Revista Brasileira de Herbicidas, v.15, n.1, p.14-25, jan./mar. 2016 (ISSN 2236-1065)
DOI: http://dx.doi.org/10.7824/rbh.v15i1.421 www.rbherbicidas.com.br

Evolution, epigenetics and resistance – troublesome weeds[1]

Evolução, epigenética e resistência – plantas daninhas problemáticas

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Abstract - The aim of the present text is to recall basic concepts about evolution, neo-darwinism and mechanisms of plant selection, pooling this knowledge into the weed science as a background which paves the way for the appearance of weed biotypes resistant to herbicides. Some questions which need to be answered regarding current concepts in weed resistance are risen. Epigenetics, secondary metabolism and environment related studies may change our view into plant resistance to herbicides.
Keywords: neo darwinism; herbicide resistance; chemical groups

Resumo - O objetivo do presente texto é recapitular conceitos básicos sobre evolução, neo darwinismo e mecanismos de seleção de plantas, conjugando este conhecimento à área de plantas daninhas como um contexto que pavimenta o caminho para o aparecimento de biotipos de plantas daninhas resistentes aos herbicidas. Algumas questões que necessitam de respostas relativas a conceitos atuais em resistência de plantas são levantadas. Estudos relacionados à epigenética, metabolismo secundário e efeitos do ambiente podem mudar nossa visão sobre a resistência de plantas a herbicidas.
Palavras-chaves: neo darwinismo; resistência a herbicidas; grupos químicos

The Agriculture as We Know

Agriculture started when man abandoned its nomad behavior and settled in certain regions, starting the cultivation of food itself (Monquero, 2014). So far, society was composed by migrating groups with herds in search for pasture. It was also at this time that the weeds have emerged, being represented by those plant species that grew spontaneously among crop plants, competing for resources such as water, light and nutrients (Ferrero et al., 2010).

Until the eighteenth and nineteenth centuries, weeds were eliminated from crops by weeding with simple tools or rudimentary equipment pulled by animals. Although its occurrence constituted problem in rudimentary agriculture, before the eighteenth century there was no clear awareness of the level of impact the occurrence of weeds caused on crop yields (Monquero, 2014).

In the eighteenth century, the occurrence of weeds was intense, and losses arising from their presence have been recognized among the major factors limiting productivity. Food shortages, due to the reduced workforce and migration from the countryside to cities, demanded a solution to this problem; the labor supply becomes limited and expensive (Collinson, 2000).

At the time, the solution was the integration of agriculture with livestock, where the diversification of the production environment provided reduction on the occurrence of invasive species to acceptable

[1] Received for publication on 28/10/2015 and approved on 10/12/2015.
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levels due to the deposition of plant stubble, crop rotation, use of organic manure, animal trampling and finally the planting of species with allelopathic properties (though this principle was still unknown) on weeds. This was the "First Agricultural Revolution" (Monquero, 2014).

In the nineteenth and early twentieth century, the cure for usually lethal diseases associated to decreasing in neonatal mortality rates, among other factors, increased growth rate and human life expectancy, resulting in a population explosion and proportional demand for food. Productivity levels of that time would not be able to meet the demand without a radical increase in acreage, which in turn was limited by manpower shortages. Intensive cropping systems were then idealized, grounded in the use of fertilizers and pesticides, genetic breeding and irrigation techniques - this was the "Second Agricultural Revolution", commonly known as "Green Revolution" (Ehlers, 1996).

The Green Revolution provided an increase in productivity and supplied the immediate demand for food, but in contrast, there was reduction in the importance of crop rotation, progressive abandonment of cover crops and manure use, the separation of animal and plant production, besides the absorption of some agricultural processes by industries.

About 70 years after the idealization of the Green Revolution, agriculture is again mired in the occurrence of pests, now resistant or tolerant to pesticides, including weeds resistant to herbicides. And it seems difficult for us to understand why agriculture reached this condition. We, technicians, are supposed to understand the biological mechanisms involved in the natural selection which turns some plant species into weeds, and to manage them based on technical planning.

On the Evolution

From the primordium through the evolutionary process, three major steps may be recognized. First there was the *single cell*, the one that started life and by itself was able to perform all basic tasks necessary for survival. After, this cell reproduced and started to form *complex individuals*, which were in simple terms formed by clusters of early cells with specialized functions (Gurevitch et al., 2009).

