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Winter wheat yield loss in response to *Avena fatua* competition and effect of reduced herbicide dose rates on seed production of this species

Ortrud Jäck[1,2] · Alexander Menegat[2] · Roland Gerhards[1]

Abstract *Avena fatua* is one of the most abundant and competitive grass weed species in cereal cropping systems worldwide. Despite its main occurrence in summer annual cereals, *A. fatua* is suspected to cause significant yield losses in winter wheat as well. Five yield loss experiments were conducted over the course of five years to investigate the impact of *A. fatua* on winter wheat yield. Two additional field studies were conducted to assess the efficacy of two ALS-inhibiting herbicides as well as of two ACCase-inhibiting herbicides at variable dose rates on *A. fatua* seed production. *Avena fatua* caused significant winter wheat yield losses of up to 40% at densities of approximately 250 plants m^{-2}. Winter wheat yield losses did not differ between years and sites. Relative *A. fatua* biomass was a better predictor for winter wheat yield loss as *A. fatua* density and biomass. Three out of four herbicides showed high efficacy against *A. fatua*, even at reduced dose rates, but *A. fatua* seed production was not directly related to herbicide efficacy. Seed production was rather influenced by the mode of action and the competitiveness of the winter wheat stand. The results showed that *A. fatua* can be a serious threat for winter wheat production in the local conditions, leading to high yield losses if not controlled. We did not find a general potential for reducing herbicide dose rates for the control of *A. fatua* in winter wheat due to variable effects on *A. fatua* seed production. The potential is highly dependent on the winter wheat competitiveness and herbicide mode of action.

Keywords ACCase-inhibitors · ALS-inhibitors · Herbicide dose–response · Wild oat

Introduction

Avena fatua L. belongs to the 10 world's worst weeds, causing high yield losses of up to 70% in cereals [1, 2]. The species is considered as the second most abundant weed in general and the most abundant grass weed in spring cereals in Europe. Regardless of its summer annual growth habit, occurrences in winter cereals have been reported as well (e.g. [3, 4]).

For *Avena* spp. and other weed species such as *Papaver rhoeas* L. and *Phalaris minor* RETZ. it has been stated that reduction in herbicide dose rates does not significantly reduce herbicide efficacy [5, 6, 7]. However, Gonzalez-Andujar et al. [8] demonstrated that *Avena sterilis* plants produce more panicles at reduced herbicide dose rates. This might cause a shift in weed population towards less herbicide-sensitive individuals in the following generations [9, 10].

Avena fatua has recently been found in winter wheat fields in Germany. Data regarding winter wheat yield loss potential and herbicide dose-dependent control efficacy are missing in these conditions. For this reason, we investigated the yield response of winter wheat to different densities of *A. fatua*. Effects of four herbicides, commonly applied in winter wheat for the control of grass weeds, were tested on *A. fatua* biomass and seed production parameters.

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Materials and methods

Yield loss experiments

Five yield loss experiments were established in southern Germany (48°44′40.8″N 8°55′26.4″E) between 2009 and 2013, with one experiment in 2009/2010 and two experiments each in 2010/2011 and 2012/2013. Winter wheat cultivar Shamane (I.G. Pflanzenzucht GmbH, München, Germany) was sown to a depth of 3 cm and at a density of 330 seeds m^{-2} in 2009 and 2010, respectively, 300 seeds m^{-2} in 2012 (Table 1). Row distance was 12 cm in all years. Depending on harvest time of the previous crop and weather conditions in autumn, winter wheat was sown between the beginning of October and the end of November. Avena fatua seeds were sown with a RTK-GPS-equipped precision seed drill (Deppe, Bad Lauterberg, Germany) between the winter wheat rows to a depth of 1.5 cm. A germination test was previously carried out to calculate the needed A. fatua sowing densities which were adjusted accordingly towards the intended target density levels. The target density levels were 0, 1–25, 26–75, 76–125, 126–225 and 226–325 plants m^{-2} in the experimental seasons 2009/2010 and 2010/2011 and were reduced to five levels in 2012/2013 due to experimental space limitations: 0, 1–50, 51–100, 101–200 and 201–300 in 2012/2013.

In 2009/2010 and 2010/2011, 150 g ha^{-1} fluroxypyr, 3.75 g ha^{-1} florasulam and 120 g ha^{-1} clopyralid (Ariane C, EC, Dow AgroScience) were sprayed to control the broad-leaved weeds. In 2012/2013, 750 g MCPA ha^{-1} (U 46 M-Fluid, SL, Nufarm) was used for this purpose. Grass weeds other than A. fatua and broad-leaved weeds that survived the herbicide treatments were removed manually. The weed-free control plots were continuously hand-weeded. Crop management was performed according to the common practice in the region. Total nitrogen fertilizer amount was dependent on residual soil nitrogen (N_{min}) and accounted for 150 kg N ha^{-1} in 2009/2010 and 2010/2011 and 170 kg N ha^{-1} in 2012/2013 split into three applications. A growth regulator (Trinexapac-ethyl 0.2 l ha^{-1} Moddus, 250 g a.i. L^{-1}, ME, Syngenta Agro GmbH, Maintal, Germany) was applied during winter wheat stem elongation.

The experiments were set up as completely randomized block design with three replications. Experimental plots had a size of 2 × 9 m divided into two parts. The larger part of size 2 × 6 m was used for grain yield assessment using a combine plot harvester. In the smaller part of 2 × 3 m, destructive measurements of weed and crop biomass were carried out. At the two-leaf-stage of A. fatua, an area of 0.5 m^2 in each plot was harvested 2 cm above ground. Winter wheat and A. fatua were separated and shoots of A. fatua were counted (except for experiment 3). The samples were dried in an oven at 80 °C for 48 h for dry biomass determination. Relative A. fatua biomass was calculated as A. fatua biomass divided by total biomass (i.e. winter wheat biomass + A. fatua biomass).

Herbicide dose–response experiments

Additionally, two dose–response experiments were carried out in season 2012/2013 at two experimental sites at the same location as the yield loss experiments. The two sites differed in soil type, crop rotation and sowing date. Site A is a low-yielding site with a loamy clay soil and average winter wheat yields of 5.5 t ha^{-1}. Previous crop was maize, resulting in a later winter wheat sowing. Site B is characterized by a loamy soil with average winter wheat yields of approximately 8 t ha^{-1}. Previous crop on this site was durum wheat. Winter wheat cultivar, sowing dates and sowing density as well as crop management were the same as in the yield loss experiments. Sowing density of A. fatua was calculated according to targeted seedling density of 50 plants m^{-2}. At site A, one herbicide treatment was conducted with 750 g MCPA ha^{-1} (U 46 M-Fluid, 500 g a.i. L^{-1}, SL, Nufarm) to control broad-leaved weeds. At site B, no additional control of broad-leaved weeds was necessary. Grass weeds other than A. fatua and new emerging broad-leaved weeds were continuously removed manually at both sites.

