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Integrated effect of crop sowing date and herbicide stress on fitness of *Bromus diandrus* Roth

Addy L. García, Aritz Royo-Esnal, Joel Torra and Jordi Recasens

Universitat de Lleida, ETSEA, Agrotecnio, Dpt. Hortofruticultura, Botánica y Jardinería. Av. Rovira Roure 191. 25198 Lleida. Spain

Abstract

Bromus diandrus Roth is a common weed species that has increased in no-tillage dry-land cereal fields in NE Spain because of the limited control options. The fitness response of plants with different emergence times (ETs) and its influence on demography has huge implications in weed management. With this subject, three ETs (F1, F2 and F3) of *B. diandrus* were established through three crop-sowing dates (D1, Oct.; D2, Nov.; D3, Dec.) for each of the three years in a barley-wheat-wheat rotation. In barley, the herbicides applied were not specific for *B. diandrus*, whereas in wheat the specific herbicide mesosulfuron-methyl plus iodosulfuron-methyl-sodium was applied. Plant density after treatments and fitness characteristics were estimated for each weed ET. Weed density decreased for later ETs and fitness was density-dependent, showing significantly higher values when a non-specific herbicide was applied, except in number of caryopses per spikelet. The increasing fitness shown by plants with later ETs and the linear relationships of vegetative biomass *vs* reproductive biomass and fecundity were disrupted by the herbicide mesosulfuron-methyl plus iodosulfuron-methyl-sodium. Plants that had survived this herbicide when wheat was growing had lower values for all the characteristics analysed. After three seasons, as a consequence of decreasing seed recruitment, a practical depletion of the *B. diandrus* population was achieved in F2 and F3 (<2.8 and <1 plants/m^2, respectively) but not in F1 (60.5 plants/m^2). This study shows the importance of delayed crop sowing to optimize the control of *B. diandrus* in cereal fields with no tillage.

Additional key words: delayed sowing; emergence time; reproductive biomass; vegetative biomass; resource allocation; no-tillage.
Abbreviations used: D1, D2, D3 (different crop sowing dates); ET (emergence time); F1, F2, F3 (different ETs considered for *B. diandrus*); RB (reproductive biomass); RE (reproductive effort); VB (vegetative biomass).
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Correspondence should be addressed to Jordi Recasens: jrecasens@hbj.udl.cat

Introduction

Direct drilling involves problems in the control of certain weed species. Some evident cases have appeared in the dry-land cereal systems in northeastern Spain, where *Bromus diandrus* Roth is widespread (Riba & Recasens, 1997; Arrúe *et al.,* 2007), proliferating in cereal crops due to the absence of effective herbicides and the introduction of conservation tillage over the past 20 years (Young & Thorne, 2004; Kleemann & Gill, 2006).

Cultivation is a useful pre-sowing weed control strategy, so under no tillage soil disturbance must be replaced with broad-spectrum herbicides, mainly glyphosate (Kleemann & Gill, 2009a). However, pre-sowing control of *Bromus* species may be limited because light inhibition of germination (Del Monte & Dorado, 2011) leads to protracted seedling establishment and evasion of early control measures (Kleemann & Gill, 2006). Furthermore, chemical control of *B. diandrus* in post-emergence is usually not effective and surviving plants are able to restore, maintain or even increase the infestations. The recent introduction of mesosulfuron-methyl plus iodosulfuron-methyl sodium offers an efficient control of *B. diandrus* (Couloume & Adrien, 2005; Rapparini *et al.*, 2006). However, this herbicide is selective in wheat but not in barley, which is the main crop in the region. Furthermore, it is not effective after the three-leaf stage of the weed (Kleemann & Gill, 2009a).

All these constraints reduce the effectiveness of control strategies against *B. diandrus* in cereal crops under no-till conditions. In the dry-land cereal systems in NE Spain, adoption of alternative weed control strategies such as crop rotation is difficult because limited rainfall allows only winter cereals to be grown. However, it has been demonstrated that delaying crop sowing results in a significant decrease in the potential competition of autumn grass weed populations and a more efficient control of newly emerged plants (Gill *et al.*, 1987; Powles & Matthews, 1996).

