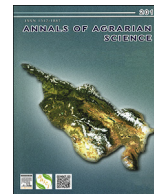




Contents lists available at ScienceDirect

Annals of Agrarian Science

journal homepage: <http://www.journals.elsevier.com/annals-of-agrarian-science>

Analysis of the metabolic resistance of *Ambrosia artemisiifolia* L. to the herbicides action

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ARTICLE INFO

Article history:

Received 5 August 2017

Accepted 14 November 2017

Available online xxx

Keywords:

Common ragweed

Metabolic resistance

Herbicide

Mode of action

Isoforms

Isoelectric

ABSTRACT

Action and aftereffect of the herbicides with different modes of action on the common ragweed population were studied in the field and greenhouse experiments. Activation of glutathione S-transferase has been detected due to the action of herbicides Harness and Guardian-Tetra both in leaves of juvenile plants and in ragweed seeds, which indicates intensive detoxification of herbicides during weed ontogenesis. Electrophoretic analysis showed that four components in protein spectra of ragweed seeds were inherent in seeds collected from herbicides-treated plants only. Using the method of isoelectric focusing, three specific peroxidase isoforms associated with a certain mechanism of herbicidal action on the parent plants were found in leaves of the next generation plants. The results confirm the intensive adaptive changes in *A. artemisiifolia* population that could provide the metabolic resistance to different modes of the herbicide action.

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Introduction

In majority of the developed countries herbicide treatment has been the most effective way to control weeds in crops over the past decades [1,2]. However, the long-term use of herbicides in large areas led to the emergence of numerous resistant populations of weeds [3]. Since a mention of the resistant biotype of *Senecio vulgaris* to simazine [4], the phenomenon of herbicide resistance has reached the level of a global problem. More than 300 herbicide-resistant biotypes of weeds have been identified in more than 270 thousand fields in 56 countries [5]. The largest number of them was found in the USA (139 of all biotypes), Australia (60 biotypes), Canada (52 biotypes) and some European countries [2]. The current situation makes us acknowledge that the herbicide-resistant weeds can significantly weaken the stability of agriculture [6], which threatens global food security [7].

Spontaneous resistance manifests itself within weed populations due to such reasons as uniformity of control methods, use of persistent herbicides, and reduction of crop rotation, use of herbicides with identical mechanism of action [8–10]. However,

the herbicide does not change the genotype of the weed, but only selects plants with some level of existing genetic resistance to a certain mechanism of action [2]. Thus, resistance to herbicides occurs in populations of weed plants as a result of evolutionary adaptation under the action of rigid selective pressure [3]. Vigueira et al. [11] consider the herbicide resistance of weeds as an example of convergent evolution, when both the same and different mutations present in plants lead to the emergence of a resistant phenotype in a group of species. Resistance of plants can be caused by changes in the three-dimensional structure of the target protein (target-site resistance, TSR) which reduces the bond to the herbicide, or does not involve the target (non-target-site resistance, NTSR), and includes biochemical modification and/or compartmentalization of the herbicide and its metabolites [3,6]. Climate change, which has become an urgent problem in recent decades in many areas [12], unexpectedly increased the risk of herbicide resistance precisely because of the increased detoxification of the herbicides [13].

In Ukraine, about 300 of the most widespread species of weed plants were found in crops, among which *Ambrosia artemisiifolia* L. (common ragweed) occupies one of leading places in the problem of eradication in the steppe Dnieper [14]. At the same time, numerous confirmations of the emergence of resistant common ragweed populations in different regions [8,15–18] indicate the

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Peer review under responsibility of Journal Annals of Agrarian Science.

<https://doi.org/10.1016/j.aasci.2017.11.005>

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global nature of the problem. Today it is known that the mutations in the enzymes structure are the basis for resistance of *A. artemisiifolia* to herbicides – inhibitors of acetolactate synthase (ALS) [18,19] and protoporphyrinogen oxidase as well [20]. Unfortunately, the mechanisms of non-target-site resistance of common ragweed as well as many other weeds have been studied extremely little, including due to the complexity of the metabolic processes [6]. The objectives of this study were (1) to detect the effects of herbicide action and after-action on biochemical and physiological properties of *A. artemisiifolia* and (2) to identify the metabolic resistance of ragweed population to different modes of action of the herbicides.

Objectives and methods

Field experiments were performed during 2014–2016 in the corn sowings on the experimental plots of Institute of Grain Crops (Dnipro, Ukraine). The plots soil was the ordinary black soil with the humus content 3.8–4.2%, and with the neutral reaction of the soil solution. Soil-applied herbicides (Harness at a dose 2.5 L/ha, and Guardian-Tetra at a dose 3.5 L/ha) were used as pre-emergence (PRE) herbicides. Foliar-applied herbicides (Starane-Premium at a dose 2.5 L/ha, Guardian-Tetra at a dose 3.5 L/ha, Stellar at a dose 1.25 L/ha, Milagros at a dose 0.18 L/ha, Lancelot at a dose 100 g/ha, and Pic at a dose 100 g/ha) were used after crop emergence as POST herbicides. Any herbicide was introduced on the control plots.

Common ragweed seeds were collected in September 2016 both from treated and control plants, and prepared for germination by the method of Van Wely et al. [19]. Seeds were kept for 2 months in wet sand at 4 °C. After that, seeds were germinated in plastic cups filled with a mixture of soil and sand (1:1) in a greenhouse with a 12-h photoperiod at 22 °C.

