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Fecundity Allocation in Some European Weed Species Competing with Crops

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Abstract: Seed production is an important element of weed population dynamics, and weed persistence relies upon the soil seed bank. In 2017 and 2018, we studied the relationship between the aboveground dry biomass of common weed species and their seed production. Weeds were selected randomly in the fields, and we surrounded the plants with a porous net to collect shed seeds during the growth season. Just before crop harvest, weeds were harvested, the plants' dry weights were measured, and the number of seeds retained on the weeds was counted. A linear relationship between the biomass and the number of seeds produced was estimated. This relationship was not affected by year for *Avena spica-venti*, *Chenopodium album*, *Galium aparine*, or *Persicaria maculosa*. Therefore, the data of the two seasons were pooled and analysed together. For *Alopecurus myosuroides*, *Anagallis arvensis*, *Capsella bursa-pastoris*, *Geranium molle*, *Polygonum aviculare*, *Silene noctiflora*, *Sonchus arvensis*, *Veronica persica*, and *Viola arvensis*, the relationship varied significantly between the years. In 2017, the growing season was cold and wet, and the slope of the regression lines was less steep than in the dry season in 2018 for most species. *Capsella bursa-pastoris* was the most prolific seed producer with the steepest slope.

Keywords: plant allometry; population dynamics; soil seed bank; weed size



Citation: Bitarafan, Z.; Andreasen, C. Fecundity Allocation in Some European Weed Species Competing with Crops. *Agronomy* **2022**, *12*, 1196. <https://doi.org/10.3390/agronomy12051196>

Academic Editors: Jose L. Gonzalez-Andujar, Guillermo R. Chantre and Ilias Travlos

Received: 30 March 2022

Accepted: 12 May 2022

Published: 16 May 2022

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1. Introduction

A plant's ability to produce seeds depends on the plant's size and its ability to survive to reproductive maturity [1–3]. Plants often need to reach a specific size before they can devote energy to reproductive tissues [4]. Above this size threshold, many plants allocate a constant proportion of additional biomass to reproductive tissues. Therefore, a plot representing the reproductive output against size would be linear with a positive slope and x-intercept [4–6]. While there may be no single unified concept of size for plants, aboveground dry biomass is a widely used measure [4,7,8].

The relationship between aboveground plant biomass and seed production has predominantly been described by linear regression models for both crops and weeds [1,8–11]. The x-axis intercept (minimum plant biomass threshold) and the slope are crucial parameters, as the intercept corresponds to the plant biomass where the plant species is unable to produce seeds, and the slope is a measure of how fast the seed production increases with increasing biomass [1,8–11]. Guglielmini (2019) studied the reproductive allometry of four annual weed species (*Digitaria sanguinalis* L. (Scop.), *Amaranthus hybridus* L., *Setaria verticillata* (L.) P.Beauv., and *Chenopodium album* L.) in greenhouse experiments. Reproduction allocation changes allometrically under highly competitive stress, as small plants failed to set seeds unless a plant biomass threshold was attained [9]. The required minimum biomass to set seeds varies considerably between species [6,11,12]. Competition between plants may alter their growth, survival, reproductive output [13], and pattern of

biomass allocation [6]. If the competition for light is strong due to a high plant density, the plant will allocate resources to become tall at the expense of seed production [8].

The soil seed bank in the uppermost 20 cm in most agricultural soils includes millions of weed seeds per ha and is the source of yearly weed problems [14]. Seed production is a major determinant of the seed bank's magnitude. For some annual weeds with short seed viability, it is probably the single most important determinant [15].

Weed seed data, representing quantification of a population, can be used in modelling and weed management decisions and might be adequate to make rough predictions of the magnitude of the weed problem in the next year [16].

Seed production by weeds under artificial conditions, e.g., pot experiments in greenhouses [9,15] may differ from plant performance under field conditions.

This project aims to estimate model parameters to describe the relationship between the biomass and seed production of fifteen common weed species growing in Europe and elsewhere. The plants were studied in wheat and oat fields in Denmark over two growing seasons. It was hypothesized that the relationship between the biomass and seed production is linear and that the slope and the intercept of the linear regression vary between weed species and between the years. Such data are valuable and necessary for creating population models, which can be used to predict the development of plant populations—for example, the development of a herbicide-resistant weed population [17,18] or invasive species [19,20].

2. Materials and Methods

2.1. Weeds in Oat Fields

The relationship between biomass and seed production of *Anagallis arvensis* L., *Capsella bursa-pastoris* (L.) Medik., *Chenopodium album* L., *Geranium molle* L., *Persicaria maculosa* Gray, *Polygonum aviculare* L., *Silene noctiflora* L., *Sonchus arvensis* L., *Veronica persica* Poir., and *Viola arvensis* Murray was assessed during the growing season of 2017 and 2018 in spring oat (*Avena sativa* L.) in two fields with sandy soils at the research station in Taastrup (55.38° N, 12.17° E), Denmark. The species were chosen because they are among the most common weeds in Denmark and Europe [14,21,22]. One field was sown on 19 April and harvested on 29 August 2017. The other field was sown on 28 April and harvested on 2 August 2018. The row spacing was 12 cm in both years. The oat cultivar was Dominik. The sowing rate was 170 kg ha⁻¹ in both years, which is the recommended seeding rate for farmers. The fields were grown organically without applying any pesticides or fertilizer.

