Biochemical Systematics and Ecology 76 (2018) 35–41

Contents lists available at ScienceDirect

Biochemical Systematics and Ecology

journal homepage: www.elsevier.com/locate/biochemsyseco

Weed suppressive traits of winter cereals: Allelopathy and competition

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ARTICLE INFO

Article history:
Received 1 February 2017
Received in revised form
2 November 2017
Accepted 5 December 2017

Keywords:
Benzoxazinoid
Triticum aestivum
Secale cereale
Triticosecale
Chromatography
Mass spectrometry

ABSTRACT

Weed suppressive potential of 33 winter wheat, 24 winter rye and 11 winter triticale cultivars recently introduced to the Scandinavian market was investigated. Competitive traits recorded were early vigor, leaf area index and crop height. Allelopathic potential was assessed by analyzing plant root and shoot material by LC-MS/MS for their content of 12 phytotoxic metabolites of the chemical group of benzoxazinoids (BX). Total BX content was highest in rye, followed by triticale and wheat. Benzoxazinoid composition varied between species with non-methoxy substituted BX dominating in rye and methoxy substituted BX dominating in wheat and triticale. Principal component analysis exhibited a clear relationship of allelopathic and competitive traits, together explaining 62% of the variance in the data set. This result underlines the need for further investigations of the relative contribution of allelopathy and competition to weed suppression in future studies.

1. Introduction

Improving weed suppressive ability of high yielding cereals could contribute to lowering herbicide use (Schulz et al., 2013). Competitive traits have been thoroughly studied to determine their contribution to weed suppression in conventional agricultural systems where fertilizer and water supply are not restricting plant growth. Early vigor, leaf area index (LAI) and canopy height were identified as the traits most strongly correlated with weed suppression of cereals (Hansen et al., 2008; Andrew et al., 2015; Mason and Spaner, 2006).

More recently, the contribution of allelopathy to the overall weed suppressive outcome has drawn attention and it has been shown that allelopathy has the potential to contribute considerably to weed suppression in cereals. For example, a screening of 453 wheat accessions using the equal compartment agar method showed that some cultivars were able to inhibit ryegrass root growth up to 90% (Wu et al., 2000b). However, allelopathic effects on weeds are very much species dependent and cumulative effects of the BX compounds and their metabolites will have considerable effects on the weed suppressive effect (Mathiassen et al., 2006; Zeng, 2014). This has led to a general agreement that weed suppressive outcome is determined by a combination of the competitive and allelopathic properties of the crop (Worthington and Reberg-Horton, 2013; Bertholdsson, 2011). However, the relative importance of allelopathic and competitive traits remains undisclosed.

In wheat, phenolic acids, short-chain fatty acids and particularly hydroxamic acids have been identified as the main groups of phytotoxic compounds (Wu et al., 2001b). Hydroxamic acids belong to the group of benzoxazinoids (BX), which also includes benzoxazolinones and lactames (Fig. 1). The chemical group of BX is abundant in Poaceae, including maize (*Zea mays*), rye (*Secale cereale*), wheat (*Triticum aestivum*) and triticale (*Triticosecale*) (Sicker et al., 2000; Wilkes et al., 1999). Benzoxazinoids have been shown to be more phytotoxic than phenolic acids (Jia et al., 2006) and are further known for their fungal growth and mycotoxin suppressive (Soltoft et al., 2008; Etzerodt et al., 2015), insect defensive (Niemeyer, 2009) and health promoting (Adhikari et al., 2015) effects.

The twelve BX chosen for analysis in the present study can be divided in non-methoxy substituted BX (BX-M): benzoxazolin-2-one (BOA), 2-hydroxy-1,4-benzoxazin-3-one (HBOA), 2,4-dihydroxy-1,4benzoxazin-3-one (DIBOA), 2-β-D-glucopyranosyloxy-1,4-benzoxazin-3-one (HBOA-glc), 2-4β-D-glucopyranosyloxy-4-hydroxy-1,4-benzoxazin-3-one (DIBOA-glc), double-

