



Hormetic and xenohormetic potential in the phytobiome of the center of origin

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Abstract A center of origin of cultivated species defined as the geographical area where a particular species originated or differentiated from another and began its domestication process. The interactions between the different factors (climate, soil, macro, and micro-organisms) present in the centers of origin have allowed the selection of specific phenotypic characteristics propitiating the adaptation of the species according to their hormetic potential. Most studies carried out in the centers of origin has been geared towards the genetic part, the search for accessions with resistance to pests and diseases, yield and agronomic attributes. New approaches such as the phytobiome study that considers the complex network of interactions inside and outside the plant combined with the use of accession search methods such as focused identification of germplasm strategy have demonstrated their potential in crop improvement.

These approaches have allowed establishing relationships between the environment, specific geographic areas, and characteristics of resistance, particularly of native breeds and wild relatives of crop plants. The study of the biotic and abiotic factors present in these sites and their application to the management of hormesis will improve the agronomic characteristics of the species and their potential for xenohormesis. The objective of this work is to share some reflections about the potential that the xenohormetic vision of the centers of origin can provide in terms of the improvement of agronomic characteristics in general and the functional features of the food obtained from the crops.

Keywords Hormesis · Xenohormesis · Center of origin · Soil · Environment

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Introduction

The sites where the plant species originated have been the interest of great scientists such as Darwin or de Candolle, but it was the naturalist and geneticist Nikolai Vavilov, who focused on identifying the places where the main crops originated (Hummer and Hancock 2015). Vavilov developed the concept of Centers of origin as the place where the differentiation and domestication of a particular crop began, and the

concept of diversification centers as the places where the greatest genetic diversity of wild relatives was present and in some cases could be the center of origin (Vavilov 1992). Its purpose, in addition to knowing the center of origin and the diversification of the main crops, was to identify individuals with special characteristics such as high yield, resistance to pests, droughts, and other biotic and abiotic factors. The exposure of plants to stress factors in the centers of origin have been key factors in the direction of the evolution of the organism, favoring its adaptation and adaptability in particularly fluctuating environments (Steinberg 2012). Besides, due to the coevolution of plants with pests and diseases, the selection of genetic material of importance for agriculture is possible (Hummer and Hancock 2015). Therefore, the centers of origin are of great importance for the improvement of crops due to the genetic diversity present in these sites (Engels et al. 2006).

On the other hand, hormesis, which is a phenomenon closely related to that indicated above, was described by Calabrese as “a biphasic dose–response phenomenon, characterized by a low dose stimulation and a high dose inhibition” (Calabrese and Baldwin 2002). This makes hormesis an essential process in evolution since it is involved in the capacity of organisms to respond adaptively to low levels of stress factors, increasing their resistance to different hazards conditions (Mattson and Calabrese 2010). The environmental factors present in the centers of origin played an important role in the selection of the species and the development of their morphological characteristics (Mercer and Perales 2010). A phenomenon linked to hormesis is xenohormesis, which refers to the transfer of defense response from one species to another through the trophic levels. The food that is taken from the plants that grow in a hormetic environment form part or activate the consumer’s defense through vegetal molecules derived from the secondary metabolism that interact with the key receptors of the consumers (Howitz and Sinclair 2008). This same effect can be observed in the trophic network that is established between the organisms present in the center of origin, including microorganisms (bacteria, nematodes, viruses, and fungi), insects, and plants. The purpose of this review is to point out and reflect on the functional balance relationships between crop hormesis versus biotic and abiotic factors and xenohormesis in the flow of trophic chains

present in the centers of origin. Additionally, the potential that the xenohormetic vision can generate in terms of agronomic characteristics will be discussed.

Methodology

The methodology, for the realization of this revision, is based on the search of articles and scientific books, which referred to the following concepts “hormesis,” “xenohormesis,” “center of origin.” In this stage of preliminary analysis, some concepts that are part of a second stage, such as phytobiome and FIGS presented, from which an additional analysis was made to complete the analysis of the paper. The third stage was to establish the conceptual relationship of the same. The last thing was to visualize the information in a diachronic and synchronous perspective, which allowed a new on the Hormetic and Xenohormetic potential of the centers of origin.