Later on, *large organisms*, composed by specialized parts, "evoluted" themselves to occupy a role into the ecosystem where they lived (Gurevitch et al., 2009). The organism that represents the origin of all offspring to date is called *last universal ancestor (LUA)*. Finally, organisms started to structure their occurrence by several mechanisms and to couple to abiotic components aiming survival, when *ecosystems* appeared.

At the beginning of the 20th century, some tried to label a community of individuals as a single organism (Clements, 1916; 1936), which was proved to be not completely true (Gurevitch et al., 2009). Although most processes depend both on organism-level and community-level behavior (Gurevitch et al., 2009), a set of individuals typically act as a set of individuals with its proper interactions, not as an "organism", although inside an ecosystem every single organism is specialized in some way aiming its own survival.

So, one is impelled to propose that up-to-date organisms are highly "evoluted", and that "evolution" is responsible for formation and prevalence of individuals adapted for survival and which are always *better* than its ancestors. We will see this is a mistake. "Evolution" is loosely defined as *the study of the transformation of species through time, including both changes that occur within species, as well as the origin of new species* (Losos, 2013). Darwin itself have not used the word "evolution" in the first edition of *On the Origin of Species* (Darwin, 1859) by means of natural selection.

Natural selection within populations refers to the situation in which individuals with one variant of a trait tend to leave more offspring that are healthy and fertile in the next generation than do individuals with an

alternative variant of the trait, and will not always lead to evolution if it is not *genetically based* (Losos, 2013). Epigenetics would say "*inherited*" as we will see later on. Thus, natural selection ultimately contributes for reducing the genetic variation within a population (Gurevitch et al. 2009), and not for increasing it (Table 1).

Table 1. Natural processes related to evolution regarding its ability to change the genetic variation.

Evolutive Process	Genetic Variation
Natural Selection	Decreases
Genetic Drift	Decreases
Mutation	Increases
Migration	Increases

Source: adapted from Gurevitch et al. (2009).

It should be noted that natural selection is the main responsible for evolution, but when it is absent, genetic drift plays also an important role (Eckert et al., 1996; Gurevitch et al., 2009). The genetic variation is important to supply a range of individuals to be tested in its aptitude to the environment, but these organisms essentially evolute when the population adapts to a given environment, which is accompanied by a reduction in genetic variation within the population while fixing those genes most favorable to that particular environment.

Reporting back to the *last universal ancestor (LUA)*, that represents the origin of all offspring to date, current organisms differ greatly from the LUA, but we can not promptly consider some current organisms more "evoluted" than others considering only the comparative distance they present from the original ancestor (LUA). In part because of this, Darwin presented his book titled as *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (Darwin, 1859). Again, no "evolution".

Not all individuals who succeed its ancestor will be more adapted to the ecosystem, although they are most likely to differ greatly from the LUA than its ancestor. This is what is called "derivation" (Ciccarelli et al., 2006). The current organism can be simply "different", not essentially "better" or most vastly fitted compared to its previous relatives (Figure 1). Some groups of orchids diverged from the LUA very early in the evolutionary history, being very often considered as the most derived group of living beings on earth (Arditti, 1992); but what is the relation with evolution?

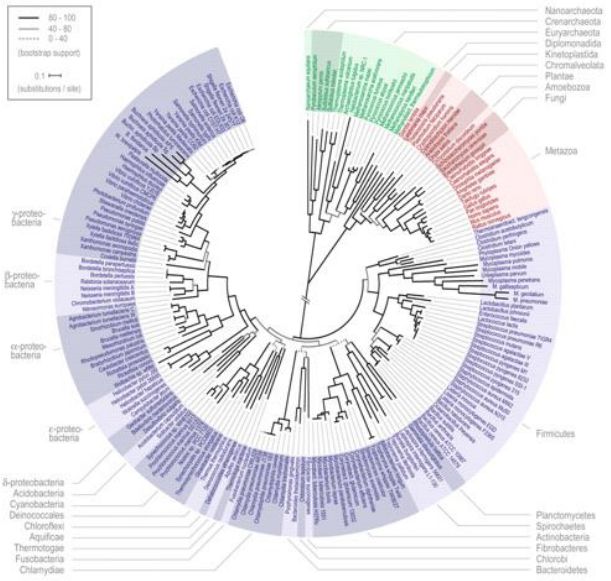

Figure 1. General schematics of the tree of life (Ciccarelli et al., 2006; Letunic and Bork, 2007). The last universal ancestor (LUA) is located at the center of the circle. For details please check the original work.

