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Glossary

ABA: Abscissic acid
ACP: Agroecological Crop Protection
AsA: Ascorbic Acid
ASC: Reduced AsA
ATP: Adenosine Tri Phosphate
DHA: De Hydro Ascorbic acid (Oxidized AsA)
EC: Electrical conductivity
Eh: Redox Potential
ET: Ethylene
G x E x M x P Interactions: Genotype x Environment x Management x Pest *sensu lato* interactions
GSH: Reduced Glutathione
GSSG: Oxidized Glutathione
ISR: Induced Systemic resistance
JA: Jasmonic Acid
NADPH: Reduced form of Nicotinamide Adenine Dinucleotide Phosphate
NO: Nitric Oxide
pH: Hydrogen potential
RAS: Root-Adhering Soil
ROS: Reactive Oxygen species
SA: Salicylic Acid

SAR: Systemic Acquired Resistance
SOM: Soil Organic Matter

Introduction

"Research is to see what everybody has seen, and think what nobody has thought" Albert Szent-Gyorgyi, Nobel prize laureate.

Since the late 19th century and until quite recently, medical microbiology was based on the assumption that a few microorganisms are pathogens while most are not. Although this binary view has now been strongly criticized, and considered untenable (Méthot and Alizon 2014), it is generally recognized that the interaction of the three factors of the host, pathogenic agent, and environment (plant disease triangle) determine whether a disease develops or not. Thus, plant stage of growth, pathogen virulence, and environmental changes result in a dynamic relationship over space and time (Agrios et al. 2005). Variations in any of the three interacting factors could significantly alter expected patterns of disease spread and development (Farber and Mundt 2017). Even if a host plant and a potential virulent pathogen are present in a certain area, serious disease epidemics will not occur unless the environment fosters their development (Bateman 1978; Keane and Kerr 1997; Agrios et al. 2005). Abiotic stresses can dramatically alter the outcome of plant-pathogen interactions and, depending on the pathosystem and stress intensity, the stress may enhance or reduce diseases. Even mild, episodic stresses can predispose plants to levels of pathogen inoculum that would not be damaging in the absence of the stress (Bostock et al. 2014). Environmental stresses also influence overall plant tolerance to insect pests (Louda and Collinge 1992).

The idea that a pathogenic organism is essentially a static or unchanging entity distinct from other types of microbes would mean that such a microorganism possessed an inherent capacity to cause disease in hosts. Pathogenicity is a dynamic feature of an interaction between a host and microbes as influenced by the environment (Agrios et al. 2005; Méthot and Alizon 2014). The role of beneficial or commensal microorganisms in plant health is now widely acknowledged, both in soil (especially the rhizosphere microbiome), and in leaves (the phyllosphere microbiome; Andrews and Harris 2000; Paszkowski 2006; Leveau 2019; Teixeira et al. 2019; Yu et al. 2019). Although knowledge of plant–plant and plant–microbe interactions has been greatly extended in recent years, the chemical communication leading to defense priming is not well-understood (Mhlongo et al. 2018) and highlights the need to further elucidate microbial functions and interactions (Toyota and Shirai 2018). Thus, two of the major questions remaining are "what makes a commensal or an opportunistic microorganism become pathogenic?" and "how do pathogenic microorganisms impact plant health?"

Understanding the impacts of stresses on plant health is, therefore, important for obtaining optimum crop production efficiency. Stress is defined as "a sudden change in the environment that exceeds the organism's optimum to cause homeostatic imbalance which must be compensated for" (Kilian et al. 2012). Homeostasis is considered an underestimated focal point of ecology and evolution (Giordano 2013) although "cellular redox homeostasis in plants" is understood to be central to the plant stress defense system (Anjum et al. 2016). More generally, Eh and pH signaling and homeostasis should be regarded as key processes in many aspects of plant biology (Rengel 2002; Foyer and Noctor 2016) since plants function in a specific Eh-pH spectrum and rely on various processes to ensure intracellular homeostasis (Husson 2013). Therefore, the redox balance in both the host and pathogen may be considered a key battlefield in determining the outcome of pathogen attack (Williams et al. 2011).

Indeed, redox potential (Eh) and hydrogen potential (pH) regulation (Eh-pH, maintenance of extra- and intra-cellular redox states) are key to both plant-pathogen (bacteria, fungi, oomycetes, and viruses) and plant-animal pest (especially insects) interactions through:

i) upstream regulation by maintaining the plant unfavorable to pest or pathogen attacks: via development of physical barriers (wax, suberin, cutin, hardened cell walls, silica, etc.) or regulation of natural openings such as stomata (Chen and Gallie 2004; Foyer 2005; Liu et al. 2007; Pollard et al. 2008; Samuels et al. 2008; Pastor et al. 2013; Coskun et al. 2019);

ii) downstream regulation after pest or pathogen attack, mainly through oxygen burst by plants and responses of pathogens-pests (Mehdy 1994; Lamb and Dixon 1997; Kuzniak et al. 2005; Kuzniak 2010; Lehmann et al. 2015; Qi et al. 2016; González-Bosch 2018; Segal and Wilson 2018) to include

iii) control of Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR) (Fobert and Després 2005; Spoel and Loake 2011; Frederickson Matika and Loake 2013) in a complex interaction with plant hormones (Srivastava et al. 2017).

In addition, sensing of the host plant by pests and pathogens can be influenced by the plant’s Eh-pH state in different ways, including emission of volatiles (Wei et al. 2014), redox associated mechanisms as in parasitic weeds (Yoder 2001), osmotic changes, and alteration of magnetic and electric fields emitted by plants which are recognized by insects (Newland et al. 2008; Greggers et al. 2013; Clarke et al. 2013), nematodes (Shapiro-Ilan et al. 2012; Ilan et al. 2013) and oomycetes (van West et al. 2002).

Cook and Baker (1983) defined disease suppressive soils as soils in which either: i) the pathogen does not establish or persist, ii) the pathogen establishes but causes no damage or iii) the pathogen causes some damage but the disease becomes progressively less severe even though the pathogen persists in soil. Two types of soil suppressiveness are known: i) general suppression, which is due to nutrient status and activity of the total microbial biomass in soil and is not transferable between soils, and ii) specific suppression owing to the activity of individual or selected groups of microorganisms and is transferable (Weller et al. 2002; Schlatter et al. 2017). While soil suppressiveness is mainly derived from the biological functions of soils (Toyota and Shirai 2018; Steinberg et al. 2019; De Corato 2021), there is plenty of evidence showing the role of both biotic and abiotic factors in disease suppression (Schneider 1982). Chemical and physical components of soil, including pH, organic matter and clay content, can operate in the suppression of plant diseases directly or indirectly through their impact on soil microbial activity (Smiley and Cook 1972; Chandrashekara et al. 2012).

The definition of soil health or quality generally includes a range of physical, chemical and biological soil properties, such as soil type, organic matter content, nutrient cycling, biological activity and soil structure, all of which impact and are impacted by soil Eh and pH (Van Bruggen and Semenov 2000; Cardoso et al. 2013; Moebius-Clune et al. 2017; Bünemann et al. 2018; Husson et al. 2018b). Methods developed to assess plant health based on the underlying stress level measured as chlorophyll fluorescence or other photo-oxidative stress markers (including photosynthetic pigments, Photosystem II efficiency, Reactive Oxygen Species -ROS-, reactive carbonyl species, antioxidant systems) are all related to Eh and pH (Husson et al. 2018a).

A previous interdisciplinary review provided evidence that Eh and pH are major drivers of soil-plant-microorganism systems (Husson 2013). This review bridged different disciplines such as soil sciences, plant physiology and microbial ecology and proposed a conceptual framework for further studies of soil-plant-microorganism functioning. The framework was based on the hypothesis that plants function physiologically within a specific internal Eh-pH range and that, along with microorganisms, they alter Eh and pH in the rhizosphere to ensure homeostasis at the cell level. Based on that review and subsequent works, we propose a conceptual model of soil-plant-microorganism system functioning driven by Eh and pH (Fig. 1):

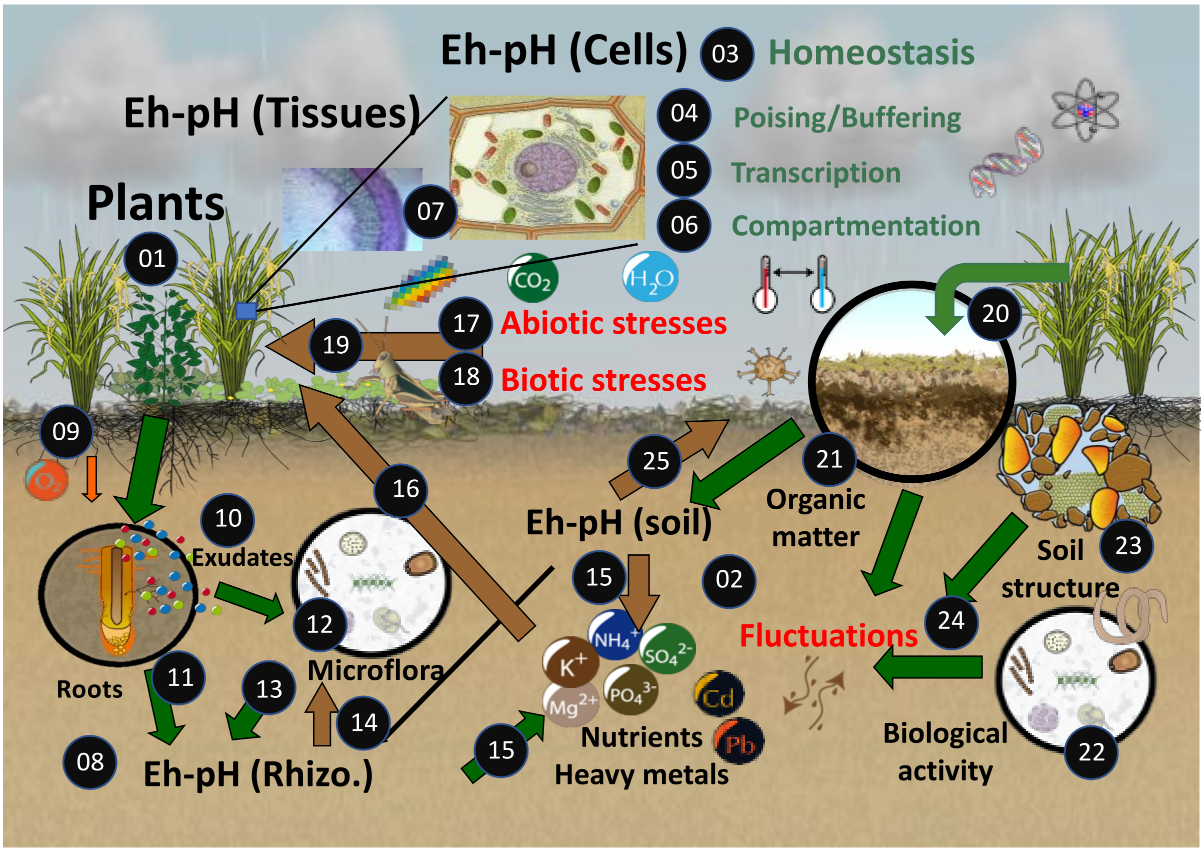


Fig. 1: The Eh-pH driven conceptual model of how the soil-plant-microorganism system could function to indicate the key role of dynamic maintenance of Eh-pH homeostasis for soil and plant health. Plants (01) grow in soil with highly fluctuating Eh-pH characteristics (02). To insure the necessary Eh-pH homeostasis at the cellular level (03), they regulate Eh and pH at short term through cascades of chemical and buffering reactions (04). When short-term buffering capacity is exceeded, there is a response at the transcript level (05). Eh-pH homeostasis is also sustained through metabolic compartmentation in the various organelles inside a cell that function at specific levels (06), and the cells evacuate the highly oxidized or reduced products from the cytoplasm through the cell walls (07). Another important process to achieve internal Eh-pH homeostasis is regulation of the external Eh-pH at the rhizosphere level (08). Under highly reduced (anaerobic) conditions, some plants (such as rice) have the ability to pump oxygen through aerenchyma cells to raise Eh in the

rhizosphere (09). Under aerobic (oxidizing) conditions, plants exudate a wide range of compounds (10). These exudates modify rhizosphere Eh-pH (11), stimulate and feed specific microorganisms (12), which further alter rhizosphere Eh-pH conditions (13). In return, soil, and especially rhizosphere, Eh-pH will largely determine the composition of the microflora (14) and the solubility and absorption of nutrients and heavy metals (15). Plant nutrition affects plant Eh-pH, especially nutrient deficiencies and toxic elements, which results in oxidative stress (16). Similarly, abiotic stresses (temperature, water, CO_2, light, etc. (17) lead to oxidative stress in the plant which leads to higher susceptibility to pests and plant pathogens. These biotic stresses (18) also lead to oxidative stress in the plant (19). In the medium to long term, plant residues (20) feed the soil microbes, alter soil organic matter (21), determine biological activity and diversity (22) and influence soil structure (23). Via these interactions, soil pH is buffered towards neutral values and soil Eh is lowered and buffered (24). Finally, soil microbes and Eh affect the fate of soil organic matter by increasing mineralization and reducing humification under oxidized conditions (25).

Changes in Eh-pH levels in plants can result from interactions among a large range of factors (edaphic, climatic and biotic). In this model, the effects of multiple stresses induce oxidative stress in the plant and result in a specific Eh-pH state. Under favorable conditions, plants will be able to sustain their homeostasis through an efficient photosynthetic process which uses solar energy to produce energy rich-glucose by combining CO_2 with H_2 from water. Oxidative stresses linked to unfavorable conditions (extreme pH, nutrient deficiency, NO_3^- absorption, metal toxicity, reduction of N, Fe, Mn, or S, pollution, low light, water stress, extreme temperatures, biotic stresses, etc.) require responses that represent an energy cost for the plant. The higher the stress, the higher the cost, creating a vicious circle where the more the plant spends energy to sustain cell homeostasis, the less energy it has to produce leaves; the smaller the leaf area, the lower the photosynthetic capacity; and the lower the photosynthesis, the lower the capacity to sustain Eh-pH homeostasis. When the various stresses overpass the plant capacity to sustain cell homeostasis, it leads to a strong imbalance that can cause severe consequences, as for example, increased susceptibility to pests and pathogens and ultimately plant death.

This paper proposes a novel conceptual framework of plant interactions with pests and pathogens that is based on the following hypotheses: soil and plant health are strongly related to Eh-pH homeostasis and plants become susceptible to pest and pathogen attacks when imbalanced Eh-pH conditions in plant compartments correspond to the specific Eh-pH conditions at which the various pests and pathogens thrive. The conceptual framework is based on four sub-hypotheses:

i) Pests and pathogens thrive in specific Eh-pH niches, i.e. spots in which the individuals of a species are exposed to a range of environmental conditions that allow microbial persistence and utilization of present resources. Species-specific phenotypic characteristics determine if a species can be found in a certain ecological niche and how it interacts with its environment (Koch and Harnisch 2016),

ii) The various plant parts (roots, shoots, stems, flowers, grains or fruits and phloem, xylem or apoplast, cells, organelles etc.) constitute different Eh-pH niches, with temporal variations,

iii) Eh-pH in various plant parts depends on the plant genotype,

iv) Environmental (abiotic and biotic) stresses alter Eh-pH in these niches.

Although redox regulation is also involved in plant-weed interactions, especially in parasitic weeds (Yoder 2001) and through redox-associated mechanisms for allelopathy (Downum and Rodriguez 1986; Cheng and Cheng 2015), we excluded weeds from this review and limit it to only two kinds of pests (pathogens and insects or nematodes) for which Eh-pH interactions are better documented.

Furthermore, the detailed processes involved in maintenance of Eh-pH homeostasis at various scales in plant/soil/microorganisms systems are not the object of this review. Especially, the critical roles of transition metals in processes related to dynamic redox regulation are not considered here. However, we would like to simply stress that metals such as Fe, Mn, Zn, Cu, Co, or Mo both regulate and are regulated by Eh-pH conditions and their homeostasis in the various plant compartments is crucial, especially in chloroplasts (Yruela 2013). Transition metals are involved in virtually all oxidation-reduction reactions through: i) physical processes, as their ability to accept or donate single electrons makes them able to overcome the spin restriction in oxidation by O_2, in accordance with Pauli's principle (Halliwell and Gutteridge 1984); ii) chemical processes, exchanging electrons and protons with a ratio different than one as the $Fe^{2+}/Fe(OH)_3$ redox couple exchanging three protons for one electron, thus impacting the electrons-protons balance (*pe*+pH) in soils (Ponnamperuma 1972); and iii) biological processes, being essential constituents of molecules involved in redox processes as chlorophyll, cytochromes and enzymes as oxidases and hydrogenases (Halliwell and Gutteridge 1984; Yruela 2013). Maintenance of Eh-pH homeostasis should therefore be regarded as a dynamic process, insured by strong interactions between physical, chemical and biological processes and related to metal ions homeostasis.

To support our underlying hypotheses, we : i) Provide an analysis of plant-pests (pests *sensu lato* that includes animal pests and pathogens) interactions from an Eh-pH perspective by reviewing the literature; ii) Report examples showing how development and attacks of pests are correlated with spatial and temporal variations in plant Eh-pH; iii) Propose evidence-based discussion of how Eh-pH homeostasis can provide a new perspective on plant health and help clarify the many Genotype x Environment x Management x Pest (G x E x M x P) interactions; iv) Explore correlations between spatio-temporal variability of Eh-pH and genotypic variations impacted by various abiotic and biotic stresses and plant susceptibility-tolerance-resistance to pests; v) Revisit mineral nutrition and plant-pest interactions from an Eh-pH perspective as well as pathogenicity and virulence; vi) Propose an original perspective on energy allocation and growth-defense tradeoff by plants based on the Eh-pH homeostasis approach and finally; vii) We review how Eh-pH conditions in the rhizosphere are the results of multiple interactions between roots and microorganisms and propose the following hypothesis: that soil structure leading to diverse Eh-pH niches and hosting a high diversity of microorganisms, is the key determinant of a soil's disease suppressiveness.

Eh-pH conditions at which pests can thrive

Plant pathogens

Each organism has an optimal Eh-pH range for its development. Pathogens having a broad host range are able to develop under a large range of Eh-pH conditions, as for instance *Pseudomonas syringae* (Morris et al. 2019). However, most pathogens are adapted to specific hosts, and have a relatively narrow optimal range of Eh-pH in which they are pathogenic (Rabotnova and Schwartz 1962). The Eh-pH conditions at which some plant pathogenic fungi and oomycetes can thrive are summarized in Table 1 while those for bacteria and viruses are reported in Table 2.

Table 1. Optimal Eh-pH conditions at which key plant pathogenic fungi and oomycetes are pathogenic. Most fungal pathogens develop under both oxidized (Eh>400mV) and acidic conditions. Necrotrophic fungi develop better in more acidic (and less oxidized) conditions than hemi-biotrophic and biotrophic fungi. A number of plant pathogenic fungi thrive in slightly acidic to alkaline conditions, as for example Gaeumannomyces, Verticillium, Colletotrichum sp. etc. Fungi developing in the apoplast develop at lower pH than those growing in the phloem. Many oomycetes develop in less oxidized conditions than their fungal counterparts, in a wide range of pH although with large species-specific variations in optimal pH. pH values in brackets indicate possible range of survival while na means non-available. These are only indications of the tendency of the main groups of pathogens. As large differences can exist between species, each pathogen should be characterized by its specific Eh-pH range of development and by its location in the plant.