Centers of origin

The botanist and geneticist N. I. Vavilov established the concept of centers of origin to refer to the place where the species or populations originated or differentiated and began its process of domestication; the latter, in the case of cultivated plants. In effect, the concept of Vavilov diversification centers defined it as places where a related species or groups have a greater variety, which could be different from the center of origin (Vavilov 1992). Vavilov established that there is a relationship between genetic diversity, geographical distribution patterns, and the origin of the crop (Engels et al. 2006). With the use of such elements, Vavilov developed his theory of centers of origin of crops and as a result proposed eight centers of origin. (I) Central East Asia includes Central and Western China, Korea, Japan, and Taiwan. (II) The Hindustani center includes the tropical zone of India, Indochina, southern China and the islands of Southeast Asia. (III) The inter-Asian center includes the interior mountains of Asia Minor, Iran, Syria, Palestine, Transjordan, Afghanistan, the interior of Asia and the northwest of India. (IV) Caucasian (V) Mediterranean Center includes countries bordering the Mediterranean Sea. (VI) Abyssinian center. (VII) Central American center that includes the south of North America and Mexico. (VIII) The Andean center including the Andes

mountain range. (Hummer and Hancock 2015). For its identification, a method of taxonomic-geographic differentiation was used, which generally consisted in the differentiation of a genus with its species and the intraspecific diversity, the determination of the genotypic composition of the species and the geographical location of its hereditary forms (Kurlovich et al. 2000). Vavilov was the first to recognize the need to collect genetic material and translate that source of scientific knowledge into an advantage for agriculture (Harlan 1971). The centers of origin harbor an important part of the diversity of the cultivated plants with a set of genes that have been of great importance for the improvement of current and future crops.

Importance of the centers of origin and its potential uses

The study of the centers of origin to understand the evolution and the role of the environment in the phenotype of the cultivars has not been carried out. However, it has already been proposed to conduct studies in the centers of origin under environmental conditions to see how the biotic and abiotic factors that change the phenotype of the plants for their diversification and domestication, this with the purpose of understanding the adaptive process of the crop traits (Chen et al. 2017). The interaction of the biotic and abiotic environmental factors and the plants allows the coevolution of the community, allowing its adaptation and specialization, reducing the effect of stress or exchanging growth and signaling factors (Braga et al. 2016). The interaction in the rhizosphere between microorganisms and the plant depends on the exchange of various compounds and genetic characteristics, for example, metabolites derived from secondary metabolism, siderophores, quorum detection system, biofilm formation or cell transduction signaling (Braga et al. 2016). The interaction with beneficial organisms allowed the plant to survive all kinds of stress from that particular environment (Ahkami et al. 2017). So, it was observed that in the rhizosphere, there are compounds that lead to chemical communication resulting in priming of defense, or induced resistance in the plant host (Mhlongo et al. 2018). Also, the health of the plant and its growth depend on the type of microorganism found in the microbiome of the rhizosphere and the function it plays in it (Mendes et al. 2013). The microorganisms present in soils vary

from one place to another, and they have been shown to be selective for plants (Hale et al. 2014). Concerning abiotic factors, in the centers of origin, there is diversity in climatic conditions. Therefore, the plants developed chemical and physical mechanisms, consistent with the biological, chemical and physical environment of their center of origin, to survive in conditions that are not present in other parts of the planet. During crop domestication and diversification, all the environmental factors mentioned above and the biological characteristics of the species (reproductive system, ploidy level, and further genetic characteristics), have been shaped the phenotypes of plants (Gepts 2006). Therefore, a relevant aspect in the study of centers of origin is to recognize a large number of beneficial organisms that are found in it and that have not yet been studied or incorporated into crop management (Mendes et al. 2013). The above is because, in the center of origin of the species, there are favorable conditions for its development, mainly for the production of secondary metabolites, because the environmental conditions are not as controlled as in conventional agriculture. The study of plant–environment–organism interactions at different fine spatial scales has shown new knowledge about the effects that mediate the productivity of plants (Surh 2011). The biotic and abiotic factors present in the centers of origin have not been studied together; neither the metabolic diversity of the crops present in these environments or the genetic potential of the plants that grow in these environments. Trying to reproduce the current environment in the centers of origin in the cultivation practices will allow developing a sustainable type of agriculture with the decrease of the use of agrochemical compounds, will allow exploiting more its nutraceutical potential and, on the other hand, the management of the resources renewable that the plant needs.

