



Review

Understanding Mechanisms of Herbicide Selectivity in Agro-Ecosystems: A Review

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Abstract: Weeds cause yield losses in desired crops through competition for sunlight, water, space, and nutrients. It is important to manage weeds in crop fields and aqua bodies using various management strategies. One of the most effective and efficient ways of managing weeds is through the use of herbicides. However, there is a need to understand the effects of these herbicides on the desired plants and/or the environment. Herbicide selectivity allows the application of herbicides in a field with both the desired crop and weeds. Herbicide selectivity is therefore described as, an application treatment at a given dosage that is toxic to some plant species but does not damage another species. However, many herbicides can be toxic at high dose rates even when applied to tolerant crops. There are several mechanisms of herbicide selectivity which are grouped into physiological and physical. Physical herbicide selectivity occurs when physical factors such as time, the position of application, plant morphological structure, and environment aid in selectivity. Physiological selectivity occurs when the plant species affect herbicide retention, penetration, movement, and detoxification. Herbicide selectivity is known to be a major cause of difficulties in controlling weeds. As a result, there is a need to understand how the environment, herbicides, and plants contribute to selectivity. This paper, therefore, provides insights into herbicide selectivity and how plants escape herbicide injury which enables species diversity.

Keywords: selectivity, physical, physiological, herbicides, penetration

1. Introduction

Herbicide selectivity is defined as the ability of some plant species to withstand a given dose while others succumb or are killed with the same herbicide concentration [1]. This enables species diversity in the environment while problematic weeds are managed or kept at levels below the economic damage of the desired crop. Patches et al. [2], defined herbicide selectivity as a treatment whose given dosage is toxic to some plant species but does not damage others. Although, most herbicides can be harmful if the dose rates are too high, even to normally tolerant plants, for example, atrazine in maize. Therefore, it can be concluded that selectivity is a process whereby herbicides kill certain plants but leave others unharmed. Herbicide selectivity can be broadly categorized into two forms that are, physiological and physical mechanisms of herbicide selectivity [3]. The physical mechanism of herbicide selectivity includes the environment, position and timing of herbicide application, and plant morphology while the physiological

mechanism of herbicide selectivity starts with differential herbicide penetration, translocation and metabolism in the plant, compartmentalization, sequestration, and altered binding sites and use of herbicide safeners [4]. When selectivity is achieved by the physical separation between the herbicide and plant, it is referred to as apparent selectivity. For example, non-selective herbicides like glyphosate and diquat, which are applied as post-emergence (POST) can damage both the crop and weeds. However, selectivity is achieved through the physical separation of the herbicide and the crop by the use of shields, cones, or time [5].

Despite some considerable work done on the use of herbicides to control weed species effectively without causing phytotoxicity to the desired crop, selectivity mechanisms of herbicides have received little attention. Understanding the importance of herbicide selectivity through the physical and physiological mechanisms is therefore vital. The objective of this paper is to uncover the knowledge, help weed scientists and farmers take advantage of herbicide selectivity as a way to protect crops from detrimental herbicide injury levels and avoid the costs of using herbicides on herbicide-resistant weed species.

2. Physical herbicide selectivity

2.1 Position selectivity

Soil-applied (pre-emergence) herbicides inhibit germination and development of weed seeds within the soil depth of 0 to 3 cm. While crop seeds are usually placed deeper, which is 5 to 10 cm. For large-seeded crops, e.g., *Zea mays* and *Phaseolous vulgaris*, are not affected by pre-emergence (PRE) herbicides e.g., metolachlor. In this case, crop seed placement depth is used as a basis of selectivity to protect the germinating crop seed from damage [6]. The herbicides form a seal zone and weed seeds within that seal zone will either not germinate or be killed by the herbicide during germination. The mechanism is called “position/depth protection selectivity” as shown in Figure 1. Selectivity is achieved provided the soil-applied herbicide does not leach easily into the root zone of the crop seed. Placement selectivity is also achieved by using granular formulated herbicides which are applied directly to the weeds with limited interference with the crop [6].

