

REVIEW

Mechanisms of multiple resistance to herbicides in *Conyza* sp. complex

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Abstract

Reports of weed resistance to herbicides have increased in recent years and differentiation in resistance mechanisms is considered to be a concern for the future of weed science. The aim of this work was to characterize the mechanisms of resistance to herbicides associated with *Conyza* sp. complex and analyze their implications. Aspects of the action of herbicides commonly used in their control will be addressed, in addition to a description of the mechanisms involved in multiple resistance in *Conyza* species.

Keywords: herbicides, horseweed, non-target-site resistance (NTSR), target-site resistance (TSR)

Herbicides are chemical compounds that act on specific points of plant metabolism, inhibiting or interrupting their development by enzymatic inhibition (Duke and Powles 2008; Cardinali *et al.* 2015; Piasecki *et al.* 2019), by mimicking endogenous growth regulatory compounds (Smith 1989) or by acting in photosystems (Kraus *et al.* 1995; Hawkes 2013).

Weed resistance to herbicides is defined as the biotype ability to continue its development and produce offspring after exposure to a certain dose of an herbicide that would be lethal to the sensitive biotype. It is an evolutionary process of the species, due to a genetic change that occurs in the species and is selected by the herbicide (Christoffoleti *et al.* 1994).

The consequence of the selection of resistant plants for world agriculture is reflected in the economic impact of such production systems, either by loss of production due to damage or competition, or by the need to use alternative tools. In the United States, losses related to resistance selection are estimated to be around US \$1.5 billion per year (Pimentel and Burgess 2014). Adegas *et al.* (2017) estimated the amount spent by Brazilian farmers, considering areas where there are

reports of resistant weeds, at up to US \$1.63 billion per year.

The complex of *Conyza* species (*Conyza bonariensis*, *C. canadensis* and *C. sumatrensis*) includes morphologically similar species which are important weeds in agricultural production systems, with the possibility of hybridization, high genetic diversity and adaptability to agricultural production systems (Lazaroto *et al.* 2008; Soares *et al.* 2015; Marochio *et al.* 2017). Characteristics such as positive photoblastic seeds, a high capacity for seed formation and wind and water dispersion favored the growth of the importance of this species (Nandula *et al.* 2006; Joris *et al.* 2016).

Conyza bonariensis is a species native to South America, which occurs abundantly in regions of Argentina, Brazil, Paraguay, and Uruguay (Kissmann and Groth 1999). *Conyza canadensis* is native to North America, with distribution worldwide, mainly in temperate zones of the northern hemisphere (Frankton and Mulligan 1987; Holm *et al.* 1997). *Conyza sumatrensis* is also native to South America, and it is dispersed worldwide throughout tropical and subtropical areas (Thebaud and Abbott 1995; Pruski and Sancho 2006) (Fig. 1).

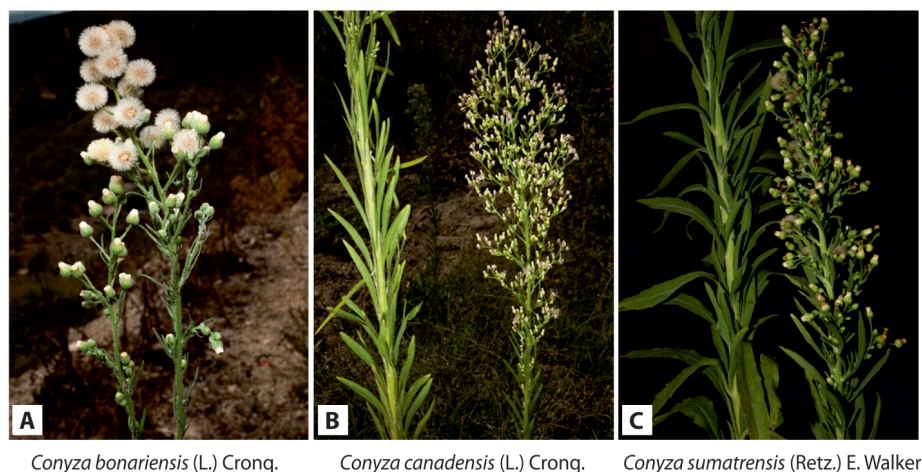


Fig. 1. The three *Conyza* species in the flowering stage: A – *Conyza bonariensis* with the cylindrical inflorescence, composed of 15–40 capitula per branch, B – *Conyza canadensis* with terminal inflorescences, sometimes with lower branches overtopping main axis and C – *Conyza sumatrensis* with the pyramidal inflorescence and widely and profusely branched, the lateral branches not overtopping the main axis