The experimental layout was a split-plot design with three replications at each site. Herbicides were randomized as main factor, and dosages were randomized as sub-plots

Table 1 Experimental details of yield loss experiments

Season	Experiment	Sowing date	Sowing density (seeds m^{-2})	Weed-free winter wheat yield (t ha^{-1})
2009/2010	1	7th Oct	330	7.4
2010/2011	2	11th Oct	330	6.4
2010/2011	3	11th Oct	330	7.3
2012/2013	4	22nd Nov	300	4.7
2012/2013	5	24th Oct	300	7.7

within the herbicide main-plots. Plots were 2 m wide and 2.5 m long. Iodosulfuron + mesosulfuron (Atlantis WG, 5.6 g kg^{-1} iodosulfuron + 29.2 g kg^{-1} mesosulfuron, WG, recommended dose rate 10.44 g a.i. ha^{-1}, Bayer CropScience), florasulam + pyroxsulam (Broadway, 22.8 g kg^{-1} florasulam + 68.3 g kg^{-1} pyroxsulam, WG, recommended dose rate 11.84 g a.i. ha^{-1}, Dow AgroSciences), pinoxaden (Axial 50, 50 g L^{-1}, EC, recommended dose rate 45 g a.i. ha^{-1}, Syngenta) and fenoxaprop-P (Ralon Super Power Plus, 63.6 g L^{-1}, EW, recommended dose rate 63.6 g a.i. ha^{-1}, Nufarm) were applied at seven descending dosages each, (100, 75, 50, 37.5, 25, 12.5 and 0% of the field rate recommended by the manufacturer). Furthermore, herbicides were applied together with their recommended additives. Dose rate of the additives was the same for all herbicide dose rates. Herbicides were applied at the 2–3 leaf growth stage (BBCH 12–13 [11]) of *A. fatua*. At the time of herbicide application, winter wheat was at growth stage BBCH 25 at site A and at growth stage BBCH 31 at site B. Herbicide application was carried out with a hand-driven plot sprayer equipped with flat-van nozzles (IDK 120-02, Lechler, Germany) and at a pressure of 320 kPa and a water volume of 200 L ha^{-1}.

Average minimum and maximum temperatures within two weeks before application were 6.4 and 22.2 °C, which dropped to 3.7 and 18.5 °C within the two weeks after herbicide application. Occasionally, light rainfall occurred.

Four weeks after herbicide treatment, *A. fatua* plants were counted within an area of 0.5 m^{-2} per plot. Subsequently, crop and weed biomass was harvested in the same area. Winter wheat has reached BBCH 47 at site A and at BBCH 55 at site B at this time. Biomass samples were separated into crop and weed, oven-dried at 80 °C for 48 h and weighted for dry biomass assessment. At the beginning of *A. fatua* seed ripening, panicles per plant were counted on five randomly chosen plants per plot. Immediately afterwards, the same plants were harvested to assess seeds per panicle. Additionally, total number of panicles per plot was counted. If there were less than five plants per plot, the assessment of panicles and seeds per panicle was done on the surviving plants. Finally, the number of seeds per plant was calculated as well as the total seed input m^{-2}.

Statistical analysis

Winter wheat yield data was transformed into relative yield loss with respect to the corresponding control treatment. The yield loss function according to Cousens [12] was fitted to the relative yield loss data following the equation:

$$\text{YL} = \frac{i \times x}{1 + i \times x/a}$$

with YL = relative yield loss and x = the independent variable, in our study relative *A. fatua* biomass, absolute *A. fatua* biomass or *A. fatua* density. The parameter i stands for the initial yield loss per unit x for $x \rightarrow 0$. Parameter a stands for the maximum yield loss (asymptote) for $x \rightarrow \infty$. Data were first fit separately for each experiment before the model was stepwise reduced to obtain common parameters for all experiments. The reduced models were compared via F test ($\alpha = 0.05$) to the full model. If the models did not significantly differ, common parameters were used for the experiments. *Avena fatua* data from dose–response experiments were analysed separately for each herbicide by performing regression analysis. A log-logistic dose–response model according to Streibig [13] was fitted with variable parameters for the different experimental sites:

$$Y = (D - C)/(1 + e^{(b \times (\log(x) - \log(e)))})$$

D = upper limit for herbicide dosage $x \rightarrow 0$, C = the lower limit of the function for herbicide dosage $x \rightarrow \infty$. The parameter e reflects the ED$_{50}$ value, i.e. the herbicide dosage at which 50% efficacy occurs, and parameter b stands for the slope around the inflection point e.

In a first step, the upper and lower limits (D and C) were tested on significant differences between experimental sites. For further analysis, data were normalized with respect to the corresponding control treatment (D) and C to allow comparison of ED-values between experimental sites, following the equation:

$$Y' = (Y - C)/(D - C)$$

with Y = the measured data and Y' = the normalized data. The above described log-logistic model was fitted to the normalized data with parameters varying with experimental sites. A Box-Cox transformation was performed to enhance heterogeneity of residuals. The model was then stepwise reduced to obtain common parameter estimates for experimental sites. The reduced models were compared via F tests ($\alpha = 0.05$) to the full model on significant differences of parameter estimates between experimental sites. ED$_{50}$ and ED$_{90}$ values were estimated from the final model and compared via F tests on significant differences between sites, in the case that parameter estimates for b or e differed significantly between experimental sites.

Herbicide efficacy was calculated from *A. fatua* residual biomass relative to *A. fatua* biomass of the untreated control.

Because winter wheat data did not show a dose–response relationship, data were analysed by analysis of variance. Data of winter wheat were first analysed separately by herbicides to test whether there were effects of dosages on biomass, number of tillers and yield. Analysis of variance models included a block effect and effects for the factors experimental site and herbicide dosage as well

as their interaction. Because effects of dosages and interaction with the experimental site were not significant for any of the herbicides, both effects were excluded from further analysis. Block effect and effects for the factors experimental site and herbicide were included. Analysis of variance was performed, and significant factors were compared with Fisher's least significant differences test ($\alpha = 0.05$).

Statistical analyses were performed using R version 3.1.1 and the package 'agricolae' for calculating Tukey's honestly significant differences [14, 15]. Dose–response analysis was performed using the package 'drc' [16].

Results

Winter wheat yield loss in response to *A. fatua* competition

The highest *A. fatua* density considered in the experiments was around 250 plant m^{-2}, but most of the densities reached less than 100 plants m^{-2}. *Avena fatua* caused significant yield losses in winter wheat in four out of five experiments (Fig. 1a–c; Table 2). It was not possible to fit the yield loss function to *A. fatua* density separately for the
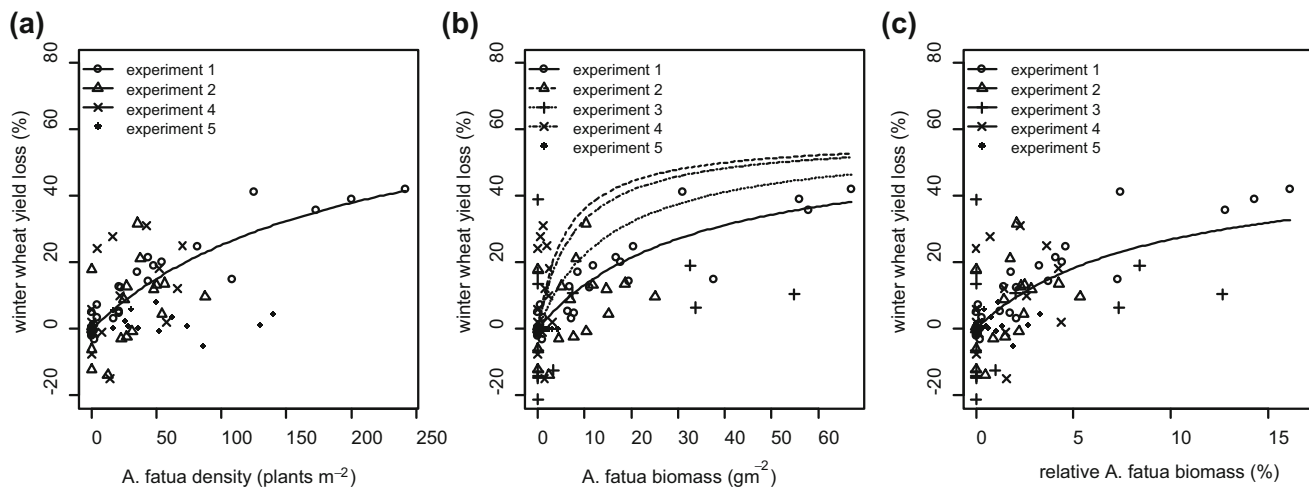