The demographic success of *B. diandrus* depends on seedling survival and fecundity, which in turn depend on the rate of emergence in autumn (Riba & Recasens, 1997). For other grass weeds, several studies (Rice & Dyer, 2001; Conley *et al.*, 2002; Gallart *et al.*, 2010) have confirmed that emergence timing affects their fitness and that percentage of seedling emergence, growth rate and fecundity differ among emerged cohorts, showing the importance of emergence time (ET) and crop competition on weed demography. Norris (2007) reported that cohorts emerging immediately after crop sowing are the main source of recruitment from the weed population and seed bank.

Several studies have reported biology of *B. diandrus* and its influence on cereal yields (Gill & Blacklow, 1984; Gill *et al.*, 1987; Kleemann & Gill, 2006; Kleemann & Gill, 2009a). However, few have analysed the effect of ET on fitness and the demographic response when crop sowing is delayed. Furthermore, the fact that mesosulfuron-methyl plus iodosulfuron-methyl sodium is only specific for wheat suggests that a study of the fitness response of surviving plants after application of this herbicide would be of interest. Potential changes in fitness and their influence on demography could have interesting implications for a *B. diandrus* management strategy that integrates cultural and chemical techniques.

We hypothesized that the date of crop sowing has significant influence on *B. diandrus* fitness and on the effectiveness of post-emergence chemical control of this weed in a cereal monocrop system. The specific objectives of this study were to determine, over three consecutive seasons, the effect of different crop sowing dates on the fitness characteristics and resource allocation patterns in *B. diandrus* in both barley, for which no effective post-emergence herbicides are available, and wheat, for which they are.

Material and methods

Study site

Experimental plots were established in a field trial in Agramunt (41°48’N and 1°07’E) (Lleida, Spain). The field is located in the Ebro Valley, 330 m above sea level, and has a semi-arid mixed continental-Mediterranean climate (Papadakis, 1966). The soil was a Fluventic Xerocrept (100-120 cm deep) (SSS, 1994), with 30.1% sand, 51.9% silt and 17.9% clay, 2.3% organic matter and a pH of 8.5. Rainfall at the site during the study period and the long-term average are presented in Table 1.

Agronomic management

Trials were conducted over three consecutive growing seasons (2008/09, 2009/10 and 2010/11) in an experimental cereal field under no-tillage. The site

Table 1. Monthly rainfall (mm) for 2008/09 to 2010/11 and monthly mean long-term rainfall (1975 to 2011) in Agramunt, Catalonia (NE Spain)

Month	**Season[a]**			**Long-term mean[b]**
	2008/09	**2009/10**	**2010/11**	**1975-2011**
October	84	69	1	50
November	31	5	0	36
December	29	112	0	30
January	56	132	0	31
February	34	39	12	18
March	55	64	36	30
April	150	26	20	48
May	5	59	27	54
June	20	76	73	38
Total Oct-June	464	582	169	378

[a] Data from 2008 to 2011 obtained from an automated weather station at the experimental field).
[b] Rainfall details averaged from 1975 to 2011 (data from 1975 to 2008 obtained from the station of the National Institute of Meteorology in Agramunt).

had been under no-tillage production for two seasons prior to the initiation of the study and had a natural infestation of *B. diandrus*. The experiment was arranged as a randomized complete block design with three replications. Each plot was 6 × 30 m and the main factor considered was the emergence time of *B. diandrus* according to three crop sowing dates (D1, D2 and D3). Respective dates in 2008, 2009 and 2010 were as follows: (D1) 20, 19, and 14 October; (D2) 7, 12, and 18 November; and (D3) 10, 3, and 13 December. Barley cv. 'Hispanic' was sown in 2008 and wheat cv. 'Bokaro' in 2009 and 2010. Cereals were sown at 180 kg seed/ha (400-450 plants/m^2). Crop sowing was performed with a no-till disc drill in rows 19 cm apart.

Doses and dates of herbicides applied in each growing season are detailed in Table 2. Mesosulfuron-methyl plus iodosulfuron-methyl sodium was applied in the 2-5 leaf stage of wheat in 2009/10 and in tillering for D1 and in 2-5 leaf stage for D2 and D3 of wheat in 2010/11. In all plots fertilizer was applied each year from February to March at 48 kg N/ha.

Weed density and fitness characteristics

The seedling populations recruited according to the three different crop sowing dates, and the emergence times (ETs) are therefore identified as F1, F2 and F3.