There are numerous reports of resistance of the three species to herbicides in several countries. There are reports of *Conyza* spp. resistance to six herbicide mechanisms of action, however, the selection of multiple herbicide resistance has become a concern, since resistant populations may have both “target-site resistance” (TSR) and “non-target site resistance” (NTSR).

The metabolic resistance mechanism (non-target site resistance) can confer resistance to herbicides not yet developed. In the case of resistance to glyphosate, which has been widely studied, at least five resistance mechanisms have been described in the species (Gage *et al.* 2019).

These mechanisms are related to the action site. In TSR there is mutation in genes that encode proteins of the action site, which affects the contact/action of the herbicide in the plant. In NTSR, it is due to reduced absorption, translocation, sequestration of the molecule in some cellular compartment or metabolic activity involved in detoxification (Kaundun *et al.* 2019; Jugulam and Shyam 2019).

Understanding the mechanisms related to weed resistance to herbicides can help to elucidate fundamental biochemical processes by which plants adapt and develop. This information can be applied in integrated management of weeds, including the creation of new technologies.

The development of genetically modified plants has proved to be very efficient. The identification and introduction of genes that confer tolerance to herbicides has been used in this process to obtain new technologies, like transgenic plants. Genetic engineering involves exploring new tools, such as the identification and silencing of these genes, interfering RNA technology, and the use of CRISPR-CAS9 (Burgos *et al.* 2017). The introduction of new technologies assists in

management due to increased possibilities of selective molecules to be used in post-emergence (Rüegg *et al.* 2007; Green and Owen 2010).

The present review aimed to describe and characterize the mechanisms of resistance to herbicides associated with the *Conyza* sp. complex and to analyze their implications in weed science.

State of *Conyza* sp. resistance worldwide

An example of plants that have both types of resistance mechanisms is the horseweed (*Conyza* sp.). It is a weed of great relevance in Brazil today, which has been causing concern among specialists due to reports of resistance to various herbicides. Species of the genus *Conyza* show worldwide resistance to different mechanisms of action of herbicides: EPSPs inhibitors, ALS inhibitors, photosystem I inhibitors, auxin mimics, PROTOX inhibitors, and photosystem II inhibitors (Table 1).

Conyza sumatrensis resistance to glyphosate and with multiple resistance to glyphosate and chlorimuron in America was first reported in 2014 (Santos *et al.* 2014a, b). In 2019, the first case of *C. sumatrensis* resistance to five mechanisms of action in Brazil was reported (Pinho *et al.* 2019). Previously, biotypes showing multiple resistance to glyphosate, chlorimuron, paraquat and an unusual symptom of a hypersensitive response have been identified, generating a rapid necrotic response hours after application of 2,4-D (Queiroz *et al.* 2019; Baccin 2020; Albrecht *et al.* 2020b). This rapid response is seen as resistance in practical terms and managed in the field.