Fig. 1 Relative winter wheat yield loss in relation to *Avena fatua* density (**a**), *A. fatua* biomass (**b**) and relative *A. fatua* biomass (**c**). Fitting of the yield loss function [12] to *A. fatua* density (**a**) was only possible when data of all experiments were merged. A separate fitting was not possible. Therefore, only one regression line is presented. **b** Shows separate regression lines for the experiments, because the

initial yield loss parameter *i* differed significantly between the experiments (Table 2). There were no significant differences between the experiments regarding winter wheat yield loss in dependency of relative *A. fatua* biomass. Therefore, only one common regression line is shown (**c**). It was generally not possible to fit the yield loss function to data of experiment 5

Table 2 Parameter estimates with corresponding standard errors and *p* values for winter wheat yield loss in dependency of *Avena fatua* density, *A. fatua* biomass and relative *A. fatua* biomass

	Parameter	Estimate	Standard error	*p* value
Avena fatua density	i	0.375	0.0815	<0.001
	a	76.639	30.1942	0.014
Avena fatua biomass	i1	1.707	0.7309	0.023
	i2	0.970	0.4251	0.026
	i3	0.364	0.2599	0.166
	i4	7.617	3.5053	0.033
	a	57.430	23.7491	0.018
Relative *A. fatua* biomass	i	5.659	1.818	0.003
	a	51.203	21.203	0.018

There is only one parameter estimate each for *A. fatua* density resulting from fitting the yield loss function to combined data from all experiments, because separate fitting for the experiments was not possible. There were significant differences for parameter *i* when the function was fit to *A. fatua* biomass data; however, parameter *a* was the same for all experiments. Winter wheat yield loss parameters did not differ between the experiments, when the function was fitted to relative *A. fatua* biomass

experiments. Therefore, the yield loss function was fitted to the combined dataset over all experiments.

For low *A. fatua* biomass, significant differences between the experiments for the initial yield loss parameter *i* were found ($p = 0.04$). However, maximum potential yield loss *a* was the same across all experiments ($p = 0.50$) (Fig. 1b). Initial yield losses ranged from 0.4 to 7.6% per g *A. fatua* dry biomass m^{-2}. Maximum potential yield loss of winter wheat caused by *A. fatua* was estimated to be 57% (Table 2). Maximum *A. fatua* dry biomass was reached in experiment 1 with 67 g dry weight m^{-2}.

When *A. fatua* biomass was converted into relative biomass, its relationship to winter wheat yield loss did not differ between the experiments ($p = 0.25$) (Fig. 1c). Initial yield loss of winter wheat was estimated to 5.7% per percent relative *A. fatua*. Maximum yield loss was 51%.

Dose–response experiments

Impact of the experimental site on winter wheat and A. fatua growth

Herbicides and dosages did not influence the number of winter wheat tillers, dry biomass and yield in the dose–response experiments. But they differed significantly between the two experimental sites. Winter wheat density and accumulated biomass at site B was significantly higher compared to site A (data not shown). Winter wheat yield
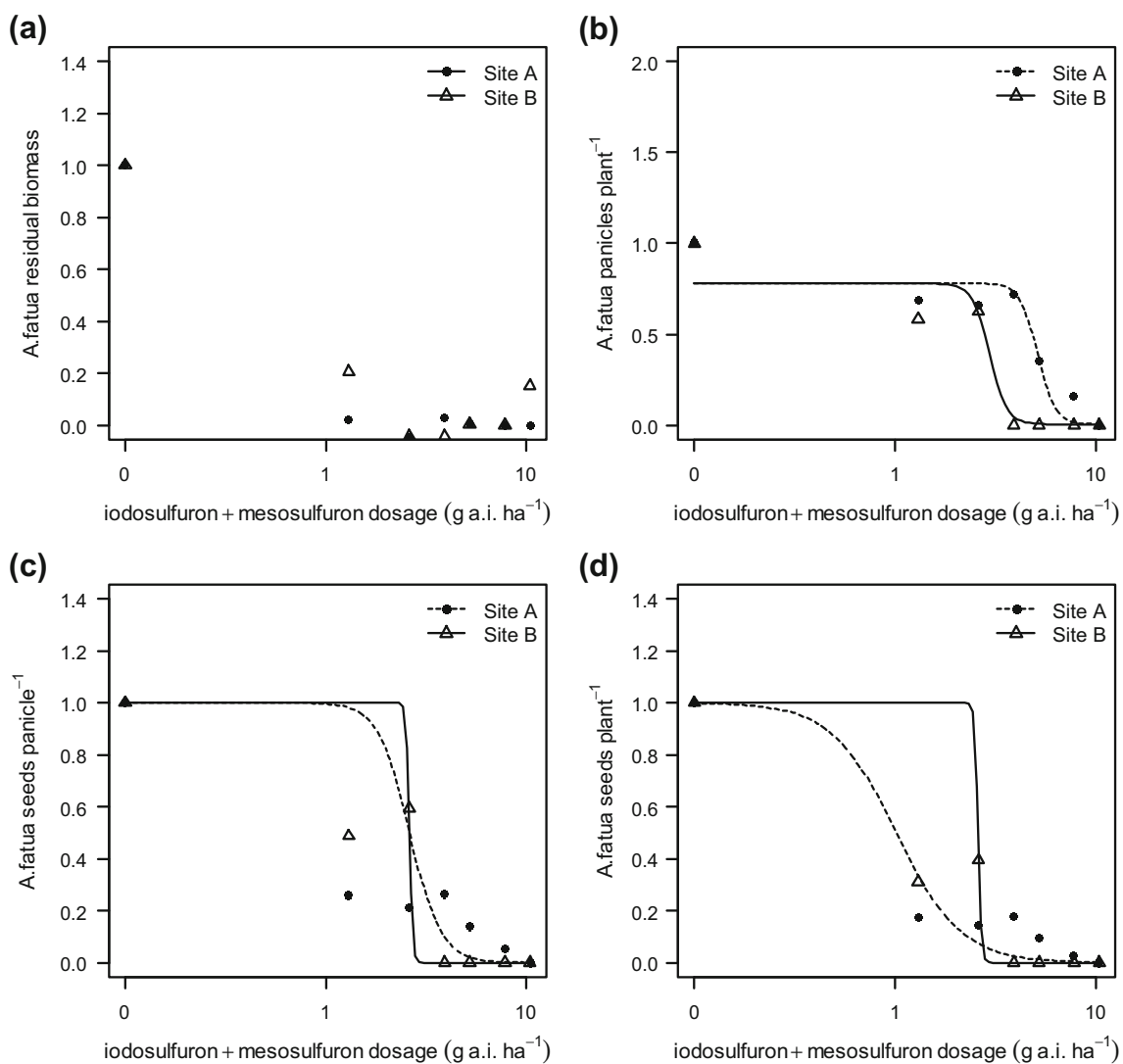
Fig. 2 Influence of variable dosages of iodosulfuron + mesosulfuron on *Avena fatua* biomass (**a**), *A. fatua* panicle production (**b**), number of seeds per panicle (**c**) and *A. fatua* seed production (**d**) at the two experimental sites site B and site A. The highest tested dosage relates to the recommended dose rate. Normalized data are shown. There was no dose–response relationship between *A. fatua* residual biomass and iodosulfuron + mesosulfuron dosage (**a**). Therefore, no regression lines are presented

was 8.7 t ha^{-1} at site B and significantly higher than at site A where winter wheat yield was 5.9 t ha^{-1}.

