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REVIEW ARTICLE

Amaranthus spp.: a genus of troublesome weeds

Chemical control of multiple herbicide-resistant *Amaranthus*: A review

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Abstract: Plants of the genus *Amaranthus* are important agricultural weeds that compromise food production worldwide. Several biological characteristics make these plants thrive in the environment and cause significant yield losses in many crops. Among the seven most important *Amaranthus* species in the Americas, four have populations with resistance to more than one mode of action (*A. hybridus*, *A. palmeri*, *A. retroflexus*, and *A. viridis*). While multiple herbicide-resistance in *Amaranthus* species is widespread, chemical control remains as one of the most important tools against those weeds. In this review, we compiled data from multiple sources on the efficacy of different herbicides across the most common modes of action that are used in *Amaranthus* management. Both PRE and POST herbicides are discussed, as well as the key factors to be considered when using each one of them. Residual PRE herbicides bring several advantages when managing *Amaranthus* species. These herbicides can avoid weed interference in the initial stages of crop development and provide a more favorable situation for weed control in POST. In addition, including PRE herbicides allows for the addition of alternative modes of action that are not available as POST treatments. Most POST herbicides have limitations regarding weed size and herbicide resistance status. Applying POST herbicides at the early growth stage of weeds is crucial to obtain efficacy. Finally, weed management sustainability depends on herbicides. Therefore, herbicide use should be combined with other weed control methods to avoid herbicide resistance evolution.

Keywords: Amaranthaceae; Herbicides, Mode of action; Multiple herbicide resistance; Pigweed; Weed management

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1. Introduction

Weeds have been selected for aggressiveness and robustness traits even before agriculture began. This selection process has been performed naturally by the environment and artificially by anthropic action (Barrett, 1983). In established ecosystems, which have suffered less disturbance overtime, there is a solid balance among the species that habit the environment, with less selection pressure on individuals, preventing that a particular species evolves into a weed. The genus *Amaranthus* belongs to the Amaranthaceae family, which includes several species that have been identified as economically important weeds worldwide (Torra et al., 2020; Reinhardt et al., 2022), especially in the American continent.

It is estimated that the genus *Amaranthus* is composed of about 70 species (Holm et al., 1997), of which approximately 10 are important as agronomic weeds, interfering in several crops, such as soybean, corn, cotton, sugarcane, orchards and vegetables (Kissmann, Groth, 1999; Chandi et al., 2013). These species are commonly known as pigweed or amaranth, "*caruru*" in Portuguese, or "*yuyo colorado*" in Spanish. In addition to their intrinsic economic importance, there has been an increased attention to these plants due to the evolution of herbicide-resistant biotypes, especially those with multiple resistance (Ward et al., 2013).

For instance, multiple resistant *A. palmeri* and *A. tuberculatus* biotypes in the United States can survive the application of five modes of action (Heap, 2022). In those cases, controlling multiple resistant plants with herbicides becomes extremely complex, given the limited options of herbicide modes of action that are still effective, requiring a deep knowledge of the control spectrum, selectivity, dose adjustment, as well as other recommendations regarding the use of herbicides.

This review is intended to contextualize the importance of the genus *Amaranthus* as a hard-to-control weed species for agricultural systems in the Americas, addressing the morphophysiological aspects of these species that confer aggressiveness characteristics when coexisting with crops. In addition, reports of biotypes of species of this genus that are resistant to herbicides will be presented, in order to outline which management strategies can be more recommended, focusing mainly on chemical control, in addition to its integration with diverse weed management practices.

2. Contextualization of the *Amaranthus* species as important weeds for agricultural systems in the Americas

The genus *Amaranthus* originated somewhere in Central and South America (Bensch et al., 2003), which explains the wide adaptation of these species to the edaphoclimatic conditions in this continent. Under favorable growth conditions (e.g.: optimum temperature and photoperiod), plants can shorten their cycle producing a greater number of propagules per plant (Taiz et al., 2015). Consequently, the infestation of these plants in an agricultural landscape can occur more quickly as a mechanism of adaption to the environment.

In Brazil there is a wide variety of *Amaranthus* species that are considered important agronomic weeds: *A. deflexus, A. lividus, A. spinosus, A. hybridus, A. palmeri, A. retroflexus,* and *A. viridis* (Table 1). Four out of seven species have populations with resistance to more than one mode of action: *A. hybridus*, *A. palmeri*, *A. retroflexus*, and *A. viridis*. In addition, while *A. tuberculatus* is not officially reported in Brazil, this is an important weed species in other countries of the American continent, such as Argentina, Mexico and the United States, with biotypes displaying multiple herbicide resistance to up to five modes of action (Heap, 2022).

Given the importance of the *Amaranthus* genus to agricultural systems, surveying and monitoring the weed infestation in the field becomes an essential strategy. Thus, understanding the biological aspects of these plants can help improving their management providing some insights on why these plants are difficult to control. This will ultimately lead to the development of diverse tools that will help farmers to implement integrated weed management concepts.

2.1 Biological aspects that contribute to decrease the efficacy of herbicides on *Amaranthus*

Weed species has been naturally selected for several aggressive characteristics over the centuries. For instance, weeds often have: competitive ability for resources that are necessary for plant growth (e.g.: water, nutrients, light), capacity to produce propagules, variable germination frequency (asynchronous), ability to emerge from deep layers of soil, propagule viability under unfavorable conditions, multiple mechanisms of reproduction and propagule dissemination, and aggressive growth (Oliveira Jr. et al., 2011). Most of these traits mentioned above are present in species of the *Amaranthus* genus, making these plants more complex to manage.

