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Rattail fescue (*Vulpia myuros*) interference and seed production as affected by sowing time and crop density in winter wheat

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Research Article

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Abstract

Field experiments were conducted in the growing seasons of 2017 to 2018 and 2018 to 2019 to evaluate the competitive effects of rattail fescue [*Vulpia myuros* (L.) C.C. Gmel.] in winter wheat (*Triticum aestivum* L.) and to assess whether delayed crop sowing and increased crop density influence the emergence, competitiveness, and fecundity of *V. myuros*. Cumulative emergence showed the potential of *V. myuros* to emerge rapidly and under a wide range of climatic conditions with no effect of crop density and variable effects of sowing time between the two experiments. Grain yield and yield components were negatively affected by increasing *V. myuros* density. The relationship between grain yield and *V. myuros* density was not influenced by sowing time or by crop density, but crop–weed competition was strongly influenced by growing conditions. Due to very different weather conditions, grain yield reductions were lower in the growing season of 2017 to 2018 than in 2018 to 2019, with maximum grain yield losses of 22% and 50% in the two growing seasons, respectively. The yield components, number of crop ears per square meter, and 1,000-kernel weight were affected almost equally, reflecting that *V. myuros*'s competition with winter wheat occurred both early and late in the growing season. Seed production of *V. myuros* was suppressed by delaying sowing and increasing crop density. The impacts of delayed sowing and increasing crop density on seed production of *V. myuros* highlight the potential of these cultural weed control tactics in the long-term management programs of this species.

Introduction

Rattail fescue [*Vulpia myuros* (L.) C.C. Gmel.] is an emerging weed problem in Europe, where it is particularly troublesome in winter annual crops. In Denmark, problems with *V. myuros* have increased significantly since it was first reported in red fescue (*Festuca rubra* L.) for seed production in the late 1990s (Mathiassen and Kudsk 2010). A survey focusing on *V. myuros* occurrence in red fescue seed samples received by seed companies from growers revealed a frequent occurrence of *V. myuros* in some regions of Denmark (Jensen and Kristensen 2013). Non-inversion tillage practices, combined with frequent cropping of winter cereals, can promote *V. myuros* infestations in Denmark (Scherner et al. 2016). Problems with *V. myuros* have also been reported in other European countries, for example, in the United Kingdom and Romania (Georgescu et al. 2016; Hull et al. 2011).

Vulpia myuros is a self-pollinating winter annual weed (Wallace 1997). The weediness of *V. myuros* is attributed to several factors, such as flexible germination requirements, a rapid growth rate early in its life cycle, vegetative growth under a wide range of temperatures and photoperiods, plasticity in vernalization requirement, high fecundity, and most importantly, tolerance to a wide range of herbicides (Dillon and Forcella 1984). It germinates rapidly under warm and humid weather conditions and can form dense stands very quickly due to weak primary seed dormancy. Seed fecundity can be substantial and results in large soil seedbanks within a single season if no control strategies are applied (Akhter et al. 2020a; Jensen and Kristensen 2013; Wallace 1997).

Vulpia myuros can interfere with crop growth by reducing yields markedly (Lawrence and Burke 2014). Due to tolerance of *V. myuros* to the widely used acetyl-CoA carboxylase– and acetolactate synthase–inhibiting herbicides (Yu et al. 2004), nonchemical control methods are considered important for successful management. Cultural practices such as stale seedbed, moldboard plowing, inclusion of spring-sown crops in crop rotations, and mulching can suppress the establishment and growth of *V. myuros* (Jensen 2010; Scherner et al. 2016). Studies with an array of different grass weed species have revealed that delayed sowing time and increasing crop density decrease weed growth and seed production (Keshtkar et al. 2017; Melander 1995; Pfeiffer et al. 1960; Walsh 2019) and crop yield loss (Wilson et al. 1990). However, the responses of *V. myuros* to delayed sowing time and increased crop density of winter cereals are unknown and represent potentially important information that can help define new integrated management strategies for management of *V. myuros*.

The impact of *V. myuros* on crop yield is essential information in the planning of integrated weed management programs, because it determines the need for in-season control (Lemerle et al. 2014). Available information on the competitive ability of *V. myuros* in winter cereals is limited to a single study that focused primarily on herbicide efficacy against *V. myuros* in winter wheat (*Triticum aestivum* L.). Yield reduction of 45% was reported from the single density of *V. myuros* (202 g dry weight m^{-2}) evaluated in the study (Lawrence and Burke 2014). This study was conducted in the northwestern United States and the results are not representative of northern European climatic conditions with dissimilar yield levels, growing seasons, crop seeding densities, and cropping systems. Even though seeds are the most important component for the survival of *V. myuros* populations, no studies have described seed production characteristics of this species. The objective of the present study was to quantify the competitive ability and fecundity of *V. myuros* in winter wheat and assess the influence of sowing date and crop density on weed interference. It was hypothesized that the competition of *V. myuros* with winter wheat can cause significant grain yield losses and competitive ability and fecundity of *V. myuros* can be manipulated through delayed sowing and increased crop density.

Material and Methods

Field Experiments

Two field experiments were carried out on a sandy loam soil at Flakkebjerg, Denmark (55.3°N, 11.4°E) in the growing seasons of 2017 to 2018 and 2018 to 2019. According to the World Reference Base (FAO) system, the soil is based on groundmorainic deposits from the last glaciation and is classified as a Glossic Phaeozem (Krogh and Greve 1999). The clay (<2 m), silt (2 to 20 µm), coarse sand (200 to 2000 µm), and fine sand (20 to 200 µm) content of the soil (0- to 25-cm) were 147, 137, 426, and 270 g kg^{-1}, respectively. The area has a temperate coastal climate, characterized by mild winters and cool summers. Before the experiments were established, the experimental field had been cultivated and farmed traditionally with cereal crops, with spring barley (*Hordeum vulgare* L.) being the preceding crop.