2.2. Weeds in Wheat Fields

The same relationship was examined for *Alopecurus myosuroides* Huds., *Apera spica-venti* (L.) P. Beauv., *Bromus hordeaceus* L., *Cirsium arvense* (L.) Scop., and *Galium aparine* L. during the growing season of winter wheat (*Triticum aestivum* L.) in two fields with clay soils at the same research station. The weed species were chosen because they are among the most common weeds in Denmark and Europe [14,21,22]. One field was sown on 27 September 2016 and harvested on 25 August, 2017. The field was fertilized with 150 kg ha⁻¹ of a combination of NPKS (22-3-8-3) on 27 September 2016, 500 kg ha⁻¹ of NPKS (22-3-10-2) on 16 March 2017, and 250 kg ha⁻¹ NPKS (33-3-10-2) on 25 April 2017. The amount of applied fertilizer is recommended to Danish farmers because of the high yield potential. The other field was unfertilized, sown on 18 October 2017, and harvested on 31 July 2018. The wheat cultivars were Elixer and KWS Cleveland in 2017 and 2018, respectively, with a sowing rate of 210 and 180 kg ha⁻¹. The fields were grown without applying pesticides.

2.3. Seed Collection

Before flowering, ten plants of each species were chosen randomly in the fields and surrounded by a trap consisting of a porous net (precision woven open mesh fabrics: SEFAR NITEX 06-475/56, Sefar, Germany; mesh opening: 475 µm-opening area: 56%) covering an area of approximately 710 cm² (Figure 1). Ten plants with approximately the same size

outside the porous net were visually observed during the season to see if they developed differently than the plants inside the traps. Twenty plants were chosen of *A. myosuroides* and *A. spica-venti*. Traps were checked each week, and seeds were collected using a portable vacuum cleaner. Every collected seed was counted until crop harvest. Just before crop harvest, weed plants were removed, the number of seeds retained on the weed plants was counted, and the aboveground plant dry weight without seeds was measured. The sum of the number of seeds shed and seeds retained on the plant was considered the total seed production.

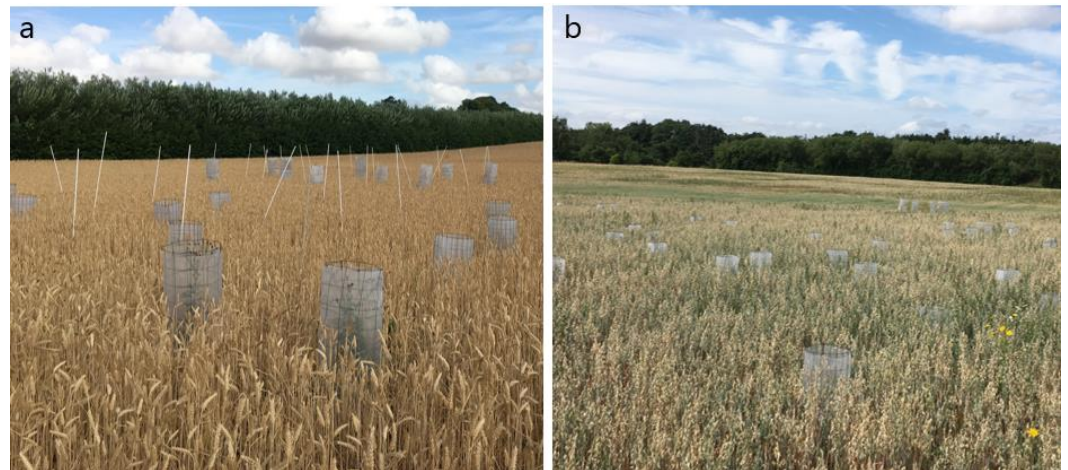


Figure 1. Seed traps placed in (a) wheat and (b) oat fields in 2018.

2.4. Weather Data

Weather data were provided from the research weather station in the area (55.67° N, 12.30° E). Figure 2 shows temperature, wind speed, and precipitation during the growth periods.

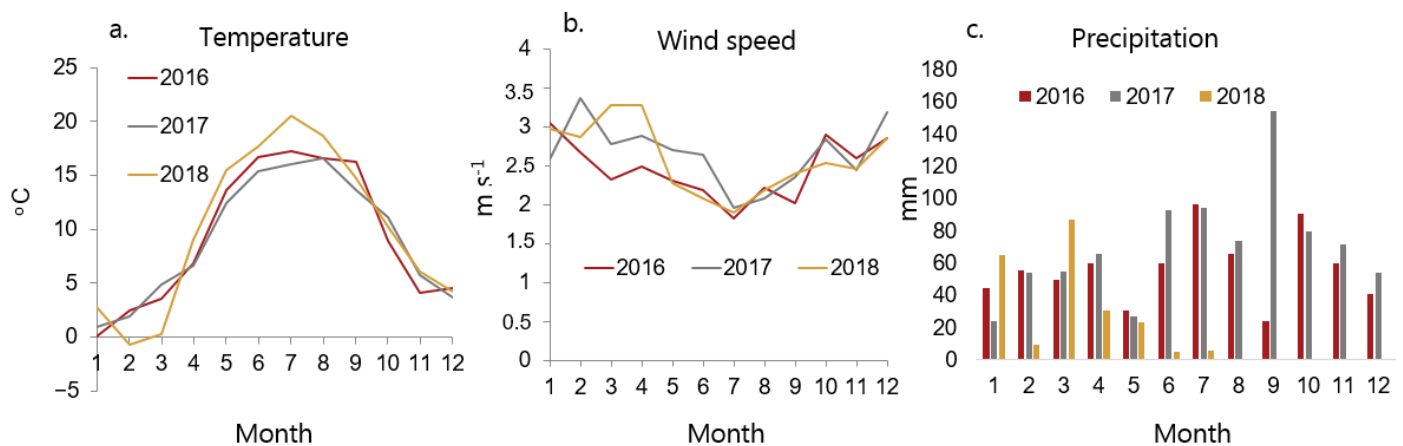


Figure 2. Weather data during the experiments: (a) daily average temperature, (b) wind speed, and (c) precipitation. Measurement height: 2, 2, and 1.5 m above ground level for temperature, wind speed, and precipitation, respectively.