Each season densities of *B. diandrus* were estimated in each plot 60 days after herbicide application within 0.1 m^2 quadrats placed at ten locations randomized by blind tossing. Each year in June, when the weeds reached their complete development and fecundity, 20 plants from F1, F2 and F3 were collected and the following biological attributes were estimated: number of stems per plant, number of spikelets per plant and stem, fecundity (caryopses per plant) and number of caryopses per spikelet. Aerial vegetative biomass (VB) and reproductive biomass (RB) per plant were also estimated. For this purpose, plants were cut at ground level, placed in a tray, separated into VB and RB and oven-dried at 65ºC for 24 hours. Reproductive effort (RE) was calculated per plant as RE = RB/VB. At maturity, panicles were collected from several plants from each ET and threshed, and 1000 caryopses were weighed when completely dry. Seed rain was calculated by multiplying final density (last density sampling before the crop harvest) by fecundity.

Allocation gradient within the panicle

Before crop harvest 20 panicles were collected from each ET and replication. Caryopses were sampled from both apical (A) and basal (B) spikelet positions on panicles, as well as both apical (a) and basal (b) caryopsis position within spikelets. Thus, the four sampling positions were Aa, Ab, Ba, and Bb. The weight of 20 caryopses situated in the same position for each ET was estimated every season. Weights are expressed per caryopsis.

Statistical analysis

ANOVA was performed using SAS (SAS Institute Inc., Cary, NC, USA) to detect differences between

Table 2. Crop sowing dates (D1, D2 and D3) and weed control methods used in the three growing seasons in the trial field

Season	Crop and sowing date	Postemergence herbicide treatment	
2008/09	Crop: Barley cv. 'Hispanic'	Isoproturon 1243 g a.i./ha plus diflufenican 69 g a.i./ha	2,4-D (444 g a.i./ha) plus MCPA (397.5 g a.i./ha) plus Dicamba (150 g a.i./ha) + Metribuzin (50 g a.i./ha)
D1	20 October	19 February	19 February
D2	7 November	19 February	
D3	10 December	19 February	
2009/10	Crop: Wheat cv. 'Bokaro'	Mesosulfuron-methyl plus iodosulfuron-methyl-sodium (15 and 3 g a.i./ha)	
D1	19 October	5 March	
D2	12 November	5 March	
D3	3 December	5 March	
2010/11	Crop: Wheat cv. 'Bokaro'	Mesosulfuron-methyl plus iodosulfuron-methyl-sodium (15 and 3 g a.i./ha)	Tribenuron-methyl plus metsulfuron-methyl (10 and 5 g a.i./ha)
D1	14 October	9 February	30 March
D2	18 November	13 April	30 March
D3	13 December	13 April	30 March

A pre-sowing herbicide treatment (one to three days before sowing) with glyphosate was applied in all plots each season, at a rate of 540 g a.i./ha and N- fertiliser was also applied in February-March 150 kg/ha.

plants with different emergence times for all the variables analysed. Because different cereals were sown and different weed managements were applied each year, the results were analysed separately for each growing season.

In cases in which ANOVA analyses were significant, LSD post-hoc tests at p=0.05 were done. Before analysis, all characteristics were transformed to satisfy the homogeneity of variance assumptions [log (x+1)], while $\mathrm{RE} = \sqrt{(x+0.5)}$ transformed. Linear regression analyses were performed between biological characteristics (VB *vs.* RB and fecundity) with the Sigma Plot program 11.0, using log (x+1) transformations.

Results and discussion

Weed density

The densities estimated 60 days after herbicide treatment differed across years and decreased significantly as the ET advanced in each season (Table 3). In 2008/09 density decreased by 71.8% between F1 and F2, by 88.0% between F1 and F3 and by 57.6% between F2 and F3. In 2009/10 density decreased by 96.2% between F1 and F2, by 99.3% between F1 and F3 and by 81.8% between F2 and F3. In 2010/11 density decreased by 95.4% between F1 and F2 and by 98.3% between F1 and F3, with no significant differences between F2 and F3. This consistent decreasing gradient of *B. diandrus* density as a function of crop sowing date is due to the greater emergence that takes place after autumn rains and the resulting reduction of the soil seed bank. These emerged seedlings are susceptible to pre-sowing control methods (Riba, 1993; Kleemann & Gill, 2006). Therefore, delayed crop sowing reduces the density of weeds competing with the crop.

