



Review

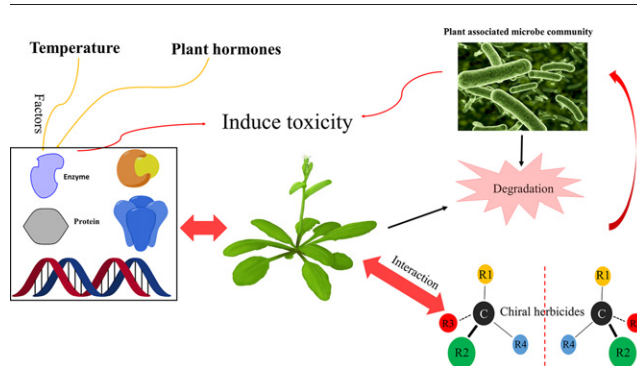
Interaction of chiral herbicides with soil microorganisms, algae and vascular plants☆

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HIGHLIGHTS

- Herbicide enantiomers behave differently toxic effects in vascular plants and algae.
- We review the current state of knowledge of herbicide enantiomers biodegradation and toxicity mechanism.
- Gathering knowledge on the enantioselective effects of herbicides will be of interest for pesticide risk assessment.
- Future work needs to develop “omics” techniques to clarify enantioselective mechanisms in chiral herbicide.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 6 October 2016

Received in revised form 13 December 2016

Accepted 13 December 2016

Available online 18 December 2016

Editor: Jay Gan

Keywords:

Chiral herbicide

Enantiomer

Enantioselective toxicology

Plant

Biodegradation

Herbicide toxicity

ABSTRACT

Chiral herbicides are often used in agriculture as racemic mixtures, although studies have shown that the fate and toxicity of herbicide enantiomers to target and non-target plants can be enantioselective and that herbicide toxicity can be mediated by only one enantiomer. If one enantiomer is active against the target plant, the use of enantiomer-rich herbicide mixtures instead of racemic herbicides could decrease the amount of herbicide applied to a crop and the cost of herbicide application, as well as unintended toxic herbicide effects in the environment. Such a change in the management of herbicide applications requires in-depth knowledge and a critical analysis of the fate and effects of herbicide enantiomers in the environment. This review article first synthesizes the current state of knowledge on soil and plant biodegradation of herbicide enantiomers. Second, we discuss our understanding of the biochemical toxicity mechanisms associated with both enantiomers in target and non-target plants gained from state-of-the-art genomic, proteomic and metabolomic tools. Third, we present the emerging view on the “side effects” of herbicides in the root microbiome and their repercussions on target or non-target plant metabolism. Although our review of the literature indicates that the toxicity of herbicide enantiomers is highly variable depending on plant species and herbicides, we found general trends in the enantioselective toxic effects of different herbicides in vascular plants and algae. The present study will be helpful for pesticide risk assessments as well as for the management of applying enriched-enantiomer herbicides.

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☆ This manuscript has been thoroughly edited by a native English speaker from an editing company (American Journal Experts). Editing Certificate will be provided upon request.

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1. Introduction

The production and release of anthropogenic chemicals into the environment are increasing. Their presence is now traceable in human tissues, as well as in wildlife worldwide. Of all agrochemicals used commercially, approximately 25% are chiral (Williams, 1996; Garrison, 2006), and chiral pesticides could account for more than 40% of all agrochemicals used in China (Ye et al., 2010). Most pesticides applied in the environment are herbicides (Zhou et al., 2010), and each year, colossal amounts (more than 10,000 tons) of chiral herbicides are applied to crops around the world (Garrison, 2006).

Chiral herbicides (see review of Ulrich et al. (2012) for a list of common chiral herbicides) are composed of one or more pairs of enantiomers that have similar physical and chemical properties in achiral environments (e.g., lipophilicity, evaporation rate, sorption on achiral molecules) but react differently with enzymes or other chiral biological molecules (Vetter, 2001; Liu et al., 2005). The interference of each herbicide enantiomer with chiral biomolecules ultimately depends on the absolute chemical configuration of each molecule (Naber and Rensen, 1988). Although most chiral herbicides are currently sold and applied as racemic mixtures rather than pure enantiomers (pure enantiomers of phenoxy herbicides are used in Netherlands and Switzerland; Liu et al. (2009)), only one enantiomer is generally active toward the target species. The inactive enantiomers can then be transported into soils and adjacent environments and could be toxic to non-target plants or other organisms (Qian et al., 2009).

Understanding the interactions between chiral herbicides and target (or non-target) organisms remains challenging due to different degradation patterns, toxic behavior and biological activities of enantiomers (Monkiedje et al., 2003; Liu et al., 2005; Diao et al., 2010b). The synthesis and critical analysis of the considerable amount of published data on the fate and toxicity of chiral herbicides is urgently needed to better understand the fate and toxicity of herbicide enantiomers. By highlighting research gaps and suggesting new research avenues, this could help with herbicide application management and ecological herbicide risk assessments (Fig. 1).

First, the present review aimed to critically discuss the current knowledge on the biodegradation of herbicide enantiomers in the environment. Second, we reviewed the toxicity effects of chiral enantiomers at the physiological, biochemical, transcriptomic and proteomic levels. Third, we presented the emerging view of the interactions between the rhizosphere microbiome and herbicide toxicity. Our aim was to focus on the environmental fate of chiral herbicides, as well as on chiral

herbicide toxicity in photosynthetic organisms to complement the literature reviews of Ulrich et al. (2012) and Ye et al. (2010, 2015), who considered the broad problems of all pesticides (insecticides, fungicides and herbicides). The present review also intended to update and expand the literature review of Liu et al. (2009), who discussed the biodegradation rates and enantioselective toxic effects of herbicides by reviewing the latest research breakthroughs on these topics with the help of new cutting-edge “omics” techniques.

2. Enantioselective herbicide biodegradation

Less persistent herbicides (soil half-life from days to months) are now increasingly being used compared to old persistent (aerobic or anaerobic soil half-life from months to years) herbicides such as atrazine, paraquat, and 2,4-dichlorophenoxyacetic acid (2,4-D), which are now restricted or banned in European countries (Wauchope, 1978; Bethsaass and Colangelo, 2006; Boyd, 2006; Kervégant et al., 2013). Due to this shift, microbial and plant biodegradation of pesticides has become an important factor when studying the fate of applied herbicides since pesticide biodegradation occurs before significant abiotic transformation (Garrison, 2006).

2.1. Biodegradation of herbicide enantiomers by the microbial community in soils

Microbial organisms in soils degrade chiral herbicides enantioselectively because different enzymes and species interact preferentially with each enantiomer (Zipper et al., 1996, 1998a, b; Nickel et al., 1997; Kohler, 1999; Fig. 2). For instance, Tett et al. (1994) reported that a consortium of three bacteria species (*Alcaligenes denitrificans*, *Pseudomonas glycinea* and *Pseudomonas marginalis*) isolated from topsoils only degraded R-mecoprop (R-MCPP) (and not S-mecoprop (S-MCPP)). Zipper et al. (1998a) further suggested that herbicide uptake and degradation may be induced by the presence of a given herbicide enantiomer concentration. They found that bacteria species isolated from soils possess three inducible membrane transporters capable of the active uptake of R-dichlorprop (R-DCPP) and R-MCPP, as well as S-dichlorprop (S-DCPP) and S-MCPP. To our knowledge, the microbial enzymes involved in herbicide biodegradation are poorly understood. Among the limited information in the literature on this topic, the soil bacterium *Sphingomonas herbicidovorans* MH has been shown to contain two different enzymes (α -ketoglutarate-dependent dioxygenase)

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