2.5. Statistical Analysis

One-way ANOVA followed by Fisher's least significant difference (LSD) test for means separation was performed using the GLM package in R version 3.6.1 (The R foundation for statistical computing, Vienna, Austria, <http://R-project.org> (accessed on 14 February 2022)) to test whether the total seed production and above ground dry weight of the plants varied significantly between the years. Variance homogeneity was assessed by visual inspection of residual plots. The significance level was set to 0.05. Visual inspection of the plotted data indicated a linear relationship between dry biomass and seed production for

all species. The relationship between the seed production and biomass was assessed using linear regression analysis for the data from each year for each species separately (1):

$$y = \alpha x + \beta \quad (1)$$

where y is the seed production, x is the biomass, α is the slope, and β is the point where the line cuts the y -axis. Data from the two years were pooled if the relationship was the same in the two years (no significant difference between the years for the slope and intercept).

3. Results

The weed plants outside the nets did not differ in size or growth shape from the plants inside, indicating that nets did not significantly affect the plants in the traps.

3.1. Weeds in Oat Fields

The average plant dry weight at crop harvest was significantly different between the years for *S. noctiflora*, *V. persica*, and *V. arvensis* (Table 1). The total seed production was significantly different between the years for *G. molle*, *P. aviculare*, *S. noctiflora*, *S. arvensis*, *V. persica*, and *V. arvensis* (Table 1).

Table 1. Average plant dry weight (g) with standard deviation (SD) and total seed production (number per plant) of weed species in oat fields in 2017 and 2018. p values shown for difference between the years.

Weed Species	Plant Dry Weight (g) (\pm SD)			Total Seed Production (\pm SD)		
	2017	2018	p -value	2017	2018	p -value
<i>Anagallis arvensis</i>	0.45 (0.49)	0.32 (0.22)	$p = 0.484$	293.2 (316.0)	428.1 (341.4)	$p = 0.371$
<i>Capsella bursa-pastoris</i>	0.80 (0.96)	1.87 (2.08)	$p = 0.156$	1456 (2091.8)	7444 (10053.5)	$p = 0.081$
<i>Chenopodium album</i>	2.40 (1.53)	5.64 (5.90)	$p = 0.109$	1875.8 (944.1)	4910.1 (4660.6)	$p = 0.058$
<i>Geranium molle</i>	0.51 (0.49)	0.31 (0.16)	$p = 0.256$	117.3 (85.1)	37.3 (65.5)	$p \leq 0.050$
<i>Persicaria maculosa</i>	1.55 (1.45)	0.89 (0.44)	$p = 0.189$	413.9 (383.2)	311.4 (173.6)	$p = 0.451$
<i>Polygonum aviculare</i>	5.55 (3.34)	3.05 (2.69)	$p = 0.082$	1514.8 (841.4)	549.9 (727.5)	$p \leq 0.050$
<i>Silene noctiflora</i>	1.49 (0.74)	0.50 (0.13)	$p \leq 0.001$	539.8 (233.8)	102.6 (56.6)	$p \leq 0.001$
<i>Sonchus arvensis</i>	13.18 (4.60)	12.48 (4.76)	$p = 0.744$	460.6 (243.5)	1954.5 (819.0)	$p \leq 0.001$
<i>Veronica persica</i>	0.70 (0.59)	0.12 (0.08)	$p \leq 0.010$	511.7 (251.0)	90.5 (45.4)	$p \leq 0.001$
<i>Viola arvensis</i>	0.81 (0.93)	0.13 (0.04)	$p \leq 0.050$	203.7 (156.8)	22.0 (20.4)	$p \leq 0.010$

A positive correlation was observed between biomass and seed production for all species (Figures 3 and 4). The slope of the linear regression (α parameter in model 1) was significantly different between the years for *A. arvensis* ($p \leq 0.001$), *C. bursa-pastoris* ($p \leq 0.001$), and *G. molle* ($p = 0.043$). The intercept (β parameter in model 1) was significantly different between the years for *A. arvensis* ($p = 0.004$), *P. aviculare* ($p = 0.012$), *S. noctiflora* ($p = 0.0013$), *S. arvensis* ($p \leq 0.001$), *V. persica* ($p \leq 0.001$), and *V. arvensis* ($p = 0.014$). Differences in slopes and intercepts of the regression line of the species in each year were also tested. In both years, they were significantly different between the species (2017: both slope and intercept ($p \leq 0.01$); 2018: both slope and intercept ($p \leq 0.001$)). The intercept was positive for some species and negative for others (Figures 3 and 4).