In 2008/09, no post-emergence effect against *B. diandrus* was observed with isoproturon plus diflufenican in barley (33.2%, 11.4% and 16.1% for F1, F2 and F3, respectively), and the decrease in weed density observed in F2 and F3 (>71%) can be attributed exclusively to the crop sowing delay. In 2009/10 and 2010/11, after the herbicide treatment, the decreasing density observed in F2 and F3 (>95% in both seasons) reflects the effect of the sowing delay and the efficiency of the chemical control by mesosulfuron-methyl plus iodosulfuron-methyl sodium. These results demonstrate that in direct drilling the control of this species with only a pre-seeding application of glyphosate is limited, but the weed density can be reduced by combining delayed crop sowing with a post-emergence application of an appropriate herbicide (García *et al.*, 2014). After three years a practical depletion of the *B. diandrus* population was achieved in F2 and F3.

Changes in fitness characteristics

Vegetative and reproductive fitness

The number of stems per plant increased significantly from F1 to F3 in 2008/09 (Table 3) as a consequence of a density-dependent response. In 2009/10 there were no significant differences between ETs and in 2010/11 significantly higher values were observed for F1 than F2 and F3. The irregular values observed in these last two seasons should be attributed to the effect of the herbicide on the surviving plants in addition to within-species competition. However, the higher value observed in 2010/11 in F1 could be attributed to other factors. As has been established for other grass weeds (Medd *et al.*, 1985; Cousens *et al.*, 1988; Izquierdo *et al.*, 2003), the strongest crop competition takes place early in the growing seasons, affecting weed tillering. The stress caused by lack of rain until February in the winter of 2010/11 reduced the competitive effect of the crop and, though the plants were smaller, they had more tillers.

Overall, a higher number of spikelets, both per plant and stem, was observed in 2008/09 than in 2009/10 and 2010/11 (Table 3). In the first season significant differences between F1, F2 and F3 were observed for both characteristics, with the lowest values in F1. On the other hand, in 2009/10 and 2010/11 the number of spikelets per stem was significantly higher in F2 and F3 than in F1. The increasing fitness response between ETs observed in the first season was not confirmed in 2009/10 and 2010/11, when plants surviving specific herbicide applications were smaller and had lower values for most fitness characteristics. In the second and third seasons unequal lower values of fitness characteristics were observed between ETs, showing that in surviving plants the allocation pattern depends more on herbicide stress than on density dependence.

Fecundity (number of caryopses per plant) was higher in 2008/09 than in the next two seasons (Table 3). Considering the three ETs together, fecundity was almost 80% lower in 2009/10 and 2010/11 than in 2008/09. Moreover, in 2008/09 a significant increasing gradient of fecundity between ETs was observed, whereas in 2009/10 only the fecundity for F1 was significantly lower than that for F2, and in 2010/11 no differences in fecundity between ETs were observed.

In 2008/09, despite the increasing fecundity of *B. diandrus* between ETs, a decreasing reduction of seed rain (seeds/m^2) was obtained as a consequence of de-

Table 3. Means and standard errors of plant density (60 days after post-emergence herbicide treatment) and fitness characteristics for three different emergence times (ET) of *B. diandrus* in a cereal field during the three growing seasons

Season	ET[a]	Density (pl/m^2)	Nº stem/pl	Nº spikelets/pl	Nº spikelets/ stem	Nº caryopses/pl	Nº caryopses/ spikelet
2008/09	F1	500.5 ± 108.6 (a)	2.9 ± 0.4 (c)	18.1 ± 1.8 (c)	6.9 ± 0.3 (b)	77.3 ± 8.1 (c)	4.3 ± 0.1 (a)
	F2	141.3 ± 30.7 (b)	3.9 ± 0.3 (b)	33.2 ± 3.1 (b)	8.5 ± 0.4 (a)	139.4 ± 10.9 (b)	4.2 ± 0.1 (a)
	F3	60.0 ± 26.8 (c)	5.5 ± 0.7(a)	49.3 ± 7.7 (a)	8.6 ± 0.3 (a)	223.6 ± 32.3 (a)	4.5 ± 0.1 (a)
2009/10	F1	563.3 ± 76.5 (a)	2.9 ± 0.3 (a)	6.9 ± 0.7 (b)	2.8 ± 0.1 (c)	13.7 ± 2.2 (b)	2.0 ± 0.2 (ab)
	F2	21.0 ± 11.1 (b)	2.9 ± 0.3 (a)	13.7 ± 1.9 (a)	5.3 ± 0.3 (a)	28.8 ± 5.2 (a)	2.1 ± 0.2 (a)
	F3	3.8 ± 2.5 (c)	2.2 ± 0.3 (a)	10.0 ± 3.2 (ab)	4.0 ± 0.6 (b)	18.3 ± 7.3 (ab)	1.4 ± 0.1 (b)
2010/11	F1	60.5 ± 19.3 (a)	6.4 ± 0.7 (a)	18.3 ± 2.0 (a)	3.5 ± 0.1 (b)	14.7 ± 2.4 (a)	0.8 ± 0.2 (a)
	F2	2.8 ± 0.9 (b)	4.4 ± 0.3 (b)	22.5 ± 2.7 (a)	4.8 ± 0.2 (a)	25.2 ± 2.0 (a)	1.1 ± 0.1 (a)
	F3	1.0 ± 0.6 (b)	4.0 ± 0.4 (b)	18.7 ± 1.9 (a)	4.6 ± 0.2 (a)	19.2 ± 3.8 (a)	1.1 ± 0.2 (a)