The experiments were arranged as a split-split plot design with three blocks. Sowing time was the main plot factor, crop density the subplot factor, and increasing weed density of *V. myuros* the sub-subplot factor; net sub-subplot size was 2.5 by 10 m. Seeds of *V. myuros* were collected from a winter wheat field near the experimental site in July 2017; seed samples were stored in paper bags at 4 C in the dark until experiments were initiated in October 2017 and September 2018. Target seedling densities of *V. myuros* were 0, 25, 75, 150, and 500 seedlings m^{-2}, and seeding rates were adjusted accordingly. To establish different seedling densities of *V. myuros*, an anticipated range of 0, 25, 75, 150, and 500 viable seeds m^{-2} were drilled at shallow soil depth after wheat sowing (on the same day). To obtain enough volume of *V. myuros* seeds for the drilling operations, grass seeds were mixed with dead seeds of Kentucky bluegrass (*Poa pratensis* L.). *Poa pratensis* seeds were killed by placing them in the oven at 100 C for 72 h. Seeding rates of *V. myuros* were adjusted based on a germination test. The factor crop density had two levels targeting 350 to 400 seedlings m^{-2} for low crop density and 450 to 500 seedlings m^{-2} for high crop density, regardless of sowing time. The range of high and low crop densities used in this study was based on the currently recommended winter wheat densities in Denmark (Keshtkar et al. 2017). Wheat ('Maribos') was sown at 12.5-cm row spacing on October 10 (normal sowing time) and November 7 (late sowing time) in 2017 and September 13 (normal sowing time) and October 3 (late sowing time) in 2018. The first experiment (October 2017 to August 2018) was characterized by a very wet autumn and a prolonged warm and dry summer, while the climatic conditions, especially temperature, were close to normal in the second experiment (September 2018 to August 2019) (Table 1). The actual sowing times reflect that early and late sowing in the growing season of 2017/2018 corresponded to late and very late sowing under normal conditions due to a very wet autumn with rainfall in September being 63% above average. Moldboard plowing was performed just before sowing; preparation of the seedbed was carried out with a rotary harrow (standard tine harrow) immediately before sowing. The crop was fertilized in April, using a mineral fertilizer containing 180 kg ha^{-1} nitrogen, 34 kg ha^{-1} phosphorus, and 86 kg ha^{-1} potassium for both experiments. Broadleaf weeds were controlled in early April using 382.5 g ha^{-1} bromoxynil (Buctril EC 225, 225 g L^{-1} bromoxynil, Bayer CropScience, Arne Jacobsens Allé 13, 2300 Copenhagen, Denmark) in 2018 and 7.5 g ha^{-1} tribenuron-methyl (Trimmer, 500 g kg^{-1}, ADAMA Northern Europe BV, Arnhemseweg 87, 3832 GK Leusden, Netherlands) in 2019. Although drought periods prevailed in the summer of 2018, periods of water stress were minimized by two irrigation events (30 mm each), one on May 21 and one on June 15.

Data Collection

Crop density was assessed at 5 wk after sowing (WAS) in two representative 1-m row lengths per plot. The density of established *V. myuros* seedlings was assessed in April in two randomly selected 0.25-m^{-2} quadrats per plot. To study the cumulative emergence of *V. myuros*, density was assessed in three fixed 0.25-m^{-2} quadrats per plot in the 2017 to 2018 growing season. In the growing season of 2018 to 2019, however, density was assessed in two fixed 0.25-m^{-2} quadrats per plot, because the results of 2017 to 2018 indicated a very low variation between quadrats. Density assessments were conducted twice per week in the first 2 WAS and then biweekly; in total, seven and six assessments were made in 2017 to 2018 and 2018 to 2019, respectively. Fixed quadrats were placed in 12 plots, where *V. myuros* was drilled at high densities (approximately 150 to 500 seedlings m^{-2}). At maturity, crop grain yield was assessed for a 1.5 by 10 m area of each plot using a plot combine (MT, Haldrup). Grain yield (kg ha^{-1}) was adjusted to 15% moisture content. The effects of crop density, sowing time, and *V. myuros* density on the yield components—number of crop ears per square meter, 1,000-kernel weight (TKW), and number of kernels per ear—were assessed at crop maturity. The grain protein content was measured using an Inframatic 9500 NIR Grain Analyzer (Perten Kungens Kurva, 141 05, Sweden) (Büchmann et al. 2001).

To study the influence of sowing time, crop density, and *V. myuros* density (defined as the density recorded in April) on seed production of *V. myuros*, five *V. myuros* plants were collected from around the center of each plot when panicles had fully emerged in mid-June. Panicle lengths were measured from the

Table 1. Mean monthly temperature and rainfall during the months of September to July in 2017–2018 and 2018–2019 compared with 10-yr means from 2011 to 2020.

Months	2017–2018		2018–2019		Long-term average 10-yr mean	
	Rainfall	Mean daily temperature	Rainfall	Mean daily temperature	Rainfall	Mean daily temperature
	mm	C	mm	C	mm	C
September	103	13	21	15	63	14
October	79	11	25	11	63	10
November	47	6	24	6	50	6
December	38	4	62	4	59	4
Subtotal (autumn and early winter)	267		132		253	
January	76	2	44	2	53	2
February	19	−1	34	4	35	2
March	48	0	91	5	37	4
April	47	9	13	8	28	8
Subtotal (late winter and spring)	190		182		153	
May	21	15	49	10	37	12
June	9	17	59	17	57	15
July	16	20	51	17	62	17
Subtotal (summer)	46		159		158	
Total	503		473		564	

collected plants, and the number of panicles per plant was assessed. The correlation between the number of seeds per panicle and panicle length was used to estimate the seed production per plant as described by Melander (1995). To establish the correlations, panicles of *V. myuros* were collected randomly from plots with the lowest (25 plants m^{-2}) and highest (500 plants m^{-2}) weed densities irrespective of crop density and sowing time. The number of seeds per panicle was assessed, and panicle length was measured. The influences of sowing time and crop density on seed number per panicle and panicle length in *V. myuros* were assumed to be nonsignificant. This assumption is supported by reports that seed number per unit length of panicle is an inherent characteristic of a weed species and that this characteristic is not influenced by crop competition or by sowing (Akhter et al. 2020b; Keshtkar et al. 2017; Melander 1995). The influence of weed density, irrespective of crop density and sowing time, on seed number per panicle length was analyzed by post hoc *t*-test. This analysis indicated a nonsignificant effect of weed density on the correlation between number of seeds per panicle and panicle length; therefore, seed production was estimated from correlations based on pooled data of 30 panicles collected from areas with the lowest and highest *V. myuros* densities. The estimated R^2 values for the relationship between seed number and panicle length were 0.66 and 0.79 in the 2017 to 2018 and 2018 to 2019 experiments, respectively (Supplementary Figure 1).

Seeds of *V. myuros* for the viability test were collected in plastic trays (13-cm diameter; Garta, Odense, Denmark) during seed shedding in July. Two trays per plot were placed in the plots with the lowest and highest weed density levels. The seeds were germinated on filter paper at alternating light and temperature (16 h at 15 C without light and 8 h at 25 C with light) after 3 mo of storage at room temperature under dark conditions. Seeds of *V. myuros* were considered viable when the radicle was 2-mm long. The viability of the nongerminated seeds was evaluated by press test (Taylor et al. 2004). *Vulpia myuros* seeds that were firm or hard were considered viable, while soft seeds without structural integrity were considered nonviable.