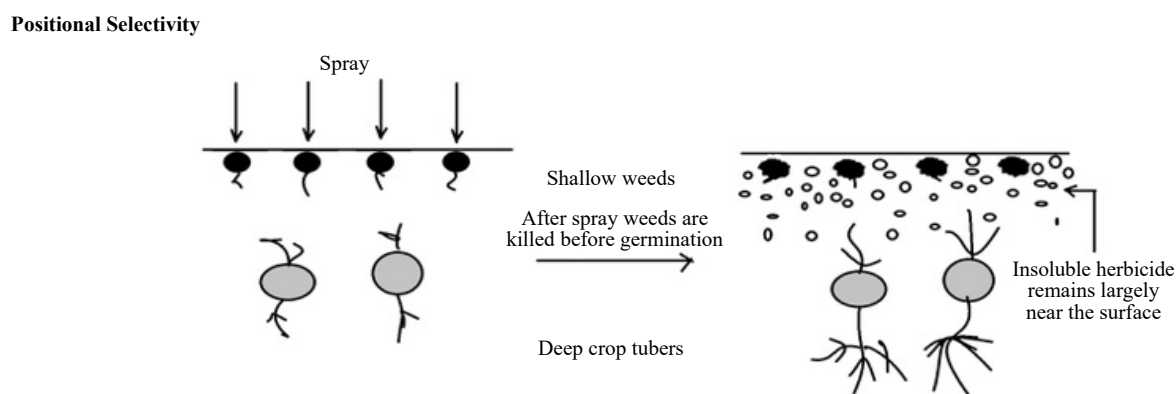


Figure 1. Position /depth herbicide selectivity [2]

2.2 Herbicide placement (application device selectivity) of non-selective herbicide

Herbicide placement refers to any factors that results in spatial separation between sensitive crop tissues or absorption sites and a toxic dosage of herbicide [7]. This is achieved through the use of herbicide shields and hooded band sprayers or cones. These are modified devices ensuring that the herbicide is directed to the weeds while the crops are shielded from the herbicide and selectivity is achieved through target spray [6]. For example, by using a spray hood/

shield glyphosate, paraquat or diquat can be made selective in wider row-spaced crops whereas the spray is directed to weeds by using herbicide cones or rope-wick applicator (Figure 2). The method is effective if the herbicide is not washed away by rainfall or irrigation water [8].

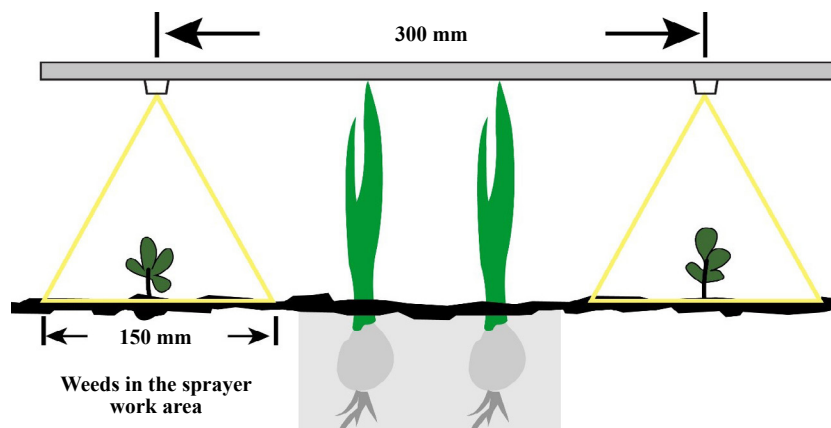


Figure 2. Herbicide shield direct the herbicide on weeds and shield the crop [9]