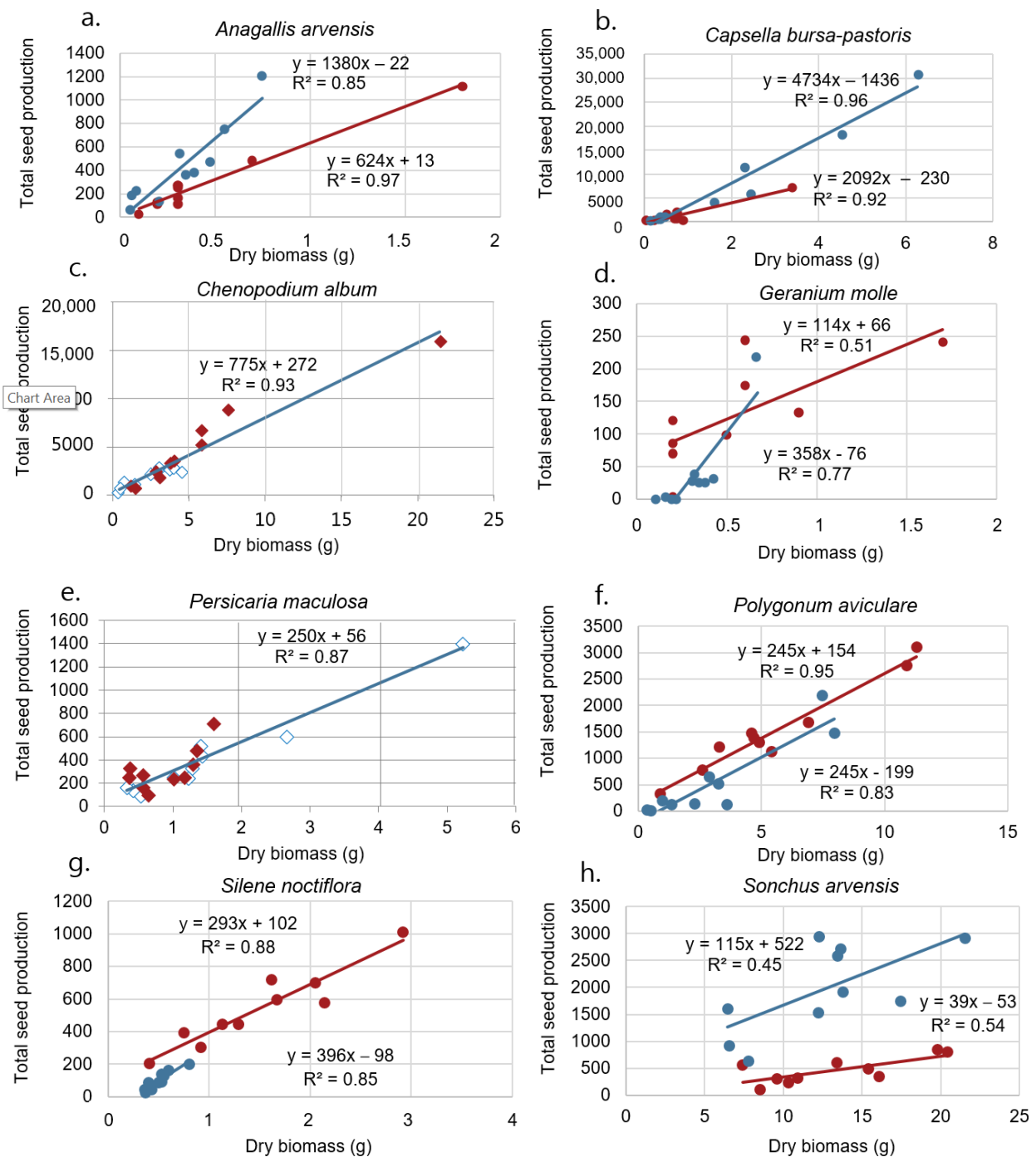


Figure 3. Relationship between plant dry biomass and seed number per plant for (a) *Anagallis arvensis*, (b) *Capsella bursa-pastoris*, (c) *Chenopodium album*, (d) *Geranium molle*, (e) *Persicaria maculosa*, (f) *Polygonum aviculare*, (g) *Silene noctiflora*, and (h) *Sonchus arvensis*. The red points correspond to observations in 2018, and the blue points correspond to observations in 2017. Regression lines are shown for both years. Where year did not affect the relationship significantly, the data from the two years were pooled together (c,e).

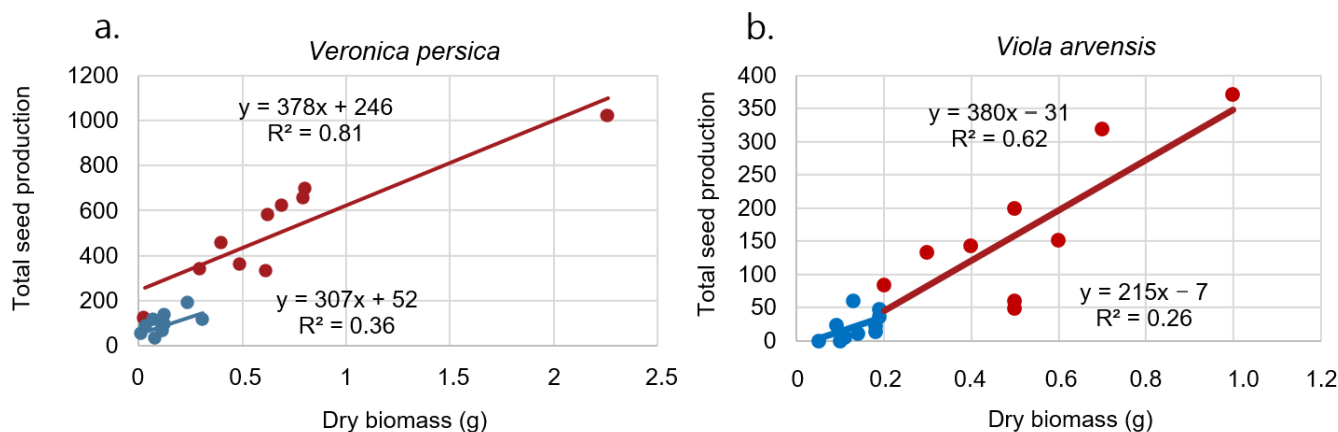


Figure 4. Relationship between plant dry biomass and seed number per plant for (a) *Veronica persica* and (b) *Viola arvensis*. The red points correspond to observations in 2018, and the blue points correspond to observations in 2017. Regression lines are shown for both years.