Species of the *Amaranthus* genus have small seeds (<1 mm), which allows them to produce a large number of these reproductive structures. For instance, *A. palmeri* is estimated to produce more than one million seeds per plant in the absence of crop competition (Nordby et al., 2007), and 250,000 seeds per plant when coexisting with soybean (Schwartz et al., 2016). This massive production of seeds in a single plant increases the possibility of observing control failures in the field. In addition, small seeds are more likely to be dispersed by different agents, such as animals (zoocory), wind (anemochory), water (hydrochory), and agronomical practices by humans (anthropocoria).

These biological characteristics have contributed to the introduction and spread of *A. palmeri* in South America. Genomic studies suggest a single introduction of *A. palmeri* into South America sometime before the 1980s, and subsequent local evolution of glyphosate-resistance in Argentina but with a secondary invasion of *A. palmeri* from the USA into Brazil and Uruguay during the 2010's (Gaines et al., 2020). In Brazil, seeds were brought unintentionally through combine importation from the US to Mato Grosso State (Gazziero, Silva, 2017). This is reinforced by Schwartz-Lazaro et al. (2017), who verified that *A. palmeri* plants can retain 98% of the seeds until the physiological maturity soybean, so that these seeds are harvested with the crop grains and spread to other areas through this operation.

Another aggressiveness characteristic that makes the control of *Amaranthus* plants more complex refers to seed dormancy mechanisms. These plants possess a very rigid seed integument, providing a mechanical restriction

Table 1 - Characterization of the main weed species of the genus *Amaranthus* occurring in Brazil[1/]

Scientific name	Common name	Resistance			Resistance report
		Single	Cross	Multiple	
A. deflexus	Low amaranth	-	-	-	-
A. lividus	Livid amaranth	-	-	-	-
A. spinosus	Spiny amaranth	-	-	-	-
A. hybridus	Smooth pigweed	-	-	EPSPs and ALS	Heap (2022)
A. palmeri	Palmer amaranth	-	EPSPS	EPSPs and ALS	Carvalho et al. (2015) Gonçalves Netto et al. (2016)
A. retroflexus	Redroot pigweed	-	ALS	ALS and PSII	Francischini et al. (2014a) Francischini et al. (2017)
		PROTOX	-	-	Heap (2022)
A. viridis	Slender amaranth	-	-	ALS and PSII	Francischini et al. (2014b)

[1/]Source: Kissmann and Groth (1999); Lorenzi (2014).

for the embryo to initiate the germination process, and subsequent emergence of the seedling (Oliveira Jr. et al., 2011). Furthermore, seed impermeability can restrict the integument from oxygen and water, and the hormonal imbalance can also contribute to seed dormancy in *Amaranthus* (Oliveira Jr. et al., 2011; Kepczynski, Sznigir, 2013). *Amaranthus* species can also present asynchronous germination (Hao et al., 2017), allowing the perpetuation of these plants in the agricultural landscape, as cultural practices would have to be implemented more often to control them.

In addition to the dormancy aspect, a rigid seed integument allows these seeds to maintain viability over long periods of time, even in extreme environmental conditions (Burnside et al., 1996). A practical example of this problem refers to the use of organic residues in agriculture from livestock such as cattle manure or chicken litter (Ronchi et al., 2010). These residues often contain *Amaranthus* seeds that can be dispersed across different areas, demonstrating the ability of *Amaranthus* seeds to remain viable even after passing through the intestinal tract of animals.

One of the most aggressive characteristics of *Amaranthus* species refers to their rapid growth rate and initial development, allowing for a greater competitiveness advantage against the crop (Horak, Loughin, 2000). While *Amaranthus* plants originate as small seedlings compared to most crops, this initial disadvantage is compensated with a higher initial growth rate. In addition, most *Amaranthus* species have multiple growing points throughout the plant (Figure 1), which makes their chemical control more difficult given that herbicides need to translocate to the growing point in order to kill the plant. This is why most labels recommend applications on smaller plants which have fewer growing points and therefore are more susceptible to herbicides.

In addition to this rapid growth, another characteristic that makes *Amaranthus* species more aggressive refers to their C4 photosynthetic metabolism. These plants display greater photosynthetic efficiency compared to C3 plants because they have no photorespiration (Taiz et al., 2015). In addition, C4 plants are more efficient on water use and CO_2 fixation under high temperatures and low water availability. Among the 10 most problematic weed species for agriculture worldwide, eight of them are C4 (Holm et al., 1977). Therefore, *Amaranthus* plants have a physiological advantage when competing with C3 crops such as soybeans, which often translates into greater ability to recover from abiotic stresses conditions such as herbicide injury.

Finally, some species of the genus *Amaranthus* display interspecific hybridization (Murray, 1960), increasing the risk for herbicide resistance allele transfer between different species. In a study conducted by Gaines et al. (2012), it was verified that the artificial crossing between *A. palmeri* glyphosate-resistant and other species of this genus (*A. hybridus*, *A. powellii*, *A. retroflexus*, *A. spinosus*, and *A. tuberculatus*), produced individuals capable of producing viable seeds, which were resistant to glyphosate. Although hybridization frequencies are low (<1.4%), taking into account the high number of seeds that *Amaranthus* normally produces, this hybridization mechanism between species is a serious problem for herbicide resistance. The rapid evolution of herbicide resistance in *Amaranthus* species also contributes to the high level of complexity when managing these plants.

