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Using panicle dry weight to estimate seed production in *Echinochloa crus-galli*

H PANNWITT*, P R WESTERMAN*†, F DE MOL* & B GEROWITT*

*Faculty of Agricultural and Environmental Sciences, Crop Health Group, University of Rostock, Rostock, Germany , and †Wageningen Plant Research, BU Field Crops, Wageningen, the Netherlands

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Summary

A better understanding of weed seed production is a key element for any long-term management allowing some weeds to shed seeds. The challenge with measuring seed production in weeds is the large effort required in terms of time and labour. For the weed species *Echinochloa crus-galli,* it was tested whether the number of seeds per panicle dry weight or per panicle length can be used to estimate seed production. Experiments were conducted in three maize fields in north-eastern Germany. The effect of factors that could influence this relationship, such as the time of seedling emergence, the density of *E. crus-galli*, the control intensity of other weeds, seed predation and field, was included. A few days before maize harvest, all panicles were removed and weighed, panicle length was measured, and for a subsample of 178 panicles, the number of seeds was counted manually. Panicle dry weight predicted the number of seeds per panicle better (R^2 = 0.92) than did panicle length (R^2 = 0.69). The other factors except for 'field' and 'seed predation' had no effect on these relationships. The relationships between seed number and panicle dry weight found in this study closely resembled those reported in an earlier study. Based on our results, we conclude that both plant traits are appropriate for the estimatation of seed production, depending on required level of precision and availablilty of resources for the evaluation of sustainable weed management strategies.

Keywords: ECHCG, barnyardgrass, maize, fecundity, panicle length, panicle weight.

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Introduction

Integrated weed management aims to maintain the control over weeds while at the same time reducing the use of herbicides whenever possible. Within this framework, an important tool is to accept weeds below economic thresholds (Barzman *et al.*, 2015). Consequently, in integrated weed management, some weeds may survive and produce seeds at the end of the season. *Echinochloa crus-galli* (L.) Beauv. (barnyardgrass) is a common weed of maize (*Zea mays* L.) (Maun & Barrett, 1986; de Mol *et al.*, 2015; von Redwitz & Gerowitt, 2018), the second most important crop in Germany (Destatis, 2018). The effectiveness of chemical control of *E. crus-galli,* the basis of weed control in commercial maize cultivation, is threatened by the high risk of herbicide resistance evolution (Claerhout *et al.*, 2016; Heap, 2018). Seeds shed from weeds that survived control, either planned due to integrated management or unplanned due to resistant biotypes, challenge us to understand the seed production of *E. crus-galli*. The seed production is important if we

Correspondence: H Pannwitt, Faculty of Agricultural and Environmental Sciences, Crop Health Group, University of Rostock, Satower Straße 48, 18051 Rostock, Germany. Tel: (+49) 381 4983171; Fax: (+49) 381 4983162; E-mail: heike.pannwitt@uni-rostock.de

want to assess weed management methods and concepts in their entirety (Norris, 2007; Norsworthy *et al.*, 2012). Data on seed production are also required for long-term predictions of weed populations via simulation models (Holst *et al.*, 2007; Freckleton & Stephens, 2009), such as the one published by von Redwitz *et al.* (2016) for *E. crus-galli*.

In weed population models that focus on a single weed species, seed production usually appears to be highly influential on population size (Gonzalez-Andujar & Fernandez-Quintanilla, 2004). Unfortunately, there are serious problems associated with the generalisation of the techniques used for estimating seed production. Ignoring this problem could lead to unrealistic model outcomes. The estimation of seed production in experiments is often limited to conditions of a single field and lack of accounting for the plasticity of weed species caused by intra- and interspecific competition and delayed emergence (Norris, 2007). This applies to *E.crus-galli*, an example of a plastic weed species that germinates and reproduces throughout the entire maize cropping season (Maun & Barrett, 1986; Norris, 1996). With delayed seedling emergence, intra- and interspecific competition increases (Bagavathiannan *et al.*, 2012). This limits the number of tillers and panicles per plant (Norris, 1992a, 1996; Clay *et al.*, 2005) and length and biomass of individual panicles (Maun & Barrett, 1986; Norris, 1996) and therefore the level of seed production of *E. crus-galli* (Bosnic & Swanton, 1997; Norris, 2007). Therefore, before applying techniques to estimate seed production, proof of concept for the ability to deal with the plasticity of the weed species is needed.