Statistical Analyses

Data from the field studies were first analyzed using an ordinary ANOVA to clarify the interactions of year with sowing time, crop density, and increasing grass weed density. Because year interacted strongly with the other three factors, and for simplicity, it was decided to analyze and present data by year. Linear and nonlinear models were used to test the effect of *V. myuros* density on the response variables in relation to sowing time and crop density. The relationship between *V. myuros* density (d) and grain yield (Y) was described using a rectangular hyperbola (Cousens 1985):

$$Y = Y_{wfree}\left[1 - \frac{id}{100(1+id/a)}\right] \quad [1]$$

where $Y_{\rm wfree}$ is weed-free crop yield, i is percentage yield loss per unit of weed density (d) as d approaches zero, and a is the maximum percentage yield loss for d increasing toward ∞.

Yield components and seed production data from the first experiment (2017 to 2018) were analyzed using a linear model (Equation 2).

$$Y = c + bd \quad [2]$$

where Y is TKW or number of crop ears per square meter or per-plant seed production, c is the intercept when weed density is zero, and b is the slope for increasing *V. myuros* density (d). Yield components and seed production data from the second experiment (2018 to 2019) indicated a curvilinear relationship and were thus analyzed using a three-parameter asymptotic nonlinear model (Equation 3).

$$Y = asym + (R_0 - asym) * e^{-e^{lrc*d}} \quad [3]$$

where Y is TKW or number of crop ears per square meter or per-plant seed production as response variables, *asym* is the lower horizontal asymptote, R_0 is the weed-free intercept, and *lrc* is the natural logarithm of the exponential rate constant.

The grain yield loss model (Equation 1) was fit using the NLMIXED procedure of SAS (SAS v. 9.4, SAS Institute, Cary, NC, USA). Remaining data analysis was performed with R statistical software v. 3.6.1 (R Foundation for Statistical Computing, Vienna, Austria, http://R-project.org) using R packages NLME v. 3.1-140 (Pinheiro et al. 2017) and LME4 v. 1.1-21 (Bates et al. 2014). The assumptions of normality and equal variance were verified graphically based on visual assessments of residual plots. Wherever the assumption of homogeneity of variance was not met, transformations were used to obtain homogeneous variances.

The model parameters were calculated using the maximum likelihood. First, a full model was generated in which parameters Y_{wfree}, i, and a in Equation 1, parameters c and b in Equation 2, and parameters R_0, lrc, and $asym$ in Equation 3 were dependent on the fixed effects of sowing time and crop density. Block was included in the model as a random term. Main and two-way interaction effects of sowing time and crop density were contrasted for each of the parameter estimates in Equations 1, 2, and 3. Based on these contrasts, nonsignificant effects were omitted from the full model, contrasting the reduced model with the full model. Justification of model simplifications were based on a likelihood-ratio test ($P < 0.05$) and the Akaike information criterion.

A two-parameter log-logistic equation (Equation 4) was fit for cumulative seedling emergence of *V. myuros* as a function of growing degree days (GDD) according to the time-to-event approach (Ritz et al. 2013):

$$E(t) = \frac{1}{1 + \exp[f(\log(t) - \log(e))]} \quad [4]$$

where E is the percent cumulative *V. myuros* emergence at a particular thermal time (t), e is the thermal time in day degrees (C) needed to attain 50% of emergence ($GERM_{50}$), and f is the slope denoting rate of emergence. The thermal time needed for initiation (10% emergence = $GERM_{10}$) and the end (90% emergence = $GERM_{90}$) of seedling emergence were estimated with 95% confidence intervals. The estimated parameters were compared by a post hoc t-test using the *Comp-Parm* function in the DRC packge in R (Ritz and Streibig 2005). The thermal time (C) (Equation 5) was calculated based on the soil temperature recorded at 3-cm soil depth using data loggers (HOBO Pendant®, 470 MacArthur Blvd, Bourne, MA 02532) installed at the experimental site at both sowing times. This analysis was implemented with the DRC package (v. 3.0-1) in the R v. 3.6.1 (Ritz et al. 2013). The base temperature of 1 C was used when calculating the accumulation of thermal time (Scherner et al. 2017b). If the mean soil temperature was at or below the base temperature, then the thermal time value was set to zero.

$$\text{Thermal time(C)} = \sum\left\{\left[\frac{\text{Maximum daily temperature} + \text{Minimum daily temperature}}{2}\right] - 1\right\} \quad [5]$$

Results and Discussion

Very different climatic conditions were recorded across two growing seasons (2017 to 2018 and 2018 to 2019) (Table 1) (DMI 2018). The weather in the first experiment (2017 to 2018) was very unusual, with uneven distribution of rainfall, the majority of which occurred in the autumn. The rainfall (mm) in the 2017 to 2018 growing season was lower than both the 2018 to 2019 rainfall and the overall long-term average rainfall of 10 yr. The deficit of precipitation in the months of May, June, and July in the growing season of 2017 to 2018 was 113 mm and 114 mm compared with 2018 to 2019 and long-term average rainfall over 10 yr, respectively (Table 1). The summer of 2018 was the warmest recorded since 1874 and unusually dry, with many days with temperatures >20 C. While the weather in the second study year (2018 to 2019) allowed timely sowing in autumn followed by a mild winter, the spring and early summer were cool, with more uniform distribution of rainfall. Consequently, very different weather resulted in significant differences between the two experiments in terms of emergence, crop–weed competition, and seed production of *V. myuros*.

Crop Population

With one exception, the winter wheat emerged uniformly within 2 to 3 WAS in both experiments. In the 2017 to 2018 growing season, due to very late sowing, crop emergence was reduced and lasted a few days longer for late sowing time than normal sowing time. In the 2018 to 2019 growing season, due to mild winters, nonsignificant differences in crop plant counts were found between sowing times. This confirms that crop density is mainly determined by seeding rate and to a very small extent by sowing time when sowing is performed before the last week of October (Melander 1995). Low and high crop densities in the 2017 to 2018 growing season were recorded as 305 and 380 plants m^{-2} at normal sowing time and 198 and 232 plants m^{-2} at late sowing time, respectively. In the 2018 to 2019 growing season, low and high crop densities were 326 and 434 plants m^{-2} at normal sowing time and 343 and 400 plants m^{-2} at late sowing time, respectively.