2.3 Chronological selectivity

Herbicide selectivity can be achieved through manipulation of the time of herbicide application (chronological selectivity). Herbicides can be applied pre-planting; post-planting and the timing of herbicide application is relative to crop growth stages [2]. This is achieved through herbicides being applied at different times. Most problematic weeds in annual crop fields are shallow-rooted and grow rapidly [10]. Therefore, the time of herbicide application is crucial for selectivity. This determines why most non-selective herbicides are applied before the crop emerges, to act as pre-cleaners to control existing weeds and ultimately allow selectivity (Figure 3). When herbicides are used as POST, selectivity is achieved as direct sprays are used to avoid damage to the field crop. The herbicide time of application in relation to the crop stage is critical, for example, pendimethalin is selective to maize, cotton, and soybean crops, when applied as PRE and not as POST. Similarly, metribuzin (Sencor) is a selective herbicide for potatoes when applied as PRE and not as POST [6].

Chronological selectivity

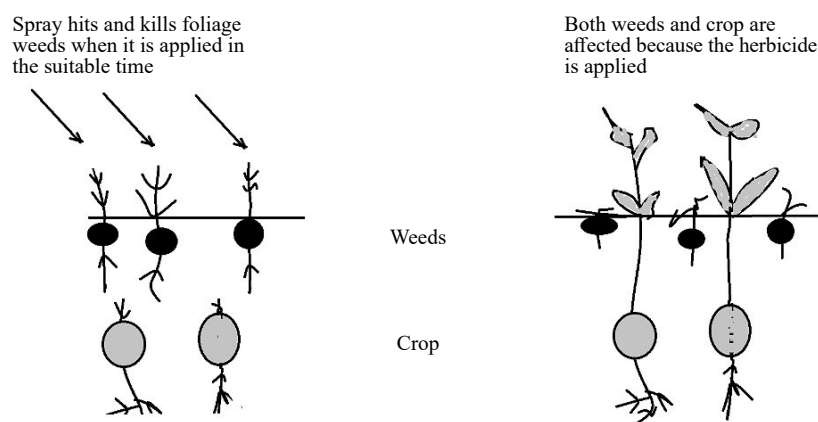


Figure 3. Non-selective herbicides are used as pre-cleaners to achieve selectivity [2]

2.4 Morphological selectivity

The location of the plant meristematic tissue determines herbicidal selectivity. In grasses, the growing points are located in the base of the plants and are protected by surrounding leaves from foliar herbicides, whilst plants with broad leaves have terminal growing points (Figure 4). This explains why 2,4-dichlorophenoxyacetic acid, and 2-methyl-4-chlorophenoxyacetic acid (MCPA) selectively affect dicotyledons (dicots) by causing abnormal growth, senescence, and eventually plant death [11].

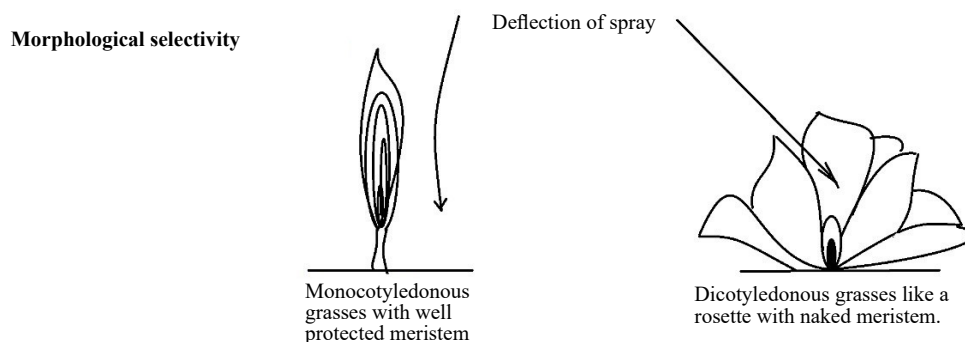


Figure 4. Morphological selectivity [2]