Despite the same amount of sown seeds, the established *A. fatua* densities differed significantly between the experimental sites with on average 34 plants m^{-2} at site A and 18 plants m^{-2} at site B. Four weeks after treatment, average *A. fatua* dry biomass in the untreated plots was 30.0 g m^{-2} at site A and significantly higher compared to site B (17 g m^{-2}). *Avena fatua* panicles per plant, seeds per panicle and seeds per plant in untreated plots did not significantly differ between the experimental sites, but tended to be lower at site B. Average number of seeds per plant of untreated *A. fatua* was 85 at site B and 110 at site A. Total seed input m^{-2} measured at the end of the season was 1700 seeds m^{-2} at site B and 5300 seeds m^{-2} at site A.

Avena fatua seed production in response to iodosulfuron + mesosulfuron dose rate

Iodosulfuron + mesosulfuron showed high efficacy against *A. fatua* at both experimental sites and throughout the tested dose rates (Fig. 2a). Due to the high efficacy, even at low dose rates, it was not possible to fit a dose–response model for these data. Residual *A. fatua* biomass was the same for all tested dosages, but complete control was not achieved.

Panicle production significantly differed between the experimental sites. At site A, panicle production was observed for dose rates below 75% of the recommended field rate, whereas at site B panicle production was inhibited until 37.5% of the recommended dose rate (Fig. 2b).

The influence of iodosulfuron + mesosulfuron dose rates on the number of *A. fatua* seeds per panicle differed significantly between the two experimental sites. ED90 values were 2.7 g a.i. ha^{-1} for site B and 3.9 g a.i. ha^{-1} for

site A ($p = 0.006$) (Fig. 2c; Table 3). At site B, seed production was inhibited at dose rates >37.5% of the recommended field rate (Fig. 2d). In contrast, any reduction in the iodosulfuron + mesosulfuron dose rate below the recommended field rate caused seed production at site A.

Avena fatua seed production in response to florasulam + pyroxsulam dose rate

Efficacy of florasulam + pyroxsulam on *A. fatua* biomass, number of seeds per panicle and seeds per plant did not significantly differ between the experimental sites (Fig. 3 a, c and d). A complete control of *A. fatua* biomass was not achieved at any of both sites, and thus, *A. fatua* produced seeds even at the recommended dose rate. There was no dose–response relationship between florasulam + pyroxsulam dose rate and number of *A. fatua* panicles per plant (Fig. 3b). However, number of *A. fatua* panicles per plant tended to be lower at site B.

Avena fatua seed production in response to fenoxaprop-P dose rate

Efficacy of fenoxaprop-P on *A. fatua* biomass, panicles per plant, seeds per panicle and total seeds per plant did not differ significantly between the two experimental sites (Fig. 4a–d). ED$_{90}$ for *A. fatua* dry biomass reduction was 15.7 g a.i. ha^{-1} which equates to 25% of the recommended dose rate (Table 3). Although differences between the experimental sites were not significant, *A. fatua* did not produce panicles at site B at fenoxaprop-P dosages as low as 37.5% of the recommended dosage. At site A, panicle production and thus seed production was inhibited at dose rates $\geq$75% of the recommended field rate. ED$_{90}$ for the number of seeds per plant was 29.1 g a.i. ha^{-1}.

Table 3 Estimates of ED$_{50}$ and ED$_{90}$ values of the tested herbicides for *Avena fatua* dry biomass, number of panicles per plant, number of seeds per panicle and number of seeds per plant

Parameter	Experimental site	Iodosulfuron + mesosulfuron		Pyroxsulam + florasulam		Fenoxaprop-P		Pinoxaden	
		ED$_{50}$	ED$_{90}$	ED$_{50}$	ED$_{90}$	ED$_{50}$	ED$_{90}$	ED$_{50}$	ED$_{90}$
Dry biomass	Site B	–	–	0.11	9.94	4.4	15.7	7.0	19.6
	Site A	–	–						
Panicles per plant	Site B	3.0	3.7	–	–	15.3	17.9	13.6	20.3
	Site A	5.1	6.4	–	–				
Seeds per panicle	Site B	2.6	2.7	1.05	2.17	20.3	24.4	10.7	15.4
	Site A		3.9					16.7	24
Seeds per plant	Site B	2.6*	2.7*	1.41	1.81	12.7	29.1	4.5	18.2
	Site A	1.0*	2.3*					9.8	21.5

Estimates are based on normalized data. If differences between the experimental sites were not statistically significant, only one common parameter estimate of the reduced dose–response model is given

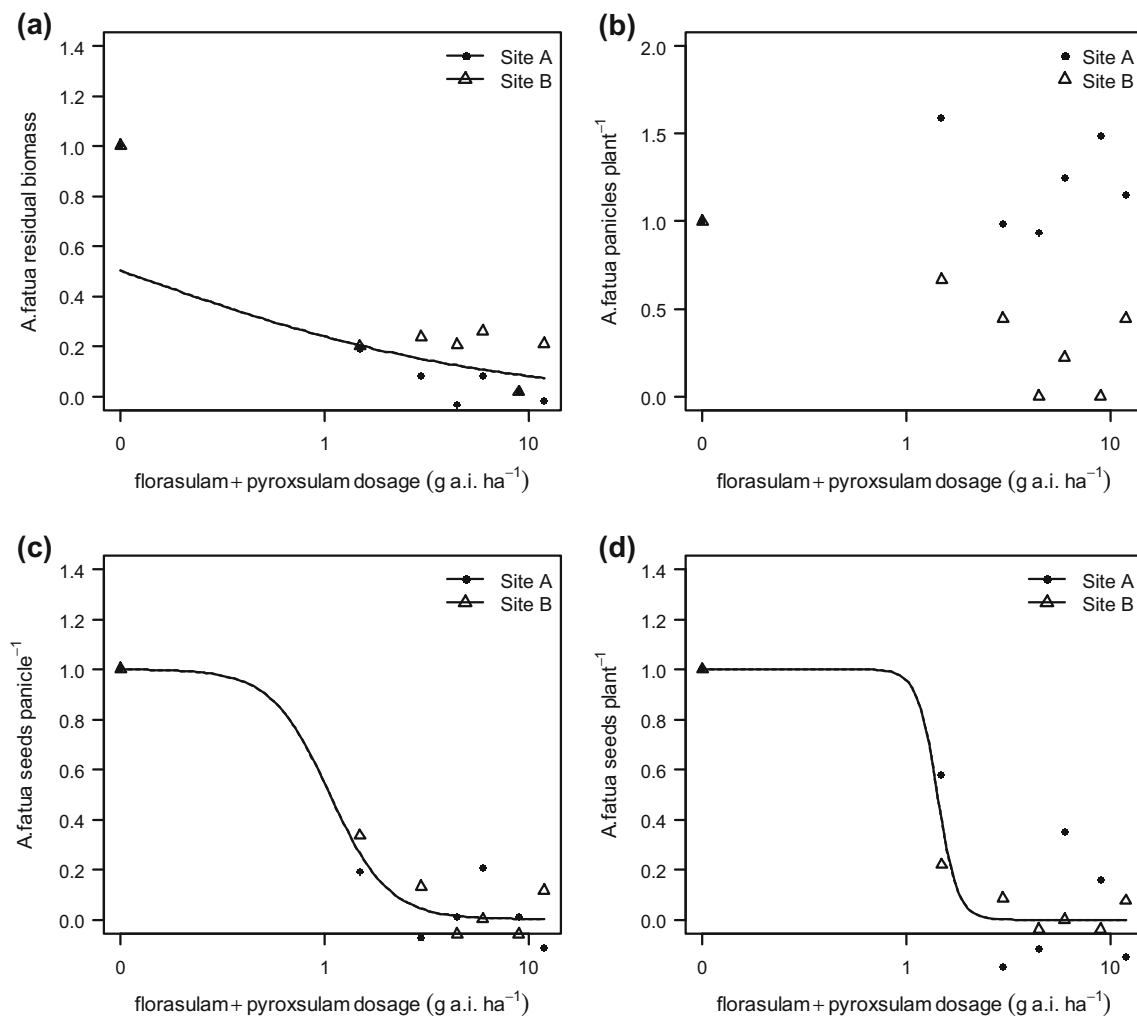* Estimates are based on curve fitting with significant lack-of-fit