2.2 Evolution of herbicide resistance in *Amaranthus* spp.

Among the greatest challenges in global agriculture is the issue related to weed species presenting resistance to herbicides. Every year, there has been a significant increase in the number of biotypes with resistance to one or more modes of action. This is the result of increased selection pressure for certain active ingredients/modes of action, and the absence of integrated weed management strategies. This causes apprehension to all agricultural stakeholders, especially those biotypes with multiple herbicide resistance (more than one mode of action), decreasing the available alternatives for chemical weed control.

Herbicide resistance in *Amaranthus* is extremely concerning. To date, *Amaranthus* species have evolved resistance to most herbicide modes of action with broadleaf activity (Table 2). The first case of herbicide

Figure 1 - Late stage *Amaranthus tuberculatus* plants have multiple growing points, which makes them more difficult to control with herbicides that need to translocate to these areas in order to provide full control

Table 2 - Global cases of single, cross and multiple herbicide resistance in *Amaranthus* species

Species	Type of resistance	Mode(s) of action (e.g.: active ingredient)[1/]
A. palmeri	Single	EPSPs inhibitors (glyphosate)
		ALS inhibitors (nicosulfuron)
		GS inhibitors (glufosinate)
		Microtubule assembly inhibitors (trifluralin)
		PSII inhibitors (atrazine)
		HPPD inhibitors (mesotrione)
		Synthetic auxin (2,4-D)
		VLCFA inhibitors (S-metolachlor)
	Cross	ALS inhibitors (imazapic and pyrithiobac)
		HPPD inhibitors (mesotrione and tembotrione)
	Multiple	ALS inhibitors (imazethapyr)
		EPSPs inhibitors (glyphosate)
		ALS inhibitors (trifloxysulfuron and pyrithiobac)
		PPO inhibitors (fomesafen)
		PSII inhibitors (atrazine)
		HPPD inhibitors (mesotrione)
		ALS inhibitors (imazethapyr)
		HPPD inhibitors (tembotrione)
		PPO inhibitors (fomesafen)
		EPSPs inhibitors (glyphosate)
		PSII inhibitors (atrazine)
		EPSPs inhibitors (glyphosate)
		EPSPs inhibitors (glyphosate)
		Synthetic auxin (dicamba)
		PSII inhibitors (atrazine)
		ALS inhibitors (thifensulfuron)
		HPPD inhibitors (mesotrione)
		PSII inhibitors (atrazine)
		ALS inhibitors (imazapic and pyrithiobac)
		EPSPs inhibitors (glyphosate)
		PSII inhibitors (atrazine)
		ALS inhibitors (chlorsulfuron)
		HPPD inhibitors (mesotrione)
		Synthetic auxin (2,4-D)
		EPSPs inhibitors (glyphosate)
		Microtubule assembly inhibitors (pendimethalim)
		ALS inhibitors (flumetsulam)
		VLCFA inhibitors (S-metolachlor)
		PPO inhibitors (carfentrazone)
		EPSPs inhibitors (glyphosate)
A. retroflexus	Single	PSII inhibitors (atrazine)
		ALS inhibitors (imazethapyr)
		PPO Inhibitors (fomesafen)
	Cross	PSII inhibitors (atrazine and metribuzin)
		ALS inhibitors (pyrithiobac and trifloxysulfuron)
	Multiple	PSII inhibitors (atrazine and prometryne)
		ALS inhibitors (trifloxysulfuron)
		ALS inhibitors (imazethapyr)
		PPO inhibitors (lactofen and fomesafen)

Continue

Continuation

Species	Type of resistance	Mode(s) of action (e.g.: active ingredient)[1/]
A. blitoides	Cross	PSII inhibitors (atrazine and simazine)
	Multiple	PSII inhibitors (atrazine and simazine)
		ALS inhibitors (chlorsulfuron)
A. albus	Single	PSII inhibitors (simazine)
A. spinosus	Single	ALS inhibitors (imazethapyr, nicosulfuron, and pyrithiobac)
		EPSPs inhibitors (glyphosate)
A. tuberculatus	Single	ALS inhibitors (imazethapyr)
		PSII inhibitors (atrazine)
		PPO inhibitors (lactofen)
		EPSPs inhibitors (glyphosate)
	Cross	ALS inhibitors (flumetsulam, imazethapyr, and nicosulfuron)
		PSII inhibitors (atrazine and cyanazine)
		HPPD inhibitors (mesotrione, tembotrione, and topramezone)
		VLCFA inhibitors (S-metolachlor and pyroxasulfone)
	Multiple	ALS inhibitors (imazethapyr and flumetsulam)
		PSII inhibitors (atrazine)
		ALS inhibitors (imazethapyr and chlorimuron)
		EPSPs inhibitors (glyphosate)
		PSII inhibitors (atrazine and metribuzin)
		EPSPs inhibitors (glyphosate)
		PPO inhibitors (fomesafen and lactofen)
		EPSPs inhibitors (glyphosate)
		ALS inhibitors (imazethapyr)
		PSII inhibitors (atrazine)
		EPSPs inhibitors (glyphosate)
		ALS inhibitors (imazamox and thifensulfuron)
		PSII inhibitors (atrazine)
		PPO inhibitors (acifluorfen, fomesafen, and lactofen)
		ALS inhibitors (cloransulam and imazamox)
		PPO inhibitors (acifluorfen, fomesafen, and lactofen)
		EPSPs inhibitors (glyphosate)
		ALS inhibitors (chlorimuron and imazethapyr)
		PSII inhibitors (atrazine)
		HPPD inhibitors (mesotrione, tembotrione, and topramezone)
		ALS inhibitors (chlorimuron and imazethapyr)
		PSII inhibitors (atrazine)
		Synthetic auxin (2,4-D, aminopyralid, and picloram)
		ALS inhibitors (imazethapyr)
		PSII inhibitors (atrazine)
		EPSPs inhibitors (glyphosate)
		PPO inhibitors (lactofen)
		ALS inhibitors (chlorimuron)
		PSII inhibitors (atrazine)
		EPSPs inhibitors (glyphosate)
		HPPD inhibitors (isoxaflutole and mesotrione)
		ALS inhibitors (chlorimuron and imazethapyr)
		PSII inhibitors (atrazine)
		Synthetic auxin (2,4-D)
		HPPD inhibitors (mesotrione and tembotrione)