3. Other physical forms of herbicide selectivity

3.1 Soil properties

The physicochemical properties of the soil are important in determining herbicide selectivity. The cation exchange capacity of soil determines which herbicides can be used to achieve selectivity. For example, trifluralin (Trif), a member of dinitroanilines herbicide group, were applied PRE or pre-plant incorporated, has an activity rate highly influenced by clay and/or organic matter content [12]. The higher the clay and/or organic matter content, the greater quantity of dinitroanilines herbicide. The herbicide may, however, be retained in the soil for too long (persistent) and released later causing adverse effects on the desired crop grown at that particular time or this may affect crop rotation [13]. Moreover, if the same amounts of herbicide are applied in soils with low clay content and/or organic matter content, the herbicide may be phytotoxic to the crop.

3.2 Prevailing climatic conditions

When POST herbicides are applied over the crop and the herbicide is retained on the plant leaf surface, its activity is affected by the environment. For example, phenoxy acetic acids formatted esters are fat soluble, when temperatures are high, leaf cuticles become more fluid and more readily penetrated by fat-soluble compounds, thus, low selectivity [14]. High temperatures and low humidity are detrimental and plants growing in these environments usually have thick cuticles, which are less penetrable cuticles. Similarly, the poorly hydrated cuticle is not easily penetrable by herbicides as well [15]. Moreover, light is an important environmental factor as it is a crucial subcomponent for photosynthesis, though uncontrollable. Therefore, many photosynthetic inhibitors are taken by the roots and good light conditions increase the opening of stomata and ultimately increase the rate of symplastic translocation of herbicides.

3.3 Leaf orientation

Foliar-applied herbicides have to remain on the leaves long enough for absorption to occur. However, the leaf architecture does determine selectivity. The shape, orientation, and chemical composition vary between plant species [2]. The erectophile (upright) plants have a stature of vertical leaf orientation, like barley (*Hordeum vulgare*) is nearly perpendicular to the soil surface, causing liquid spray droplets to fall off the plant easily compared to dicotyledonous

plants which are planophiles, and makes the herbicides less selective because the applied herbicide has a longer leaf surface exposure time, thereby increasing herbicide absorption [6]. In addition, plants with hairy leaf surfaces prevent direct/quick contact with spray droplets, for example, the velvet leaf (*Abutilon theophrasti*) [14]. However, when hairy surfaces are moisture-saturated, herbicide entry may be promoted because hairiness delays evaporation. It is postulated that thick leaf cuticles allow crop herbicide selectivity, however, the cuticle composition and hydration are more important for herbicide absorption [7].

3.4 Plant stage of growth

Plants are susceptible to herbicides differently through their growth and development. At the early stages of plant growth, many plants are less selective to herbicides [2]. This is believed to be attributed to plant tenderness, exposed growing points, and not fully adapted to the environment. For example, thiadiazine group of chemicals like Bentazone or Basagran, when applied to soybean and groundnut crops, has to be done at the second to third trifoliate leaf stage. Earlier application (at the dicot stage) may damage the crop. Similarly, older weed plants have a high herbicide selectivity and may resist herbicide application. This can be due to the fact that as plants grow, they develop a thick cuticle and waxy leaf which inhibits the process of penetration [16]. Furthermore, as a plant grows, it will have an increase in the number of leaves, this can also reduce the herbicide full cover spray (the ability of herbicide to get to all productive leaves), thereby reducing herbicidal translocation. Moreover, the leaves may also shield the meristematic tissue [7]. More so, as plants grow older, they develop a deep root system that reduces the absorption and apoplastic translocation. Perennial weeds are more sensitive to foliar-applied herbicides during the active growth period than early stages [8, 16].

4. Physiological herbicide selectivity

Some authors refer to physiological mechanisms as a biological factor that involves processes that affect the activity and/or the breakdown of the herbicide [17]. These include: differential rate of herbicide absorption, differential rate of herbicide translocation, differential rate of applied herbicide deactivation, and specific herbicide protoplasmic resistance.