There are weed species that were controlled by herbicides, but from a given moment on, they were no longer controlled: the so-called resistant plants to herbicides. Natural selection, according to Darwin's theory, often occur at the *individual level*; they differ in terms of fitness and genetic answers which are measured by observations on the differences among individuals in the same population from one generation to the other (Gurevitch et al., 2009). We will get back to this, as epigenetics presents an alternative explanation.

Horseweed (*Conyza* spp.) and sourgrass (*Digitaria insularis*) are the most striking

examples of resistant plants to herbicides in the Brazilian tropical agriculture. Are they "evoluted", "derived", "adapted", "selected"? A proposal applied to the weed science is presented in Table 2, which is subjected to further discussion. In fact, genetic changes that lead to resistance to herbicides are usually so small compared to the genetic pool of the organism that is usually considered as a microevolution (Dekker, 2009), although this is a controversial concept.

Table 2. Effectiveness of natural processes on the occurrence of weed species resistant to herbicides: a proposal.

Natural Process[1]	Summarized Definition[2]	Comments
Selection	1: gametic and zygotic differential mortality; non-random differential reproduction of different genotypes in a population; 2: When traits have a genetic basis, adaptive traits become universal to the population.	The primordial happening on establishment and dominance of resistant types under a selecting agent.
Adaptation	1: adjustment to environmental stress; 2: morphophysiological character modification which improves survival and reproductive efficiency.	Resistant types are not most adapted to the environment, but essentially to survive to the selecting agent. Most resistant types are equal to or less fitted than the susceptible type to the environment.
Derivation	1: Temporal continuity and discontinuity of the living beings on the tree of life; 2: History of evolutionary relatedness among groups of organisms; 3: Phylogenetic distance between the current organisms and the last universal ancestor.	The binomial nomenclature does not change from the susceptible to the resistant type. From this scope the level of derivation for both types is equal. It is hard to say if the genetic alteration suffered by the resistant type turns it most distant from the last universal ancestor than the susceptible one. Derivation seems to be of little importance for the issue of weed resistance to herbicides.
Evolution	1: Any gradual change; 2: Any cumulative change in organisms or populations through generations; 3: Change in the frequency of genes in a population.	Eyes would be a dispensable part for a fish which lives in deep dark water, for example, because it would be of no use and could even be easily injured. For this fish other senses would be more important. The resistant weed type surely evoluted to adapt to the main stress which was causing death for the species: the selecting agent, but it is not "worse" or "better".

[1]Adapted from Gurevitch et al. (2009); [2]Adapted from Cicarelli et al. (2006), Dekker (2009) and Florio (2013).

How human labor and management decisions affect weed population regarding "evolution"? How is it linked to the occurrence of pests resistant to pesticides?

On the Ecotypes and Biotypes

As already pointed out, natural selection tends to reduce the genetic variation into a population since it increases the frequency of the alleles responsible for the superior fitness while those associated to inferior traits are discarded (Gurevitch et al., 2009). Natural selection can also increase or decrease the variation between populations, since traits fixed into each one of the populations will depend mostly on the environment they are growing (Darwin, 1859). This ultimately opens the door

for the differentiation of species in the long term (speciation), process which is based on natural selection, mutation, genetic drift and migration (Table 1). In the short to middle term, however, it leads to the formation of ecotypes.

The term "ecotype" describes populations of the same species from distinct habitats or locations, which present genetically based differences in appearance and function (Gurevitch et al., 2009). The term "biotype" appeared to describe responses of pests to cultivars and other variants of their food plants (Claridge and Hollander, 1983), and seems to be more connected to the genetics than to phenotype; its concept is also very different when related either to individuals or to populations, which demand some caution in its use.

There is also a proposed hierarchy regarding species, ecotype and biotype, in that order. In a wide simplification, ecotype regards to a population of a given species adapted to a given environment, while biotype is formed by the varieties of that species in the population, also under the same environment (Yochelson et al., 1983).