Fig. 3 Influence of variable dosages of florasulam + pyroxsulam on *Avena fatua* biomass (**a**), *A. fatua* panicle production (**b**), number of seeds per panicle (**c**) and *A. fatua* seed production (**d**) at the two experimental sites site B and site A. The highest tested dosage relates to the recommended dose rate. Normalized data are shown. There were no statistical differences between the experimental sited for dose–response relationships with *A. fatua* residual biomass (**a**), seeds panicle^{-1} (**c**) and seeds plant^{-1} (**d**). Therefore, only one regression line for both experimental sites is shown. There were no dose–response relationships for *A. fatua* panicles plant^{-1} at either site, which is why **b** shows no regression lines

Avena fatua seed production in response to pinoxaden dose rate

There was no significant difference of pinoxaden efficacy on *A. fatua* biomass between the experimental sites. ED_{90} was 19.6 g a.i. ha^{-1}, which equates to around 44% of the recommended field dose. Influence of pinoxaden on *A. fatua* panicle production did not significantly differ between the sites. However, as for fenoxaprop-P, there was no panicle production at site B at 37.5% of the recommended field dosage, whereas at site A panicle production was inhibited only at dosages >75% of the recommended field dosage (Fig. 5b). ED_{50} for the number of *A. fatua* seeds per panicle was significantly lower at site B ($p < 0.001$). Also, the required pinoxaden dosage for

90% reduction in number of seeds per panicle (ED_{90}) was significantly lower at site B compared to site A ($p < 0.001$; Table 1; Fig. 5c). Consequently, the response of the number of *A. fatua* seeds per plant differed significantly between the two sites. ED_{50} for the number of seed per plant was 4.5 g a.i. ha^{-1} at site B and 9.8 g a.i. ha^{-1} at site A. ED_{90} were at 18.2 and 21.5 g a.i. ha^{-1}, respectively, and similar to the ED_{90} of *A. fatua* dry biomass reduction.

The influence of herbicide efficacy on *A. fatua* seed production differed between the two experimental sites (Fig. 6a). At site A, seed production clearly increased with decreasing herbicide efficacy, whereas this trend was not so obvious at site B. There were only small differences in *A.*
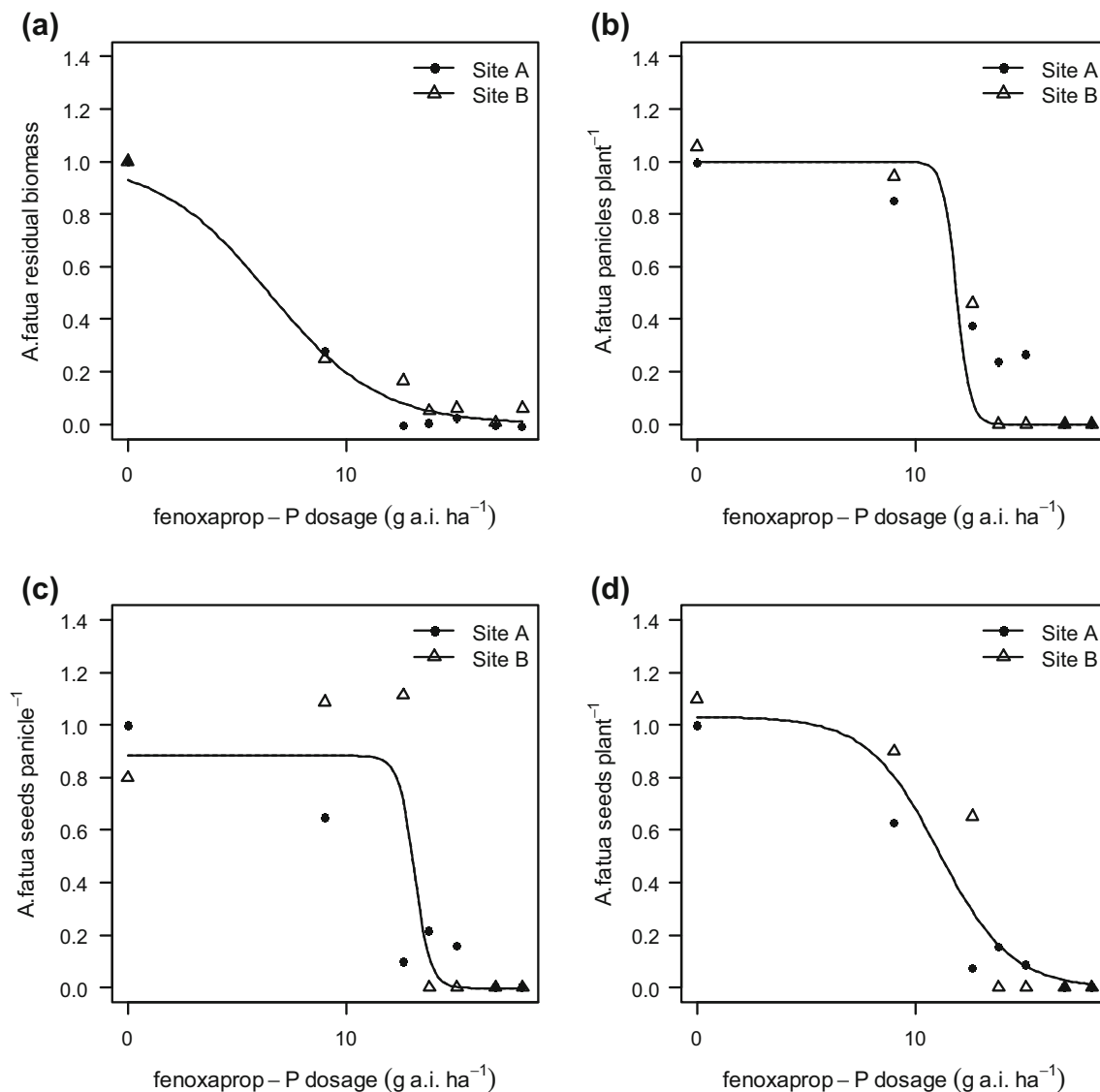
Fig. 4 Influence of variable dosages of fenoxaprop-P on *Avena fatua* biomass (**a**), *A. fatua* panicle production (**b**), number of seeds per panicle (**c**) and *A. fatua* seed production (**d**) at the two experimental sites site B and site A. The highest tested dosage relates to the recommended dose rate. Normalized data are shown. There were no statistical differences in the dose–response relationships for all parameters between the experimental sites. Therefore, only one regression line for both sites is presented in each (**a**)–(**d**)

fatua seed production at herbicide efficacies above 50%. The influence of herbicide efficacy on seed production also differed between the two tested groups of herbicides, i.e. ALS-inhibitors and ACCase-inhibitors (Fig. 6b). ALS-inhibitors tremendously reduced *A. fatua* seed production at all efficacy levels and seed production was not efficacy-dependent, but *A. fatua* produced seeds even at highest efficacy levels (>98%). The influence of ACCase-inhibitors on *A. fatua* seed production was efficacy-dependent. Efficacy levels above 80% revealed high suppression of seed production with medians at 0, but at lower efficacy levels seed production increased. Below 50% efficacy of ACCase-inhibitors, seed production was similar to that of the untreated control treatment.