4.1 Differential penetration

Differential penetration occurs in plants and is a mechanism of herbicide selectivity. Herbicides on plant foliage must cross several natural barriers before ultimately reaching their specific biochemical site of action [18]. The pathway of absorption and translocation is more tortuous for some herbicides than others [16, 18]. This depends, to some extent, on the morphological and physiological characteristics of individual plants in relation to the herbicide. Ransom [6], believed that the greatest variability in the rate of herbicide absorption among plants occurs after foliar application. Herbicide uptake is genetically controlled and environmentally influenced by morphological characteristics. These include leaf angle, leaf area, and pubescence on the leaf surface. This is the first line to determine the maximum potential herbicide dose rate to be intercepted and retained by a plant [16].

The distribution of herbicide molecules within the plant is also an important factor in selectivity. In cotton plants, lenticular glands and trichome hold high concentrations of triazines and substituted ureas lowering the concentration at the site of action [17, 19]. Herbicides that get deposited on plant surfaces must first penetrate the non-living barriers on the outer part of a plant which are the cuticle and stomata. However, stomata entry is not important as there is a difference in stoma opening due to field conditions and the maximum opening of the stomata may be different from the time depending on the herbicidal application [20]. This, therefore, explains why cuticle penetration is of more importance. Choudhury [21] highlighted that the cuticle is a complex layer that is an open, sponge-like structure made up of a lipid frame within interspersed pectin (water-soluble strands) and possible open pores. It also allows both aqueous and lipid routes of herbicide penetration.

Epicuticular waxes are hydrophobic, thus, leaves are not readily wettable but the addition of adjuvants improves herbicide penetration [2, 19]. The pores on the cuticle can fill up in a water-saturated atmosphere to provide an

accessible water diffusion continuum. When a plant is under stress, pores fill with air which acts as a barrier but the lipid route will be still available [17]. Moreover, cuticle thickness varies from plant to plant even on the same plant. As the leaves mature cuticle composition and thickness differ, thus having an impact on herbicide selectivity. Roots also have a cuticle though it is less thick than the ones on leaves and does not have a waxy layer, making it more permeable than foliar cuticle [17]. Thus, differential penetration is influenced by waxy surfaces, hairy leaf surfaces, and cuticle characteristics.

4.2 Differential translocation

Translocation is the movement of water, sugars and dissolved organic solutes in a plant from one region to another. This movement can be apoplastic or symplastic and herbicides are also translocated using the same pathways, which is some distance before reaching the specific site of biochemical action. Choudhury [21] alludes that the apoplastic pathway is the non-living pathway where the herbicide is translocated through intercellular spaces, which is a continuous network of cell walls and xylem tissue that functions as the conduit for water and mineral transport from the roots to the shoots. The symplast is a continuous network of living cells and includes the plasmodesmata and phloem that translocate sugars and other organic solutes from the leaves and storage organs to other parts of the plants [16]. Thus, after absorption, herbicides must therefore translocate, for a short distance, from the epidermis to the vascular bundles.

Herbicides absorbed through the roots have an additional barrier, the endodermis [17]. The endodermal cell walls are impregnated with suberin that creates the Casparian strip which is impermeable to herbicide penetration. In order for the herbicide to enter the vascular bundles from here, it has to by-pass the Casparian strip, by penetrating the cell membrane and using the symplastic pathway to reach the xylem or phloem for long-distance translocation [2]. Herbicides translocate extensively in both pathways but when being translocated over a long distance they become predominant in one system over the other. Some herbicides may become trapped in the symplastic pathway due to ionization. After ionization, they become anionic and cannot penetrate across the membrane thus remaining in the cytoplasm.