Continue

Continuation

Species	Type of resistance	Mode(s) of action (e.g.: active ingredient)[1/]
A. tuberculatus	Multiple	PPO inhibitors (acifluorfen, fomesafen, and lactofen)
		ALS inhibitors (imazethapyr)
		PSII inhibitors (atrazine)
		EPSPs inhibitors (glyphosate)
		HPPD inhibitors (mesotrione)
		PPO inhibitors (fomesafen)
A. viridis	Multiple	ALS inhibitors (trifloxysulfuron)
		PSII inhibitors (atrazine and prometryne)
A. powellii	Single	PSII inhibitors (atrazine)
	Cross	PSII inhibitors (atrazine and metribuzin)
		ALS inhibitors (imazethapyr and thifensulfuron)
	Multiple	PSII inhibitors (atrazine and metribuzin)
		ALS inhibitors (imazethapyr)
A. blitum ssp. *oleraceus*	Single	PSI inhibitors (paraquat)
		PSII inhibitors (atrazine)
		ALS inhibitors (imazethapyr)
A. cruentus	Single	PSII inhibitors (atrazine)
A. hybridus	Single	ALS inhibitors (imazethapyr)
		EPSPs inhibitors (glyphosate)
		PSII inhibitors (atrazine)
	Cross	ALS inhibitors (imazethapyr, chlorimuron, and flumetsulam)
		PSII inhibitors (atrazine, bentazon, and bromoxynil)
		Synthetic auxin (2,4-D and dicamba)
		PPO inhibitors (fomesafen, lactofen, and sulfentrazone)
	Multiple	ALS inhibitors (imazethapyr)
		EPSPs inhibitors (glyphosate)
		Synthetic auxin (2,4-D and dicamba)
		EPSPs inhibitors (glyphosate)
		ALS inhibitors (imazethapyr)
		PSII inhibitors (atrazine)

[1/] Source: Adapted from Heap (2022). PSII, photosystem II; ALS, acetolactate synthase; EPSPS, 5-enolpyruvylshikimate-3-phosphate synthase; HPPD, hydroxyphenylpyruvate dioxygenase; VLCFA, very-long chain fatty acid.

resistance in *Amaranthus* occurred in the United States in 1972, in which an *A. hybridus* biotype evolved atrazine resistance in corn (Heap, 2022). Since then, resistance to several other modes of action has been reported including PSII, ALS, EPSPS, Auxin, microtubule, HPPD, and VLCFA. More recently, an *A. palmeri* biotype from Arkansas, USA evolved glufosinate resistance, the first time ever that resistance to this mode of action was reported for a broadleaf species (Barber et al., 2021).

Among the herbicide resistance cases in all species of the genus *Amaranthus*, *A. palmeri* and *A. tuberculatus* are the two species with the highest number of cases, followed by *A. hybridus*. This behavior may result from the greater dispersion that these species present globally, when compared to others belonging to the same genus (Montgomery et al., 2020). While the first two species are more common in North America, *A. hybridus* is often found in South America.

While PSII and ALS resistance have been reported in most species of the genus *Amaranthus*, glyphosate resistance has caused more problems in terms of dimension. Out of the eleven *Amaranthus* species with resistant to at least one mode of action, four are glyphosate resistant: *A. hybridus*, *A. palmeri*, *A. tuberculatus*, and *A. spinosus*. More recently, HPPD, auxin and PPO resistance have evolved in *A. palmeri* and *A. tuberculatus* biotypes from North America. The cascade of resistance evolution in *Amaranthus* is a response to the selection pressure imposed by the repetitive use of one mode of action to manage resistance another (Hausman et al., 2016). Multiple resistance to ALS, PSII and EPSPs inhibitors is the most common among all species. In *A. palmeri* and *A. tuberculatus*, some biotypes have multiple resistance to up to five distinct modes of action (Heap, 2022).

Regarding the mechanisms involved in the process that confers resistance to *Amaranthus* to the herbicides, it is emphasized that this is dependent both on factors related to the plant species, as well as on the mode of action of the herbicide (Larran et al., 2022). In general, for synthetic auxins and HPPD inhibitors, factors linked to non-target site mechanisms are involved in the resistance process. In contrast, for PPO, ALS and EPSPs inhibitors, most of the reported cases are conditioned to the occurrence of mutations in the genomics of the species, which confer insensitivity of the weeds to the herbicides. Therefore, it is clear the need for change into a more sustainable management in addition to chemical weed control, otherwise, we will continue to stack herbicide resistance traits into weed species such as *Amaranthus*.