Vulpia myuros Cumulative Emergence

Crop density had no effect on the cumulative emergence of *V. myuros*, and the data were therefore pooled across crop densities, and parameter estimates were compared between sowing times (Table 2; Figure 1). In the 2017 to 2018 growing season, *V. myuros* seeds sown at normal and late sowing times initiated emergence ($GERM_{10}$) at the same time (124 and 123 thermal time [C], respectively); however, time to complete the emergence ($GERM_{90}$) was more rapid at late sowing time (196 C) than normal sowing time (303 C). Similar to the previous growing season, in 2018 to 2019, *V. myuros* initiated emergence ($GERM_{10}$) at the same time at the two sowing times (138 and 132 C, respectively), however, the influence of sowing time on duration of *V. myuros* emergence was reversed. For instance, time to complete the emergence ($GERM_{90}$) was greater for late sowing time (393 C) than for normal sowing time (303 C). The rate of emergence indicated that in the 2017 to 2018 growing season, *V. myuros* seed sown at late sowing time showed very rapid emergence rate ($f = -9.5$) compared with normal sowing time ($f = -4.9$). In contrast, differences in emergence rates were minor in the 2018 to 2019 growing season, with $f = -5.6$ at normal sowing time and $f = -4.0$ at late sowing time.

As late sowing time in the growing season of 2017 to 2018 corresponded to very late sowing under normal conditions (November 10), *V. myuros* seeds encountered more cold days and probably required more days for the accumulation of the heat units required to initiate emergence ($GERM_{10}$). After the initial germination, seeds of *V. myuros* completed emergence ($GERM_{90}$) more rapidly than at normal sowing time. The potential of *V. myuros* to emerge at low temperature has also been reported in previous studies, where *V. myuros* emerged at 1 C (Scherner et al. 2017b) or 0 C (Ball et al. 2008). Although *V. myuros* seeds sown at late sowing time exhibited a rapid emergence rate and finished emergence earlier in the 2017 to 2018 growing season, the total number of seedlings was lower compared with normal sowing time. However, in the more normal 2018 to 2019 season, sowing time had no effect on the total number of seedlings of *V. myuros*.

The rate and duration of emergence are key factors influencing weed competitiveness, susceptibility to different control practices, and generative potential (Forcella et al. 2000). The current study showed that *V. myuros* emerged rapidly with lower GERM90 values at normal sowing and late sowing times (303 and 393 C,

Table 2. Regression parameter estimates from the log-logistic model for cumulative percentage emergence of *Vulpia myuros*.[a]

	Regression parameters[b]					
	f (95% CI)		GERM10 (95% CI)		GERM90 (95% CI)	
Sowing time	2017–2018	2018–2019	2017–2018	2018–2019	2017–2018	2018–2019
				C		
Normal sowing time	−4.9 b (−5.34, −4.5)	−5.6 a (−6.1, −5.0)	124 a (116–132)	138 a (131–145)	303 a (284–322)	303 b (284–322)
Late sowing time	−9.5 a (−10.4, −8.5)	−4.0 b (−4.4, −3.7)	123 a (119–128)	132 a (122–142)	196 b (189–203)	393 a (364–422)
Significance level[c]	P < 0.001	P < 0.001	P = 0.16	P = 0.35	P < 0.001	P < 0.001

[a]Data from two crop densities were pooled for each sowing time in each year (2017–2018 and 2018–2019).
[b]$E(t) = 1/(1 + \exp[commacommaf(\log(t) - log(e))])$. *E* is the cumulative emergence at a particular thermal time *t*, *e* is the thermal time in day degrees (C) needed to attain 50% emergence, and *f* is the rate of emergence. Regression parameter values followed by different letters indicate significant difference across sowing times within a year.CI, confidence interval; GERM10, and GERM90, thermal time (C) needed for 10% and 90% *V. myuros* emergence, respectively.
[c]Parameter estimates were compared by *t*-tests at the 5% level of significance.

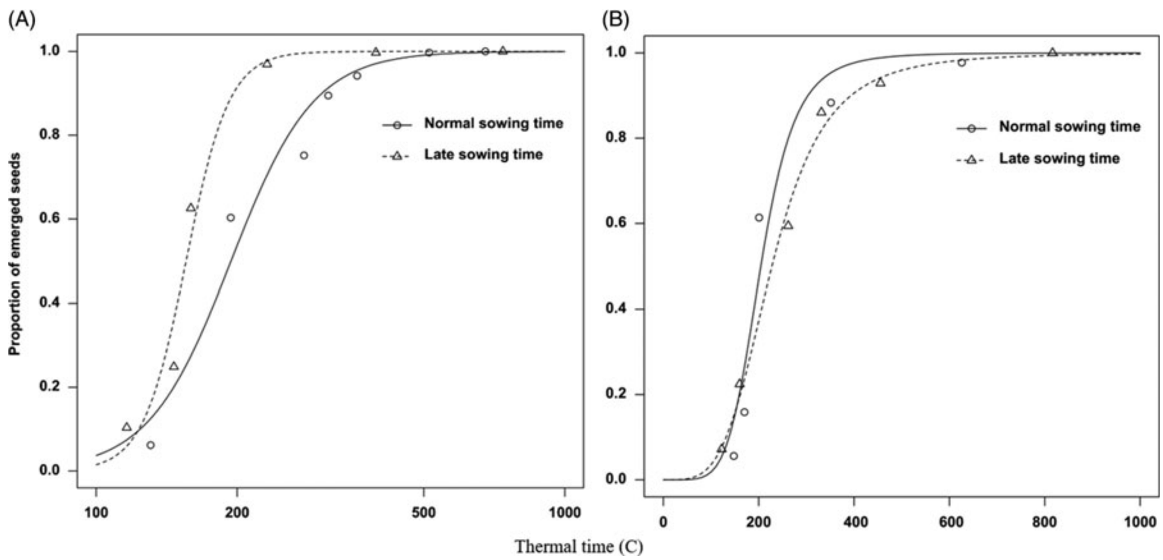

Figure 1. Cumulative emergence dynamics of *Vulpia myuros* at normal sowing time and late sowing time in relation to thermal time (C) in 2017–2018 (A) and 2018–2019 (B). Regression equation and parameter estimates described in Table 2.