Hormesis and xenohormesis

Hormesis is defined as an adaptive response represented by a biphasic dose–response to a determining factor of stress in which low-dose induce stimulation and high-dose induce inhibition, and the responses can be induced by direct stimulation of the hormesis or resumed by an overcompensation stimulation hormesis (Calabrese 2018). Hormesis also explains phenotypic changes in all organisms under the effect of any

stress factor that have the objective of maintaining homeostasis and increasing the survival of an organism. Hormesis is a universal process that is present across biological systems and stressors (Garzon and Florez 2013). Although the beneficial/harmful effects should not be part of the definition of hormesis, the hormetic potential has been represented as an advantage in evolution. That is, the hormesis gave the organisms the ability to adapt in a given place and eventually the hormetic potential, depending on the plasticity, gives greater adaptability of pre-existing characteristics and greater evolutionary potential of the species over time (Calabrese and Baldwin 2002). Vavilov (1992) hypothesized that the geographical location where the greatest number of species/varieties of cultivated plants are found is likely to be recognized as the center of origin of that group of cultivated plants. The diversification of the species is given by all the environmental factors and the greater genetic variation, which translates into the greater potential of adaptation. The plasticity, because it allows the organisms to be close to the adaptive state, serves as a basis for adaptation (Ho and Zhang 2018). Due to the above, hormesis is key in the evolution of the species in the centers of origin, as it is reflected in the plasticity that allowed it to adapt fully to these sites. Currently, the studies of plant hormesis has been carried out using chemical stress factors (pesticides, heavy metals, herbicides, elicitors), physical (temperature, UV light, drought), and biological (part or entire organisms) (Belz and Duke 2014; Abbas et al. 2016; Rodriguez-Salus et al. 2016; Vargas-Hernandez et al. 2017; Agathokleous et al. 2019). Although there are no reports of studies of hormesis related to stress factors in the centers of origin, many of the biotic and abiotic factors studied were present in the centers of origin through the evolution of the plants. The plant response to the above stress factors depends on the type, duration, and dose of the stimulus in addition to the stage of development of the plant and its biological organization (Chelli-Chaabouni 2014).

Meanwhile, xenohormesis explains the hormesis interspecies; that is, heterotrophic organisms can sense some compounds synthesized by autotrophic organisms in response to stress (Howitz and Sinclair 2008). It has also been proposed that xenohormesis is given by the recognition of stress through the evolutionarily adaptive modulation of the enzymes and receptors pathways in organisms, rather than the detection of

low doses of stress (Howitz and Sinclair 2008). Many molecules derived from secondary metabolism in plants have as their main function to protect against pathogenic organisms functioning as phytoalexins (Surh 2011). Animals exploit the secondary metabolism of plants against different types of stress that disturb their homeostasis (Forbey et al. 2009). Due to several organisms have the ability to synthesize secondary metabolites, including plants, microorganisms or fungi (O'Connor 2015), a different view can be assumed about the xenohormesis among the trophic networks of the organisms (Fig. 1). That is, xenohormesis can be passed from autotrophic to heterotrophic, autotrophic–autotrophic, and heterotrophic to heterotrophic and heterotrophic to autotrophic organisms. Some metabolites produced by fungi, as well as those derived from plants can be used as pharmaceuticals. The biological properties that have been studied in fungi are antitumor, cardiovascular, immunomodulatory, anti-allergic, anti-diabetic, and hepatoprotective properties (Kaul et al. 2017).