In the first year, the regression line for *A. arvensis*, *C. bursa-pastoris*, *P. maculosa*, and *P. aviculare* had an R^2 of 0.9. The lowest R^2 was related to *G. molle* and *S. arvensis* (both $R^2 = 0.5$). In the second year, the regression line for *C. album* and *C. bursa-pastoris* had the highest R^2 (both $R^2 = 0.9$), and the lowest R^2 was related to *V. arvensis* ($R^2 = 0.2$) (Figures 3 and 4).

Different weed species responded differently to the weather conditions. The perennial weed, *S. arvensis*, had larger biomass and seed production in the dry season. Seed production was significantly higher in the rainy season (2017) compared to the dry season (2018) for *G. molle*, *P. aviculare*, *S. noctiflora*, *V. persica*, and *V. arvensis*, while biomass was significantly increased for *S. noctiflora*, *V. persica*, and *V. arvensis*. Some species showed more variation between seasons than others did. Biomass was similar between both years for *G. molle* and *P. aviculare*. The season affected neither biomass nor seed production of *A. arvensis*, *C. album*, *C. bursa-pastoris*, and *P. maculosa* (Table 1).

3.2. Weeds in Wheat Fields

The average plant dry weight at crop harvest was significantly different between the years for *A. myosuroides*, *A. spica-venti*, *C. arvense*, and *G. aparine* (Table 2). The total seed production was significantly different between the years for *A. myosuroides*, *A. spica-venti*, and *G. aparine* (Table 2). We only found *B. hordeaceus* in the wheat field in 2017.

Table 2. Average plant dry weight (g) with standard deviation (SD) and total seed production of weed species in wheat fields in 2017 and 2018. *p*-values shown for difference between the years.

Weed Species	Plant Dry Weight (g) (\pm SD)			Total Seed Production (\pm SD)		
	2017	2018	<i>p</i> -value	2017	2018	<i>p</i> -value
<i>Alopecurus myosuroides</i>	1.95 (1.47)	6.17 (2.75)	$p \leq 0.001$	953.3 (663.8)	3337.6 (1415.1)	$p \leq 0.001$
<i>Apera spica-venti</i>	0.69 (0.71)	4.59 (1.56)	$p \leq 0.001$	1191.9 (952.4)	5678.7 (2610.5)	$p \leq 0.001$
<i>Bromus hordeaceus</i>	2.55 (1.75)	No plants	—	894.2 (627.9)	No plants	—
<i>Cirsium arvense</i>	31.84 (19.03)	16.97 (7.65)	$p \leq 0.05$	None	1647.6 (588.4)	—
<i>Galium aparine</i>	8.34 (8.36)	0.53 (0.25)	$p \leq 0.01$	616.5 (627.9)	37.3 (16.4)	$p \leq 0.01$

Cirsium arvense did not produce any seeds in 2017. We observed a positive correlation between biomass and seed production for all five species (Figure 5). The intercept was only significantly different between years for *A. myosuroides* ($p = 0.03$). The intercept was positive for some species and negative for others (Figure 5).