There are often remarkable differences in some concepts among different areas of knowledge, this being also true when the basic science of Biology is faced with the applied science of Agriculture. Weed science researchers label a "type" of weed which acquired resistance to a herbicide as "biotype", compared to its non-resistant relative. Weed science related books may define ecotype and biotype in slightly different ways than biology, disregarding hierarchy, but by the end the term "biotype" seems really to be the most appropriate from both biological and agricultural point-of-view regarding resistant "types" of plants to herbicides.

Ecotype defines a population of a given species adapted to a given environment, but most resistant populations of weeds are not generated in the micro-region where they are reported: they are often brought into by contaminated machinery, soil samples, seeds or animals, besides water or wind. Resistant weed populations are mainly dispersed rather than generated into each and every location. Thus, we seem to really have resistant "biotypes" to the herbicides, since most of the time the resistant population came from a given environmental ecotype originally located elsewhere.

On the Resistance to Herbicides

Herbicides are used to enhance productivity of crops by controlling weeds which compete with cultivated plants for water, light and nutrients (Shimizu et al., 2011). *Resistance to Herbicides* is the inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the population (Vargas et al., 2009).

Organic herbicides arrived at the market in 1932 with the Dinitro-o-cresol (DNOC), which was extremely toxic to humans (EPA, 2000). Successful chemical weed control, however, was achieved only with the discovery of the herbicidal activity and availability to the market of 2,4-D in 1946 (Monquero, 2014). The first weeds resistant to herbicides (2,4-D), *Commelina diffusa* and *Daucus carota*, were reported in 1957 (Vargas et al., 2009). Since then the list of plant species with biotypes resistant to herbicides have increased exponentially.

Herbicides are considered not to be directly responsible themselves for the appearance of resistance in plants since they are majorly the selecting agent of genetic variations which naturally appeared into the population (Powles and Holtum, 1994; Silva and Silva, 2007). However, in the Animal Science, teratogenic agents are studied, being those physical, mechanical or chemical agents that cause malformation to the embryo resulting in monstrous forms (Rodrigues et al., 2011), including intoxication, radiation, infectious diseases and chemical agents.

For plant somatic embryogenesis (which is not of first concern for the evolution of plant

biotypes resistant to herbicides), Jain et al. (2000) reported that the intensity of cell divisions and the formation of large embryogenic protusions under treatment with 2,4-D may influence the formation of abnormal embryo types. In that study, somatic embryos in medium containing 2,4-D resulted in abnormalities of embryo morphology and malformation of shoot apex and cotyledons. In fact, induced mutations are used to promote additional genetic variation for breeding programs since 1927, resulting in genetic variations not possible to be differentiated from the naturally occurring ones (Allard et al., 1960). This author cites colchicine and mustard gas as chemical mutating agents.

For now, under the light of the current knowledge, the problem for the evolution of plant biotypes resistant to herbicides is the recurrent and persistent use of these compounds, which increases the selection pressure. But this affirmation, sooner or later, may need to be reviewed under the light of new epigenetic scientific data. We'll get back to this later.

One should remember that Darwin's natural selection is build on three concepts: (1) phenotypic variation, (2) fitness differences associated to that variation, and (3) genetic background for that variation (Darwin, 1859; Gurevitch et al., 2009). Although unlikely (under the light of the current knowledge) that herbicides would cause mutations which would be transferred to seeds and result in the establishment of mutated plants (because of moment of application, dose, etc…), this deserves future attention as new data is generated.

By means of selecting mechanisms earlier pointed-out, often a plant into the population will present a given genetic configuration which will guarantee its survival under the application of the herbicide. Resistance can be genetically distinct; a target-site single-gene based, or conversely non-target site based which relies on enhanced herbicide metabolism rates and other specific mechanisms (Shimizu et al., 2011; Busi et al., 2013).

The mechanisms of plants, which confer resistance to herbicides (lower herbicide absorption, translocation or metabolism, compartmentalization, target site mutation), is also vastly discussed in herbicide resistance textbooks (Powles and Holtum, 1994; Vargas et al., 2009; Busi et al., 2013). Summarizing, diverse patterns of herbicide resistance, in genetic terms, can be evident at either the individual or the population level (Petit et al. 2010a,b).