respectively) under normal field conditions than, for example, annual bluegrass (*Poa annua* L.) (754 C), another common grass weed in Denmark (Scherner et al. 2017b). Rapid emergence gives *V. myuros* a competitive advantage over winter cereals early in the growing season (Dillon and Forcella 1984). The rapid germination at late sowing time in the 2017 to 2018 growing season reflects that *V. myuros* can germinate under low temperature and light conditions. These findings are similar to observations by Dillon and Forcella (1984), who reported that *V. myuros* emerged rapidly and under a wide range of light and temperature conditions. Similarly, a recent study showed *V. myuros* germination under wide range of temperature, light, and pH conditions (Weller et al. 2019). The effect of sowing time on the emergence of *V. myuros* reported in our study was inconsistent across years, probably because of very different growing conditions in the two growing seasons. In practice, the main objective of delayed sowing is to reduce weed competitiveness by reducing weed densities, delaying weed growth relative to crop growth, and reducing the survival of grass weeds during the winter (Melander et al. 2005). However, this effect cannot be expected in the present experiment, in which dry weed seeds were seeded at the time of crop seeding (Melander 1995). Non-dormant weed seeds naturally present in the soil are already imbibed and ready to germinate immediately after seedbed preparation, and this could influence emergence pattern, especially the time of initiation of emergence. In practical farming, preparing a seedbed but delaying sowing time (stale or false seedbed) means that many *V. myuros* seeds, due to their rapid germination rate, will emerge before and can be controlled mechanically or chemically before crops are sown. A study conducted in Denmark indicated that a stale seedbed could reduce density of *V. myuros* up to 80% (Jensen 2019).

Crop Grain Yield

The competitive ability of *V. myuros* based on initial yield loss per unit of weed density (i) and maximum yield loss (a) was not affected by postponing sowing and increasing crop density in the two growing seasons (Figure 2). In the 2017 to 2018 growing season, the estimated i and a parameter values were 0.43 and 21.72%, respectively; in the 2018 to 2019 growing season, the corresponding values were 0.45 and 49.81%, respectively. In 2017 to 2018, the weed-free yield (Y_{wfree}) was significantly different between sowing times but solely at late sowing time between the two crop densities. The estimated Y_{wfree} values were 10,750 kg ha^{-1} at normal sowing time, and 7,010 and 5,900 kg ha^{-1} at high and low crop density, respectively, at late sowing time in 2017 to 2018 (Figure 2A). The weed-free yield (10,260 kg ha^{-1}) was not influenced by sowing time or by crop density in 2018 to 2019 (Figure 2B).

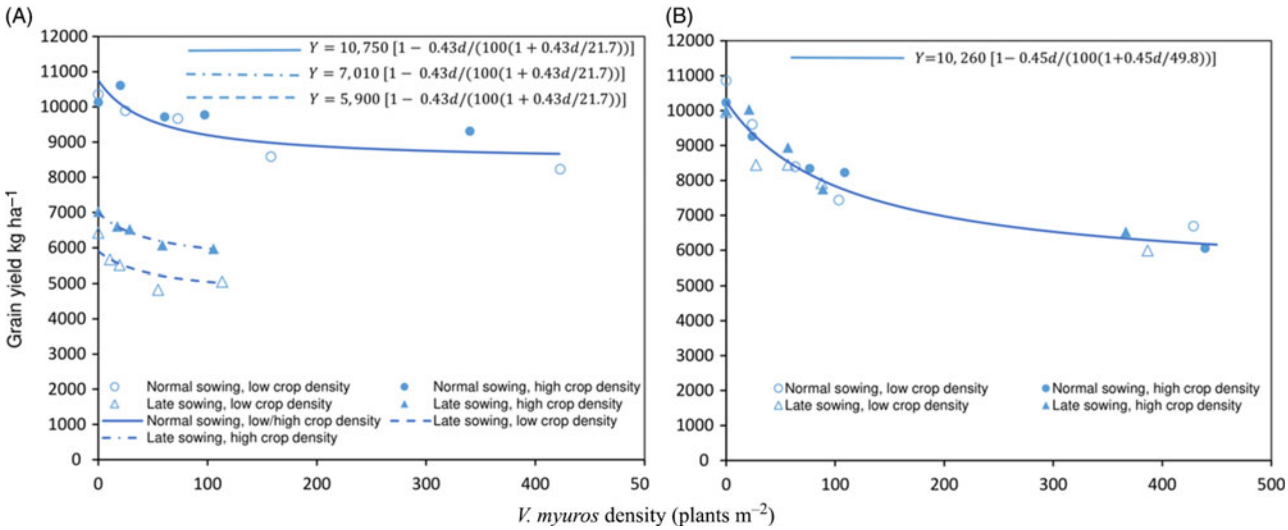

Figure 2. Relationships between crop grain yield (kg ha^{-1}) and *Vulpia myuros* density at two sowing times and crop densities in winter wheat in the growing seasons of 2017–2018 (A) and 2018–2019 (B). Data were fit to the rectangular hyperbola model (Equation 1).

A similar initial yield loss per unit of weed density (*i* parameter) in 2017 to 2018 and 2018 to 2019 indicated that *V. myuros* competitiveness was consistent at low weed densities. In contrast, a lower maximum yield loss (parameter *a*) in 2017 to 2018 compared with 2018 to 2019 likely indicates a relatively higher intraspecific competition between *V. myuros* plants at higher densities in 2017 to 2018 than in 2018 to 2019. The very different climatic conditions in the two growing seasons could explain this variation. The lower maximum yield reduction in 2017 to 2018 was most likely due to a more intense intraspecific competition for soil moisture between *V. myuros* plants. A simulation study showed that severe and frequent droughts shifted the competition in favor of deep-rooted winter wheat over shallow-rooted blackgrass (*Alopecurus myosuroides* Huds.) (Stratonovitch et al. 2012), and it is likely that the dry spring of 2018 was more stressful to the shallow-rooted *V. myuros* (Ozanne et al. 1965; Rossiter 1966) than the deep-rooted winter wheat. The estimated weed-free yields at normal sowing times were approximately the same in the two growing seasons, suggesting that the two irrigations erased the potential effect of drought on grain yield in 2017 to 2018. In 2018 to 2019, cool weather and more uniform distribution of rainfall during spring and early summer likely decreased the intraspecific competition for soil moisture between *V. myuros* plants, which may have promoted *V. myuros* competition with the crop. The positive relationship between competition and amount of rainfall across the two experiments reflected the higher sensitivity of *V. myuros* to drought. A previous study by Lemerle et al. (1995) described other possible factors such as variation in height, accumulated biomass, root proliferation, leaf area, nutrient uptake, and rate of phenological development for the variation in competitive effects of grass weeds between two growing seasons. Indeed, *V. myuros* accumulated more biomass in 2018 to 2019 than 2017 to 2018, reflecting that *V. myuros* used resources more efficiently in 2018 to 2019. On average *V. myuros* accumulated 52 and 122 g m^{-2} biomass at lowest weed density and 285 and 428 g m^{2} biomass at highest weed density in 2017 to 2018 and 2018 to 2019, respectively. The other factors listed by Lemerle et al. (1995) were not recorded in the present study.