Pest type		**Affected tissues**	**Species**	**Organs**	**pH**	**Eh (mV)**	**References**
Fungi	Necrotrophic	Apoplast	*Sclerotinia* spp (Mold, rot)	Stems, roots, leaves, fruits	3-4	500-600	(Webb 1921; Howlett et al. 2001; Suzuki et al. 2003; Saharan et al. 2007; Yadeta and Thomma 2013; Alkan et al. 2013; Lebreton et al. 2014; Armijo et al. 2016; Knight and Sutherland 2016; Bousset et al. 2019; Zhang et al. 2020)
			Rhizoctonia spp (Various diseases)	Roots, Seeds	4.5-5.5	350-450	
			Leptosphaeria maculans (Blackleg, canker, rot)	Cotyledons Young leaves	4-5.5	450-600	
			Botrytis cinerea (Grey mould)	Green tissues	4.1-5.9	500-550	
		Epidermis, Hypodermis Xylem Phloem	*Fusarium* spp (Rot) *Fusarium oxysporum* (Wilt)	Roots	5-8	400-500	
		Endodermis Xylem Phloem	*Gaeumannomyces* spp (Take all)	Roots, stems	6-7 Specific	na	
		Epidermis, Xylem, Phloem	*Alternaria* spp (Early blight, leaf spot)	Stems, leaves	5-8	400-550	
	Hemi-biotrophic	Apoplast Xylem	*Magnaporthe oryzae* (Rice blast)	Leaves, roots, grain (glumes)	6-7 (5-8)	300-500	(Venard and Vaillancourt 2007; Diéguez-Uribeondo et al. 2008; Wicklow et al. 2009; Xie et al. 2010; Miyara et al. 2012; Landraud et al. 2013; Yadeta and Thomma 2013; Lebreton et al. 2014; Bousset et al. 2019)
		Xylem	*Verticillium* spp (Wilt)	Roots, stems	6-9	400-600	
		Apoplast, Fiber cells, Xylem, Phloem (function of the species)	*Colletotrichum* spp (Antrachnose)	Leaves, stems, roots (specific)	7-8 (3-9.2) Conidia: 5-6. Variable with strains. Able to alkalinize	na	
	Biotrophic	Apoplast	*Puccinia graminis* (Cereal rusts) *(Obligate)*	Green tissues Stems	4-7.5 Variable with growing medium	na	(Webb 1921; Gebrie 2016)
			Blumeria graminis (Mildews) *(0bligate)*	Leaves	<5.5	Resistant -25mV *vs* susceptible	(Felle et al. 2004)

		Epidermis	*Ustilago maydis* (Smut)	Leaves	5.1-5.5 Strain specific	na	(Geiser et al. 2014)
			Erysiphe graminis (Powdery mildew)	Leaves	5.6	265-325	(Benada 1966; Arabi and Jawhar 2002)
Oomycetes	Necrotrophic	Epi- and endodermis, Apoplast, Xylem, Phloem	*Pythium* spp (Damping off)	Seeds, roots, stems	6-6.5 (3 - 9) specific	Using nitrate Cathodo-tactic (*P. aphadni-dermatum*)	(Van West et al. 2003; Kong et al. 2009; Van Buyten and Höfte 2013; Krasnow and Hausbeck 2017; Ah-Fong et al. 2019)
	Hemi-biotrophic	Apoplast, Xylem	*Phytophthora* spp (Mildew)	Roots, tubers, leaves	6-6.5 Specific *P. citricola*: 9 *P. tropicalis*: 5 *P. palmivora*:4 -6	<350 mV (*Ph. infestans*) Using amino-acids Anodo-tactic (*P. palmivora*)	(Morris et al. 1995; Simpfendorfer et al. 2001; Van West et al. 2003; Benada 2012; Ah-Fong et al. 2019)
	Biotrophic	Apoplast	*Albugo candida* (White rust)	Green tissues	6.5 (3.5-9.5)	na	(Endo and Linn 1960)

Table 2. Some Eh-pH conditions where various types of plant pathogenic bacteria and viruses can develop. Many plant pathogenic bacteria grow under more reduced (lower Eh) conditions than their fungal counterparts, in alkaline or slightly acidic plants or plant parts. These conditions are met in reduced (anaerobic) soils, and correspond to relatively oxidized plants as nutrient balanced plants are reduced (pe+pH<10). Viruses develop under both reduced and alkaline conditions, that also correspond to conditions found in reduced soils, but in strongly oxidized plants as the phloem is buffered at very low Eh in nutrient balanced plants. The listed Eh-pH values are indicative of where microorganisms are pathogenic on plants although some of them (notably Gram-negative bacteria) can thrive under different Eh-pH conditions, especially in reduced soil conditions for bacteria, and then become pathogenic when conditions become more oxidized.

Aerobic conditions correspond to pe+pH >10 according to Rabotnova and Schwartz (1962). pe+pH is equivalent to the chemical notion of rH_2 or to correct Eh to pH 7, which better characterizes oxidation in organic chemistry than Eh alone. At 25°C, pe +pH = Eh(V)/0.059 + pH. Electrical neutrality corresponds to pe+pH=14 or Eh@pH7=402mV (Husson et al. 2016).

Pest type		**Affected tissues**	**Species**	**Organs**	**pH**	**Oxidation (pe+pH)**	**References**
Bacteria	Proteobacteria (Gram-negative)	Apoplast	*Pseudomonas syringae*	Leaves, roots, seedlings, Seeds	Large range. Apoplastic alkalization induced lesions	Oxic and microoxic = aerobic and facultative anaerobic	(Rabotnova and Schwartz 1962; Gour et al. 2000; Bové and Garnier 2003; Gnanamanickam 2006; Hogenhout and Loria 2008; Bueno et al. 2012; Yadeta and
			Xanthomonas spp		5-9	Aerobic	
			Ralstonia		7-8	Aerobic	

			solanacearum				Thomma 2013; Geilfus et al. 2020)
		Apoplast,	*Erwinia* spp	Leaves, fruits, tubers	7.5 (5-9) Shifts >8 upon infection	Facultative anaerobic, fermentative	(Nachin and Barras 2000; Shrestha et al. 2005; Matthysse 2006; Bueno et al. 2012; Hwang et al. 2017; Wang et al. 2018)
			Agrobacterium tumefaciens	Roots, stems, trunks	5.5	Aerobic Able to respire nitrogen oxides	
		Xylem limited	*Xylella fastidiosa*	Leaves	6.5-6.9	Aerobic	(Wells et al. 1987)
		Phloem limited	*Candidatus Liberibacter crescens*	Leaves, roots, tubers	5.8-6.8	Strictly aerobic	(Haapalainen 2014; Bendix and Lewis 2018; Cruz-Munoz et al. 2019; Molki et al. 2019)
			Candidatus Liberibacter asiaticus		Neutrophilic Alkalization of hemolymph to 8.1	Micro-aerophilic Facultative aerobic	
	Firmicutes (Gram+)	Phloem limited	*Candidatus Phytoplasma* *Spiroplasma*	Leaves, roots	6	Micro-aerophilic	(Wissenschafts et al. 1999; Bové and Garnier 2003; Hogenhout and Loria 2008; Jha and Sonti 2009; Sen et al. 2015; Bendix and Lewis 2018)
	Actino-bacteria (Gram+)	Xylem and apoplast	*Clavibacter michiganensis* *Corynebacterium sepedonicum*	Leaves, seed, roots, tubers	7-8 in culture Up to 5 in xylem Acidification of extracellular pH to 4.5 in Potato	Aerobic	
Viruses		Phloem Epidermis cells	Tomato Spotted Wilt Virus	Leaves	7 (>6 and < 9)	<200 mV	(Best and Samuel 1936; Best 1968; Opalka et al. 1998; Brugidou et al. 2002; Steinmetz et al. 2006; Zechmann et al. 2007; Király et al. 2008; Clemente-Moreno et al. 2013; Gillet et al. 2013; Liao et al. 2015; Wilts et al. 2015; Berthelot et al. 2019)
			Various viruses (Tobacco Mosaic Virus, Cowpea Mosaic Virus, Plum Pox Virus, Turnip Mosaic Virus, etc.)		Swollen at high pH Reduced by low pH	Controlled by antioxidant, increased by ROS Transmission activation is operated by a redox switch	
		Phloem and xylem Epidermis cells	Rice Yellow Mottle Virus	Leaves, stems	Swollen, unstable at basic pH in cytosol (7.5) Compact, stable at acidic pH in vacuoles (5)	Favored by H_2O_2	

Insect pests

Although it is well-known that insect pest interactions with plants are affected by both regulation and balance of pH (Harrison 2001), and by redox signaling (Zebelo and Maffei 2015), little is known about the influence of the combined Eh-pH levels (reflected in pe+pH) of the plant parts that insects feed upon.

The redox state of the apoplast exerts a strong influence on the extent of the plant response to aphid infestation in terms of altered cell wall composition and nutritional quality (Rasool et al. 2017). Eh-pH conditions affect plant digestibility by insects, and redox active components such as phenols are regarded as antifeedant, digestibility reducers and toxic (Fürstenberg-Hägg et al. 2013; Usha Rani and Pratyusha 2013; Napoleão et al. 2017). The Eh-pH in insect intestinal tracts is related to digestive enzymes and reflects different digestive strategies. The effects of plant allelochemicals, especially phenols, on insect herbivores are influenced by gut redox conditions. Therefore, the regulation of gut redox conditions is an important adaptation strategy of insect herbivores to the plant chemical defenses that must be included in the analysis of plant-insect interactions (Appel and Martin 1990). Herbivores may have multiple strategies to deal with foliar phenolics such as a "reducing strategy" in which reducing conditions in the gut prevent phenolic oxidation, and an "oxidative or polymerization strategy" in which phenolics are oxidized and rapidly polymerized. Herbivores feeding on foliage with a high concentration of readily oxidized and polymerized phenolics and low concentration of nutrients (e.g., many trees) may use the oxidative polymerization strategy. Conversely, herbivores feeding on foliage with a low concentration of phenolics but high concentration of nutrients for reducing potential (e.g., many herbs) may employ the reducing strategy (Appel 1993). Saprophytic larvae of *Penthetria holosericea*, which feed selectively on decomposed leaves and their own microbe-rich faeces, present very alkaline (pH>11) conditions with moderately low Eh (230 mV) and thus, have a high pe+pH (>15) in the midgut. These conditions differ fundamentally from those of detritivorous and humivorous insects which host a highly active, fermentative microbiota in their alkaline midgut or hindgut compartments (Šustr et al. 2014).

In a study of Lepidopteran larvae, midgut pH of *Helicoverpa zea*, *Heliothis virescens* and *Hyphantria cunea* (Noctuidae) revealed significant differences between insect species, but no host plant effect (geranium, cotton, clover or soybean), since all were strongly alkaline at pH 9.3 to 10.6 (Johnson and Felton 1996a). In contrast, midgut Eh was influenced by both insect and host plant species. Midguts of larvae feeding on clover and soybean had more positive potentials, with redox values about 100 mV higher than those of larvae feeding on geranium. In this interaction, much of the variation in midgut redox conditions was due to the redox activity of host plant chemicals at the alkaline pH of the gut (Johnson and Felton 1996a).

Midgut Eh-pH, in relation to plant Eh-pH, therefore, can help discriminate insects based on their feeding mode and capacity to cope with an oxidized diet. Adults or nymphs of sucking insects preferentially feed on plant parts at neutral to basic pH, e.g. the phloem (Giaquinta 1977; Gerendás and Schurr 1999). They dislike strongly reduced plants or plant parts that are rich in phenols and ascorbic acid (Farkas et al. 1960). It is interesting that these insects often are vectors of viruses that require high pH.

Also, a lower level of ROS and a higher antioxidant potential in the adult than in the larval midgut indicate stage specificity in the management of oxidative stress as reported for *Leptinotarsa decemlineata* (Coleoptera, Chrysomelidae), the Colorado Potato Beetle, which has a midgut with low pH of 5.38 to 6.30, and pe+pH of

5.93 to 6.95 (Krishnan et al. 2007). Phytophagous Lepidopteran larvae have a higher midgut pH, with a low Eh and pe+pH for a specialist such as *Manduca sexta* with a pH of 8.0 to 9.3, an Eh of -188 to -88 mV and a pe+pH of 5.8 to 6.8. In contrast, generalists have a high Eh and pe+pH, for example, *Lymantria dispar* with a pH of 7.9 to 8.2, an Eh: +214 to +238 mV and a pe+pH of 11.6 to 12.2. Another example is *Papilio glaucus* with a pH of 9.8 to 10.1, an Eh of +17 to +57 mV and a pe+pH of 10.4 to 11.0 (Appel and Martin 1990).

Regarding phytophagous insects, little is known about the Eh-pH levels of the plant parts they feed upon. Johnson and Felton (1996b) reported midgut Eh and pH values for 13 Lepidopteran, two Coleopteran, one Orthopteran and one Isopteran species feeding on natural host plants or plant-derived foods. Table 3 reports new information published in the literature.

Table 3. Eh-pH physicochemical status of some phytophagous-saprophagous insect midguts (based on literature published following the review by Johnson and Felton 1996b).

Insect species	**Order & Family**	**Food source**	**Midgut Redox (Eh: mV)**	**Midgut pH**	**References**
Leptinotarsa decemlineata	Coleoptera; Chrysomelidae	Leaves-mesophylla	Adults: -177 to 0 Last instar larvae: +32 to +38	Adults: 5.37 - 6.4 Last instar larvae: 5.38 - 6.30	(Krishnan et al. 2007, 2009)
Melolontha melolontha	Coleoptera: Scarabaeidae	Roots	+220 to +340	7.9 - 8.2	(Egert et al. 2005)
Pachnoda ephipppiata	Coleoptera: Scarabaeidae	Soil organic matter	-190 to +180	8.4 - 10.7	(Lemke et al. 2003)
Pachnoda marginata	Coleoptera: Scarabaeidae	Soil organic matter	-200 to -100	9.5 – 11.7	(Cazemier et al. 1997, 2003)
Penthetria holosericea	Diptera: Bibionidae	Soil organic matter	+20 to +60	11	(Šustr et al. 2014)
Agrotis ipsilon	Lepidoptera; Noctuidae	Stem-collar	+171 to +250	9 - 9.75	(Ellakwa 2014)
Spodoptera littoralis	Lepidoptera; Noctuidae	Leaves-mesophylla	-131 to +370	8.2 - 8.8	(Krishnan and Kodrík 2006)
Acrididae (23 spp)	Orthoptera; Acrididae	Leaves-mesophylla	+179 to +327	5.90 - 7.33	(Appel and Joern 1998)
Reticulitermes flavipes	Isoptera: Rhinotermitidae	Soil organic matter	+80 to +200	6.5 to 7.0	(Ebert and Brune 1997)
Cubitermes ugandensis	Isoptera: Termitidae	Soil organic matter	+350 to 400	6.0	(Kappler and Brune 2002)

Similar information is not available for phloem-feeding species (e.g. aphids), since studies were conducted mainly for insects whose body size allows gut dissection (e.g. Lepidoptera, Orthoptera, and some Coleoptera, particularly Scarab beetles). Although Isoptera have a small body size there is interest in studying their digestive processes because they involve symbiotic microbiota (in the hindgut). Still, there are some reservations about the accuracy of Eh measurements for the latter (Eutick et al. 1976; Veivers et al. 1980; Brune et al. 1995). In addition, information is often lacking as to whether redox potentials indicated in these studies are Eh (according to the Standard Hydrogen Electrode) or potentials measured via the reference electrode (Ag-AgCl or calomel). Information on Eh-pH midgut conditions is also missing for species whose diet differs between immature and adult stages, e.g. chafer beetles (*Pachnoda spp*.), cockchafers (*M. melolontha*) or blackbeetles (*O. nasicornis*). *L.*

decemlineata is the only species studied for both adults and larvae even though they both feed on the same plant organs. Nevertheless, the positioning of this species on the Eh-pH map is consistent with that of *E. varivestis* (Murdock et al. 1987; Johnson and Felton 1996b; Krishnan et al. 2009). The positioning of the 23 species of Orthoptera is also consistent with that of *L. migratoria* (Bignell 1984; Johnson and Felton 1996b; Appel and Joern 1998).

Overall, it is difficult to draw overarching conclusions of phytophagous-saprophytic insects based on their taxonomy, feeding-style or developmental stage (an exception is Colorado beetle chewing-biting larvae and adults). This is due either to a complete lack of information on piercing-sucking species, independent of adults or nymphs or a partial lack of information on chewing-biting species for which diet differs between immature and adult stages: chafer beetles (*Pachnoda* spp.) are soil saprophytes at the larval stage and aerial herbivores at the adult stage; cockchafers (*M. melolontha*) or blackbeetles (*Oryctes nasicornis*) are root-feeding or saprophytic as larvae but aerial herbivores as adults. For example, information on chewing-biting Lepidopteran caterpillars-worms is available only for larvae (since adults generally do not feed on plant parts) while the information is available only for adults for chewing-biting grasshoppers.

Gastropods and nematodes

Charrier and Brune (2003) showed that two phyllophageous species of starved helicid snails (Gastropoda and Pulmonata), (*Helix pomatia* and *Cornu aspersum*, syn. *Helix aspersa*) had a pH increasing from the crop (an expanded portion of the alimentary tract used for the storage of food prior to digestion) to the distal intestine of pH 6.4 and 7.4, respectively. In the saprophagous *Elona quimperiana*, the pH along the gut axis remained acidic (5.1–6.6). Oxygen was not detected in the gut lumen of any of these species to highlight anaerobic conditions. This clearly illustrates that the morpho-anatomical differentiation of the intestinal tract corresponds to different physicochemical microenvironments. The increasing alkalinity along the gut should have repercussions for the microbial communities colonizing the intestine. Intestinal microbiota, in turn, may cause changes in the pH of the host tissue during anaerobiosis (Pörtner 1987; Charrier and Brune 2003).

Nematodes perceive and respond to pH and redox potential gradients in the soil or rhizosphere (Hua et al. 2020). Detrimental nematodes seem to require oxidized conditions as suggested by the negative impact of reduced conditions during anaerobic soil disinfection (Di Gioia et al. 2016; Browne et al. 2018), the efficient antioxidant defense systems of spring barley in response to stress induced by *Heterodera filipjevi* (Labudda et al. 2020), the high nematicide activity of reduced organic acids (Oka 2010), or the requirement of peroxiredoxins from *Meloidogyne incognita* for its successful development (Dubreuil et al. 2011). Many plant pathogenic nematodes such as *Heterodera glycines*, *Meloidogyne incognita* or *M. hapla*, thrive at low (4.5 to 5.5) pH (Hua et al. 2020). The greatest numbers of *Pratylenchus alleni* colonized soybean roots at pH 6.0. *Hoplolaimus galeatus* and members of the Tylenchinae-Psilenchinae survived best at soil pH 6.0, while numbers of the Dorylaimidea were greatest at both pH 6.0 and 8.0. Non-stylet nematodes (Rhabditidae and Cephalobidae) were recovered in greater numbers from pH 8.0 soil (Burns 1971).

Spatial and temporal variability of Eh and pH in plants: identification of Eh-pH niches

Studying the effect of plant age and leaf position on susceptibility to wheat stripe rust, Farber and Mundt (2017) suggested that the distribution of the rust could be driven more by differences in host susceptibility than by propagule dispersal. Benada (2017) hypothesized that Eh and pH are major players in plant physiology and pathogen resistance in order to explain the variable changes in resistance that occur during ontogeny of the host and environment that involve: i) the disease gradients on a plant, ii) the evolution of susceptibility of organs during ontogeny and growth, and iii) the difference in resistance of individual plant cells and relatively swift changes of its resistance within a couple of hours. From an evolutionary point of view, the circadian rhythmic cell is a hydro-electro-chemical oscillator driven or synchronized by sunlight with a temporal compartmentation of metabolism and a network of metabolic sequences to compensate for oxidative stress (Wagner et al. 2000). It is, therefore, not surprising to observe a strong spatial and temporal variability of Eh and pH in plants.

Spatial variability of Eh and pH in plants

Plants have five key nutrient tissues, namely the phloem, xylem, leaf apoplast, root apoplast, and cellular organelles that serve as nutrient reservoirs. Each of these are the target of certain pathogens and pests (Fatima and Senthil-Kumar 2015). The nutrient content in these tissues differ in types of minerals and carbon sources (sugars, amino- and organic acids, and organic alcohols) (Fatima and Senthil-Kumar 2015), all of which affect Eh or pH. Eh and pH have been recognized as important factors defining ecological niches for microorganisms (Köpke et al. 2005; Vartoukian et al. 2010; Cardinale 2011; Jones et al. 2015; Koch and Harnisch 2016). The difference in Eh-pH between roots and shoots, as well as between apoplast, xylem and phloem, can therefore be used to characterize Eh-pH niches.

Eh-pH niches: Roots vs shoots or grains

The assessment of redox state based on ratios of ASC/DHA (reduced *vs.* oxidized AsA) or GSH/GSSG (reduced *vs.* oxidized Glutathione) ratios logically shows that roots (i. e. non photosynthetic organs) are more oxidized than leaves (i.e. photosynthetic organs) in maize (Ahmad et al. 2016), soybean (Borella et al. 2019), sunflower (Ortega et al. 2017), onion (García et al. 2020) and poplar (Morabito and Guerrier 2000). Roots show tremendous variability in rhizospheric-apoplastic pH, especially in relation to nitrogen mineral nutrition. There is strong acidification related to NH_4^+ absorption and pronounced alkalization related to NO_3^- absorption (Marschner et al. 1986). Masiello et al. (2008) measured a higher carbon oxidation state in maize grains than in maize stover. Internal oxygen concentrations are lower within bulky storage organs such as fruits (apple, banana) or tubers than other tissues. This results in different oxygen gradients within growing potato tubers which have a very low oxygen level in the center of the tuber (Geigenberger 2003).

