



Weed suppression by Canadian spring cereals: relative contribution of competition for resources and allelopathy

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Abstract

Integrated and more sustainable weed management practices are in great demand all around the globe. The adoption of more weed-suppressive cereal cultivars could be part of an integrated weed management strategy. Recently, a study was published analysing the relative contribution of above-ground competition and allelopathy to weed suppression of Scandinavian winter cereals at the field level. The present study used the same approach with Canadian spring wheat and triticale cultivars, and confirmed the results of the previous study. The competitive traits such as leaf area index, crop height and early vigour, and the allelochemicals belonging to the chemical group of benzoxazinoids measured in the root zone were of equal importance to explain the variance of weed biomass at the field level. In addition, a dendrogram showed large genetic variability for competitive and allelopathic traits in the Canadian spring cereals, providing the genetic basis for the initiation of breeding programmes for more weed-suppressive cultivars.

Keywords *Triticum aestivum* · *Triticosecale* · benzoxazinoid · HPLC–MS/MS · Field trial

Introduction

The interest in sustainable weed control strategies, which can be implemented as part of integrated pest management strategies to reduce the reliance on chemical weed control, has recently increased (Lamichhane et al. 2016).

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Exploitation of the crop's own abilities to suppress weeds by competition for light, space and nutrients and/or allelopathic interactions forms a weed control measure which would be easily implementable (Andrew et al. 2015). The specific crop traits conferring weed suppression have been extensively reviewed and described in the literature (Andrew et al. 2015; Worthington et al. 2014; Bertholdsson 2011). Recently, the relationship of competitive and allelopathic traits with weed-suppressive effects was studied applying a novel approach where the competitive and allelopathic variables of interest were measured at the field level and relative contributions of each trait were calculated using multivariate statistics (Reiss et al. 2018a). The competitive crop traits included in the former and present study are crop height, leaf area index (LAI) and early vigour. As allelopathic traits, allelopathic compounds belonging to the chemical group of benzoxazinoid (BX) were analysed. The group of BX was chosen as it has been identified as the most potent phytotoxic compounds produced by the *Poaceae* (Jia et al. 2006).

The present study analysed the weed suppressiveness of three Canadian spring wheat cultivars and seven breeding lines (hereafter referred to as cultivars) and two spring triticale cultivars based on the same methodology as the recent work of Reiss et al. (2018a). For integrated weed management (IWM) strategies to be successfully implemented, it

is, however, not sufficient to be easily implementable but knowledge on robustness to a range of crop varieties and climatic conditions is also of major importance (Swanton et al. 2008). Therefore, adopting a similar methodological approach was of benefit as it allowed us to compare the weed-suppressive effects of winter cereals to spring cereals, winter annual weeds to spring annual weeds and wet coastal climate to dry continental climate. Consequently, we hypothesised that the relative contribution of the competitive and allelopathic traits of interest was stable across the two continents.

To confirm this hypothesis, the objectives of this study were:

1. to measure three competitive crop traits LAI, early vigour and crop height, BX exudation and weed abundance in Canadian spring wheat and spring triticale cultivars, under standard cropping conditions,
2. to quantify BX concentrations in crop shoots, roots and soil with HPLC–MS/MS and
3. to determine the relative contribution of competition and allelopathy to the weed suppressiveness of ten spring wheat and two spring triticale cultivars.

Materials and methods

Field trials

Field trials were conducted in 2017 at the Agriculture and Agri-Food Canada, Lethbridge Research and Development Centre in Lethbridge, Alberta, Canada. The set-up included ten Canadian spring wheat and two Canadian spring triticale cultivars (Table 1). The experimental design was a completely randomised block design with weed presence/absence as block. The experiment was sown on the 24th of

May with 250 seeds per m² and a plot size of 4 m². Weed species sown into the experiment were *Chenopodium album* Lamb's quarters (LQ); *Avena fatua*, Wild oat (WO) and *Sinapis alba*, Mustard (WM). WO was sown at 130, WM at 50 and LQ at 140 seeds per m², respectively. Natural monocotyledonous weeds were almost not present and natural dicotyledonous (DI) weeds were combined to one biomass measurement. The most common natural weed was the dicotyledonous species *Amaranthus palmeri*, Palmer's pigweed. The competitive traits NDVI and LAI, and crop height were measured in the absence of weed on the 28th of June 2017, the 17th of July and the 19th of July, respectively. Soil, root and shoot samples for BX analysis were collected on the 5th of July and weed biomass was measured on the 12th of July.