[a] Emergence times (ET) were established each season in function of crop sowing date. F1, mid-October; F2, mid-November; F3, early December. Fitness characteristics estimated in June before crop harvest. Different letters between ETs for the same season indicate significant differences (p<0.05).

creasing density: 38678 for F1, 19700 for F2 and 13414 for F3 (data not shown). In that year F1 fecundity was in agreement with the results of Riba (1993), who collected plants in similar cereal fields to those of the present study. By contrast, fecundities were much lower when an effective herbicide was applied in 2009/10 and 2010/11. Similar decreasing results were obtained for Australian populations of this species by Kleemann & Gill (2009b), who recorded fecundities of 71 and 22 caryopses per plant in populations not treated and treated with mesosulfuron-methyl herbicide, respectively.

Despite the significant increase in fecundity observed between ETs in 2008/09, the number of caryopses per spikelet was statistically similar (from 4.2 to 4.5) (Table 3). However, this reproductive attribute showed lower values in the next two seasons. In 2009/10, the number of caryopses per spikelet for F2 (2.1) was significantly higher than for F3 (1.4). In 2010/11, no significant differences between ETs were observed (the number ranged from 0.8 and 1.1). The stability of the number of caryopses per spikelet between ETs in the first season demonstrates that it was not affected by plant competition whereas the variation of these values in 2009/10 and 2010/11 were caused by herbicide effect. Similarly, Torra & Recasens (2008) observed stable values of the number of seeds per capsule in corn poppy (*Papaver rhoeas*) despite the decreasing performance and reproductive fitness in function of cohort emergence and crop competition. These results suggest that despite the changes in fitness characteristics according to competition, the plant keeps a regulation mechanism that guarantees a minimal fecundity. Dyer *et al.* (2012), analysing the growth response to interspecific competition of *Bromus tectorum*, observed that the allocation of components for reproduction was maintained even when interspecific competition had a large negative effect on target plant growth. It may therefore be feasible to assume a similar modulating response in an intraspecific competition scenario.

Vegetative and reproductive biomass

Overall, higher values of VB and RB were observed in plants in 2008/09 than in the next two seasons (Table 4). For VB this reduction was 88% in 2009/10 and 84% in 2010/11. For RB, overall, the decrease was 69% and 34%, respectively.

In 2008/09, VB increased significantly from F1 to F3 (from 41.5 to 121.5 mg). In 2009/10, it only increased from F1 (7 mg) to F2 (14 mg). In 2010/11 no significant differences were found between ETs but the maximum value was observed for F2 (16.0 mg). The highest value of RB was observed in 2008/09, with a significant increase from early to late ETs (from 30.5 for F1 to 64.0 mg for F3). In the next two seasons, RB was significantly higher for F2 than for F1 (Table 4).

The RE differed between ETs depending on the cropping season, averaging 0.65 in 2008/09, 1.53 in 2009/10 and 3.02 in 2010/11 (Table 4). Furthermore, there was a significant decreasing gradient in RE between F1-F2 and F1-F3 in 2008/09. Decreasing RE in response to ET was confirmed by Riba (1993), who compared summer and winter cohorts of this species. However, performance of plants that survived the specific herbicide application showed higher values of RE (regardless of ET) in 2009/10 and 2010/11 than in 2008/09. These values reflect the reproductive penalty caused by herbicides, which force the surviving plants to make a greater effort to produce seeds.