Table 1. Reports of herbicide resistance in *Conyza bonariensis*, *C. canadensis* and *C. sumatrensis* worldwide (Heap 2014)

Country	Year	Site of action	Active ingredient
<i>Conyza bonariensis</i>			
Spain	1987	PSII	simazine
Egypt	1989	PSI	paraquat
Japan	1989	PSI	diquat and paraquat
Israel	1993	PSII	atrazine and simazine
Israel	1993	ALS	chlorsulfuron
South Africa	2003	PSI	paraquat
South Africa	2003	EPSPs	glyphosate
Spain	2004	EPSPs	glyphosate
Brazil	2005	EPSPs	glyphosate
Israel	2005	EPSPs	glyphosate
Colombia	2006	EPSPs	glyphosate
USA	2007	EPSPs	glyphosate
USA	2009	EPSPs and PSI	glyphosate and paraquat
Greece	2010	EPSPs	glyphosate
Portugal	2010	EPSPs	glyphosate
Australia	2011	EPSPs	glyphosate
Australia	2011	EPSPs	glyphosate
Argentina	2012	EPSPs	glyphosate
Australia	2016	PSI	paraquat
<i>Conyza canadensis</i>			
Japan	1980	PSI	paraquat
France	1981	PSII	atrazine
Switzerland	1982	PSII	atrazine and simazine
United Kingdom	1982	PSII	Simazine
Poland	1983	PSII	Simazine
Czech Republic	1987	PSII	atrazine
Spain	1987	PSII	atrazine and simazine
France	1988	PSII	linuron
Belgium	1989	PSII	atrazine
Canada	1993	PSI	paraquat
Israel	1993	ALS and PSII	atrazine, chlorsulfuron, imazapyr, metribuzin, pyriithiobac-sodium and sulfometuron-methyl
USA	1994	PSI	paraquat
Belgium	1998	PSI	paraquat
Poland	2000	ALS	imazapyr
USA	2000	EPSPs	glyphosate
USA	2001	ALS	chlorimuron-ethyl and cloransulam-methyl
USA	2002	PSII	atrazine, diuron and simazine
USA	2002	PSII	diuron
USA	2003	ALS and EPSPs	chlorimuron-ethyl, cloransulam-methyl and glyphosate
Brazil	2005	EPSPs	glyphosate
China	2006	EPSPs	glyphosate
Spain	2006	EPSPs	glyphosate
Czech Republic	2007	EPSPs	glyphosate
USA	2007	EPSPs and PSI	glyphosate and paraquat
Canada	2010	EPSPs	glyphosate

Table 1. Reports of herbicide resistance in *Conyza bonariensis*, *C. canadensis* and *C. sumatrensis* worldwide (Heap 2014) – continuation

Country	Year	Site of action	Active ingredient
Poland	2010	EPSPs	glyphosate
USA	2010	EPSPs and ALS	glyphosate, thifensulfuron-methyl and tribenuron-methyl
Italy	2011	EPSPs	glyphosate
Portugal	2011	EPSPs	glyphosate
Canada	2011	ALS and EPSPs	cloransulam-methyl and glyphosate
Greece	2012	EPSPs	glyphosate
Japan	2014	EPSPs	glyphosate
USA	2014	EPSPs and PSI	glyphosate and paraquat
Hungary	2016	EPSPs	glyphosate
South Korea	2017	EPSPs	glyphosate
France	2019	EPSPs	glyphosate
<i>Conyza sumatrensis</i>			
Taiwan	1980	PSI	paraquat
Japan	1986	PSI	diquat and paraquat
Malaysia	1990	PSI	paraquat
Sri Lanka	1998	PSI	paraquat
Spain	2009	EPSPs	glyphosate
Brazil	2010	EPSPs	glyphosate
France	2010	EPSPs	glyphosate
Brazil	2011	ALS	chlorimuron-ethyl
Brazil	2011	ALS and EPSPs	chlorimuron-ethyl and glyphosate
Greece	2012	EPSPs	glyphosate
Brazil	2016	PSI	paraquat
France	2016	ALS	flazasulfuron, iodosulfuron-methyl-sodium, mesosulfuron-methyl and penoxsulam
France	2016	ALS and EPSPs	flazasulfuron, glyphosate, iodosulfuron-methyl-sodium, mesosulfuron-methyl and penoxsulam
Brazil	2017	PPO	saflufenacil
Brazil	2017	ALS, PSI and EPSPs	chlorimuron-ethyl, glyphosate and paraquat
Brazil	2017	PSII, PSI, PPO, EPSPs and AUXIN	2,4-d, diuron, glyphosate, paraquat and saflufenacil
Paraguay	2017	ALS, PSI and EPEPs	chlorimuron-ethyl, glyphosate and paraquat
Australia	2018	PSI	paraquat
Australia	2018	EPSPs	glyphosate
Turkey	2018	EPSPs	glyphosate