Another complicating factor when measuring seed production is the immediate seed shed of *E. crus-galli* as soon as seeds are ripe. Thus, the timing to measure seed production becomes crucial. Gathering seeds too soon and a certain proportion of the seeds will not be ripe yet, gathering seeds too late and a certain proportion of seeds has been shed already. Both can lead to underestimation of (viable) seed production. A correct estimation of seed production requires a measuring technique that either involves the collection of all seeds during the whole process of seed shed or that is independent of the time of seed shed.

Direct methods to estimate seed production, such as sticky boards or pans, are generally inexact due to seed losses, especially at low seed densities (Norris, 2007). An alternative is counting all seeds per plant or m^2. Because this method is extremely time-consuming, researchers have been searching for more efficient methods that are based on the allometry of plants, that is the relationship between seed production and individual vegetative or reproductive biomass (Thompson & Stewart, 1981; Weiner *et al.*, 2009), panicle dry weight or panicle length (Norris, 1992b; Forcella *et al.*, 2000).

Norris (1992b) established relationships between seed production and panicle length and panicle dry weight for *E. crus-galli* when the plant was growing in a pure stand. His experiments were conducted in the Mediterranean climate of the Central Valley of California, USA. It is unknown whether the relationships he found are applicable to the conditions in north-eastern Germany, or whether they are applicable for *E. crus-galli* grown under competition with crops or other weed species. For a methodology to be generally applicable, the relationships between seed production and the panicle traits (e.g. panicle length or panicle dry weight) need to be solid under a range of field conditions.

Environmental differences between the two locations, California (USA) and north-eastern Germany, and genetic differences between populations may alter the relationships between seed number and panicle dry weight/panicle length. Furthermore, the relationships between seed number and panicle dry weight or length is expected to be influenced by intra- and interspecific weed competition because competition influences plant morphology.

For the objective of the study, optimising the estimation of seed production, data of the number of seeds per panicle trait of *E. crus-galli* were compared on two scales, that is large scale (USA vs. Europe) and small scale (field within Germany). For seed production per panicle, the relations determined by Norris (1992b) were calibrated with experimental data from different fields in north-eastern Germany. To estimate the implications of using different relationships for seeds per panicle, these relationships were applied to more of our field experimental data, plants per area and estimated their seed production.

Materials and methods

Field management

Field experiments were conducted in three commercial maize fields that were minimally tilled and had been under continuous maize cultivation for at least 3 years. Field management was similar among all three fields. On 4–7 May 2015, maize (9 seeds m^{-2}) was sown in rows 75 cm apart and 5 cm deep in the soil. Before maize seeding, the seedbed was prepared, but only in the rows, using a rotary tiller (16 cm width). This ensured that the soil between rows remained undisturbed and that weed seeds moved neither horizontally nor vertically. Similarly, to avoid movement of seeds, no organic fertiliser was applied prior to crop sowing.

The crop was fertilised with mineral fertiliser (field 1, 20 kg ha^{-1} N and 40 kg ha^{-1} P; field 2, 140 kg ha^{-1} N and 60 kg ha^{-1} K; field 3, 70 kg ha^{-1} N and 70 kg ha^{-1} P) approximately 4 weeks after sowing, when the maize plants had three leaves. In the middle of September 2015, the height of three randomly chosen maize plants per plot (see below) was measured, and the mean height (±SE) was calculated to be 168 ± 2 cm (n = 216) in field 1, 200 ± 1 cm (n = 216) in field 2 and 186 ± 2 cm (n = 211) in field 3. For more details about field properties, such as soil types and locations, see Pannwitt *et al.* (2017).