The determination of herbicide selectivity among plants may be due to differential rates and extent of translocation which is influenced by the source-sink relationship and these vary amongst plants. The apoplastic pathway relies on the rate of transpiration of a plant, so herbicide movement does depend on the transpiration stream [18]. Thus, most of the apoplastically translocated herbicides are soil applied. Differential apoplastic translocation after root uptake plays a role in determining the selectivity of several herbicides. An example of limited translocation as a mechanism of herbicide selectivity was exhibited between flurodifen-resistant groundnut and susceptible cucumber [22]. It was proven that selectivity was due to the limited translocation of flurodifen from roots to the groundnut's leaves before it could enter the chloroplast [19].

4.3 Compartmentalization/sequestration

The applied herbicide can be inactivated either through binding to a plant molecule or by being removed from metabolically active region of the cell to inactive region in the cell where the herbicide will be of no effect for example the vacuole (Figure 5). Zimdahl [18], explained that in some instances, herbicides are compartmentalized after absorption and are immobilized in roots or tissues of tolerant plant species where damage is minimized. In a number of cases, weeds have shown selectivity to glyphosate through altered target sites and vacuole sequestration [6].

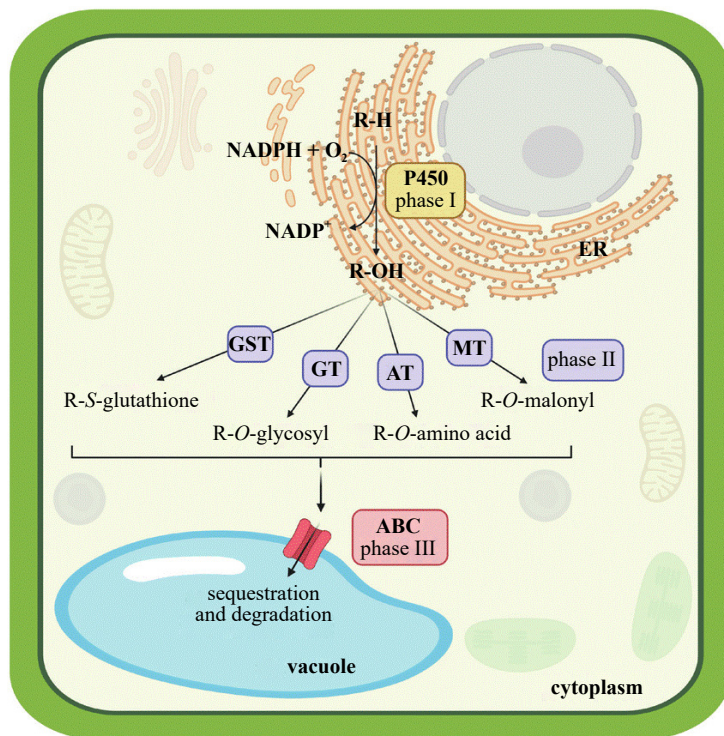


Figure 5. Herbicidal sequestration [13]

4.4 Altered binding sites

Altered target site of action is whereby a single nucleotide mutation in the gene encoding a protein bound by an herbicide can result in a single amino acid change, disrupting the ability of the herbicide to bind to the protein without disabling the enzyme function (Figure 6) [18]. The first discovered altered target site was in photosystem PSII inhibiting herbicides, which compete with plastoquinone for binding on the D1 protein and thereby inhibit PSII electron transport [10].