3. Chemical control of multiple herbicide resistant *Amaranthus* spp.

Based on the context presented above regarding the relevance of *Amaranthus* species to agricultural systems, this section will present chemical control strategies that aim at reducing the selection pressure on diverse populations. In addition, the integration with cultural, mechanical, and other methods will be presented as they form the basis for sustainable weed management. When it comes to sustainable weed management using herbicides, there are some basic concepts such as rotating and mixing modes of action in both PRE and POST, use of the full label rate, and use of adjuvants that are recommended for each herbicide (Norsworthy et al., 2012). The adoption of these practices itself will not eliminate the risk for resistance but reduce selection pressure and help manage existing resistance issues (Takano et al., 2021).

In the following sections, we present important aspects regarding chemical weed management of *Amaranthus* by modes of action recommended for PRE and POST. In order to summarize all of the information, we compiled literature data demonstrating chemical control of both herbicide resistant and susceptible *Amaranthus* biotypes. More importantly, the information described below is not intended to serve as a recommendation, and each situation must be discussed with a certified professional prior to the implementation of the best weed management option.

3.1 Efficacy of PRE herbicides on *Amaranthus* species

The commercialization of genetically engineered crops in the early 2000's allowed farmers to selectively use broad spectrum herbicides such as glyphosate and glufosinate in POST of many important crops such as soybean, corn and cotton. Consequently, weed management was simplified and most farmers abandoned the use of PRE herbicides because glyphosate was extremely effective in POST. This paradigm shift caused problems such as yield losses due to weed interference in the early stages of crop development, higher weed density by the time of the POST treatment, and consequently the increased selection pressure on weed populations. Therefore, the reincorporation of PRE herbicides into the weed control program is essential for the effective and sustainable management of *Amaranthus* (Figure 2).

PRE herbicides normally present greater efficacy because they work in very early stages of plant development, when weeds are most susceptible to their phytotoxic effects. Therefore, the use of PRE herbicides plays a crucial role on resistance management, especially those cases involving resistance to more than one mode of action (Tranel, 2021). PRE herbicides become even more important for *Amaranthus* management given their small seed size, which reduces their ability to survive an herbicide application. Interestingly, some PPO resistant *A. palmeri* and *A. tuberculatus* biotypes are controlled with the label rate of PPO inhibitors in PRE, but not in POST (Lillie et al., 2020), emphasizing the importance of the application timing on *Amaranthus* management.

The most common modes of action that are used for *Amaranthus* management in PRE are ALS, PSII, HPPD, PPO, VLCFA, and microtubule inhibitors. Although resistance to those modes of action have been reported in *Amaranthus*, many of them are still effective on several populations, and therefore, are widely used worldwide. We compiled examples of herbicides within the most common modes of action that are recommended for *Amaranthus* control in PRE and their respective efficacy levels on *A. hybridus*, *A. palmeri*, *A. retroflexus*, and *A. viridis* (Table 3).

Figure 2 - Control of *A. viridis* with PRE herbicides and cover crop prior to soybean planting

Table 3 - Data compilation regarding the performance of herbicides controlling different herbicide-susceptible *Amaranthus* species in PRE. Herbicides are classified according to their respective mode of action

Active ingredient	*A. hybridus*	*A. palmeri*	*A. retroflexus*	*A. viridis*
ALS inhibitors				
Chlorimuron	Green	Green	Green	Green
Diclosulam	Green	Green	Green	Green
Flumetsulam	Green	Green	Green	Green
Imazethapyr	Green	Green	Yellow	Green
PSII inhibitors				
Ametryn	Green	Green	Green	Green
Amicarbazone	Green	Green	Green	Green
Atrazine	Green	Green	Green	Green
Diuron	Green	Green	Green	Green
Metribuzin	Green	Yellow	Green	Green
Prometryne	Green	Yellow	Green	Green
DXS inhibitors				
Clomazone	Red	Yellow	Red	Red
HPPD inhibitors				
Isoxaflutole	Yellow	Green	Yellow	Yellow
PPO inhibitors				
Fomesafen	Green	Green	Green	Green
Flumioxazin	Green	Green	Green	Green
Oxyfluorfen	Yellow	Yellow	Green	Green
Sulfentrazone	Green	Green	Green	Green
Microtubule inhibitors				
Pendimethalin	Green	Green	Green	Green
Trifluralin	Yellow	Yellow	Green	Green
VLCFA inhibitors				
S-metolachlor	Green	Green	Green	Green
Pyroxasulfone	Green	Green	Green	Green
Synthetic auxin				
2,4-D	Yellow	Yellow	Green	Yellow

Green: control greater than 80%; Yellow = control ranging between 50 and 80%; Red: control less than 50%.

Source: Whitaker et al. (2011); Lorenzi (2014); Gray et al. (2013); Mahoney et al. (2014); Larran et al. (2017) Gonçalves Netto et al. (2019).