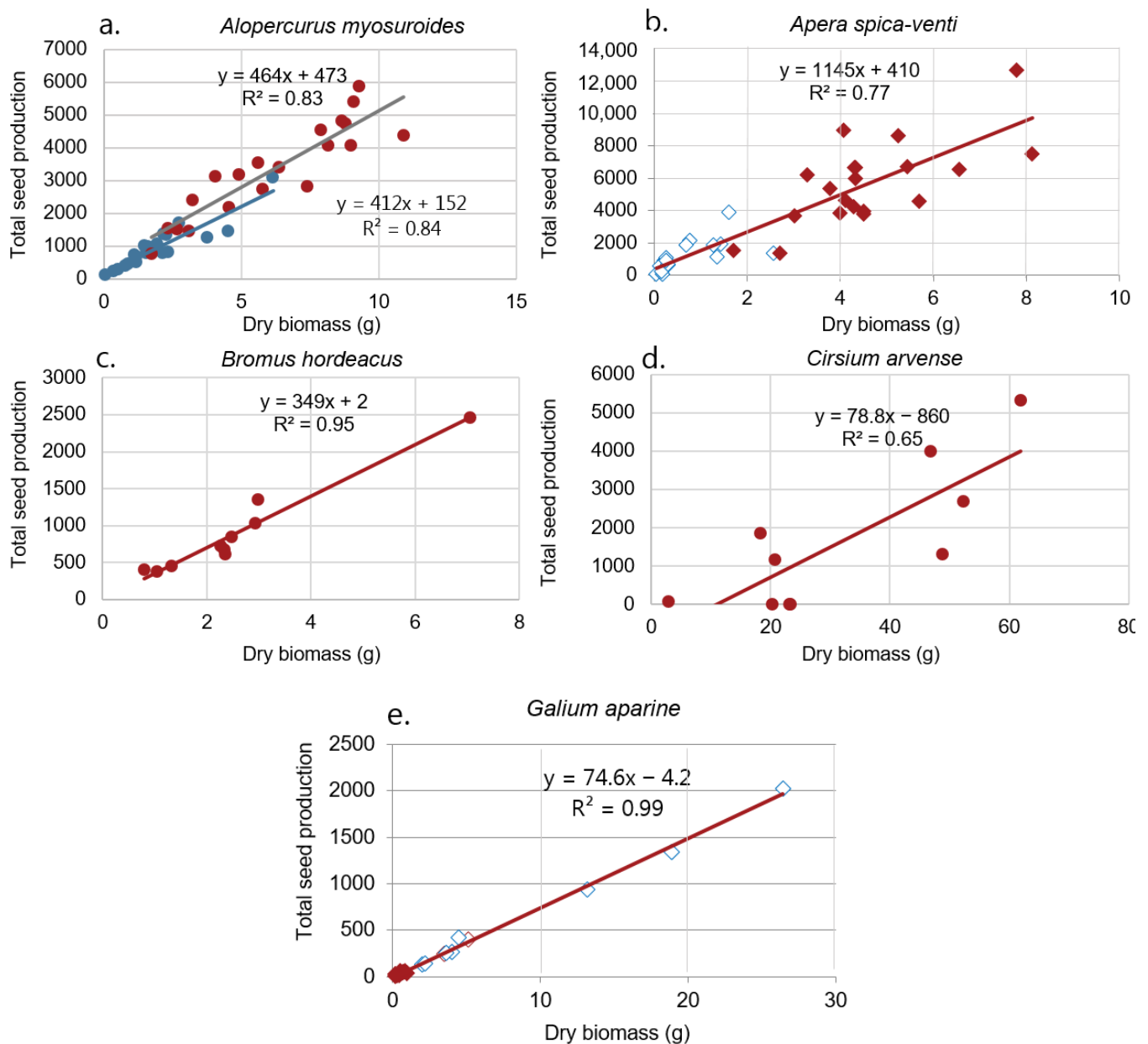


Figure 5. Relationship between plant dry weight and seed number per plant for (a) *Alopecurus myosuroides*, (b) *Apera spica-venti*, (c) *Bromus hordeaceus*, (d) *Cirsium arvense*, and (e) *Galium aparine* growing in two wheat fields. The red points correspond to observations in 2018 and the blue points correspond to observations in 2017. Regression lines are shown for both years. Where year did not affect the relationship significantly, the data from the two years were pooled together (b,e). *Bromus hordeaceus* was only observed in 2017 and *C. arvense* only produced seeds in 2018.

The dry season enhanced the growth and seed production of the two grass weeds *A. myosuroides* and *A. spica-venti*, which produced significantly more biomass and seeds than the rainy season. Biomass and seed production was substantially higher in the rainy season (2017) compared to the dry season (2018) for *G. aparine*.

4. Discussion

4.1. Weather Conditions

Figure 1 shows seed traps in the fields. Different weather conditions in the two growing seasons resulted in different biomass and seed production of the weed species in

the two years. In 2017, the summer in Denmark was cold, wet, and cloudy with no days with temperatures >30 °C. In 2018, the summer was unusually dry, warm and sunny, with many days having temperatures higher than 30 °C (Figure 2). It was the warmest summer since 1874 [23].

In the dry and warm weather in 2018, the wheat and oat plants became drought-stressed, resulting in less growth and thinner stands, creating more space and light for the weeds. Irrigation was not an option on the fields. Wheat and oat plants, along with weeds, matured earlier in 2018, resulting in harvest occurring two and four weeks earlier, respectively, than in 2017.

In 2018, the growth period was about 37 days longer than in 2017, which contributed to explaining why the size of weeds and seed production were significantly higher, as most weeds continue to set flowers and seeds if growth is not interrupted.

Wind may cool the leaf surface and reduce growth rate or supplement plants with carbon dioxide, enhancing their growth. The wind is also a major disturbance in many plant ecosystems and can play a crucial role in plant regeneration. Cereals and other herbaceous crops can often recover after wind damage [24]. However, the wind speed did not differ much between the two seasons (Figure 2). Therefore, we assume that the wind only contributed insignificantly to the observed variation in plant growth between the two years.

4.2. Regression Models

The graphical representation of the raw data suggested the application of a linear model in all the cases. For all species, a linear model described the data relatively well. The linear regressions varied widely in slope, intercept, and R^2 between weed species (Figures 3–5). Several species had positive x-intercepts, indicating a threshold size for reproduction, while there were also populations with negative x-intercepts (positive y-intercept) (Figures 3–5). Thompson et al. [25] have recorded similar results. However, a line does not describe the relationship correctly at low biomasses because the plant must produce a certain amount of biomass before producing seeds. Genetic variation within the species and different growing conditions within the fields may affect the estimation of the model parameters.

4.3. Weeds

Only a few scientific references were found about the relationship between biomass and seed production under field conditions for the studied common European weeds, probably because most weeds shatter their seed continuously during the summer months and the seeds need to be collected continuously. Otherwise, seeds might be spread by the wind or moved or eaten by seed predators [26,27].

4.3.1. Weeds in Oat Fields

Anagallis arvensis

Anagallis arvensis was the only species in the oat field where the slopes and the intercepts were significantly different in the two seasons (Figure 3a). It is a relatively small plant species with small seed production. The weed has declined significantly in Danish fields during the last century [28].