Leaf Eh-pH also has high spatial variability. Husson et al. (2018a) plotted the spatial distribution of Eh and pH in rice plants and showed that average leaf pH decreased from younger leaves (located on the upper part of the canopy) to the older ones (located on the lower part of the canopy). The youngest leaves had the highest Eh values, which were negatively correlated with their length (the shorter the leaf, the higher the Eh value). The last fully expanded leaf had the lowest Eh, and Eh of mature leaves increased with leaf age, with the lowest leaves being the most oxidized (higher Eh). The tip of the leaves was also more acidic and in a reduced (lower pH and Eh) than the base. This corroborates the results of Benada (1967, 2017) who measured the lowest redox potential in the second upper leaf of wheat and barley during stem elongation, while the lowest value was in the top leaf when the ear appeared in wheat. In dicotyledons such as bean (*Phaseolus vulgaris*), 3-days-old intact plantlets had greater antioxidant protection by antioxidant proteins (thioredoxin, glutathione reductase, peroxiredoxin) than 9-day-old individual cotyledons (Karmous et al. 2017). Overall, while the mean Eh-pH measured at leaf level or the redox state at leaf or root level provides useful information on plant health (Husson et al. 2018a), this knowledge does not provide information on intra-organ variability of Eh and pH. Nevertheless, such information is needed since the various types of pathogens or pests do not all colonize or feed on the same plant organs.

Eh-pH niches within organs: phloem, xylem and apoplast

Eh-pH conditions in phloem, xylem and apoplast are summarized in Table 4. The phloem is strongly buffered at high pH and low Eh. In contrast, the xylem pH is acidic but its Eh-pH varies relative to external conditions, especially soil Eh-pH. The apoplast is acidic and more oxidized but apoplast Eh-pH varies relative to tissue age and function (elongating tissues are more acidic) and is poorly buffered.

Table 4. Homeostasis level, buffering capacity and processes involved in Eh-pH regulation in phloem, xylem and apoplast

Location	**pH-Eh**	**Homeostasis Buffering capacity**	**Physiological processes**	**References**
Phloem	pH	7.5 to 8.5 Strongly buffered 5.0 to 6 in Citrus	High pH needed for active transport system coupling sucrose translocation across the plasma membrane (phloem loading) to the proton motive force generated by the H^+-pumping ATPase Phloem loading of sucrose is pH-dependent, and is markedly inhibited at an apoplast pH of 8 compared to pH5	(Giaquinta 1977; Bush 1992; Gerendás and Schurr 1999; Hijaz and Killiny 2014; Killiny 2017; Cruz-Munoz et al. 2019)
	Eh	Low Eh: 50-90 mV 50 to 150 mV lower than apoplast Strongly buffered Micro-aerophilic	Related to sucrose, amino acid and accumulation of Salicylic Acid (SA) Important transport conduit for mobile redox signals inducing SAR (SA, lipid-derived molecules, ascorbate, glutathione, ROS, Systemic Wound Response and Systemic Acquired Acclimation Low internal O_2 in the vascular bundle.	(Wright and Fisher 1981; Fromm and Bauer 1994; Schmidke et al. 1999; Van Dongen et al. 2003; Van Bel and Gaupels 2004; Hafke et al. 2005; Rocher et al. 2006; Gaupels et al. 2017; Bendix and Lewis 2018)
Xylem	pH	5.0-6.0 Weakly buffered	Strongly fluctuates with composition of dominant ions in the xylem sap, uptake of inorganic ions (especially nitrogen), external conditions (microclimatic factors) and stresses	(Gloser et al. 2016; Pandit and Mukkherjee 2016)

	Eh	Related to soil Eh and pH Weakly buffered	Has a lower concentration of organic compounds (sugars, peptides and proteins) than the phloem. The difference between xylem pH and soil pH creates a difference in redox potential (50 to 200 mV) between xylem and soil (corresponding to the Nernst's equation). For a xylem at pH6 when soil pH is lower than 6, the xylem Eh is lower than soil the Eh and when soil pH is higher than 6, xylem Eh is higher than soil Eh, with approximatively -60 mV pH^{-1}	(Love et al. 2008; Pandit and Mukkherjee 2016)
Apoplast	pH	4.5-6.0 Buffered Variable with tissues 5.2 for rice, 5.75 for barley	Regulated through H^+-ATPase pumps and influenced by photosynthesis. Result of a complex interaction between ion transport, H^+-buffering, H^+-consumption, and H^+-production. pH regulation is energy costly Low apoplast pH in elongating tissues are associated with growth. Lower apoplastic pH compared to the cytosolic pH has a crucial control effect on redox properties of protein cysteine thiols and overall redox conditions. Palisade apoplast pH is higher than stomatal and epidermal apoplast pH	(Grignon and Sentenac 1991; Mühling et al. 1995; Felle 2005; Geilfus and Mühling 2011; Landraud et al. 2013; Visnovitz et al. 2013; Janku et al. 2019)
	Eh	100-250 mV 50-150 mV higher than phloem Weakly buffered	Predominantly determined by a high concentration of ASC; the production of ROS, an active process in the apoplast that is controlled by either a plasma membrane-bound NADPH oxidase or a set of peroxidases in the cell wall; and large numbers of thiol groups present on the proteins of the plasma membrane with a potential capacity 10 orders of magnitude lower than the phloem capacity	(Fromm and Bauer 1994; Felle 2001; Hafke et al. 2005; Potters et al. 2010; Gjetting et al. 2012; Foyer and Noctor 2013)

The low antioxidant efficiency in the apoplast allows ROS to easily accumulate and provides a condition for ROS signaling. Therefore, the apoplastic ROS-antioxidant homeostasis is actively engaged in the reception of, and reaction to, many biotic and abiotic stresses (Podgórska et al. 2017). Similarly, pH signals light intensity changes, drought, lack of oxygen, and the presence of symbiotic partners or microbial attackers (Felle 2001). The plant apoplast is the first site of direct contact with a pathogen and is thus an interface that mediates the first crosstalk between host and pathogens to perform a crucial role in initiation and coordination of many defense responses (Bolwell et al. 2001; Gupta et al. 2015). Any deviations from the basal cellular redox balance may induce responses that continuously readjust cellular functions; however, diversion of resources to stress responses may limit growth and may thus be detrimental to the plant. The ultimate outcome of these responses must therefore be tightly controlled by the redox signaling networks between organellar and apoplastic signaling systems (Sierla et al. 2013). This is also valid for pH that acts as a messenger in situations where pH changes are preconditions for certain processes, e.g., the gravity response, activation of certain transporters in stomatal movements, and possibly for growth in general (Felle 2001).

Intra-cellular variability of Eh-pH

Eh-pH conditions in the cell organelles are summarized in Table 5. Cell Eh-pH is strongly buffered to permit marked differences and interplay between organelles.

Table 5. Homeostasis level, buffering capacity and processes involved in Eh-pH regulation in the cytoplasm, mitochondria and chloroplast

Organelle	pH-Eh	Homeostasis level	Physiological processes	References
Cytoplasm	pH	7.2-7.5 Strongly buffered	Proton pumps in the plasma membrane and tonoplast provide intracellular pH homeostasis and maintenance of a transmembrane proton gradient. Many plant functions (nutrient and sugar transport, cell elongation, organ development) are highly dependent on the ability of individual cells to control pH in the cytosol and in the apoplast. The cytosolic antioxidant system shields the nucleus from chloroplast ROS signals. Photosynthetic ROS signals and redox imbalances are buffered by cytosolic antioxidants. Whether they reach the nucleus depends on the rate of ROS-formation and strength of the cytosolic antioxidant system	(Felle 2001; Hinsinger et al. 2003; Baier and Dietz 2005; Schwarzländer et al. 2008; Gjetting et al. 2012)
	Eh	-320 mV to -312 mV Strongly buffered	Organic acid metabolism equilibrates the redox potential in plant cells but also transfers redox equivalents between cell compartments supporting various metabolic processes	(Schwarzländer et al. 2008; Jubany-Mari et al. 2010; Igamberdiev and Bykova 2018)
Mito-chondria	pH	7.8-8 (matrix) Strongly buffered	The mitochondrial matrix and chloroplast stroma need to keep a relatively basic environment around pH 8 for optimization of biochemical reactions occurring in these two compartments The generation of a proton gradient across the inner mitochondrial membrane is an essential energy conservation event that couples the oxidation of carbohydrates and fat to the synthesis of ATP. There is a close metabolic interaction and redox exchange between chloroplasts and mitochondria	(Schwarzländer et al. 2008; Santo-Domingo and Demaurex 2012; Su and Lai 2017)
	Eh	-360 to -310 mV in unstressed plants Strongly buffered	Mitochondria are at the center of redox dependent processes as they generate ROS that drive redox-sensitive events and respond to ROS-mediated changes in the cellular redox state	(Schwarzländer et al. 2008; Handy and Loscalzo 2012; Müller-Schüssele et al. 2020)
Chloroplast	pH	7 in the dark to 7.8-8 in the light	The chloroplast is buffered at pH 8 for optimization of biochemical reactions	(Su and Lai 2017)
	Eh	-400 to -340 <-300 to -240 mV in the dark Very dynamic signaling compartment sensing perturbations at the	The chloroplast stroma is highly reducing, thanks to large amounts of ascorbate, glutathione and other antioxidants. Interplay among apoplastic and chloroplastic redox signaling networks is a key mechanism in plant stress responses. Depending on the photo-oxidative strain, up to almost 100% of the photosynthetically transported electrons can be diverted into the antioxidant defense system that is involved in the synthesis of	(Johnson 2003; Baier and Dietz 2005; Noctor et al. 2007; Sierla et al. 2013; Dietz et al. 2016; Foyer and Noctor 2016; Serrano et al. 2016; Lu and Yao 2018)

		subcellular level and to integrate a multitude of intracellular signals	important mediators of plant defense responses such as nitric oxide (NO), salicylic acid (SA), jasmonic acid (JA) and absicic acid (ABA), as well as secondary messengers including calcium and ROS.	

Cellular redox imbalances are usually induced by environmental changes that can be clearly observed in chloroplasts and mitochondria, which are also key players in the regulation of cytosolic and extracellular redox states (Tsang et al. 1991; Dietz 2003). Thus, the photosynthesizing chloroplast functions as a conditional source of important redox and ROS information, which is exploited to tune processes inside the chloroplast, cytosol and nucleus (Dietz et al. 2016). It is interesting that oxidizing conditions in the chloroplast correlate with a high reduction state (Baier and Dietz 2005).

Temporal variability of Eh and pH in plants

Photosynthesis is the primary reduction reaction by accumulating electrons and protons. All variations in photosynthetic activity (related to temperature, light, nutrition, etc.) affect the redox state and pH of the plant. Reduced photosynthesis leads to oxidation and alkalization while efficient photosynthesis in optimal conditions will lead to more acidic and reduced plants (Mühling et al. 1995; Mullineaux and Rausch 2005). Thus, both the ROS and antioxidant levels have diurnal changes. Abrupt variations in temperature and light intensity may lead to ROS accumulation due to disruption of the photosynthetic and respiratory electron transport chains (Kocsy et al. 2013). In rice leaves, Eh and pH (and thus, pe+pH) were high at the end of the night (absence of photosynthesis). Both Eh and pH decreased in the morning, reached a low plateau during the day and increased again at the end of the day (Husson et al. 2018a). This is consistent with: i) hourly and seasonal variations in photosynthesis as reported by Bernacchi et al. (2006) who reported a raise in instantaneous carbon assimilation in the morning that reached a high plateau during the day but decreased at the end of the afternoon, and ii) the increase of petiole pH in grapevine during the day, as reported by Masoero and Cugnetto (2018).

Annual, seasonal or irregular fluctuations in environmental conditions also alter the plant's cellular redox state (Kocsy et al. 2013) and antioxidant responses (Ferreira and Domingos 2012). As for Eh, the pH of xylem sap from several species shows seasonal variations, being more acidic in the spring than in the rest of the year (Wilkinson 1999).

Plant age is also an important factor in understanding Eh-pH variation. In the early stage of growth, germination is accompanied by extensive changes in the redox state of seeds. Proteins present in an oxidized form in dry seeds are converted into the reduced state following imbibition of water (Alkhalfioui et al. 2007) so that seed acidification coincides with germination (Footitt and Cohn 1992). With aging, peroxidation of lipid complexes present in seed reserves liberates fatty acids which, at the moment of germination, are transformed by lipolysis into alcohols, aldehydes and ketones (Norton and Harman 1985; Davet 2004). On rice, Husson et al. (2018a) showed that aging of organ (leaf) and at the plant level, was related to acidification and oxidation (increase in Eh) which was consistent with variations in chlorophyll content and net assimilation of CO_2 in leaves at different ages (Backhausen and Scheibe 1999).

Genotypic variability of plant Eh-pH

In analyzing almost two dozen species, Cornelissen et al. (2011) showed that leaf pH was a species-specific trait with interspecies differences of over 2 pH units. Masoero and Cugnetto (2018) also reported high variability of raw pH across 49 species. The grapevine, *Vitis vinifera*, appeared as the most acidic species (pH 3.68) while maize (4.84), potato (5.77), lettuce (5.97), basil (6.08), cauliflower (6.10) and pumpkin (6.38) were less acidic.

Data regarding the differences in redox state-leaf Eh are limited but show differences between:

i) species: Leaf redox potential was 80 mV higher in sunflower than in wheat (Benada 2017). Furthermore, the antioxidant content (both AsA and GSH) was higher in the rhizomes of anoxia tolerant *Iris* sp. compared with cereal roots that have a higher amount of oxidized DHA. Similarly, rice roots had a lower AsA/DHA ratio (meaning more oxidized conditions) than wheat with values of 0.3 and 0.7, respectively under aerobic conditions (Blokhina et al. 2000). Deciduous leaves had a higher carbon oxidation (Cox) state than coniferous leaves while goldenrod (*Solidago canadensis* L.) had a much lower Cox than red clover (*Trifolium pretense*; Masiello et al. 2008);

ii) varieties: In rice, Nerica 4 (*Oryza sativa* type *japonica x O. glaberrima*) variety grown under various conditions (fertilization, growing season) and at different ages had a lower Eh, pH and pe+pH in their last fully developed leaf than those of IRBLTA-2Pi (*O. sativa sub. Indica*; Husson et al. 2018a).

Environment and plant Eh-pH

Cellular redox homeostasis is affected by abiotic factors that can affect the ROS level (and their reaction products) at varying levels in the major energy organelles such as chloroplast and mitochondria (Das et al. 2015; Anjum et al. 2016). Oxidative stress may occur under high light intensities over long time periods, during drought, waterlogging, cellular toxicity (under soil contamination or air pollution) or mineral deficiency (Elstner and Osswald 1994). Leaf Eh is altered by external factors such as light, temperature, moisture, nutrition, etc. (Benada 2017). Based on all this, the following section reviews how plant Eh-pH can be affected by abiotic and biotic stresses.

Abiotic stresses and plant Eh-pH

Climatic conditions and plant Eh-pH

A non-exhaustive list of reports that highlight how stresses related to low or high light intensity or temperature lead to plant oxidation (increase in Eh and pe+pH) and alkalization in relation to decreased photosynthesis is summarized in Table 6.

Table 6. Effects of light intensity and temperature on plant Eh-pH

Stress		Impact	Mechanisms	References
Low or very high light intensity	Eh	Increased Eh	Stomatal closure via abscisic acid pathway; reduced photosynthesis by reduced CO_2 availability; reduced photorespiratory carbon metabolism; photosynthetic generation of biologically damaging molecules	(Ort 2001; Benada 2017; Maai et al. 2019)
	pH	Increased apoplast and	Influence of photosynthesis on	(Raghavendra et al.

		xylem pH Decreased cytosol pH Increased vacuolar pH	Plasmalemma H^+-ATPase. Heat induced electrical signals. Variable between C3 and C4 plants and according to CO_2 concentration	1993; Mühling et al. 1995; Grams et al. 2009; Aubrey et al. 2011)
Low or high temperature	Eh	Increased Eh (+8 to 10 mV in *A. thaliana* cytosol and nuclei after 5 days at 42°C vs 22°C)	Disruption of cellular homeostasis and photosynthesis; increase in photorespiration; overproduction of ROS; decrease in chlorophyll content; photoinhibition; interference with carbohydrate metabolism; stomatal closure, inhibition of Rubisco activity	(Allen and Ort 2001; Noctor et al. 2007; Hemantaranjan et al. 2014; Awasthi et al. 2015; Benada 2017; Soengas et al. 2018; Babbar et al. 2021)
	pH	Increased pH	Reduced photosynthesis by extreme temperatures. Increase in leaf pH with decreasing temperature (pH= 5.1 at 35°C increasing to 6 at 10°C)	(Masoero and Cugnetto 2018)

Extreme water conditions usually lead to increased Eh and pH, except for roots under waterlogged conditions that result in asphyxia (Table 7). Drought and waterlogging also strongly impact plant nutrition through alteration of soil-rhizosphere Eh-pH that determines the form and solubility of major elements and micronutrients (Husson 2013).

Table 7. Effects of drought and waterlogging-submersion on plant Eh-pH

Stress		**Impact**	**Mechanisms**	**References**
Drought	Eh	Strong oxidation	GSSG/GSH increased 2.6-fold in maize leaves and 2.3 in roots after 12 days of drought. Decreased photosynthetic rate increased production of superoxide anion and hydrogen peroxide by twofold In *Arabidopsis thaliana*, cytosolic Eh was significantly raised from -312 mV to -302 mV after 11 days of water stress, although cytosolic Eh is strongly buffered	(Jubany-Mari et al. 2010; Li et al. 2014; Ahmad et al. 2016)
	pH	Usually, increase in plant pH. Variable with plant species	Leaf and root pH increase in some drying plants by unknown processes; however, a leaf pH decrease is reported for grapevine, *Arabidopsis thaliana*, *Pisum sativum* and *Trifolium repens* and poplar. There is a nonlinear relationship between leaf xylem sap pH and soil water content in *Brassica napus* and *Raphanus sativus*, but no change in *Helianthus annuus*	(Wilkinson and Davies 1997; Bahrun et al. 2002; Gloser et al. 2016; Secchi and Zwieniecki 2016; Masoero and Cugnetto 2018)
	Electrical Conductivity (EC)	Increase in xylem EC	Accumulation of sugars in the xylem apoplast observed under water stress conditions is controlled by xylem pH and lower xylem pH is related to loss of xylem transport function to eventually result in accumulation of sugars, thus raising xylem EC	(Secchi and Zwieniecki 2016)
Waterlogging Submersion	Root Eh	Strong reduction Asphyxia	Reduced oxygen (O_2) availability in plant roots creates a barrier for gas diffusion into plant cells, inhibiting free gas	(Thomson and Greenway 1991; Blokhina et al.

			exchange for photosynthesis and respiration and induces changes in plant water relations. Reduction in aerobic respiration. Depletion of AsA and GSH and lowering of the redox status of root cells, stronger in the root stele since aerenchyma can provide O_2 for respiration in the cortex.	2000; Vozáry et al. 2008)
	Leaf Eh	Increase, oxidation	A decline in net photosynthesis decreases stomatal conductance, transpiration, and the intercellular partial pressure of CO_2 in leaves. Production of nitric oxide (NO), hydrogen peroxide (H_2O_2) or other ROS. Alteration of ascorbate-glutathione related parameters during anoxia but restored during re-oxygenation	(Igamberdiev et al. 2005; Salazar et al. 2015; Paradiso et al. 2016)
	pH	Decrease in cytoplasmic pH Increase in apoplastic pH	Energy crisis, tolerance of which varies from plant to plant. Switch to anaerobic respiration. Production of lactate and ethanol by glycolysis. Rapid acidification of the cytoplasm (half a pH unit), depending on H^+ pump activity and lactate production. Acidosis can cause cell death. Apoplastic alkalization decreases the proton motive force thus reduces the transport mediation of energy-rich compounds	(Felle 2006)

Edaphic conditions and plant Eh-pH

Overall, leaf pH proved to be species-specific but remarkably constant for a given species grown on soils at pH ranging from 3.67 to 6.51 (Cornelissen et al. 2011). Both high and low soil-rhizospheric pH led to oxidation of wheat leaves (Bhuyan et al. 2019). pH regulation mobilizes numerous H^+-pumps all of which employ the same universal physical principles of converting redox energy into proton pumping (Thomma et al. 2011). Thus, leaves of wheat seedlings grown under extremely acidic or strongly alkaline-stress showed strong oxidative damage compared with the control at pH 7.0. A sharp increase in H_2O_2 content (134 and 90%) and in malondialdehyde - a stress indicator produced from lipid peroxidation (199% and 194%) - were observed at both an extremely acidic (pH 4.0) and strongly alkaline pH (pH 8.5), respectively (Bhuyan et al. 2019). Leaves of rice grown under aerobic conditions (high soil Eh, low soil pH, no water stress) had a higher Eh (20mV higher) and lower pH (-0.2 to -0.4 pH units) compared with those of plants grown under anaerobic conditions (low soil Eh and high soil pH; Husson et al. 2018a). High soil pH leads to higher xylem Eh than soil Eh while low pH leads to lower xylem Eh than soil Eh. At constant soil Eh, high soil pH leads to xylem oxidation (Love et al. 2008).