Experimental design

In 2015, seed production was measured in a completely randomised block design. Each field consisted of six blocks (10.5 × 13.5 m) with 12 plots (1.5 × 1.5 m) each that were 10 m apart. Different densities of seeds of *E. crus-galli* (300, 600, 1200, and 2400 seeds m^{-2}; Appels Wilde Samen GmbH, Darmstadt, Germany) were applied to two plots per block in August 2014. No seeds were added (control) in four plots per block. Seed predators, such as carabid beetles and rodents, can be active in the fields and affect the density of applied seeds. Therefore, they were excluded from half of the plots by a 60-cm-high plastic frame.

In the spring and summer of 2015, following seed addition in 2014, the effect of interspecific competition with other weed species on seed production of *E. crus-galli* was tested by (i) eliminating all other weeds (treatment 1), or (ii) allowing other weeds after the crops had three leaves (treatment 2). For this purpose, half the blocks were kept weed free (except for *E. crus-galli*) by a combination of selective herbicide treatments and hand weeding (see below), while in the other half, weed management stopped after 1–4 June. Two weeks before crop seeding, a non-selective herbicide (Glyphosate, 450 g a.i. L^{-1}, Glyphos Supreme, FMC, Germany) was applied in both treatments. This treatment most likely had no effect on *E. crus-galli* because at that time, no seedlings of *E. crus-galli* had emerged. When the crop had developed three leaves (1–4 June), leaf- and soil-active herbicides (Tritosulfuron, 250 g a.i. kg^{-1}, Arrat, BASF, Germany, and Dicamba, 500 g a.i. kg^{-1}, Dash, BASF, Germany) were applied in both treatments. When the crop had six leaves (29–30 June), a leaf-active herbicide (Bromoxynil, 225 g a.i. L^{-1}, Bromotril 225 EC, ADAMA, Germany) was applied additionally, but only to treatment 1. After that, late-emerging weeds of species other than *E. crus-galli* were manually cut to ground level every second week in treatment 1.

To test the effect of the timing of seedling emergence (cohorts), seedlings of *E. crus-galli* were marked using a differently coloured toothpick for each emergence cohort, every second week. Cohort 1 included individuals of *E. crus-galli* that had emerged before maize planting on 4 May; cohort 2 included individuals counted from 5 May until 1 June; cohort 3 included individuals that emerged between 2 and 30 June; and cohort 4 included individuals that emerged between 1 and 31 July. Seedlings that emerged in August were not considered for analysis because these plants did not produce seeds. Similarly, seedlings that emerged immediately after sowing of *E. crus-galli* in the autumn of 2014 were not considered because they died in winter and produced no seeds.

Seed production

Panicles were checked for flowering from July to October 2015. Each flowering panicle was wrapped in a perforated and air-permeable bag (Crispac bag, 150 × 305 mm, pores ∅ 2.00 mm, Baumann Saatzuchtbedarf, Waldenburg, Germany) to avoid seed losses. All panicles were cut and collected a few days before maize harvest. The number of adult plants, that is plants that produced panicles, was counted per cohort and plot. Panicles were separated from the culm of the adult plants by cutting them approximately one cm below their lowest rachis. Panicles were oven-dried (30°C) for 24 h and stored at room temperature until they were analysed.

A total of 6491 panicles of *E. crus-galli* were harvested. For each panicle, the dry weight was determined by weighing to an accuracy of ±10 mg and length was measured from the attachment point of the lowest rachis to the tip of the panicle.

To determine the relationship between seed number and panicle dry weight or length, a subsample of 178 panicles was drawn from all panicles. The sample was not completely random; the subsample always included small-, medium- and large-sized panicles from all treatments and all cohorts. The number of caryopses per panicle, which we refer to as seeds per panicle, was determined by stripping the seeds from the panicles and separating apparently broken or empty seeds from intact (full, sound and heavy) seeds and counting the intact seeds manually.

