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Review Article

Integrating Plant Nutrients and Elicitors for Production of Secondary Metabolites, Sustainable Crop Production and Human Health: A Review

Ávila-Juárez Luciano*, Torres-Pacheco Irineo, Ocampo-Velázquez Rosalía Virginia, Ana Angélica Feregrino-Pérez, Andrés Cruz Hernández and Guevara-González Ramón Gerardo*
Biosystems Engineering Group, Division of Graduate Studies, School of Engineering, Universidad Autónoma de Querétaro, C.U Cerro de las Campanas, S/N, Colonia Las Campanas. C.P. 76010. Santiago de Querétaro, Querétaro, México
*For correspondence: ramon.guevara@uaq.mx

Abstract

Plants are essential sources of bioactive substances that promote health. For economic reasons, farmers usually focus on obtaining higher yields rather than crop nutraceutical quality. The application of non-essential elements (NEEs) is a technique used to increase secondary metabolites (SMs) in plants. This technique includes variations of the essential elements ratios in a nutrient solution or the inclusion of elicitors, such as salicylic acid or methyl jasmonate. Elicitor use is controversial because plants grow differently in inert substrates, *in vitro* and soil. Soil contains essential elements (EEs) and NEEs that can enhance SM synthesis and increase nutraceutical plant quality. However, any technique that modifies plant metabolism can decrease yields. Thus, developing techniques to increase both agricultural product yield and quality is necessary. This review aims to demonstrate the necessity for a new recipe or "cocktail" of plant nutrients based on EEs and NEEs, and elicitors apply to achieve both a high yield and crops nutraceutical quality.

Keywords: Elicitors; Essential chemical elements; Non-essential chemical elements; Secondary metabolites

Introduction

Since the "Green Revolution," agriculture has been influenced by land mechanization, genetically improved crops, and the excessive use of fertilizers and pesticides which are harmful to the environment (Floros *et al.*, 2010). Such changes have increased agricultural yields (Dayan *et al.*, 2009) because of the more rapid growth of crops (Stefanelly *et al.*, 2010). Moreover, improved plant care and optimal climate handling have improved the conditions for plant growth (Bennett *et al.*, 2012) and reduced the production of secondary metabolites (SMs).

Plants are an essential source of nutrients and secondary metabolites (SMs) (Patra *et al.*, 2013), frequently referred as bioactive compounds, such as alkaloids, phenolic compounds (PCs) and terpenes (Jahangir *et al.*, 2009). Certain SMs reduce the risk of disease, including colon cancer (Russell and Duthie, 2011) and, reduce blood pressure, serum lipids, diabetes mellitus, obesity (Perez-Vizcaino and Duarte, 2010) and cardiovascular diseases (Bernal *et al.*, 2011).

Organic products contain additional SMs when compared with conventional products. The main difference between organic agriculture (OA) and conventional agriculture (CA) is that former uses more plant-friendly pesticides with lower residual effect, with crop growth medium as soil. Soil contains essential (EEs) and non-essential elements (NEEs) in inadequate ratios for plant nutrition, and under stress conditions, plants produce more SMs (de Costa *et al.*, 2013). Moreover, SMs alter normal growth, resulting in decreased crop yields. However, organic products have better nutraceutical quality, but OA cannot always satisfy the demand for horticultural products because a) certain crop yields are approximately 30% of the obtained in CA (Ramos-Solano *et al.*, 2010) and b) OA occupies less than 5% of the cultivable land (Connor, 2008).

Currently, various techniques are being used to increase SMs in plants, including varying ratios of EEs or adding NEEs in the nutrient solution (NS), soil or directly to the plant and applying elicitors such as jasmonic acid (JA), salicylic acid (SA) or nitric oxide (NO) and their derivatives. However, there is a risk of causing an increase or decrease in the yield and SM production by the use of these techniques. The application of elicitors is a widely used technique. However, the SM production in plants growing in soil, *in vitro* or in inert substrates varies, with more SMs usually produced in soil.

In a broad sense, "elicitor", for a plant refers to chemicals from various sources that can trigger physiological and morphological responses (Zhao *et al.*, 2005). For instance: methyl jasmonate (MeJ) (Heredia and Cisneros-Zevallos, 2009), JA (Saw *et al.*, 2010), SA, and hydrogen peroxide (H_2O_2) (Jeong and Park, 2005) act as elicitors. Elicitors mimic the action of plant signaling

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molecules (Ruiz-García and Gómez-Plaza, 2013) and produce reactive oxygen species (ROS) (Yoshioka *et al*., 2011) that stimulate the plant to produce defense hormones and enzymatic or non-enzymatic antioxidant mechanisms to mitigate ROS effects. A similar effect is caused in the soil by NEEs.

Therefore, the agricultural industry should focus on obtaining high yields with greater nutraceutical quality to promote public health. In the present review, we present the relationship of EEs and certain NEEs in SM production and review the application of elicitors in plants cultivated in soil, inert substrates or *in vitro* and the relationship between elicitors, EEs and NEEs on secondary metabolite production in plant.