Salt stress is a major plant stress that also leads to oxidation and alkalization. There is a rapid increase in H_2O_2 and superoxide radical in Indian mustard (*Brassica juncea*) under severe salt stress conditions where an oxidative burst occurred within 30 mn and increased membrane damage up to 2.8, 7.8 and 9.0 fold, within 30 minutes, 2 and 24 hours after stress induction, respectively (Ranjit et al. 2016). The decline in maize leaf growth under salt stress was due to an inhibition of H^+-pumping activity and increase in apoplastic pH of leaves (Pitann et al. 2009). In *Vicia faba*, alkalization was acropetally moved to the leaves after first arriving in the older leaves where it spread systemically throughout the entire apoplast, starting from the leaf base towards the tip. The alkalization then increased ABA in the leaf apoplast and guard cells (Geilfus 2017). Apoplast pH affected functionality by reducing the stomatal pore size in *Vicia faba* during the onset of Cl^- salinity via effects on ABA. Based on this mode of action, it was hypothesized that, under conditions of soil salinity, Cl^--inducible alkalization of the leaf apoplast reduces the transpiration rate and, thus, reduces the uptake of Na+ and Cl^- from the soil solution (Geilfus 2017).

Aluminum (Al) is a major plant growth-limiting factor in acid soils (Melakerberhan et al. 1995). The primary site of Al accumulation and toxicity is the root meristem. Al triggers lipid peroxidation and ROS production in roots, inhibits respiration and depletes ATP (Yamamoto et al. 2003). In barley, alleviation of aluminum toxicity by hydrogen sulfide was related to elevated ATPase and suppressed oxidative stress (Dawood et al. 2012). Several other toxic elements are known to lead to plant oxidation, including cadmium (leading to formation of callose in phloem cells), zinc, mercury, and antimony (Cuypers et al. 2001; Benitez-Alfonso et al. 2011; Sobrino-plata et al. 2014; Ortega et al. 2017).

In general, high levels of metal ions such as Co, Cu, Fe, Mn, Mo, Ni,and Zn, and trace levels of toxic metals (Pb, Cd, Hg, As, Cr, Ag, Al, Cs, Sr, U) have been reported to negatively affect plant growth, metabolism, development, and overall productivity, due mainly to accelerated ROS formation and, to a lower extent, through other reactions (Anjum et al. 2014). High soil pe+pH also increases Cd availability from increased bacterial activity (Wang et al. 2020). Finally, GSH is a key antioxidant for the plant to cope with mercury and cadmium stress (Sobrino-plata et al. 2014). Likewise, the ascorbic acid (AsA) redox system efficiently protects the plant and plays a key role in metal-metalloid stress tolerance (Chen et al. 2017b). A deficiency of GSH and AsA leads to susceptibility to toxic elements such as Cadmium (Jozefczak et al. 2015).

Mineral nutrition and plant Eh-pH

Mineral nutrition impacts plant photosynthesis and, as a consequence, plant Eh-pH. Any kind of N, P or K deficiency leads to plant oxidation. While N deficiency results in alkalization, P or K deficiency results in acidification (Table 8). The concentration of amino acids and sugars in the apoplast of leaf and stem tissue may increase with Ca, B, Zn or K deficiency (Huber et al. 2011), which leads to an increase in EC. Furthermore, Si content decreases with excess applications of N, which can also affect disease tolerance (Gupta et al. 2017). Besides the availability of N, the form in which it is absorbed by the plant influences soil Eh-pH and has a dramatic impact on plant physiology (Marschner et al. 1986).

Table 8. Impact of mineral nutrition (N, P, K) on plant Eh-pH

Element	**Variable**	**Effect of deficiency**	**Physiological processes**	**References**
N	pH	Increases root and shoot xylem pH by 0.2-0.3 units	N deprivation decreases whole plant transpiration which can potentially close stomata	(Dodd et al. 2003; Huber and Thompson 2007)
	Eh	Oxidation and altered antioxidant responses	Deprivation leads to changes in phenolic metabolism and oxidative status Varying patterns of superoxide dismutase isoforms.	(Huber and Thompson 2007; Kováčik and Bačkor 2007)
P	pH	Acidification	Promotion of root elongation by	(Anuradha and

			acidification; pH control of anthocyanins	Narayanan 1991; Chen et al. 2013)
	Eh	Oxidation and altered antioxidant responses	Alterations in photosynthetic physiology, including reductions in CO_2 assimilation rates, down-regulation of photosynthesis-related genes and photoinhibition at the photo-system II level. Photo-oxidative stress is characterized by an increased production of ROS in chloroplasts	(Kováčik and Bačkor 2007) (Hernández and Munné-Bosch 2015)
K	pH	Acidification	K is an alkalizing element, and high K nutrition leads to higher plant pH	(Ward 1960)
	Eh	Oxidation and altered antioxidant responses	K enhances antioxidant defense in plants and protects them from oxidative stress Accumulation of soluble sugars in K-deficient plants in both leaves and roots	(Kováčik and Bačkor 2007; Amtmann et al. 2008; Hasanuzzaman et al. 2018)

The form of nitrogen absorbed by the plant and the solubility of essential elements are related not only to the type of fertilizer applied but also to soil Eh-pH conditions. The main form of N absorbed is mainly determined by pe+pH with a balance between both forms being reached close to pe+pH=14 (Husson 2013). Drought limits biological activity and thus leads to a raise in soil Eh and pe+pH, with a strong negative impact on Fe and Mn solubility, and increased nitrification. For example, a four-fold reduction in nitrate reductase activity was observed following 6 days of severe drought (Li et al. 2014). In contrast, submersion causes a strong and rapid decrease in soil Eh, with a slight raise in pH, leading to low pe+pH, thus to reduced, soluble Fe and Mn, and to ammonification (Ponnamperuma 1972; Cottes 2019). Thus, the dominant form of mineral nitrogen in soil is nitrate in dry-oxidized-alkaline soils and ammonium in waterlogged-reduced-acidic soils.

Nitrate absorption strongly alkalizes plant roots and shoot (apoplast) while ammonium absorption leads to strong acidification, with a strong impact on other nutrients solubility-absorption. Absorption of nitrate is an active process that increases root respiration to reduce Eh in the rhizosphere while leading to shoot oxidation (Table 9).

Table 9. Impact of N-form of nutrition (NH_4^+ vs NO_3^-) on plant Eh-pH

Form	**Variable**	**Impact on plant**	**Processes**	**Impact on other nutrient availability**	**References**
NO_3^-	pH	Strong alkalization of the roots-rhizosphere (up to +2 pH units) Alkalization of shoots, leaf apoplast	Release by roots of OH^- to compensate for the negative charge absorbed with NO_3^- Strongly basic hydroxides resulting from assimilation of NO_3^- in the leaf	Decrease in Fe, Mn, Bo, Cu, Zn, Ca and P solubility - absorption	(Marschner et al. 1986; Marschner 1995; Foyer and Noctor 2013; Elmer and Datnoff 2014; Singh and Schulze 2015; Geilfus 2017; Sun et al. 2020)
	Eh	Roots-rhizosphere reduction Shoots oxidation	Activation of pumps for active N absorption increases root respiration (oxygen consumption). Reduction of NO_3^- to NH_4^+ requires 8 electrons, and 8 to16 ATP. Nitrate as N-source generates higher energetic cost (+5 to 12%) for assimilation, reduction to amino acid and pH control, as compared to		

			ammonium nutrition. NO_3^- increases photorespiration		
NH_4^+	pH	Strong acidification of the roots-rhizosphere (up to -2 pH units) Acidification of shoots, leaf apoplast	Release by roots of H^+ to compensate for the positive charge absorbed with NH_4^+	Decreases in P, K, S, Ca, Mg and Mo solubility-absorption NH_4^+ absorption is antagonist to cations as Ca^{2+}, Mg^{2+} or Mn^{2+}	(Marschner et al. 1986; Marschner 1995; Zou and Zhang 2003; Li et al. 2013; Elmer and Datnoff 2014; Singh and Schulze 2015)
	Eh	Reduction of the shoots Oxidation of the roots	Absorption of strongly reduced NH_4^+, reduced energetic cost for protein formation Activation of ATP-H^+ pumps for pH regulation, consuming electrons		

Biotic stresses and plant Eh-pH

As with abiotic stresses, biotic stresses usually lead to apoplast alkalization and oxidation. Infection by viruses, bacteria or fungi impact photosynthetic activity in various ways. The generation of ROS (an oxidative burst) in response to microbial pathogen attack is a ubiquitous early part of the resistance mechanisms of plant cells. ROS, especially hydrogen peroxide (H_2O_2), seem to play a dual role in plant defense by eliciting localized death-limitation of host plant cells and pathogens and by acting as a diffusible signal for the induction of antioxidant and pathogenesis-related genes in adjacent plant tissues (Hernández et al. 2016). A second component of the resistance mechanism is extracellular alkalization, occurring as a result of the Ca^{2+} and proton influxes, and the K^+ efflux common to most elicitation systems as one of the earliest virus responses (Bolwell et al. 2002).

In an advanced stage of viral infection, photosynthetic rates of diseased plants only attain 75 to 80 % of those of the healthy plants, on a leaf area basis. This reduced photosynthesis can be related to loss of chloroplast (chlorosis, as in viral and bacterial infection), loss of leaf area (destruction as in the case of necrotrophic fungi or bacteria), occlusion of the vascular system, or stomata closure (Goodman et al. 1967; Hernández et al. 2016). Plants infected by fungi, bacteria or viruses also display a common response, namely an increase in respiration, one of the most general physiological phenomena of diseased plants (Goodman et al. 1967).

Similarly, an oxidative response also occurs following an attack by herbivores as *H. zea* (Bi and Felton 1995). A general disturbance of redox balance is induced in tissues also by aphid feeding, including the accumulation of oxidases and phenolic substrates and loss of reducing activity and protein (Jiang and Miles 1993). Overall, following insect attacks, ROS accumulate in apoplastic as well as in symplastic regions. Apoplastic burst of ROS acts as a first barrier against subsequent attack by pathogens and herbivores (War et al. 2012). A systemic suppression of photosynthesis is often associated with caterpillar herbivory where oxidative modifications are observed (Thivierge et al. 2010), e.g. oxidation of ascorbic acid (Goggin et al. 2010). Aphids also oxidize plant phenolic monomers that act as their deterrent, into inert polymers (Jiang 1996). Finally, wounded plants secrete sap with a characteristic acidic pH of 5.0 to 5.8 and high content of different phenolic compounds such as lignin and flavonoid precursors. Plants typically respond to wounding, including that caused by sucking insects, by mobilizing and oxidizing phenolic compounds (Miles and Oertli 1993; Hwang et al. 2017).

Eh-pH homeostasis: a unifying perspective on Genotype x Environment x Management x Pest (G x E x M x P) interactions

We consider Eh-pH homeostasis as a unifying process that attempts to shed light on the multiple processes related to plant-pest interactions. A model of these interactions is proposed based on the assumption that plants become susceptible to pests when imbalanced Eh-pH conditions in their compartments match the specific Eh-pH ranges at which the various pests can thrive, usually in oxidized plants (high *pe*+pH). Once attacked, a major defense reaction of plants is a localized oxidation of the pathogen or wounds.

Hence, this "redox" model (Fig. 2) correlates: i) the Eh-pH conditions of the plants in their various compartments (roots, shoots, stems, grains, fruits and apoplast, xylem, phloem, cell, and organelles) which are the result of genotype, age, management practices and the various stresses related to the abiotic and biotic environments, their intensity and their duration; ii) the specific conditions at which specific pests can thrive depending on the pest type, their reproductive cycle, metabolism and living style (soil-borne vs air-borne, biotrophic-hemi-biotrophic-necrotrophic, intracellular-extracellular, chewing-sucking, etc.).

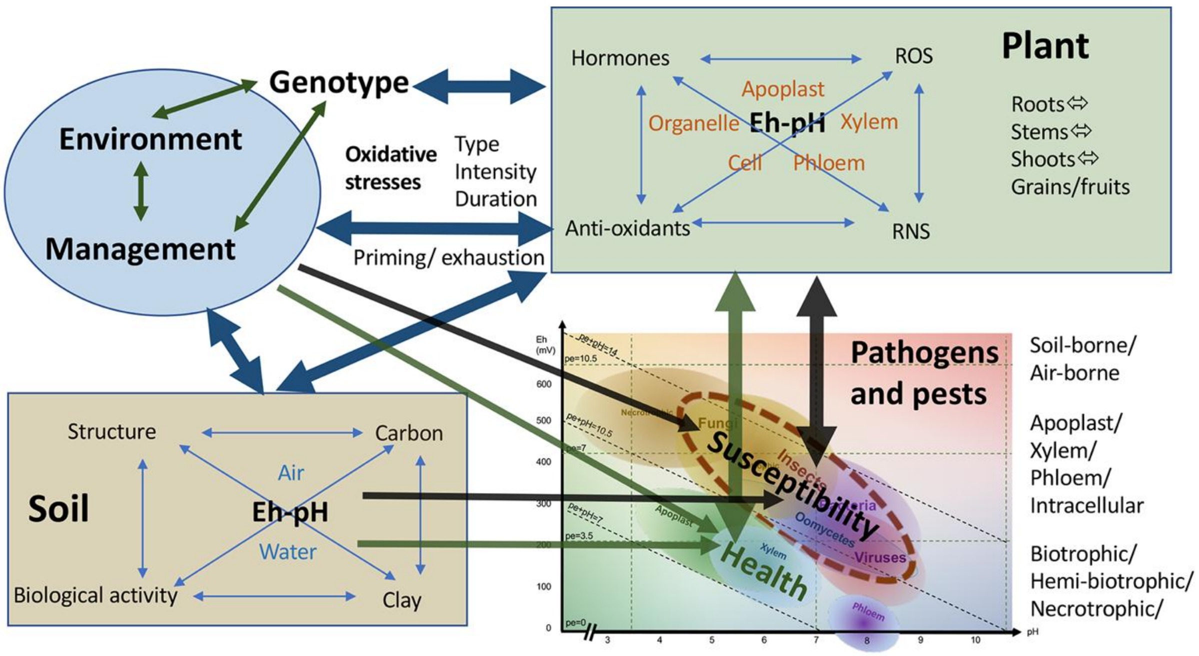


Fig. 2: Model of GxExMxP interactions in a "Redox" perspective. Environment and management practices impact soil Eh-pH (water and air in interaction with soil structure, carbon, biological activity and clay). Environment (management practices) and soil Eh-pH induce oxidative stresses in plants, which together with genotype affect plant Eh-pH in the various plant compartments through interactions between ROS, RNS, hormones and antioxidants. These antioxidants can be primed or inversely exhausted in relation to type, duration and intensity of the various stresses. In this model, plants become susceptible when imbalanced Eh-pH conditions in plant compartments match the specific Eh-pH conditions at which the various pests can thrive.

The effects of the multiple and complex abiotic and biotic factors and their interactions can be integrated into these simple parameters to provide a powerful tool for analyzing *GxExMxP* interactions in a temporal and spatialized perspective.

Can spatio-temporal variability in plant Eh-pH explain locations-periods of plant susceptibility-tolerance-resistance to various pests?

The "Eh-pH zones", where the various types of pests can thrive in space (relation to the various plant parts) and time is summarized in Fig. 3.

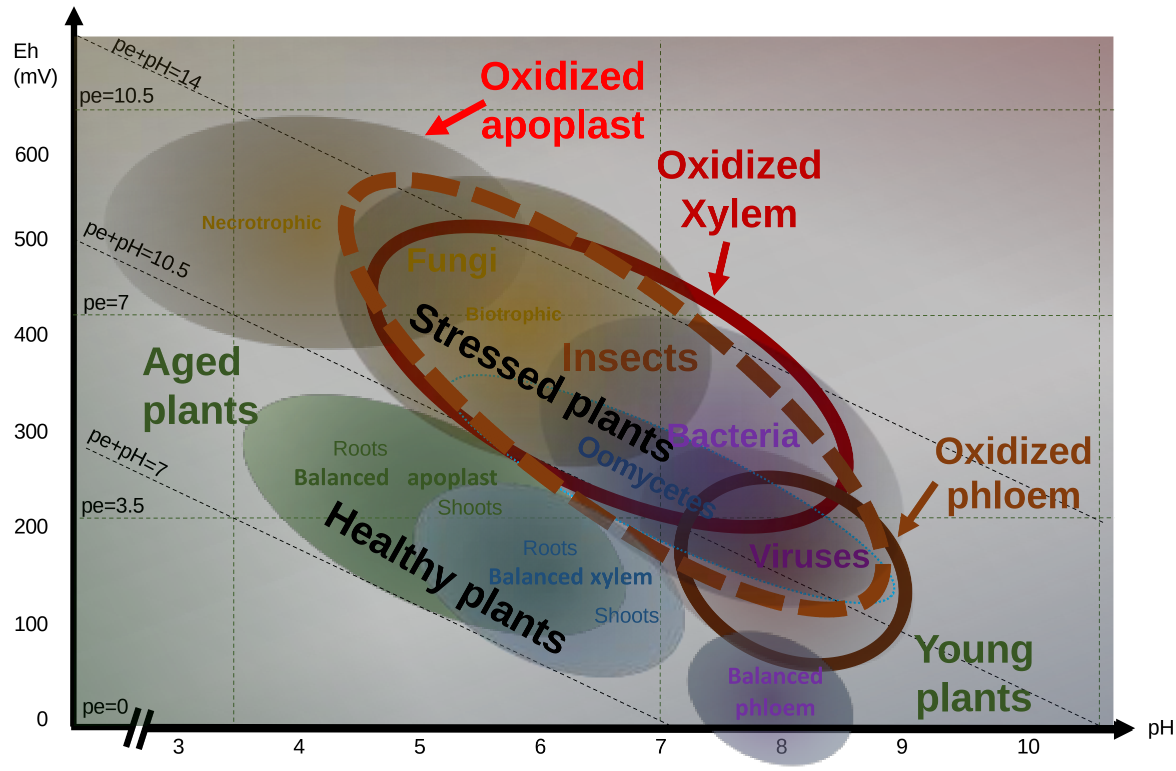


Fig. 3. Eh-pH map of indicative zones where the main groups of pests can thrive, corresponding to oxidized plants. Adapted from section 2 (Tables 1 and 2) and section 3. Viruses develop in alkaline phloem and possibly xylem, as do most bacteria. Inversely, most fungi prefer the acidic and more oxidized apoplast. Oomycetes often thrive in moderately oxidized apoplast, usually at higher pH than their fungal counterparts. Insects have different preferences, according to their feeding mode: xylem or phloem sucking insect at higher pH and lower Eh compared with biting-chewing insects; larvae at lower pe+pH and higher pH compared with adults. These are only tendencies for the main groups of pathogens and pests, as optimal Eh-pH conditions are specific. Although some pathogens are ubiquistic, able to develop in a large range of Eh-pH conditions, most pathogens can develop only in a specific, narrow Eh-pH range (Rabotnova and Schwartz 1962).

The spatial variations in plant Eh-pH correlate well with, and may explain the spatial distribution of pests within plant organs as illustrated by four examples: i) the initial development of fungi (fungal wilt pathogens) in the apoplast (more acidic and oxidized than the vascular system), and where many soil-borne fungi are necrotrophic (developing in the more acidic-oxidized conditions of the roots) while most of the biotrophic pathogens, such as rusts and powdery mildews, occur on the above-ground portions of the plants that are less acidic and oxidized than the roots (Raaijmakers et al. 2009); ii) the preferential development of many Gram-positive bacteria, including phytoplasma and proteobacteria, in the alkaline phloem and in the xylem, which rapidly become alkaline upon various stresses (Bové and Garnier 2003; Padan et al. 2005), iii) the invasion of plants by obligate intracellulars, e.g. viruses, through the alkaline and reduced phloem (Hipper et al. 2013); and iv) the feeding habits of insect vectors of these pathogens, which are xylem (bacteria) or phloem (viruses and bacteria), such as sucking insects (Garnier et al. 2001; Wielkopolan and Obre 2016).