Mechanisms of action of herbicides and changes in metabolism in resistant *Conyza* spp. biotypes

There are several mechanisms of resistance described in *Conyza* spp. (Table 2). Sometimes several mechanisms are involved in the resistance to a single mechanism of action. Genetic variability and the possibility of hybridization between species is one factor that can contribute to the selection of resistance to

herbicides that occurs increasingly among *Conyza* species (Soares *et al.* 2015).

The mechanisms involved in the resistance of *C. sumatrensis* to Protox inhibitors and auxin mimics are still unknown. In other species, the mechanism of resistance to Protox inhibitors is defined as a mutation in the PPX2 gene (Giacomini *et al.* 2017).

The overexpression of the gene regulating the production of the enzyme EPSPs (Sammons and Gaines 2014), insensitivity of the enzyme EPSPs (Kaspary *et al.* 2016), alteration in the uptake and transport of the

Table 2. List of resistance mechanism described in *Conyza* spp. worldwide

Site of action	Active ingredient	Resistance mechanism	Reference
EPSPS	glyphosate	enzyme insensibility	Kaspary <i>et al.</i> (2016)
		overexpression of EPSPs gene	Dinelli <i>et al.</i> (2008); González-Torralva <i>et al.</i> (2014); Sammons and Gaines (2014)
		vacuolar sequestration	Ge <i>et al.</i> (2010); Ge <i>et al.</i> (2014); Kleinman and Rubin (2017)
		antioxidant enzymes activity	Piasecki <i>et al.</i> (2019)
		differential uptake and translocation, metabolism	Ferreira <i>et al.</i> (2008); Preston and Wakelin (2008); González-Torralva <i>et al.</i> (2012), Cardinali <i>et al.</i> (2015); Moretti and Hanson (2016)
ALS	cloransulam, chlorimuron, imazethapyr, imazapyr, chlorsulfuron, pyriithiobac, mesosulfuron, thifensulfuron, tribenuron, flazasulfuron, iodosulfuron, metsulfuron, penoxulam	ALS mutations (altered target site): amino acid substitution	Osuna and De Prado (2003); Zheng <i>et al.</i> (2011)
PSI	paraquat, diquat	activity of antioxidant system	Fuerst <i>et al.</i> (1985); Vaughn and Fuerst (1985); Shaaltiel and Gressel (1986); Pölös <i>et al.</i> (1988); Turcsányi <i>et al.</i> (1994); Ye and Gressel (1994); Szigeti <i>et al.</i> (1996); Pereira (2019)
		reduced translocation and vacuolar sequestration	Moretti and Hanson (2016)
PSII	atrazine, simazine, linuron, metribuzin, sulfometuron, diuron	mutation at <i>psbA</i> gene (Ser 64 to Gly)	Gawronski <i>et al.</i> (1992); Heap (2014)
		gene mutation (Ser 264 to Gly)	Matzrafi <i>et al.</i> (2015)
		structural alteration of atrazine-binding and change in lipid composition of thylakoid membranes	Lehoczki <i>et al.</i> (1984)
		D1 protein mutation and limited conversion of xanthophyll cycle components	Váradí <i>et al.</i> (1994); Darkó <i>et al.</i> (1996)
PPO	saflufenacil	unknown	–
Auxin	2,4-D	unknown	–

herbicide in the plant, possibly due to morphological changes between resistant and susceptible biotypes (Ferreira *et al.* 2008; Cardinali *et al.* 2015; Moretti and Hanson 2016; Baccin 2020), sequestration of the herbicide and compartmentalization in the vacuole by means of specific transporters (Ge *et al.* 2010, 2014) and enzyme activity of the antioxidant system are the mechanisms ascribed to glyphosate resistance in horseweed (Piasecki *et al.* 2019).