Data analysis

To select the best predictor of the number of seeds per panicle, regression models of log-transformed panicle dry weight and log-transformed panicle length were analysed separately, including their respective second-

degree polynomials. Seed predators were able to access ripe, heavy panicles hanging outside the plastic frames in field 1; therefore, plots with frames from field 1 were excluded from regression analysis. Models that could accommodate skewed error distributions were tested: (i) a generalised linear regression model (GLM) with a quasi-poisson distribution; (ii) a GLM with a negative binomial distribution; (iii) a linear regression model (LM) after Box-Cox transformation of the response variable; and (iv) a LM after log transformation of the response variable. Explanatory variables included weed cohort (1–4), field (1–3), weed seed density (300, 600, 1200 or 2400 seeds m^{-2}), interspecific competition with other weed species (±), weed seed predation (±) and first-order interactions. Model selection was done via backward selection using the *F* test (models 1, 3, and 4) or the chi-square test (model 2), with $\alpha \leq 0.01$ as the test criterion.

When all data were analysed together, panicle dry weight did better than panicle length in describing seed production per panicle. Therefore, further analyses focussed on panicle dry weight as the main predicting variable of seed count. Because of significant interactions between field and panicle dry weight, further field-specific model selection and subsequent analysis were carried out. All final models met the model assumptions (linear relationship assumption, normal distribution of residuals, homoscedasticity and absence of influential values).

Calibrating seed production data from Norris (1992b)

To compare our *E. crus-galli* seed data from Germany with data from California (Norris, 1992b), we combined and converted Norris's model equations. Norris related the number of florets and the seed dry weight per panicle to the structural dry weight of the panicle, that is the dry weight without the seeds, as follows:

$$\left\{\begin{array}{c}\log(\text{numflor}) = 0.98 + 0.96 \times \log(\text{strucbiom}) \\ \log(\text{weightseeds}) = 1.12 + 1.03 \times \log(\text{strucbiom})\end{array}\right\}, \quad (1)$$

where numflor = number of total florets per panicle, weightseeds = weight of seeds + aborted seeds per panicle (mg per panicle), and strucbiom = panicle structural dry weight (mg per panicle).

From 1, it follows that the total panicle dry weight (*B*), that is the sum of the dry weight of the structure, the seeds and the aborted seeds, is

$$B = \exp(1.12 + 1.03 \times \log(\text{strucbiom})) + \text{strucbiom}. \quad (2)$$

Under the assumption that *numflor* is equal to the number of seeds (*S*), it follows from 1 that

$$\log(\text{strucbiom}) = (\log(S)) - 0.98)/0.96. \quad (3)$$

The insertion of Eqn 3 into Eqn 2, subsequent simplification and changing the units to (g per panicle) results in

$$\log(B) = \log((\exp(1.073 \times \log(S) + 0.069) + \exp(1.042 \times \log(S) - 1.021))/1000). \quad (4)$$

Solving Eqn 4 for *S* is analytically impossible. Therefore, Eqn 4 was used to compare Norris's and our results graphically (Fig. 1).

Using the regression models to estimate seed production

To provide an example of an application of our regression models, the number of seeds produced per plant and the number of seeds produced per m^2 were estimated. This was done only for plots that excluded seed predators and had been seeded with 600 seeds m^{-2} (six plots per field). We had no information on the number of panicles per individual adult *E. crus-galli* plant. However, for each plot, information was available on (i) the number of *E. crus-galli* plants per cohort and per m^2, (ii) the proportion of these plants that were adult, (iii) the number of panicles per m^2 and to which cohort they belonged, (iv) the dry weight of each of these panicles, and (v) our regression lines relating panicle dry weight to seeds per panicle based on a sample of these panicles. This allowed the estimation of means and standard errors ($n = 6$). The information was used as follows: the selected regression lines relating panicle dry weight to the number of seeds per panicle (Fig. 1) were used to estimate the number of seeds for each panicle ($n = 896$) that was bagged in any of the plots. This process was repeated using the relationship established by Norris (1992b). Next, for each field, seed production per cohort and per m^2 was calculated by adding up the seeds produced by all panicles per field and cohort and per m². The number of seeds per plant is the number of seeds per m² divided by the number of adult plants per m^2. Then, the number of panicles per adult plant was calculated as the number of panicles per m^2 divided by the number of adult plants per m^2 per field and cohort. The number of seeds per panicle was calculated by the number of seeds per adult plant divided by the number of panicles per adult plant for each field and cohort. The calculation of the number of seeds per panicle and seeds per m² was repeated by using the relationship established by Norris.