Sustainable Agriculture

Current agriculture practices require a shift towards sustainability models. Plant nutrition should focus on obtaining high yields and crops with greater nutraceutical value usually high in SMs than what are currently produced. Plants grown under OA conditions contain more SMs than produced under CA (Vallverdú-Queralt *et al*., 2012). Amendments containing NEEs as rare elements (REs) are used in OA. These elements cause stress in the plant (Wang *et al*., 2007a) and increase the amount of SMs (Challaraj *et al*., 2010a); however, the induced stress can also result in a lower yield. However, OA cannot adequately satisfy the demand for vegetables. An alternative could be to work with the CA techniques with a consideration for yield and nutraceutical quality. Therefore, sustainable agriculture must be promoted. In recent years, researchers have focused on the relationship between fruit and vegetable consumption and on identifying plant compounds that promote health benefits (García-Mier *et al*., 2013). These compounds are categorized into three groups: alkaloids, polyphenols, and terpenes broadly termed as secondary metabolites (Table 1).

Table 1: Categories of secondary metabolites in plants and their effects on health

SMs group	Health benefit	Reference
Alkaloids	Antioxidant	Herraiz and Galisteo, 2003
	Rheumatoid arthritis	Wang *et al*., 2007b
	Anticancer	Kabashima *et al*., 2010
	Anti-inflammatory activity	Yang *et al*., 2007
	Hypertension	Monteiro *et al*., 2012
Polyphenols	Antimutagenic	Feregrino-Pérez *et al*., 2011
	Antioxidant	Krinsky and Johnson, 2005
	Anticancer	Fresco *et al*., 2006
	Antimicrobial	Veloz-García *et al*., 2010
	Anti-inflammatory, Anti-itch	Sur *et al*., 2008
	Hypocholesterolemic	Jiao *et al*., 2010
	Antidiabetic activity	Kobori *et al*., 2009
Terpenes	Antitumor activity	Lage *et al*., 2010
	Protection against eye diseases	Krinsky and Johnson, 2005
	Antimicrobial	Mathabe *et al*., 2008
	Antidiabetic activity	Patil *et al*., 2011

SMs: secondary metabolites

The role of SMs is to protect the plant from stress. For example, ascorbic acid protects metabolic processes from damage caused by hydrogen peroxide (H_2O_2) and other toxic oxygen derivatives (Ahmad *et al*., 2010). Diets based SMs provide benefits by preventing or reducing certain diseases in humans. For example, green tea contains catechins that prevent chronic age-related disorders, such as cardiovascular disease (Hodgson and Croft, 2010), mediate vascular inflammation and atherosclerosis through different actions (i.e., anti-hypertensive, anti-lipemic, anti-inflammatory, anti-proliferative and anti-thrombogenic) (Moore *et al*., 2009; Naito and Yoshikawa, 2009) and prevent the invasion of certain cancers (Khan and Mukhtar, 2008).

Universal Nutrient Solutions in Agriculture

In 1939, Arnon and Stout published the "essential" elements for plants. Since then, recipes for "universal nutrient solutions" (UNSs) have been introduced, such as the by Hewitt (Steiner, 1961) and Steiner (1984). The latter recipe is widely used in agriculture research and is formed by 12 essential chemical elements: N, P, K, Ca, Mg, S, Fe, Mn, B, Cu, Zn and Mo. Currently, UNSs are produced with the maximum 12 essential chemical elements. However, differences exist between various chemical element concentrations. For example, FAO UNS has 34% more N than of Steiner. In contrast, Kilinc UNS has 70% and 77% less N and K, respectively than Steiner UNS (Table 2). Thus, choosing the most appropriate UNS for research, remains difficult because of variations between solutions. An ionic imbalance of elements in the solution could potentially affect the performance or production of compounds of interest.

Plant nutrition is a complex process that involves these essential elements in addition to carbon, oxygen and hydrogen. In the absence of these elements, plants cannot complete their life cycles (Arnon and Stout, 1939). Therefore, fertilization programs provide optimum amounts of fertilizer to increase visual quality and yield; however, such programs are insufficient. Changes in human populations have caused increases of chronic degenerative diseases, and a new method of producing crops is necessary that can potentiate yields but also produce food with high nutraceutical value capable of contributing to public health.

Nutritional Management: Is it the Right Tool to Increase SMs in Plants?

The increase in SMs is achieved by manipulating the ionic proportions of the chemical elements in the NS (Table 3). However, use of such techniques requires careful management because synergism or antagonism can be induced between chemical elements and can cause deficiencies or toxicity resulting in a decrease of yield.