The significantly lower weed-free and average grain yields at late sowing time in 2017 to 2018 are in accordance with previous studies in which delaying winter wheat sowing beyond the optimal sowing time always reduced grain yield (Fielder 1988; Spink et al. 2000). The significantly greater weed-free yield at high crop density at late sowing time in 2017 to 2018 can be explained by the observation made by Spink et al. (2000) that if individual plant growth was reduced due to a delay in sowing, a higher crop density was required to achieve greatest attainable yields. In 2018 to 2019, the mild winter (Table 1) could possibly explain why neither sowing time nor crop density had any influence on weed-free yields. In contrast with our study, higher crop densities have been shown to effect competitiveness of grass weeds such as *A. myosuroides* and rigid ryegrass (*Lolium rigidum* Gaudin) (Keshtkar et al. 2017; Walsh 2019). The main aim of higher crop density is to provide a dense and competitive crop stand against weeds (Walsh 2019). However, in 2017 to 2018, the late-sown crop plants were less competitive due to suboptimal growing conditions, which could partially explain the lack of influence of crop density on *V. myuros* interference. In 2018 to 2019, a mild winter and cool and rainy weather in April through June (Table 1) likely resulted in less intraspecific competition for soil moisture among *V. myuros* plants. Therefore, *V. myuros* may have maintained a competitive advantage over the crop. In practice, it is likely that effects of late sowing on *V. myuros* density would be greater than observed in the present study, because emerged weeds would be controlled before sowing.

This is the first weed–crop interaction study with *V. myuros* using an additive design with increasing *V. myuros* densities. This study helps rank the competitiveness of *V. myuros* relative to other major grass weeds of winter wheat in northern Europe such as silky bentgrass [*Apera spica-venti* (L.) P. Beauv.], *A. myosuroides*, and Italian ryegrass [*Lolium perenne* L. spp. *multiflorum* (Lam.) Husnot] Lam. The competitive ability of the four grass weeds was found to be different based on the *i* and *a* parameters estimates listed in Table 3. *Vulpia myuros* is clearly the least competitive among problematic grass weeds, as it has overall lower competitive indices (*i* and *a* parameter) values. At higher weed densities, *L. perenne* was the most competitive species with the greatest potential maximum yield losses (parameter *a*). The highest *i* parameter value for *A. spica-venti* indicates its superior competitiveness at low weed densities. Based on these limited data, we propose the following ranking: *A. spica-venti* > *L. perenne* >

Table 3. Regression estimates of the effect of increasing densities of *Vulpia myuros*, *Apera spica-venti*, *Alopecurus myosuroides*, and *Lolium perenne* on winter wheat grain yield.[a]

Weed species	Year	Regression estimates[b] *i*	*a*	Reference
		—% plant $^{-1}$m^{-2}—	—%—	
V. myuros	2017–2018	0.43 (0.25)	21.72 (4.52)	This study
	2018–2019	0.45 (0.07)	49.81 (3.28)	
A. spica-venti	1991	2.19 (0.95)	71.02 (10.23)	Melander 1995
A. myosuroides	1991	0.55 (0.25)	55.03 (5.50)	Zanin et al. 1993
L. perenne	1989–1991	0.37 (0.12)	91.73 (19.90)	Zanin et al. 1993

[a]This table shows the competitive ability of *V. myuros* and other grass weeds based on the *i* and *a* parameters estimates from the same equation (Cousens 1985).
[b]$Y = Y_{wfree}[1 - id/100(1 + id/a)]$ Parameter Y_{wfree} is weed-free crop yield, *i* is percentage yield loss per unit of weed density (*d*) as *d* approaches zero, and *a* is the maximum percentage yield loss for *d* increasing toward ∞. Standard errors are presented in parentheses.

A. myosuroides > *V. myuros*. This ranking offers insight into the potential problems associated with *V. myuros* in comparison to other problematic grass weeds. Although *V. myuros* ranked lowest of the four grass weed species, it can still cause grain yield losses up to 50%.

There was no impact of *V. myuros* interference on protein content in either growing season, except at early sowing in the 2017 to 2018 growing season, when grain protein content decreased linearly with increase in *V. myuros* density (data not shown). In addition, overall protein content tended to be higher at low crop density than at high crop density. This was expected, because fewer crop plants can take up more nitrogen, and our results are in line with those of Kolb et al. (2012), who also found highest protein contents at lowest crop density in wheat.

Yield Components

An effect of sowing time was observed on number of crop ears per square meter and TKW in the 2017 to 2018 growing season but not in 2018 to 2019 (Figure 3). No effect of crop density on crop ears per square meter and TKW was observed in either growing season, with one exception. Where main effect of crop density was observed on crop ears per square meter in the 2018 to 2019 growing season, crop ears per square meter in weed-free plots (weed-free intercept, R_0; Equation 3) were significantly lower at low than high crop density (Figure 3B). The observed decrease in number of ears per square meter and TKW and their relationship with sowing time followed a trend similar to grain yield reduction due to *V. myuros* interference, whereas this trend was not seen for crop density (Figures 2 and 3).

To investigate the contribution of yield components to the overall grain yield, a separate Pearson's correlation analysis of yield components with grain yield was performed for each sowing time for each year (Table 4). In the 2017 to 2018 growing season, a significant positive correlation was found between grain yield and number of crop ears per square meter at both normal sowing (r = 0.45) and late sowing times (r = 0.50). However, the correlation (r = 0.47) between grain yield and TKW was only found to be significant at normal sowing time (P = 0.012). In the 2018 to 2019 growing season, the reduction in crop yield was closely correlated to the reduction in number of ears per square meter (r = 0.83 and r = 0.86 at normal sowing and late sowing times, respectively), and TKW (r = 0.76 and r = 0.70 at normal sowing and late sowing times, respectively). There was no correlation between grain yield and the number of kernels per ear at either sowing time in 2017 to 2018; however, a significant negative correlation was found in 2018 to 2019 at normal sowing time (r = −0.36) and late sowing time (r = −0.46).

The significant positive correlation between grain yield and number of ears per square meter and TKW indirectly demonstrates that *V. myuros* interference with wheat occurs at both early and late crop growth stages (Table 4). Early *V. myuros* competition could have prevented tillering and caused mortality of whole plants or tillers before ear emergence, as also seen in wheat competing with winter wild oat [*Avena sterilis* L. ssp. *ludoviciana* (Durieu) Gillet & Magne] (Armin and Asghripour 2011). *Vulpia myuros* interference with winter wheat at late growth stages is most probably due to a shading effect (Supplementary Figure 2), as also seen for *A. spica-venti* in winter wheat (Melander 1995). It tends to grow taller than winter wheat and senesces later than other grass weeds such as *A. myosuroides* (Akhter et al. 2020b). Interestingly, the only variable indicating a significant negative correlation with grain yield was number of kernels per ear in 2018 to 2019. A possible explanation is that in 2018 to 2019, weed competition reduced the number of ears per square meter more than TKW (Table 4). Therefore, there could have been an increase in primary tillers with a proportionally higher number of kernels per ear at higher weed densities, as discussed by Cousens et al. (1988).