Statistic tools used

All analyses were done in R version 3.1.2 (R Core Team, 2017). The package 'MASS' (Venables & Ripley, 2002) was

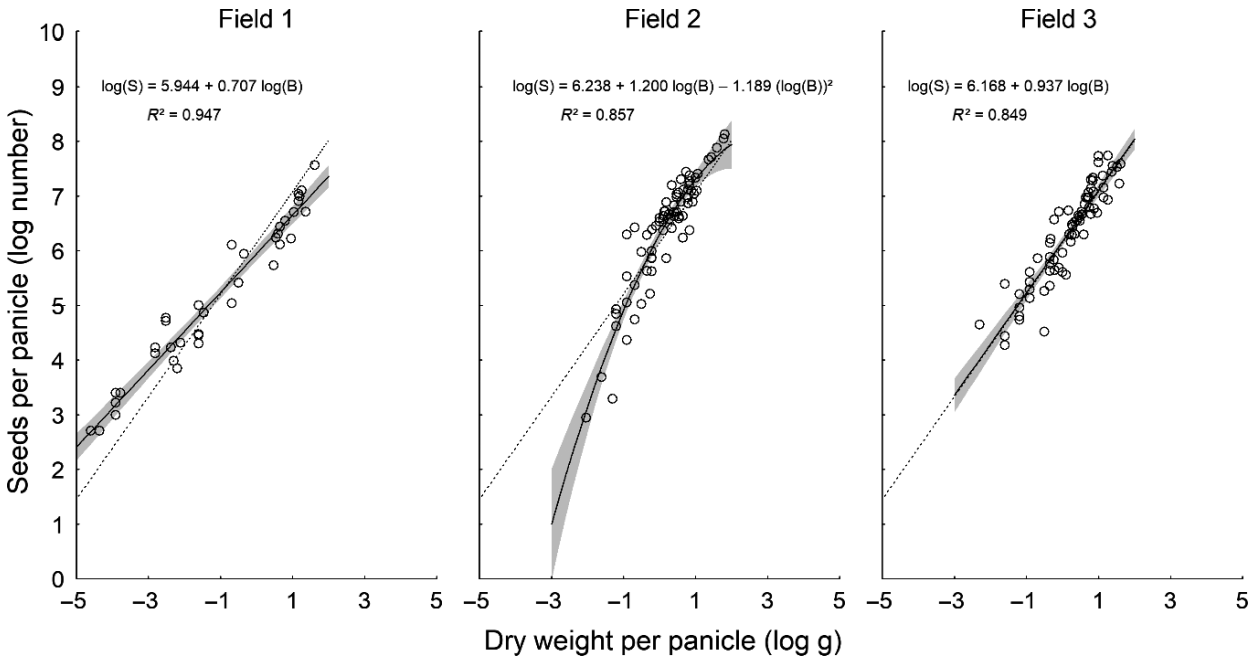

Fig. 1 Number of seeds (S) per panicle of *E. crus-galli* depending on panicle dry weight (B) in three fields. Regression line with 95% confidence interval. The dotted lines display the relationship derived from Norris (1992b) ($\log(B) = \log((\exp(1.073 \times \log(S) + 0.069) + \exp(1.042 \times \log(S) - 1.021))/1000)$).

used for the negative binomial model, and the package 'emmeans' (Lenth, 2018) was used to compare the slopes of different regression models.

