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Protective responses induced by herbicide safeners in wheat

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ABSTRACT

Safeners are agrochemicals which enhance tolerance to herbicides in cereals including wheat (*Triticum aestivum* L.) by elevating the expression of xenobiotic detoxifying enzymes, such as glutathione transferases (GSTs). When wheat plants were spray-treated with three safener chemistries, namely cloquintocet mexyl, mefenpyr diethyl and fenchlorazole ethyl, an apparently identical subset of GSTs derived from the tau, phi and lambda classes accumulated in the foliage. Treatment with the closely related mefenpyr diethyl and fenchlorazole ethyl enhanced seedling shoot growth, but this effect was not determined with the chemically unrelated cloquintocet mexyl. Focussing on cloquintocet mexyl, treatments were found to only give a transient induction of GSTs, with the period of elevation being dose dependent. Examining the role of safener metabolism in controlling these responses, it was determined that cloquintocet mexyl was rapidly hydrolysed to the respective carboxylic acid. Studies with cloquintocet showed that the acid was equally effective at inducing GSTs as the ester and appeared to be the active safener. Studies on the tissue induction of GSTs showed that whilst phi and tau class enzymes were induced in all tissues, the induction of the lambda enzymes was restricted to the meristems. To test the potential protective effects of cloquintocet mexyl in wheat on chemicals other than herbicides, seeds were pre-soaked in safeners prior to sowing on soil containing oil and a range of heavy metals. Whilst untreated seeds were unable to germinate on the contaminated soil, safener treatments resulted in seedlings briefly growing before succumbing to the pollutants. Our results show that safeners exert a range of protective and growth promoting activities in wheat that extend beyond enhancing tolerance to herbicides.

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1. Introduction

Safeners are an important group of agrochemicals used extensively in cereals to protect crops from damage caused by selective herbicides without compromising weed control efficacy (Davies and Caseley, 1999; Edwards et al., 2005; Hatzios, 2003; Hatzios and Burgos, 2004). The mechanism of safener action most widely accepted is that these chemicals enhance crop tolerance by inducing the expression of proteins involved in the metabolism of herbicides, thus accelerating their detoxification (Davies and Caseley, 1999; Hatzios and Burgos, 2004). Amongst these 'safened' enzymes, the best studied are the glutathione transferases (GSTs) which catalyze the conjugation of herbicides with the endogenous tripeptide glutathione (Cummins et al., 1997; Davies and Caseley, 1999; DeRidder and Goldsbrough, 2006). Such conjugation has been demonstrated in barley (Scalla and Roulet, 2002), maize (Fuerst et al., 1993; Scarponi et al., 2006), wheat (Cummins et al., 1997; Pascal and Scalla, 1999), the wheat progenitor *Triticum tauschii* (Riechers et al., 2003; Xu et al., 2002), and rice (Wu et al., 1999). In addition, it is known that safeners enhance the expression of other classes of detoxifying enzymes including the cytochrome P450 mixed function oxygenases (Persans et al., 2001), type 1 glucosyltransferases (UGTs) (Brazier et al., 2002) and ATP-binding cassette (ABC) transporter proteins in a range of plants (Coleman et al., 1997; Riechers et al., 2010).

One intriguing characteristic of safeners is their apparent species specificity, with different classes of chemistry being developed for use in each of the major cereal crops (Riechers et al., 2010). In addition, for each given species a number of different safener chemistries have been developed. For example in wheat (*Triticum aestivum* L.), the quinolinoxycarboxylic acid cloquintocet mexyl, as well as the unrelated compounds mefenpyr diethyl and fenchlorazole ethyl have been widely used as post-emergence safeners (Fig. 1). All these compounds are used to safen aryloxyphenoxypropionate (AOPP) herbicides which inhibit the essential enzyme acetyl CoA carboxylase. All chemical classes of safener are known to functionally exert their protective effect by enhancing herbicide detoxification in wheat. For example, cloquintocet mexyl is known to increase the rate of hydroxylation, ether cleavage, and

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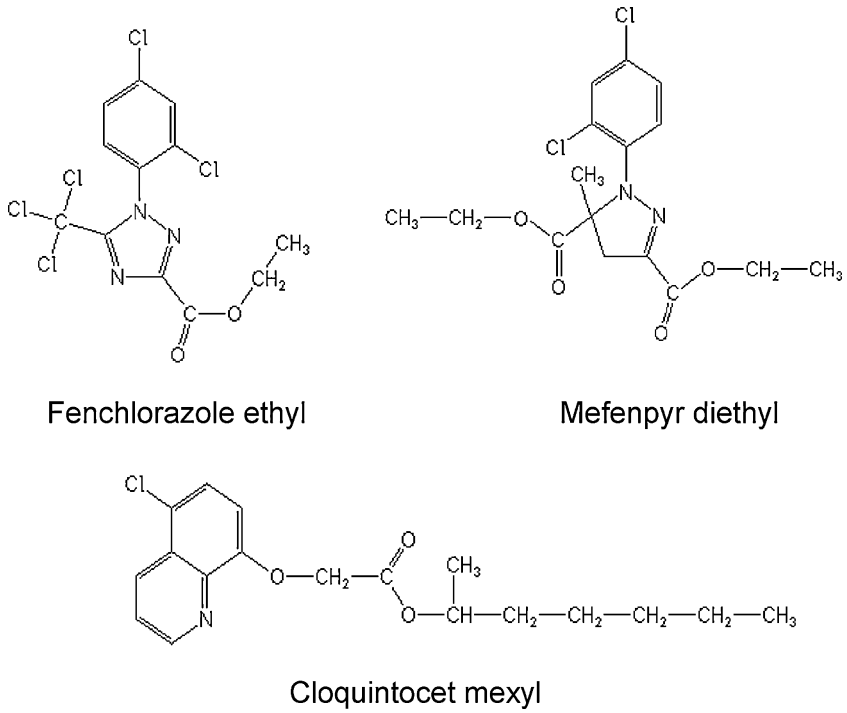