Similarly, the spatial distribution of pests, between organs, is correlated to Eh-pH niches. Examples are: i) the resistance to wheat stripe rust (*Puccinia striiformis f. sp. tritici*,) within same-aged plants was lower on the uppermost leaf than in the second leaf, while it was even higher in the third leaf [These **leaves** are not the same 'age'] (Farber and Mundt 2017), in accordance with higher Eh levels in the young and not fully developed leaves; ii) the highest infection by Rice Yellow Mottle Virus in the flag leaf (oxidized, alkaline; Joseph et al. 2011), iii) the higher resistance of rice to bacterial blast (*Xanthomonas campestris pv. oryzae*), in old, mature leaves compared with young leaves (with low Eh and high pH (Koch and Mew 1991); and iv) the highest resistance to thrips (*Frankliniella occidentalis*) of the youngest fully opened *Capsicum* leaves compared to older leaves (van Haperen et al. 2019).

Temporal variations in plant Eh-pH are also correlated to timing of susceptibility-tolerance-resistance, and Eh-pH alteration with age could be involved in the processes implied in ontogenic resistance at plant or organ level. Some aged plants naturally develop acidic and less reduced conditions, which could explain the acquired immunity of plants against bacterial diseases (thriving in alkaline and moderately reduced conditions) with aging. This has been described with *Xanthomonas campestris* in rice (Koch and Mew 1991) and in *Arabidopsis thaliana* (Hess et al. 2005), which requires intercellular accumulation of SA. Interestingly, in tomato, age-related resistance to *Phytophthora infestans* has been related to ethylene (ET) and SA (Shah et al. 2015). Plant-leaf aging is related to acidification that matches with the higher susceptibility of young rice plant-leaves to viruses (thriving in alkaline conditions), as exemplified for Rice Yellow Mottle Virus (Joseph et al. 2011). Likewise, young grapevine leaves present a high Grapevine Fanleaf Virus level during the whole vegetative period while mature leaves, tendrils and flower-berry clusters do so only at the beginning of the vegetative period (Krebelj et al. 2015). In contrast, the decreasing susceptibility of grapevine leaves to *Erysiphe graminis* while aging (Calonnec et al. 2018) could be related to lower Eh in the fully developed leaves (Husson et al. 2018a). This is also true for the increasing susceptibility of aging rice plants to *Helminthosporium oryzae* and *Magnaporthe oryzae* (formerly *Pyricularia oryzae*; Padmanabhan and Ganguly 1954). Temporal variability in plant Eh-pH may also explain that *Capsicum* plants start to develop resistance to thrips (*Frankliniella occidentalis*) once they are between 4- to 8-weeks-old (van Haperen et al. 2019). Likewise, cabbage plants aging from 3 to 9 weeks increased pre-imaginal mortality of the moth, *Plutella xylostella*, (Lepidoptera) and reduced its larval development rate, pupal weight and fecundity (Campos et al. 2003). Finally, an Eh-pH perspective on modulation of plant immunity by light, circadian rhythm and temperature could also be valuable by providing insights into the important role of circadian rhythm in the plant defense system against pests (Hua 2013; Lu et al. 2017).

Can genotypic differences in plant Eh-pH explain susceptibility, tolerance or resistance to pests?

As for spatio-temporal variations, genotypic variability in plant Eh-pH is correlated to and may explain differential susceptibility to the various types of pests. Under this Eh-pH perspective, it can be hypothesized that any pathosystem is related to specific plant Eh-pH values. Masoero and Cugnetto (2018) reported a predisposition towards fungal infection when the pH was more acidic, with grapevine (pH 3.69) and apple (pH 5.04) as model plant species. They also reported a tendency towards bacterial infection when the pH was less acidic, as exemplified for pear (pH 5.52). The high propensity of tomato to bacterial and viral diseases (Blancard 2012) might also be related to its high pH (5.46), in addition to a strong increase in xylem pH under extreme water conditions (i. e. up to 7.0 and 8.0 under flooding and drought, respectively; Wilkinson 1999; Jackson et al. 2003). The differences in Eh-pH values among plant species might also explain why aerial hemibiotrophic and biotrophic fungi are specialized to a limited number of hosts, with similar Eh-pH conditions. For instance, the hemibiotrophic *M. oryzae* is limited to rice, a few other cereals including wheat (Debona et al. 2012), or wild grasses such as *Leersia hexandra*, *Echinochloa crusgalli*, or *Brachiaria mutica* (Jashvantlal 2008). This pathogen does not develop, for instance, on cruciferous species such as rapeseed (*Brassica napus*) that has different Eh-pH conditions. In contrast, the causal agents of phoma stem canker of rapeseed (*Leptosphaeria maculans* and *L. biglobosa*), major biotrophic fungi, are limited to brassicas and do not develop on cereals (Rouxel and Balesdent 2005). Furthermore, the low Eh in rice might explain why this plant is not infected by *Sclerotinia sclerotiorum*, a, necrotrophic and damaging plant pathogen that can infect 383 species in 225 taxonomic genera and 64 plant families (Purdy 1979).

A second hypothesis can also be proposed that, besides the specific recognition processes depending on host and plant pathogen genotypes, varietal resistance, tolerance and susceptibility to pests is related to differences in basal Eh-pH and genetic capacity of the variety to sustain a balanced Eh-pH. For instance, the rice variety Nerica 4 sustains a low Eh and pH and is resistant to several strains of the rice blast pathogen while the more oxidized rice variety IRBLTA-2Pi was highly susceptible to some strains of the pathogen (Fukuta et al. 2019). Similarly, greater varietal resistance of wheat to the blast pathogen was related to a more efficient antioxidative system in the removal of excess ROS generated during the infection process of *M. oryzae*, limiting cellular damage caused by the fungus (Debona et al. 2012).

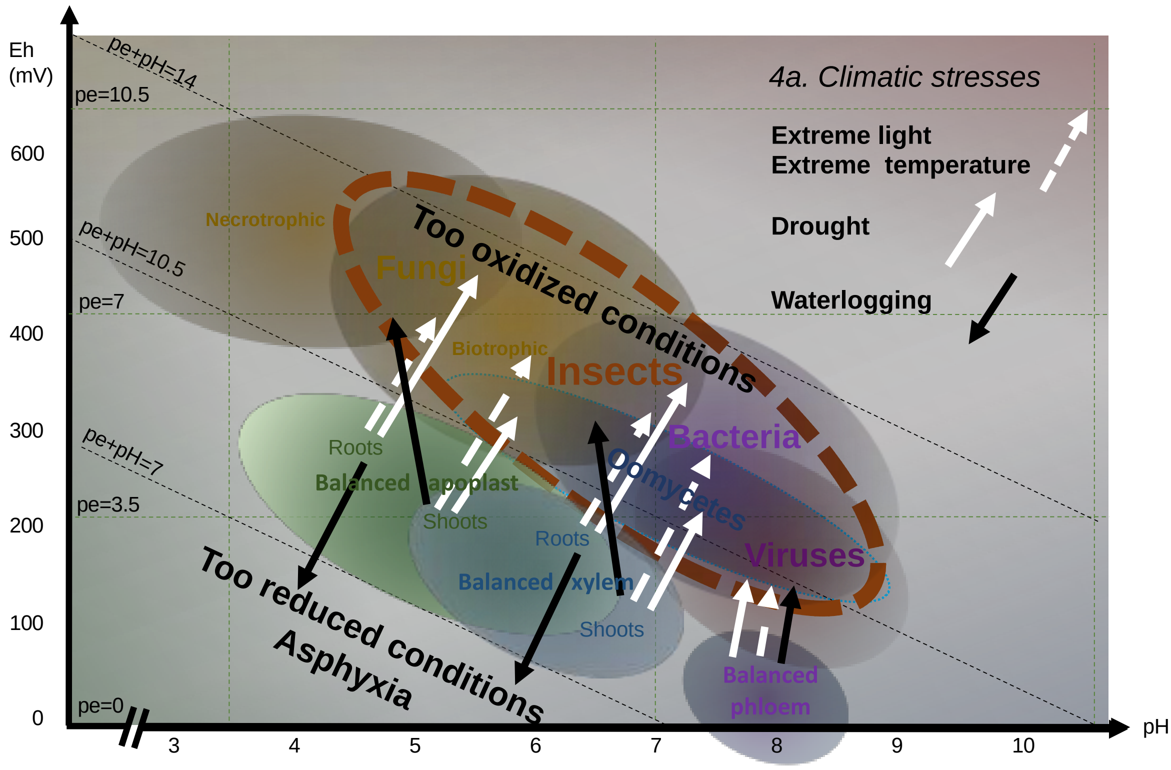
However, it should be clearly stated that these are only major trends observed, which should not be generalized without caution. They are based on "mean" plant Eh-pH conditions, diffferences between varieties can be as important as differences between species, and local conditions in the different plant compartments also have to be considered, and related to specific pathogens or pests and their requirements.

Can Eh-pH imbalance related to abiotic stresses explain plant susceptibility, tolerance and resistance to pests?

A common feature in the response to all stresses is the onset of oxidative stress through the production of ROS (Carvalho et al. 2015; Sewelam et al. 2016). One of the earliest responses of plants to pathogens, wounding, drought, extremes of temperature or physical and chemical shocks is the accumulation of ROS such as superoxide, hydroxyl radicals, hydrogen peroxide, singlet oxygen, etc. The oxidative stress that often ensues with and following infection is a widespread phenomenon. It is extensively observed in plants exposed to most, if not all, biotic and abiotic stresses (Shao et al. 2008). Plants synthesize a large pool of antioxidants such as ascorbate, tocopherol, and proteinaceous thiols (thioredoxin, peroxiredoxin and glutaredoxin) that interact with

ROS to maintain redox homeostasis (Kapoor et al. 2015). Thus, during stress, the requirements for energy increases with the intensity of respiration from exergonic processes, and plant's entropy also increases (Dragičević 2015). As a consequence, most abiotic stresses generally result in oxidation with an exception being in roots during waterlogging-flooding. Similarly, abiotic stresses, most often, lead to apoplast alkalization. This systemic pH increase may be a secondary effect without functional implications that results from ion movements or proton-pump regulation. There is increasing evidence that apoplast alkalization is part of a mechanism to withstand stress (Geilfus 2017).

A schematic summary highlighting the impacts of major abiotic stresses on plant Eh-pH homeostasis is presented in Figure 4 with zones indicating where the main pest groups can thrive optimally. It is important to recognize that waterlogging, drought (Fig. 4a) and salinity (Fig. 4b) stresses are most directly encountered by roots although the effects may be manifest throughout the plant (Bostock et al. 2014). This is also the case when soil imbalances occur (pH, Eh, mineral deficiency, toxic elements etc.). In contrast, light, temperature (Fig. 4a) and air pollution are most directly encountered by aerial parts. This Fig. 4 illustrates how plants could become susceptible to various diseases following abiotic stresses in relationship to oxidation, or inversely, why waterlogging reduces diseases caused by fungi such as *Fusarium poae* (Martínez et al. 2019).



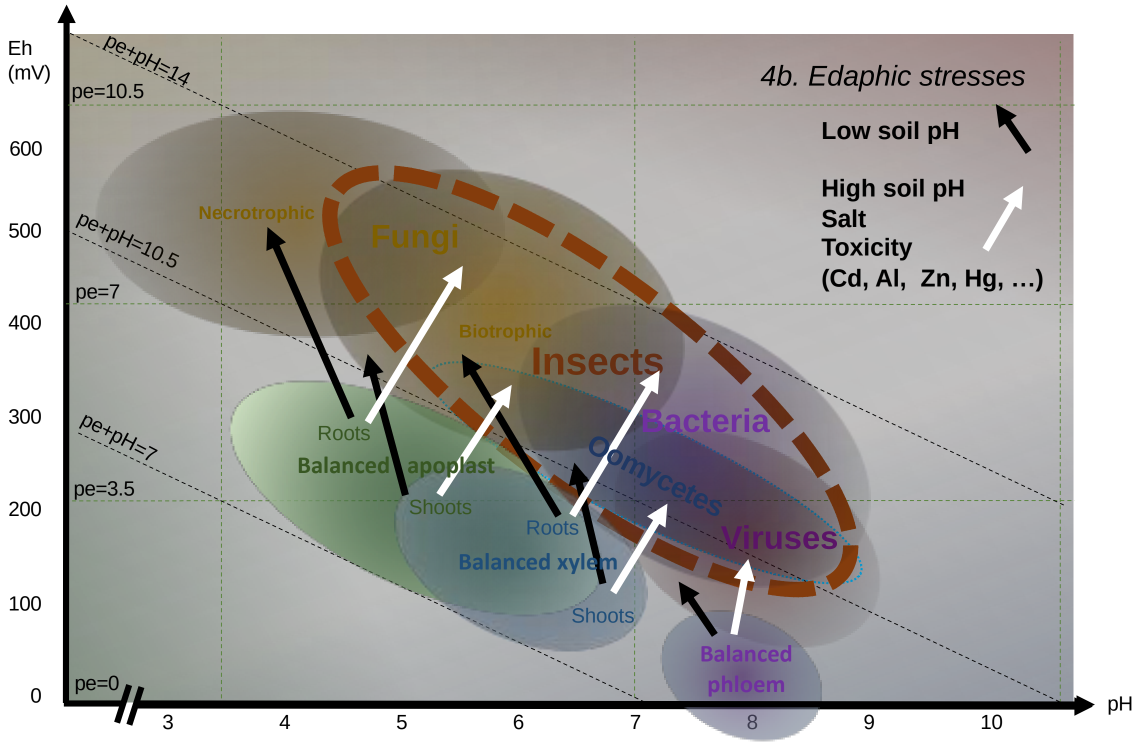


Fig. 4: Impact of abiotic stresses leading to unbalanced redox conditions in plant parts (pH-Eh map) in relation zones indicating optima where the main pest groups can thrive (adapted from Tables 1 and 2). 4a. Climatic stresses. 4b. Edaphic stresses. Edaphic stresses often lead to plant oxidation and increased plant susceptibility except for waterlogging that results in root asphyxia and, shoot oxidation or acidification. Low soil pH leads to further acidification in the rhizosphere, while high soil pH results in further alkalization of the rhizosphere.

Variations of plant Eh-pH following stress has been correlated with increased susceptibility to various types of pests (Schoeneweiss 1975). Abiotic stresses can predispose plants to potentially aggressive hemi-biotrophic pathogens to result in severe disease despite very low levels of inoculum. Perhaps the most pronounced impact of abiotic stress is to facilitate diseases caused by opportunistic or facultative pathogens and those present in association with their hosts such as epiphytes or endophytes (Lamichhane 2015). An example is the root- and crown-infecting pathogens *Pythium ultimum* and *Fusarium spp*.; air-borne pathogens, such as *Alternaria* spp. and *Botrytis cinerea*; and many canker-causing pathogens of woody perennials (Bostock et al. 2014). For instance, summer heat is conducive to epidemics of cytospora canker of *Alnus* (Worrall et al. 2010).

In contrast, abiotic stresses can also result in reduced incidence or severity of diseases caused by obligate or biotrophic, pathogens. Exceptions are diseases caused by some viruses, fungi, and nematodes (Bostock et al. 2014). Thus, pathogen infection on already drought-stressed plants can either result in plant resistance to pathogens, through drought-induced activation of basal defense mechanisms or, inversely, can result in susceptibility due to a weakened basal defense (Bertrand 1976).

To understand how abiotic stresses, including the edaphic ones, can either increase or decrease plant susceptibility to various pests, a dynamic approach is required and additional parameters must be considered, namely: i) the intensity and duration of the stress since abiotic stresses occurring prior to infection affect susceptibility of plants in different ways; ii) the synergistic occurrence of multiple stresses and their combined effects (Lamichhane 2015); and iii) availability of anti-oxidant pools in the plant, their ability to counterbalance the oxidative stresses and their possible exhaustion.

Predisposition, acclimation, priming effect, exhaustion and death in a "redox" perspective

Stress may affect plant diseases through a range of effects on the pathogen, host, or the host-pathogen interaction. The concept of predisposition implies an effect on the host rather than on the pathogen (Sorauer 1974). Stresses or nutrition that cause stomatal closure or formation of a thicker cuticle may prevent invasion by pathogens. In some cases, however, pathogens may enter a plant regardless of stress and affect disease development more than infection (Schoeneweiss 1975). Drought-induced pathogen resistance is presumably due to enhanced induction of antimicrobial and PR-proteins activated by drought. These compounds can protect plants during early stages of pathogen infection. Plant susceptibility to drought may be attributed to high levels of ABA in drought stressed plants since this hormone interferes with pathogen-induced plant defense signaling and thereby reduces the expression of defense-related genes (Ramegowda and Senthil-Kumar 2015).

Bostock et al. (2014) developed a model of plant response to integrate the general adaptation syndrome with the concept of disease severity, disease duration and disease predisposition. In this model, there is an alarm stage following an abiotic stress event which corresponds to the maximum predisposition before the acclimation-resistance stage (maximum resistance) to conclude with a final collapse, exhaustion and death stage.

In an Eh-pH perspective (Fig. 5a), this could be seen as a first phase for the increase in ROS (and ABA) that is followed by the production of antioxidants and phytoalexins by the plants (acclimation stage, maximum resistance). The collapse stage could be regarded as the exhaustion of the antioxidant capacity of the plant that leads to a further increase in oxidation level. The collapse, exhaustion and death phase could, therefore, be split into two sub-phases: i) a high susceptibility phase that could still be reversible, especially to viruses and necrotrophic pathogens, that is related to strongly oxidized conditions upon exhaustion of antioxidants, and ii) a death phase related to irreversible oxidation. Furthermore, the high production of antioxidants following ROS activation after a moderate stress could have a priming effect to induce a greater capacity to respond to further stimulus, lowering the plant redox state, and, thus, preparing it for a rapid response in case of pest attacks. One hypothesis could be that plants that sustain a lower Eh level can more readily produce reduced primary and secondary metabolites such as phenolics, SA and phytoalexins or redox regulated molecules such as plant pathogenesis-related proteins (Fobert and Després 2005; Balmer et al. 2015). Indeed, compounds that induce priming are reported to promote stronger and faster responses to stress by modulating the oxidative environment and interacting with signaling pathways mediated by SA, JA and ET (González-Bosch 2018).

Stress intensity, stress duration, multiple stresses and cumulating oxidative stresses

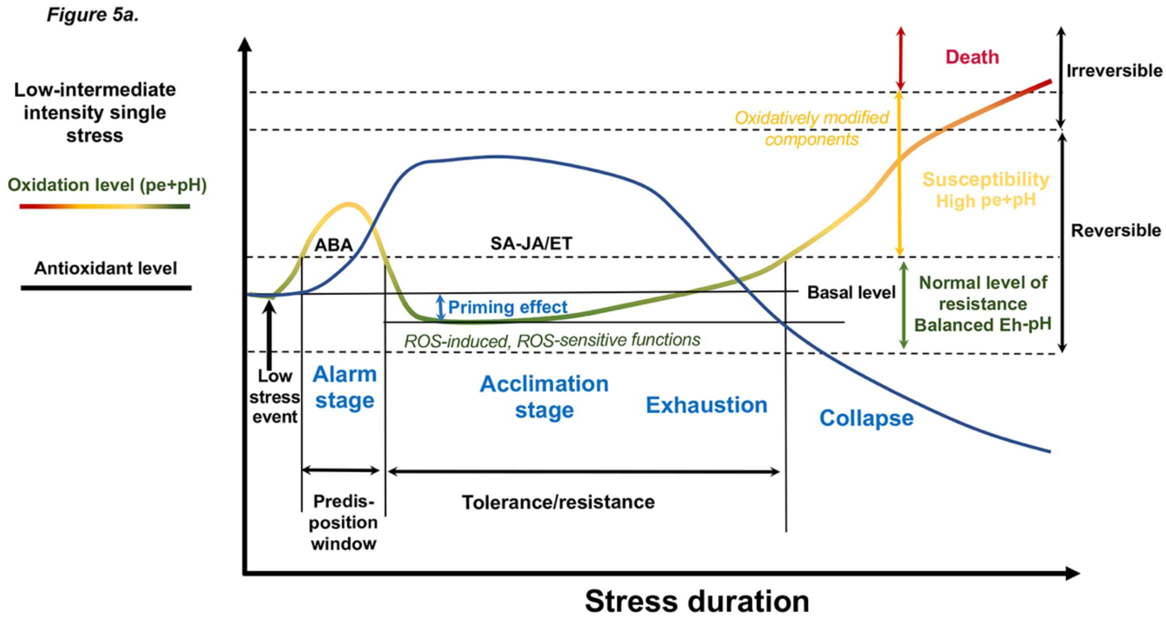
Under natural conditions, biotic and abiotic stresses frequently co-occur. As a consequence, common molecular signaling pathways governing adaptive responses to individual stresses can interact (Nguyen et al. 2016). A mechanism to study multiple-stress interactions (Bateman, 1978) recognizes that plant responses to a combination of stresses such as heat and drought may differ from those to individual stresses. Abiotic stress applications are likely to influence plant-pathogen interactions and vice versa (Prasch and Sonnewald 2015). For instance, when applied in combination, drought and herbivory had an additive effect on specific processes involved in secondary metabolism and defense responses, including protease inhibitor activity (Nguyen et al. 2016). Abiotic and biotic stress interactions can occur at multiple levels, depending on the type of stress (osmotic, ionic), growth characteristics, infection strategy of the pest (biotroph-necrotroph, mode of infection by direct penetration or through plant openings such as stomata, etc.) or infection stage of the host (Kissoudis et al. 2014).