Table 2: Universal nutrient solutions for hydroponics

Chemical Element	Hoagland and Arnon, 1950	Hewitt, 1966	Kilinc, 2007 (1)	Steiner, 1984	Kilinc, 2007 (2)	FAO, 1990	Jensen, 1985
mg L^{-1}							
N	210	168	50	167	150	150-225	106
P	31	41	26	31	31	30-45	62
K	234	156	66	277	234	300-500	156
Mg	48	36	10	49	30	40-50	48
Ca	160	160	33	183	100	150-300	93
S	64	48	5	111	15	NA	64
Fe	2.5	2.8	2.6	1.33	8	3-60	3.8
Mn	0.5	0.55	1.6	0.62	5	0.5-1	0.81
B	0.5	0.54	0.5	0.44	1.5	0.4	0.46
Cu	0.02	0.064	0.66	0.02	2	0.1	0.05
Zn	0.05	0.065	1	0.11	0.3	0.1	0.09
Mo	0.01	0.048	0.066	0.048	0.2	0.05	0.03

NA: not available

Plant Nutrition with Macronutrients

Nitrogen (N) is the only element used as a cation (NH_4^+) or anion (NO_3^-). Nitrogen influences growth and morphological development (Gifford *et al.*, 2008), primary and secondary plant metabolism (Giorgi *et al.*, 2009). The link between primary and secondary metabolic pathways in plants is considered to occur through phenylalanine ammonia-lyase (PAL), which explains the concurrent increase of flavonoid activity with increased PAL activity (Lillo *et al.*, 2008). Nitrogen is highly consumed by plants, and non-optimal concentrations of N can lead to losses of yield.

Productivity is also limited under phosphorus (P) deficiency (Chen *et al.*, 2008) and as part of energy rich molecules such as adenosine triphosphate (ATP), nucleic acids and phospholipids, it is involved in primary metabolism (Wu *et al.*, 2003). The symptoms of plant P deficiency are the production of anthocyanins and decreases of development.

Potassium (K) is essential for the synthesis of proteins, glycolytic enzymes and for photosynthesis (Hu *et al.*, 2005). It acts as a coenzyme and activates different precursor enzymes of metabolic pathways (Bussakorn *et al.*, 2003), and its partial or total deficiency has been associated with increased antioxidant enzymes (AOEs). Potassium might play a special role in the process of carotenoid biosynthesis by activating several enzymes regulating carbohydrate metabolism as well as the precursors of isopentenyl diphosphate, pyruvate and glyceraldehyde 3-phosphate (Fanasca *et al.*, 2006).

Calcium ions (Ca) have been adopted as a secondary messenger and represent a versatile signaling molecule in eukaryotic organisms (Dodd *et al.*, 2010). It is involved in several plant physiological processes, acts as an indicator and translator, and is present in sensory proteins that decode specific stimuli (Batistič and Kudla, 2012). Low levels of Ca in the NS increase AOEs levels. However, within the cellular structure, non-optimal concentrations of Ca cause fruit damage; for example, “blossom end rot” in tomato results in the total loss of the product.

Magnesium (Mg) is involved in vital plant functions such as 1) phosphorylation for ATP formation in chloroplasts, photosynthetic fixation of carbon dioxide, protein synthesis, chlorophyll formation, phloem restoring, partitioning and assimilation of photosynthetic products, generation of oxygen reactive forms and photo-oxidation of leaf tissues and activation of enzymes such as ribulose-1.5-diphosphate carboxylase (RuBP) (Cakmak and Yazici, 2010). It is also part of the molecular structure of chlorophyll, and its absence causes severe plant stress that leads to increased AOEs production. In certain cases, the absence of Mg in the NS reduces carotenes and increases AOEs, such as superoxide dismutase (SOD), peroxidase (POD) and ascorbate peroxidase (APX) (Tewari *et al.*, 2006).

Likely, sulfur (S) is converted to cysteine in plants, the main substrate for the synthesis of compounds that contain S (Nikiforova *et al.*, 2005), such as methionine, glutathione, nicotinamide, phytochelatins and phytoalexins (Rausch and Wachter, 2005).

Plant Nutrition with Micronutrients

The application of micronutrients in plants has been strengthened, and the effects of these micronutrients on SM production depend mainly on the concentration and type of element (Table 4). Similar to macronutrients, inaccurate concentrations of micronutrients can cause crop damage related to toxicity because plants require micronutrients in small amounts.

Iron (Fe) is an essential element and its absence reduces productivity in photosynthetic organisms (Jeong and Guerinot, 2009). Fe is a co-factor for proteins involved in cellular processes such as respiration, photosynthesis and cell differentiation (Broadley *et al.*, 2012). It is required by AOEs because it catalyzes the reactions of electron transfer (Halliwell, 2006).

Copper (Cu) is part of the structure of certain proteins, mainly those involved in photosynthesis (plastocyanins) and respiration (cytochrome oxidase) and in the electron transport chain (Pilon *et al.*, 2006).

Zinc (Zn) is the only metal present in six enzyme categories: oxidoreductases, transferases, hydrolases, lyases, isomerases and ligases (Auld, 2001). Zn is a co-factor of these enzymes groups involved in respiration, photosynthesis and hormone biosynthesis (Broadley *et al.*, 2007).

The role of boron (B) in plants include sugar transport, cell wall synthesis and integrity, lignification, carbohydrate metabolism, ribonucleic acid (RNA), indoleacetic acid, phenolic metabolism, and it is incorporated in the cellular membrane (Ahmad *et al.*, 2009).

Molybdenum (Mo) is necessary in biochemical and physiological processes (Sun *et al.*, 2009) and is an essential component of mononuclear enzymes, metabolic processes and cycles of carbon, N and S (Liu *et al.*, 2010). At high concentrations, Mo can induce the production of SMs (Yu *et al.*, 2012).