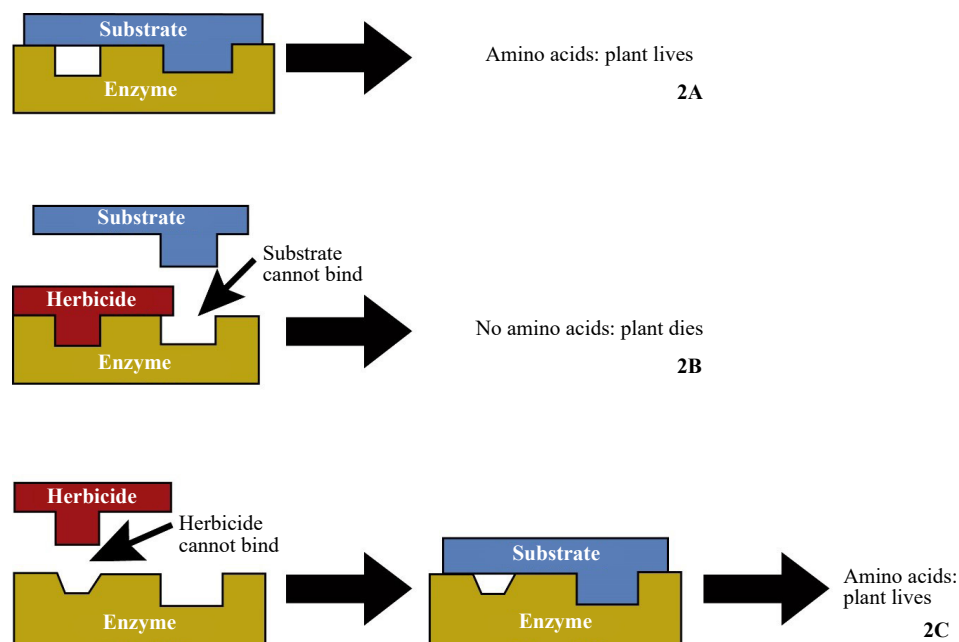


Figure 6. Herbicide altered site of action [13]

4.5 Differential metabolism

Differential metabolism is the most common mechanism that contributes to herbicide selectivity. In this case, the plant is able to alter or degrade the chemical structure of the herbicide through enzymatic, and occasionally non-enzymatic, reactions that render them to be more phytotoxic. For example, 2,4-dichlorophenoxybutyric acid (2,4-DB) is converted to 2,4-dichlorophenoxyacetic acid (2,4-D) by redroot pigweed [19]. Moreover, the enzyme cytochrome P450 monooxygenase which is a membrane-bound haem-protein catalyzes an oxy-reduction reaction by adding a single atom of oxygen to a hydrophobic herbicide thereby making it hydrophilic and less toxic [17].

4.6 Safeners

Safeners (antidotes) are chemical agents that reduce the injury level of herbicides to crop plants by a physiological or molecular mechanism, without compromising weed control efficacy. These are used for the protection of large-seeded grass crops, such as corn, grain sorghum, and rice, against pre-plant-incorporated or pre-applied herbicides of the thiocarbamate and chloroacetanilide families [23]. Furthermore, safeners are also used to protect wheat against POST applications of aryloxyphenoxypropionate and sulfonylurea herbicides. Safeners induce co-factors such as glutathione and herbicide-detoxifying enzymes such as glutathione S-transferases, cytochrome P450 monooxygenases, and glucosyl transferases [20]. Herbicide safeners at times are used with specific herbicide active ingredients, for example, benoxacor is used to protect crops against damage by *S*-metolachlor [21]. In addition, safeners enhance the vacuolar transport of glutathione or glucose conjugates of selected herbicides.

5. Conclusion

The use of herbicide technology is one of the most efficient and cost-effective ways of controlling weeds. However, there is a need to understand how plants and other weed species escape from herbicidal damage. Herbicide selectivity provides knowledge on how certain species escape herbicidal damage thus determining the choice of herbicides. Moreover, herbicide selectivity can also help to reduce the harmfulness of herbicide on a desired crop through placement selectivity, herbicide sequestration, use of safeners, and altering plants' herbicide binding sites. However, it is without reason that when herbicides are applied, crop losses (phytotoxicity) might occur. Therefore, it is important to assess the herbicide selectivity of plants to reduce crop phytotoxicity and herbicide wastage.

Conflict of interest

The authors declare no conflict of interest.

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