Seed Production

Vulpia myuros density had a significant effect on per-plant seed production in both years, except at late sowing time in the 2017 to 2018 growing season, where no relationship between weed seed production and weed density was observed (Figure 4). In 2017 to 2018, the linear relationship between seed production and *V. myuros* densities was influenced by crop density at normal sowing time, with average seed production being higher at low than at high crop density (Figure 4A), while crop density had no effect on seed production at late sowing time (data not shown). At late sowing time in 2017 to 2018, the average per-plant seed production in *V. myuros* was around 1,000, which was comparable to normal sowing time and much lower than in 2018 to 2019. At late sowing time in 2017 to 2018, sowing was very late, resulting in a poor crop stand that provided less competition, allowing *V. myuros* to produce a similar number of tillers and panicles at both sowing times. In 2018 to 2019, seed production in *V. myuros* was influenced by sowing time and crop density (Figure 4B). The estimated R_0 (intercept) and *asym* (lower asymptote) parameter values (Equation 3) depended neither on sowing time nor on crop density, while *lrc* (rate of decline in seed production from R_0 to *asym*) depended on both parameters. For instance, *lrc* was higher for high crop density than for low crop density, which suggested that high crop density reduced seed production. Similarly, *lrc* was higher for late sowing time, which indicated that delayed sowing reduced seed production in *V. myuros*.

The per-plant seed production in *V. myuros* was greater in 2018 to 2019 than in 2017 to 2018, with an average seed number per plant of 1,000 and 1,700 in 2017 to 2018 and 2018 to 2019, respectively. The difference in seed production between the two experiments was explained by differences in weed biomass production

Table 4. Coefficients of Pearson's correlation between winter wheat grain yield and yield components.

	2017–2018		2018–2019	
Yield components	Normal sowing time	Late sowing time	Normal sowing time	Late sowing time
Number of ears per square meter	0.45 (P = 0.014)	0.50 (P = 0.005)	0.83 (P < 0.001)	0.86 (P < 0.001)
1,000-kernel weight	0.47 (P = 0.012)	0.14 (P = 0.463)	0.76 (P < 0.001)	0.70 (P < 0.001)
Number of kernels per ear	0.083 (P = 0.674)	0.18 (P = 0.371)	−0.36 (P = 0.052)	−0.46 (P = 0.010)

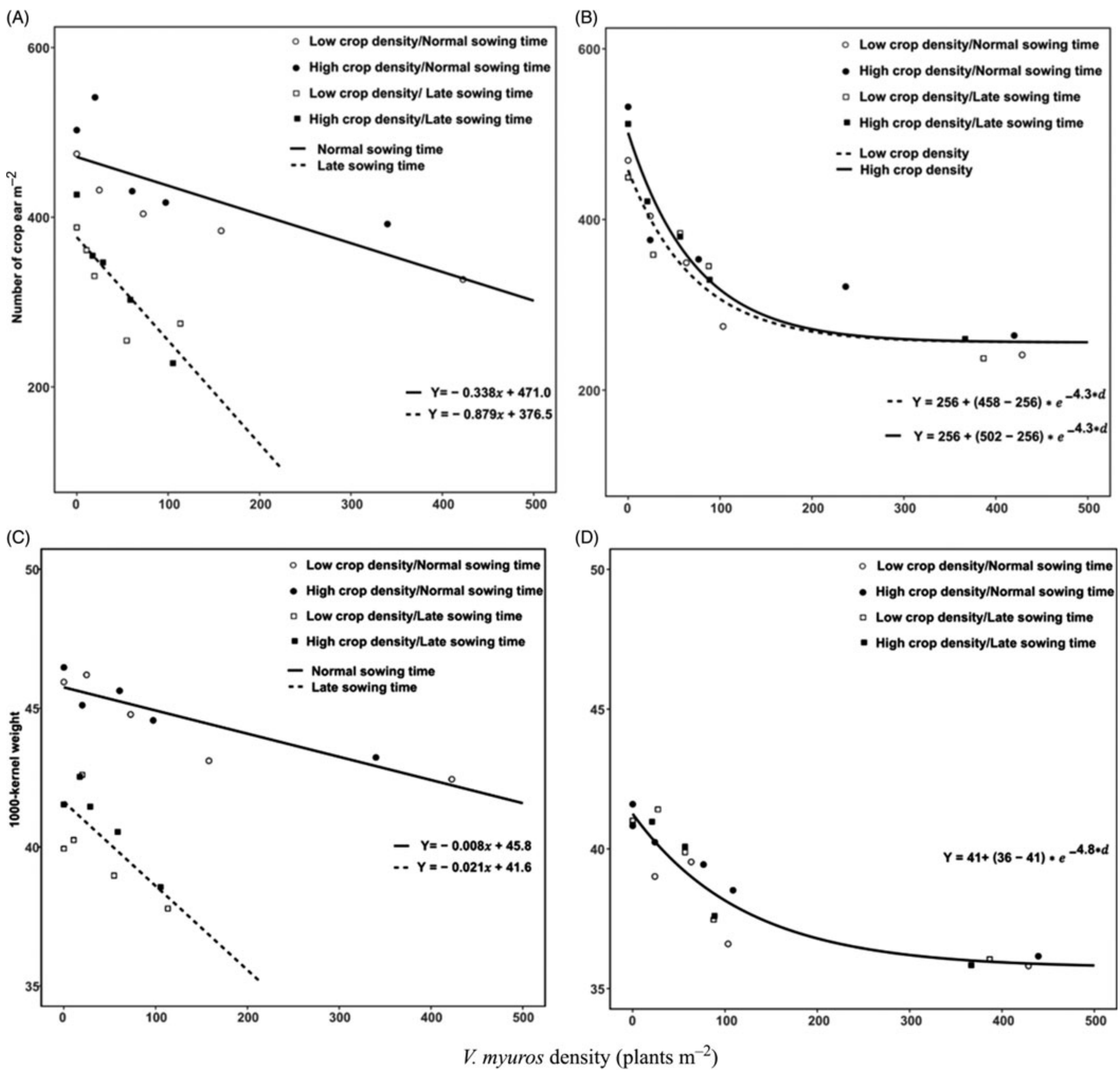

Figure 3. Relationships between yield components and *Vulpia myuros* density at two sowing times and crop densities in the growing seasons of 2017–2018 (A and C) and 2018–2019 (B and D). Number of crop ears per square meter (A and B) and 1,000-kernel weight (C and D) data are shown with fitted curves. Data from the growing seasons of 2017–2018 and 2018–2019 were fit to the linear regression (Equation 2) and asymptotic nonlinear regression (Equation 3) models, respectively.

across the two study years, as *V. myuros* accumulated more biomass in 2018 to 2019 than in 2017 to 2018. A similar relationship between weed biomass and weed seed production has been reported by Walsh (2019).