Manganese (Mn) is involved in the metabolism of approximately 35 enzymes (Hebbern *et al.*, 2009), and it acts as a metal catalyst and protein activator (Barber, 2003). Manganese participates in the following processes: activation of enzymes involved in N metabolism (i.e., glutamine synthase and arginase), gibberellic acid and RNA biosynthesis, polymerase activation and fatty acids biosynthesis (Hansch and Mendel, 2009).

Use of Non-essential and Beneficial Elements

Beneficial elements cause growth retardation, enzymatic activity changes (Gopal and Rizvi, 2008) and photosynthesis disorders (Ganesh *et al.*, 2008). Beneficial elements are used to increase SMs; for example, the content of α-tocopherol, asparagine and tyrosine (Hédiji *et al.*, 2010), isocitrate dehydrogenase (ICDH), citrate synthase (CS), fumarase, malate dehydrogenase (MDH) and phosphoenolpyruvate carboxylase (PEPC) increases in tomato plants (López-Millán *et al.*, 2009) when 100 µM Cd is used in the NS. Hibiscus plants grown in soil with 20 mg kg^{-1} cobalt (Co), showed increased anthocyanins, and a similar effect occurs when 50 ppm nickel (Ni) is applied in the same crop (Aziz *et al.*, 2007). In bean plants, 0.06 mM mercury (Hg) in the SN increases the contents of α-tocopherol, ascorbic acid and retinol, and this response appears to be concentration dependent (Zengin and Munzuroglu, 2005). Silicon (Si) is often used as a beneficial elements in various crops because its effectiveness. Si increases biomass (Eneji *et al.*, 2008) and provides resistance against plagues (Savvas *et al.*, 2009) and heavy metals (Nwugo and Huerta, 2008). Si induces AOEs production (Soylemezoglu *et al.*, 2009), such as SOD and catalase (CAT), which protect plant tissues (Al-Aghabary *et al.*, 2004). In alfalfa plants with an NS that contains 1 mM Si, the content of SOD, CAT and POD increases and glutathione reductase (GR) decreases (Wang *et al.*, 2011a). Selenium (Se) is another BE; however, its role has not been completely defined (Malik *et al.*, 2010). Se promotes resistance to abiotic factors (Yao *et al.*, 2009). For example, when Se is used in the NS of soybean at a concentration of 5 µM, an increase in SOD, CAT, APX and glutathione peroxidase (GPX) activities is observed (Malik *et al.*, 2012).

Use of Rare Elements

Rare elements (REs) are homogeneous elements with similar chemical properties and include lanthanides, scandium and yttrium. Their use in agriculture is currently increasing, and mixtures of REs can be found in the market. These REs increase SOD, POD, total phenols (TP) and carotenoid content in corn (Challaraj *et al.*, 2010a), modify plant enzymatic activity (Gopal and Rizvi, 2008), and promote the activation of antioxidant mechanisms such as AOEs or SMs. The effect of rare elements on plants varies depending on the element and its dosage. For instance, cerium (Ce), lanthanum (La) and neodymium (Nd) can increase the yield and fruit quality in certain concentrations and in some crops (Wang *et al.*, 2007a); however, can cause toxicity in high concentrations.

In bean plants, gradually increasing La concentrations of the root NS (0.25, 0.5, 1, 2, 4, 8 and 12 mg L^{-1}) results in increase of SOD, APX and GPX (Wang *et al.*, 2011b). Taxol content increase when 1 mM of Ce^{4+} is applied to cells of *Taxus cuspidata* (Yang *et al.*, 2009). In rice, the use of Ce^{4+} in the NS leads to an increase of SOD, CAT and malonyldialdehyde (MDA) (Xu and Chen, 2011). In radish plants, the use of terbium (Tb^{3+}) (5 mg L^{-1}) increases the activity of ascorbate and decreases guaiacol content (Wang *et al.*, 2009).

Rare elements also increase the absorption of ions that may be beneficial for SM synthesis. For example, Ce^{3+} usage results in an increase of K, Mg, Ca, Cu, Fe and Mn content (Wang *et al.*, 2008), and are applied to infertile soils to improve the availability of essential elements. Similar to beneficial elements, the increased dosage of rare elements can be toxic to plants.

Towards a New Cocktail of Necessary Nutrients (CNN)

In current agricultural practices, NS with essential elements, and the optimal EE concentrations required to develop NS for commercial crops are known and have produced increases in yield. However, to develop horticultural functional foods, new techniques that produce higher contents of SMs in crops are necessary. One method is to vary EE concentrations and another method incorporates non-essential elements such as rare elements in the nutrient solution.