Capsella bursa-pastoris

Capsella bursa-pastoris was the most prolific seed producer, with a slope of 4734 (Figure 3b). Very small plants are able to produce seeds, and if the growth season is long, as it was in 2018, the plants become large and produce a huge number of small seeds (seed weight 0.1 mg). Hence, the variation in plant size and seed production was very large (Table 1). Its occurrence has increased significantly in Danish fields [28], probably due to the immense shift from summer to winter annual crops, which favor winter annual species. *Capsella bursa-pastoris* is mostly a summer or winter annual tetraploid and is predominantly

inbreeding [29]. It has a worldwide distribution, avoiding only the hot and wet tropics. It is one of the most frequent and widespread flowering plants on earth [30].

Chenopodium album

For *C. album*, the slopes and the intercepts did not vary significantly between the seasons and, consequently, data were pooled for the two years (Figure 3c). Like *Capsella bursa-pastoris*, *C. album* is able to produce seeds on very small plants, and plants having a long growth season may become large and produce a large number of seeds (Table 1). The largest plant weighed 21.46 g and produced 15,932 seeds. Several researchers have studied the size dependency of sexual reproduction of *C. album*. Grundy et al. [31] also found a linear relationship between seed production of *C. album* and aboveground dry weight. Seed production was mostly independent of planting density, crop competition, and growing season. The linear relationships were consistent from population to population. Relatively stable biomass and seed production offer some indications that a general relationship may be possible for use as a predictor of seed production for *C. album* [29]. Similar stability of the biomass/seed production relationship has also been shown by Rasmussen [32] for *C. album* competing with barley, even when herbicides had been used at sublethal rates. Guglielmini et al. [9] also found that seed production increased linearly with higher biomass and lower competition for *C. album*. They found, like us, that the linear regression was not different between the years for *C. album* even though plant growth and seed production were higher in the first year. They reported an intercept of zero (y -axis intercept when $x = 0$ was zero) and a slope of 1122. Aarssen and Taylor [8] studied the fecundity allocation of 21 herbaceous plant species of natural populations in Canada, including *C. album*. They estimated almost the same slope and R^2 for *C. album* (0.95 and 857.5, respectively) as we did (0.93 and 775.07, respectively). Aarssen and Taylor [8] estimated the intercept to be -3.5 , which is considerably different from what we found (272.2).

Geranium molle

The regression lines did not fit well for *G. molle* ($R^2 = 0.77$ in 2017, $R^2 = 0.50$ in 2018) (Figure 3d). Geraniums produce about five seeds per flower and disperse the seeds by forcibly ejecting them for several meters (1–4 m) [33]. The dispersal mechanism may explain the poor fit of the regression lines. Some seeds have probably escaped by being ejected out of the seed nets. A lid on the seed net would have prevented the seeds from leaving the nets but may have reduced light and hence plant growth compared to plants outside the nets.

Persicaria maculosa

The growing season did not significantly affect biomass and seed production (Figure 3e). The biomass variation and seed production were about the same for the two years despite the different weather conditions. Genotypes in this species express a wide range of functionally appropriate phenotypic plasticity in response to light, moisture, and nutrient conditions [34,35].

Polygonum aviculare

Polygonum aviculare is an annual weedy species showing extensive genetic variation in seed and leaf size. The variation in cell size and/or gibberellin content might be the mediators of the correlation found between seed size, leaf size, and growth parameters within this species [36]. The hot summer in 2018 favored the species (Figure 3f). *Polygonum aviculare* colonizes a wide range of open, man-made habitats, which differ in the type and intensity of disturbance regime [36,37]. In western Europe, genotypes with tiny seeds and small leaves tend to occur in trampled sites such as footpaths and cart tracks [38]. Plants with larger leaves occur in two kinds of untrampled habitats: in sites subject to frequent weeding activities, they are represented by short-lived genotypes with a high biomass

allocation to seed; in more stable sites with a denser plant cover, they are represented by genotypes with a longer life span and a higher biomass allocation to vegetative organs [38,39].

Silene noctiflora

There was a large difference in biomass and seed production between the two years (Figure 3g). *Silene noctiflora* thrived well in the warm summer in 2018 but poorly in the wet and cold summer in 2017. Salisbury [40] reported that in plants of *S. noctiflora* examined in England, the mean number of seeds per capsule was 182 (SE = 3) and the mean number per plant was 2587 (SE = 206), which is a considerable higher seed number per plant than we observed.

Sonchus arvensis

Sonchus arvensis is a perennial species propagating by seeds, but it also produces vegetative shoots from rhizomes. Perennials' above- and belowground biomass allocation strategies may affect the aboveground biomass/seed production relationship. However, we only included the aboveground biomass. Still, we observed a positive correlation between aboveground plant biomass and seed production (Figure 3h). A positive correlation between seed production and aboveground biomass has been reported for many herbaceous perennials e.g., [8,41–43].

Veronica persica

There was a significant difference between biomass and seed production in 2017 and 2018 (Figure 4a). The cold summer resulted in small plants and low seed production. Lutman et al. [44] studied seed production by *V. persica* and other weed species in 12 experiments in England. These species were grown in the field either on their own or in competition with a range of arable crops, though mainly winter wheat. Using the average plant weights in the different crops and these regression parameters, it was calculated that *V. persica* growing in all the tested crops would produce 700–1400 seeds plant⁻¹ (plant dry weights 0.7–1.5 g). The data for the weight of *V. persica* in winter wheat (1.2 g) indicated that it would produce 1115 seeds plant⁻¹. In contrast, when growing without intra- or interspecific competition from the crop or other weeds, *V. persica* produced 4100 seeds per plant (plant dry weight 5.5 g). Accordingly, the seed production was, in general, larger than we recorded.