Regarding resistance to the herbicides inhibiting the enzyme acetolactate synthase (ALS), present in the biosynthesis of the amino acids alanine, leucine and valine, the change in the sequence of the amino acids that make up the enzyme, in specific positions, leads to a change in the binding site, making the herbicide

unable to couple in the region and consequently losing its effect, since there is no interruption in metabolism (Osuna and De Prado 2003; Zheng *et al.* 2011).

Reports of paraquat resistant weeds date back to 1980, with resistant *Conyza* biotype found in Taiwan. Since then, the resistance of *Conyza* to paraquat has occurred in several countries: Hungary (Pölös *et al.* 1988), Taiwan, Japan, Egypt, Malaysia, Canada, United States (Moretti and Hanson 2016), Belgium, Sri Lanka, South Africa, Australia, Brazil and Paraguay (Pereira 2019; Pinho *et al.* 2019; Zobiolo *et al.* 2019; Albrecht *et al.* 2020a, b). It has been noted that paraquat resistance probably applies to diquat, since they are not only part of the same mechanism of action, but are also of the same chemical group, therefore, very similar.

The rapid action of this herbicide is related to its action on the complex of Photosystem 1 located on the thylakoid membrane, inside the chloroplast, as a false electron acceptor of photosynthesis, being a preferential electron acceptor of ferredoxin. After reduction, paraquat di-cation becomes a mono-cation radical, transferring an electron to molecular oxygen, producing reactive oxygen species (Summers 1980). The state of oxidative stress is reached by plants due to the intense formation of free radicals and changes in proteins are initiated due to a chain of reactions. Lipid peroxidation caused by reactive oxygen species destroys the double lipid layer of the cell membrane, threatening homeostasis.

The toxic effect of paraquat on plants is due to the oxidation-reduction reaction, transferring electrons to NADP, forming NADPH in addition to superoxide radicals. The partial reaction of oxygen for electrons that escape the respiratory chain forms reactive oxygen species (ROS), which when present in large quantities cause serious damage to DNA, proteins and lipids (Finkel and Holbrook 2000).

At the cellular level, oxidative damage can lead to disruption of growth, senescence and cell death. Defense systems have evolved in plants to combat the accumulation of these reactive oxygen species, but all the enzymes in the antioxidant system are not sufficient to neutralize the production of ROS, generating oxidative stress. SOD (superoxide dismutase) corresponds to a whole family of enzymes present in both cytosol and mitochondria, and acts by catalyzing the dismutation of the superoxide radical into hydrogen peroxide and oxygen. The increase in the enzymatic activity of the antioxidant system of plants is one of the described resistance mechanisms (Fuerst *et al.* 1985; Vaughn and Fuerst 1985; Pereira 2019).

Moretti and Hanson (2016) mention that the presence of a single mechanism acting on more than one herbicide with a different mechanism of action is of concern regarding the management of this species. In investigating the multiple resistance to glyphosate and paraquat in *Conyza*, the authors describe sequestration of glyphosate and paraquat in the vacuole, occurring similarly to the mechanism reported in ryegrass, *Lolium rigidum* (Yu *et al.* 2007), where two tonoplast transporters would be involved, each one with affinity to a determined herbicide.

It is suggested that the transport of paraquat by tonoplasts into the vacuole occurs due to the similarity of the herbicide molecule to polyamines, especially due to the distance between positively charged nitrogen atoms, under the physiological pH (Powles and Yu 2010). Polyamides are stored in vacuoles and due to the physiological and biochemical importance of the compound, there is a great regulation in the transport flow across the tonoplast membrane (Kusano and Suzuki 2015).

The described mechanisms of resistance to PSII are all related to changes in the site of action of the molecule by mutations in genes or proteins, which prevents the action of herbicides in plants.

After the application of auxin-mimicking herbicides, there is oxidation of the actin cytoskeleton by the hydroxyl radicals generated due to increased expression of the xanthine oxidase enzyme (Pazmiño *et al.* 2013; Rodríguez-Serrano *et al.* 2014). The treated plant shows a continuous increase in levels of auxin signaling, followed by symptoms of rapid uncontrolled tissue development and leaf hyponastic response, with growth inhibition and death (Grossmann 2010).