Results

Relationship between panicle dry weight and seed production on a small scale

Of all tested models, the LM with log transformation was the most parsimonious and revealed the highest R^2 or pseudo-R^2 (explained deviance of GLMs); thus, further analysis focussed on LM. When data of all fields were analysed together, the number of seeds per panicle was best described by panicle dry weight (R^2 = 92%). Using panicle length instead of dry weight as an explanatory variable explained less of the variance (R^2 = 69%; Table 1). Analysis per field showed that only the tested variable on panicle traits, namely panicle dry weight and panicle length, could explain the number of seeds per panicle. All other tested variables, that is weed cohort, weed seed density, interspecific competition with other weed species, weed seed predation and first-order interactions, did not significantly explain the number of seeds per panicle.

Field-specific models based on panicle dry weight are shown in Fig. 1. In all fields, the number of seeds increased with panicle dry weight, but the slopes of the regression lines differed significantly among all three fields (P (χ^2) < 0.05). This indicates that plants differed between fields in the allocation of resources to seeds.

Table 1 Analysis of variance of best-selected linear regression model to describe the log number of seeds per panicle by plant traits (panicle dry weight (B) or panicle length (L)) and other explanatory variables (field (1–3), weed seed predation (±) and first-order interactions)

Parameter	df	*F* value	*P* value
Panicle dry weight (R^2 = 92%)			
Log(B)	1	1724.617	<0.001
Log(B^2)	1	18.475	<0.001
Field	2	5.120	0.007
Weed seed predation (±)	1	0.622	0.431
Log(B) × field	2	21.741	<0.001
Log(B) × weed seed predation (±)	1	12.878	<0.001
Log(B^2) × field	2	9.412	<0.001
Residuals	167		
Panicle length (R^2 = 69%)			
Log(L)	1	309.163	<0.001
Log(L^2)	1	8.910	<0.001
Field	2	0.882	0.144
Log(L) × field	2	5.506	<0.001
Log(L^2) × field	2	3.064	0.001
Residuals	169		

Relationship between panicle dry weight and seed production on a large scale

The confidence interval of our regression models differed significantly from the model described by Norris (1992b) in two of the three fields. If the regression model by Norris (1992b) would have been used, then seed production would have been underestimated for lighter panicles (≤0.3 g panicle dry weight) and overestimated for heavier panicles (≥0.7 g panicle dry weight) in field 1. In contrast, in field 2, seed production would have been overestimated for lighter panicles (≤0.5 g panicle dry weight) and underestimated for heavier panicles (between 0.9 and 3.5 g panicle dry weight).

Using the regression models to estimate seed production

Seed production by *E. crus-galli* differed between fields as the adult plants in field 1 produced, on average, 590 (± 161) seeds per plant (n = 6); those in field 2 produced 1638 (± 403) seeds per plant; and those in field 3 produced 2483 (± 341) seeds per plant. Lowest seed production was obtained in field 1 (58 157 ± 8064 seeds m^{-2}), followed by field 2 (130 888 ± 16 960 seeds m^{-2}), and being highest in field 3 (203 643 ± 37 739 seeds m^{-2}). The total number of adult plants per m^2, the number of panicles per adult plant and the number of seeds per panicle were higher in field 3 than in fields 1 and 2 (Table 2). In field 2, the number of panicles per adult plant and the number of seeds per panicle was higher than field 1 (Table 2).

In all three fields, the main contributor to seed production per m^2 was the number of plants that emerged in cohort 2 (field 1, 77%; field 2, 78%; and field 3, 54%), followed by the number that emerged in cohort 3 (field 1, 22%; field 2, 10%; and field 3, 46%). In field 2, seeds from plants that emerged in cohort 1 contributed only 12% to seed production, and in field 1, cohort 4 contributed only 1%. The number of panicles per adult plant and number of seeds per panicle gradually decreased, comparing all fields, in the following order: cohort 2 > cohort 3 ≈ cohort 1 > cohort 4 (Table 2).