On the Selection of Resistant Biotypes

Plant species are often geographically differentiated (subspecies, ecotypes, etc.) as a result of natural selection operating upon genetic variability (Simmonds, 1979), which is in turn maintained by heterozygosity supplemented by introduction of external genes (Kuckuck et al., 1991). The mechanism a resistant biotype is selected from a group of plants will depend if it comes from individual-level or population-level selection. The way resistant biotypes are selected resembles the way geneticists select superior material in breeding programs by using, among other methods, (1) individual plant selection, or (2) population selection (Allard, 1960).

Individual plant selection relies on the matter that the genetic diversity which paves the way for selection comes from the spontaneous heritable changes which occur slowly and randomly. For plant breeding, the new variety obtained by individual plant selection is constituted from a single pure line (Simmonds, 1979), and relies both on productivity and survival abilities. For population selection, the population is exposed to the selecting agents and those plants most adapted to the given stress tend to survive; it relies most on the survival ability of plants into the population (Allard, 1960).

Back to the evolution of resistance to herbicides in plants, two general selecting mechanisms arise from the super-over-simplified essay on plant breeding previously

presented: (1) high-level and (2) low-level selection, respectively by high and low doses of herbicides.

The high-level selection occurs under heavy occurrence of the selecting agent (factor), which for weed resistance is given by high herbicide doses. It relies on the matter that all plants into a population will die under the application of the super-dose of the herbicide but the one with the genetic alteration (usually by mutation), which will survive and reproduce (Figure 2a); thus, the proportion of plants in the field gradually shifts from the susceptible to the resistant biotype as the selecting factor is repeatedly applied (Figure 2b). It is an individual selection since the susceptible plants will continuously die at every herbicide application while the resistant individuals survive and seed.

The low-level selection occurs when sub-lethal doses of the herbicide (as the selecting factor) is repeatedly applied to the field. In this case, as most biological phenomena follow the normal distribution (Becker, 2015), the dose is not enough to promote elevated levels of control and only the naturally most susceptible proportion of the plants will die, while the also naturally most tolerant proportion will survive and seed (Figure 3). After successive selection cycles the population as a whole will be so tolerant to the herbicide that it fulfills the requirements for the concept of *resistance to herbicides* (Vargas et al., 2009). In this selection method a whole population is selected, thus it tends to be a poligenetic resistance.

Some aspects about weed resistance to herbicides may need to be updated in view of current knowledge. It is a fact that science changes every day, and concepts often need to be re-evaluated. The first aspect is the appearance of biotypes resistant to herbicides; the *Brazilian Herbicide Resistance Action Committee* bibliography (HRAC-BR) (Christoffoleti, 2008) describes that the appearance of weed biotypes resistant to herbicides is conditioned to a genetic change into the population, imposed by pressure selection under the application of the *recommended dose of the herbicide*. As demonstrated, resistance seems to be developed by distinct means also for doses higher or lower than those at the herbicide label. Because of this – among other aspects, herbicide label doses should be respected.