Plants can absorb non-essential elements, and if present in an inadequate range, either in the soil or NS,

Table 3: Effect of different concentrations of macronutrients in plants for the production of secondary metabolites

Element	Plant	Doses	Effect	Reference
N	Broccoli	0	Flavonoids ↑	Jones *et al*., 2007
	Cabbage	0	Flavonoids ↑	WeiFeng, 2009
	Lettuce	0	Flavonoids ↑	Chiesa *et al*., 2009
	Olive tree	0	Flavonoids ↑	Fernández-Escobar *et al*., 2006
		9.58 meq L^{-1}	Mannitol ↑	Boussadia *et al*., 2010
	Tomato	0	Flavonoids ↑	Simonne *et al*., 2007
		3.25 mM	Carotenoids ↓	Khavari-Nejad *et al*., 2013
P	Lentil	0	PC and anthocyanins ↑	Sarker and Karmoker, 2011
	Tomato	0.7 mM	β- carotene and xanthophyll ↓	Khavari-Nejad *et al*., 2013
K	Millet	0	CAT, GPX and APX↑	Heidari and Jamshidi, 2011
	Tomato	4 mM	Carotenoids ↓	Schwarz *et al*., 2013
	Basil	5 mM	Phenols, rosmarinic acid and anthocyanins ↑	Nguyen *et al*., 2010
	sunflower		soluble solids ↑	
		25 Kg ha^{-1}	SOD, CAT and GPX ↑	Soleimanzadeh *et al*., 2010
Ca	Millet	0	POD and CF ↑	Finger *et al*., 2006
		5 mM	PC ↓	
	Tomato	0.1 mM	SOD and DAR ↑	Mestre *et al*., 2012
			CAT, APX and GR ↓	
	Eggplant	0.5 meq L^{-1}	Total phenols and PPO ↑	Pratima *et al*., 2002
	Tobacco	5 mM	Total phenols, POD and PPO ↑	Ruiz *et al*., 2003
	cherry	80 mM	Phenols, flavonoids, anthocyanins and ascorbic acid ↑	Aghdam *et al*., 2013
Mg	blackberry	0	Carotenoids ↓	Tewari *et al*., 2006
	Sunflower		SOD, POD and APX ↑	
	Lettuce	0	Glutathione, SOD, APX, GPX and CAT	Chou *et al*., 2011
		60 mg L^{-1}	Lactucopicrin ↑	Seo *et al*., 2009
S	Arabidopsis	0	β-alanine, putrescence, raffinose, glutamine, α- tocopherol and β-sitosterol ↑	Zhang *et al*., 2011a
	Beans	0	Carotenoids ↑	Juszczuk and Ostaszewska, 2011
	Peas	200 mg $plant^{-1}$	saccharose ↑	Scherer *et al*., 2006

PC: phenolic compounds; CAT: catalase; SOD: superoxide dismutase; GPX: glutathione peroxidase; APX: ascorbate peroxidase; POD: peroxidase; DAR: ascorbate reductase; GR: glutathione reductase; PPO: polyphenol oxidase. ↑ represents an increase; ↓ represents a decrease

Table 4: Effect of different concentrations of micronutrients on secondary metabolite production in plants

Element	Plant	Doses	Effect	Reference
Fe	Rapeseed	0	AP, POD, SOD and AA ↑	Tewari *et al*., 2013
			CAT ↓	
	Plum	0	Asparagine, alanine, glutamine, and organic acids ↑	Jiménez *et al*., 2011
			SOD and APX ↑	
	sweet potato	9 mmol L^{-1}	CAT ↓	Adamski *et al*., 2012
Cu	Poppy	2 mmol L^{-1}	Carotenoids ↑	Cambrollé *et al*., 2011
	grapevine	2.5 mmol L^{-1}	Carotenoids ↓	Cambrollé *et al*., 2013
	mustard seed	50 µM	Ascorbate and SOD ↑	Feigl *et al*., 2013
	rice	50 µM	Ascorbate and SOD ↑	Thounaojam *et al*., 2012
		100 µM	GPX, APX and GR ↑	
Zn	wheat	3 mM	POD, CAT and APX ↑	Li *et al*., 2013
	Beetroot	50 µM	MDH, PEPC, ICDH and CS ↑	Sagardoy *et al*., 2011
	Tomato	100 µmol L^{-1}	Carotenoids, APX and GR ↑	Cherif *et al*., 2011
B	Tobacco	0	GDH, glucose and fructose, organic acids, phenols and amino acids ↑	Beato *et al*., 2011
	Orange tree	2.5 µM	Carotenoids, saccharose, DHAR and CAT ↑	Han *et al*., 2008
	Carrot	5 µM	AA ↓	Eraslan *et al*., 2007
	Corn	4 mM	SOD and CAT ↑	Esim *et al*., 2013
			POD ↓	
	Linen	450 mM	PAL, PPO and POD ↓	Heidarabadi *et al*., 2011
Mo	*Glycyrrhiza uralensis* Fisch	5.2 mg L^{-1}	GA and squalene ↑	Wang *et al*., 2013
	Tomato	0.5-1 mg kg^{-1}	Yield	Sandabe and Bapetel, 2008
Mn	Clover	5.2 µM	GPX ↑	Dorling *et al*., 2011
	Pea	50 µM	GOGAT, CAT and APX ↑	Gangwar *et al*., 2010
	Grape	30 mM	PPO, CAT and POD ↓	Mou *et al*., 2011