Discussion

The objective to optimise the estimation of seed production calls for a solid method, delivering results not affected by the plasticity of weed species due to competition or time of emergence, environmental variations and genetic differences. Moreover, it should be easy to handle. We first discuss how robust the methods based on panicle traits, namely dry mass and length, are to estimate seed production per panicle on a large scale (i.e. across continents) and then compare the differences occurring on a small scale (i.e. across fields). We then evaluate the methods to assess seed production in light of its foreseen purpose of integrated weed management.

Relationship between panicle dry weight and seed production on a large scale

Comparing Norris' model with the model we developed, the relationship between panicle dry weight and seed production per panicle was equally closely related among the two climates, different field managements, differences in the competition with the crop and populations of *E. crus-galli* between the two continents (Europe and USA) and was not influenced by the year of the study (1992 vs. 2015). Panicle dry weight explained seed production per panicle in both models equally well. The models developed in this study, describing the number of seeds per panicle as a function of panicle dry weight or length, were not influenced by the plasticity of *E. crus-galli,* that is variation in plant morphology due to intra- and interspecific competition and time of emergence. Panicle dry weight, however, predicted seed production per panicle more precisely than did panicle length. Thus, on a large scale, panicle dry weight resulted in a more robust model for the estimation of seed production than panicle length.

Relationship between panicle dry weight and seed production on a small scale

However, when comparing the relationship between panicle dry weight and seed production per panicle on a small scale, the slopes of the relationship varied between the three experimental sites. When seed production was estimated in our fields using the model developed by Norris, very different estimates were obtained for two of the fields than when our own models were used. Apparently, differences on a small scale can have consequences for the total amount of seeds produced. Seed production per m^2 would have been overestimated by 41% and underestimated by 14% in fields 1 and 2, respectively, if the equation developed by Norris (1992b) would have been used.

On a small scale, competition by other weeds, seed density or presence/absence of seed predators could not explain differences in seed production. This indicates that other factors influencing growing conditions in each field altered the slope of the relationship between seed number and panicle dry weight, resulting in field-specific values. While growing conditions

Table 2 Adult plants per m^2, panicles per adult plant, seeds per panicle and seeds per m^2 for each cohort (1, early May; 2, May until the beginning of June; 3, June; and 4, July) of *E. crus-galli* in three fields (1, 2 and 3) at a sowing density of 600 seeds per m^2

Field	Cohort	Plants (m^{-2})	Panicles ($plant^{-1}$)	Seeds ($panicle^{-1}$)	Seeds (m^{-2})	Seeds in Norris ($panicle^{-1}$)	Seeds in Norris (m^{-2})
1	2	31 ± 5.232	2 ± 0.132	586 ± 45	45 028 ± 8732	862 ± 81	65 941 ± 13 232
	3	66 ± 12.426	1 ± 0.138	192 ± 47	12 934 ± 2386	245 ± 67	16 183 ± 3285
	4	9 ± 2.996	1 ± 0.066	22 ± 6	195 ± 92	12 ± 5	109 ± 63
2	1	16 ± 4.000	2 ± 0.000	514 ± 64	15 912 ± 2054	444 ± 47	13 824 ± 2050
	2	48 ± 9.179	3 ± 0.660	761 ± 78	102 284 ± 16 027	651 ± 63	87 466 ± 13 226
	3	15 ± 3.040	1 ± 0.359	517 ± 103	12 692 ± 5487	450 ± 80	11 054 ± 4642
3	2	22 ± 8.983	4 ± 0.877	852 ± 101	109 462 ± 50 090	830 ± 100	1 066 87 ± 48815
	3	61 ± 6.746	2 ± 0.596	621 ± 46	94 181 ± 18 764	606 ± 45	91 718 ± 18 278

Seeds per panicle and the number of seeds per m^2 were estimated by regression models in each field and the regression model from Norris (Fig. 1; $n = 6$; field 2, cohort 1, $n = 2$; mean ± standard error).