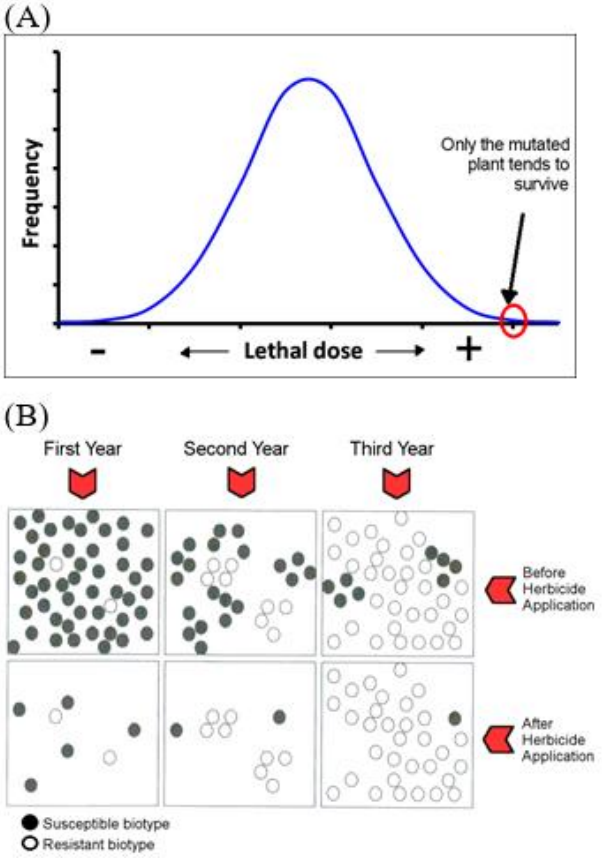

Figure 2. Normal distribution of plants susceptibility to herbicides as dose is increased. The population dies under high doses of herbicides, except the mutated single plant (A). Biotype shifts from the susceptible to the resistant biotype following the initial plant selection and under the application of the selecting factor (B). Source (B): adapted from Christofffoleti (2008).

The second aspect which may need review is about differentiating tolerant and resistant biotypes. The HRAC-BR (Christoffoleti, 2008) suggests that when a

susceptible biotype which differs from the uncontrolled one in terms of Growth Rate 50 (GR_{50}) and Lethal Dose 50 (LD_{50}) is present, it is resistance; if not, it is tolerance. This definition raises two questions: (1) resistance is to be considered only when it comes from genetic mutation, disregarding population selection? Not always the susceptible biotype will be present.

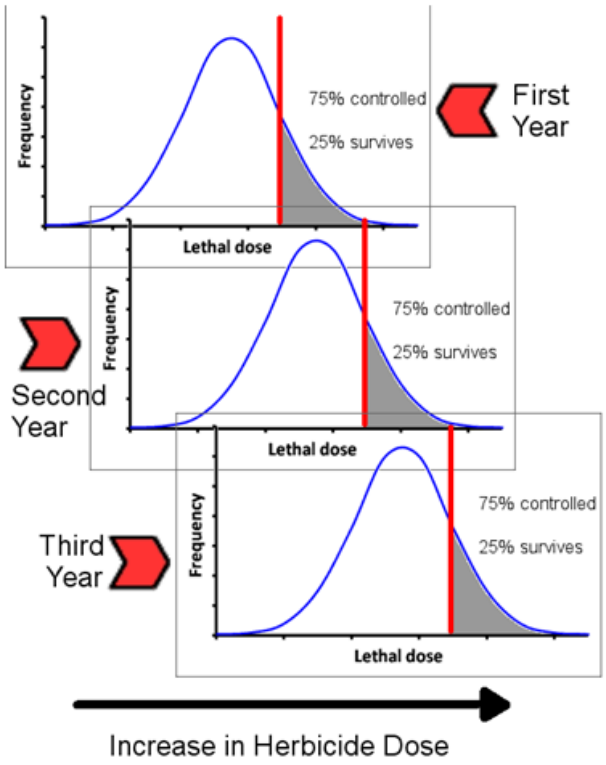

Figure 3. Need for increasing the herbicide dose in order to keep 75% control for weed individuals into a population in successive generations (years). Every year, the 25% naturally most tolerant plants will survive and reproduce, increasing the mean of susceptibility to herbicide in its offspring population.

And (2) differences in GR_{50} and LD_{50} may serve as tools to differentiate high-level and low-level resistance? The proposed answers are (1) *No*, and (2) *Yes*. There is, however, some scientific background for experimentation to prove before these answers can be accepted.

On the Easiness of Selecting Resistant Biotypes

The speed of resistance evolution is influenced by herbicide use history, dose applied, associated and agronomic practices; the weed biology as population growth rate, genetic diversity, and reproductive mode; and population genetic factors (Jasieniuk et al., 1996), besides the selecting mode (high or low level selection).

The *Resistance Risk* for each herbicide chemical groups (maybe for individual compounds) – not only at herbicide mechanism level, is an important matter which deserves attention from the scientific community but have been somewhat ignored by weed science.

There is need to make available for technicians a list which classifies herbicides (associated to its chemical group) by its probable risk of selecting resistant biotypes, aiming for scientifically based herbicide rotation schemes to be used in the field.

This subject was brought into by Valverde et al. (2000) from field observations in Central America while studying resistance of *Echinochloa colona* to herbicides and since then no advances appear to have been made in the subject, although there is a general agreement this is of first concern regarding weed resistance issues. In Table 3, summarized data regarding herbicide group risk of developing resistant biotypes is presented, but unfortunately, the first attempt of classification, the *Resistance Risk* has no strong scientific background to date.