Molecular and biochemical studies indicate that there are extensive overlaps in abiotic and biotic stress responses and there is some evidence for a universal stress response transcriptome for which a model involving the recruitment of ROS and phytohormones to sequentially engage defense responses has been proposed; however, it is unclear how the sequence is disrupted by predisposing stress events (Bostock et al. 2014). Plants use common pathways and components in the stress-response relationship. This phenomenon, which is known as cross-tolerance, allows plants to adapt or acclimate to a range of different stresses following exposure to one. Redox signals appear to have a central role in these common pathways (Pastori and Foyer 2002).

In their seminal review on enhancing crop resilience to combined abiotic and biotic stress, Kissoudis et al. (2014) showed that stress factors affect the homeostasis of chemical signals in the apoplasm such as Ca^{2+}, ROS, and pH levels. A combination of abiotic stress with pathogen infection potentially derails hormone and systemic ROS homeostasis. Under multiple stresses, the intensity of one stress affects the plant's responses to further stresses. For instance, plants exposed to mild drought stress activate the basal defense response that enables them to defend against pathogen infection. In contrast, severe drought causes leakage of cellular nutrients into the apoplast that facilitates successful pathogen infection (Ramegowda and Senthil-Kumar 2015).

Considering both the oxidative stress and the regulation of antioxidant systems, Lushchak (2014) proposed four levels of an intensity-based classification of oxidative stress, namely: i) a basal oxidative level; ii) a low intensity oxidative stress, in which markers of ROS-induced and ROS-sensitive functions can be measured; iii) an intermediate intensity oxidative stress, and iv) a high intensity oxidative stress where markers of oxidatively modified components dominate.

In the proposed hypothesis in this paper we integrate the various models and classifications through an Eh-pH perspective. Consideration of oxidative stresses in combination with plant responses (antioxidant systems in interaction with hormones) results in a dynamic and spatialized plant Eh-pH model (Fig. 5). In this model, low to moderate stress after an alarm stage (predisposition upon oxidation), leads to the production of antioxidants (in relation to ABA) and priming of plant defense mechanisms and decreased plant susceptibility in an acclimation stage in which SA, JA-ET induce SAR-ISR.



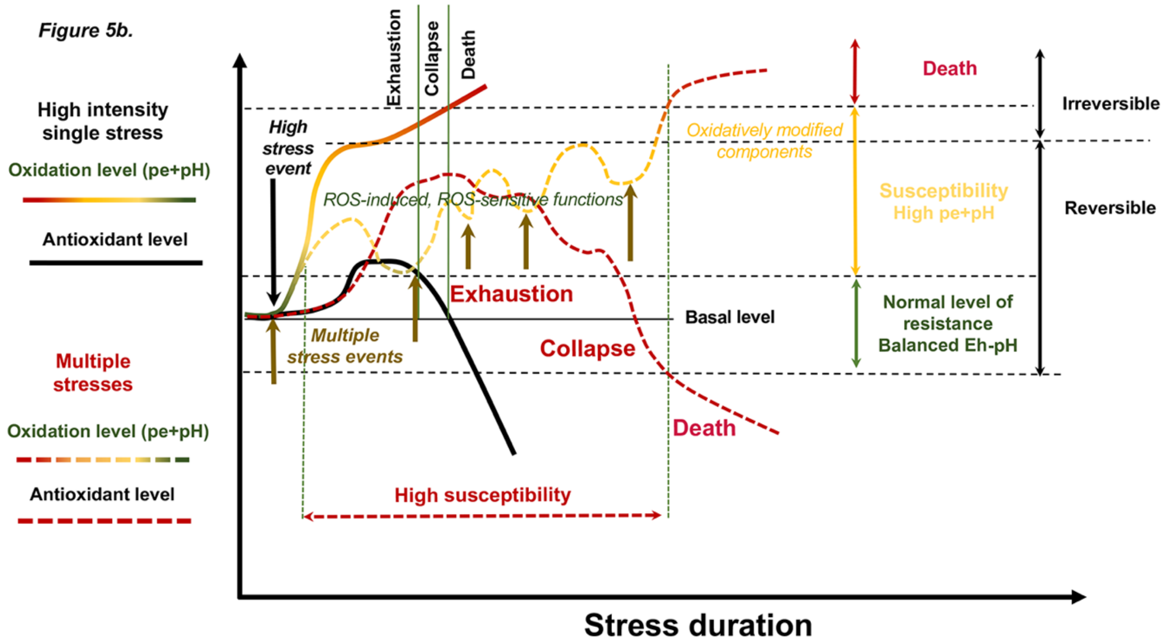


Fig. 5. Model of plant responses to abiotic and biotic stresses and disease predisposition by combining models from Bostock et al. (2014) and Lushchak (2014) in an Eh-pH perspective. 5a. Low to intermediate stress intensity of long duration. 5b. High stress intensity and multiple stresses. Production of antioxidants after a moderate stress induces an acclimation stage, but exhaustion of the antioxidant pool. Upon high intensity, multiple stresses or long stress duration leads to plant cell collapse and death. The stronger the abiotic stress or the higher the number of simultaneous stresses, the faster the exhaustion (the shorter the tolerance-resistance phase). The longer the stress or more consecutive stresses, the higher the risk of exhaustion of antioxidants. As long as ROS-induced and ROS sensitive functions can be sustained, oxidation-susceptibility can be reversed. Upon exhaustion of antioxidant pools, strong oxidation leads to irreversible collapse and death.

High intensity stress or multiple combined stresses lead to a rapid increase in oxidative stress and a rapid exhaustion of plant antioxidant pools and results in increased susceptibility to pests, without possibility of acclimation (Fig. 5b). Several observations suggest that there is a critical glutathione status below which the accumulation of pathogen-defense related molecules is inhibited and, consequently, disease resistance is impaired (Noctor et al. 2011). Similarly, consecutive multiple stresses, or prolonged single stress lead to progressive exhaustion of antioxidant capacity and increased plant oxidation to ultimately result in irreversible collapse and death.

Photosynthesis, the primary mechanism for reduction, is also fundamental in restoring the antioxidant pools by regenerating NADPH (Reduced Nicotinamide Adenine Dinucleotide Phosphate; mid-point potential: Em NADP+/NADPH= -320 mV) which then results in regeneration of GSH (Em GSSG/GSH: -230 mV) and ASC (Em DHA/ASC: + 90 mV; Noctor 2006). Paradoxically, chloroplasts produce various forms of ROS, and photosynthesis also produces H_2O_2 in the peroxisomes because of photorespiration (Exposito-Rodriguez et al. 2017). These ROS play an important role in signaling, but they also need to be scavenged to sustain redox homeostasis. Removal of H_2O_2 in chloroplasts occurs through ASC-dependent and TRX-dependent pathways (Foyer and Shigeoka 2011). One of the effects of oxidative stress is to decrease chlorophyll biosynthesis (Aarti et al. 2006) so that oxidative stresses generally decrease photosynthesis. Following exhaustion of antioxidant pools, redox imbalance negatively alters photosynthesis and thus alters the plant's capacity to regenerate antioxidant pools.

This model of Eh-pH homeostasis, as a central component of plant health, proposes a coherent perspective by deciphering the multiple interactions between abiotic stress and plant susceptibility, tolerance and resistance to pests. The model introduces a framework explaining how abiotic stresses can alter plant–pest interactions by enhancing host plant susceptibility or, inversely, by priming tolerance to pests in relation to antioxidant pools in the plant. This model may also be useful to decipher the poorly understood interactions among multiple biotic stresses acting simultaneously or, to the contrary, to understand how some pests may alter plant response to abiotic stresses (Pandey et al. 2017).

Can Eh-pH imbalance related to biotic stress explain biotic-biotic interactions and cohorts of pests?

Studies of plant–pathogen interactions have historically focused on simple models of infection involving single pathosystems. In contrast, in the wild, microbes are part of complex multispecies consortia-communities (Lamichhane and Venturi 2015). Plant infections often involve multiple species or genotypes and exhibit complexities that are not captured in individual pathosystems (Abdullah et al. 2017). Simultaneous infection of a single plant by various pathogens has been recognized as an important modulator of host resistance and a driver of pathogen evolution (Tollenaere et al. 2017). Even commensal bacteria can enhance virulence of opportunistic pathogens via cross-metabolism. For example, *Streptococcus gordonii* enhances the bioavailability of oxygen during infection to allow *Aggregatibacter actinomycetemcomitans* to shift from a primarily fermentative to a respiratory metabolism that promotes its growth and persistence (Stacy et al. 2016). Mechanistically, respiratory metabolism enhances the fitness of *A. actinomycetemcomitans in vivo* by increasing ATP yields via central metabolism and creating a proton motive force (Stacy et al. 2016). Furthermore, host plant nutrition can significantly influence the growth and condition of phytophagous insects that influence their susceptibility to pathogens (Shikano et al. 2010).

The recognition of Eh-pH niches specific to each pest could help decipher the three main types of interactions in co-infection systems (Seabloom et al. 2015; Abdullah et al. 2017): i) competition, in which competing pathogens develop physical barriers or utilize toxins to exclude competitors as reported for *Fusarium verticilloides* and *Ustilago maydis* in maize (Jonkers et al. 2012). This may involve interactions between pests that have different Eh-pH optimum conditions with each one altering these conditions to enhance its fitness for its own benefit at the expense of the others; ii) cooperation, whereby pathogens beneficially interact, by providing mutual biochemical signals essential for pathogenesis. This could be regarded as pathogens having similar Eh-pH optimum conditions. Similar Eh-pH niches could potentially explain the many fungi-fungi, virus-virus and bacteria-bacteria synergistic interactions as reviewed by Lamichhane and Venturi (2015) or mixed infections for example as reported for Rice Yellow Mottle Virus and *Xanthomonas oryzae* in rice (Tollenaere et al. 2017); and iii) coexistence, whereby pathogens can stably coexist through niche specialization.

Similarly, the Eh-pH perspective proposes a framework to explain how a pathogen can render a host: i) more vulnerable to other pathogen attacks, as is the case of *Pseudomonas syringae* predisposing plants to invasion by the necrotrophic ascomycetes *Alternaria brassicicola* or *Albugo candida* that allow subsequent infections by several opportunistic pathogens (Abdullah et al. 2017). This induced susceptibility by development of the first pathogen might be attributed to a further imbalance of Eh-pH in the various plant compartments (apoplast, xylem, phloem, intracellular); ii) more resistant through the induction of a systemic defense-signaling cascade that restores Eh-pH conditions unfavorable to pathogens that confers resistance to subsequent attacks, as exemplified by *Pseudomonas fluorescens* (Ongena et al. 2005).

The Eh-pH homeostasis hypothesis could also help explain how above-ground infestation of whitefly (*Bemisia tabaci*) in peppers (*Capscicum annuum*) can induce below-ground resistance against the gram-negative *Ralstonia solanacearum* that develops in an aerobic, alkaline condition through SA-dependent signaling, that leads to an increase of root-associated gram+ bacteria (Yang et al. 2011). This perspective may also explain how a host plant's nutritional status can significantly influence the growth and condition of phytophagous insects and, consequently, the susceptibility of the latter to pathogens (Shikano et al. 2010). Finally, this hypothesis might help clarify the 'crosstalks' among hormones involved in plant defense and help improve the model of SA-mediated defense against biotrophs and JA-ET-mediated defense against necrotrophs. The latter model is currently regarded as being too simplistic since defense responses are thought to be fine-tuned not only to particular plant–pathogen combinations (Abdullah et al. 2017), but also to multiple biotic and abiotic stresses and co-infections.

Revisiting mineral nutrition and plant-pest interactions with an Eh-pH perspective

Interactions between mineral nutrition and plant pests include how nutrient supply alters pest prevalence and influences competitive interactions among coinfecting pathogens (Lacroix et al. 2014). However, several reviews (Datnoff et al. 2007; Huber and Haneklaus 2007; Amtmann et al. 2008; Dordas 2008; Spann and

Schumann 2010; Huber et al. 2011; Elmer and Datnoff 2014; Gupta et al. 2017; Shah 2017) highlight inconsistent and, in some cases, contradictory results because (i) no information was available whether the supply of these nutrients was low, optimal or excessive relative to plant needs; (ii) the form of N or other nutrients supplied (e.g., ammonium or nitrate which are metabolized differently) were not provided; and iii) lack of consideration for differences in infection patterns between obligate and facultative parasites (Huber et al. 2011). Other sources of inconsistency can be related to interactions between elements (co-application, antagonism, synergy), the time of application (Amtmann et al. 2008; Elmer and Datnoff 2014), the crop developmental stage at the time of nutrient application (Dordas 2008); soil type and general growing conditions, especially pH, and other possible plant stresses (water, temperature, biotic stress, etc.). Furthermore, the mode of entry of the pathogens, and the plant tissue involved first (leaf or root, apoplast, xylem or phloem) and the plant physiological stage at which they develop. Although the effect of these situations may be well known, they frequently are not considered in the published studies. Many of these studies attributed the form of N to pH conditions even though Eh conditions are as important as pH relative to N forms. For example, the NH_4^+ form is dominant at low pe+pH (<14) while NO_3^- dominates at higher pe+pH (Husson, 2013).

An Eh-pH perspective in relation to plant nutrition and entry point of pathogens that defines various types of pests and characterizes spatio-temporal variations in a plant’s susceptibility or resistance to them and feeding modes of pests, could shed light on these interacting processes and identify consistencies that are currently lacking. This section illustrates the importance of a spatialized and dynamic Eh-pH perspective by providing a few examples.

N nutrition and plant-pest interactions in an Eh-pH perspective

Nitrogen availability for plants is one of the most important factors influencing disease development (Elmer and Datnoff 2014; Gupta et al. 2017); however, the mechanisms by which N affects disease development remains elusive and sometimes appears inconsistent (Gupta et al. 2017). Nitrogen-deficient plants may not provide the nutrient environment necessary for obligate pathogens, whereas nitrogen excess may inhibit the production of defense responses to other pathogens (Elmer and Datnoff 2014). Nitrogen is an essential component of amino acids, enzymes, hormones, phenolics, phytoalexins, and proteins. Interestingly, all of these molecules have direct effects on disease development (Elmer and Datnoff 2014; Gupta et al. 2017), and are involved in redox homeostasis.

Most of the conflicting reports regarding the role of nitrogen in plant disease may be due to a failure in recognizing and reporting the form of nitrogen used in the experiments (Elmer and Datnoff 2014). In their review of nitrogen and plant diseases, Huber and Thompson (2007) highlighted that application of nitrogen under unspecified form resulted in an increased and decreased disease level in 20 and 22 cases, respectively. Similarly, NH_4^+-N application resulted in an increased and decreased disease level in 8 and 16 cases, respectively. Likewise, NO_3^--N application led to an increased and decreased disease level in 11 and 9 cases, respectively. Earlier, Huber and Watson (1974), reported an increase and decrease in diseases level due to NH_4^+ nutrition in 24 and 20 cases, respectively while they reported an increase and decrease in diseases due to NO_3^- in 20 and 24 cases, respectively.

A careful consideration about how the N-form impacts plant Eh-pH homeostasis in its different compartments provides an interesting perspective that helps disentangle the interactions between N-form of nutrition and pests and pathogens (Fig. 6).

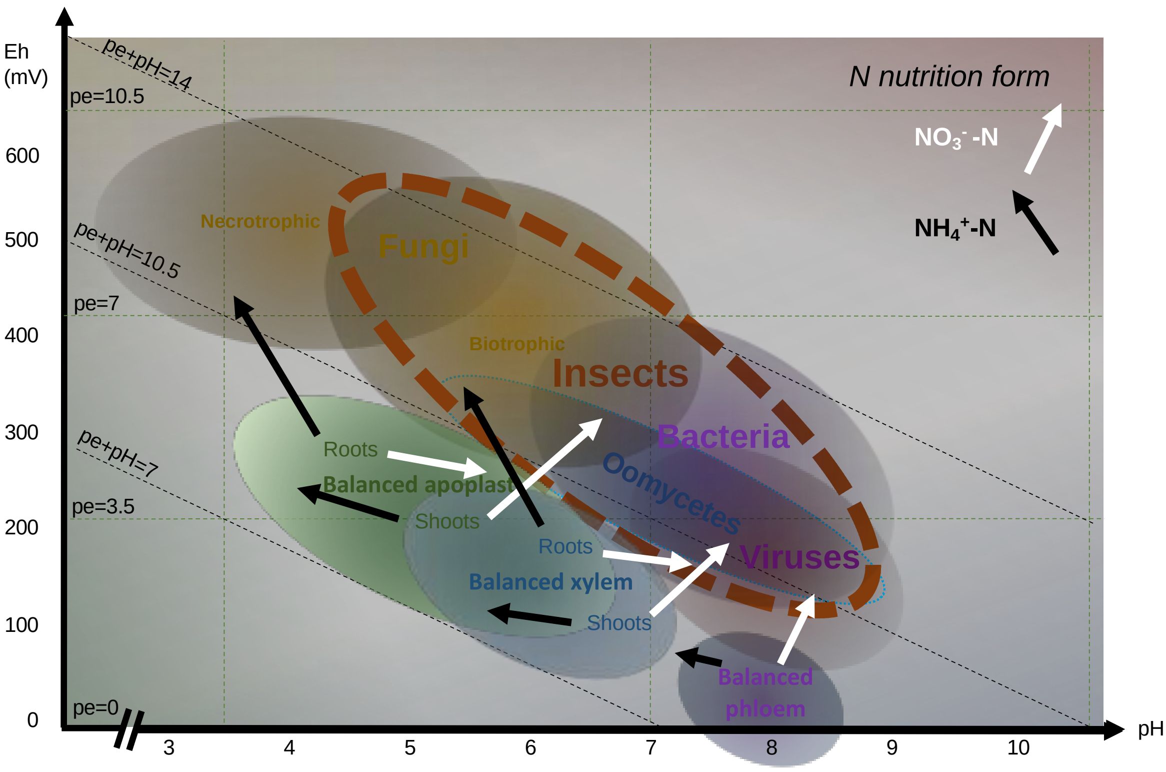


Fig. 6: Impact of N-form of nutrition, creating unbalanced redox conditions in plant parts (pH-Eh map) in relation to optimum zones where the main groups of pathogenic microorganisms and pests can thrive. NH_4^+ absorption (red arrows) leads to plant acidification, reduction (decreased pe+pH) of shoots but oxidation of roots. NO_3^- absorption (yellow arrows) leads to plant alkalization, with shoots oxidation and roots reduction (Table 9). More generally, absorption of cation leads to acidification and absorption of anion leads to alkalization, as biochemical and biophysical stat mechanisms maintain stat status in the plant. However, nitrogen as a remarkadely stronger impact than other elements as NH_4^+ and NO_3^- amount to 80% of the total anions and cations assimilated by plants (Marschner 1995).

By considering the type of pests and the part of the plant they infect first, we present clear patterns of disease severity (Huber and Watson 1974) that are in accordance with local Eh-pH conditions induced by N-form of nutrition:

- Soil-borne fungi that penetrate plants from the roots (*Rhizoctonia* spp., *Fusarium* spp., *Armillaria* spp., *Sclerotinia spp.* spp., *Helminthosporium* spp., *Cercosporella* spp., *Thielavopsis* spp., *etc.*) are decreased by nitrate and increased by ammonium (14 cases out of 16). This is in agreement with increased root pH and decreased root Eh by nitrate nutrition given that these fungi thrive at low pH and high Eh, and that ammonium nutrition leads to strong rhizosphere acidification. In contrast, soilborne fungi increased by nitrate nitrogen and actinomycetes such as *Gaeumannomyces spp*. and *Streptomyces spp.* are reduced by ammonium.