Discussion

Avena fatua caused significant yield losses in winter wheat in four out of five experiments. In experiment 5, we did not observe any winter wheat yield losses, although *A. fatua* densities exceeded 100 plants m^{-2}. This was probably due to a vigorous growth and high competitiveness of the winter wheat crop on this site which caused a low relative biomass of *A. fatua* even at high densities.

The results indicate that the yield loss potential of *A. fatua* did not differ between experiments and years, but was rather dependent on the crop-weed biomass ratio. This is in line with previous findings on crop-weed competition. It has been shown that crop yield loss related to weed density
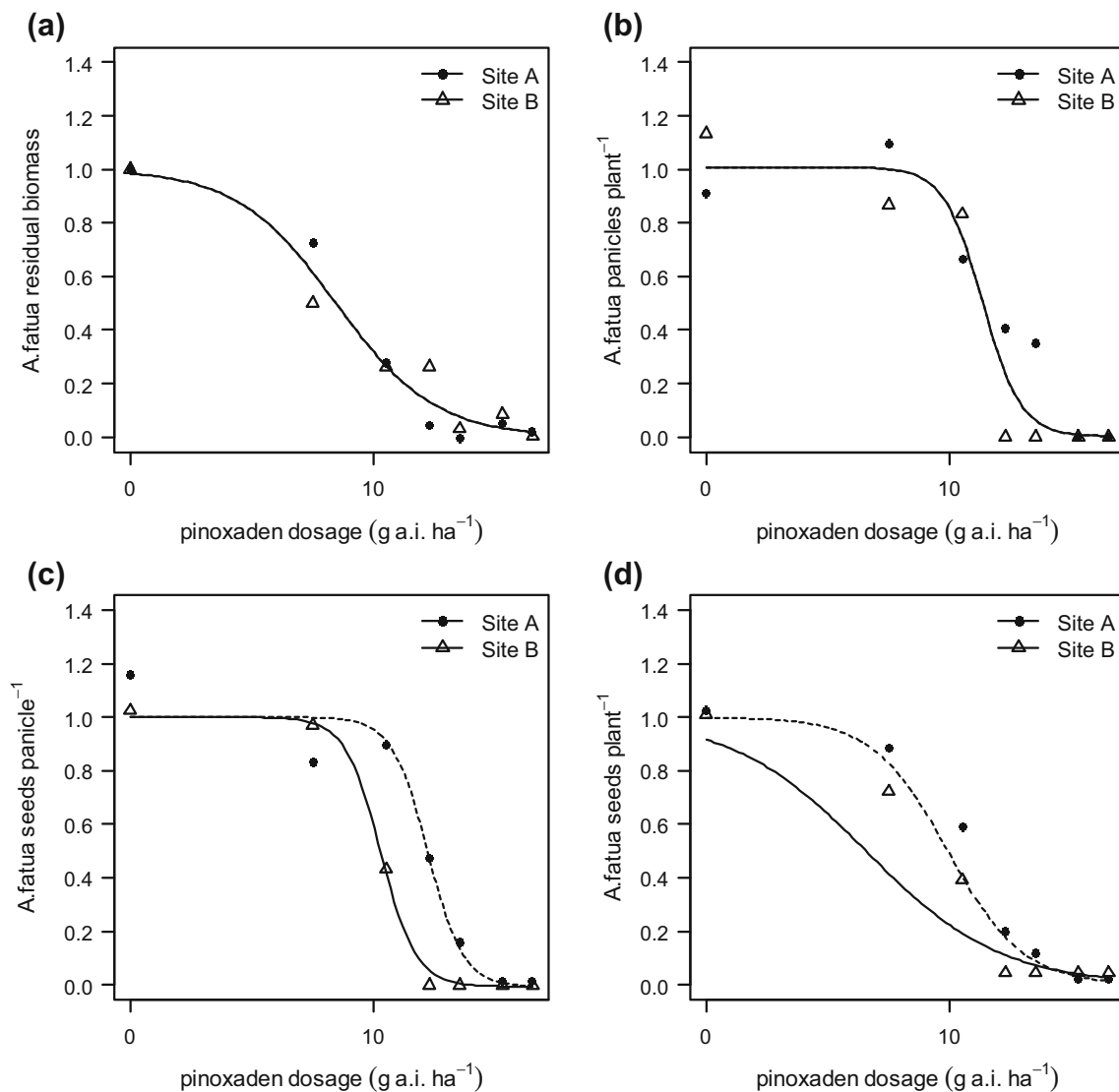
Fig. 5 Influence of variable dosages of pinoxaden on *Avena fatua* biomass (**a**), *A. fatua* panicle production (**b**), number of seeds per panicle (**c**) and *A. fatua* seed production (**d**) at the two experimental sites site B and site A. The highest tested dosage relates to the recommended dose rate. Normalized data are shown. There were no statistical significant differences in the dose–response relationships for *A. fatua* residual biomass (**a**) and panicles plant^{-1} (**b**) between the experimental sites. Therefore, only one regression line for both sites is shown. Dose–response relationships for *A. fatua* seeds panicle^{-1} (**c**) and seeds per plant^{-1} (**d**) differed significantly between the experimental sites, which is why there are separate regression lines shown for each site

varies significantly, mainly being associated with different emergence times of weeds and thus their size and competitiveness relative to the crop. Lotz et al. [17] have shown that relative weed leaf area better describes yield loss compared to weed density, because weed competitiveness is taken into account. Similarly, Lutman et al. [18] found relative weed biomass being a much more precise predictor for crop yield loss than weed density. Our data support this conclusion. It was not possible to fit the yield loss function separately for each experiment when *A. fatua* density served as independent variable, but only if the data of all experiments were merged. In contrast, fitting to data on

relative *A. fatua* biomass was possible for each experiment (Fig. 1; Table 2).