Table 4. Means and standard errors of vegetative biomass (VB), reproductive biomass (RB) and reproductive effort (RE) per plant for *B. diandrus* with different emergence times (ET) at the end of three cropping seasons.

Season	ET[a]	VB (mg)	RB (mg)	RE
2008/09	F1	41.5 ± 4.5 (c)	30.5 ± 3.0 (c)	0.77 ± 0.02 (a)
	F2	77.0 ± 6.0 (b)	45.0 ± 3.0 (b)	0.62 ± 0.02 (b)
	F3	121.5 ± 23.0 (a)	64.0 ± 10.0 (a)	0.57 ± 0.02 (b)
2009/10	F1	6.5 ± 1.0 (b)	10.0 ± 1.0 (b)	1.63 ± 0.14 (a)
	F2	14.0 ± 2.5 (a)	20.5 ± 3.0 (a)	1.51 ± 0.10 (a)
	F3	8.5 ± 1.5 (ab)	13.0 ± 4.0 (ab)	1.45 ± 0.15 (b)
2010/11	F1	11.5 ± 1.5 (a)	22.5 ± 2.5 (b)	2.30 ± 0.27 (b)
	F2	16.0 ± 2.0 (a)	41.0 ± 5.0 (a)	2.62 ± 0.16 (ab)
	F3	11.5 ± 1.0 (a)	29.5 ± 2.5 (ab)	4.14 ± 0.87 (a)

[a] Emergence times (ET) were established each season in function of crop sowing date. F1, mid-October; F2, mid-November; F3, early December. Different letters between ETs for the same season indicate significant differences (p<0.05). Characteristics estimated in June before crop harvest.

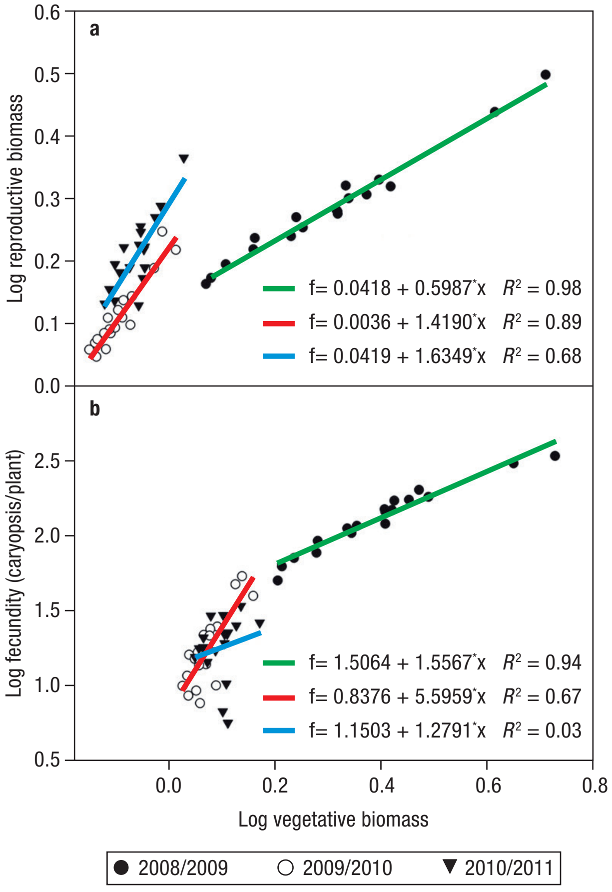

Figure 1. Linear regressions between vegetative and reproductive biomass (a) and between vegetative biomass and fecundity (b) of *Bromus diandrus* for three different cropping seasons: 2008/09, 2009/10 and 2010/11.

Figure 1a shows a positive linear relationship between VB and RB, with R^2 values ranging from 0.68 to 0.98 across years. In 2008/09, the plants were bigger and the relationship comprised greater ranges of values of vegetative and RB than in 2009/10 and 2010/11. However, the slope was more pronounced in 2009/10 and 2010/11, when plants were forced to produce a minimum effective RB from a lower VB. Similarly, positive regressions between VB and fecundity (Fig. 1b) were obtained for the three seasons (R^2 range from 0.43 to 0.94). A greater range of values was obtained in 2008/09, corresponding to plants with higher VB and fecundity. However, in 2009/10 and 2010/11 the more pronounced slopes are in agreement with the lower range of values of both characteristics.