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https://doi.org/10.1016/j.bse.2017.12.001
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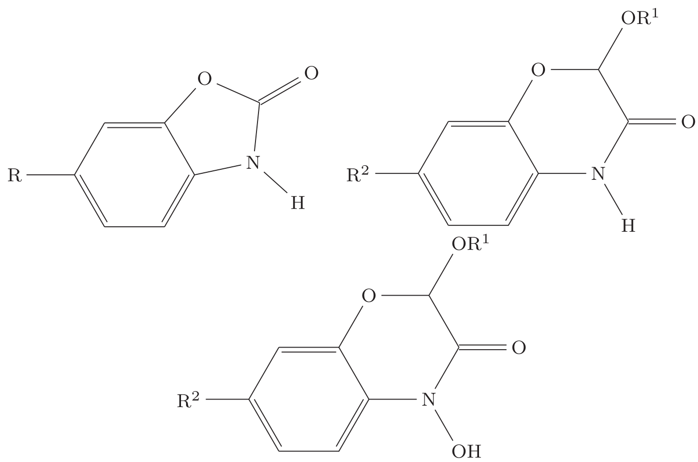

Benzoxazolinones		Lactames			Hydroxamic acids		
R	Abbreviation	R1	R2	Abbreviation	R1	R2	Abbreviation
H	BOA	H	H	HBOA	H	H	DIBOA
OCH_3	MBOA	H	OCH_3	HMBOA	H	OCH_3	DIMBOA
		Glc	H	HBOA-glc	Glc	H	DIMBOA-glc
		Glc	OCH_3	HMBOA-glc	Glc	OCH_3	DIMBOA-glc
		Glc-hex	OCH_3	HBOA-glc-hex[a]	Glc-hex	OCH_3	DIMBOA-glc-hex[a]

[a] Structure not fully elucidated.

Fig. 1. Chemical structures of the 12 BX compounds analyzed.

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).

To date, quantification of BX in cereal plant material and root exudates is in many cases insufficient due to a restriction to few compounds, mainly DIBOA and DIMBOA, or poor methodology with comparatively high detection limits (Belz and Hurle, 2005a; Brooks et al., 2012; Burgos and Talbert, 2000; Burgos et al., 1999; Reberg-Horton et al., 2005) etc. demanding a critical mindset when conclusions on allelochemic characteristics are drawn.

Benzoxazinoid content in Scandinavian winter wheat and winter rye cultivars has been extensively studied (Mogensen et al., 2006; Carlsen et al., 2009), but detailed investigations on the BX composition of winter triticale cultivars are limited. Triticale is of special interest, as it is the intergeneric hybrid between the female parent wheat and the male parent rye, providing the accessibility of interspecies germplasm for further breeding aims (Oettler, 2005; Bertholdsson, 2011). The official Danish trials for disease monitoring (SEGES, 2015) provide a unique possibility to study a collection of recent high yielding and promising cultivars of winter wheat, winter triticale and winter rye on the Scandinavian market managed according to general farming practice. The cultivars are grown side by side at several locations in the country, allowing for the comparison of a broad range of cultivars and to be able to come to conclusions on species specific traits and their correlations. As these disease observation trials are kept weed free, this study is solely focusing on the measurement of the allelochemic and competitive traits that have previously been shown to be weed suppressive. Further, it has been shown that weed suppression is highest in rye, intermediate in triticale and lowest in wheat (Dhima et al., 2006; Lemerle et al., 1995). In contrast, it was recently shown that triticale on average had higher allelopathic properties than rye (Bertholdsson, 2011; Bertholdsson et al., 2012). This illustrates that a lot remains to be elucidated about the causes of the weed suppressive potential of triticale and how this can be attributed to its ancestors rye and wheat.

The objective of this study was to determine the weed suppressive potential of high yielding winter wheat, winter triticale and winter rye cultivars by i) analyzing the composition of benzoxazinoids in the winter cereals wheat, triticale and rye ii) monitoring early vigor, canopy height and LAI, traits that have been associated with high weed suppressiveness (Andrew et al., 2015) and iii) examining the relationship between above-ground morphological traits and allelopathic properties.

2. Materials and methods

2.1. Experimental setup and sample collection

The field experiments were conducted in 2014/15 at two locations in Denmark, Flakkebjerg (55.3253 N, 11.3913 E) and Tølløse (55.60753 N, 11.801784 E). The set up was a completely randomized block design with species as blocks and cultivars as experimental unit. The experiments were sown at 24.09.2014 and 06.10.2014 at Flakkebjerg and Tølløse, respectively. Total plot size was 30 m^2 in Flakkebjerg and 20 m^2 in Tølløse. Sowing density of winter wheat was 350 or 245, of winter rye was 250 or 175 and of winter triticale was 300 germinable seeds per m^2 for non-hybrid and hybrid cultivars, respectively. Plots were kept weed free with herbicide applications and remaining crop management was carried out according to standard procedures. Weather conditions at both locations can be found as supplementary material.