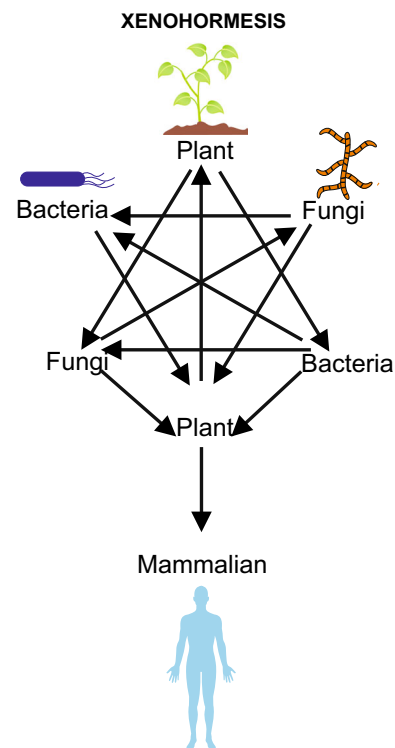


Fig. 1 Xenohormesis trophic networks of the organisms

The adaptive mechanism of plants through specific metabolic pathways

The development of plants is intimately related to the environment to which they are exposed during their life cycle, giving a specific response depending on the stimulus to which they are exposed (Chelli-Chaabouni 2014). These stimuli can be classified as biotic or abiotic and considered as stress when they are part of a sub-optimal environmental condition (Bohnert and Sheveleva 1998). The plant response to stress to a stress factor depends on several factors, including the type, duration, and dose of the stimulus in addition to the stage of development of the plant and its biological organization (Chelli-Chaabouni 2014). Although there are features that are present in various organisms, little is known about the trajectories step by step through which complex features arise in nature (Weng 2014). The development of organisms in different stress conditions depends on the adaptation strategies that they have developed over time (Mocali et al. 2017). The differentiation of organisms consists of morphological differentiation as well as metabolic. Metabolism is a property of life that is represented as a network of chemical transformations that are mediated by enzymes (Weng 2014). Plants exploit their metabolism to produce a large number of compounds for adaptation (Weng 2014). The distribution of the products of the secondary metabolism is important for the taxonomy, but its appearance reflects the integrations in a given phylogenetic framework (Wink 2003). The molecular mechanisms that allow the diversification of defense secondary metabolites are gene and genome duplications and consequent exaptation (or 'neofunctionalization'); accumulation of point mutations; and multilocus control leading to variation in metabolic products (Speed et al. 2015). When a type of stress is sensed by the cell, there is a response to stress as a defense reaction to an environmental force (s) that results in damage of the macromolecules, the response results in an increase of the tolerance or removal of the damaged cells. The interaction between the plants and their environment is mediated by the biography of secondary metabolism products as an adaptive plastic response to their environment (Sampaio et al. 2016). At very short space scales, the habitat of a species can differ enormously in terms of stress factors, which have the ability to impose natural selection on several traits and may cause genetic differentiation within a

population (Wos and Willi 2018). In relation to the factors of biotic origin with which plants interact, coevolution plays a very important role in explaining the diversity of secondary metabolites related to defense (Speed et al. 2015).

On the one hand, the plants focus their efforts on the synthesis of toxins to counteract the pathogens while they develop surviving strategies to resist the toxins of the same (Speed et al. 2015). Defense compounds in plants that are secondary metabolites, which are derived from promising metabolites use a limited number of metabolic pathways acquiring diversification through the addition of different combinations of functional groups (Wink 2016). The synthesis of this type of compound is the main characteristic of the immune system of plants, counteracting the effect of stress-mediated by microorganisms or environmental factors. The main pathways for the synthesis of defense compounds are the phenylpropanoids, the isoprenoids, and the alkaloids, being inducible or the former, phytoanticipins, and phytoalexins, respectively (Iriti and Faoro 2009). Therefore, the adaptive mechanism of plants through specific metabolic pathways, as a final expression in the behavior or phenotype of a species determined in its center of origin, is obviously the product of the genetic pile of the species and the direct action of the environment and the interaction of environmental factors and their incidence on the biological entity. Therefore, the adequate management not only of the genotype but also of all the environmental factors must be reflected in production systems in which it can be oriented towards performance, quality or a balance between yield and quality, but always with a sense that the productive activity is in harmony with the environment.