AP: alkaline protease; POD: peroxidase; SOD: superoxide dismutase; AA: ascorbic acid; CAT: catalase; APX: ascorbate peroxidase; GPX: glutathione peroxidase; GR: glutathione reductase; MDH: malate dehydrogenase; PEPC: phosphoenolpyruvate carboxylase; ICDH: isocitrate dehydrogenase; CS: citrate synthase; GDH: glutamate dehydrogenase; DHAR: dehydroascorbate reductase; PAL: Phenylalanine ammonia-lyase; GA: glycyrrhizic acid; PPO: polyphenol oxidase; GOGAT: oxoglutarate aminotransferase glutamate. ↑ represents an increase; ↓ represents a decrease

stress will result in ROS production. Under normal and primarily under stress conditions, ROS are detoxified by a group of enzymatic antioxidants, such as SOD, APX and CAT, and non-enzymatic antioxidants (Fig. 1), such as

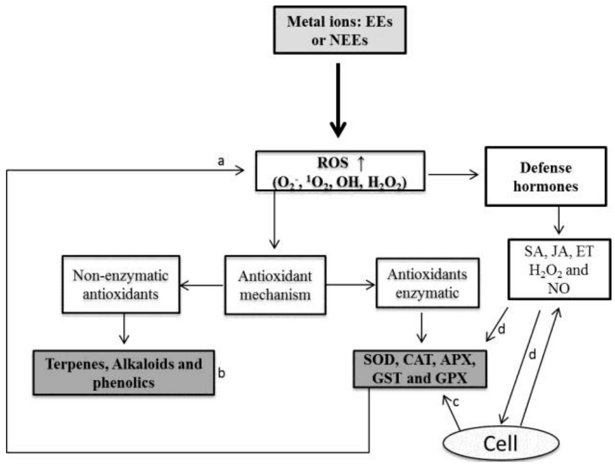

Fig. 1: Metal ion signaling pathway and specific response mechanism: a) degradation/accumulation; b) activation/deactivation of compounds; c) activity increase or decrease; d) regulation of antioxidant enzymes. EEs: essential elements; NEEs: non-essential elements; ROS: reactive oxygen species; SOD: superoxide dismutase; CAT: catalase; APX: ascorbate peroxidase; GST: glutathione S-transferase; GPX: glutathione peroxidase; SA: salicylic acid; JA: jasmonic acid; ET: ethylene; H_2O_2: hydrogen peroxide; NO: nitric oxide

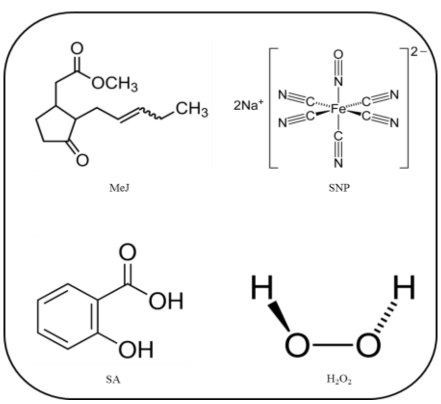

Fig. 2: Elicitor chemical structures, MeJ: methyl jasmonate; SNP: sodium nitroprusside, a donor of nitric oxide; SA: salicylic acid and H_2O_2: hydrogen peroxide

ascorbic acid, glutathione, carotenoids and tocopherols (Miller, 2010).

Non-essential elements (mainly Res) activate plant response genes, alter plasmatic membrane potential (Kenderesová *et al*., 2012), and induce ROS and Ca-signaling (Rodrigo-Moreno *et al*., 2013) in response to ion effects. The production of antioxidant defenses triggered by the presence of certain non-essential elements depends on the type and concentration of the element but also on the plant species (Rodríguez-Serrano *et al.*, 2009). Thus, the antioxidant mechanism can be inhibitory or stimulatory (Schützendübel and Polle, 2002).

It has been shown that if non-essential elements are present in the soil or NS, can be absorbed by plants. Sheppard *et al.* (2010) found the following non-essential elements in tomato fruit: Ag, As, Ba, Cd, Ce, Cl, Co, Cr, Cs, La, Li, Mo, Na, Nb, Nd, Ni, Pb, Pr, Rb, Sb, Se, Sm, Sn, Sr, Tb, Th, Tl, U, V, Y, Yb and Zr. Similar results were also found by Matos-Reyes *et al.* (2010), Demir *et al.* (2010) and Bressy *et al.* (2012).

Current common practice includes cultivating plants with recipes that contain non-essential elements in the NS. In China, rare elements have been used to increase the quality and yield of crops for several years. However, it is important to consider the adverse effect that NEEs have on crops because their optimal concentration and time of application and effect on each type of crop is currently unknown.

Non-essential elements most likely cause a hormetic effect, which is a plant response to doses with low dose-stimulation and high doses-inhibition of growth (Poschenrieder *et al.*, 2013). By including NEEs such as As, Se, Cr, Al and Pb in the NS, yield increases, and it is likely stimulation in an adaptive compensation process (Poschenrieder *et al.*, 2013). Studies have suggested stress-induced growth mainly because of excess metals; however, few studies have analyzed the physiological state and molecular mechanisms of the stimulant response to accurately assess the action of ions in the plant.

Based on these data, it may be possible to develop a recipe or "cocktail" of nutrients containing essential and non-essential element to increase plant SMs without affecting the yield. Physiologically, ROS can be induced in the plant to activate antioxidant mechanisms, thus generating functional foods. However, it is difficult to calculate the amount of SMs to induce at the expense of yield because an increase in ROS is usually accompanied by plant damage.