appeared to alter panicle dry weight, the number of seeds per panicle always remained closely related to panicle dry weight. Different field conditions caused shifts in the timing of seedling emergence, the number of panicles per plant and the number of seeds per panicle. As expected, the timing of seedling emergence influenced seed production of the adult plants of *E. crus-galli*. With delayed emergence, seed production declined because late-emerging plants produced fewer panicles per plant and fewer seeds per panicle. Similar effects have been described for *E. crus-galli* in maize, rice and cotton fields where late-emerging weeds had to compete with the crop, especially for light (Norris, 1992a, 1996; Bosnic & Swanton, 1997; Clay *et al*., 2005; Bagavathiannan *et al*., 2012). Thus, our analyses showed that growing conditions clearly altered panicle dry weight; but in each field, the number of seeds per panicle was always closely related to the panicle dry weight.

In summary, the relationship between panicle dry weight and the number of seeds per panicle appears to be surprisingly solid when compared at a large, continental scale, but can differ at a small, regional scale.

The objective to establish a reliable and straightforward method to estimate seed production is difficult to achieve in the case of *E. crus-galli*. In this study, panicle dry weight did better than panicle length in predicting seed production per panicle. The difference in the percentage of explained variance was substantial with 69% (panicle length) and 92% (panicle dry weight). In contrast to the study by Norris (1992b), in this study, the total panicle dry weight was measured by including the dry weight of the seeds. This way of measuring panicle dry weight requires a much better timing and is more time consuming than simply measuring panicle dry weight without seeds or panicle length, which can be measured after seed shed. Alternatively, panicle dry weight excluding the seeds is less time-consuming. Norris (1992b) waited until full seed shed, which lasted for approximately 3 weeks, to measure the number of seeds by panicle length and panicle dry weight without seeds. By using either length or dry weight without seeds as independent variables, Norris (1992b) found no difference in the explained variance (94%) of the models for seeds produced per panicle. Compared to Norris's study, the growth of *E. crus-galli* in the current experiment was limited by several variables, such as different densities of *E. crus-galli*, presence of the crop, herbicide application and seed predation. During model selection, each of these variables was dropped one at a time. Intra- and interspecific competition, however, changed the relationship between seeds per panicle and panicle length in a way that made the error in the model increase. Measuring panicle dry weight including seeds, however, requires that all seeds are still on the panicle. This method is more appropriate for *E. crus galli* plants grown under arable cropping conditions. Panicles of *E. crus-galli* were formed over a period of up to 9 weeks and the seeds did not mature simultaneously. This requires either frequent sampling or bagging the panicles, as done in this experiment. Seeds in this study did not fully shed until harvest. Rubbing the panicle to separate fixed seeds is again time-consuming and can partly destroy the panicle structure.

Our study gives new insights into the pros and cons of different methods that can be used to estimate seed production in *E. crus-galli*. Both methods, that is based on a relationship between seed number and panicle dry weight or panicle length, have their advantages and disadvantages, depending on the users demand for precision and work load.

1 Panicle length can be used if the estimate of seed production does not have to be very precise or seeds have already shed. This method would be sufficient if a quick and rough estimate of seed production is required, for instance to compare the efficiency of weed control measures within a field.

2 Total panicle dry weight is a more precise estimator of seed production. This method should be used when high accuracy and precision is needed and sufficient time and labour is available. We recommend it as the method of choice in research if different influences within one field on weed demography should be modelled, such as crop management (e.g. mechanical weed control) or seed losses caused by seed predation (Pannwitt *et al.*, 2017).

3 Applications of population dynamic simulation models intend to predict long-term developments. Field-specific calibration of seed production is an unfulfillable request for this type of application. Even so, long-term simulation models can profit from the results of this study, as the correspondence of estimated seeds per panicle with Norris and our data are good news for these applications. Predicting seed production very precisely and accurately is valuable in itself, but cannot replace weak data on numerous other life-cycle parameters requested in these simulation models. We conclude that the accuracy in predicting seed production based on panicle traits is satisfying for their purposes. In long-term scenario applications, research resources should be allocated sensibly to quantify all population dynamic parameters.

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