortality and fecundity were higher than in field 1. Our results are in line with findings on *Ambrosia trifida* L., in which in-field conditions strongly influenced life-cycle transitions, i.e., seedling mortality and loss of fecundity [40]. In field 1, we observed that soil moisture was lower than in fields 2 and 3 [41]. The low soil moisture hampers individual plant growth, biomass [42], and related fecundity [43,44], and, thus, the constant final seed production per unit area.

4.4. Implications for Weed Management

Evaluating our results from an agricultural perspective, the main issue for integrated weed management is to maintain the abundance of seedlings under a certain threshold. For *E. crus-galli* in maize fields in Germany, a threshold level is given (e.g., six seedlings according to [45]). In our study, seed predation affected the number of seedlings, but failed to keep the weeds below this threshold. To accelerate seed predation, farmers can extend the period of access to seeds on the soil surface for predators. Delaying the time of crop harvest, for example, increases this period. A cover crop under sown in maize can provide a canopy protecting seed feeders from being predated by a higher taxa and seeds from being incorporated in the soil by rain splashes. For controlling weeds, however, simply relying on targeting the seed stage by seed predation is not enough, as weeds can compensate for the losses. To limit the growth of a plant population, several studies suggested an 80 to 100% reduction in transitions between all life stages [17,28,46]. Model analysis testing the effect of multiple weed management strategies to reduce the reliance on herbicides in Abutilon theophrasti Medik. populations indicated that seed predation of 40%, combined with crop rotation, reduced herbicide use, and no-till, reduced the population [17]. Therefore, efficient weed control should target many life stages, rather than focus on the seed stage only. Additional management strategies are useful to keep the number of weeds low even in other development stages. In maize crops, for example, farmers mainly use herbicides to control weeds at the seedling stage. In modern and integrated weed management, however, one of the principles is to use as little herbicide as possible [47]. Seed predation reduces the entry of new seeds into the seedbank, and thus the number of emerging seedlings. This improves the efficiency of herbicides because herbicides target weed plants at low densities better than at high densities [48]. Thus, mortality at the seed stage can indirectly reduce the use of herbicides.

Furthermore, our results illustrate the consequences of insufficient management strategies targeting the seedling stage. We assume that if *E. crus-galli* seedlings m⁻² escape weed management in maize crops, populations compensate for the targeted seedlings. The reasons for weeds escaping management strategies are diverse, but failed herbicide application is one of the most intractable problems. Escaped seedlings will increase the weed population towards a constant final seed production. Our results give new insights that help farmers to understand the behavior of *E. crus-galli* if management fails.

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Appendix A



Figure A1. Experimental design showing the arrangement of the six blocks. In three blocks (grey) intraspecific competition and in the other three blocks (white) interspecific competion was initiated. Each block consist of 12 plots where half of them is surrounded by a plastic frame to prevent the acces of seed predators. Seed predators were trapped using Pitfall and Sherman life traps. In each plot we sowed a different density of *E. crus-galli* indicated by the number 0, 300, 600, 1200, 2400 seeds m⁻².

Life-Stage Parameter	Parameter Explaining Parameter		F Value	p Value	
$\log(\text{seedlings m}^{-2})$					
$R^2 = 81\%$	intercept	1	5.938	0.016	
	field	2	11.470	< 0.001	
	log(spring seedbank m ⁻²)	1	80.576	< 0.001	
	predation	1	20.037	< 0.001	
	field $\times \log(\text{spring seedbank m}^{-2})$	2	7.153	0.001	
	field \times predation	2	4.909	0.009	
	residuals	135			
log(adult plants m^{-2})					
$R^2 = 81\%$	intercept	1	10.123	0.001	
	field	2	2.645	0.075	
	log(seedlings m ⁻²)	1	63.533	< 0.001	
	field $\times \log(\text{seedlings m}^{-2})$	2	7.388	< 0.001	
	residuals	138			
log(fecundity)					
$R^2 = 92\%$	intercept	1	358.929	< 0.001	
	field	2	18.224	< 0.001	
	$\log(adult plants m^{-2})$	1	75.644	< 0.001	
	predation	1	6.780	0.010	
	$\log(adult plants m^{-2})^2$	1	24.489	< 0.001	
	log(adult plants m^{-2}) ² × predation	1	4.197	0.043	
	field $ imes$ log(adult plants m ⁻²)	2	5.243	0.006	
	field \times predation	2	8.150	< 0.001	
	residuals	133			
log(seed production m^{-2})					
$R^2 = 64\%$	intercept	1	1028.152	< 0.001	
	field	2	94.102	< 0.001	
	$log(adult plants m^{-2})$	1	8.547	0.004	
	predation	1	1.799	0.182	

 $\text{field} \times \text{predation}$

residuals

2

137

12.162

< 0.001

Table A1. Analysis of variance (type 3) of the best-selected linear regression model to describe the log number of a life stage (seedlings m^{-2} , adult plants m^{-2} , fecundity, seed production m^{-2}) and other explaining variables (field, log previous life-stage, weed seed predation, and first-order interactions).

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