Viola arvensis

Viola arvensis plants were all small, producing a small number of seeds in 2017 (Figure 4b). Lutman et al. [45] found a linear relation ($R^2 = 0.956$). The slope of the line for the plants growing without competition was over 1.0 and was significantly higher than for the samples from within the winter wheat crops, which were <1.0. Plants of this weed growing alone had an average dry weight of 29.3 g plant⁻¹ and thus produced 3714 seeds. *Viola arvensis* growing in normal density winter wheat weighed 2.6 g and produced 465 seeds, which is about the same relationship as we found (Figure 4b). Plants competing with each other as well as with the wheat, weighed <1 g, and consequently, their seed production was low—97–169 seeds per plant. Integrating the highest weed populations in the normal density wheat crop (c. 200 plants m⁻²) into these calculations resulted in an estimated seed production of c. 7400 seeds m⁻² [44].

4.3.2. Weeds in Wheat Fields

Alopecurus myosuroides

Even plants with little biomass produced seeds, and the linear regression fitted the data for both years well (Figure 5a). Moss [45] found that head numbers and head length were significantly correlated with total seed production. Head length, but not head number assessments, were also significantly correlated with viable seed production. Moss [46] suggested a quantitative model for the population development of *A. myosuroides* based

on seed cycle data from field experiments. The model includes a density dependent relationship between plant and head numbers. Heads m^{-2} (y) were found to be related to plants m^2 (x) by the equation: $y = B \times (1 + \alpha x)$, where $B = 3.88$ and $\alpha = 0.0018$.

Apera spica-venti

For *A. spica-venti* the slopes and the intercepts did not vary significantly between the seasons and, consequently, data were pooled (Figure 5b). Even tiny plants were able to produce seeds. Seeds are small (2.4 mm \times 0.6 mm) and weigh about 0.1 mg. Thompson et al. [25] reported some evidence of nonlinearity of size-dependent reproductive output for *A. spica-venti*. Although the linear regression did not fit our data well ($R^2 = 0.77$), our data showed no indication of nonlinearity.

Bromus hordeaceus

Unfortunately, the *B. hordeaceus* was only observed in the dry and warm year (2018) (Figure 5c). The linear regression fitted well to the data ($R^2 = 0.95$). Ewing and Menke [47] found that drought treatments diminished seed production, but some germinable seeds were produced under severe drought. Drought effects were carried over to the next generation because stressed plants produced smaller seedlings.

Cirsium arvense

In 2017, the plants did not produce any seeds (Figure 5d). The low temperatures and high precipitation in the summer months seemed to have blocked seed setting. *Cirsium arvense* is a perennial weed, the success and persistence of which derive from an extensive, far-creeping, and deep rooting system which ensures survival and rapid vegetative spread under a wide range of soil and management conditions. Therefore, it does not exclusively depend on seed production for surviving unto the following season. In general, *C. arvense* has the reputation of producing only a few viable seeds per flowerhead [48]. Klinkhamer et al. [49] found that seed production of flowering plants of *Cirsium vulgare* varied strongly between years. The percentage of plants that were noticeably damaged by herbivores also varied between years and caused a reduction of the seed production by 80% in 1982 and 15% in 1984.

Galium aparine

The linear regression fitted the data ideally for *G. aparine* ($R^2 = 0.9959$). One reason could be that all seeds were still on the plants at harvest. In 2018, the plants did not produce much biomass, but could still produce seeds (Figure 5e). In a study of population dynamics of *G. aparine* in West Germany, seed counts were higher on sites that had been cropped with sugar beet than on sites under grain production [50]. Seed production was lowest in spring barley (9 seeds plant^{-1}) and highest in sugar beet (2170 seeds plant^{-1} , corresponding to the same range as we recorded depending on the plant biomass).

5. Conclusions

The relationship between biomass and seed production could be described with a linear function for all weed species. The slope and the intercept of the linear regression varied between species and between the years.

This biomass/seed production relationship was not affected by year for *A. spica-venti*, *C. album*, *G. aparine*, and *P. maculosa*. Therefore, the data of the two seasons were pooled and analyzed together. For *A. myosuroides*, *A. arvensis*, *C. bursa-pastoris*, *G. molle*, *P. aviculare*, *S. noctiflora*, *S. arvensis*, *V. persica*, and *V. arvensis*, the relationship varied significantly between the years. In 2017, the growing season was cold and wet, and the slope of the regression lines was less steep than in the dry season in 2018 for most species. *Capsella bursa-pastoris* was the most prolific seed producer with the steepest slope.

We have provided information on seed production of several common weed species. Such data are valuable and necessary for creating population models. The collected

data can be used to predict the development of plant populations in combination with other data—for example, the development of a herbicide-resistant weed population or invasive species.

It would be valuable to study other populations of the same weed species in other regions and under other environmental conditions, as the genetic variation in weed populations can be large and ecological factors significantly influence seed production. Therefore, the data from one single location cannot be used to generalize the relationship between biomass and seed production for a weed species adapted to a wide range of environments and a large area of distribution.

Author Contributions: C.A. was responsible for funding acquisition and the design of the experiment. Z.B. conducted the practical work, processed the data and wrote the first draft of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was a part of the project: 105 SWEEDHART-Separation of weeds during harvesting and hygienisation to enhance crop productivity in the long term. The activity was conducted under the “Joint European research projects in the field of Sustainable and Resilient Agriculture” under ERA-NET Cofund FACCE SURPLUS 2015. We thank Innovation Fund Denmark for financial support.

Data Availability Statement: Data are available from the corresponding author.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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