Among the ALS inhibitors with residual activity in the soil, diclosulam, imazethapyr, chlorimuron, and others have excellent efficacy controlling *Amaranthus* in PRE (Carvalho et al., 2006). Even though some ALS inhibitors such as trifloxysulfuron and pyrithiobac are recommended for POST application in cotton, they have also demonstrated PRE activity on *A. hybridus*, *A. viridis*, *A. deflexus*, and *A. lividus* control (Francischini et al., 2013). Unlike PPO resistance, ALS resistant *Amaranthus* sp. biotypes are not controlled even when applications are performed in PRE (Francischini et al., 2019). This is probably due to the ALS resistance mechanism involving a target site mutation that often provides high levels of resistance even in PRE applications. Similarly, PSII resistance in A. retroflexus is not affected whether atrazine and prometryne are applied PRE or POST (Francischini et al., 2019). In contrast, PSII susceptible biotypes of *A. hybridus*, *A. lividus*, *A. spinosus*, and *A. viridis* are well controlled with diuron and prometryne when applied PRE in cotton (Raimondi et al., 2010).

HPPD inhibitors are also an alternative mode of action to control *Amaranthus* in PRE. Even though HPPD resistant biotypes are documented, most cases involve POST herbicides such as mesotrione and tembotrione (Table 2). Therefore, other carotenoid inhibitors applied in PRE such as clomazone (DXS inhibitor) and isoxaflutole can be alternatives to control *Amaranthus*, depending on crop safety requirements for each active ingredient (Senseman, 2007). Clomazone applied in PRE demonstrated efficacy on *A. hybridus*, *A. lividus*, *A. spinosus,* and *A. viridis* but residual activity was shorter compared to other herbicides (Raimondi et al., 2010). On the other hand, PRE application of clomazone provided poor control of *A. palmeri* in contrasting soil textures, whereas isoxaflutole showed excellent control under both sandy and clay soils (Gonçalves Netto et al., 2019).

Soil applied PPO inhibitors have been used to manage weed resistance to other modes of action (Sosnoskie, Culpepper, 2014). Sulfentrazone and flumioxazin in PRE provided excellent control of *A. palmeri* in a sandy soil (Gonçalves Netto et al., 2019). Oxyfluorfen provided at least 27 days of residual activity on *A. hybridus*, *A. lividus*, *A. spinosus* and *A. viridis* (Raimondi et al., 2010). In addition, PRE application of fomesafen provides selective control of *A. palmeri* in cotton, allowing the use of this herbicide in the US (Sosnoskie, Culpepper, 2014), and in Brazil (Oliveira Neto et al., 2015).

Residual herbicides targeting microtubule assembly and VLCFA metabolism are also efficacious on *Amaranthus* species. For instance, S-metolachlor, trifluralin and pendimethalin provided excellent control of several *Amaranthus* species. However, the residual activity of these herbicides varied depending on the soil characteristics and the application rate (Francischini et al., 2019; Gonçalves Netto et al., 2019). In contrast, alachlor provided more than 30 days of residual activity on *A. viridis*, and poor control of *A. hybridus*, *A. lividus* and *A. spinosus* when applied in PRE (Raimondi et al., 2010).

Some of the synthetic auxin herbicides display residual activity in the soil (Osipe et al., 2017). The genetically modified crops with resistance to 2,4-D and dicamba allows for the selective control of *Amaranthus* in PRE with these synthetic auxin herbicides. Even though synthetic auxin herbicides are mainly recommended in POST, these products also display a relatively short residual activity in the soil that can help managing weeds in PRE (Lorenzi, 2014).

Based on the abovementioned, it is evident that several options are available for residual control of *Amaranthus* in PRE applications for different crops. Including PRE herbicides in the weed control program allows for resistance management by adding more options of effective modes of action in the toolbox. These herbicides also prevent initial weed interference with the crops, which often leads to yield losses (López-Ovejero et al., 2019). In addition, residual herbicides decrease the weed density and size, which facilitates weed management in POST. However, PRE herbicides require more technical expertise because their efficacy depends on several factors such as the application rate, the soil characteristics, the presence of crop residues, and others.

3.2 Efficacy of POST herbicides controlling *Amaranthus* species

The management of *Amaranthus* with POST herbicides should be done in the early growth stages of the weed species. Most herbicides have restrictions regarding the efficacy levels on late POST control (Table 4). A single POST

Table 4 - Data compilation regarding the performance of herbicides controlling different herbicide-susceptible *Amaranthus* species in POST. Herbicides are classified according to their respective mode of action