NEEs and Elicitors are Necessary for SMs Production

Several methods exist that increase SMs in plants, such as using elicitors (Table 5). Chemical elicitors, including SA, JA, NO, and MeJ, may interact with receptors in plants, activating defense response **(**Ruiz-García and Gómez-Plaza, 2013). For instance, NO is involved in abiotic stress, as are heavy metals (Zheng *et al*., 2008). NO also interacts with ROS in various ways and may serve as an antioxidant and ROS scavenger during environmental stress (Zheng *et al*., 2010). Additionally, elevated NO down regulates K^+/Cl^- influx, and promotes K^+/Cl^- efflux and Ca^{2+} release during stomatal closure (Sokolovski and Blatt, 2004). NO regulates mineral absorption, particularly at concentrations of 50 µM, and enhances shoot uptake of Mg, Cu, Ca and Fe (Liu *et al*., 2015). Moreover, NO regulates genes related to plant growth and ion absorption (Besson-Bard *et al*., 2009). MeJ is a naturally occurring plant growth regulator that modulates chlorophyll degradation and anthocyanin biosynthesis (Ruiz-García *et al*., 2012). MeJ has been also involved in NH_4^+ accumulation in rice leaves (Hung and Kao, 2007). NH_4^+ is released through the action of PAL, the

Table 5: Effects of chemical elicitors on plant antioxidant enzymes/secondary metabolites

Plant	Elicitor (dose)	Effect	Reference
Tomato	NO: 100 µM	Chelate reductase ↑	Graziano and Lamattina, 2007
Tomato	NO: 20 µM	CAT, POD, SOD and APX ↑	Zhao *et al*., 2011
Tomato	NO: 100 µM	Chelate reductase ↑	Graziano and Lamattina, 2007
Tomato	NO: 20 µM	CAT, POD, SOD and APX ↑	Zhao *et al*., 2011
Tomato	SA: 100 µM	CAT and POD ↑	Ortega-Ortiz *et al*., 2007
Tomato	SA: 10 mM	Vitamin C and °Brix ↑	Javaheri *et al*., 2012
Tomato	SA: 500 µM	Soluble solids ↑	Yildirim and Dursun, 2009
Tomato	MeJ: 0.1 µM	Quercetin ↑	Horbowicz *et al*., 2011
Strawberry	MeJ: 300 µM	Resveratrol ↑	Wang *et al*., 2007c
Cucumber	H_2O_2: 1.5 mM	SOD, GH and APX ↑	Zhang *et al*., 2011b
Cucumber	H_2O_2: 1.5 mM	POD, DHAR and APX ↑	Gao *et al*., 2010

H_2O_2: hydrogen peroxide; NO: nitric oxide; SA: salcylic acid; MeJ: methyl jasmonate; POD: peroxidase; CAT: catalase; APX: ascorbate peroxidase; SOD: superoxide dismutase; GH: glutathione; DHAR: dehydroascorbate reductase.↑ represents an increase; ↓ represents a decrease

Table 6: Production of bioactive compounds and/or antioxidant enzymes by elicitation in plants grown in soil, *in vitro* or in substrate

Cultivation Medium	Plant	Elicitor	Bioactive Compounds/AOEs(difference from control)*	Reference
Soil	*Artemisia annua*	2 mmol NO	Total chlorophyll, artemisinin content, POD, SOD and CAT ↑	Aftab *et al*., 2012
Soil	*Brassicacampestris*	50 mmol H_2O_2	CAT and MDA↑	Chun-Yan *et al*., 2007
Soil	*Glycine max*	2% (SO_2+NO_2)	PC ↑	Hamid and Jawaid, 2009
Soil	*Lycopersicon esculentum*	0.5 mM SA	Chlorophyll ↑	Yıldırım and Dursun, 2009
Soil	*Lycopersicon esculentum*	10^{-4} M SA	Lycopene and vitamin C =	Javaheri *et al*., 2012
Soil	*Syzygium samarangense*	5 mM H_2O_2	Flavonoids, anthocyanins, total phenols and carotenoids↑	Khandaker *et al*., 2012
Soil	*Zea mays*	100 ppm SA	Chlorophyll ↑	Rao *et al*., 2012
Substrate: UNS	*Lycopersicon esculentum*	100 µM SNP	Proline, chlorophyll, MDA, CAT, LOX, APX and GPX =	Kazemi, 2012
In vitro	*Fagopyrum esculentum*	10^{-6} M MeJ	Acids: caffeic, gallic, syringic, feluric, coumaric acid, and quercetin =	Horbowicz *et al*., 2011
In vitro: NS	Cucumis sativus	100 M SNP	SOD, CAT, GPX, APX, DHAR, AsA and GSH =	Lin *et al*., 2012
In vitro	*Physalis peruviana*	0.1 mg L^{-1} JA or 1 Mm SA	4□- hydroxy-withanolides E =	Piñeros-Castro *et al*., 2009
Substrate: UNS	*Glycine max*	100 µM SA or SNP	Flavonoids, anthocyanins, LOX and SOD =	Simaei *et al*., 2012
In vitro	*Lycopersicon esculentum*	1 mM SA	Total chlorophyll and carotenoids totals =	Shahba *et al*., 2010
Substrate: UNS	*Lycopersicon esculentum*	100 µM SNP	SOD, POD, CAT y APX =	Zhang *et al*., 2009
Substrate: UNS	*Cucumis sativus*	1.5 mM H2O2	SOD, CAT, GSH-PX, GR and AsA =	Zhang *et al*., 2011b