FIGS, genotyping and population analysis linked to environmental variables

The Focused Identification of Germplasm Strategy (FIGS), is a novel that approach has allowed the identification of accessions with a better adaptive response. The FIGS is a method of searching through filters in Geographic information system (GIS) and gene banks. The searches are done under the hypothesis that many of the accessions collected from the environment evolved in these sites, and their adaptive traits have been determined by the selection pressure

that was present in the environment origin (Bari et al. 2012). FIGS has led to the detection of a relationship between geographic areas and the incidence of resistance, particularly of native breeds and wild relatives of crop plants (Bonman et al. 2007). This link between the environments has been shown to link the morphological traits in barley (*Hordeum vulgare* L.) to the ecoclimatic pattern of the original collection sites (Endresen 2010; Endresen et al. 2011). The focused selection of the selection of subsets of the germplasm strategy is proposed as an alternative approach to the selection, evaluation of rare traits, and useful in crop improvement. Many adaptive features can be linked to agro-climatic parameters (Table 1).

The plant environment: the phytobiome

As has been mentioned, the environment of the plant is determined both by living organisms and by the physical conditions present in the ecosystems. The communities of organisms and the physical conditions constitute these areas or ecosystems of this set that are found in and around the plants, which as a whole have been called Phytobiome (Fig. 2; Leach et al. 2017). Phytobiome is structured as a complex network of interactions that links crops with microorganisms, soil,

climate, animals, plants, and other environmental factors (Marla 2017). This complex network of interactions is established, regulated, and inhibited through the production and perception of physical and chemical signals (Leach et al. 2017). The biological interactions include competition, predation, and pathogenesis to mutualism and symbiosis processes; on the other hand, these are influenced by abiotic factors such as soil composition, temperature, humidity, irradiation, and wind (Leach et al. 2017). Interactive relationships between plant and environmental factors over time have allowed creating a process of constant adaptation. Stress factors present in the phytobiome induces the process of hormesis creating adaptive responses to counter the same or different stress factor (Table 2).

Soil

The soil is a factor composed of a very complex matrix of elements that plays a very important role in the plant. Soil is a natural body constituted by a mineral fraction and an organic fraction, is the basis of most ecosystems and determines how an ecosystem will look in terms of animal and plant life (Schoonover and Crim 2015). The rocks in the terrestrial surface, that

Table 1 Study of the FIGS in some crops

Accessions	Variable	Filters	Adaptive response	References
<i>Vicia faba</i>	Drought	Moisture-limited environments, wetter sites	Higher, leaf area, stomatal density, stomata area, transpiration rate and fertility	Khazaei et al. (2013)
Bread wheat	wheat aphid (<i>Diuraphis noxia</i>) resistance (RWA)	Countries where RWA has been reported Agro-climatic zone classifications of arid, semi-arid and semi-humid Country groups at different elevations	IG-41578, IG-41603, IG-43273 (Pakistan), IG-107147 (Iran), IG-138374 (Uzbekistan) and IG-138998 (Iran) showed a high level of resistance to RWA	El Bouhssini et al. (2009)
Wheat and barley	stem rust (<i>Puccinia graminis</i> Pers.) in wheat (<i>Triticum aestivum</i> L. and <i>Triticum turgidum</i> L.) and net blotch (<i>Pyrenophora teres</i>) in barley (<i>Hordeum vulgare</i> L.)	Monthly mean values for temperature (temp), minimum temperature, maximum temperature, precipitation, and the derived bio-climatic layers	Improve the efficiency of field screening trials	Endresen et al. (2011)
Wheat	Powdery mildew resistance	Sites with incidence powdery mildew	Resistance against at powdery mildew race	Bhullar et al. (2009)