The experimental sites used for the dose–response experiments differed significantly regarding winter wheat yield and competitiveness. This was partly due to different sowing dates with earlier sowing at site B. Additionally, site B is a more favourable site for winter wheat cropping with generally higher yields. At the time of herbicide application, winter wheat at site B was already at the beginning of stem elongation, while at site A, wheat was still in the tillering phase. We cannot fully explain the differences in emergence rate and biomass production of *A. fatua* between the sites although lower winter wheat

Fig. 6 *Avena fatua* seed
production for different
herbicide efficacy classes
averaged across herbicides for
both experimental sites (**a**), and
averaged across sites for the two
tested herbicide groups (ALS-
inhibitors
(iodosulfuron + mesosulfuron
and florasulam + pyroxsulam),
ACCase-inhibitors (fenoxaprop-
P and pinoxaden)) (**b**)
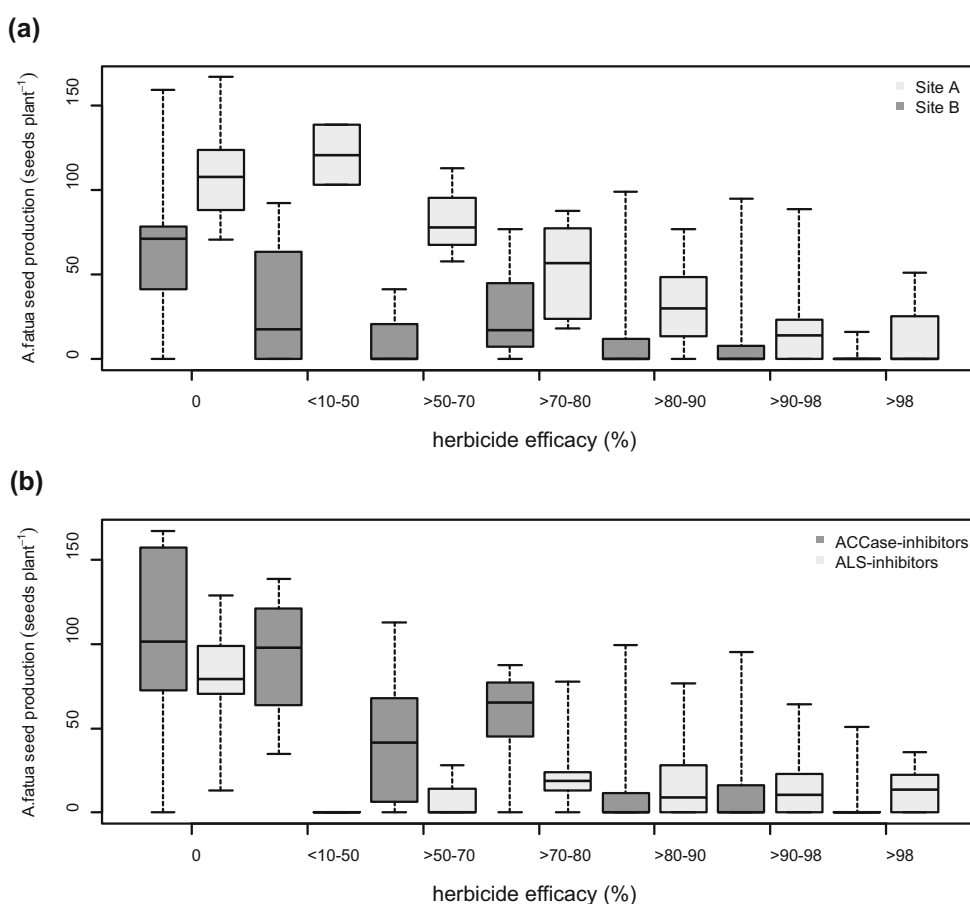
density and competitiveness could explain why *A. fatua*
densities were twice as high at site A than at site B.
According to Page et al. [19], differences in the microcli-
matic conditions due to different landscape positions of the
sites could also have influenced the emergence rates of *A.
fatua*. These results demonstrate the plasticity of *A. fatua*
and demonstrate that in case of dispersal of this weed in
Germany different biological behaviour is expected
depending on the field management, as also found in other
countries [20].

Lemerle et al. [21] showed that herbicide efficacy is not
influenced by wheat cultivars differing in competitiveness
in seasons where herbicide efficacy is generally high. In
seasons with reduced herbicide efficacy, biomass reduction
of *Lolium rigidum* was higher in more competitive wheat
cultivars compared to less competitive ones. Similarly,
O'Donovan et al. [22] showed that both ALS- and
ACCase-inhibitors' efficacy on *A. fatua* increased with
higher spring wheat seeding rate. Despite the very different
winter wheat growth and competitiveness between our
experiments, we did not find an effect of crop competi-
tiveness on herbicide efficacy. The effect on *A. fatua*
residual biomass was the same at both sites. Efficacy of the
tested herbicides was high even at reduced dose rates, so

that the effect of wheat competitiveness might not have
come into effect. *Avena fatua* seed production tended to be
lower in competitive winter wheat stand (Site B). This is in
line with findings of reduced *A. fatua* soil seed banks at
higher wheat seeding rates implying reduced seed return
[22]. It has been shown for other weeds as well that crop
competition reduces weed seed production [23].

Beside the experimental site, also the mode of action of
the herbicides influenced the dependency of *A. fatua* seed
production on herbicide efficacy. Seed production was not
influenced by the efficacy of ALS-inhibitors, whereas *A.
fatua* seed production increased with decreasing ACCase-
inhibitor efficacy. The results suggest that treatment with
ALS-inhibitors caused growth inhibition, whereas treat-
ment with ACCase-inhibitors at the same efficacy level led
to regrowth and subsequent seed production.

There is a high probability for herbicide efficacy
underestimation when considering short-term effects on
plant biomass solely. Several studies could show that seed
production is often more reduced by herbicides compared
to weed biomass [24, 25, 26, 27]. The presented results
suggest that this is only true for *A. fatua* under high crop
competition. At less competitive sites, the opposite effect
was observed, i.e. higher seed production at the same

efficacy level, which was probably due to recovery of *A. fatua* plants. These results show that *A. fatua* seed production was not directly related to residual biomass and thus herbicide efficacy, but dependent on interaction with the crop and herbicide mode of action.

Avena fatua seed production after application of reduced herbicide dose rates is bearing the risk of herbicide resistance development, in particular non-target-site resistance [10, 28]. Cases of herbicide-resistant *A. fatua* have been reported for several European countries such as Belgium, France, Germany, Poland, UK and Turkey [29]. Non-target site resistance is believed to be of polygenic nature, involving several gene loci and to require some generations of sexual reproduction for enrichment of resistance alleles in single plants [30, 31]. *Avena fatua* is mainly self-pollinating, and outcrossing rates are only between 0.05 to 0.08% in wheat and hence contribution of outcrossing to evolution of resistance is assumed to be low [32]. However, Beckie et al. [33] found evidence for non-target-site-based resistance in *A. fatua* biotypes from Canada to ALS- and ACCase-inhibitors. Busi et al. [34] recently presented results on recurrent selection of *A. fatua* with low doses of diclofop-methyl. When *A. fatua* was treated with below-labelled dosages having reduced efficacy, *A. fatua* exhibited a LD_{50} in the third progeny generation being 2.3 times higher than in the parental generation. Furthermore, they found slight cross-resistances to ALS-inhibitors. These recent data show that the risk of non-target site resistance development in *A. fatua* due to reduced efficacy cannot be excluded.

Our results highlight that *A. fatua* is a competitive weed in winter wheat leading to high yield losses if not controlled. We found potential for reducing herbicide dose rates for control of *A. fatua* in winter wheat, which was however dependent on the site. Three of the four tested herbicides completely inhibited seed production at dose rates of 37.5% of the recommended dose rate or higher in the competitive winter wheat stand. This potential was not given at the site with a less competitive winter wheat stand. Furthermore, the results showed that making decision on using reduced herbicide dosages for weed control should not only be made on herbicide efficacy data but also on their effect on seed production, because herbicide efficacy (biomass reduction) and seed production were not directly related to each other. Otherwise, the risk of unwanted seed return rises as possibly the risk of evolution of polygenic resistance. The results reveal a potential of herbicide dose reduction in the competitive winter wheat stand, because crop competition reduced *A. fatua* seed production also at reduced efficacy levels. In the less competitive stand, however, highest efficacy was necessary to prevent seed return.