Active ingredient	*A. hybridus*		*A. palmeri*		*A. retroflexus*		*A. viridis*	
	$POST_{Early}$	$POST_{Late}$	$POST_{Early}$	$POST_{Late}$	$POST_{Early}$	$POST_{Late}$	$POST_{Early}$	$POST_{Late}$
ALS Inhibitors								
Chlorimuron	Green	Green	Green	Yellow	Green	Yellow	Green	Yellow
Cloransulam	Green	Green	Green	Yellow	Yellow	Red	Green	Yellow
Imazethapyr	Green	Green	Green	Green	Green	Red	Green	Green
Metsulfuron	Green	Green	Green	Yellow	Green	Green	Green	Green
Nicosulfuron	Green	Green	Yellow	Yellow	Green	Green	Green	Green
Pyrithiobac	Green	Green	Green	Yellow	Green	Green	Green	Green
Trifloxysulfuron	Green	Green	Green	Yellow	Green	Green	Green	Green
PSII inhibitors								
Atrazine	Yellow	Yellow	Green	Green	Green	Green	Green	Yellow
Bentazon	Yellow	Yellow	Yellow	Red	Green	Green	Green	Yellow
PSI inhibitors								
Diquat	Green	Green	Green	Green	Green	Green	Green	Green
Paraquat*	Green	Green	Green	Green	Green	Green	Green	Green
HPPD inhibitors								
Mesotrione	Green	Green	Green	Yellow	Green	Green	Green	Yellow
Tembotrione	Green	Red	Green	Yellow	Green	Yellow	Green	Yellow
PPO inhibitors								
Carfentrazone	Green	Green	Green	Yellow	Green	Green	Green	Green
Fomesafen	Green	Green	Green	Green	Green	Green	Green	Green
Flumiclorac	Yellow	Red	Green	Yellow	Yellow	Red	Yellow	Red
Flumioxazin	Green	Red	Green	Yellow	Yellow	Red	Green	Yellow
Lactofen	Green	Green	Green	Yellow	Green	Green	Green	Green
Saflufenacil	Green	Yellow	Green	Green	Green	Green	Green	Green
EPSPs inhibitors								
Glyphosate	Green	Green	Green	Green	Green	Green	Green	Green
GS inhibitors								
Glufosinate	Green	Green	Green	Green	Green	Green	Green	Green
Synthetic auxin								
2,4-D	Green	Green	Green	Green	Green	Green	Green	Green
Dicamba	Green	Green	Green	Green	Green	Green	Green	Green
Triclopyr	Green	Green	Green	Green	Green	Green	Green	Green

$POST_{Early}$: Early postemergence application (2 to 4 leaves); POS_{Late}: Late postemergence application (4 to 8 leaves); Green: control greater than 80%; Yellow = control ranging between 50 and 80%; Red: control less than 50%. * Active ingredient with registration canceled in Brazil.
Source: Grichar (1997); Lorenzi (2014); Gonçalves Netto et al. (2019); Kumar et al. (2020).

application on early-stage plants (2-4 leaves) of *Amaranthus* is often enough to provide complete control of these plants. In contrast, controlling larger plants (>8 leaves) requires the use of herbicide combinations or even sequential applications of different herbicides (e.g.: treatment with a systemic herbicide followed by a contact herbicide).

To date, there are several herbicides recommended for *Amaranthus* management in POST applications. The most common modes of action that are effective on those species are ALS, PSII, HPPD, PPO, EPSPS, GS inhibitors and synthetic auxins. In response to the widespread evolution of EPSPS and ALS resistance in many *Amaranthus* populations across the globe, herbicides targeting HPPD, PPO, GS and synthetic auxins have become widely used for managing these plants, leading to the evolution of resistance to these modes of action. However, not all populations are resistant to all of these modes of action, which makes the herbicide recommendations more specific for each region and even for each field, depending on the herbicide resistance situation in each case.

For ALS susceptible *Amaranthus* biotypes, most herbicides within that mode of action are efficacious on these species in POST applications (Table 4). Pyrithiobac and trifloxysulfuron provided excellent control of both *A. lividus* and *A. hybridus* when applications were conducted at the 2-4 leaf stage (Braz et al., 2012). A dramatic reduction in efficacy levels was observed when plants were treated at later stages of development, especially in *A. lividus*, which was more tolerant to the ALS inhibitors compared to *A. hybridus*. Once again, resistance to ALS inhibitors is widespread across *Amaranthus* populations. Therefore, these herbicides should be used following best management practices to avoid the evolution of resistance in these fields.

Similarly, herbicides targeting PSII can provide excellent control of *Amaranthus* populations that have not yet evolved resistance to these herbicides. In general, atrazine provides excellent control of *Amaranthus* species, especially with the addition of mineral oil to the spray solution, which enhances herbicide uptake by the plant (Gonçalves Netto et al., 2019). Bentazon is another example that can be used to control *Amaranthus*. However, this herbicide only works in early POST applications due to its limited translocation in plants (Grichar, 1997).

There has been only one case of resistance to PSI inhibitors in *Amaranthus* species globally, a paraquat-resistant *A. blitum* ssp. *oleraceus* population from Malaysia (Heap, 2022). This makes PSI inhibitors an alternative for *Amaranthus* management in POST. Because paraquat has been banned in several countries, including Brazil, diquat becomes the only commercial herbicide within this mode of action (Camargo et al., 2020). Diquat is a non-selective broad-spectrum contact herbicide that is recommended in burndown applications in both agricultural and non-agricultural areas (Gitsopoulos et al., 2014). This herbicide also has limited translocation and should be used on small plants at the early stage of development or in a sequential application following the first application with a systemic herbicide (Mendes et al., 2020).

HPPD inhibitors are another mode of action that can be used for HPPD-susceptible *Amaranthus* management. Resistance to HPPD herbicides has been documented in *A. palmeri* and *A. tuberculatus*. HPPD herbicides such as mesotrione and tembotrione are commonly tank-mixed with atrazine, which often provides a synergistic effect due to increased herbicide uptake (Armel et al., 2007; Chahal et al., 2019). Both mesotrione and tembotrione should be applied onto small weeds when using these herbicides in POST, given that larger plants tend to escape from the herbicide treatment.

PPO inhibitors have been used to manage multiple herbicide resistant *Amaranthus*, to other modes of action such as ALS, PSII and EPSPS. Because PPO inhibitors are contact herbicides with limited translocation, POST applications should be done at early stages of plant growth. For instance, fomesafen, lactofen, flumiclorac, and saflufenacil provided excellent control of *A. palmeri* at the 2-4 leaf stage, but plant survival was observed when these herbicides were applied at the 6-8 leaf stage (Gonçalves Netto et al., 2019).