The herbicide 2,4-D acts on the plant simulating the effect of auxin, a plant growth regulator. This herbicide acts on the plasma membrane, inducing a protein (protein G), which is responsible for cytoskeleton modulation through the arrangement of actin microfilaments and microtubules. Thus, after protein induction, a breakdown of the cell occurs and this effect is noticeable in plants by its hyponastic response. 2,4-D also acts directly on the cell nucleus, inducing the production of ethylene and ABA through the activation of signaling, leading to the intense production of reactive oxygen species, which act by collapsing the plasma membrane and with this, wilting and subsequent tissue death. The evolution of symptoms from application to death of the plant can take days or weeks (Song 2014; Foloni 2016).

In *C. sumatrensis* an unusual response to the herbicide 2,4-D has been observed and this response is related to environmental conditions during application (temperature and light). After application of the product, necrotic symptoms occur quickly in the leaves, which resemble the rapid response after the application of glyphosate in *Ambrosia trifida* in the United States (Moretti *et al.* 2018; Van Horn *et al.* 2018; Queiroz *et al.* 2019; Pinho *et al.* 2019).

The accumulation of hydrogen peroxide occurs quickly in the leaves after treatment with the herbicide (Queiroz *et al.* 2019; Baccin 2020). Changes in the volume and storage of starch in the chloroplasts of *C. sumatrensis* occurs after application of 2,4-D and these symptoms were also identified in *A. trifida* presenting rapid necrosis to glyphosate. A carbon source is required to induce necrosis and translocation of the herbicide is also involved in the resistance mechanism of *A. trifida* to glyphosate (Moretti *et al.* 2018; Van Horn *et al.* 2018).

The rapid accumulation of ROS after the application of 2,4-D, causes lipid peroxidation and the production of these reactive oxygen species is related to the occurrence of necrosis in *C. sumatrensis*. The rapid necrosis resembles the programmed cell death response (Moretti *et al.* 2018; Queiroz *et al.* 2019).

Resistance to auxin herbicides may be related to changes in auxin influx and efflux carriers and ABC

transporters, but the mechanism involved in resistance in *C. sumatrensis* remains unknown (Titapiwatanakun and Murphy 2009; Cho and Cho 2013). In *Arabidopsis thaliana*, mutations in genes encoding auxin receptors and transporters can generate plants resistant to auxin-mimicking herbicides (Roux and Reboud 2005; Walsh et al. 2006; Kubes et al. 2012; Yu and Wen 2013).

The differential perception of herbicides to the plasma membrane was identified in a population of *Brassica kaber* (Mithila and Hall 2005). Alterations in the auxin signaling pathway have been identified in a population of *Echinochloa crus-galli* (Xu et al. 2013). In *Sisymbrium orientale*, resistance to 2,4-dichlorophenoxyacetic acid (2,4-D) appears to be related to a single gene, not yet identified (Preston and Malone 2014).

Due to the complexity of the mode of action of auxin herbicides, the evolution of resistance in weeds is often related to mechanisms unrelated to the binding site (Gaines et al. 2020). The mechanisms of weed resistance include reduced absorption, reduced translocation, detoxification and changes in the binding sites, but there is a great lack of molecular and biochemical knowledge on this subject (Gaines et al. 2020). The complete characterization of the mechanisms of resistance to herbicides in *C. sumatrensis*, still lacks further research, therefore, the search for answers and solutions continues.

The use of correct practices and the adoption of a technological package will help to reduce the occasional effects caused by the competition of horseweed species with the cultural package of cultures. The lines of research that should be intensified are related to the identification of cultural practices that provide a competitive advantage for the crop of interest, in relation to the weeds in them, aiming to reduce the dependence on herbicides to carry out the control, which, according to the review, becomes inefficient due to the selection of resistant biotypes, with different resistance mechanisms.

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