Sample analysis

Sample collection, preparation, extraction and analysis were conducted as described in Reiss et al. (2018a). The compounds quantified in soil, root and shoot material belonged to the group of BX which can be divided into non-methoxy-substituted BX (BX-M): benzoxazolin-2-one (BOA), 2-hydroxy-1,4-benzoxazin-3-one (HBOA), 2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA), 2- β -D-glucopyranosyloxy-1,4-benzoxazin-3-one (HBOA-glc), 2-4 β -D-glucopyranosyloxy-4-hydroxy-1,4-benzoxazin-3-one (DIBOA-glc), double-hexose derivative of DIBOA (DIBOA-glc-hex) and double-hexose derivative of HBOA (HBOA-glc-hex) and methoxy-substituted BX (BX + M): 6-methoxy-benzoxazolin-2-one (MBOA), 2-hydroxy-7-methoxy-1,4-benzoxazin-3-one (HMBOA), 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA), 2- β -D-glucopyranosyloxy-7-methoxy-1,4-benzoxazin-3-one (HMBOA-glc) and 2- β -D-glucopyranosyloxy-4-hydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA-glc). Additionally, also their degradation products, the phenoxazinones

Table 1 Cultivars and their origin included in the field experiment in Lethbridge, Canada

Species	Cultivar	Source	Pedigree
Wheat	AAC Foray	AAC Foray	CPS03hnF4 5123.032/5701PR
Wheat	AAC Penhold	AAC Penhold	5700PR/HY644-BE//HY469
Wheat	FL62R1 ^a	FL62R1	QG 22.24 R1/Alsen//SS Blomidon/Alsen
Wheat	AC Stettler	AC Stettler	Prodigy/Superb
Wheat	FS7011 ^a	WB28479	FL62R1/AC Stettler
Wheat	FS10010 ^a	WB28320	FL62R1/AC Stettler
Wheat	AYT-1-273 ^a	WB22707	HW21//Vesper/FL62R1
Wheat	AYT-1-274 ^a	WB22708	HW21//Vesper/FL62R1
Wheat	AYT-1-277 ^a	WB22715	HW21//Vesper/FL62R1
Wheat	AYT-1-281 ^a	WB22732	HW21//Vesper/FL62R1
Triticale	AAC Delight	AAC Delight	03P110/Tyndal
Triticale	AC Ultima	AC Ultima	Drago/Ibex//Civet2

^aExperimental lines

2-acetylamino-3H-phenoxazin-3-one (APO) and 2-amino-7-methoxy-3H-phenoxazin-3-one (AMPO) were analysed in soil according to the protocol described in Reiss et al. (2018a).

Statistical analysis

Statistical analysis was conducted as described in Reiss et al. (2018a). The dendrogram (Supplementary Figure 1) was calculated with the scaled and centred dataset also used for the PCA analysis. Jaccard distance and Ward's method were used to divide the clusters.

Results

Competitive and allelopathic traits

Wheat contained significantly less BX concentration in shoot, root and soil materials, compared to triticale ($F(1,3022) = 23.39, p < 0.0001$). Independent of cereal species, root samples had significantly higher BX concentrations than shoot and soil samples ($F(2,3021) = 103.3, p < 0.0001$). Crop height at maturity and LAI were not significantly different between crop species ($F(1,32) = 0.436, p = 0.50$); $F(1,134) = 0.006, p = 0.94$). Moreover, triticale cultivars had a significant higher NDVI, compared to wheat ($F(1,178) = 225.2, p < 0.0001$).

Visualisation of the data structure

The results of the PCA analysis including the competitive traits such as crop height, NDVI and LAI, the BXs measured in the root zone and weed biomass measurements of sown and natural weeds are visualised in the biplot in Fig. 1. The first two principle components explained 56 % of the variance in the dataset. Weed biomass clustered together with the four wheat cultivars sharing the same pedigree (AYT-) (Table 1) and the wheat cultivar AAC Foray. The two triticale cultivars AAC Delight and AC Ultima had loadings on the two first components that were similar to the loadings of the BX's measured in the root zone. Consequently, BXs measured in the root zone are found in close proximity to the two triticale cultivars in the biplot in Fig. 1. Weed biomass of the model weed species (WM, WO, LQ) was highly loaded on both PC-axes and clustered together with the wheat cultivar AAC Foray. The cultivars AAC Penhold and FL62R1 were located isolated from the other cultivars opposite of the weed biomass measurements.

Using the same variables as in the PCA analysis, a dendrogram was calculated (Supplementary Figure 1). Interestingly, the two triticale cultivars AAC Delight and AC Ultima were clustering together with the wheat cultivar AAC Foray.