Susceptible biotypes are also controlled with EPSPS and GS inhibitors such as glyphosate and glufosinate, respectively. Glyphosate shows great efficacy even on large plants, but glufosinate is a contact herbicide with limited translocation (Takano et al., 2020a). Therefore, plant size, herbicide dose and environmental conditions should be considered when using glufosinate. While glyphosate resistance is widespread in *Amaranthus*, glufosinate resistance is still evolving with a limited number of cases globally (Barber et al., 2021). The efficacy of glyphosate and glufosinate can be improved with the addition of ammonium sulfate to the tank (Pline et al., 2000). Tank-mixing glufosinate with low doses of PPO inhibitors has shown synergistic effect on controlling *A. palmeri* and *A. tuberculatus* (Takano et al., 2020b).

Finally, synthetic auxins are another option for *Amaranthus* control in POST applications, especially in genetically modified crops with resistance to 2,4-D or dicamba. While a single application of these herbicides can provide efficacy, tank-mixing synthetic auxins with glyphosate has shown synergistic effect for several broadleaf species including *Amaranthus* (Cahoon et al., 2015).

4. Integrated weed management practices for *Amaranthus* control

Given the large number of herbicide-resistance cases reported in different *Amaranthus*, it is evident the need for integrated solutions to control weeds and avoid the evolution of resistant populations. Therefore, crop management strategies that reduce the spread of weed species and improve the crop's ability to suppress weed infestation are essential for the sustainability of agriculture. Acquiring certified seeds, cleaning agricultural machinery, and avoiding the introduction of weed seeds from other areas are best management practices that should be implemented in any agricultural field (Oliveira Jr. et al., 2011; Takano et al., 2018).

Cultural practices involve the use of equilibrated fertilizers, adoption of rapid-growth cultivars, adjusting crop density and row spacing, and any agronomic practice that create a favorable environment for the crop (Braz et al., 2019a). While these practices are not able to completely suppress weed infestation *per se*, they can facilitate weed control with herbicides by reducing weed density and size, which is especially important when it comes to *Amaranthus* management. In addition, cover crops can provide a layer of crop residue on the soil surface, suppressing weed emergence both physically and chemically (allelopathy) (Oliveira Jr. et al., 2014). In *A. hybridus* and *A. retroflexus*, seeds showed a reduced ability to germinate in the absence of light (Gallagher, Cardina, 1998). This is caused by the effect of red light (660 nm) and far-red light (730 nm) on the seed phytochrome, which alters the active (Fvd) and inactive (Fv) form, stimulating germination under a high ratio of Fvd/Fv (Figure 3) (Oliveira Jr. et al., 2011). In addition, it is well known that cover crop associated with herbicide mixture and rotation are extremely powerful against multiple herbicide resistant weeds (Marochi et al., 2018) (Figure 2).

Mowing is another alternative to control large and flowering plants of *Amaranthus*. This strategy has been successfully adopted for glyphosate-resistant *Digitaria insularis* plants (Raimondi et al., 2019). Weed mowing can prevent seed production and reduce selection pressure on weed populations evolving herbicide resistance. Systemic herbicides often provide better control on regrowing and fully active plants (Braz et al., 2019b).

In summary, *Amaranthus* represent a major group of weed species that can cause enormous losses in global agriculture. Herbicides are powerful tools for managing *Amaranthus* but the overreliance on these chemicals often lead to herbicide resistance in this genetically diverse plant genus. Residual herbicides bring several advantages for *Amaranthus* management, including reduction in initial weed interference and facilitating weed control in POST. These herbicides can also increase the number of alternative modes of action, given that *Amaranthus* have evolved resistance to many POST herbicides. Increasing diversity in the weed control toolbox is the only way to overcome herbicide resistance and obtain sustainability in weed management for global agriculture.

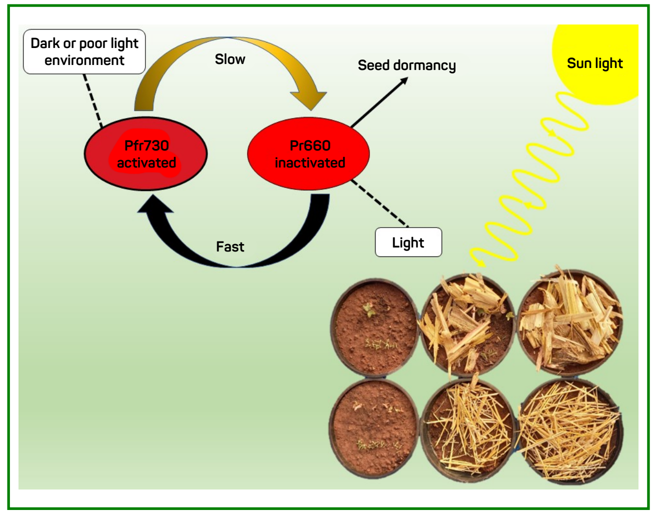

Figure 3 - Suppression of *A. hybridus* emergence by increasing quantities of corn (top) and wheat (bottom) crop residue. Some *Amaranthus* species are positive photoblastic, depending on light to activate and trigger germination

Author' contributions

Both authors contributed equally to writing the manuscript.

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