The steeper slopes and the lower and narrower range of values observed reflect the effect of selective herbicides on the surviving plants. These relationships allow prediction of seed production based on the weed biomass (Thompson *et al.*, 1991; Norris, 2007). In our case the behaviour of plants surviving herbicides has interesting implications for studies of weed population dynamics –where variables as RB and fecundity across years become determinant– and also for the construction and outcomes of bioeconomic models, as has been studied by Torra *et al.* (2010).

Overall, in 2008/09 values of weight of 1000 grains were 24.2% higher than in 2009/10 and 31.3% higher than in 2010/11 (Table 5). In 2008/09 a significant decreasing gradient from F1 (17.62 g) to F3 (14.87 g) was observed, while in 2009/10 the significant differences did not follow a gradient in function of the ET, with the highest values being observed in F2 (13.76 g) and the lowest in F1 (10.86 g). In 2010/11 there were no significant differences between ETs. In 2008/09, the decreasing gradient in weight of 1000 grains as a function of the moment of seedling establishment was related to the increasing fecundity observed, and simultaneously to the plant density of each ET. Riba (1993)

Table 5. Weight (g) and standard errors of 1000 caryopses of plants of *B. diandrus* with different emergence times (ET) for three different cropping seasons.

ET[a]	2008/09	2009/10	2010/11
F1	17.62 ± 0.27 (a)	10.86 ± 0.13 (c)	11.97 ± 0.80 (a)
F2	15.96 ± 0.19 (b)	13.76 ± 0.30 (a)	10.98 ± 0.15 (a)
F3	14.87 ± 0.15 (c)	12.09 ± 0.03 (b)	10.32 ± 0.32 (a)

[a] Emergence times (ET) were established each season in function of crop sowing date. F1: middle October, F2: middle November, F3: early December. Different letters between ETs for the same season indicate significant differences (p<0.05). Characteristics estimated when plants were completely developed.

also observed lower seed weight when fecundity was higher in *B. diandrus*. However, this correlation was not observed in 2009/10 and 2010/11, when the fecundity in general was much lower. Moreover, a complementary expression of the decreasing fitness should be obtained through further analysis of the seed dormancy and viability from plants surviving herbicide treatments. No records are available yet, but they will be of practical interest in studies of population dynamics of *B. diandrus*.

From a long-term perspective, the changes in fitness characteristics observed highlight the importance of integrating two different strategies to control *B. diandrus* populations in cereal systems. In general, delaying crop sowing and later ETs lead to an increase in vegetative and reproductive fitness characteristics as a density-dependent response; however, the lower seed rain allows a reduction of the population demography across seasons. In a scenario in which added stress is also present due to a herbicide effect, the fitness response could be practically disrupted and seed recruitment becomes very difficult.

Allocation within the panicle

In general, a decreasing gradient of caryopsis weight was observed according to seasons (Table 6). Considering all positions and the three ETs together, the mean caryopsis weight was 15.90, 11.02 and 10.64 mg, respectively, for 2008/09, 2009/10 and 2010/11. An ET effect was only observed in 2008/09 for all the positions considered, with greater values for F1 than for F2 and F3. In 2008/09 and 2009/10 a position effect was observed within each ET (except in F1 in 2009/10), while in 2010/11 no significant differences were found between the four positions considered. In 2008/09 similar patterns of allocation were observed in the three ETs. The heaviest caryopses were those from the bottom of spikelets situated in apical position in the panicle (*Ab*), followed by those in the lowest position in spikelets situated in basal position in the panicle (*Bb*), whereas the weight of caryopses in apical position in both apical (*Aa*) and basal position (*Ba*) of the spikelet in the panicle was lower than that of caryopses in position *Ab*, in most cases with a significant difference.

Without a specific herbicide application (season 2008/09), a significant gradient of resource allocation as a function of caryopsis position in the panicle was observed for each ET. Caryopses from apical spikelets were heavier, regardless of their position within them. This could be interpreted as a result of the different

Table 6. Mean weight (mg) and standard errors of one caryopsis according to the apical (*a*) or basal (*b*) position of caryopses in the spikelet and the apical (*A*) or basal (*B*) position of the spikelet in the inflorescence of plants of *B. diandrus* with different emergence times (ET) for three growing seasons.