References

1. Beckie, H. J., Francis, A., & Hall, L. M. (2012). The biology of Canadian weeds. 27. *Avena fatua* L. (updated). *Canadian Journal of Plant Science, 92,* 1329–1357.
2. Holm, L. G., Plucknett, D. L., Pancho, J. V., & Herberger, J. P. (1991). *The world's worst weeds. Distribution and biology.* Malabar: Krieger Publishing Company.
3. Cavalieri, A., Lewis, D. W., & Gulden, R. H. (2013). Residual weeds in winter wheat in Manitoba. *Canadian Journal of Plant Science, 93,* 1195–1200.
4. Schroeder, D., Mueller-Schaerer, H., & Stinson, C. S. A. (1993). A European weed survey in 10 major crop systems to identify targets for biological control. *Weed Research, 33,* 449–458.
5. O'Donovan, J. T., Harker, K. N., Blackshaw, R. E., & Stougaard, R. N. (2003). Effects of variable tralkoxydim rates on wild oat (*Avena fatua*) seed production, wheat (*Triticum aestivum*) yield, and economic return. *Weed Technology, 17,* 149–156.
6. O'Donovan, J. T., Harker, K. N., Blackshaw, R. E., & Stougaard, R. N. (2003). Influence of variable rates of imazamethabenz and difenzoquat on wild oat (*Avena fatua*) seed production, and wheat (*Triticum aestivum*) yield and profitability. *Canadian Journal of Plant Science, 83,* 977–985.
7. Travlos, I. S. (2012). Reduced herbicide rates for an effective weed control in competitive wheat cultivars. *International Journal of Plant Production, 6,* 1–14.
8. Gonzalez-Andujar, J. L., Fernandez-Quintanilla, C., Bastida, F., Calvos, R., Gonzales-Diaz, L., Izquierdo, J., et al. (2010). Field evaluation of a decision support system for herbicidal control of *Avena sterilis* ssp. *ludoviciana* in winter wheat. *Weed Research, 50,* 83–88.
9. Kudsk, P. (2014). Reduced herbicide rates: Present and future. In *Proceedings 26th German conference on weed biology and weed control,* Julius-Kühn-Archiv 443, 37–44.
10. Manalil, S., Busi, R., Renton, M., & Powles, S. B. (2011). Rapid evolution of herbicide resistance by low herbicide dosages. *Weed Science, 59,* 210–217.
11. Hess, M., Barralies, G., Bleiholder, H., Buhr, L., Eggers, T., Hack, H., et al. (1997). Use of the extended BBCH-scale—General for the description of the growth stages of mono- and dicotyledonous weed species. *Weed Research, 37,* 433–441.
12. Cousens, R. (1985). A simple model relating yield loss to weed density. *Annals of Applied Biology, 107,* 239–252.
13. Streibig, J. C. (1988). Herbicide bioassay. *Weed Research, 28,* 479–484.
14. De Mendiburu, F. (2014). Agricolae: Statistical procedures for agricultural research. R package version 1.2-1. http://CRAN.R-project.org/package=agricolae.
15. R Core Team. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

16. Ritz, C., & Streibig, J. C. (2005). Bioassay analysis using R. *Journal of Statistical Software, 12,* 1–22.
17. Lotz, L. A., Christensen, S., Cloutier, D., Fernandes-Quintanilla, C., Legere, A., Lemieux, C., et al. (1996). Prediction of the competitive effects of weeds on crop yields based on the relative leaf area of weeds. *Weed Research, 36,* 93–101.
18. Lutman, P. J. W., Risiott, R., & Ostermann, H. P. (1996). Investigations into alternative methods to predict the competitive effects of weeds on crop yields. *Weeds Science, 44,* 290–297.
19. Page, E. R., Gallagher, R. S., Kemanian, A. R., Zhang, H., & Fuerst, E. P. (2006). Modeling site-specific wild oat (*Avena fatua*) emergence across a variable landscape. *Weed Science, 54,* 838–846.
20. Harker, K. N., O'Donovan, J. T., Irvine, R. B., Turkington, T. K., & Clayton, G. W. (2009). Integrating cropping systems with cultural techniques augments wild oat (*Avena fatua*) management in barley. *Weed Science, 57,* 326–337.
21. Lemerle, D., Verbeek, B., & Commbes, N. E. (1993). Interaction between winter wheat (*Triticum aestivum*) and diclofop to reduce the cost of annual ryegrass (*Lolium rigidum*) control. *Weed Science, 44,* 634–639.
22. O'Donovan, J. T., Blackshaw, R. E., Harker, K. N., & Clayton, G. W. (2006). Wheat seeding rate influences herbicide performance in wild oat (*Avena fatua* L.). *Agronomy Journal, 98,* 815–822.
23. Wilson, B. J., Peters, N. C. B., Wright, K. J., & Atkins, H. A. (1988). The influence of crop competition on the seed production of *Lamium purpureum*, *Viola arvensis* and *Papaver rhoeas* in winter wheat. *Aspects of Applied Biology, 18,* 71–80.
24. Boutin, C., Strandberg, B., Carpenter, D., Mathiassen, S. K., & Thomas, P. J. (2014). Herbicide impact on non-target plant reproduction: What are the toxicological and ecological implications? *Environmental Pollution, 185,* 295–306.
25. Carpenter, D., & Boutin, C. (2010). Sublethal effects of the herbicide glufosinate ammonium on crops and wild plants: Short-term effects compared to vegetative recovery and plant reproduction. *Ecotoxicology, 19,* 1322–1336.
26. Carpenter, D., Boutin, C., & Allison, J. E. (2013). Effects of chlorimuron ethyl on terrestrial and wetland plants: Levels of, and time to recovery following sublethal exposure. *Environmental Pollution, 172,* 275–282.
27. Rotchés-Ribalta, R., Boutin, C., Blanco-Moreno, J. M., Carpenter, D., & Sans, F. X. (2015). Herbicide impact on the growth and reproduction of characteristic and rare arable weeds of winter cereal fields. *Ecotoxicology, 24,* 991–1003.
28. Busi, R., Neve, P., & Powles, S. (2013). Evolved polygenic herbicide resistance in *Lolium rigidum* by low-dosage herbicide selection within standing genetic variation. *Evolutionary Applications, 6,* 231–242.
29. Heap, I. (2016). The international survey of herbicide resistant weeds. www.weedscience.com. Accessed September 6, 2016.
30. Délye, C., Jasieniuk, M., & Le Corre, V. (2013). Deciphering the evolution of herbicide resistance in weeds. *Trends in Genetics, 29,* 649–658.
31. Petit, C., Duhieu, B., Boucansaud, K., & Délye, C. (2010). Complex genetic control of non-target-site-based resistance to herbicides inhibiting acetyl-coenzyme A carboxylase and aceto-lactate-synthase in *Alopecurus myosuroides* Husd. *Plant Science, 178,* 501–509.
32. Murray, B. G., Morrison, I. N., & Friesen, L. F. (2002). Pollen-mediated gene flow in wild oat. *Weed Science, 50,* 321–325.
33. Beckie, H. J., Warwick, S. I., & Sauder, C. A. (2012). Basis for herbicide resistance in Canadian populations of wild oat (*Avena fatua*). *Weed Science, 60,* 10–18.
34. Busi, R., Girotto, M., & Powles, S. B. (2016). Response to low-dose herbicide selection in self-pollinated *Avena fatua*. *Pest Management Science, 72,* 603–608.