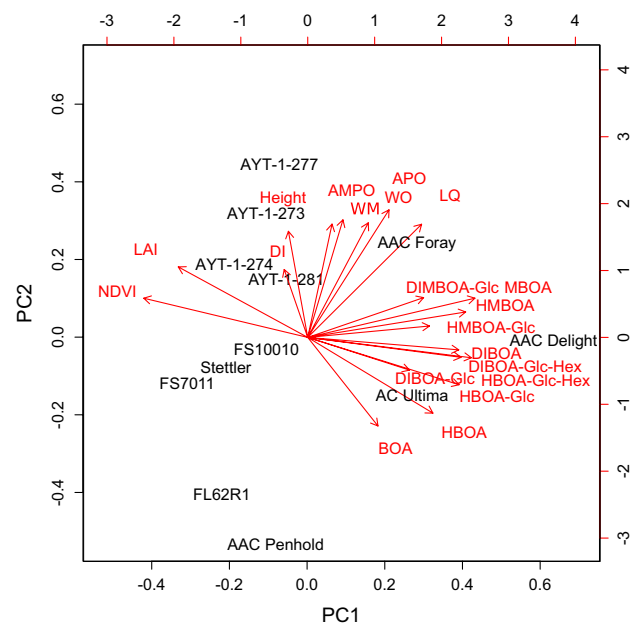


Fig. 1 Biplot of a principal component analysis conducted on the competitive and allelopathic traits of ten Canadian spring wheat and two spring triticale cultivars. PC1 explained 40% and PC2 16% of the variance in the dataset

The four cultivars (AYT-) sharing the same pedigree were located in close proximity and at the same branch as the triticale cultivars.

Contribution of the single variables to explain the variance in weed biomass

Partial least squares regression was calculated for model weed species and dicotyledonous natural weeds separately, and the regression was conducted both on the complete dataset with wheat and triticale cultivars and exclusively for wheat cultivars (Table 2). The models conducted on the complete dataset explained around 60% of the variance of weed biomass and differed significantly from the models based exclusively on the results with the wheat cultivars, explaining only between 35 and 55% of the variance of weed biomass ($F(1,26) = 23.36, p < 0.001$).

In the models on the complete dataset, competitive and allelopathic variables together explained about 60% of the variance of the model weeds LQ, WM and WO, and 54% of the natural dicotyledonous weeds (DI). Contributions of the single traits were not different between weed species ($F(3,60) = 0.53, P = 0.66$) and their individual contributions to the models did not differ ($F(15,48) = 1.71, P = 0.08$).

In the wheat cultivar-based models, contributions differed significantly between weed species ($F(3,60) = 5.11, p = 0.003$) resulting in a significantly higher explanation of variance of LQ biomass. However, also with these models,

Table 2 Contribution of the competitive and allelopathic traits in % to explain the variance in weed biomass. Different letters indicate significant differences between weed species $\alpha=0.05$

Cereals included	Triticale and wheat				Only wheat			
	LQ	WM	WO	DI	LQ	WM	WO	DI
Weed species								
Groups	a	a	a	a	b	a	ab	a
Compounds								
MBOA	3.18	5.18	3.68	3.60	3.49	2.16	4.16	2.52
HMBOA	2.70	4.55	3.66	3.90	4.21	1.48	3.92	2.23
APO	5.51	4.49	3.38	2.70	4.62	3.91	2.85	3.73
AMPO	3.63	4.10	3.02	0.68	3.93	3.47	1.99	4.00
BOA	3.59	2.69	3.76	2.31	1.42	2.23	3.60	1.65
HBOA	4.65	2.40	4.10	2.65	3.74	0.87	3.61	0.70
DIBOA	3.77	4.45	4.40	4.74	1.94	2.39	1.86	3.10
DIMBOA-Glc	2.17	2.88	3.06	4.17	3.71	1.80	2.96	1.64
HBOA-Glc	4.67	3.43	4.09	3.35	4.42	2.49	4.80	1.27
HMBOA-Glc	2.89	3.17	2.73	4.18	4.02	2.67	3.27	1.94
HBOA-Glc-Hex	3.84	4.45	4.58	4.92	4.54	1.68	4.13	0.76
DIBOA-GLc-Hex	3.70	4.45	4.54	4.62	4.01	2.84	1.42	3.26
DIBOA-Glc	4.19	2.67	3.03	2.00	3.85	3.33	3.01	4.08
Height	1.91	2.99	3.05	4.16	2.12	2.60	4.12	2.71
LAI ^a	5.24	2.96	4.29	2.64	2.92	2.44	1.17	1.35
NDVI ^b	4.88	4.34	4.97	3.91	2.11	1.80	2.36	0.21
Total	60.51	59.20	60.33	54.53	55.04	38.14	49.22	35.15

Total contribution is the sum of the contribution of all competitive and allelopathic variables

^aLeaf Area Index

^bNormalised Difference Vegetation Index

relative contribution of the single competitive and allelopathic variables did not differ significantly ($F(15,48) = 1.127, p = 0.36$)

Discussion

The ANOVA on BX concentrations (Supplementary Table 1) and the biplot of the PCA (Fig. 1) confirmed the conclusions of previous Danish and Australian studies that triticale had higher BX concentrations, compared to wheat (Reiss et al. 2018b; Wilkes et al. 1999). Furthermore, higher concentrations in root tissue, compared to shoot tissue, were also in line with two Danish studies (Reiss et al. 2018a, b).