Fig. 2 The phytobiome consists of a complex network of interactions that links crops with microorganisms, soil, climate, animals, plants, and other environmental factors. The

interactions are mediated by physical cues and signals chemical in nature, including lipids, peptides, polysaccharides, and secondary metabolites

with the time and by means of a set of processes of weathering, determine the formation of the ground, disintegrate and alter also by the action of biotic and abiotic factors. The classification of the soils considers the chromatic aspects, the texture, the age, and the predominant factors in their development (Hartemink 2015). These factors are different between the soil types, and many have an effect on the physical characteristics (aggregate structure, porosity, and bulk density), chemical products (nutrients supply and cycles) and biological (microbial and enzymatic activities, soil fauna) (Jiang et al. 2014). For example, the structure of the soil determined by the size of the particle reflects both the form and the physical and chemical arrangement of the climate, as well as its capacity to retain and transmit liquids and organic and inorganic substances (Schoonover and Crim 2015). Aggregates are secondary particles formed by the

combination of mineral particles with organic and inorganic substances. The complex dynamics are the result of biotic and abiotic factors (Baiamonte et al. 2015). Aggregation stability increases with the organic carbon surface and soil clay and cation exchange capacity (Bronick and Lal 2005). Aggregates, in addition to physically protecting organic matter, influence microbial communities, oxygen diffusion, and water flow determine the absorption and desorption of nutrients (Baiamonte et al. 2015). On the other hand, plants modify the environment in which they grow, modifying the characteristics of the substrate in a physical and chemical way. These modifications are part of the biogeochemical cycles and the formation of the soil by producing weathering agents affecting the structure by creating pores in the soil improving the stability of aggregates (Weidenhamer and Callaway 2010). Its positive effect on soil

Table 2 Adaptive responses of crops to different types of environmental factors

Stress factor	Crops	Adaptive responses	References
<i>BIOTIC</i>			
<i>B. pumulis</i> , <i>P. pseudoalcaligenes</i>	Rice	Enhance the stability of the plant cell membrane for the survival of the plant under salt stress	Jha and Subramanian (2016)
<i>Bacillus megaterium</i> , <i>Bacillus thuringiensis</i> , <i>Pseudomonas putida</i>	<i>Trifolium repens</i>	Increasing plant drought tolerance	Ortiz et al. (2015)
<i>Paenibacillus xylanexedens</i> , <i>Enterobacter cloacae</i>	<i>Phoenix dactylifera</i> L.	Increasing plant the survival of the plant under salt stress	Yaish et al. (2015)
<i>Ochrobactrum</i> sp., <i>Antoea agglomerans</i> , <i>Bacillus thuringiensis</i> , <i>Pseudomonas fluorescens</i>	<i>Capsicum annuum</i> cv. Demre, <i>Solanum lycopersicum</i> cv. Marmande	Effects against bacterial spot disease caused by <i>Xanthomonas euvesicatoria</i>	Akköprü et al. (2018)
<i>Pseudomonas putida</i>	<i>Cucumis sativus</i>	Effects against bacterial disease caused by <i>Pseudomonas syringae</i> pv. lachrymans	Akköprü and Ozaktan (2018)
<i>ABIOTIC</i>			
Atmospheric CO ₂ levels	Potato	The tuber yield increase in potatoes under no water restriction	Finnan et al. (2015) and Kimball (2016)
Early mild water restriction	Potato	Enhance water stress resistance and tuber yield	Xu et al. (2011) and Yactayo et al. (2013)
Increase temperature	Woody plants	Enhanced growth, productivity, and health overall	Yuan et al. (2018)
Salinity	<i>Cynara cardunculus</i>	Leaf phenolic content was significantly increased	Hanen et al. (2008)
Low doses of gamma radiation	Tomatoes	Stimulate germination and substantially increase fruit number	Wiendl et al. (2013)