- Fungi of aerial parts and xylem-apoplast (*Poria = Stenocarpella* spp., *Verticillium* spp.) are increased by nitrate and decreased by ammonium (4 cases over 4). This is in accordance with lower Eh in aerial parts of ammonium-fed plants.
- Soil-borne oomycetes are either decreased by nitrate and increased by ammonium (*Aphanomyces* spp., *Phytophthora* spp.: 3 cases out of 3) or increased by nitrate and decreased by ammonium (*Pythium* spp.: 2 cases out of 2). This is in agreement with the facts that zoospore's germination is optimal for this pathogen at high pH of 7-8 (Davet 2004). Likewise, *Aphanomyces* spp. infection is the most severe at low soil pH (<6.5; Payne et al. 1994). Finally, zoospores of *Phytophthora palmivora* are anodotactic while those of *Pythium aphanidermatum* are cathodotactic (van West et al. 2002).
- Virus-like diseases are decreased by ammonium application (5 cases out of 6) while they are increased under nitrate nutrition (2 cases out of 2). This confirms that the acidification and reduction of aerial parts of the plant under ammonium nutrition, while many viruses require alkaline and oxidized conditions.
- Foliar and vascular bacterial pathogens (*Pseudomonas* spp., *Erwinia* spp., *Corynebacterium* spp.) are increased by nitrate application (4 cases out of 5) consistent with the increased pH related to nitrate nutrition, where most pathogenic bacteria thrive at high pH.
- Nematode galls are increased by nitrate and decreased by ammonium nutrition (2 cases out of 2). This confirms an increased root pH by nitrate fertilization (and inversely acidification by ammonium) and that *Heterodera glycines* is favored by high pH (Pedersen et al. 2010).

Similar conclusions can be drawn from the review by Huber and Thompson (2007). These authors reported increased disease with nitrate and decrease with ammonium nutrition of air-borne fungi such as *M. oryzae, Alternaria macrospora, Monilinia vaccinia-corymbosi, etc.*, viruses and nematodes (*Pratylenchus penetrans*), and a decrease with nitrate. Ammonium nutrition of soil-borne fungi (*Fusarium* spp., *Rhizoctonia* spp., etc.) had the opposite effect. Thus, this dynamic and spatialized Eh-pH perspective can help decipher multiple contrasting interactions. For instance, in winter wheat, foliar and ear disease severity were positively associated with plant N uptake, use of mineral fertilizers, use of low leaf phenolic-flavonoid concentration, and short-straw variety "Solstice" (overall consistant with oxidized growing conditions in plants). In contrast, severity of the same diseases were negatively associated with the inputs of composted farm yard manure, leaf phenolic-flavonoid concentrations, and use of the long-straw variety "Aszita" which is rich in the phenols and flavonoids that maintain plants in a reduced condition (Rempelos et al. 2020).

Nitrogen application also strongly affects insect damage. Plant nutritional quality and plant defenses that directly act on herbivores are altered by nitrogen fertilization, and herbivorous insects can distinguish plants receiving different nitrogen applications. Nitrogen fertilization results in higher occurrence and more crop damage from herbivorous insects by reducing plant resistance, and also increases sucking pests in 55% of the studies (Shah 2017). This is in agreement with an increase in Eh and pH conditions in nitrate-fed plants. This Eh-pH homeostasis perspective could also be used to analyze the incidence of insect pests under mineral vs organic fertilizations (Altieri and Nicholls 2003).

Micronutrients and plant-pest interactions in a Eh-pH perspective

Manganese is a good illustration of the benefit in considering Eh-pH to decipher relations between mineral nutrition and plant pests. Mn absorption is strongly influenced by soil-rhizosphere Eh-pH conditions, and is soluble only in its reduced form (Mn^{2+}), at low pe+pH. Mn has a tremendous impact on plant Eh-pH. Of central importance are its structural, redox and electron transport roles in photosynthesis, which results in the splitting of water and electron harvesting during the light reaction. Aside from Mn superoxide dismutase and a few Mn containing enzymes, Mn functions primarily as an activator of enzymes, including dehydrogenases, transferases, hydroxylases and decarboxylases (Thompson and Huber 2007).

Due to its role in plant Eh-pH regulation, it is not surprising that Mn availability reduces diseases in 89% of the cases (reviewed by Thompson and Huber (2007)). All the conditions leading to Mn reduction and, thus to its increased availability, decreased the development and severity of pathogenic fungi such as *Gaeumannomyces graminis* and *M. oryzae*. Interestingly, these pathogens possess the ability to oxidize Mn, and their virulence depends on this capacity. Mn oxidation was, thus, highly correlated with fungal virulence and disease development (Thompson and Huber 2007). The battle for Mn between host and bacterial pathogens, in relation to oxidative stress, was, indeed, a major determinant defining the outcome of infections (Juttukonda and Skaar 2015).

Other essential micronutrients in redox regulation have a strong impact on a large range of pests. Examples are sulfur (Bloem et al. 2005), copper and boron, which were reported to decrease diseases in 93 and 91% of the studied cases, respectively (Datnoff et al. 2007).
The first-row transition metals—manganese (Mn), iron (Fe), cobalt (Co), nickel (Ni) and copper (Cu)—provide the necessary redox and catalytic activity for many important biological processes (Ranieri et al. 2001; Bárcenas-Moreno et al. 2011; Gerwien et al. 2018). A process aptly named 'nutritional immunity' makes the host actively sabotage and counteract metal uptake by microorganisms and it can also fight invaders by deploying toxic levels of certain metals. Iron, Cu and Mn, for example, are intrinsically toxic via Fenton chemistry (generation of oxygen radical species from hydrogen peroxide, catalyzed by the metal), leading to oxidative damage to the microbes at high metal concentrations (Gerwien et al. 2018). Finally, silicon, which has been reported to play an important role in resistance to fungal and bacterial diseases, and to herbivory (Epstein 1994; Fauteux et al. 2005; Sakr 2016; Liu et al. 2017), is also known to improve antioxidant capacity and redox homeostasis (Manivannan et al. 2018; Soundararajan et al. 2018). For example, silicon induces resistance of cassava to bacterial blight by altering antioxidant enzyme activity (Njenga et al. 2017).

Revisiting pathogenicity and virulence in an Eh-pH perspective

The Eh-pH perspective described herein provides a simple answer to the question "what makes commensal or opportunistic microorganisms become pathogenic?" The answer is that "A commensal or opportunistic microorganism becomes pathogenic when it encounters or can develop Eh-pH niches favorable for its development".

This hypothesis is supported by the fact that pH has now been recognized as a key factor in reducing fungal pathogenicity (Fernandes et al. 2017). In addition, cellular redox balance may serve as an inducer for the defense-related genes, including pathogenesis-related proteins (Foyer 2005). Oxalic acid indirectly aids *Sclerotinia sclerotiorum* pathogenicity by acting as a signaling molecule via manipulation of host ROS (Williams et al. 2011). Furthermore, ROS and redox regulation are also involved in the perception of pests and activation of plant defense. For instance, mitogen-activated protein kinase cascade, involved in pattern-triggered and effector-triggered immunity, is activated and regulated by ROS (Bigeard et al. 2015; Liu and He 2017).Indeed, the Rice Yellow Mottle Virus-encoded viral suppressor of RNA silencing P1 is a protein with redox-dependent flexibility (Gillet et al. 2013).

It can also be hypothesized that the virulence of a pathogen is related to its ability to alter and sustain host plant Eh-pH to its benefits despite the plant attempts to make it unfavorable, especially during the oxidative burst in the hypersensitive response (Torres et al. 2006). This is observed with *Sclerotinia sclerotorium* and *Botrytis cinerea* through oxalic acid production (Mbengue et al. 2016; Wang et al. 2016), or in bacteria through production of thiol antioxidants such as GSH and detoxification enzymes that consume ROS (Reniere 2018). Fungal pH modulations of the host environment regulate an arsenal of enzymes to increase fungal pathogenicity. This arsenal includes genes and processes that compromise host defenses, contribute to intracellular signaling, produce cell wall-degrading enzymes, regulate specific transporters, induce redox protectant systems, and generate factors needed by the pathogen to effectively cope with the hostile environment within the host (Alkan et al. 2013). The ability of the pathogen to actively increase or decrease its surrounding pH allows it to select the specific virulence factor, out of its vast arsenal, to best fit a particular host (Prusky and Yakoby 2003).

The evolution of pathogenicity towards novel hosts may be based on traits that were originally developed to ensure survival in the microorganism's original habitat, including former hosts (Van Baarlen et al. 2007). An Eh-pH perspective could help understand cross-kingdom host jumps or why and how pests can expand their host range. This perspective can also provide new insights on the "disease triangle" that integrate pathogenicity, host susceptibility, and environment. This can be done by stating that compatible interactions between a pathogen and a host will only result in disease symptoms when environmental conditions are also fulfilled (Van Baarlen et al. 2007). This review suggests that Eh-pH are major determinants of environmental conditions impacting pest-host interactions.

Microorganisms thriving in slightly reduced and acidic conditions could be commensal or even beneficial to plants in such situations; however, they may become detrimental when Eh-pH conditions change (especially increase in pe+pH) to alter their interactions. This could be the case for Cyanobacteria which exhibit characteristics of higher plants (photosynthetic organisms) as well as bacteria. These bacteria are able to reduce the effect of salinity by producing extracellular polysaccharide or compatible solutions, increase rice seed germination in drought situations, and remove pollutants (heavy metals and pesticides) from soil and water (Singh et al. 2016). Faced with biotic stresses, cyanobacteria are capable of producing a diversity of chemical compounds efficiently in addition to releasing various enzymes, competing for rhizosphere space and activating plant defense responses by interacting with plant roots. All these features represent an exploitable strategy against pests in agriculture (Singh et al. 2016). In the event of soil oxidation, however, this group of bacteria can contribute to iron starvation of plants because Cyanobacteria require large amounts of iron and have developed very efficeent mechanisms for iron uptake. They are very competitive with plants for this essential nutrient element (Kranzler et al. 2013).

Revisiting energy allocation and growth or defense trade-off with an Eh-pH perspective

The plant immune system should be tunable because the immune response is costly, making unnecessary activation a burden on plant fitness (Nobori and Tsuda 2019). An Eh-pH approach may provide a new perspective on the growth versus defense trade-off in plants as reviewed by Huot et al. (2014). A model of plant energy allocation under various conditions is proposed in Fig. 7, based on the Eh-pH perspective.

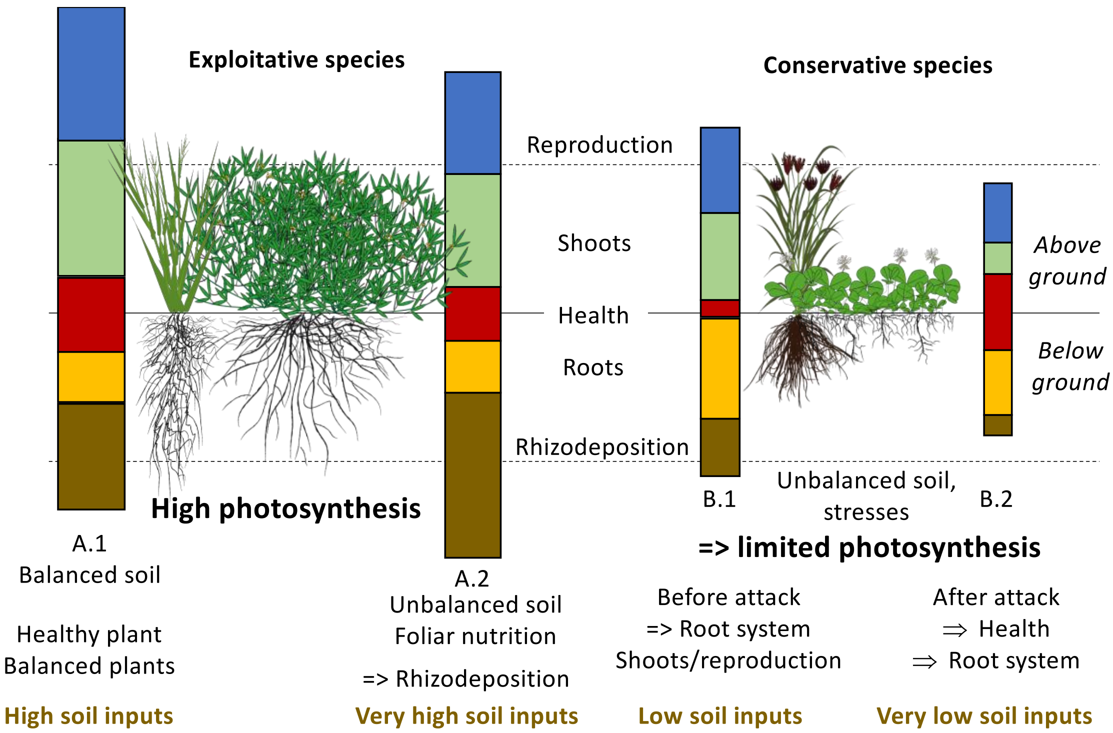


Fig. 7. Hypothesized model of energy allocation to reproduction, growth, health and rhizodeposition as a function of growing conditions. The energy investment distribution and aboveground-belowground interactions in this Fig. vary with plant strategies. A1: Under optimal soil conditions, the high energy produced by very efficient photosynthesis permits a balanced distribution of energy between vegetative growth, reproduction, health and root exudation, with the latter "feeding" the soil microorganisms. High amounts of exudates are released in the rhizosphere, but the high vegetative growth increases photosynthetic capacity, and thus energy production in a very sustainable cycle. Energy rich plants (balanced pH, Eh and pe+pH) are not attractive to pests and are able to sustain interactions unfavorable to pathogens since they accumulate secondary metabolites and also are not attractive to insects. A2: When soil imbalance is (partially) compensated for by efficient fertilization (especially through foliar application of elements in an accessible form), high photosynthesis can be

achieved. In order to restore the necessary soil balance, plants allocate a higher percentage of photosynthetic products to root exudation that selects and feeds a rich and balanced microflora. However, deficiency in various nutrients, including micronutrients, increases exudation of sugars, amino acids and phenolics (Cakmak and Marschner 1988; Carvalhais et al. 2011)*, at the expense of resources needed by the plant for growth and reproduction. B1: When photosynthesis is limited by various abiotic stresses (low light, extreme temperature, or soil imbalance that leads to nutrient deficiency, toxicity, etc.), energy production is low. In the absence of a pest, the available energy is mainly allocated to shoot and root growth and reproduction, with less, rhizodeposition to alter soil conditions favorable for plant health. The low energy allocated to plant health leads to high pH or high pe+pH and makes the plant attractive to pests and susceptible to pathogens. B2: Upon pest attack, the energy available for the plant is further decreased due to the reduction of photosynthetic activity, reduction of photosynthetic leaf tissues surrounding necrotic lesions, and reorientation of plant metabolism by the pathogen (Bastiaans and Kropff 1993; Berger et al. 2007). The plant then allocates most of its energy towards pest containment which limits its vegetative growth and, as a consequence, its photosynthetic capacity further. In a vicious circle, lower photosynthesis increases plant Eh-pH imbalance to increasing its susceptibility to pests.*

This model is based on a series of observations. First, the spatial variability of Eh-pH in plants is consistent with a new perspective of defense predicting that the allocation of defensive chemistry within a plant is a function of tissue or organ value in terms of fitness. In other words, tissues with higher predicted value (young leaves with high photosynthetic activity, thus lower Eh-pH, have significantly higher concentrations of defensive chemicals compared to less valuable older tissues (McCall and Fordyce 2010). Second, ruderal plants growing on highly disturbed soil, are anticipated to spend most of their energy in reproduction rather than in mutualism (rhizodeposition). Competitor plants are expected to invest their energy mainly in growth but also in defense (health) and mutualist microorganisms. At the end of the spectrum, stress tolerators growing in soil with low disturbance are anticipated to primarily invest their energy in pest defense and feeding mutualist microorganisms (De Deyn 2017).

Under favorable soil conditions, the plant traits that govern carbon and nutrient exploitation generally dominate. These traits include fast growth, low C:N root:shoot ratio, low secondary metabolite content, short lifespan, and short litter residence time (De Deyn et al. 2008). Plants having such a strategy regarding acquisition, use and conservation of nutrients, are regarded as exploitative plants (Guyonnet et al. 2018a). Where soil resources (nutrients, water, oxygen, pH) limit growth, plant traits that govern carbon and nutrient conservation generally dominate and are characterized by slow growth, high C:N root:shoot ratios, high secondary metabolite content, long (organ) lifespan and long litter residence time (De Deyn et al. 2008). These species exude less carbon in the rhizosphere but the exudate composition is different. Such species are regarded as conservative species. Under stress conditions such as drought, exploitative species reduce their growth and root exudation faster than conservative species to benefit from mycorrhizal symbiosis and increased fungal abundance. Upon long term-extreme stress, conservative species are expected to reduce their growth, exudation and transfer of C to microbes and thereby impacting mycorrhizal symbiosis. Under similar conditions, exploitative species will respond by root death, reduced growth and less root exudation and C transfer to microbes. On termination of stress, conservative species, although they have unaltered exudate quality, will resume C transfer to microbes, re-establish mycorrhizal symbiosis, and slowly regrow. Despite altered root exudate quality, exploitative species will transfer high amounts of C to microbes, favor Plant Growth Promoting Rhizobacteria and recreate a high bacterial abundance. This permits rapid mineralization of dead roots, microbes and native soil organic matter that releases large amounts of N and accelerates regrowth (Williams and de Vries 2019). All this illustrates the strong interplay between roots and the soil microbiome.

Eh-pH in the rhizosphere: interplay between roots and microbiota

On the asssumption that homeostasis is a focal point of ecology and evolution (Giordano 2013), the concept of Eh-pH homeostasis could bring an interesting perspective of soil-plant-microorganism interactions. In all ecosystems, plants transform the surrounding soil to make and maintain a habitat more favorable for growth (Marschner 1995). To this objective, plants shape the microbiome composition by selecting for specific microorganisms from the total pool of microorganisms in the bulk soil. These are then assembled into communities in the rhizosphere (Berg and Smalla 2009; Dini-Andreote and Elsas 2013). On the other hand, bacteria have developed various adaptation strategies to thrive in different rhizosphere niches (Jacoby et al. 2017). Microbial communities in the rhizosphere of different plant species growing on the same soil are often different, and some plant species can create similar communities in different types of soil. Even within species, different genotypes can develop distinct microbial communities in their rhizosphere. This suggests that plants are able to shape the composition of the microbiome in their rhizosphere (Berendsen et al. 2012), in such a way that both microbial density and activity in the rhizosphere are much higher than in bulk soil (Paungfoo-Lonhienne et al. 2010; Marschner 2011). Since root exudates play a key role in the establishment of plant-microorganisms interactions (Guyonnet et al. 2018a; Nobori and Tsuda 2019), plants probably shape common microbial communities as a result of these exudates (primary and secondary metabolites). Those that come from plant photosynthates are rich nutrient sources and include carbohydrates, organic acids and amino acids (Paszkowski 2006). Soil pe+pH contributes significantly to determine soil enzyme activities and differences in microbial composition and function (Wang et al. 2020).

Parameters such as pH, redox, ionic strength, water potential, and the concentration of nutrients and organic compounds are different in the rhizosphere compared to bulk soil (Jones et al. 2004). Under imbalanced soil conditions, plants alter rhizosphere Eh-pH towards neutral conditions (Krasil'nikov 1958; Hinsinger et al. 2003; Husson 2013). They do this through root exudates, as a result of passive diffusion or release under active processes for a specific purpose (Fischer et al. 1989; Jones et al. 2004). In both cases, plants rely strongly on microorganisms to alter and buffer rhizopshere soil Eh-Ph. Microorganisms are: i) adapted to specific Eh-pH conditions (and their fluctuations), ii) able to sense redox signals (redox-taxis), and iii) able to alter and adapt Eh and pH of their surrounding environment to their requirements to a much greater extent than other living organisms (Krasil'nikov 1958; Rabotnova and Schwartz 1962; Alexandre and Zhulin 2001; Pidello 2014). Indeed, soil bacteria are able to create networks with tiny electronic connections between electron donors and acceptors which is critical to electron transfer via electrical currents (Li et al. 2017). These networks enable microbial communities to rapidly eliminate electrons coming from their metabolic processes and transport them to distant electron pumps (Ball 2007; Ntarlagiannis et al. 2007). Soil microorganisms largely govern redox kinetics by producing enzymes that speed up redox reactions to release energy (Burgin et al. 2011; Gianfreda

2015). Under well-structured and biologically active soils, water bounding can be expected, knowing that bound water has a catalytic action and is known to facilitate electron and proton transfers (Ball 2008). These redox reactions between connections are also facilitated through soil electrical conductivity which is related to nutrient content, salinity, organic matter, pyrogenic carbon, cation exchange capacity, residual humidity, soil texture and soil compaction (Husson 2013). Electrical currents have actually been measured between roots and arbuscular mycorrhizae (Berbara et al. 1995).