The protein composition of common ragweed seeds was studied by the method of gradient electrophoresis in a polyacrylamide gel (SDS-PAGE) in accordance with Laemmly [21].

Method of isoelectric focusing (IEF) described by Righetti [22] was used to study the isoforms of peroxidase in leaves of the next-generation common ragweed plants, grown in the greenhouse without herbicide treatment.

Activity of glutathione S-transferase (GST, EC 2.5.18) was measured by the method of Habig et al. [23] with 1-chloro-2,4-dinitrobenzene (CDNB) as a substrate. 200 mg of plant material was triturated with Tris-buffer, pH 8.0, containing 0.1% PVP, and centrifuged for 20 min at 10,000 rpm and 4 °C. The assay mixture containing Tris-buffer, 100 µl of GSH, and 200 µl of sample was incubated during 10 min at 30 °C. Optical density change was detected at 340 nm during four minutes after addition of 100 µl CDNB, and the enzyme activity was expressed in nkat/g DW (dry weight) in seeds or in nkat/g WW (wet weight) in leaves. Determination of the enzyme activity was performed in three replicates. Significance of the differences was estimated using Student's t-test ($P < 0.05$), and was indicated by an asterisk (*).

Results and analysis

In the field experiment, the number of juvenile plants of *A. artemisiifolia* and level of the metabolic processes in weed leaves differed significantly depending on herbicide classes, mechanisms of action, and variant of herbicide treatment (Table 1).

The PRE-herbicides Harness and Guardian-Tetra reduced the number of juvenile weed plants by no more than 60% of the control level. The active substance in these herbicides is acetochlor belonging to the chloroacetanilides and inhibiting the synthesis of the fatty acids. Herbicides with this mechanism of action have been used for many years on the experimental plots, which may explain

their low effectiveness. However, the activity of glutathione S-transferase was the greatest in the plants treated with PRE-herbicides Harness and Guardian-Tetra, exceeding the control level by 1.5 and 1.4 times. Catalyzing the glutathione conjugation with xenobiotic, GST provides one of the key ways of their detoxification [24]. Since the intensive biochemical herbicides modification indicates the formation of a metabolic (non-target-site) resistance in the treated plants [3,5,6], GST activation in leaves of common ragweed plants can testify to similar processes due to acetochlor action.

In comparison with Harness individual action, sequential treatment with Harness and the POST-herbicides Starane and Lancelot was accompanied by a decrease in weed number 4.2 and 2.5 times respectively, and decrease in GST activity 1.5 times in both variants. Herbicides Starane and Lancelot have a different structure, but are combined by auxin-like mechanism of action. So, the use of the auxin-like POST herbicides can be an effective method of controlling *A. artemisiifolia* at the plots with long-lasting application of acetochlor.

As for the herbicide Guardian-Tetra, its foliar applying, in comparison with soil applying, was almost 3 times more effective in reducing the weed number. On the contrary, GST activity in the ragweed leaves was reduced due to POST treatment, amounting to about 90% of the control. It seems that terbutylazine (auxin-like component of the herbicide) did not affect the juvenile weed plants in the cause of soil-applying, which could be due to a decrease in the penetration and translocation of the herbicide, and also contribute to the development of resistance.

The polycomponent herbicide Stellar, first applied on the experimental plots, provided the greatest decrease in juvenile plants number together with a slight GST activation. Obviously, the combined action of topramesone inhibiting the growth point of the plants and auxin-like dicamba caused an irreversible imbalance of phytohormones and subsequent weed elimination.

In our study, variability in the properties of seeds collected from plants of *A. artemisiifolia* was established (Table 2). Seed weight was declined on most plots, especially due to effect of the herbicide Guardian-Tetra: more than 40% below control both with the soil and foliar applying. An increase in seed weight of 14% was founded only on the plots where a tank mixture of the herbicides Milagro (inhibitor of ALS) and Lancelot (ALS-inhibiting together with auxin-like action) was applied. Since seed size polymorphism is of adaptive importance [25], variability of common ragweed seed weight like the previously revealed vital differentiation of ragweed seeds [26] can contribute to weed population survival under the herbicide action. This conclusion is confirmed by the data of Matyukha et al. [14] that in the steppe Dnieper area during 1991–2001, with the annual herbicide application, the total number of weed seed germs in topsoil increased 1.5 times, while common ragweed seeds increased 2.4 times.

GST activity in seeds from ragweed plants treated with Harness (PRE) + Starane (POST) and Guardian-Tetra (PRE and POST) exceeded control level by 30%, 15% and 8%, respectively, indicating an increase in metabolic detoxification in weed population. The results are in agreement with the data [24] according to which metabolic resistance is often manifested to the herbicides of various chemical classes and mechanisms of action. GST activation in seeds of common ragweed can also be combined with the biosynthesis of specific isoforms which play a key role in the multiple herbicidal resistances (MHR), as Cummins et al. [27] noted. Thus, formation of seeds in the field experiment indicates that the population of *A. artemisiifolia* is likely to have simultaneous resistance to several different modes of herbicide action, including auxin-like, inhibition of the fatty acids synthesis, and ALS inhibition.

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