*Bioactive compounds/enzymes efficiency differences, in different culture medium (significant difference p<0.05). Note: no elicitor was applied al control. AOE: antioxidant enzyme; NO: nitric oxide; SA: salicylic acid; MeJ: methyl jasmonate; JA: jasmonic acid; PC: phenolic content; SOD: superoxide dismutase; CAT: catalase; SO_2: sulfur dioxide; NO_2: nitrogen dioxide; NS: nutrient solution; UNS: universal nutrient solution; POD: peroxidase; GSH-PX: glutathione peroxidase; SNP: Sodium nitroprusside (NO donor); LOX: lipoxygenase; MDA: malondialdehyde; GPX: glutathione peroxidase; DHAR: dehydroascorbate reductase; GSH: glutathione; APX: ascorbate peroxidase; AsA: ascorbic acid; ↑ represents an increase; ↓ represents a decrease; = represents the control effect

first enzyme in the phenylpropanoid biosynthesis pathway (Hahlbrock and Grisebach, 1979).

Plants produce signaling molecules such as SA, JA and NO, and the content of these molecules increase when the plant is under stress. Compounds such as chitosan, harpin and 1-methylcyclopropane have been also identified, and provide benefits when exogenously applied to the plant. These benefits include protection against plague or diseases or support of metabolism. These compounds mimic the action of signaling molecules such as SA and JA and their derivatives. These also interact with plant receptors that activate defense mechanisms, such as TP and flavonoids (Liu *et al.*, 2005). Signaling molecules such as methyl jasmonate (MeJ), SA, H_2O_2 and NO currently used exogenously to increase the SMs content in crops, and these molecules are known to regulate the production of AOEs and SMs (Fig. 1). These molecules have different characteristics (Fig. 2), but in some crops, these produce similar effects (see Table 5).

In hydroponic crops, the increased SMs in elicited plants are barely noticeable. However, the increase of SMs is significant when elicitors are used in plants growing in soil or compost (Table 6), and Turra *et al.* (2011) showed that compost contains REs. The increase of SMs may occur because soil contains certain NEEs and REs that helps to activate SM synthesis pathways. Rare elements are involved in plant metabolism and increase ion absorption, protein synthesis, chlorophyll *a* and *b* content, plant yield, and enzyme activity (POD and SOD) (Challaraj *et al.*, 2010b).

Plants respond differently to elicitors i.e., certain SMs are activated in certain plants and the same SMs can be deactivated in others (Table 6). Signal perception is the first step in the elicitation process and leads to a transduction cascade by which plants respond to stimuli and activate kinases and produce ROS, ion flow and cytoplasm acidification (Vasconsuelo and Boland, 2007). However, if the plant is elicited and the necessary material (some chemical element) is not found in the soil or NS, the expected response to the stimuli will not occur. When the plant is elicited, one of two actions occurs: certain elements classified as non-essential are present in the ion flux, and they can stimulate SM synthesis; or NEEs present in a minimum quantity exert pressure in the cell that favors a secondary metabolism pathway. Plants cultured in substrates or *in vitro* with NS, even when an elicitor is used, do not indicate an increase in SMs (compared to the non-elicitor control), which may result from missing a certain metabolite biochemical pathway chemical element that is necessary for activation (Table 6). However, the elicitation of plants grown in soil usually produce a favorable response in terms of SM production, which may be explained by the presence of NEEs, such as EBs or REs, in soils, and these NEEs participate directly and indirectly in the production of SMs.

Conclusions

Plants generate SMs to protect cells from the harmful effects caused by ROS, and SMs also have beneficial health effects. OA produces horticulture products with greater amounts of SMs, but such agricultural techniques are inadequate to satisfy the global demand, whereas the NS used in CA are insufficient to produce fruits and vegetables with high nutraceutical value. The use of a technique that may increase plant SMs, such as varying the ionic EE ratio or adding NEEs in the NS, results in lower yield. Applying only elicitors, such as MeJ, NO and SA, forces the plant to produce SMs but causes lower yields. Certain NEEs can be included in the NS, and elicitors can be applied to plant foliage. Thus, NEEs could enhance ROS production and elicitors could activate antioxidant mechanisms. Thus, the production of ROS and bioactive compounds, such as terpenes, alkaloids and phenols, would be equilibrated.

According to reports found in the literature, the application of elicitors and the presence of NEEs in the NS or soil are necessary to increase and potentiate SM production. Therefore, the coordinated combination of these two techniques is required for the production of SMs. However, ions must be identified that can be added to the NS without being transferred to the edible part of the plants or concentrations of such ions must be determined that are low enough to avoid health damage. In addition, this new cocktail must not have a negative impact on the environment. Thus, the new NS should increase yield and produce food with higher nutraceutical qualities capable of preventing human diseases.

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