aggregates consists of (1) entangling fine particles in stable macroaggregates, (2) promoting wetting and drying cycles rearranging the soil particles, (3) adding organic matter, (4) supporting microorganisms in the rhizosphere (5) providing food for the edaphic fauna (Amézketa 1999). During the life cycle of the plants, they add organic matter in the form of leaf litter and secretions in the soil, increase the storage potential and retention of nutrients in the soil. The products secreted in the soil by the roots are generally known as root exudates (Walker et al. 2003). The chemical composition of the exudates varies between species and phenological status, as well as environmental conditions, but may include a range of labile sugars, organic acids and amino acids (Girkin et al. 2018). The ability to secrete a wide range of compounds is one of the most important characteristics of the roots of plants, these compounds represent from 40 to 60% of all the

photosynthetically fixed carbon that is transferred to the soil (Keiluweit et al. 2015). Therefore, the soil, in itself is a determining factor of possible metabolic routes inside and outside the plant and in turn linked to survival, which determines at a given time an evolutionary direction.

Organic matter

The organic matter or organic fraction of the soil is constituted by a mixture of organic compounds in a constant state of transformation. It is generally used as an indicator of soil quality because it plays an important role in the maintenance and physical integrity of the soil (Li et al. 2018). The acidic organic acids of the soil are an important part of the organic fraction; they have a relevant impact on the availability of nutrients and soil ecology (Adeleke et al. 2017).

The organic matter in the soil improves the environment for beneficial microorganisms, increases the development of the populations and biodiversity. As it is a source of energy for microorganisms, it increases its activity as aggregate formers that improve soil properties (Medina and Azcón 2010). Therefore, it is a relevant factor in the possibilities of certain routes of biosynthesis in plants in a given center of origin, so that necessarily it also affects a certain evolutionary direction.

Microorganisms

The organic matter that composes the soil are the compounds derived from living organisms, and within this category are the microorganisms present in the soil as nematodes, fungi, and bacteria. Microorganisms control processes, such as decomposition and nutrient cycling. Microorganisms control processes, such as decomposition and nutrient cycling (Kaiser et al. 2016). These represent approximately 1% of their weight and are involved in the exchange of substances and energy in the soil (Gagelidze et al. 2018). They are a pillar in ecosystems, their diversity and structure are determined by different biotic or abiotic factors, such as climate or vegetation (Delgado-Baquerizo et al. 2018; Li et al. 2018). The soil microbiota plays a fundamental role in the physical and chemical processes in the soil. They promote the formation of soils through the erosion of rocks by means of three mechanisms: mechanical damage, water retention, and acidification by metabolites (Yanwen et al. 2017). The activities of microbes in the weathering of rocks and minerals can be called bioweathering.

In most cases, these interactions are close to the surface of the soil interactions with biotic and abiotic factors that regulate the habitat and determine the availability of resources for the maintenance of life (Gadd 2010). The decomposition of organic matter constituted by vegetable, animal, and microbial remains is one of the most important microbial activities in the soil; the microbial activities of decomposition are related to the cycle of elements that constitute the biomass of living beings with biochemical functions and essential structures (Gadd 2010). The speed of decomposition is determined by three main factors: soil organisms, the physical environment, and the quality of organic matter. In

the decomposition process, different products are released: carbon dioxide (CO₂), energy, water, nutrients from plants and organic compounds that affect the properties of the soil, favoring the stability of aggregation, increasing the capacity to attract and retain nutrients (Khatoon et al. 2017). The beneficial microorganisms for plants through different types of interactions (symbiotic, endophytic, associative) are involved in the acquisition of nutrients, increase the chances of germination of seeds, generally, strengthen their growth and improve their response to the various biotic and abiotic stress factors (Souza et al. 2015). Microorganisms are sources of a diversity of different Metabolites. Of these biologically active compounds, most are produced by bacteria, for example is that of *Streptomyces*, which produced secondary metabolites, which specific functions with the interaction bacteria-plant-environment and as toxic substances and signaling (Miao and Davies 2010). Within the beneficial or non-pathogenic microorganisms for the plants are plant growth-promoting rhizobacteria (PGPRs) and fungi (PGPFs) and biological control agents (BCAs) (Russ et al. 2012). An appreciation derived from the above allows making clear that microorganisms provide metabolic pathways complementary to those of a plant determined in its place of origin, and therefore logically affect a particular evolutionary direction.