Season	ET[1]	Caryopsis position			
		Ab	***Bb***	***Aa***	***Ba***
2008/09	F1 *	20.33 ± 0.14 (a)	19.04 ± 0.56 (ab)	18.33 ± 0.41 (ab)	16.94 ± 0.40 (b)
	F2 **	17.65 ± 1.20 (a)	16.24 ± 0.36 (ab)	13.86 ± 0.48 (bc)	11.95 ± 0.58 (c)
	F3 **	17.16 ± 0.84 (a)	14.86 ± 0.12 (ab)	13.00 ± 0.67 (bc)	11.39 ± 0.36 (c)
2009/10	F1	13.27 ± 1.41 (a)	11.51 ± 0.05 (a)	10.96 ± 0.58 (a)	8.53 ± 0.22 (a)
	F2	14.60 ± 0.04 (a)	12.66 ± 1.40 (ab)	9.22 ± 0.84 (b)	8.18 ± 0.42 (b)
	F3	13.73 ± 0.47 (a)	12.47 ± 0.05 (ab)	8.78 ± 1.92 (ab)	8.32 ± 1.09 (b)
2010/11	F1	12.26 ± 1.53 (a)	10.73 ± 1.72 (a)	11.71 ± 1.93 (a)	11.15 ± 1.64 (a)
	F2	9.86 ± 0.81 (a)	11.13 ± 0.29 (a)	9.76 ± 0.27 (a)	9.87 ± 0.62 (a)
	F3	10.54 ± 0.29 (a)	10.51 ± 1.06 (a)	9.83 ± 0.89 (a)	10.38 ± 1.03 (a)

[1] Emergence times (ET) were established each season in function of crop sowing date. F1, mid-October; F2, mid-November; F3, early December. Different letters between caryopsis positions for the same ET mean significant differences (p<0.05). Asterisks indicate that values from cohort F1 in season 2008/09 were significantly different (p<0.05) from values from F2 and F3 for any of the caryopsis positions considered. Characteristics estimated when plants were completely developed.

moment when the spikelets started to develop and the inflorescence was still inside the plant: spikelet production follows a downward direction, starting the development from the highest (apical) positions of the inflorescence, when the vegetative apex is transformed into the reproductive apex, as has been defined for several grasses (Pujol, 1998). For other grasses, González-Rabanal *et al.* (1994) and Recasens *et al.* (2007) confirmed that these differences in seed position in the panicle resulted in further differences in seed dormancy. During development, seeds in different positions may experience different temperatures and/or water content, and differences in resource partitioning, which could influence their dormancy status. This further assessment in *B. diandrus* could provide new knowledge on how the position of caryopses on the panicle promotes changes in dormancy regardless of environmental factors.

Furthermore, during the first season a decreasing gradient of caryopsis weight was observed from the basal to apical positions in the spikelet. These differences depend on the sequential process of floral development within the spikelet. In rice, these differences in grain weight within the spikelet are attributed to an intra-spikelet competition for assimilates pre- and post-anthesis (Calderini & Reynolds, 2000). The absence of these differences in *B. diandrus* when the specific herbicide was applied (2009/10 and 2010/11) could be explained by a disruption of the source-sink balance during the period of grain filling. The high number of spikelets without filled grains observed in plants that survived the herbicide (data not shown) is evidence of this process.

Implications for management

Delaying the crop sowing date reduces not only the density of *B. diandrus* and the weed pressure on the crop, but also the recruitment of new seeds to the seed bank. In the absence of a specific herbicide, plants that emerged late showed higher fecundity, a decrease in reproductive effort and a decrease in 1000-grain weight. However, their contribution to the final seed recruitment was lower than those of earlier-emerged plants, for which higher densities were established. Delaying crop sowing (until mid-November) should be considered as an efficient management tool for controlling this species in a cereal monocrop in no-tillage systems. The application of mesosulfuron-methyl plus iodosulfuron-methyl sodium when wheat sowing is delayed increases efficiency due to delayed plant phenology and reduced weed density, and also reduces the fitness of surviving plants.

One constraint of delaying the crop sowing date is the possible yield reduction. However, in our experiment the delayed sowing did not lead to a yield penalty: on the contrary, higher yields were obtained due to the avoidance of the competitive effect of the weed (data not shown). In all cases, a balance between crop yield and weed control should be established in order to maximize profits.

In our study, after three growing seasons the *B. diandrus* population was practically depleted in the field. Implementation of cultural and chemical strategies in no-tillage systems may improve integrated weed management programmes in dry-land arable fields where options for growing crops alternative to cereals are limited.

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