On Epigenetics and Science Advacement

It is a fact Science moves on every day; all theories help knowledge to advance but none is written on stone. Darwin based his theory on the *Origin of Species by Means of Natural Selection* mostly on individual behavior; the continuous *Struggle for Life, from Scarceness to Death*. Lamarck, fifty years earlier than Darwin, remarked that "evolution" is based on a

cooperative interaction between organisms and the surrounding environment. He was largely ridiculed throughout History, but this is not a contradiction.

Lamarck never affirmed all changes in parents would be transmitted to their offspring; he affirmed the offspring would retain traces of the non-genetic changes when it was necessary for survival (Balter, 2000). Beyond this, protocooperation reported between some species (Ryan, 2002) may help proving Clements was also not completely wrong in his "superorganism" theory. In fact, Darwin's blind spot was probably having not considered the environment effect on organisms at the deserved extension. This, evidently, does not blurs the bright of his theory.

Table 3. Summarized data regarding the risk of generating a resistant plant biotype as a function of herbicide mechanism of action.

HRAC Group	Herbicide Group	Years for Resistance [1]	Resistance Risk [2]
A	ACCAse inhibitors	6 - 8	High
B	ALS inhibitors	4	High
C	Photosystem II inhibitors	10 - 15	High
D	Photosystem I inhibitors	10 - 15	Moderate
F	Carotene biosynthesis inhibitors	~ 10	Low
K1	Tubuline inhibitors	~ 10 - 15	Moderate
O	Synthetic auxin	~ 20	Low

[1]Adapted from Powles and Holtum (1994) and Preston (2005); [2]Adapted from Valverde et al. (2000). Resistance risk is subjective and considers that (a) as most specific the site of action of an herbicide, (b) as most applied (field scale) the mechanism of action, and (c) as longer the residual effect and lower the degradation, as higher the risk of resistance appearance.

In addition, until recently the general consensus was that genes were transmitted only to the offspring, and only through reproduction, but recent discoveries proved genetic transference among species, making difficult to qualify "species" under the light of current knowledge (Pennisi, 2001). The concern about this is that genetically modified organisms (GMOs) in agriculture were introduced into the environment and we do not know exactly how these genes will be spread.

Finally, epigenetics (literally "control over the genetics") seems to explain that the environment may influence genes although they do not cause changes to its structure. Among several epigenetic mechanisms, one seems to be of concern for plant resistance to herbicides: gene silencing. According to traditional concepts, when an embryo is formed, its epigenomics is completely erased and rewritten from its ADN, except for some genes whose epigenetic marks are maintained (University of Utah, 2015). An experience with mice showed that environment may present stronger influence on the organism than genetic mutations (Waterland and Jirtle, 2003). Could resistance to herbicides be present in the offspring by similar means?

Why do some cases of plant resistance to herbicides seem to appear from nowhere already as multiple resistance? We promptly assume that the genotype which was introduced was already resistant to a single mechanism of action, and locally developed resistance to another one; but the secondary metabolism of plants may be more dynamic than mutations (Délye et al., 2013) and we are not giving a dime for it in our studies on weed resistance to herbicides. There seems to be initial suspicion

to date that multiple resistance may come from single events, ADN-related or not.

A single phrase may describe the fault that could be limiting our knowledge into plant resistance to herbicides: *the environment, associated to secondary metabolism and epigenetic mechanisms, may play a most significant role into plant resistance to herbicides than we anticipate*. There is no doubt to date that epigenetic inheritance occurs in plants (University of Utah, 2015).

Final Remarks

The current way we manage agricultural fields are not sustainable, being the majorly responsible for the appearance of resistant weed biotypes, and need to be changed. Evolution adapts organisms to the environment where they live with its own stresses, but "evolution" does not mean "better".

Natural selection and genetic drift turn species most adapted to the environment they are into, while mutation and migration supply the genetic variations which is the background for these processes. Selection is the primordial happening on establishment and dominance of resistant types under a selecting agent.

Resistance may come from high-level or low-level selection, respectively from individual or population selection. Herbicide dose labels need to be respected. Some current concepts regarding weed resistance need improvement. There is a need to improve herbicide classification by their risk of selecting resistant biotypes. Epigenetics, secondary metabolism and environment related studies may change our view into plant resistance to herbicides.

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