The results of the measurements of competitive traits of Canadian spring cereals were also in line with earlier studies on Scandinavian winter cereal species. The ANOVA analyses of both studies showed that there were no significant differences in crop height and LAI between wheat and triticale, but triticale soil coverage was significantly higher in early spring, compared to wheat.

The two first components of the PCA analysis of Canadian cereal cultivars explained about 10% less of the total variance when compared to the PCA analyses conducted on Scandinavian cultivars (Reiss et al. 2018a). The reason for

this might be that rye was included as an additional species in the trials with Scandinavian cultivars, leading to a wider variation within traits. Nevertheless, the overall trends visualised in the PCA on Canadian spring cereals were comparable to those observed for the Scandinavian winter cereals. Weed biomass clustered together with wheat cultivars and allelopathic compounds with triticale cultivars.

Various approaches have been applied to investigate competitive or allelopathic weed-suppressive traits but only a few with the objective to determine both traits for the same cereal species (Bertholdsson 2011; Worthington et al. 2014). Both studies used bioassays to assess allelopathic traits. Worthington et al. (2014) concluded that allelopathic traits were of minor importance, whereas Bertholdsson (2011) found significant effects of allelopathic traits on weed growth and in a further study they concluded that there is breeding potential to increase the allelopathic potential of wheat (Bertholdsson et al. 2012). However, the first study measuring competitive, as well as allelopathic traits at the field level, was the Danish studies by Reiss et al. (2018a) and Reiss et al. (2018b). They used multivariate statistics to determine the relative contribution of competitive and allelopathic traits measured under standard cropping conditions in winter wheat, triticale and rye, and concluded that allelopathic and competitive traits contributed equally to

explain the weed-suppressive effect of the cereals (Reiss et al. 2018a). The PLSR analysis conducted on the Canadian wheat and triticale cultivars revealed that contributions of allelopathic and competitive traits were not significantly different, i.e. of equal importance explaining differences in weed biomass. Consequently, the trials on Canadian spring cereals are in line with the results obtained for Scandinavian winter cereals (Reiss et al. 2018a). The PLSR model, solely applied to Canadian spring wheat, revealed that variance in weed biomass of the dicot LQ was best described. This is in line with earlier results on Scandinavian winter cereals, where wheat described weed biomass of dicot weeds significantly better than triticale and rye (Reiss et al. 2018a). In contrast, weed-suppressive variables of Canadian wheat cultivars described weed biomass of the natural weed population by only 35%, which was the lowest percentage found in the analysis. One possible explanation might be that the most dominant dicot natural weed species was *A. palmeri*, which is very aggressive in its growth and hence less affected by the level of suppressiveness of a cereal cultivar. Even though a validation of this hypothesis was not within the scope of this study, it provides an example of the limitations of the integration of weed-suppressive cultivars as part of an integrated weed management strategy. Crop traits, conferring competition and allelopathy may not have measurable effects on the fitness of very competitive weed species.

In contrast to the earlier studies on Scandinavian cultivars, we had access to the pedigree information of the Canadian cultivars and the dendrogram in (Supplementary Figure 1) clearly illustrates that the data collected reflects differences between cereal cultivars. The result shows that there was a high degree of variability of weed-suppressive traits in the available gene pool of recent Canadian wheat and triticale cultivars, which is a precondition for initiating breeding programmes for increased weed-suppressive cereal cultivars.

Conclusions

In summary, it is concluded that there were no significant differences in the relative contribution of competitive and allelopathic traits to suppression of weed biomass of Canadian spring cultivar species. In other words, all traits were equally important explaining weed suppressiveness of the ten spring wheat and two spring triticale cultivars. Similar results were found with Scandinavian winter cereal species grown in competition with winter annual weed species under a wet coastal climate very different from the dry continental climate of Central Canada. This suggests that these traits

remain stable across continents which, in an IPM context, is important because results with wheat, triticale and rye are generalisable and can be applied in other conventional cropping contexts. Moreover, analysis of the genetic ancestry of the cultivars included revealed that there was a high degree of variability of weed-suppressive traits, providing preconditions for the initiation of cereal breeding programmes for increased weed-suppressive cultivars.

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