Long-term control of annual weeds depends on reducing seed production (Szekeres 1991). Crop competition is an important factor in limiting seed production of grass weeds by suppressing their growth and development (Walsh 2019). The impact of crop density

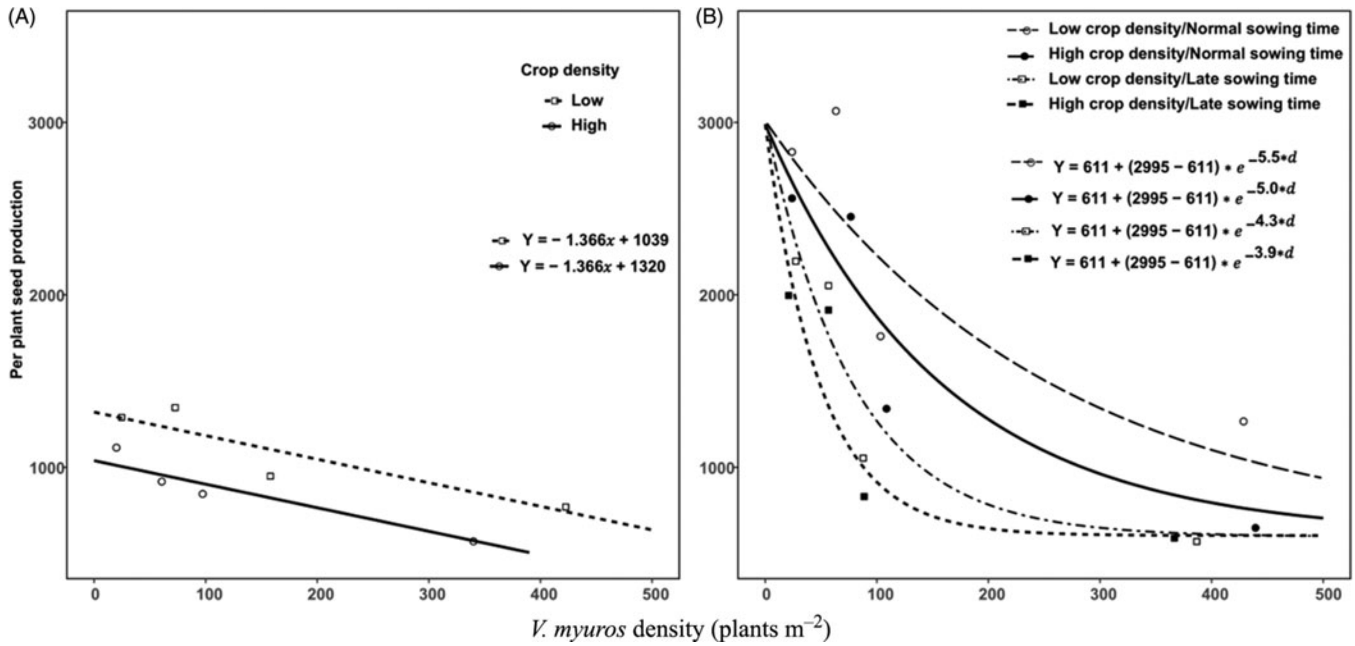

Figure 4. Relationships between the per-plant seed production and *Vulpia myuros* density at two crop densities solely at normal sowing time in the growing season of 2017–2018 (A) and at two sowing times and crop densities in 2018–2019 (B). Data from the growing seasons of 2017–2018 and 2018–2019 were fit to the linear regression (Equation 2) and asymptotic nonlinear regression (Equation 3) models, respectively.

on seed production in *V. myuros* was generally consistent across two experiments. Previous studies with grass weeds have also indicated that increasing crop density limits weed growth and seed production (Keshtkar et al. 2017; Pfeiffer et al. 1960; Walsh 2019). The potential of delayed sowing to reduce seed production was observed in 2018 to 2019, when late sowing significantly hampered seed production. Suppression of seed production by increasing crop density and delayed crop sowing has been reported for other grass weed species such as wild oat (*Avena fatua* L.), *A. spica-venti*, *A. myosuroides*, *L. rigidum*, and ripgut brome (*Bromus diandrus* Roth) (Keshtkar et al. 2017; Melander 1995; Walsh 2019).

The *V. myuros* seed viability experiment indicated no influence of weed density, sowing time, or crop density on the viability of the *V. myuros* seeds. On average, 94% and 96% of *V. myuros* seeds sampled in winter wheat were viable in 2017 to 2018 and 2018 to 2019, respectively. The high percentages of viable seed reported in the present study are in line with reports of Laude (1956), who found 98% of *V. myuros* seeds viable after a 2-mo period of afterripening. Field trials were initiated around 4 and 16 mo after seed collection in the growing seasons of 2017 to 2018 and 2018 to 2019. Hence, it is expected that the afterripening requirement was met in both experiments (Scherner et al. 2017a). Secondary dormancy due to seed storage for more than a year may have influenced establishment in the second experiment; however, a germination percentage of more than 90% suggests that it is not likely that storage conditions influenced the results in the second study year.

High individual fecundity and high seed viability demonstrate the potential of *V. myuros* to rapidly form large populations from even a few uncontrolled individuals within a field. Due to the lack of effective in-crop herbicide options, there is an urgent need for effective nonchemical weed control methods to manage *V. myuros*. Decision making concerning control of *V. myuros* in winter wheat under northern European conditions should consider not only the potential for in-season yield loss, but also the long-term effects of seed production. Elimination of seed production is critical for long-term success in managing *V. myuros*. The results from the current study highlighted the significance of sowing date and crop density for suppressing seed production in *V. myuros*. Nevertheless, sowing date and crop density cannot stand alone and have to be combined with other cultural practices such as crop rotation, moldboard plowing, and mulching to achieve effective control of *V. myuros* (Jensen 2010; Scherner et al. 2016). The information gained from the current study adds to the general understanding of the *V. myuros* biology and interference with winter wheat and can be used to optimize integrated management strategies for this species.

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Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2020.84

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