When facing biotic stresses, plants react by changing the chemistry of their root exudates to assemble health-promoting microbiomes (Rolfe et al. 2019). Besides, plant roots alter soil structure, aeration and humidity to create microhabitats which can be seen as many Eh-pH niches (Krasil'nikov 1958; Fischer et al. 1989) compatible with microorganisms of various Eh-pH requirements. The joint activity of roots and microbes promotes physico-chemical heterogeneity in the rhizosphere with its spatial and temporal diversity in the local soil microhabitat (Dini-Andreote and Elsas 2013). While stochastic community assemblies dominate in homogeneous environments, deterministic community assembly processes are the rule in heterogeneous environments, hence, creating selective pressure for microorganisms (Dini-Andreote et al. 2015).

Plant roots, microbes and earthworms determine soil aggregation, especially near the surface of their biopores, either by enhancing aggregate diversity or by its homogenization. Roots lead to the formation of subpolyeders and shrinkage-induced cracks due to water uptake while earthworms form tiny platy and sheared structures because of their intermittently swollen body shape (Haas and Horn 2018). Close to the biopore surface (<1mm), roots have an acidifying effect while earthworms have an alkalizing one. The interaction of both lead to neutral to slightly acid pH and a neutral Eh at approximately 400 mV. Within the microaggregates, roots lead to higher Eh (600 mV) while earthworm activity leads to a more neutral Eh around 400-450 mV (Haas and Horn 2018). In return, microorganisms further alter and buffer Eh-pH conditions, especially in the rhizosphere which is a hotspot of biological activity (Krasil'nikov 1958). Hence, a direct effect of microorganisms is achieved through the production of biofilms and indirectly through improvement of aggregation, stabilization of soil structure (thanks to bacterial polysaccharide and fungal glycoprotein glues), increased water retention (thanks to biological mesoporosity increase), and resistance against erosion that create a diversity of Eh-pH niches (Pidello 2014; Clocchiatti et al. 2020).

Improved Eh-pH conditions and, consequently, enhanced plant nutrition and health, lead to increased photosynthesis, plant production and root exudation to further favor microbial growth and diversity in a virtuous cycle (Fig. 8). This entire process of soil transformation starts from seed germination: germinating seeds profoundly modify their environment and their microbiota as they constitute important sources of nutritious exudates, a great part of which is volatile. Exudate production increases with the quantity of reserve substances stored in the seeds,; thus, it varies with seed size and is species-dependent (Davet 2004; Nelson 2018). Production conditions, age of the seed and storage conditions can lead to physiological differences between two genetically identical seed lots. Increased moisture content and storage temperature leads to oxidation, higher pH and loss of viability (Nagel et al. 2019).

The ‘lifestyle’ of the plant needs to be considered in order to put all of this information into perspective. Conservative species exude more amino acids, while exploitative species exude more primary metabolites (sugar, organic acids) and this composition differential can be critical in regulating the plant’s microbiota (Guyonnet et al. 2018b). By exuding more carbon into the rhizosphere, exploitative species attract more taxa in root tissues and in the rhizoplane (Root-Adhering Soil, RAS), and they stimulate more taxa involved in Soil Organic Matter (SOM) degradation by a “priming effect” mechanism. They select more specific SOM degraders, exclude consumers in the RAS and root inhabiting bacteria than conservative species, and they increase denitrifying activity in the RAS (Guyonnet et al. 2018b). Organic acids cause significantly greater increases than sugars do in the detectable richness of the soil bacterial community and lead to larger shifts in the composition of dominant taxa. The greater response of bacteria to organic acids may be due to the higher amounts of added carbon, solubilization of soil organic matter or shifts in soil pH (Shi et al. 2011). Inversely, the root exudation pattern and root respiration are altered by microorganisms such as mycorrhizae or bacteria (Jones et al. 2004; Korenblum et al. 2020).

These interactions occur at different time scales, at medium or long term in the process of soil aggregation and weathering although they are also important at relatively short-term. Loss of C from the plant to the rhizosphere is a rapid process: photosynthetically fixed C can be detected in the rhizosphere in less than 1 hour after photosynthetic fixation and reaches maximum exudation rates after 3 h. Likewise, microbial turnover of root exudates in the soil is very rapid, with a half-life of between 0.5 and 2 h for most sugars, amino acids and organic acids (Jones et al. 2004).

Endophytic microbes (mostly bacteria and fungi) present on asymptomatic plants have also been shown to: (i) obtain nutrients in soils and transfer them to plants in the rhizophagy cycle and other nutrient-transfer symbioses; (ii) increase plant growth and development; (iii) reduce oxidative stress of hosts; (iv) protect plants from diseases; (v) deter feeding by herbivores; and (vi) suppress growth of competitor plant species (White et al. 2019). Plant roots can not only incorporate large organic molecules including proteins and DNA, but are also able to take up non-pathogenic microorganisms into root cells where they are degraded and used as as a nutrient source (Paungfoo-Lonhienne et al. 2010). This rhizophagy cycle is an oxidative process in plants for nutrient extraction from symbiotic microbes (White et al. 2019).

Root exudates drive the soil-borne legacy of aboveground pathogen infection (Yuan et al. (2018). After five generations of *Arabidopsis thaliana* inoculated aboveground with *Pseudomonas syringae pv tomato*, the causal agent of bacterial speck of tomato, bacterial communities of both rhizosphere and bulk soil were altered by the infection of this bacterial pathogen. These changes were the result of greater exudation of amino acids, nucleotides, and long-chain organic acids as well as the lower exudation of sugars, alcohols, and short-chain organic acids. The sixth generation of *A. thaliana* was grown on the same pathogen-conditioned soil but was uninfected by the bacterial pathogen. The sixth generation of the plant had increased levels of jasmonic acid (a defense-regulating phytohormone), and improved disease resistance compared with plants grown on control-conditioned soil (five generations of *A. thaliana* uninfected by Pst). This clearly demonstrates the capacity of plants to favor beneficial rhizosphere communities via modification of plant exudation patterns in response to exposure to aboveground pathogens to the benefit of subsequent plant generations (Yuan et al. 2018).

The rhizosphere microbiome results from an interplay between soil and seed microbiota, beneficial and pathogenic microorganisms colonizing aerial parts of plants, and root exudation; all of which appears to be largely regulated by Eh and pH. Microorganisms play a key role in the numerous interactions between plant and soil, but soil is in part derived from the activity of plants (Fig. 8) since they supply organic matter and play a pivotal role in weathering rocks and minerals (Lambers et al. 2009).

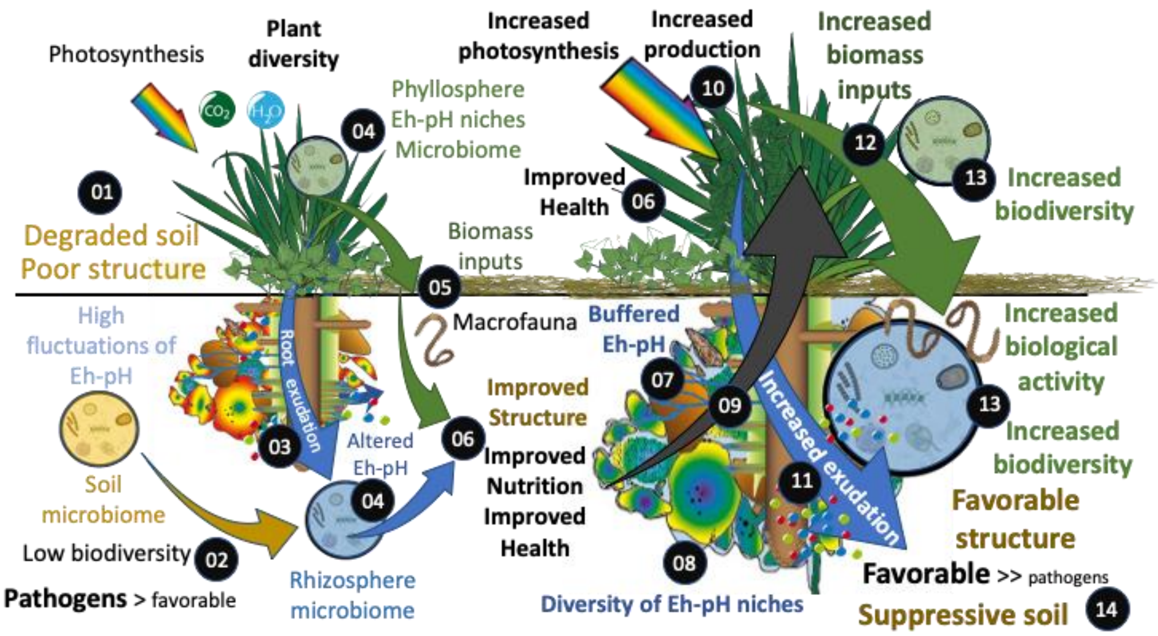


Fig. 8: Schematic presentation of the soil-plant-microorganism system showing the central role of photosynthesis by plant that provides the "fuel" for soil system regeneration. On degraded soils (01), poor structure and high Eh-pH fluctuations lead to low diversity of the soil microbiome, with pests dominating beneficial organisms (02) to result in poor plant growth. As a consequence, plants have limited capacity and energy to sustain an efficient pest or pathogen defense system, leading to poor plant health. Increasing photosynthetic activity by various means leads to increased root exudation (03) that alters Eh-pH and allows the development of a diversity of microorganisms in the rhizosphere and phyllosphere (04). The inputs of biomass on the soil surface from decaying plant parts create a litter (05) that, promotes the development of active macrofauna. Together with the active macrofauna, feeding on root exudates microorganisms in the rhizosphere improve soil structure, plant nutrition and plant health (06). The improved soil structure and active microbiota buffer the Eh-pH, both in soil and plants (07) to create a diversity of Eh-pH niches (08) and food supplies for microorganisms. All of this activity favors the completion of major biogeochemical cycles and increases plant defense against pests. Improved soil structure, plant nutrition and health (09) result in increased photosynthesis and biomass production (10). Consequently, both root exudation (11) and biomass inputs on the soil surface (12) are enhanced to further fuel the development of biological activity and biodiversity (13) while improving

soil aggregation, plant nutrition and plant health in a virtuous cycle. Beneficial organisms largely dominate pests, leading to suppressive soils (14).

Are balanced and diverse Eh-pH niches hosting a highly diverse microbiome the key determinant to soil suppressiveness?

Competitive interactions in soil microbial communities are regarded as the major driving factor of general soil suppressiveness. To infect root tissue, pathogens have to compete with members of the rhizosphere microbiome for available nutrients and microsites (Chapelle et al. 2016). In disease-suppressive soils, pathogen activity is strongly restricted by specific rhizosphere microorganisms. For instance, the rhizosphere microbiome of sugar beet seedlings grown in a soil suppressive to the fungal pathogen *Rhizoctonia solani* showed that *Oxalobacteraceae, Burkholderiaceae, Sphingobacteriaceae* and *Sphingomonadaceae* were significantly more abundant in the rhizosphere upon fungal invasion and that stress-related genes (ppGpp metabolism and oxidative stress) were upregulated in these bacterial families (Chapelle et al. 2016). It was postulated that the pathogenic fungus induces directly or via the plant, stress responses in the rhizobacterial community that lead to shifts in microbiome composition and to activation of antagonistic traits that restrict pathogen infection. Several root-colonizing microorganisms are known to improve the plants response to pathogens (Meisner and De Boer 2018). Upon pest attack, plants are able to stimulate protective microorganisms and enhance microbial activity that suppresses pests in the rhizosphere (Berendsen et al. 2012). Natural antibiotics are weapons in the microbial warfare in the rhizosphere that are integral to plant health (Cha et al. 2016). Plant response to increased pathogen abundance depends on the microbial community colonizing the root, which is affected by the amount and composition of rhizodeposits. For example, iron-mobilizing coumarins exudated by *A. thaliana* shape their root bacterial community by inhibiting the proliferation of a relatively abundant *Pseudomonas* species via a redox-mediated mechanism (Voges et al. 2019). Redox-active phenazine compounds also play a role in the persistence and survival of *Pseudomonas* spp. in the rhizosphere and, inversely, plant-beneficial phenazine-producing *Pseudomonas* spp. are proficient biocontrol agents of many soilborne pathogens (Biessy and Filion 2018). Melatonin, an amphiphilic antioxidant produced by cellular organisms able to scavenge both oxygenated and nitrogenated compounds, may decrease the deleterious physiological effect of various abiotic stresses through modulation of antioxidative enzymes and enhancement of organic acid anion exudation. In addition it may differentially modify some bacterial and fungal communities (Pisoschi and Pop 2015; Zhang et al. 2017; Madigan et al. 2019).

Redox states affect substrate availability and energy transformation and, thus, play a crucial role in regulating soil microbial abundance, diversity, and community structure (Song et al. 2008). Redox potential fluctuations are common in soils, and microbial community acclimation or avoidance strategies for survival shape microbial community diversity and biogeochemistry (DeAngelis et al. 2010). By characterizing redox-related soil microbial communities along a river flood plain continuum, Song et al. (2008) observed that, microorganisms, in general were highly abundant, diverse, and distributed more evenly in the oxic layers than the anoxic ones. The lower diversity in the anoxic than the oxic soils was primarily attributed to differences in oxygen availability in these soils. The decrease in abundance with increasing oxygen and substrate limitation, however, was considerably more drastic than the decrease in diversity, suggesting that growth of soil microorganisms is more energy demanding than maintenance (Song et al. 2008). Although indigenous soil bacteria are highly adapted to fluctuating redox regimens and generally possess physiological tolerance mechanisms allowing them to withstand unfavorable redox periods, soil bacterial communities loose significant diversity under sustained or frequent anoxic conditions (Pett-Ridge and Firestone 2005). pH is also a major driver of microorganism diversity in soil, and appears to be more important than nutrients in shaping bacterial communities in agricultural soils, including their ecological functions and biogeographic distribution (Wang et al. 2019). Fast changing Eh-pH conditions are therefore expected to be detrimental to biological activity and diversity. Soil structure resulting from the interactions of plant roots, associated macrofauna and microbial activity to strongly impact Eh-pH dynamics, appears to be a key determinant of soil health.

The loss of organic matter and degradation of soil structure due to soil tillage (Reicosky et al. 1997; Johannes et al. 2017) lead to low buffering capacity and thus, strong fluctuations in soil Eh and pH (Husson 2013). Fiedler et al. (2003) measured a pronounced decrease in soil Eh (-100 to -200 $mV.h^{-1}$, -800 mV in 3 days) as a result of water saturation following precipitation events, and an inverse raise in soil Eh in drying soils. Together with mean soil Eh, strong fluctuations of soil pH occur with changes in soil humidity, especially upon saturation (Tano et al. 2020). These fast-changing conditions strongly affect microbial populations and growth. Under rapidly fluctuating conditions, microbial populations can be periodically activated and inactivated, which, in turn, quickly alters the nature and rate of key biogeochemical transformations (Pett-Ridge and Firestone 2005). Physiological responses to stress have costs at the organismal level that can result in altered ecosystem-level C, energy, and nutrient flows. These large-scale impacts result from direct effects on active microbes' physiology and through stability of the active microbial community (Schimel et al. 2007). Plants can not always adapt to fast-changing Eh-pH conditions and, consequently, face multiple stresses that render them susceptible to multiple pests and pathogens.

Inversely, under well-structured soils that are rich in organic matter with active root systems, a large diversity of Eh-pH niches can harbor a diverse and highly active biological community. This provides essential ecological services that allow plants to sustain their Eh-pH homeostasis. For instance, plant- and root-associated microorganisms enhance plant mineral nutrition and carbon cycling through redox alteration (Marschner 1995; Schimel and Schaeffer 2012; Xi et al. 2016; Jacoby et al. 2017). The biogeochemical cycles of carbon, nitrogen, sulfur, and phosphorus appear to be driven by the "FeIII–FeII redox wheel" in dynamic redox environments (Li et al. 2012). Arbuscular mycorrhizal fungi improve redox homeostasis in rice through regulation of ROS scavenging activities that help the host release glutathione (Li et al. 2020). *Trichoderma* species, are involved in redox processes that confer resistance to redox stresses and facilitate redox homeostasis (Cardoza et al. 2010; Singh et al. 2013). This beneficial effect is reduced by (oxidizing) abiotic stresses for *Trichoderma harzianum*-induced resistance to downy mildew in grapevine (Perazzolli et al. 2011).

Well-structured soils that offer a large range of Eh-pH niches and host a highly diverse microbial community, have been regarded as plant disease suppressive soils (Cook 2014; Löbmann et al. 2016). Oxygen gradients (in space and time) lead to the assembly of a microbial community that is dominated by populations that are able to endure in both aerobic and anaerobic conditions (Chen et al. 2017a). Effective oxygen consumption, combined with the formation of microaggregates, sustains the activity of oxygen-sensitive anaerobic enzymes and leads to the direction of unsorted redox processes (i.e. not following the “redox tower” that would cause ecological niches of prokaryotes that consume electron acceptors in a thermodynamically determined order), within and between populations (Chen et al. 2017a). Various ecological services can be simultaneously ensured at any time by the rich soil biodiversity in a balanced environment.

Conclusions and future perspectives

Although causality cannot be demonstrated with the available literature, the literature does report many spatio-temporal correlations between Eh-pH conditions and plant susceptibility, tolerance and resistance to pests across various stress conditions that could support our initial hypothesis that Eh-pH homeostasis is central to soil and plant health. The Eh-pH homeostasis model is strengthened by the fact that this model: i) represents a unifying paradigm that comprises a large range of processes in a very logical and consistent manner; ii) encompasses various other models in crop protection (priming-exhaustion, optimal defense theory, susceptibility-tolerance-resistance, soil legacy, etc.); iii) enlightens our understanding of these processes without contradicting any observation or current knowledge; and, finally iv) provides a useful perspective to disentangle G x E x M x P interactions.

The new perspective this model proposes could help: i) plant pathologists and entomologists understand plant-pathogen and plant-pest interactions, and develop new approaches to pest management; ii) epidemiologists and modelers refine their models; iii) breeders improve and accelerate breeding for improved plant resistance, adaptability and tolerance to various stresses, pests and pathogens; and enhance energy allocation between growth and defense in selected varieties; iv) plant nutrition specialists design advanced fertilizers adapted to pH-Eh conditions of a given soil to meet the requirements of a given crop; and v) agronomists develop agroecological crop protection (ACP; Deguine et al. 2017) or biodiversity-based agriculture by developing ecosystem services provided by biological diversity based on a redesign of the farming system (Wezel et al. 2014; Duru et al. 2015).

Overall, an Eh-pH perspective could become a very powerful tool to develop a “one health approach” (Mackenzie and Jeggo 2019; Ratnadass and Deguine 2021) as the same parameters explain fundamental processes and could be used to characterize the “health” of soils (Husson et al. 2018b), plants (Husson et al. 2018a), animals and humans. This is consistent with the increasing recognition of the importance of Eh and pH homeostasis in health (Aoi and Marunaka 2014; Ursini et al. 2016; Kruk et al. 2019) and the role of microbiota and pathobiota in healthy and unhealthy host immune responses (Littman and Pamer 2011).

This review emphasizes the importance of jointly considering Eh and pH in further studies since most studies conducted to date disconnect these two interacting parameters. In order to accomplish this, improved measurement methods and other tools are needed to assess plant and soil Eh-pH conditions. These could include spectrometric methods to overcome limitations of electrochemical ones for plants and the use of bio-indicators as natural vegetation species to surmount problems related to the high spatio-temporal variability in soils.

Declarations

Funding

Not applicable

Conflicts of interest/competing interests

The authors declare having no conflict of interest

Availability of data and material

Not applicable

Code availability

Not applicable

Compliance with ethical standards

All authors read and approved the final manuscript

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