Fig. 1. The herbicide safeners cloquintocet mexyl, fenchlorazole ethyl and mefenpyr diethyl used in wheat.

glucosylation of the AOPP clodinafop propargyl (Kreuz et al., 1991), whilst fenchlorazole ethyl increased the cleavage by glutathionylation of the related herbicide fenoxaprop ethyl. In each case, whilst the safeners have been individually shown to enhance the activities or expression of several classes of herbicide-metabolising enzymes, there have been no reported attempts to compare the relative efficacy of these chemicals in inducing detoxification responses either qualitatively or quantitatively. It is also clear that whilst wheat safeners are predominantly used commercially to enhance tolerance towards a specific partner herbicide, this protective ability extends to multiple classes of chemistry. For example, in addition to safening the AOPP herbicide fenoxaprop ethyl in wheat, mefenpyr diethyl also increases the selectivity ratio of the unrelated sulfonyl ureas mesosulfuron-methyl and iodosulfuron methyl-sodium by enhancing their detoxification (Hacker et al., 2000).

Using cloquintocet mexyl, mefenpyr diethyl and fenchlorazole ethyl as different classes of safener (Fig. 1), we now address whether or not distinct chemistries invoke different responses in detoxifying enzymes in wheat. We then use different treatment regimes to test the longevity and dose dependence of response and evaluate the ability of safeners to protect wheat from soil borne chemical pollutants in addition to herbicides.

2. Materials and methods

2.1. Chemicals and related analysis

Safeners were purchased from Greyhound Chromatography & Allied Chemicals (Birkenhead, UK). The detergent formulant Biopower® was provided by Bayer Crop Science (Cambridge, UK). To prepare cloquintocet acid, a solution of cloquintocet-mexyl (100 mg, 0.3 mmol) was dissolved in tetrahydrofuran:H_2O (1:1, 5 mL) and treated with LiOH (30 mg, 1.2 mmol) at room temperature. The resulting solution was stirred for 3 h then diluted with water. The aqueous layer was first extracted with Et_2O (3 × 5 mL), then acidified (pH 1) with 1 M HCl and extracted with DCM (3 × 5 mL) and finally neutralised (pH 7) with solid $NaHCO_3$ and extracted with DCM (3 × 5 mL). The aqueous layer was then subjected to reverse phase (C-18) chromatography to afford the title compound as a white solid (65 mg, 93%). The sample was analysed and its authenticity confirmed by NMR using a Varian Inova instrument δ_H (500 MHz, d_6-DMSO) 8.95 (1H, s, Ar–H), 8.57 (1H, d, *J* 8, Ar–H), 7.80 (1H, bs, Ar–H), 7.70 (1H, d, *J* 8, Ar–H), 7.20 (1H, d, *J* 8, Ar–H), 4.42 (2H, s, CH_2) and by mass spectrometry on a Waters Acquity TQD *m*/*z* (ES^+) 240 ($[^{37}Cl]M^+$) 238 ($[^{35}Cl]M^+$) as described previously (Brazier-Hicks et al., 2008). For the extraction of safener metabolites, wheat tissue was ground up in liquid nitrogen using a pestle and mortar, extracted in 3× (w/v) methanol and then centrifuged (3000 × *g*, 5 min) to remove cell debris. The metabolites in the resulting supernatant were analysed using an Acquity UPLC™ linked to a Waters Q-TOF Premier mass spectrometer as described (Brazier-Hicks et al., 2008).

2.2. Plant growth and treatment

Wheat seeds cv. Einstein were obtained from Nickerson-Advanta LTD (Lincolnshire). For post-emergence safener treatments, seeds were imbibed in water for 1 h prior to planting. For pre-emergence treatments, the seeds were soaked for 24 h in 0.1% (v/v) aqueous acetone, with or without, the safener present. For standard studies, seeds were sown on John Innes loam-based compost N° 2. For studies with chemically contaminated soil, test samples from the field were kindly donated by ConocoPhillips (Seal Sands, Middlesborough TS2 1UH). The soil samples had been monitored for metal and organic content over the 5-year period prior to assay (Table 1). The contaminated soil was then mixed with sharp sand, at a ratio of 4:1, to improve soil consistency. In each case, seeds were sown on the surface of the soil and covered with a thin layer of horticultural sand, prior to placing in an environmental chamber (Sanyo MLR-350H) at 25 °C with 60% humidity and a photoperiod of 16 h light (150 $\mu E\,m^{-2}\,s^{-1}$) and 8 h dark. For post-emergence treatment, 7-day-old wheat shoots were sprayed with a hand held misting pump to run-off with 0.1% (v/v) Biopower® and 0.1% (v/v) acetone containing the safener at a final concentration of 10 mg L^{-1}

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