Climatological conditions

Nowadays, plants generally in their natural environment are exposed to multiple factors of biotic stress (plague and diseases) and abiotic factors (high and low temperatures, droughts, floods, lack of light, and nutrient deficiencies (Kumar et al. 2018). The sessile life of the plants has allowed developing a variety of mechanisms to tolerate different stress factors (Atkinson and Urwin 2012). Plants can adjust to new conditions against different stress factors through phenotypic plasticity (Nicotra et al. 2010). The plasticity response in plants begins with the detection of an external stimulus through receptors in the plasma membrane, such as G proteins (Martínez-Bastidas et al. 2017). These initiates a signaling cascade that activates the transcription of genes, depending on the level and the stimulus, epigenetic processes such as DNA methylation can be activated, changes in the population of small RNAs that can alter gene

expression (Nicotra et al. 2010). The ability of plants to sense the surrounding environment and respond appropriately at different levels of interaction allows plants to establish a homeostatic system (Zipfel and Oldroyd 2017). To maintain the levels of homeostasis, plants can adjust multiple aspects of their morphology and physiology. The plants, in response to the lack of light, can present changes in the leaves. These changes are present in an increase in the total leaf area per unit of biomass to increase the area of light capture.

On the contrary, the rate of photosynthesis per area shows a negative response to improve efficiency in respiration and carbon use (Freschet et al. 2018). The combination of low temperatures and light is considered one of the most challenging stress factors for plants causing alterations; however, the plants have developed mechanisms that allow for homeostasis between the contribution and the use of energy (Míguez et al. 2015). The response induced in plants by variable environments can respond through adaptive plasticity in short time and in a long time through the evolved process (Gremer and Venable 2014). The plasticity is genetically controlled, hereditary, and of potential importance for the evolution of the species. The understanding of the changes induced by the different biotic and abiotic factors in the traits of the plants allows the understanding to answer the unknowns about ecology and evolution in the wild species and is useful to design strategies such as the manipulation of the plasticity in the species of crops (Nicotra et al. 2010). In the case of the climatic component of the environment, it can be perceived that it is one of the sources of stress or mitigation for the plants, so that, in the way in which these selection instruments behave in the center of origin, they are shaping the evolutionary process. Currently, the studies in situ in the centers of origin to understand the domestication and diversification are very few (Chen et al. 2017). For example, the Andes region is the most important site for potato diversification, it has different uncertain climates, and this allows genetic diversity to be high. Within the various climate, scenarios are droughts, frosts, hailstorm, or excess rainfall (Quiroz et al. 2018). Studies have been reported on how the changes in climatic conditions in this place lead to the acclimation or phenotypic plasticity of potatoes in terms of physiological responses that select plant traits to cope stress factors (Quiroz et al. 2018).

Conclusions

Until now, the centers of origin have been used to take advantage of genetic resources exclusively to confer resistance, performance, etc. and the environment and its interactions have been disdained to influence the same characteristics, for the improvement of production processes. The genetic variation determines the adaptability that is reflected in the potential of hormesis manifested in greater plasticity respect of the changes that are reflected in the centers of origin. We must take advantage of the phenomenon of hormesis not only for the defense of plants but also to improve the functional qualities of the food. Therefore, it is necessary to put efforts into the study of the environmental conditions present in the centers of origin or situ studies, and their integration in the hormesis phenomenon, to increase the agricultural attributes, without the corresponding effort of the genetic part.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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